Food and Agriculture Organization
of the United Nations

VOLUME ONE

THE POLLINATION OF CULTIVATED PLANTS

A COMPENDIUM FOR PRACTITIONERS

POLLINATION SERVICES FOR SUSTAINABLE AGRICULTURE
EXTENSION OF KNOWLEDGE BASE

POLLINATOR SAFETY IN AGRICULTURE

THE POLLINATION OF CULTIVATED PLANTS

A COMPENDIUM FOR PRACTITIONERS

Volume 1

Edited by
David Ward Roubik
Smithsonian Tropical Research Institute,
Balboa, Ancon, Republic of Panama

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME 2018

The text was prepared as part of the Global Environment Fund (GEF) supported project 'Conservation and management of pollinators for sustainable agriculture, through an ecosystem approach' implemented in seven countries – Brazil, Ghana, India, Kenya, Nepal, Pakistan and South Africa.

The project was coordinated by the Food and Agriculture Organization of the United Nations (FAO) with implementation support from the United Nations Environment Programme (UN Environment).

First edition: 1995

Second edition: 2018

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ISBN 978-92-5-130512-6

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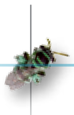

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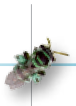

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CONTRIBUTORS

M.L. Adriano-Anaya

Universidad Autonoma de Chiapas, Centro de Biociencias, Carretera a Puerto Madero Km 2.0, Tapachula, 30700, Chiapas, Mexico

M.A. Aizen

Laboratorio Ecotono, Centro Regional Universitario Bariloche (CRUB), Universidad Nacional del Comahue and Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), CP 8400, San Carlos de Bariloche, Río Negro, Argentina

L. Bergamini

Universidade Federal de Goiás-UFG, Departamento de Botânica, Goiânia, GO, Brasil

D. J. Biddinger

Pennsylvania State University Fruit Research and Extension Center, Entomology, 290 University Drive, Biglerville, PA 17307, Pennsylvania State University, Department of Entomology, 501 ASI Building, University Park, PA 16801, USA

B. Blochtein

Pontificia Universidade Católica do Rio Grande do Sul, Av. Ipiranga, 6681 – 90619900, Porto Alegre, RS, Brasil

M. Brand

Natural History Department, Entomology, Iziko Museums of South Africa; 25 Queen Victoria Street, P.O. Box 61, Cape Town, 8000, South Africa

S.L. Buchmann

Departments of Entomology, and of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA

D.M. Burgett

Oregon State University, Corvallis, Oregon 97350, USA

L.A. de O. Campos

Universidade Federal de Viçosa, Departamento de Biologia Animal, Viçosa, MG, Brasil

M.J. de O. Campos

Universidade Estadual Paulista-UNESP, Departamento de Ecologia, Rio Claro, SP, Brasil

J.H. Cane

USDA, Bee Biology and Systematics Lab, Utah State University, Logan, Utah 84322-5310, USA

M.C. Cavalcante

Universidade Federal Rural de Pernambuco, Serra Talhada, PE, Brasil

C.R. Cervancia

Institute of Biological Sciences, University of the Philippines, Los Baños, Philippines

S.A. Cunningham

CSIRO Ecosystem Sciences, Box 1700, Canberra, ACT, Australia

A.R. Davis

Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, Canada

M.S. Deprá

Universidade Estadual do Norte Fluminense Darcy Ribeiro-UENF, Laboratório de Ciências Ambientais, Campos dos Goytacazes, RJ, Brasil

A. van Doorn

BumbleConsult, the Netherlands

M.A. da S. Elias

Universidade Federal de Goiás-UFG, Departamento de Botânica, Goiânia, GO, Brasil

A.C. Fajardo, Jr.

Institute of Biological Sciences, University of the Philippines, Los Baños, Philippines

E.V. Franceschinelli

Universidade Federal de Goiás-UFG, Departamento de Botânica, Goiânia, GO, Brasil

B.M. Freitas

Universidade Federal do Ceará – UFC, Departamento de Zootecnia – CCA, Campus Universitário do Pici, Bloco 808, CEP 60.356-000 Fortaleza – CE, Brasil

L. Freitas

Jardim Botânico do Rio de Janeiro-JBRJ, Rio de Janeiro, RJ

M.C. Gaglianone

Universidade Estadual do Norte Fluminense Darcy Ribeiro-UENF, Laboratório de Ciências Ambientais, Campos dos Goytacazes, RJ, Brasil

L.A. Garibaldi

Sede Andina, Universidad Nacional de Río Negro (UNRN) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mitre 630, CP 8400, San Carlos de Bariloche, Río Negro, Argentina

J. Grajales-Conesa

Universidad Autonoma de Chiapas, Centro de Biociencias, Carretera a Puerto Madero Km 2.0, Tapachula, 30700, Chiapas, Mexico

L. de Guzman

USDA-ARS Honey Bee Breeding, Genetics, and Physiology Lab, 1157 Ben Hur Rd., Baton Rouge, LA, 70820-0000, USA

M. Guzmán-Diaz

Universidad Autonoma de Chiapas. Centro de Biociencias, Carretera a Puerto Madero Km 2.0, Tapachula, 30700, Chiapas, Mexico

L.D. Harder

Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4, Canada

A. Hassan Jalil

Koperasi Meiponi K.L. Bhd., Kuala Lumpur, Malaysia

T.A. Heard

Honorary Associate, Social Insects Lab, School of Biological Sciences, Macleay Building A12, University of Sydney, NSW 2006, Australia

M.M. Henao

Laboratorio de investigaciones en Abejas (LABUN), Departamento de Biología, Universidad Nacional de Colombia, Sede Bogotá, Colombia

J. Hipólito

Laboratório de Biologia e Ecologia de Abelhas; Instituto de Biologia – Departamento de Zoologia, Universidade Federal da Bahia (UFBA); Rua Barão de Geremoabo, S/N, Campus de Ondina; CEP 40.170-110 Salvador, BA, Brasil

D.W. Inouye

Department of Biology, University of Maryland, College Park, MD 20742-4415, USA

J. Jaramillo

Laboratorio de investigaciones en Abejas (LABUN), Departamento de Biología, Universidad Nacional de Colombia, Sede Bogotá, Colombia

N.K. Joshi

Pennsylvania State University Fruit Research and Extension Center, Entomology, 290 University Drive, Biglerville, PA 17307, Pennsylvania State University, Department of Entomology, 501 ASI Building, University Park, PA 16801

M. Kasina

Kenya Agricultural Research Institute, NARL, P.O. Box 14733-00800 Nairobi, Kenya

P.G. Kevan

Alexander Building, School of Environmental Sciences, University of Guelph, Guelph, Ontario N1G 2W1, Canada

L.H.P Kiill

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) Semiárido, Petrolina PE, Brasil

R. Krell

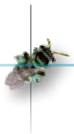
FAO, Rome, Italy

C. Krug

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Ocidental, Manaus, AM, Brasil

P. Kwapong

Department of Conservation Biology and Entomology (CBE), School of Biological Sciences Sciences, University Post Office, University of Cape Coast, Cape Coast, Ghana



R.P. Macfarlane

Buzzuniversal, 33 Woodside Common; Christchurch, New
Zealand

D.J. Martins

Turkana Basin Institute – Stony Brook University, NY
11794 USA, Insect Committee of Nature Kenya, National
Museums of Kenya & Mpala Research Centre P O Box 555
Nanyuki 10400 Kenya

M. Maués

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA)
Amazônia Oriental, Belém, PA, Brasil

J.K.S. Mbaya

National beekeeping station, P.O. Box 34188, Nairobi,
Kenya

B.G. Meyrelles

Universidade Federal de Viçosa, Departamento de
Biologia Animal, Viçosa, MG, Brasil

P.C. Montagnana

Universidade Estadual Paulista-UNESP, Departamento de
Ecologia, Rio Claro, SP, Brasil

J.E. Moreno

Smithsonian Tropical Research Institute, Balboa,
Republic of Panama

G. Nates-Parra

Laboratorio de investigaciones en Abejas (LABUN).
Departamento de Biología, Universidad Nacional de
Colombia, Sede Bogotá, Colombia

C. M. Silva-Neto

Instituto Federal de Educação, Ciência e Tecnologia de
Goiás, Cidade de Goiás, GO. Brazil

P. Nunes-Silva

Pontificia Universidade Católica do Rio Grande do Sul,
Av. Ipiranga, 6681 – 90619900, Porto Alegre, RS, Brasil

R. Ospina Torres

Laboratorio de investigaciones en Abejas (LABUN),
Departamento de Biología. Universidad Nacional de
Colombia, Sede Bogotá, Colombia

I. Ovando-Medina

Universidad Autonoma de Chiapas. Centro de
Biociencias. Carretera a Puerto Madero Km 2.0,
Tapachula, 30700, Chiapas, Mexico

L. Packer

Department of Biology, York University, 4700 Keele
Street, Toronto, Ontario M3J 1P3, Canada

G.P. Patricio

Universidade Estadual Paulista-UNESP, Departamento de
Ecologia, Rio Claro, SP, Brasil

C. Pigozzo

Centro Universitário Jorge Amado (UNIJORGE),
Av. Luiz Viana Filho, Campus Paralela,
CEP. 41.745-130, Salvador, BA, Brasil

C.S.S. Pires

Embrapa Recursos Genéticos e Biotecnologia, Cx. Postal
02372 – Brasília – DF, CEP 70.849-970, Brasil

V.C. Pires

Instituto do Meio Ambiente e Recursos Hídricos da
Bahia, Rua Viena, nº. 425, Bairro Dinnah Borges –
Eunálopis – BA, CEP 45.820-970, Brasil

E. J. Rajotte

Pennsylvania State University, Department of
Entomology, 501 ASI Building, University Park, PA
16801, USA

M.F. Ribeiro

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA)
Semiárido, Petrolina PE, Brasil

M. Rincon-Rabanales

Universidad Autonoma de Chiapas, Centro de
Biociencias, Carretera a Puerto Madero Km 2.0,
Tapachula, 30700, Chiapas, Mexico

A. Rodriguez-C.

Laboratorio de investigaciones en Abejas (LABUN),
Departamento de Biología, Universidad Nacional de
Colombia, Sede Bogotá, Colombia

D.W. Roubik

Smithsonian Tropical Research Institute, Balboa,
Republic of Panama

M. Salvador-Figueroa

Universidad Autonoma de Chiapas, Centro de
Biociencias, Carretera a Puerto Madero Km 2.0,
Tapachula, 30700, Chiapas, Mexico

D. Sammataro

USDA-ARS Carl Hayden Honey Bee Research Center, 2000
E. Allen Road, Tucson, AZ 85719-1596, USA

A.C. dos Santos

Embrapa Amazônia Oriental, Belém, PA, Brasil

R.C. Sihag

Department of Zoology, CCS Haryana Agricultural University, Hisar 125004, India

E.M.S. Silva

Universidade Federal do Vale do São Francisco, Petrolina, Brazil

F.O. da Silva

Universidade Federal de Sergipe, Campus do Sertão, Núcleo de Educação em Ciências Agrárias e da Terra, Rodovia Engenheiro Jorge Neto km 0, Silos, 49680-000, Nossa Senhora da Glória, SE.

P.N. Silva

Universidade Federal de Viçosa, Departamento de Biologia Animal, Viçosa, MG, Brasil

C.I. da Silva

Universidade Federal do Ceará – UFC, Departamento de Zootecnia – CCA, Campus Universitário do Pici, Bloco 808, CEP 60.356-000 Fortaleza – CE, Brasil

K.M.M. Siqueira

Universidade do Estado da Bahia, Campus III DTCS, Juazeiro. Av. Egard Chastinet s/n São Geraldo 48905-680 – Juazeiro, BA, Brasil

E.R. Sujii

Embrapa Recursos Genéticos e Biotecnologia, Cx. Postal 02372 – Brasília – DF, CEP 70.849-970, Brasil

H. Taki

Department of Forest Entomology, Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan

L.I. Vargas-Lopez

Universidad Autonoma de Chiapas, Centro de Biociencias, Carretera a Puerto Madero Km 2.0, Tapachula, 30700, Chiapas, Mexico

J.A. Vazquez-Ovando

Universidad Autonoma de Chiapas. Centro de Biociencias. Carretera a Puerto Madero Km 2.0, Tapachula, 30700, Chiapas, Mexico

B.F. Viana

Instituto de Biologia, Universidade Federal da Bahia – Campus de Ondina, Rua Barão de Geremoabo s/n, 40170-210 Salvador, BA, Brasil

S. Witter

Fundação ZooBotânica do Rio Grande do Sul, Salvador França, 1427 – 90690 –000, Porto Alegre, RS, Brasil

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PREFACE TO THE SECOND EDITION

Pollinators such as bees have been declining in diversity, if not abundance, ever since people began to replace their habitats with those suited for human use. Humans are largely responsible for this problem and, thus, might also be expected to remedy it. How to achieve this, however, is not yet exactly clear. Furthermore, there is now increasing awareness that an intact ecosystem has values determined by social, political, economic and a host of other human devices, which are often in conflict with ecological processes that form and maintain ecosystems and the services they provide to humanity [1–3].

Many advocate the use of "sustainable" approaches in crop pollination. However, it is prudent to draw on the knowledge of experts in related fields. One such group is the sustainable forestry cadre, which encompasses both the so-called developed and developing worlds. In their words, [4] sustainable forestry is not the same as sustainable forests. In the present context, sustainable pollination is not the same as sustainable pollinators. Which pollinators are to be sustained, how and for whom?

There are obvious trade-offs. In the case of agriculture, managed pollinators are brought in when local pollinator numbers are too low in the surrounding environment to pollinate crops at an acceptable level. However, when the environment itself is the source of pollinators, and property boundaries are already set, some difficult decisions are required. How much land or habitat should remain underutilized by agriculture or other activities to sustain pollinators? In other words, how many crops or other materials can be voluntarily sacrificed for the sake of producing fruit and seeds that are only obtained from pollination by wild animals? In larger farms or monocultures, the question is more complex, but similar. If fewer pollinators result in a smaller yield, is it less costly to increase planting density or area, to hire a pollinator service provider (PSP) or to sacrifice arable land for "pollinator reserves" [5]? Finally, biocides almost invariably reduce pollinator populations [6, 7]. Is the cost of such chemical input compensated by the increased saleable produce and the profit margin, compared to lost production due to a pollination/pollinator deficit?

As if this were not already complicated enough, bee keepers are hard pressed to maintain their profit margins, which seem to hover at a level of net profit being just shy of 10 percent of the gross profit [8]. In other words, no one is getting rich, but commercial beekeeping is sustainable – meaning that it can continue and is not going "into the red". The fact that nature is deemed sustainable only when such a decline is avoided is a sure sign of trouble. Nature must not only continue, but advance by a process known as natural selection, to keep pace with the mounting challenges posed both by environmental change and human impact. Without the appropriate habitat and populations it supports, that cannot occur.

The present compendium for practitioners shows the reader how to strive to maintain important checks and balances, taking into consideration pollinators in croplands, both large and small, and within the world's temperate and tropical realms. While it describes a range of methods and goals, it does not advocate any particular product or copyrighted item. Thanks are due to FAO for its service in furthering applied pollination science, and to B. Gemmill-Herren, who managed to initiate the Global Pollination Project and provide FAO with professional expertise, thus continuing to support this work.

David W. Roubik

David W. Roubik
Smithsonian Tropical Research Institute,
Balboa, Ancon, Republic of Panama

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A NOTE ON REFERENCES

Several of the chapters included in this publication appeared in earlier forms in the previous edition of this Compendium: *Pollination of Cultivated Plants in the Tropics* (1995). The presentation of the references in these chapters has remained the same, with the inclusion of newer publications where these are mentioned in the text. New chapters and sections use a numbered reference system. All chapters have been revised and updated for this second edition.

ACKNOWLEDGEMENTS

Funding for **Chapter 4** (D.J. Biddinger, E.G. Rajotte and N.K. Joshi) was provided by a State Horticultural Association of Pennsylvania grant, an USDA-SCRI Research and Extension grant (PEN04398) on native pollinators, an USDA-NRCS Conservation Innovation grant with the Xerces Society for Invertebrate Conservation, and a current regional USDA-SCRI Coordinated Agricultural Project grant (MICL05063) on integrated crop pollination. The authors thank Dr. Sheena Sidhu, Department of Entomology, University of California, Riverside, CA for reviewing a previous draft of this chapter.

The work for **Chapter 7.1** (*M. Kasina*) was carried out within the Kenya Pollination Project (KPP), which forms part of the Global Pollination Project, and is financially supported by GEF and implemented in seven countries, including Kenya, by UNEP through FAO Rome. The author thanks the team involved in project implementation at Kakamega, Mt Kenya and Kilimambogo, as well as the national project coordination team, and the farmers who agreed to participate in the project.

The study that comprises **Chapter 7.3** (*D.J. Martins*) was conducted as part of an analysis of insect diversity and plant-pollinator interactions in the Turkana Basin at the Turkana Basin Institute. The following student volunteers from Hillcrest Secondary School assisted with fieldwork: N. Morey, E. Stephanou and T. Maseland. The Nachekichok Women's Group are also thanked for allowing the project team to work on their farms. Assistance, useful comments and insights and support were provided by S.C. Collins, R. Leakey, M. Leakey, L. Leakey, I. Angelei, P. Lomosingo, A. Powys, M. Kasina, M.N. Mutiso, W. Kinuthia, J. Mamlin and S.E. Mamlin, and the scientists and staff of the East African Herbarium, National Museums of Kenya, the Whitley Fund for Nature, National Geographic Society and Nature Kenya.

Chapter 9.3.1, the study on Brazil nut (*Bertholletia*) in the Amazon (*M. Maués, M.C. Cavalcante, A.C. dos Santos and C. Krug*), was made possible by support from Embrapa, CNPq – Process n° 556406/2009-05, and the Global Pollinator Project GEF/UNEP/FAO/MMA, FUNBIO.

The authors of **Chapter 9.3.4** (*R. Ospina-Torres, J. Jaramillo, A. Rodriguez-C., M.M. Henao and G. Nates-Parra*), a study of passion fruit on Colombia, would like to offer their thanks to the Universidad Nacional de Colombia (DIB and Departamento de Biología) and COLCIENCIAS for funding the study (DIB 8003251; COL 1101-52128758) and to GNP and ROT and the Young Researcher (JJ). They also thank the team of the Bee Research Laboratory (LABUN) for their support. They are grateful to Scott Bridges for his translation and editorial assistance, and to David Roubik for his invitation to participate in this publication and for his editorial comments. The owners of the crops are also thanked for their collaboration.

Chapter 9.3.4 (*M.C. Gaglianone, E.V. Franceschinelli, M.J.O. Campos, L. Freitas, C.M. Silva Neto, M.S. Deprá, M.A.S. Elias, L. Bergamini, P. Netto, B.G. Meyrelles, P.C. Montagnana, G.P. Patricio and L.A.O. Campos*) resulted from the CNPq project (556057/2009-0) and the Tomato Pollinators Network Research in Brazil, as part of the Project "Conservation and Management of Pollinators for Sustainable Agriculture, through an Ecosystem Approach", supported by the Global Environmental Facility Bank (GEF), coordinated by FAO with implementation support from UNEP, and supported in Brazil by the Ministry of Environment (MMA) and the Brazilian Biodiversity Fund (Funbio). Thanks are due to G.C.G. Delaqua, M.F. Marques, A.P. Hautequestt, M.C.M. Morais, L.F. Ferreira, I.R. Stanciola, G. Paiva, B.B. Grisolia, F.G. Brocanelli and M.A. Pizano for their assistance in the field and laboratory, and to the farmers that allowed the study on their proprieties. Grateful thanks are also due to G.A.R. Melo, F.A. Silveira, S.R.M. Pedro and F.F. Oliveira for taxonomic identification. EMATER and RioRural/SEAPPA/RJ and FAPERJ (MCG: E-26/112.652/2012) are thanked for logistical and financial support. M.C.Gaglianone, L. Freitas and L.A.O. Campos are grateful to CNPq for the PQ productivity scholarships.

Chapter 9.3.11 contains information gathered over 20 years of research on cashew pollination through projects supported by different institutions and in partnership with academics, researchers, students and cashew growers to whom the author (B.M. Freitas) is indebted. Part of the content presented here resulted from the CNPq-Brasilia/Brazil projects 521946/96-4, 305062/2007 and 7556042/2009-3, and the Cashew Pollinators Network Research in Brazil, as part of the Project "Conservation and Management of Pollinators for Sustainable Agriculture, through an Ecosystem Approach", which is supported by the Global Environmental Facility Bank (GEF), and coordinated by FAO with implementation support from the United Nations Environment Programme (UNEP) and supported in Brazil by the Ministry of Environment (MMA) and the Brazilian Biodiversity Fund (Funbio). The author thanks the Brazilian National Research Centre for Tropical Agro-Industry (EMBRAPA/CNPAT) for use of its experimental station to conduct field research and the supportive help of its staff over many years. The author is also grateful to CNPq-Brasilia/Brazil and CAPES-Brasilia/Brazil for M.Sc. and Ph.D. sponsorship for the students involved in the projects and the British Council (NE Brazil) and CNPq-Brasilia/Brazil for travel grants.

The author of **Chapter 11** (*A. vanDoorn*) offers his thanks to H.H.W. Velthuis for critically reading the manuscript.

The authors of **Chapter 15** (*C.I. da Silva and B.M. Freitas*) would like to thank many people and institutions involved with their studies of carpenter bees and their role as pollinators over the last two decades. B.M. Freitas would like to thank his former and present students for their dedication, passion fruit growers F. Ferreira Neto, J.B.C. Nunes and V.C. Aquino for their interest and collaborative work in the field trial, and CNPq–Brasilia/Brazil for supporting project # 467275/2000-9 and CNPq–Brasilia/Brazil, CAPES–Brasilia/Brazil and FUNCAP–Ceará/Brazil for the M.Sc. and Ph.D. sponsorship of students involved in the projects. C.I. da Silva would like to thank FAPEMIG–MG/Brazil for its financial support.

The Editor wishes to express a particular acknowledgment to Dr. Barbara Gemmill-Herren for devoting much effort and input to these works, both while at the FAO and in her continuing dedication to the global pollination field.

Part I

INTRODUCTION

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Chapter 1

LESSONS LEARNED OVER THE LAST 20 YEARS

D.W. Roubik

1.1 SUSTAINABLE POLLINATION AND POLLINATORS

The year 2012 marked the 50th anniversary of a landmark book by Rachael Carson entitled *Silent Spring*, which first drew attention to the real dangers of biocides. Today, lessons regarding the hazards of toxic pesticide are still being re-learned, with the consequences of usage most evident in pollinators. In 1995, FAO published *The Pollination of Cultivated Plants in the Tropics*, which introduced readers to various aspects of natural and insect pollination. Now, over 20 years later, it is timely to revise, update and expand this publication. While there is much new information to be added to the knowledge base on pollination, much of what was known 20 years ago bears repeating.

The practical concerns of pollination studies are not difficult to understand. The largest crops – rice, wheat, sugar cane and corn – are pollinated by wind, but the proportion of crops that requires pollination by animals has increased steadily. Only a few crops used for fruit, seeds or fibre (e.g. olives, pistachio, pineapple and banana) have no need for pollination by animals [4, 5]. The utility of pollination also extends to crops beyond food and fibre. For example, a number of important biofuels (aside from sugarcane and corn) benefit from pollinators including: sunflower, canola, African oil palm, coconut, *Jatropha* and soybean [6, 7, 44 and see Chapter 9.3].

Yet, problems still arise in getting the pollinator-pollination message across, despite concerted efforts [8–24]. Notwithstanding progress in farming techniques and diverse farm management strategies, many limitations persist in basic and applied knowledge of pollinators and their environment, especially among small farms. In such environments, pollinators cannot be rented or purchased; they must be incorporated into farming itself. And if they are lost, *some* (see below) will likely vanish forever. Most of the pollinators in any kind of agro-ecosystem certainly seem to require conscious attention and management innovations, if not intervention or regulation.

Not all pollinators are amenable to management, however. Those that are possess certain distinguishing characteristics that require attention, especially now. The main pollinators serving agriculture in addition to "pollen bees" (Chapter 4) are "persistent pollinators". They nest along roadways, open areas, human-created landscapes and often forage in weedy vegetation. They are pre-adapted to disturbances such as land clearing or aridity, and opportunistically use available nesting and food resources during much of the growing season. Their pioneer habits make them potentially invasive and able to fill biological gaps and loose niches. Individuals and companies that have achieved economic success as "PSPs" produce and sell adaptable or at least manageable bees, such as *Apis, Osmia, Centris, Xylocopa, Bombus* and *Megachile*. Such species forage on a wide range of plants and crops and are amenable to nesting in spaces expressly created for them. Most importantly, they appear to compensate for biodiversity loss in pollinator species by their sheer number and persistence, a fact that is still underappreciated.

Thus, it is true that, over the short term, pollination may be preserved at the expense of certain pollinators by substituting the rich diversity of pollinators in natural systems with certain "default pollinators" in agricultural systems. A conservationist views such novel pollinators as a mixed blessing, because they may displace the original pollinators. Many of those original pollinators, however, prefer their normal habitat and will be primarily found there, not in the agro-ecosystem. Although the most flexible species will remain accessory pollinators in agriculture and silviculture, more sensitive species will not be found nearby. The majority of pollinators, outside of particular reserves, will be a small subset of the original pollinators in any geographic area. These will be the pollinators that are managed, and will include the most adaptable and opportunistic species that rapidly colonize, reproduce and compensate for environmental stressors. In rare cases, they might also include species that can partly withstand biocides, fire, rising global temperature and tillage. The most obvious alternative scenarios in the agro-pollination network seem implausible: people are unlikely to abandon farming in favour of forest gardening within semi-natural communities; the continuation of widespread habitat poisoning until all wildlife, including pollinators, is driven to extinction seems inconceivable; and agronomists are unlikely to find the means of converting all important crops into self-pollinating or pollen-free varieties. Pollinators, some of them living in the wild and some of them under human care, will continue to form the basis for successful agriculture and silviculture. The only rational definition of success is sustainability, in its best sense.

1.1.1 Tropical and temperate zones

When the first edition of this book was completed, in 1993, several important facts were evident. The majority of plants cultivated in the tropics had not received much attention with respect to pollination requirements, breeding system or pollinators. Most cultivated plants and their fruit, seed and edible parts had therefore survived without applied human knowledge or management. This statement also applied – and still applies – reasonably to the temperate zone, in addition to the tropics and subtropics [25–31]. Moreover, although agrarian knowledge is formidable on fruit, nut, vegetable and seed crop management [32, 33], the paucity of concrete pollination data for tropical and temperate crops remains unchanged. Several new chapters here serve to demonstrate the range of important tests and variables that are needed to supply that badly needed, detailed information on pollination.

Because tropical crops grown in the highlands usually originate in the temperate zone, tropical pollination information already contains much that is relevant to temperate climates. At the same time, the tropical crops consumed in the temperate zone are much more diverse than temperate zone crops consumed in situ. It is therefore important to study and monitor them, especially in the global marketplace. One region and set of practices also informs others, which constitutes a significant advantage for the goal of sustainable pollination and sustainable pollinators worldwide.

In the tropics, the last 20 to 30 years mirror past dynamics in the temperate zone with at least one major difference. A basic ecological turning point is approaching: the tropics are quickly losing a significant proportion of natural habitats, including a large part of the world's species [34], and routinely depend upon this often underappreciated wildlife. Temperate latitudes have already passed through changes that led to the adoption of different, manageable pollinators, either to supplement or replace those in agricultural settings. As Krell (Chapter 10.5) points out, creating infrastructure for improving pollination is expensive and difficult, and the best alternative is to conserve pollinators while they still exist (Chapter 3.1). While the situation in the temperate zone is being managed – more or less – this is often not the case in the tropics as far as pollinators and pollination are concerned. Economies in these regions are, therefore, especially vulnerable to a pollinator decline [e.g. 35]. However, one distinct advantage in the tropics is the continuous breeding and activity of pollinators and plants. If this persists, and does not have to be artificially restored, there are many benefits, including potential recovery following negative impacts.

Somewhat contrary to the above scenario, there have been significant new advances in applied and managed pollination, at least at the descriptive level. Some of the most comprehensive and detailed efforts relate to tropical zones. For instance, a catalogue of Neotropical bees led to a broad summary of passion fruit management in Brazil, and also to an enumeration of common bees found at flowering crops in that diverse tropical country [99, 119, 120]. In the temperate zone, detailed manuals now supply the natural history enthusiast with the means to identify species of bumblebees [36]. The subjects of pollinator application, restoration and gardening to fulfil pollinator needs have been treated by recent introductory guides and manuals, both supported with international funding and by societies dedicated to pollinators and their conservation, and are generally available on the World Wide Web [e.g. 86, 107, 109, 119].

This revised edition of the original compendium, first published in 1995, examines the tropical and temperate zones together. It incorporates and updates several sections from the first edition and adds many new chapters and authors. These emphasize not only the present state of knowledge and its application but, in general, approaches and methods for *getting things done* in various farming environments. In order to introduce those subjects to a new generation of readers, the following paragraphs outline the general similarities and differences of tropical and temperate zones.

Pollinators can be divided essentially into two groups: those dedicated to visiting flowers and those that make only occasional use of them. Bees, certain wasps and flies are the *only* animals that specialize in harvesting pollen, using its protein to make their offspring. These insects are indispensable for pollination. They remove pollen from the anthers, handle it and occasionally pass it on to a receptive stigma, but otherwise pollen is destined for brood, the earth or personal consumption by such dedicated flower visitors.

The tropics are distinguished not only by continuous growing seasons, and a potentially greater build-up of diseases or herbivores, but also by a much wider variety of general pollinators – primarily honey-making social bees with colonies active year round [17, 22, 37, 38]. Those bees are termed "general pollinators" because they may interact with a large proportion of the local flowers. More importantly, such bees recruit hundreds to thousands of colony members on the best available blooms. This results in distinctive behaviour with bees visiting flowers and leaving in a comparatively abrupt manner, particularly in large patches such as croplands. Once the blooms are over or if they have not satisfied the colony, the bees continue their search for more. Colonies can live for years and reproduce, visiting one flower species after another or many at the same time.

In the temperate zone, other bee groups and varied pollinating animals often seek a narrower variety of flowers. However, in both the temperate zone and among certain tropical habitats and species, the individual pollinator has a brief active season. During a favourable period at any point on the globe, a particular bee or other flower-visiting animal may reproduce and then disappear from view for around 48 weeks. Such varied pollinator schedules call for fundamental differences in management outlook and approach in croplands. The tropics and some subtropical areas are naturally endowed with bees that visit flowers throughout the year; however, their value as adequate or manageable pollinators, as shown in several chapters here, is only now being realized.

Among all the world's pollinators – including flies, wasps, bees, beetles, thrips, butterflies and moths, through bats, birds, marsupials and the odd ant, crickets, cockroaches, squirrels, lizards and molluscs – about half of tropical flowering plants depend on bees. This proportion rises in farms and wildlands of the temperate zone, where the majority of flowering plants are visited and pollinated by bees, birds and flies. When searching for crop pollinators with the aim of increasing their abundance – and believing that this will also help pollinate native flora – a fairly rigorous plan of study and experimentation is needed to provide evidence that such hopes are well founded. Although this area remains beyond the scope of the present publication, the tools needed to investigate the subject are presented here and have been updated since the original edition.

1.1.2 Pollinator backup and restoration

Although animals pollinate flowers everywhere, among crops the most widely employed pollinator is usually a single species of honey bee. This social animal provides a critical backup role in the pollinator realm. As a manageable bee that also produces marketable honey and wax, *Apis mellifera* has few counterparts in the pollinator world – most notably the tropical and subtropical "stingless honey bees", now increasingly utilized. Those honey-making animals are equally regarded as a basis for "productive conservation", perhaps because they have multiple uses and provide economic benefits. They may be good for sustaining a certain kind of agriculture, much as teak plantations prevent erosion or leguminous cover crops improve soil nitrogen, but whether they should constitute the principal basis for agricultural pollination is rightly questioned (see Chapter 3).

Although crops that require animal pollination do not provide the bulk of food for human consumption, their individual nutritional value is often higher [35, 39]. At the high end of crop value, biofuels and seed, fruit, nut and beverage crops increasingly demand bees and other pollinators, which must be managed to fulfil such demands [29, 40–45].

By diversifying the species that are put to work for those purposes, and by working to understand their biology, experts come closer to finding adequate insurance for both human needs and general conservation. Perhaps some time in the future, pollinators managed for crop production or invasive ones that have naturalized (e.g. megachilids, bumblebees or honey bees in the Americas, Australia, New Zealand and elsewhere) may provide a backup or even the sole pollination services for certain native wildland plants, as they now readily support a variety of invasive flora. The vast crop fields, if varied in their composition and managed in a "pollinator friendly" manner, may in turn help to restore *some* pollinators to their native habitat. The essential fact remains that a species in an assemblage is sustainable in the proper community, while all else is unsustainable without added input. This publication is an effort to define the parameters of that needed human input.

1.2 THE EXTENT OF PROGRESS TO DATE

1.2.1 An ecological overview

Fifty years ago, it was known that pollinators for agricultural plants can fail, just like the rains or a vernalization period, and that growers often "place all their eggs in one basket" – at least for a year or two [45]. Then, as now, small farmers in tropical zones cut and burn forest to sow crops in a cycle resembling "predatory farming" [46] – using up one set of resources and then passing to another, but at a small scale and with a rapid farm recovery period. However, more extensive land use by more people, and greater demands, leads to soil and land becoming increasingly depleted.

Less traditional and larger-scale styles of farming spread thus rapidly removing existing habitats and organisms, including pollinators, more or less completely and for relatively long periods. All such practices inevitably affect huge landscapes, but the tropics and the temperate zone also harbour substantial areas of natural vegetation and wildlife. These natural ecosystems nonetheless experience drought, flooding and a certain degree of regular, substantial fluctuation.

Figure 1.1
SCENES OF HUMANS, CULTIVATION AND POLLINATORS FROM AROUND THE GLOBE

Above left depicts a mating and nesting aggregation of the giant honey bee, *Apis dorsata*, in Asia, and a mating drone with queen flying nearby. Flies and stingless honey bees (meliponines) are shown below, working on the flowers of mango. Shaded coffee plantings, pollinated by diverse bees, are presented along with forest clearing and burning, traditional tillage and beekeeping with a hive of honey bees, and the chemical applications of herbicide and pesticide (by air) in paddy rice, next to a young plantation of African oil palm, pollinated by beetles and not requiring biocide utilization (in the Neotropics, contrasted with Asia and Africa). Ripe fruit of mangosteen, mango, cashew and lychee are shown.

Source: Drawing and design by F. Gattesco and D.W. Roubik

Figure 1.2
WHAT THE BEES HAVE GIVEN US

Food is shown in the form of honey and pollen from both stingless honey bees (above right), with two worker bees in flight and a fecund, non-flying queen next to a few brood cells and honey pots, while the worker *Apis mellifera* (above left) flies near its comb and brood containing a few drones and queens. Food and beverage take the form of products of plants whose flowers bees forage from and deliver pollen to (below left), with a worker bumblebee cradled next to some coffee beans and leguminous seeds. Seeds for growing plants with multiple uses are also shown (bottom right), including forage for livestock (the "leafcutter" bee female shown at its nest, a managed pollinator for lucerne), biofuels (sunflower seeds), and squash and melon seeds.

Source: Drawing and design by F. Gattesco and D.W. Roubik

They are by no means stable, regardless of latitude or elevation, and their original pollinators and floral resources experience peaks and lows. Thus, an important contrast with agricultural areas is not only the presence of abundant native pollinators, including some that are managed, but an abundance suitable for pollination. That relative stability is certain to be a goal of management, rather than a given feature obtained merely by preserving pollinator reserves or management areas.

A curious "boom or bust" resource pattern also exists for flower visitors. Of particular relevance to the main subject of this publication is the important role played by ENSO (El Niño–Southern Oscillation) events [59, 74] in heavily agricultural areas, particularly in Southeast Asia, tropical America and Africa. An extensive flowering period occurs every few years, in which a large variety of woody plants flower concurrently, usually within a few months. Among mass flowering crops, and in those natural systems affected by the dry years of ENSO, pollinators are attracted in large numbers to resources that last only a short time. There, the pollinators are forced to adjust though a combination of food hoarding, diapause (hibernation) and dispersal (migration, especially the honey bees), when no such large resource blooms occur. In the temperate zone, in general, most pollinators are highly seasonal, and their adult activity matches that of preferred floral resources [106]. A brief active pollinator period in the drier regions often follows rain showers. In the moister regions, the emergence of adult insects that pollinate flowers coincides most often with a dry period. Thus, while agricultural ecosystems are challenging habitats for pollinators to persist within, they are not entirely different from the challenges of resource swings in natural environments, to which pollinators have always had to adjust. As discussed below, the threat of agricultural chemicals poses an entirely different kind of challenge, found only in human-created ecosystems.

1.2.2 Major shifts in pollination landscapes

The world is now experiencing a "sea change" in the pollination landscape, and must decide how to usher in the best alternatives to the original, natural communities. Two contemporary events, in addition to much publicized and debated pesticide use and habitat conversion, are having a strong global impact on pollinators and pollination. One is repeated introduction of Asiatic native honey bee pests (primarily *Varroa*, a large parasitic mite) westward, where they readily switch their host to the Western hive bee, *Apis mellifera*. In addition, these parasitoids attack that species in situ, within Asia, where the Western hive bee is often relatively defenceless (see Chapter 16). The other significant impact is Africanization of honey bees in the Neotropics. The ecology of this introduced bee species creates pervasive yet varied changes, and provides the first feral population of stinging honey bees in most of the Americas [22, 47–56, and the present publication]. Those bees are not amenable to crop pollination achieved by trucking (i.e. transporting over roadways) colonies in large numbers, because they are too dangerous. They can, however, be cultivated along with crops in a suitable setting, or their hives moved on a small scale.

Global agricultural intensification and the accompanying fungicide, herbicide, rodenticide, miticide, bacteriacide and insecticide (collectively called biocide or pesticide) treatments, plant growth regulators, fruit thinners, fertilizers and the ploughing of land, have had mostly predictable effects [46, 57–70]. When former pollinators are pushed out, other pollinators need to be brought in [69, 70]. In cases where those pollinators present problems or are not in abundant supply when needed, the cause and effect may be clear, but adequate solutions may be less obvious and seldom work out satisfactorily. Meanwhile, research and outreach continue to highlight important topical problems and needed additional research and management aimed at pollinators, as emphasized repeatedly in this publication. Pollinator wellbeing requires serious study and long-term commitment [16, 71–77, 101, 112], but more pollinators are needed *now* for agriculture.

In North America and Africa, in particular, pollinated fruit and vegetables are major crops both in net value to growers and in total tonnage [78, see also Chapter 7.3]. Generally, however, wind-pollinated wheat, rice, sugarcane, corn, barley, millets and other grains or tree crops, such as walnuts, remain the major world crops. Dense plantings ensure that pollen is transferred among individuals by wind. As long as the farmer stays ahead of the pests, parasites, soil depletion, temperature extremes and moisture deficits that such croplands experience, pollination seems guaranteed. And yet, until herbicide-resistant pollination units are invented [1–3, 66], or pesticide-resistant strains of honey bees are available (parasite and pathogen resistant varieties are known, see Chapter 16), no pollinator or pollination service should be taken for granted. While the attractive notion (for growers) persists that someday many crops will be pollination-free or parthenocarpic, or prompted to fruit uniformly by inexpensive commercial growth hormones or regulators, or that honey bees will resist whatever environmental or other obstacles are thrown at them, all such ideas ultimately *assume that no new economic factors, weather patterns, pathogens or natural enemies* will arise. Likewise, they assume that the flexibility and survival of pollinator populations, currently known simply as "health", will not decline from genetic or nutritional issues. Most biologists, growers and resource managers presumably know better. Furthermore, certain proven sustainable practices remain superior because of their economy, flexibility and durability. Pollinators are part of the sustainability equation, but which pollinators merit this status and which human inputs will maintain them is only now being established.

1.3 THE POLLINATION FACTOR IN CROPLANDS

1.3.1 Crop harvest constraints

What happens when numerous seeds and fruit are produced in a stand of animal-pollinated plants? Growers are generally content; however, the type of produce and its commercial sale largely determine final outcome and income. One result of a larger crop is that the fruit may be smaller and less attractive or, when regional production reaches a peak, the market price declines. Another is that, in the following year, the perennial fruit and nut trees will bear less fruit and seeds, an outcome known as alternate bearing (see glossary). A third consequence, although rare, is that the plant will die (this occurs in peaches and cacao, among others, when nearly every flower sets a fruit); however this situation is impossible in all but artificial pollination experiments. Nevertheless, the observation underscores the relationship between short-term and long-term production from a cultivated plant. The critical question of which level of pollination is most beneficial for both short and long-term productivity often remains poorly understood, at least for perennial plants under cultivation.

1.3.2 The nature of agricultural sustainability

A major consideration in attaining sustainability concerns slow fruit and seed production.[1] Fruit growers have been known to drive a stake into their trees (causing stress) to gain more profit from a season's blooming, and are actively seeking possible solutions to perceived underproduction. Can production rates or success be augmented and is this a sustainable solution to production shortfall? More study can provide evidence of pollinator decline and pollination shortcoming, versus a limitation related to plant physiology or farming practice. However, in agricultural plots – in contrast to natural mixed habitats of diverse species – the *relatively* sustainable (i.e. multiyear) value of any one season must be carefully assessed. Where there are fewer and fewer pollinators, questions arise as to which kinds are still available, which existed previously, how the performance and consistency of either group might be rated, and what it costs to replace them. Those are by no means new themes (see Chapters 2.2 and 3.2), but they have been the subject of considerable study since the first edition of this book was published (see Further reading).

At the population level, almost no studies have been made on the abundance (versus diversity or species

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[1] Short-term pollinator deficits are addressed in several chapters of this publication (e.g. Chapter 3.1).

richness) of pollinators over three or more successive years. This is an important subject because pollinators and their resources naturally vary between years. Such variation may be cyclical and predictable, difficult to predict or may indicate certain plants "take a break" due to their biology after producing a relatively large fruit or seed crop. Some of the great climatic drivers of bee and flower population cycles occur sporadically, and in cycles of a few to several years or even decades. Of these, there also are very few studies, for example, of the general flowering phenomenon in Southeast Asia. Nonetheless, yearly crop yield management involves attempts to optimize flowering and final fruit production in a relatively stable system, at least in the development of a particular management scheme (see Chapters 4 and 6 in particular). If the few population studies are sorted into "relatively stable and natural" habitats, versus those that are "human-induced and probably unstable", there is little to allow for a statistical comparison. Yields may be subject to fine-tuning and rational planning, or they may be beyond human control. In truth, a pollinator deficit may be remedied with more careful cultivation or management of pollinators. Obtaining more produce from a plant, in the case of a perennial, also means that its life expectancy is possibly shortened [32, 33]. Plants are replaced at an appreciable cost, thus having a bumper crop one year may result in an economic deficit the next, or later when those plants require removal and replacement, or more care.

1.3.3 A taxonomic impediment for crops

Local crop pollination requirements and pollinator performance vary considerably, as highlighted in this compendium. One reason involves the differing needs of botanical cultivars. A recognized cultivar has a certified name, enabling farmers to buy its seeds with confidence. But not every cultivar of a given crop has the same breeding system or pollination requirements. Among mango and apple with their thousands of cultivars, for example, some depend entirely on flies for pollination while bees are responsible elsewhere, and female flowers of certain cultivars produce fruit without pollination or pollen. Each of these is the same generic crop wherever it is grown, and has the same common and scientific name. However, in this case biology supersedes scientific nomenclature and necessitates a focus on the detailed knowledge and nomenclature of named cultivars. It is known that pollinator and pollination requirements differ among plants of the same genus or family. That this is sometimes true for individual populations within a given species should come as no surprise.

1.3.4 Crop pollination ecology

Pollen-free clonal crops are certainly used widely, along with many that self-pollinate within the flower (see Chapter 2.1 and Part V). Those apparently self-sufficient cultivars are developed by plant breeders, whenever possible, but so-called "hybrid vigour" remains a mainstay of many crops and their commercial seeds. Genetic inbreeding within any crop usually produces less and less adapted individuals. Because crops are biological entities, despite their modification and selective breeding, they need an adequate fund of genetic variation to adapt to challenges in their life and over generations. In addition, hybrid seeds cannot exist without cross-pollination, which is often impossible by wind or abiotic agent, or by agrochemical means. In the world's farms and plantations, aside from a few widely grown commercial species (banana, pistachio, seedless grape, date palm, oil palm, agave, olive, certain citrus, papaya), bees supply most of the necessary natural and managed pollination, and the means of producing abundant hybrid seeds via outcrossing – the movement of pollen between plants. In fact, many plants that do not necessarily need bees – those that self-pollinate – are nonetheless aided in their seed, fruit and fibre production when bee-pollinated or outcrossed. Field examples are given in the present book (e.g. Chapters 3 and 9.3) and additional outstanding examples include coffee and lettuce [54, 79]. Growers often appreciate this, and some have experimented and learn to make sure there are at least honey bees present. Even if inefficient by some standards, honey bees are almost never a waste of effort, unless better pollinators are found and propagated for their contribution to yield and vigour [70].

Pollination service providers (PSPs) design management schemes for large farms in a variety of settings that have evolved at a steady and sometimes rapid pace (e.g. see Chapter 4). Outstanding success in greenhouse or glasshouse production of tomatoes – among a few dozen crops – has made bumblebees star performers due to persistent study and management over the course of a century (Chapter 11). The alfalfa leafcutter bee, a lucerne pollinator, was imported to the Americas accidentally from Europe in the 1930s and later became the most intensely managed non-*Apis* bee in the world [41, 80]. *Osmia*, another megachilid bee known as a Mason bee – due to its plastering of nest cells with mud – is stored artificially in the resting or diapause stage during the cold season, then released en masse in extensive croplands during the spring bloom [19, 20, 41, 80, and Chapter 3.1]. Such benchmark events have been accompanied by the combined impetus of the Internet and World Wide Web, and the blossoming of detailed and original, comprehensive works on pollination, pollinators, the environment and food production over recent decades. Stingless bees, the foremost honey-making bees on the planet, are now receiving serious consideration as more than tropical curiosities [22, 81, 82 and Chapters 13–15]. In addition, international pollination initiatives and networks are now operational worldwide. New scientific journals are focusing on beekeeping in diverse settings, bees in general, applied pollination work, conservation, applied ecology, and the economics of crop and farming stability. The welfare of pollinators has finally been incorporated into the perception of human welfare.

However, it is not possible to be certain about the stability of pollinators. They are seldom under our control and often do not prefer or meet the needs of crops put before them. In at least two decades, one of the major pollinating species, *Apis mellifera,* has been markedly affected by a variety of stresses, yet they survive and maintain considerable diversity [83]. Recent information points to possible disease, primarily viral "spillover" from Western hive bees – and also bumblebees kept by growers largely for greenhouse operations – to a few other bee species [84, 85 and Chapter 11]. No pandemic involving bees in general has ever been found.

The view that agricultural pollinators are livestock is being replaced with a more realistic view towards maintaining habitat quality for pollinator populations (Chapter 3 and Part II). In the long run this seems desirable. Recognizing the general level of ignorance regarding pollinator conservation or restoration, most experts stress the importance of conserving nature as a whole, and trust that this foresight, fraught with ignorance though it is, will allow nature and its processes to conserve pollinators and correct some of the problems.

Much of the modern scramble to retain bees in the environment is tied to their honey production, as well as agricultural advantages. This rationale is founded on basic economics, and not necessarily the requirements of forestry, agronomy, conservation or sustainability [86–90]. Such "productive conservation" or the application of pollinators to multiple needs and desires occurs in habitats that are no longer natural or fully intact. The concept of a mature and diverse ecosystem versus a more disturbed environment is of importance for this general theme, but seems poorly understood. For instance, a large part of the tropics is thought to be pristine, although this is not the case [90, 91]. When a natural patch of wildlife or vegetation is present, it is often located in an area that has already been used and altered by humans, even in the recent past. There are secondary forest species that persist despite disturbances such as land clearing, burning, fragmentation and local climate change. Most species alive today have in fact experienced drastic changes during their evolutionary and ecological history, the largest driven by repeated periods of glaciation over the past few million years. Glacial conditions in these remote times created drier and cooler habitats, while forests retreated and open habitat increased. During such periods the landscape was populated with different groups of organisms. Today, the search for new pollinators to be managed requires both honey production and pollination by bees adapted to change and manipulation (Part IV). An ice-age analogue is now being created by human activity [34, 92] and pollinators tolerant of such a disturbance will gradually predominate. The wild bees that persist under these conditions, most of them solitary but some of them social with perennial colonies, are likely to be those adapted to edge or open habitats, where their nesting resources and food plants are concentrated. Some social bees including the highly social honey-making species that form long-lived colonies will continue to hoard food or migrate between floral habitats, and thereby survive dearth periods. Agricultural lands, notwithstanding pollutants and pesticides, continually test and select for certain kinds of flower-visiting animals, largely by eliminating those that are ill adapted to abrupt or progressive habitat modification. The future has places for both colonial and other bees, and efforts to help them may occasionally prove decisive.

1.3.5 Prospects in pollination biology

Prominent worldwide habitat conditions include burgeoning human populations, not unlike human arrival in the Americas just 15 000 years ago. However, as the students of two decades in Central Amazonian experimental forest plots and elsewhere report, the present marks an unprecedented pace and scale of change [34, 89, 91]. Can biotic elements keep up and survive in the tropics and elsewhere? Will most native pollinators be stripped from the landscape by competition with invasive honey bees? Species that seem to be on the rise include Africanized honey bees, *Apis cerana, A. dorsata, A. florea* or *A. indica*, flies, small halictid bees, persistent populations of solitary and stingless honey bees, and long-range foragers such as *Xylocopa*, *Centris, Amegilla* and *Bombus*. Will flowering plants evolve self-pollination in response to pollinator loss or deficit? More importantly, is there any general restoration model available and can such restoration projects, which include pollinators, be cost-effective?

The tropics, particularly the Neotropics, are now repeating the temperate zone history of urbanization and retreat from smallholder agricultural plots and family farms. These abandoned lands may generate more native habitat – at a low successional stage – and eventually become biocide-free environments or be brought into large-scale development [92]. Conversely, traditional family farming is still the dominant practice in much of the tropics.[2] The world may "green up" a little as a result of land-use change, but an old-growth forest or natural prairie, even in relatively small areas, needs decades to centuries to form and perform its proper function. The concern is how to deal with the interim regarding the pollination of current crops.

Within secondary growth forest and other regenerating habitats, there is a good chance that more pollinator species may thrive, due to loss of their natural enemies after community simplification. Successional stages of natural communities seem to include a greater abundance of fewer pollinators, which thereby replace more species foraging and pollinating at lower rates, in the more advanced or complex communities. This scenario is now a factor in planning for pollination futures [89]. Certain generalists may replace specialists, to an extent, through their flexibility or evolutionary change.

Modelling pollination in natural habitats is a useful tool for realizing a sharper focus on crop and wildlife management, including pollinators and their resources [93, 94]. Concurrently, the practical experience of farmers who recognize the value and goal of pollination service provides abundant empirical data and insight presented in recent FAO publications (see the References and Chapter 7). Fortunately, such organizations motivate scientific extension work and promote cooperation across continents through a number of farsighted projects aligned with international pollinator initiatives.

Technicians and growers are currently more sensitized to the fact that pollination is just as important to their livelihoods as other kinds of farm management. Extension and outreach efforts confirm the concept and validity of pollination. As illustrated

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[2] See www.fao.org/assets/infographics/FAO-Infographic-IYFF14-en.pdf

in the case studies presented in this publication, pollination is a broad theme with consistent and predictable features. Above all, if there is no provision for pollinators, then the management of farms or wildlands – in any real sense – is precarious and incomplete. Manuals or compilations such as this one can be used to inform and train those interested, who may, in turn, then present the facts to future farmers, pollination activists, professional pollination service providers, and officials or governments responsible for management and policy.

A noteworthy difference from the previous book, published in 1995, is that food, fuel and beverage crops are accorded greater emphasis, resulting in the removal of some content on timber, forage and medicinal cultivated plants. Because most plant names and a wealth of information are now easily accessible via the Internet, and the more credible sources follow international standards and norms, there seems little reason to repeat them here where a general online query will suffice. These are essential steps in an overall enterprise of providing information, cross-checking, and confirming trends and facts. Much is sure to change and will certainly improve. While the present scope of this compilation precludes discussion of wider themes, it reviews major advances in pollination biology, with some consideration of policy and management in the tropics, subtropics and the temperate zone. Commercial crops and certain techniques and tools are discussed in detail, along with general methods, experiments and theory. While this publication is not a husbandry manual for pollination service providers, or a set of guidelines for applications of chemical input to management questions, it does attempt to outline the practices and concerns of this vital human activity.

1.4 HOW TO USE THIS BOOK

The first part of the book reviews general issues, applied pollination, and makes suggestions or general recommendations on pollination for agriculture and conservation. More detailed information is then presented for particular crops, organized by geographic region and crop type. Pollination successes and challenges are identified and examined. Pollinator management is given its own section, followed by a section on research techniques, a further look at theory and the identification of pollen – the materia prima of cultivated plants – from a practical point of view. As formal or written agreements seem essential for crop pollination and professional pollination service providers, a first annex presents a basic pollination contract, and a second presents crop pollen species descriptions and documents the requisite voucher material and common and scientific names for pollen of cultivated plants depicted here for microscopic, taxonomic reference and pollinator study (Annex 2).

A number of relatively new and pertinent resources are available online. For example, Canada provides concise information for many animal pollinated crops at http://pollinator.ca/canpolin/ – a model that will hopefully motivate further work in this field.[3] The World Wide Web has truly permitted entry to an era of rapid enlightenment. It is of particular value for research, for example, with regard to establishing the scientific names of living things, and the publications and laboratory websites of authors. Caution should be exercised, however, when consulting "grey" literature and consulting websites offering services free of charge. Random searches for specific answers to crop cultivation or pollination needs are not encouraged. While these may be forthcoming or are sometimes available, the real tests and implementation take time, and are not assisted by quick or superficial answers. That biologists and other professionals will transform the current "Anthropocene" age into the needed "Biologicene", based on field tests and science, is a worthy goal, encapsulated in the following message: "When he [or she] enters a forest or meadow he [she] sees not merely what is there, but what is happening there" (Paul B. Sears, "Deserts on the March", 1935).

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[3] Another promising example is a pollination report for passion fruit produced at the national level: www.iea.usp.br/pesquisa/grupos/servecossistemas/publicacoes/manejo-dos-polinizadores-e-polinizacao-de-flores-do-maracujazeiro (in Portuguese).

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Chapter 2

POLLINATION, POLLINATORS AND POLLINATION MODES: ECOLOGICAL AND ECONOMIC IMPORTANCE

2.1 POLLINATION: A GENERAL OVERVIEW

R.C. Sihag

Angiosperms are credited with the most beautiful gift of nature – they have flowers. The latter, though scientifically of reproductive relevance, have much greater significance in the ecosystem and for human society. As Richards remarks (1987, p. 66):

> An outstanding feature of Angiosperms is the amazing diversity in forms and colour that has been adopted by the inflorescence, sufficient to inspire great art, fuel a major industry and serve as a solace for suffering mankind. Yet the flower is merely a sex organ, and never has any function except to promote reproduction by seed, usually sexually. The beautiful, weird, sinister, astounding forms that flowers have acquired are strictly pragmatic, and have encouraged the ecological diversification, and dominance, of the flowering plants.

This quote underlines the ecological importance of flowers.[4] If the authentic paleontological and present ethological records can prove (and they do) that the evolution and perpetuation of this floral diversity is due to pollinators, this surely demonstrates their importance. Likewise, if it is also proved that pollinators help to increase the seed yield of many crops, this should underline their economic importance.

In angiosperms, pollination is an important event that acts as a prerequisite to sexual reproduction. Pollen performs the same function in plants that sperm does in animals. Successful pollen transfer is therefore very important. However, pollen is a non-motile spore: it must be transferred from anthers (the seat of their production) to the stigma (the seat of their germination) by a vector.

Different plant species exercise different pollination modes, and the benefits accrued depend upon the kind of pollen transferred. While self-pollination normally tends to increase homozygosity, pollen from other flowers, plants or genotypes should increase heterozygosity. Self-pollination generally sacrifices plant quality (particularly in outcrossers), while outcrossing helps to increase hybrid vigour, resulting in healthier and stronger plants (although this is not always the case). The type of pollination also determines the chances of gene recombination and exchange between individuals. In changing environments, gene recombination (and therefore

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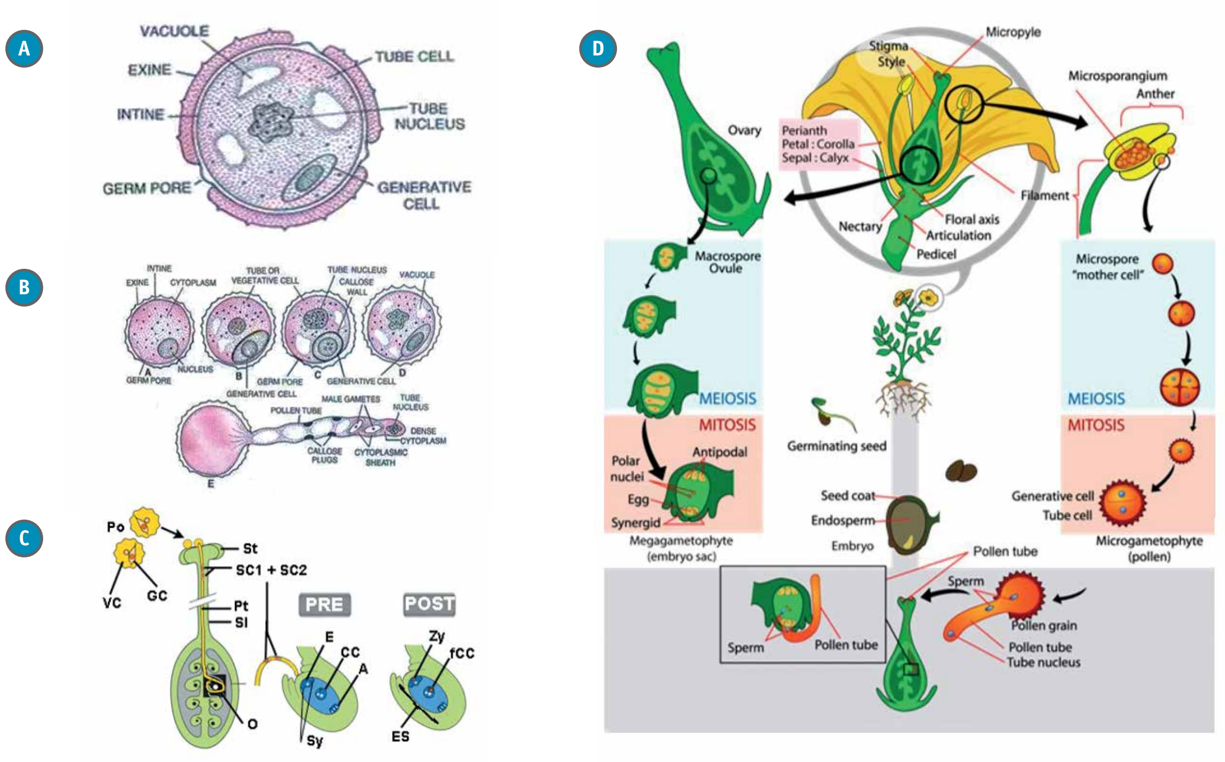
Figure 2.1
SCHEMATIC REPRESENTATION OF POLLEN, FERTILIZATION AND REPRODUCTION IN THE ANGIOSPERM LIFE CYCLE



(A) eukaryotic pollen cell; (B) pollen grain and germination; (C) angiosperm fertilization (Po = pollen grain, VC = vegetative cell, GC = generative cell, St = stigma, Sl = style, Pt = pollen tube, SC1/SC2 = sperm cells, O = ovule, E = egg, ES = embryo sac, Sy = synergides, A = antipodal cells, CC = central cell, Zy = zygote, fCC = fertilized central cell, and PRE/POST = before and after fertilization); (D) complete angiosperm life cycle

Source: A and B taken from "Stamen: male reproductive organ in flowering plants", article shared by Puja Mondal, www.yourarticlelibrary.com/biology/stamen-male-reproductive-organ-in-flowering-plants/11816.

cross-pollination) should provide an opportunity to produce strains better suited to new conditions, and is therefore an ecological necessity. In changing pest scenarios with rapidly evolving resistance to pesticides, especially in the tropics, gene recombination and heterozygosity through cross-pollination are reliable means to increase crop yield. Literally, they provide certain crops with the opportunity to keep up with or escape their enemies.

This section reviews pollination modes and pollinators, along with their ecological and economic importance. The use of complex terminology for pollination ecology is avoided where possible, although such terms are used elsewhere in the present book (see also the Glossary). The discussion is limited to descriptions of the importance of pollinators and pollination modes in crops grown to produce seeds and fruit.

2.1.1 The flower

Before exploring the benefits of pollination it is important to first understand how flowers work and how they relate to pollination and pollination modes. These subjects are explored in more detail in Chapters 5–7.

A typical hermaphrodite (bisexual) flower has four parts:

- *Calyx*: The calyx (consisting of sepals) is normally green and provides protection to other floral parts during the bud stage.

Figure 2.2
FLIES POLLINATING A STRAWBERRY

Native flies on a native strawberry of the USA, Pacific Northwest, drawn from photograph.

Source: Drawing and design by F. Gattesco and D.W. Roubik

- *Corolla*: The corolla (consisting of flower petals) is the coloured part of the flower, which provides the primary attraction and stimulus for pollinators.
- *Androecium*: This is the male part of the flower. It consists of anthers that hold pollen and function as the seat of male spores.
- *Gynoecium*: This is the female part of the flower and carries the female gamete – the ovule – in the ovary. Pollen is received at the distal tip called the stigma, where the former germinates for fertilization.

2.1.2 Pollination modes and pollinators

Pollination is the process of transferring pollen from the anthers to the stigma. The agent provoking this transfer is called the pollinator. Normally, angiosperms exhibit two kinds of pollination mode:

- When pollination takes place within a flower it is called *self-pollination* or selfing (Figure 2.1). Self-pollination takes place if: (i) the flowers are bisexual and have stigmas and anthers at the same heights (the stamens and the style are of the same length); (ii) both sexes mature simultaneously (protandry or protogyny are absent); and (iii) contact of newly dehisced anthers (releasing fresh pollen) with the receptive stigma is imminent. Proximity of anthers to stigma under the above conditions should result into self-pollination. If selfing results in fertilization, this should indicate at least some occurrence of strict inbreeding.

- When pollen from one flower is carried to the stigma of another, the process is termed *cross-pollination* or outcrossing. Here an external agent is required to accomplish the pollen transfer.

There are two kinds of outcrossing: (i) when crossing occurs between flowers of the same plant (this process is genetically equal to selfing although a foreign pollen vector is required); and (ii) when crossing occurs between flowers of two different plants. Outcrossing is important in plants where either flowers or plants are unisexual; anthers and stigma of the same flower are at different heights (i.e. stamens and style are of different lengths); sexes mature at different times (presence of protandry or protogyny); there is no contact of dehisced anthers with stigma of the same flower during their functional phase; and, above all, plants are self-incompatible (i.e. pollen from a plant cannot be utilized by its own flowers).

Outcrossing is brought about by two kinds of agents: abiotic and biotic. Abiotic pollinating agents are inanimate physical forces. Thus, abiotic pollination is generally "random", or at least is not directed specifically between flowers. Different kinds of abiotic pollination have been recognized:

- Gravity pollination (*geophily*) is found in self-pollinated plants. Here, some pollen is expected to fall on the receptive stigmas of other flowers due to gravity and may pollinate the flowers. However, geophily is highly unreliable and is a rare and insignificant pollinating agent.
- Water pollination (*hydrophily*) is found only in some water plants where inflorescences float or are submerged. However, many freshwater plants produce aerial inflorescences.

Wind-pollination (*anemophily*) is found in many plant families including crop plants – especially grasses. Characteristics of plants using the wind-pollination method include: (i) a reduced leaf surface area; (ii) exposed flowers; (iii) reduced perianths; (iv) long stamens and sometimes explosive anther dehiscence; (v) smooth, dry pollen grains that may bear air sacs; (vi) lack of nectaries and nectar in flowers; and (vii) flowers having no colour or scent.

The relative disadvantages of the wind pollination method are: (i) low accuracy; (ii) pollen concentration declines with distance from the emitting source; (iii) pollen is intercepted by all surfaces in the line of dispersal; and (iv) pollen availability may diminish with height for flowers of wind-pollinated trees.

In the case of biotic pollinating agents, animals perform the task of pollination (zoophily). Biotic pollination is highly accurate, but has a higher cost: nectar in addition to pollen must be offered to pollinators by the plant, which often has large and colourful flowers. Pollen vectors such as bees are characterized by high floral constancy.

Characteristics of plants using the biotic pollination mode include: (i) the production of relatively small amounts of pollen; (ii) the existence of some kind of relationship between the pollen vector and pollination unit (see Sections 2.1.2-2.1.4); (iii) significant variation in size and external appearance of pollen, which is usually sticky; and (iv) flowers with attractive colours and odours that also produce nectar. Biotic pollination naturally falls into several distinct classes:

- pollination by insects (entomophily) such as beetles (cantharophily), flies (myophily), bees (melittophily), butterflies (psychophily) and moths (phalaenophily);
- pollination by invertebrates such as snails and slugs (malacophily);
- pollination by vertebrates such as birds (ornithophily) and bats (chiropterophily).

Entomophily has played a major role in the evolution of angiosperms. The other pollination modes are considered to be secondary derivatives of entomophily. Among these modes, bee pollination is the most effective primarily for two reasons: first, bees visit flowers to gather food and thus seek flowers at all times, and second, the flower constancy of bees (their persistence in seeking flowers of one species) is very high.

All these forms of pollination modes are present in nature, but are scattered in space and time. For example, ornithophily is best witnessed in Australian and Neotropical forests, with hummingbirds and large nectar-producing flowers the best example. Different pollinating animals are in fact associated with different sizes and shapes of flowers and are usually effective pollinators of these flowers, regardless of the species and their origin. These relationships vary from the most specialized to the least specialized types, as illustrated in much of the pollination literature and elsewhere in this book.

2.1.3 The ecological importance of pollinators and pollination modes

Pollination modes and pollinators strongly influence ecological relationships, genetic variation in the plant community, floral diversity, speciation, plant evolution and ecosystem conservation (see Section 2.2). Pollination modes (e.g. abiotic or biotic) have a very broad range of effects, some of which are discussed below.

The role of selfing: Because selfing provides no chance of gene recombination, successful inbreeding over generations leads to genetic impoverishment (i.e. loss of variability) and limited possibility for adaptation in new situations. Inbreeding may also become a starting point for the formation of a successful inbreeding species. The chances of the former remain larger than the latter. Obligate selfing is a rare event and is found in a small minority of plants. However, individual species may show high levels of selfing, which may exceed 99 percent of all fertilizations. Examples include wheat, barley, oats and beans. Selfing is normally found in opportunistic annual plants.

Repeated selfing renders the majority of species less vigorous, when measured in terms of height, weight or reproductive and survival capabilities. Inbreeding depression occurs in organisms that are normally "outcrossers" and much less in those that have evolved to be "selfers". Selfing is a secondary derivative of outcrossing. Environmental changes that resulted in the failure of self-incompatibility among outcrossers led to the evolution of selfing in plants.

The role of wind-pollination (anemophily): Like selfing, anemophily is considered a later derivative of a widespread, pre-existing condition – in this case, biotic pollination. Retention of floral colour and scent, a well-formed corolla, effective and simultaneous wind and insect pollination, and similar features in a wind-pollinated plant, indicate its recent development and a connecting link between biotic pollination and anemophily. Sudden environmental change resulting in failure of pollination is considered to be the fundamental cause of anemophily. However, unlike selfing, anemophily provides some chances of genetic recombination through outcrossing. Anemophily might be considered a highly wasteful pollination mode because the pollen falls randomly. However, a recent analysis shows that this is not the case, and it is precisely its greater economy that promotes the evolution of anemophily wherever possible. Nonetheless, large amounts of energy and material are used in the production of massive amounts of pollen and feathery styles on flowers. In compensation the perianths are highly reduced and rudimentary. Therefore, floral features are greatly restricted. As a consequence, anemophiles exhibit low floral diversity.

Effective anemophily requires dry weather and either low plant species richness or a large number of individuals in a relatively small area. The frequency of anemophily increases with both latitude and elevation. Wind pollination is generally uncommon in lowland tropical environments, especially in rain forests, and is dominant in temperate deciduous and boreal forests. These latter forests show low plant and floral diversity.

The role of animal pollinators (zoophily): The majority of extreme floral adaptations are directed towards animal visitors. Animals accurately transport a high proportion of the relatively small amount of pollen produced over large distances to a tiny stigmatic target. Accordingly, zoophily provides the best chances of gene recombination. Pollination by animals goes hand in hand with floral diversity and its perpetuation. In species-rich communities with a low level of ecological dominance by individual plant or animal species, biotic pollen dispersal predominates. This is why, for example, alpine grasslands and Mediterranean and tropical forests are populated by attractive flowers and show high floral diversity.

In more productive and stable communities, the proportion of specialist flowers is slightly higher, indicating the availability of more reproductive niches. Such communities will tend to have a greater number of species in each pollination syndrome. The diversity of reproductive niches available in a habitat is necessarily a major component in floristic richness.

Pollinating animals also play a highly important role in speciation (new species formation). Selfing and wind pollination are considered to have no role in this process and generalist animal pollinators play only minor roles. With regard to the interdependent relationships of pollination syndromes and pollinators, specialized associations, even if only temporary, are vital.

The mutual adaptation of flowers and pollinators and their interdependence are considered to be the result of long and intimate co-evolutionary relationships. Various paleontological records now clearly show that many flower forms evolved due to the selective pressure of pollinators over geological periods. Non-specialized, flower-visiting animals were followed by highly specialized visitors, ultimately culminating in the specialized blossom and pollinator classes found today (Chapter 5).

Pollinators and ecosystem conservation: As described above, there are several specialized pollinator and blossom classes. These classes and the existence of several pollination syndromes highlight the interdependence of pollinators and plants. In such systems, pollinators promote the perpetuation of plants by making their sexual reproduction a success. This is because successful reproduction is the major currency in the life of an organism, and failure to reproduce impairs individual fitness. Therefore, the conservation of pollinators should imply the conservation of plant species, and vice-versa. The conservation of plants and pollinators upholds species diversity in the ecosystem. A species-rich ecosystem with high species diversity is considered to be the most stable. This is the normal state of the tropics. Conservation of pollinators and their host plants should therefore imply the conservation of ecosystems.

2.1.4 The economic importance of pollinators

The economic importance of pollinators has now been fully recognized and realized in agriculture. The list of crop plants that either rely completely on pollinators or benefit from their pollinating visits is vast. By increasing their seed and fruit yield through cross-pollination and the fecundity and survival benefits that these bring, pollinators are also receiving benefits. The relationship is self-sustaining. Since human populations depend directly on agriculture for food, fibre and other articles, and population growth has heightened the need for these commodities, the importance of pollinators in modern times has increased several times over. Honey bees and some solitary bees can now be managed successfully and utilized for the pollination of crops. Their necessity is felt whenever it is established that they increase yield, especially in crops that are self-incompatible or otherwise in need of visitors to their flowers.

Table 2.1 presents a list of crops grown in the tropics – fruits, vegetables, oil seeds, forage, fibres and spices. The benefits accrued to these crop plants, and hence the importance of pollinators in agriculture, is indicated as the percentage increase in yield.

Table 2.1

COMMON WORLD CROPS, BREEDING SYSTEM AND BENEFITS FROM POLLINATORS

FRUIT CROPS		
Acerola	*Malpighia glabra*	1–3% (S), 6.7–55% (H), 6.7–74% (C)
Almond	*Prunus dulcis*	No bees, no fruit formation
Apricot	*Prunus armenica*	Benefited from BP
Blackberry	*Rubus*	Benefited from BP
Cashew	*Anacardium occidentale*	55.5% (S), need BP
Cherimoya	*Annona cherimola*	6% (OP), 44–60% (H)
Cherry	*Prunus*	20–35% (S), 49% (H)
Chestnut	*Castanea*	1.3% (S), 68%(OP), 34.9% C(H)
Kiwifruit	*Actinidia deliciosa*	CE
Citrus	*Citrus*	40–60% (H), 80-100% (OP)
Coconut	Cocos nucifera	CE
Date	*Phoenix dactylifera*	CE
Grape	*Vitis vinifera*	1.7 seeds/cage, 1.8 (BP), 1.8 (OP) (BE)
Guava	*Psidium guajava*	CE
Jamun	*Syzygium vulgare*	CE
Jujube	*Ziziphus jujuba*	CE
Litchi	*Nephelium chinensis*	0.01–0.03% (BE), 0.7–11.2% (BP)
Mango	*Mangifera indica*	C increases fruit set
Muskmelon	*Cucumis melo*	1.6 crates/A (BE), 242 crates/A (BP), CE
Pawpaw	*Asimina triloba*	CE
Papaya	*Carica papaya*	CE
Passion fruit	*Passiflora*	CE
Peach	*Prunus persica*	BP increases yield
Watermelon	*Citrullus lanatus*	CE

VEGETABLE CROPS		
Balsam pear	*Momordica charantis*	CE
Beet	*Beta vulgaris*	BP increases seed yield 14%
Cabbage	*Brassica oleracea*	CE
Carrot	*Daucus carota*	128 lb/A (IE), 435 lb/A (TI), 711 lb/A (OP), 840 lb/A (BP)
Chayote	*Sechium edule*	CE
Cucumber	*Cucumis sativus*	CE
Egg plant	*Solanum melongena*	C increases production
Lettuce	*Lactuca sativa*	C increases seed yield
Onion	*Allium cepa*	9.8% (BE), 93.4% (BP)
Pumpkin	*Cucurbita*	6.8% (BE), 61.2% (BP), CE
Radish	*Raphanus sativus*	CE
Tomato	*Solanum esculentum*	Buzz pollination essential
Turnip	*Brassica rapa*	CE
Loofah	*Luffa cylindrica*	CE
White Gourd	*Benincasa hispida*	CE
Bottlegourd	*Lagenaria siceraria*	CE

OILSEED CROPS		
Flax	*Linum usitatissimum*	BP increases seed yield 22.5–38.5%
Niger	*Guizotia abbyssinica*	BP increases yield
Rapeseed, Canola and Mustard	*Brassica*	64.7 seed set (BE), 95.3% (BP)
Oil palm	*Elaeis guineensis*	CE
Olive	*Olea europaea*	C increases fruit set
Peanut	*Arachis hypogaea*	BP increases seed yield 6–11%
Safflower	*Carthamus tinctorius*	32–47% (BE), 100% (BP)
Sesame	*Sesamum indicum*	BP increases seed yield
Sunflower	*Helianthus annuus*	311 lb/A (BE), 931 lb/A (OP)

"PULSE" CROPS		
Broad bean	*Vicia faba*	BP increases seed yield
Cicer milkvetch	*Astragalus cicer*	2.3% (S), 12.4%, (H), 23.1% (C)
Pigeon pea	*Cajanus cajan*	BP increases seed yield 10%

SPICES, CONDIMENTS AND BEVERAGES		
Black pepper	*Piper nigrum*	BP essential
Cacao	*Theobroma cacao*	CE
Carambola	*Averrhoa carambola*	C obligatory
Cardamom	*Elettaria cardamomum*	11% (BE), 67% (BP)
Chicory	*Cichorium intybus*	0% (S), 61% (OP)
Clove	*Syzygium aromaticum*	CE
Coffee	*Coffea*	61.7% [*within branch*] (BE)
Coriander	*Coriandrum sativum*	C obligatory
Fennel	*Foeniculum vulgare*	BP increases seed yield 7 times
Kolanut	*Cola acuminata*	CE
Methi	*Trigonella corniculata*	0.09 kg/plot (BE), 6.2 kg/plot (BP)
Pimento	*Pimenta dioica*	19 berries (BE), > 1 000 berries (BP)
Tea	*Camellia sinensis*	CE
Vanilla	*Vanilla pompona*	CE
FORAGE CROPS		
Alfalfa	*Medicago sativa*	0.3 kg/A (BE), 20.3 kg/A (BP)
Berseem	*Trifolium alexandrinum*	0.27-0.64 seed/head (BP), 19.58–70.54 seed/head (BE)
Lespedeza	*Lespedeza*	C level 61.480.9%
Vetch	*Vicia*	BP increases seed production
FIBRE CROPS		
Cotton	*Gossypium*	2.3–3.4% (BE), 0–53% (BP)
Kenaf	*Hibiscus cannabinus*	C helpful in yield
Sisal	*Agave*	C necessary
Sunn hemp	*Crotalaria juncea*	2.6% (OP) 65% (BP)

Notes: BE = bees excluded; BP = bee pollination; C = cross-pollination; CE = cross-pollination essential; H = hand pollination; IE = all insects excluded; TI = tiny insects permitted; OP = open pollination; and S = self-pollination.

A companion table listing known pollinators for global crops grown for human consumption be found in A.M. Klein *et al.* 2007. Importance of pollinators in changing landscapes for world crops, *Proceedings of the Royal Society B*, 274(1608). doi: 10.1098/rspb.2006.3721.

2.1.5 Conclusion

Pollination involves the transfer of pollen from anthers to the stigma. Self-pollination is of little ecological or economic significance to many plant species, and when followed by self-fertilization it can cause inbreeding depression. This is a result of homozygosity, which provides no chance for gene recombination. Therefore, variability in the plant species is impoverished. The homozygous individuals have stunted growth and low yield in many of the wild and cultivated plant species. Cross-pollination, on the other hand, leads to heterozygosity and provides chances of gene recombination. This may increase variability in a plant population and provides opportunities for the evolution of new varieties, strains and even species. Heterozygosity in cultivated crops is expected to increase hybrid vigour, resulting in more healthy plants with higher seed yield. Aside from monospecific croplands of wind-pollinated species, cross-pollination by wind, water or gravity is of often of little importance due primarily to its random nature. However, pollination by insects can have great significance in the evolution of flowering plants and many floral, vegetative and genetic traits. All other biotic and abiotic pollination modes are secondary derivatives of zoophily – the animal transport of pollen grains. The presence of a wide variety of pollinators and pollination syndromes has contributed to present-day floral diversity in the tropics and subtropics. Among the animal pollinators, bee pollination (melittophily) is of great significance in agriculture, increasing seed production in many entomophilous and anemophilous crops. The conservation of pollinators and pollination services for plants is essential to preserve floral diversity in the ecosystem. Managed pollination should be accorded a high priority, in order to increase the crop yields of seed and fruit.

2.2 CONSERVING POLLINATORS FOR AGRICULTURE, FORESTRY AND NATURE

P.G. Kevan

Pollination is a pivotal, keystone process in almost all biotically productive terrestrial ecosystems. These include the most remote wildernesses of the Arctic to the most highly managed farming operations, such as hydroponics in greenhouses. Pollination is at the centre of a multi-spoked wheel that has human, livestock and wildlife consumers at its circumference. Other relationships of importance to maintaining the health of ecosystems include fungal and microbial interactions with roots affecting plant growth and nutrition, biophysical interactions in the soil, biophysical interactions between life and the atmosphere, plant propagule (seeds, etc.) dispersal by animals, the role of forests and multifarious pollution problems.

In recent years, conservation concerns over pollination have received increasing attention. This concern has been triggered in part by recognition of the value of pollination to agriculture. Figures calculated for Australia, Canada and the United States, mostly in regard to honey bees, show that the value of pollination far exceeds that of hive products such as honey. Recognition of this issue in Europe prompted several pioneering studies. However, the economics of animal pollination in agriculture within any one country are complex and difficult to assess. Regardless, agriculture and other equally vital economic ventures are dependent on a variety of pollinators, including the most generally important, honey bees. The total value of animal pollination to world agriculture has not been estimated, but the value to the global health of ecosystems is beyond measure.

The demise of pollinators is the consequence of four major human activities: (i) pesticide use, (ii) habitat destruction, (iii) diseases, and (iv) competition from introduced flower visitors. The majority of related information is drawn from temperate regions, but the same problems can be assumed to be equally or more severe in the tropics (see Chapter 3). The aim of this chapter is to review briefly the information available on each factor and place into perspective the potential consequences of ignoring the impacts to date.

Another issue in pollinator conservation is increasing recognition by scientists and others that "non-honey bees" are important as crop pollinators. However, the lack of general acceptance of the greater efficiency of other pollinators for certain crops, and the failure to recognize that some crops are poorly, if at all, pollinated by honey bees have hampered appropriate developments towards pollinator conservation for agricultural productivity.

2.2.1 Pesticides

The dangers associated with pesticides, especially insecticides, and pollinators are well documented and understood, especially with regard to European honey bees. Roubik et al. (2014) and other recent works have summarized the current available information (see Preface and Chapters 1 and 4). Johansen and Mayer (1990) wrote a highly informative book on the subject with an emphasis on the United States. Information has been published on most pesticides used worldwide regarding their toxicity to European honey bees, and sometimes other bees. In fact, many pesticide containers bear labels highlighting the associated dangers to pollinators.

Recent trends in many parts of the world towards reducing the use of pesticides in agriculture and forestry have lessened the overall incidence of pollinator poisonings. However, the problems are still severe in developing countries. It must also be remembered that pesticides constitute an integral part of integrated pest management practices (IPM) for crop protection in modern agriculture and forestry. The dangers must still be kept in mind and a constant vigilance maintained.

Many pesticide problems seem to stem from accidents, carelessness in application and deliberate misuse despite label warnings and recommendations (see Chapter 4). As pesticide application becomes increasingly regulated and users are required to take safety courses before certification, the problem should diminish. However, in many countries regulations are wanting, lax or ignored. General problems are exacerbated by the free availability in developing countries of pesticides that are outmoded or illegal elsewhere. In agricultural settings, pesticide use can be easily monitored and controlled by: (i) responsible agents of the agrochemical industries who manufacture and sell pesticides, (ii) diligent applicators who pay heed to labels, recommended application rates, and warnings about pollinator poisonings and human health, (iii) government extension agents, and (iv) other persons interested in agriculture and pollination services including the general public.

Issues in non-agricultural settings and agroforestry are more complex because of the importance of a wider diversity of pollinators, both wild and managed. One example of a well-understood situation occurred in eastern Canada where fenitrothion, sprayed against spruce budworms that were defoliating forest trees, had devastating side effects on wild, native pollinators of commercial blueberry fields. The effects were also immediately felt on the pollinators servicing the sexual reproductive needs of native vegetation. A number of different plant species of the forest and forest margins suffered reduced fruit and seed set, which in turn would be expected to impact wildlife by depriving them of natural quantities of food. The effects on pollinators resulting from extensive applications of pesticides against other major pests, such as forest defoliators, locusts and grassland herbivores, have received only minimal investigation.

2.2.2 Habitat destruction

Habitat destruction affects pollinator populations, as with populations of any organism, in three ways: (i) destruction of food sources; (ii) destruction of nesting or oviposition sites; and (iii) destruction of resting or mating sites.

The destruction of food sources is best illustrated by examples of the removal of vegetation, which provides pollinator with food when crops are not in bloom in agricultural areas. The vegetation removed is frequently regarded as unwanted, as weeds or as competition for the crop plants, yet is invaluable to pollinators and other beneficial insects. Kevan (1986) made special reference to these problems with respect to biological control, IPM and pollination in the tropics. The negative effects on pollinator populations in agricultural areas of removing "unwanted" vegetation have been documented, in particular, for Europe and North America (see Chapter 4).

The destruction of nesting and oviposition sites has been documented in central Canada for the demise of populations of leafcutter bees (Megachilidae), which were left without nesting sites in stumps and logs as fields of alfalfa expanded; in Europe for bumblebees as the amount of relatively undisturbed land in hedgerows and greenbelts declined; and in the tropics for the inadequate pollination of cacao by midges in plantations from which oviposition substrates or rotting vegetation had been too fastidiously removed.

Examples of the destruction of special mating or resting sites pertain to pollinators with rather special requirements and to those associated with rare plants. Although this problem is suspected to be real, documentation is not available and evidence would be difficult to obtain without specialized research.

The general issue of habitat destruction for pollinators has evoked concern on a broad scale. Janzen's 1974 article "The deflowering of Central America" exemplifies the problem. He points to a vicious cycle of reduced vegetation for pollinator resources, reduced pollination of vegetation, the demise of plant reproductive success, and reductions in seed and fruit set. These result in the failure of re-vegetation with the expected level of biodiversity. This cycle applies to all parts of the world where pollination by animals forms an integral part of the ecosystem. Nevertheless, recent publications on the conservation of insects and other animals give short shrift to pollinators and all but ignore the consequences of their demise. In the context of the present publication, this attitude is very difficult to understand.

2.2.3 Pollinator diseases

Mite diseases of honey bees have evoked major concern, as trachael mites and *Varroa* have spread at alarming rates. The impact of such diseases on honey bee colonies is well documented, but little information is available on the effects on pollination. It has been suggested that many amateur and small-scale beekeepers will abandon their activities because of the additional complexities of bee management associated with monitoring for mite diseases and controlling them once detected. Furthermore, chemical control of mites may not be acceptable to producers of pure honey.

The necessary changes to beekeeping, which is mostly in the hands of small-scale operators widely dispersed over the agricultural landscape, seem to be resulting in fewer beekeepers and lower distribution of free pollination from bees in their hives. There are already complaints from parts of the United States about inadequate numbers of honey bees for pollination of pome, stone and small, soft fruit crops. Pollination services may come to be provided by commercial beekeepers at an additional cost to the grower and consumer (see Chapter 10).

This scenario would apply to beekeeping operations in other parts of the world where non-native diseases have invaded the native stocks of honey bees. In India, the possible transfer of diseases from European honey bees to the Asiatic hive bee (*Apis cerana*) was suggested as the cause of the demise of the latter to the detriment of honey production.

Great care is needed for the introduction of honey bees from one part of the world to another. The spread of honey bee diseases from place to place and between species is mostly attributable to human activity (e.g. *Varroa* in western Asia, Europe, and North and South America, and trachael mites in North America, etc.). Quarantine protocols are well established in some countries, but are unfortunately lacking in others. Bailey and Ball (1991) provided a key work on bee pathology worldwide, and the subject is advancing with new information and protocols (see Chapter 16).

Leafcutter bees also suffer from diseases. The most important are the many chalk brood fungal varieties, such as that affecting the alfalfa leafcutter bee, *Megachile rotundata*. This disease has a major impact on the culture of the bees, and diagnosis facilities have been established in certain places (e.g. western Canada) where these bees are highly important to pollination in agriculture. Research on diseases affecting other managed pollinators, such as orchard bees (*Osmia*) and bumblebees (*Bombus*), is assuming importance as these pollinators take on a role in agricultural crop production.

The importance of disease in the regulation of populations of native pollinators is unknown. The same can be said regarding the roles of other natural enemies, such as the many parasitic wasps that attack natural populations of all kinds of bees, but are much more concentrated and capable of creating adverse effects in commercially established populations of solitary bees. However, a wide variety of pathogens, parasites, parsitoids and predators attack native bees and other pollinators in nature.

2.2.4 Pollinator competition

The most studied of the competitive interactions between pollinators as they relate to pollination is that of the effect of the Africanized (naturalized hybrid African x European) honey bees on native pollinators and European honey bees in South and Central America. The apparent reductions in abundance of native bees in the Neotropics after the invasion of Africanized bees was first pointed out by Roubik (1978), who subsequently placed the phenomenon in a broader context (2009). However, the issue of the competitive interactions of African bees with native pollinators in South and Central America seems complex.

In Australia, there has been debate recently over the effects of the introduced European honey bee on the native flora and fauna of pollinators. Some conclude that there is justification for the concern that European honey bees have caused reduction in the pollination of some native plants, especially those pollinated by birds, by removing the sought-after nectar and causing changes in their populations and foraging habits. The issue of effects on native pollinating insects is less clear from the botanical side, but the same trends are evident with respect to the native bees.

2.2.5 Diversification of pollinators

Although it must be conceded that honey bees are the most valuable pollinators in agriculture, they are not the sum total of crop pollination. Numerous examples illustrate this point including the greater efficiencies of orchard bees for pome fruit pollination, alfalfa leafcutter bees for alfalfa pollination, bumblebees for pollination of tomatoes and other solanaceous crops in greenhouses, blueberry bees for blueberries and carpenter bees for passion fruit. The lack of pollination brought about by honey bees for oil palm, various annonaceous fruit crops, red clover and other crops with flowers too deep for honey bees to access, as well as bat-pollinated durian, provide further evidence of the need to consider alternative pollinators for many crops. This issue is particularly important for the tropics because the natural pollination mechanisms of a large proportion of plants (crops and others) are not understood.

2.2.6 Conclusion

The conservation of honey bees, other domesticated bees, wild bees and other pollinators raises an important issue in the global context of agricultural and natural sustainable productivity. It is extremely important that apiculturists expand their horizons to embrace the culture of alternative species and the importance of other pollinators in agriculture. The significance of pollinators and the adverse affects that habitat destruction, poisoning, disease and competitive interactions with alien species have on pollination processes, need to be fully acknowledged by biologists, ecologists, agriculturalists and the general public, within the new spirit of global, environmental sustainability and conservation of biodiversity.

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Chapter 3

SUSTAINABLE YIELDS, SUSTAINABLE GROWTH OR NEITHER?

3.1 THE POTENTIAL FOR INSECT POLLINATORS TO ALLEVIATE GLOBAL POLLINATION DEFICITS AND ENHANCE YIELDS OF FRUIT AND SEED CROPS

L.A. Garibaldi, S.A. Cunningham, M.A. Aizen, L. Packer and L.D. Harder

3.1.1 Introduction

Land use has changed at an unprecedented rate during the past century. Agricultural lands, pastures, tree plantations and urban areas have expanded concomitantly with the consumption of agricultural products, energy, water and chemical inputs [1]. Those changes have caused widespread environmental degradation and major biodiversity loss that affect the ecosystem services on which human livelihoods depend [1], including crop pollination by wild insects [2, 3]. This chapter provides a general framework for understanding the contribution of animal pollination to crop yield. It also describes global patterns of pollinator abundance and diversity, pollinator dependence, pollination deficits, and the pollination efficiency of honey bees (*Apis mellifera*) and wild insects. It concludes with recommendations for improved agricultural sustainability from the enhancement of pollinator biodiversity, pollination services and crop yield.

3.1.2 Pollen as a resource that limits crop yield

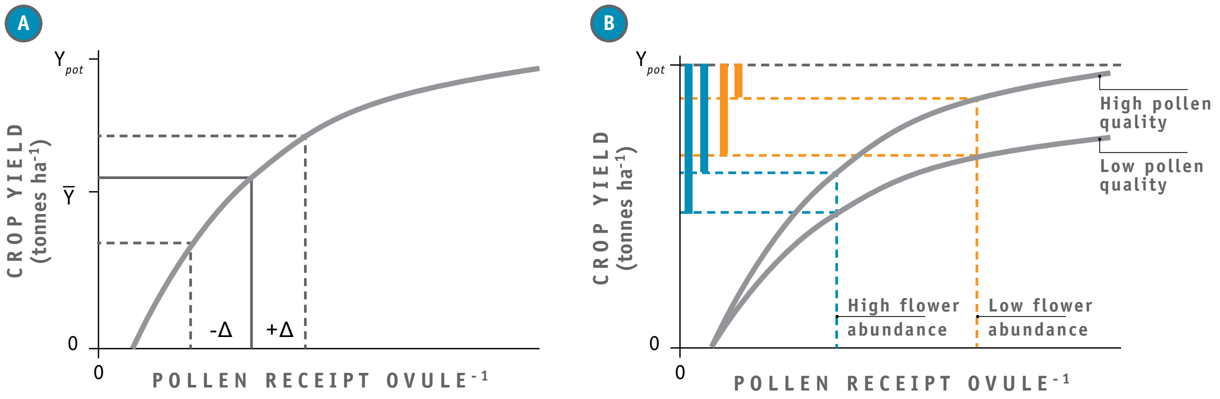
Crop yield (tonnes ha^{-1}) [1 tonne = 1.1 US tons] increases asymptotically with the delivery of resources in general, and for most fruit or seed crops with the pollen delivered to the stigmas [4–10]. The relation can be summarized generally as

$$Y = Y_{pot} \cdot (1 - e^{-b \cdot Pollen})$$

where Y is realized yield, $Pollen$ is the mean number of pollen grains per stigma, and b governs the rate of approach to the "asymptote, Y_{pot}, which is the potential yield (Figure 3.1a). Given such a saturating relationship, the temporal (e.g. among years) or spatial (e.g. among agricultural fields) variation in pollen receipt both increases variability (reduces stability) of crop yield, and reduces its mean. The latter result arises because the yield increase resulting from Δ units of pollen receipt above the average during a good year (+Δ in Figure 3.1a) is smaller than the yield decrease caused by pollen receipt Δ units below the average during a bad year (–Δ in Figure 3.1a).

Figure 3.1

CROP YIELD INCREASES WITH POLLEN QUANTITY AT A DECELERATING RATE, WITH PREDICTABLE IMPLICATIONS FOR THE RESPONSES OF MEAN YIELD AND YIELD STABILITY TO VARIATION IN POLLINATION AND POLLEN QUALITY



(A) Variability in pollen receipt (Δ) increases yield variability, but also reduces its mean ($\bar{Y}$), where $\bar{Y}_{pot}$ is the potential yield. (B) Effects of pollen quality and flower abundance. The blue and orange rectangles indicate the pollination deficit (potential minus the realized yield) under high and low flower abundance, respectively.

Source: L.A. Garibaldi

Pollination deficit is thus a shortfall in the yield of fruit and seed crops which could be alleviated by improved pollination, expressed here as the difference between potential and realized yield (Figure 3.1b) [11]. The model described above can be elaborated to incorporate the influence of pollen quality, which can affect pollination deficit through change in ovule fertilization and embryo development [8, 12]. Unlike pollen quantity, better pollen quality, resulting in enhanced cross-fertilization and reduced inbreeding depression [8, 12], can increase both potential yield *Ypot* and the rate of increase in crop yield with increasing pollen quantity, as influenced by *b* (Figure 3.1b). Thus, even if other inputs are provided, a reduction in the quantitative component of pollination deficit will not maximize yield unless pollinators deliver a sufficient quality of pollen. Management practices mostly ignore this component of pollination deficit; however, encouraging pollinators that move frequently among plants will improve overall pollen quality and reduce the deficit [13, 14]. Further enhancement of outcrossing rates might be achieved by considering the floral display, inflorescence architecture and particularly the genetic composition of the cultivated crop. Finally, management practices usually enhance the abundance of crop flowers per hectare, which may alleviate pollination deficits by promoting pollinator arrival or recruitment (i.e. higher pollinator attractiveness). However, these practices more commonly increase deficits by saturating the local pollinators, thus reducing the number of visits per flower, and therefore pollen receipt per ovule. In other words, the combination of monocultures with sparse, poor pollinator assemblages exacerbates the pollination limitation experienced by many crops (Figure 3.1b). Practices should therefore not try to increase floral resources, unless other measures are in place to increase the abundance and/or diversity of pollinators.

3.1.3 Pollinator dependence in fruit and seed crops

As with wild plants, fruit and seed crops, which are the subject of this volume, differ greatly regarding the extent to which animal pollinators increase yield, ranging from little or no improvement (e.g. obligate wind or self-pollinated crops such as walnuts or cereals) to complete dependence (e.g. Brazil nut, cocoa, kiwi, melon and papaya) [15]. In general, animal pollination enhances the sexual reproduction of about 90 percent [16, 17] of all angiosperms. Among crops, the estimates are similar, amounting to 85 percent of 264 crops cultivated in Europe [18] and 70 percent of 1 330 tropical crops, many of which have not received study [19]. Globally, animal pollination enhances the yield of 75 percent of the 115 most important crops, as measured by food production [15, 20] and economic value [21], including crops with a high domestication investment, such as soybean, sunflower and canola [13, 22, 23].

Such estimates consider crops to be of two kinds – completely unaffected by animal pollination, or at least partially dependent on animal pollination, whereas from a farmer's perspective the pollinator dependence of crops varies quantitatively. This dependence can be measured according to the extent of yield reduction in the absence of pollinators (percent dependence) compared to potential yield (Figure 3.1). The contribution of animal pollination to global agriculture has been estimated based on the pollinator dependence of the 87 most important crops, using yearly data for 1961–2006 provided by the Food and Agriculture Organization of the United Nations (FAO) [20]. Those crops were classified into five (average) dependency categories: 0 (no dependence), 5 percent, 25 percent, 65 percent and 95 percent (extremely high dependence) [15]. Thus, with no animal pollination, the estimated reduction in total agricultural production – considering these different categories of dependency – is 3 percent to 8 percent, depending on the year and local economic perspective [20]. These estimates are lower than previous ones by about 30 percent, which were derived without considering the degree of pollinator dependence [15]. However, the extra cultivated area needed to compensate for the < 10 percent production loss, under a hypothetical scenario of complete pollinator collapse, is much higher because of the lower yields of pollinator-dependent crops [20]. The increased area ranges from 15 percent to 42 percent, with the largest estimates for developing countries, where two-thirds of global agricultural land is farmed [20]. Furthermore, analyses of temporal trends for cultivated area and production reveal that, although animal pollination accounts for a relatively small share of total crop production, agriculture became steadily more pollinator dependent (> 50 percent increase) during 1961–2006 [20]. Therefore, the expansion of cultivated area, driven in part by pollinator loss, contributes to global environmental degradation, particularly in developing countries.

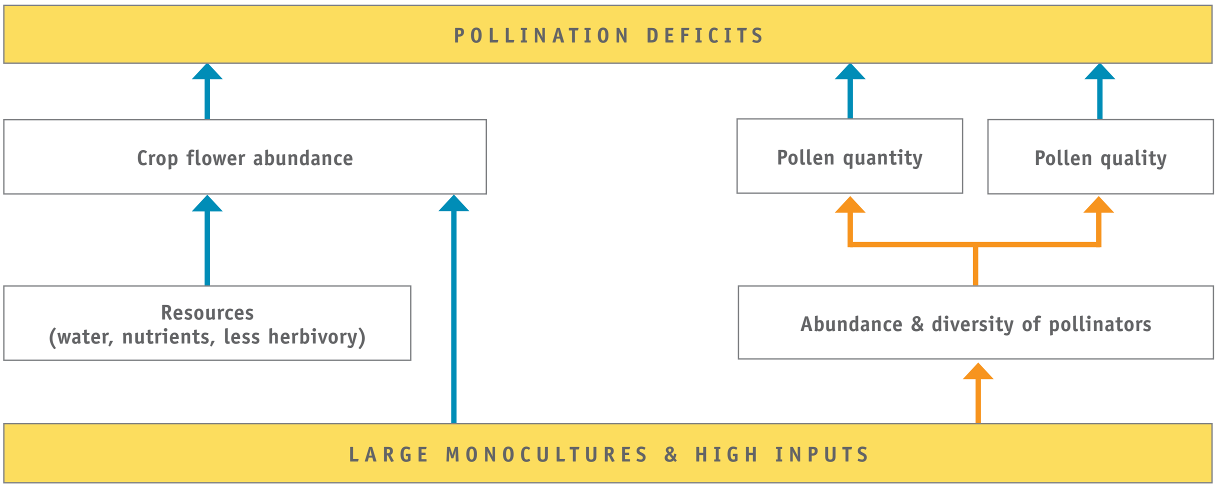
3.1.4 Are pollination deficits common?

The preceding section describes the magnitude of the pollination deficit that would occur if all pollinators disappeared. By analysing temporal trends in the growth and stability of crop yield, this section asks whether pollination deficits are common [24].

Pollination deficits are common among wild plants [25] and are thus expected among crops in general. Indeed, pollination deficits occur frequently in natural pollinator communities and ecosystems [25], just as crops can be nutrient limited even in non-degraded soils [26]. Despite many floral mechanisms that promote efficient pollen transfer, cross-pollination is intrinsically an uncertain process [9]. However, pollination deficits are aggravated in agricultural landscapes for several reasons. First, intensively managed agricultural landscapes usually provide poor habitats for pollinators [2, 3]. Furthermore, unlike crop loss due to herbivores, weeds, pathogens and their vectors, which are usually highly regulated by agricultural practices, pollination is usually subject to only minimal management and occurs almost entirely naturally, as an "ecosystem service" [27]. Worsening this situation, pollinator abundance and diversity are declining in many agricultural landscapes [2, 28, 29], further reducing the quantity and quality of pollen delivered to flowers [30] (Figure 3.2). Finally, current agricultural practices often involve the cultivation of extensive and massively flowering monocultures, increasing pollination demands for brief periods [19, 31]. The demands cannot be satisfied by the local pollinator pool (Figure 3.2), which is itself diminished by the practice.

Figure 3.2

POSSIBLE CONSEQUENCES OF AGRICULTURAL PRACTICES TO POLLINATION DEFICITS



Agricultural landscapes often are homogeneous environments including large monocultures and high chemical inputs, which may either cause pollinator deficits or alleviate some of them (see text). The blue arrows indicate most positive inputs, while orange arrows suggest where abundance, diversity and pollen factors may be negatively afected, while still contributing to overall crop production.

Source: L.A. Garibaldi

Given such conditions, crops with greater pollinator dependence will have a lower mean and stability of yield growth than less dependent crops, despite other practices that increase yield in most crops, such as fertilizer application and irrigation [24]. This prediction is supported by FAO data collected annually from 1961 to 2008, comprising 99 crops that accounted for 95 percent of global cultivated area during 2008. As a consequence of the lower mean and stability of yield growth, the cultivated area increased at a faster rate for crops with higher pollinator dependence such that production can match the demanded levels. That is, yield growth decreased but area growth increased with crop pollinator dependence (see [24] for more details). These results reveal that insufficient and variable pollination quantity and (or) quality reduce yield growth of pollinator-dependent crops, decreasing the temporal stability of global agricultural production, while promoting compensatory land conversion to agriculture.

The conversion of land to agriculture, described above, leads to a concomitant reduction in natural and semi-natural areas within agricultural landscapes, and decreases the abundance and richness (number of species) of wild pollinators (Figure 3.2). Such land conversion increasingly isolates crop plants from wild pollinators, aggravating pollination deficits (Figure 3.2). In particular, a synthesis of 29 studies [2] reveals that a 1 km separation between natural and semi-natural areas reduces flower visitor richness by 34 percent, visitation rates to crop flowers by all insects except honey bees by 27 percent, and the proportions of a plant's flowers or ovules that develop into mature fruit or seeds (fruit and seed set, respectively) by 16 percent [2]. Such separation similarly reduces spatial and temporal pollination stability, defined as the inverse of spatial variation within fields or of among-day variation within fields, respectively. Specifically, spatial stability decreases by 25 percent, 16 percent and 9 percent for richness, visitation and fruit set, respectively, whereas temporal stability decreases by 39 percent and 13 percent for richness and visitation, respectively [2]. To the extent that pollination deficits and low pollination stability have stimulated any change in agricultural practice, they have traditionally been addressed by managing a single pollinator species, usually honey bees, which are the most abundant crop pollinator species worldwide [2]. Potential effects of distance to source for honey bees are circumvented by deployment in crop fields and, during floral scarcity, by food supplements and other management measures (see Chapter 20). In addition, honey bees forage farther than most wild pollinators, and can locate and use discrete flower patches scattered in the landscape by means of scouting and directed recruitment [32–34]. However, whether an application of honey bees reduces most potential deficits efficiently remains an open question (see Part IV).

3.1.5 Can honey bee management alone reduce pollination deficits?

Honey bees occur both as wild and managed colonies nesting in transportable hives. Hived colonies can be placed in almost any habitat, depending on the demand for commercial pollination or honey production. Therefore, honey bees can alleviate the negative effects of isolation from natural or semi-natural areas on crop seed or fruit set. However, focusing on honey bees alone for pollination management may not provide sustainable pollination for several reasons.

First, an increased abundance of honey bees complements, but evidently does not replace, the pollination provided by diverse assemblages of wild insects. Wild insects pollinate most crops more effectively than honey bees, as revealed by a recent global synthesis of 600 fields in 41 crop systems [35]. In that study, fruit set varied positively with flower visitation by honey bees in only 14 percent of the sampled crops. In contrast, flower visitation by wild insects increased fruit set in every study crop. The relatively weak influence of honey bees detected by this analysis may reflect their tendency to limit single foraging bouts to small flower patches, and sometimes the flowers of a single plant [13, 14]. If this occurs regularly, cross-pollination is limited and elevated self-pollen interference and inbreeding depression are likely (Figure 3.1) [8].

Second, even for crops pollinated by honey bees, the current commercial availability of colonies may not suffice. Despite a global increase in the number of hives of approximately 50 percent during the last five decades, global agriculture dependent on animal pollination has tripled [36]. These disparate rates strongly suggest a rapidly expanding demand for pollination services provided by wild insects and other pollinators. Furthermore, honey bee numbers have increased unevenly among countries, with strong growth in major honey-producing countries, such as Argentina, China and Spain, but declines elsewhere, including the United Kingdom, the United States and many western European countries [36, 37]. Growth in honey bee numbers in one country is unlikely to contribute to the pollination of crops in another, although many queens and nuclei are distributed internationally (Chapter 16). In most countries except the United States [38], beekeepers profit more from producing honey than from renting colonies for pollination. Therefore, as is increasingly realized, the use of honey bees as crop pollinators will remain low unless payments for pollination increase.

Third, species of flower visitors respond differently to environmental change (response diversity), and thus biodiversity plays an important role in stabilizing ecosystem services, including crop pollination [39]. Indeed, some studies predict an increased role for wild bees given global warming [40]. Another study reported contrasting responses of wild insects and honey bees to wind conditions [41], such that this response diversity may stabilize crop pollination. The effects of response diversity may be especially relevant in the tropics, where impacts of climate change on pollinators are expected to be the greatest [42]. In summary, wild insects play a critical but underappreciated role in modern agriculture, and their importance will increase even more in the future. It is therefore essential to make better use of them for crop pollination.

3.1.6 Why do wild insects contribute to crop yield?

Fruit and seed set are key components of crop yield and reflect pollination success when other resources (e.g. nutrients) are not limiting factors [43]. Positive effects of wild insects on fruit set occur regardless of geographic location, sample size of the study, relative proportion of honey bees in the pollinator assemblage (their relative dominance), pollinator dependence of the crop, or whether the crop species is herbaceous or woody, native or exotic [35]. Such consistency is expected from the generalized nature of plant-pollinator interactions, whereby multiple pollinator species can profit from pollen and nectar of the same plant species [44]. This generalization does not mean that all pollinators interacting with a given crop are equally effective, but rather that various pollinators have comparable pollination efficiency.

The number of pollinator species (species richness) by itself may increase the mean and the stability of crop yield through several mechanisms [45]. First, a rich pollinator fauna displays more individual niche complementarity, with a variety of pollinators active across different flower patches and during different periods, individual days or a crop's entire flowering season, thus providing more consistent pollination overall [39, 46, 47]. Second, different pollinator species can act synergistically. For example, wild insects enhance the pollination behaviour of honey bees, presumably by un-aggressively displacing them from flowers, thus potentially driving both pollination quantity and quality, and enhancing outcrossing [13, 14, 30]. Third, because of a simple sampling effect, richer pollinator assemblages are more likely to include an efficient pollinator for a given crop than poor species assemblages [48]. By these and other mechanisms [49, 50], pollinator diversity contributes critically to an increased, sustained yield.

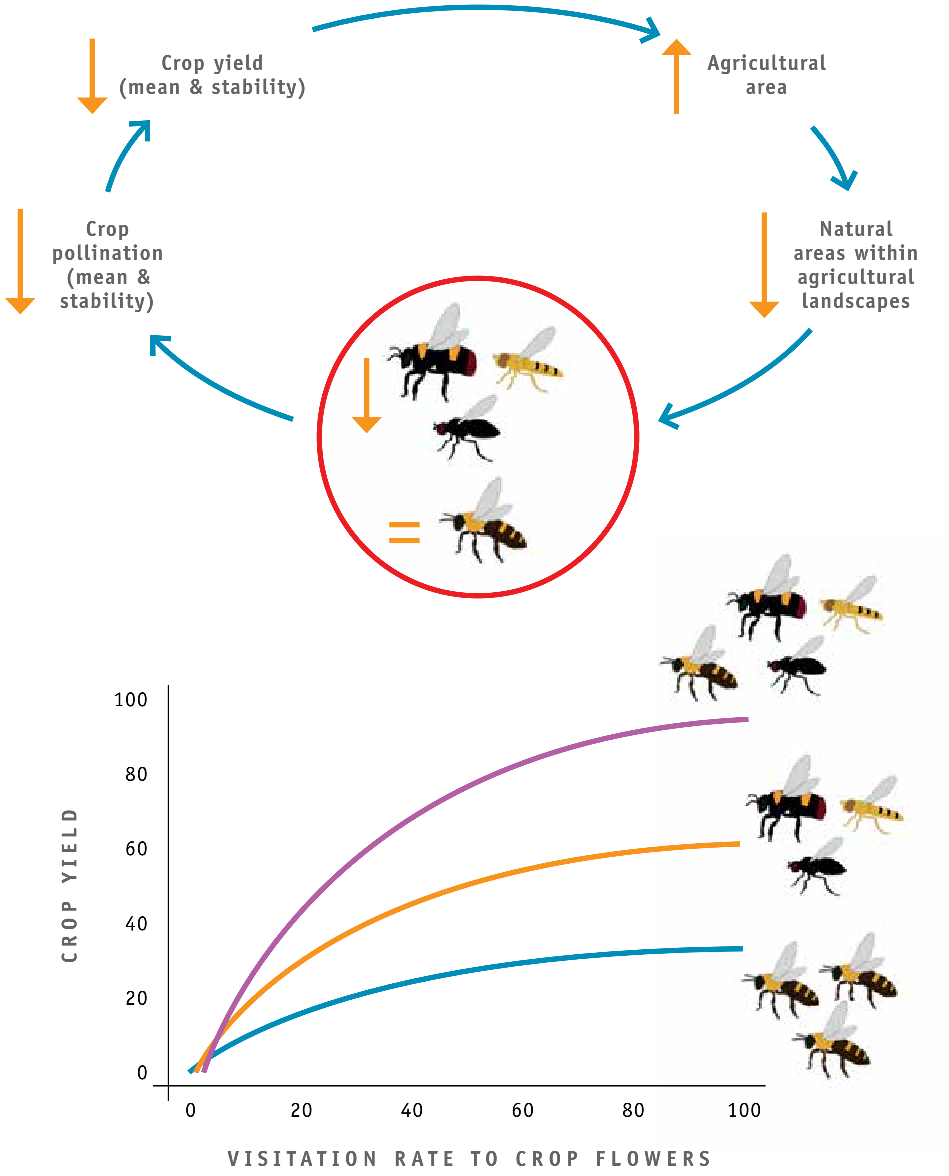
3.1.7 Sound practices that reduce pollination deficits

Land use changes during the past century have aggravated pollination deficits. Global fertilizer and herbicide use and the irrigation of crop areas have increased rapidly during recent decades, concomitant with the cultivation of mass-flowering crops [1]. In particular, herbicides – which have seen the most rapid growth in use among pesticides worldwide – are also implicated in the creation of agricultural environments devoid of pollen and nectar resources [50]. As discussed above, the combination of monocultures with sparse, poor pollinator assemblages exacerbates the pollination limitation experienced by many crops (Figure 3.3). In addition to the lack of habitat heterogeneity in those landscapes, high pesticide input further impoverishes wild insect assemblages (Figure 3.3). As argued here, the introduction of exotic pollinators does not seem to be an environmentally sensible practice to mitigate pollination deficits.

Varied practices increase the abundance and species richness of wild insects [51]. Indeed, wild pollinator species richness and flower visitation rate – a reflection of pollinator abundance – correlate strongly across agricultural fields [35]. Therefore, practices that enhance species richness may also increase aggregate pollinator abundance, and vice versa. Practices that should enhance the carrying capacity of habitats for wild insect assemblages and associated crop pollination services include:

- conservation and restoration of natural and semi-natural areas within landscapes dominated by crops [2, 3];
- planting hedgerows and flower strips along field edges [52–54];
- the addition of nesting resources (e.g. reed internodes) [55];
- implementation of organic practices within landscapes dominated by conventional farming [23, 56–58];
- the development and implementation of pollinator safety guidelines when applying insecticides [59–63];
- enhancement of farmland heterogeneity [39, 56, 64, 65];
- reduction of crop field size [66];
- actions to increase flowering plant richness within crop fields [14, 61, 62, 67, 68].

Figure 3.3
THE CYCLE OF WILD POLLINATOR DECLINE IN AGRICULTURAL SYSTEMS AND ITS EXPECTED CONSEQUENCES FOR CROP YIELD



Pollen limitation hinders yield growth of pollinator dependent crops, decreasing temporal stability of production, and promoting compensatory land conversion to agriculture at the expense of natural and semi-natural areas. These land use changes decrease the species richness and abundance of wild pollinators (represented by upper three insects in red circle) and crop pollination, but do not affect honey bee abundance (represented by lower insect in red circle). Increasing the visitation rate (visits flower^{-1} hour^{-1}) of only honey bees adds pollination and crop yield (tonnes ha^{-1}), but does not compensate for pollination losses from fewer wild insects.

Source: L.A. Garibaldi, reprinted from [50]

The effectiveness of such practices is context dependent, and relatively more successful when and where background floral resources, and natural nesting substrates, are scarce [69]. Where diverse floral resources are already available, preserving this diversity is likely to be the most cost-effective mitigation practice. In general, the effectiveness of large-scale practices (e.g. restoration of semi-natural areas) depends on smaller scale practices (e.g. increasing plant diversity within fields), and vice versa. The effects of such management depend on how far the various pollinators will fly from their nests, which is poorly studied. Flight distances are expected to vary positively with body size [70]. However, strong fidelity to small habitats, irrespective of body size, has also been documented [71]. Therefore, small-scale practices can strongly affect pollinators and crop pollination [52, 72]. Maintenance of biodiversity in agricultural landscapes is expected to support ecosystem services generally, and there is already strong evidence [35] that this is the case for the diversity of wild insects and the pollination services they provide.

3.1.8 Natural history of bees and their potential for crop pollination

Bees (Hymenoptera, Anthophila) are the single most important group of pollinators because they depend on flowers for nourishment at all active lifecycle stages, and visit flowers regularly and consistently. Nevertheless, the estimated > 20 000 species of bees [73] do not have equivalent potential as effective crop pollinators because of differences in geographic ranges and natural history, including abundance, phenology and habitat requirements. Thus, from an agricultural rather than a purely conservation perspective, management practices that promote suitable species are more likely to result in improved yields.

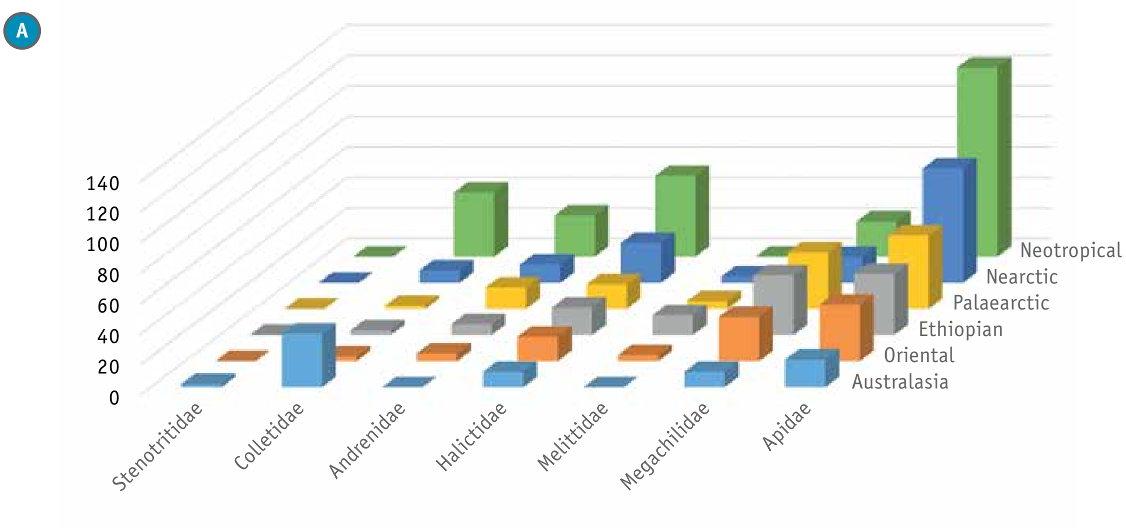
Bees are not equally spread geographically, but instead are most diverse in arid and semi-arid habitats, perhaps as a consequence of their purported evolutionary origin in drier parts of Gondwana [74, 75]. The preponderance of different bee taxonomic groups also varies with habitat and continent. Some higher-level taxa are geographically restricted, such as Stenotritidae and Euryglossinae, which are native only to Australia (Figure 3.4). Others are restricted, or largely restricted, to specific biomes. Stingless bees, Meliponini, are almost entirely tropical whereas the most species-rich bee genus, *Andrena*, is largely a north-temperate taxon (Figure 3.5a). Still other taxa are almost ubiquitous: *Hylaeus* is found on all continents except Antarctica, which has no bees.

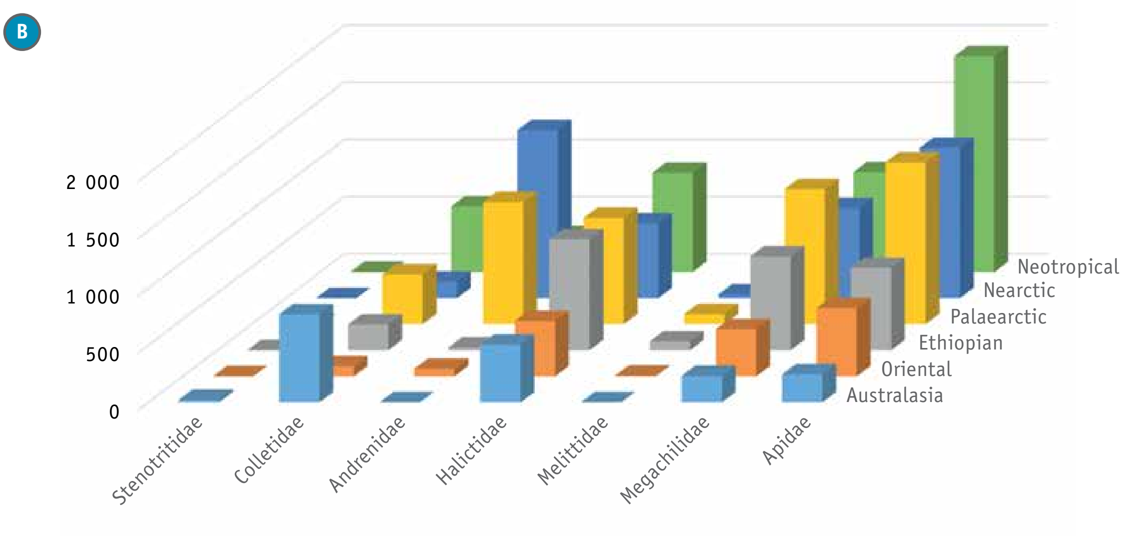
To be suitable for crop pollination, wild bees must be active simultaneously with crop flowering. Eusocial bees are often more suitable in this regard, because they are active throughout the growing season. They include the native *Apis* and *Bombus* species that extend from northern Africa to Asia, and in the case of *Bombus* also into the Americas. Those genera have had their ranges extended further by human introduction (below), and commonly exploit crops [35]. Most social Halictini, on the other hand, have pulses of activity, although their nests are often closed between brood-producing periods [76]. Solitary bees with a single generation per year rarely forage for more than a few weeks, and the activity periods of specialist species are often tightly linked to the flowering periods of their preferred hosts. Nevertheless, such phenological matching can be used to advantage for crop pollination if a specialist species frequents wild relatives of the crop, as is the case for the nomiine *Dieunomia* and sunflowers [77].

The activity periods of solitary bees also vary taxonomically. For example, although most *Andrena* are active during spring, North American species of the subgenus *Cnemidandrena* fly during late summer or autumn [78]. Similarly, species of the *Colletes inaequalis* group are among the first bees active during spring in northeastern North America [79], whereas species of the *Colletes succinctus* group are active during late summer and autumn in Europe [80]. Such phenological characteristics exclude many bee species as potential crop pollinators, despite their contribution to the pollination of native plant species.

Figure 3.4

NUMBERS OF GENERA (A) AND SPECIES (B) OF BEES OF DIFFERENT FAMILIES FROM DIFFERENT ZOOGEOGRAPHICAL REALMS



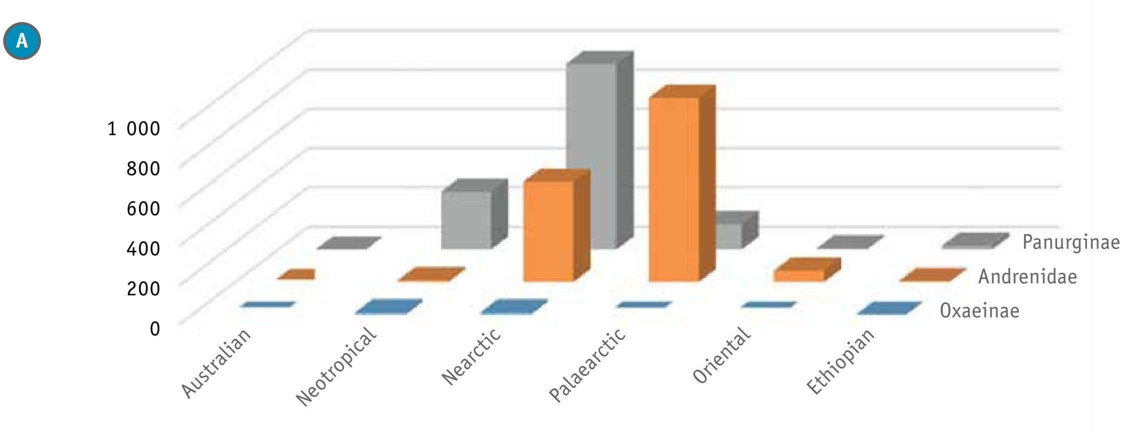


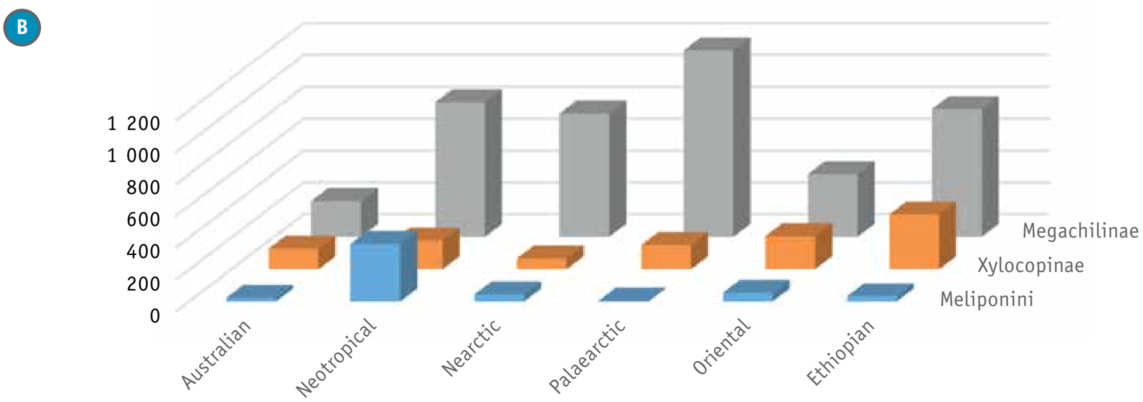
These data were obtained from [129] with the different regions delimited by national boundaries as close to those of the realms as possible. The greater generic diversity in the Neotropics for Colletidae, Halictidae and Apidae is evident, as is the low generic diversity of bees, except the Colletidae, in Australia. The pattern for species shares some similarities, such as the high diversity of Apidae in the Neotropics, but also some differences, such as the diversity of Halictidae in the Ethiopian realm. Some of the variation among regions likely reflects different intensity of study of bee taxonomy

Source: L.A. Garibaldi, reprinted from [50]

Figure 3.5

GEOGRAPHIC VARIATION IN THE NUMBERS OF SPECIES IN (A) THE THREE SUBFAMILIES OF ANDRENIDAE AND (B) THE THREE TAXONOMIC GROUPS OF BEES TO WHICH MOST MANAGED BEES BELONG (OTHER THAN *APIS* OR *BOMBUS* SPP.) AND FROM WHICH ADDITIONAL SPECIES MAY BE MOST SUITABLY EXAMINED FOR USE IN CROP POLLINATION





Source: L.A. Garibaldi

In addition to food requirements, the maintenance of viable wild bee populations in agricultural landscapes requires the provision of suitable nesting conditions. All Andrenidae, Melittidae and Stenotritidae, as well as the vast majority of Halictidae, nest in soil.

However, details of the preferred soil type, degree of shading and so on are known for comparatively few species [81, 82]. As a result, appropriate management practices are unclear. It is noteworthy that the most intensively managed ground-nesting pollinator, the alkali bee (*Nomia melanderi*), has specific and somewhat unusual substrate requirements, including silty, sub-irrigated soils with salty surfaces [83] (Chapter 5). Other ground-nesting bees used for crop pollination include *Amegilla* spp. for tomatoes in Australian greenhouses [84] and cardamom in India [85] and New Guinea [86], and both *Augochloropsis* and *Exomalopsis* for tomato pollination in Mexico [87] among others (see Part III).

Some bee subfamilies nest primarily in wood or pithy stems, including most Hylaeinae, Megachilinae and Xylocopinae, which makes them particularly amenable to management, because suitable materials can be readily provided. The first of these are comparatively hairless bees that carry foraged pollen internally, and so are not suitable for crop pollination. *Xylocopa* are effective pollinators of blueberry and passion fruit (see Chapters 9 and 15), as well as greenhouse tomatoes and melons [88]. However, the clearing of woody debris prior to planting of passion fruit vines, a usual agricultural practice, results in crop failure [89]. In contrast, *Xylocopa* in artificial domiciles have been introduced effectively into passion fruit orchards in Brazil [90]. They also colonize unoccupied nest sites within the fields, although the placement of unoccupied nests in fields does not attract bees from outside [90].

Megachilidae have the largest number of managed solitary bees, but are also the family with the most diverse nesting requirements [91, 92]. Most species nest in pithy stems or holes in wood, but for some species almost any cavity is used for nesting (they have even been found in the fuel lines of downed aircraft [93]). There is a large literature on the use of alfalfa leafcutter bees and various orchard bee species [94, 95], but one recent study also demonstrates the importance of nest dispersion. Specifically, *Osmia lignaria* (the "Blue Orchard Bee") prefers to nest in plots with a high density of nest boxes (100 per plot) with few cavities (100 per box), rather than in plots with a lower density of nest boxes (25 per plot) with many cavities (400 per box), despite the same overall density of potential nest sites [96]. Such details of nest box design and spacing will impact bee reproductive success and potential for sustainable management.

The use of wild bees as agricultural pollinators must embrace more aspects of their biology than mentioned above. Those of particular relevance are population dynamics [97] and features of the mating system, such as the potential impact of diploid males [98] on the persistence of small bee populations. Variation in ecological traits among bees of different taxonomic groups must be considered when habitat is modified to enhance crop pollination by native bees. Consequently, the expanded use of wild bees in food production will require increased expenditure on basic taxonomy and natural history [99]. Tropical stingless bees (Meliponini) provide a prime example. These eusocial bees have long been managed for honey production [100, 101], and one genus, *Melipona*, is increasingly used for pollination of crops such as tomato, eggplant and *Capsicum* peppers [102–105]. Their use is expanding in Africa [105, 107], Australia [106] and Latin America [101, 108] (see Part IV). The group includes hundreds of species that may be used in agriculture (Figure 3.5b). However, the pollen and nectar preferences of only few species are known, and even less is known about their pollination performance on particular crops [109].

3.1.9 Bee introductions

Motivated first by desire for honey and then by crop pollination problems, humans have promoted a few bee species and moved them beyond their original ranges. Accidental introductions can lead to successful colonization, even from a single, mated female [110]; however, some of the most problematic invasions have followed purposeful introduction for honey production or crop pollination [111, 112]. Most notably, honey bees and *Bombus terrestris* native to the Western Palaearctic have been spread around the world with human assistance. Both domesticated and wild varieties of honey bee are now nearly ubiquitous, and several European *Bombus* species have become naturalized in North and South America, Japan, New Zealand and Tasmania [113, 114]. In some regions, the alien bees have become superabundant, such as Africanized honey bees in the Neotropics [114–116] and *B. terrestris* in Patagonia [111]. In these cases, invasive bees overexploit flowers of both native and crop species, in some instances reducing fruit set because of intensive pollen theft [117] or flower damage [10]. Although exotic bees usually comprise only a small proportion of local bee diversity [118, 119], their abundance at a site can thus increase dramatically over time [114, 120] and spread rapidly upon introduction [111, 121], with the potential for large-scale ecological [47] and agricultural impacts [122].

In addition to reducing fruit and seed set as a result of over-visitation [10], introduced pollinators may diminish the reproduction of both cultivated and wild plants if they displace more effective native pollinators. Evidence for such impacts is varied. It is not clear whether the natural abundance of native bees decreases following invasion of the Africanized honey bee [47, 113, 114, 123]. Furthermore, visitation by wild bees to crop flowers sometimes varies independently of honey bee visitation [34]. However, invasion of Africanized honey bees has changed the preferences of native plant species by wild insects [47, 114]. Other studies have shown that the presence of managed honey bees can reduce the reproduction or fecundity of native bees, presumably though resource competition [124]. More seriously, the abundance of medium and large-bodied native bees declined following the arrival of *B. terrestris* in Israel in 1978 [125]. Similarly, the invasion of northwest Patagonia by *B. ruderatus* and then by *B. terrestris* during the last two decades has driven the native bumblebee *B. dahlbomii* to the brink of extinction [111]. The latter population collapse probably resulted from the susceptibility of the native bumblebee to pathogens transmitted from the invading congeners, rather than resource competition [126].

In summary, bee introduction can impose high environmental costs, while its benefit for crop pollination is arguable. As discussed, honey bees are often not particularly efficient pollinators. Their importance is likely to be greatest when the native pollinator community is so reduced that only managed honey bee hives can replace the missing ecosystem service. Introduced bumblebees can be highly damaging to flowers when abundant, or cause the demise of other, more efficient, pollinators. Little information is available on the impact of other introduced bees [113], but available evidence suggests that future pollinator introduction should be strongly discouraged. Instead, pollination management practices should, wherever possible, promote diverse and healthy assemblages of native pollinators.

3.1.10 Conclusion

Humanity faces a major challenge as agricultural intensification and growth of cultivated areas increase to satisfy greater demands from a human population of growing size and affluence [127, 128]. However, with long-term, sustainable agricultural practices, higher agricultural production does not necessarily require further loss of biodiversity or major environmental degradation [127, 128]. Crop yield (tonnes ha^{-1}) is a key driver of farm profits, livelihoods and agricultural decisions, which influence land use at both local and global scales. This chapter discussed how yield could be limited by pollen quantity and quality. Pollination deficit is the difference between realized yield and potential achieved under optimal pollen quantity and quality conditions. Pollination deficits can arise for crops because, unlike other limits, such as nutrients and pests, pollen delivery is not managed directly in most agricultural systems. Consistent with these observations, global patterns of yield reveal that pollination deficits are common for crops dependent on animal pollination.

Pollination deficits reduce the yield growth of pollinator-dependent crops and also promote the cultivation of a larger area to satisfy production demands. Indeed, planting of pollinator-dependent crops is expanding three times faster than the managed honey bee population, potentially exacerbating chronic pollination deficits exhibited by many crops. As a consequence, crop yield increasingly depends on pollination services provided by wild insects, which contribute significantly to fruit or seed set, regardless of crop origin (exotic or native) and life history traits (herbaceous or woody, etc.). Honey bees supplement the role of wild insects but cannot replace them, so that efforts to maximize pollination require the conservation or enhancement of all available pollinators. However, managed and wild populations of pollinators are declining in many agricultural landscapes, and further introductions of alien species should be discouraged because of their manifold environmental impacts. This situation strongly motivates conservation or restoration of natural and semi-natural areas within agricultural landscapes.

Restoration is promoted through land use heterogeneity, the addition of diverse floral and nesting resources, and respect for pollinator safety when applying pesticides and herbicides. Natural history traits of local wild pollinators can often be used to improve the effectiveness of pollinator-supporting practices. In general, the potential management of wild bees for crop pollination is still largely unrealized. Practices that enhance wild insects and associated crop pollination will usually provide resources for managed honey bee colonies, and can also enhance other ecosystem services, thereby creating positive feedback between healthy agricultural environments and high and stable crop yields.

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3.2 ALTERNATIVES TO ARTIFICIAL POLLINATOR POPULATIONS

R. Krell

3.2.1 Introduction[5]

Agricultural practices have undergone drastic changes over the last 100 years. The push towards mechanization in recent decades has seen ever-larger areas devoted to the cultivation of single crops with the aim of maximizing profit, alongside increased use of chemical fertilizers, herbicides and pesticides. Higher and higher production goals ignored the long-term effects on pollinators, with the pollination requirements of many crops taken into consideration only once changes in cultivation practices demonstrated new production limits. In the meantime, numerous natural pollinator populations were diminished or lost. Until very recently, honey bees were still considered dangerous and damaging to fruit orchards, and while the tremendous progress made in understanding the beneficial interactions of insects and plants has given rise to many potential applications, these have yet to be implemented.

Although exploitative agricultural practices similar to those described above have long been promoted in both tropical and subtropical developing countries, many regions are still undergoing the process of transformation. Other areas have come under pressures such as population growth or desertification, which also result in drastic changes to habitats.

This section presents ideas related to pollinator needs and for improving degraded habitats and those still to be transformed. Such a discussion cannot neglect social, technical and other environmental concerns. At the same time it is beyond the scope of this book to consider all possible aspects. Therefore, emphasis is placed on ideas and principles that should be considered by planners, technicians and others involved in making sustainable agriculture and multiple, sustained, non-destructive use of forests a reality. The concepts necessarily include subjects such as biological pest control and the promotion of less capital-intensive farming practices (e.g. intercropping, rotation and cover-crop plantings). These ideas require a new but not necessarily more difficult approach to improving agricultural efficiency. They also depend on a better understanding of the biological, physical and social interactions underlying all agricultural production.

Suggesting practices such as the foregoing examples to village communities and countries which have much more pressing problems may seem idealistic, particularly when such practices are not employed in other more stable industrialized countries not facing continuous emergency situations. However, traditional agriculture often resembles closely modern approaches that minimize dependence on agricultural chemicals and destructive land-use practices, albeit at a reduced scale. The goal is to highlight alternatives to increased agricultural production at any cost. Fortunately, methods exist that can be employed without the need for large-scale, long-term scientific studies, huge investments or loss of productivity, and rely instead on common sense.

It seems unreasonable to place an additional burden on the shoulders of the weakest link in the chain, the primary producer. Instead, a communal or concerted effort could be promoted by providing other benefits, such as better prices, greater access to markets and privileged access to the omnipresent subsidies. This also requires a change in the attitude of local politicians, bankers and merchants, as well as those countries and organizations that function as the primary source of finance, buyers, teaching and technology transfers. In this way, improvement in pollinator availability becomes a "global" problem in the purest sense. As with all global problems, the solution necessarily begins with the smallest details and changes in the attitudes of each and every one of us.

The following sections present a range of ideas which can be tested, improved upon and transferred to relevant stakeholders for active implementation, as well as to others for inclusion in a more global, complete plan of development.

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[5] For ease of reading, principal and general references are included at the end of the section.

3.2.2 Mechanical pollination and chemical pollination

Pollination by hand may be feasible under a certain limited circumstances and for small-scale production such as home gardens. On a larger production scale it is not profitable. Traditional date palm pollination or sometimes passion fruit and special hybrid seed production, as well as orchid propagation, including *Vanilla*, is done by hand. Increasing use is made of insect pollinators, even for greenhouse production. Mechanical pollination of fruit trees (apples and peaches) with large blowers has been attempted, but never incorporated into commercial enterprises. Thus, hand or mechanical pollination will remain restricted in application and cannot replace pollinators in agriculture on a large scale.

3.2.3 Habitat management for wild pollinators

The natural pollinators of wild plants and agricultural crops include a wide variety of organisms, not just bees and certainly not just honey bees. But aside from the pollinators whose populations can be manipulated or managed in large numbers, there exist a wide array of bee and non-bee pollinators capable of pollinating agricultural crops. Not the least important among theses are a variety of flies. Over a hundred different insect species can be observed on the flowers of certain fruit trees, although not all contribute significantly to their pollination. Maintaining such a diverse insect fauna increases the chance of sufficient pollination without the need for additional pollinator populations.

In order to ensure a sufficient number of wild pollinators, their habitats must be preserved and maintained. This means that the adult and larval stages of the pollinators need to locate food (often highly specific flowers, leaves, other insects, etc.). For many pollinators, nesting sites are also required. Some insects require certain soil conditions to survive during one of their life stages. For migratory species such as certain varieties of hummingbird or Asian and African honey bees, the habitats needed at each extreme of the migratory range must be preserved to ensure that sufficient numbers return during the next migratory season. In short, it is crucial to know the life history and requirements of species to ensure their conservation and multiplication. This is a demanding task even for the much less diverse fauna of the better-studied temperate climates. Fortunately, as long as the original plant cover of wildlands is preserved, much of the diversity will maintain itself.

What is the best way to determine the correct size of habitat for these purposes? Opinions are divided on this matter. Because few definitive scientific studies will be completed in the available time, the only safe approach is to conserve the largest possible area. Minimum requirements for some of the better-studied larger animals and ecosystems are known. For example, insect populations probably do not need the same size of habitat as certain mammalian predators. However, since many insects depend on other plant and animal species, they likely need somewhat extensive habitats for their survival. As more information is amassed about beneficial insects and other animals, the capacity of experts to prepare smaller habitats for them will increase.

In the event that only small islands of non-cultivated land can be maintained, it may be necessary to selectively plant and control species in those habitats to maintain pollinator populations that better suit the needs of these special environments (see also Part IV). If the more important natural pollinators for the crops are known, plant species used by these pollinators can be planted or maintained selectively. This approach would ensure the availability of flowers at the correct time. These selected habitats need more advanced planning in land use and also require more management, as they are less stable, being largely artificial. The lower the level of management possible in an area, the larger the area will have to be in order to maintain the required species diversity and abundance.

The composition of reserves or protected habitats will differ across regions and climates, but all should share a few common characteristics:

- a large diversity (to the extent possible) of local or locally adapted plants;
- freedom from exposure to pesticides;

- connection between habitat "patches" to enable species exchange, migration, etc.;
- sufficient numbers and distribution of such habitats in order to provide benefits to many agricultural producers.

The economic benefit of protected habitats cannot be justified only by the provision of pollinators and resulting production increase, particularly if only a few crops planted benefit from abundant pollinators. Additional values have to be found and a plausible intrinsic value for the local population, since monetary values are often of less importance. In order to make the additional effort worthwhile for the farmer, these small pieces of "unused" or "unaesthetic" land should preferably have another direct benefit, such as the provision of water, firewood, fruits, fodder, windbreaks, soil improvement or erosion control. If sustainable habitats are to be created or preserved, intrinsic values might include:

- traditional use of plants and forest for hunting
- food reserves for years in which crops fail
- medicinal resources
- ceremonial or religious uses.

Thus, the reserve size or species composition of such habitats might also be determined by intended alternative uses and established values.

While large reserves, such as biosphere reserves and World Heritage reserves, can and must conserve entire ecosystems, many small habitats can also preserve natural, beneficial pollinator species where they are needed. The smallest such habitats are field boundaries, hedges between fields and forest edges with various stages of successional plant growth. Following in size are fallow fields, planted forest patches for firewood and other communal or private uses, forests along river edges (riparian forests) and other pockets of more or less managed natural forests, preferably all connected to each other.

Hedges: Hedges play important roles in traditional agricultural systems in extreme climatic or geographical conditions, such as steep slopes or windswept plains. Their benefits can also be enjoyed in tropical climates. Apart from possible aesthetic values, hedges act as food and nesting resources for a large variety of animals, including pollinators such as birds, bats and insects. They also include windbreaks and livestock fences, provide erosion control, may stabilize dunes and water runoff, and produce firewood, fodder, fruits and medicinal plants.

Hedge communities can be chosen by observing local habitats and selecting those species most closely matching the desired hedge environment. The woody or shrubby hedge species should be chosen according to the major benefits expected from the hedge. Among suitable plant species, those that improve soil, provide rich nectar and pollen sources or have the most diverse use, may be preferred. Orientation of the hedgerows may follow land contours, property boundaries or be positioned to avoid (or enhance) the shading of cultivated plants.

Companion species should be planted or seeded according to the shade the mature hedge will provide. Naturally, shade-tolerant species should be in the centre of the hedge and on the side receiving more shade during the hottest part of the day. Some maintenance may be required to prevent one species from dominating and eliminating all others. But it is important to avoid weeding by completely destroying any plant cover, so common in tropical countries. The possible creation of natural hazards by providing new sites for poisonous snakes or stinging insects should also be taken into consideration. Sensible control by the elimination of such hazards is usually feasible.

Single or multiple-species hedges are frequently used for erosion control where they directly contribute to increased agricultural production, not only through feeding and protecting beneficial insects, including pollinators, but also through maintaining or improving soil and providing additional crops or food.

Fast-growing species that are easy to establish are preferred, especially if they are nitrogen-fixing legumes such as *Gliricidia sepium*, *Calliandra calothyrsus*, *Acacia decurrens* or *Desmodium rezonii*. These species give nectar and are actively sought by important pollinators like *Xylocopa* and *Apis*. The trees also can be pruned for mulching, animal fodder and firewood. Hedge pruning often determines whether species come to flower and provide nectar for bees. Selecting woody plants that act as pollinator food sources is sensible, as long as management of the hedges allows for flowering. The width of the hedge may vary with its overall function from a single row of planted sticks to a couple of metres.

Field boundaries: Field boundaries, in contrast to hedges, may or may not consist of perennial or woody species. They can be cultivated as boundaries by ploughing, cutting or spraying to maintain selected beneficial plant species for weed, pest and soil control, as well as to provide alternative food sources for pollinator species. Their width and maintenance may change more frequently with the rotation of crops.

Roadsides may cover considerable areas in some countries. These surfaces can be managed by cutting, which is fairly expensive, or by seeding and selective planting in order to maintain growth in certain successional stages. This allows them to serve functions similar to those of field boundaries, hedges or even small forest patches.

Home gardens: Due to their size, home gardens do not usually contribute much to feeding large pollinator populations. However, when entire villages plant flowering hedges around their homes, as well as fruit trees and bushes, and cultivate other flowers and certain vegetables, these habitats provide limited support for pollinator populations. Most of all, they constitute a source of food when there are few or no wild flowers nearby. This can be particularly helpful for beekeeping with species such as the Asia *Apis*, stingless bees and many non-*Apis* pollinators.

Riparian forests: Riparian forests grow in the immediate vicinity of a creek or river and perform an important ecological function by preventing soil runoff into the creeks, thus keeping water clear and less contaminated by agrochemicals.

Soil runoff not only constitutes a loss to the farmer, but also a threat to fish and other aquatic fauna. The soil changes the river bottom and the river course, and fills up reservoirs and lakes. Accordingly, trees on steep slopes or ravines should never be removed, and borders of 30 m to 100 m should be maintained, even on level riverbanks. Local conditions relating to flooding, aquatic life, river changes, land orientation and rainfall patterns must be considered. In addition, possible alternative uses of these areas, as described below for small forest patches, must be taken into consideration when planning the size of these borders.

Thus, leaving riparian forests untouched brings many ecological benefits, including the provision of unusually rich sources of nectariferous plant species and nesting sites for many kinds of pollinators. Where these habitats have already been destroyed, it is worthwhile replanting water edges with native tree and shrub species. Selecting the right species constitutes an active area of new research in much of the world.

Small forest patches: Forest vegetation can also be planted near agricultural fields. As is the case with natural forest, these patches can present a multitude of uses in addition to maintaining pollinators. Selecting only the fastest growing species used for firewood or timber production produces results similar to the planting of highly selective monocultures for agricultural production. Conversely, the application of sustained yield concepts considers the benefits of selected species for the soil, alternative uses, and the habitats provided by the forest patches for other crops and healthy populations of plants and animals. Mixed plantings should allow some undergrowth management. Future crop breeding might select for forest undergrowth conditions, thus simulating multilevel natural forests.

The classic eucalypt or pine groves do not present the best solution in most situations (either over the short term or long term), as these plants are selected for maximum rate of biomass production, which is only one among many important criteria. Even though most *Eucalyptus* species provide abundant nectar, their pollen is deficient in nutrients and very few companion plants can grow in the understory of these trees. As such, they provide no sources of cover, forage or alternative food for many kinds of animals. Soil quality and the water table are often negatively influenced and no other benefits can be obtained from the barren ground until many years after cutting.

In contrast, many fast-growing indigenous tree species permit various other uses of the land and the tree crop. Carefully selected species can even improve soil conditions through nitrogen fixation and organic matter deposition. More information on species selection, characteristics and requirements is available from a variety of information centres and networks.[6] The directory of world honey plants by Crane, Walker and Day (1984) allows cross-referencing of some species also known to be good producers of nectar or pollen.

A variety of experimental approaches have been employed for the establishment of small forest patches, mostly with an emphasis on multiple use of existing forests, forest conservation, community forestry, agroforestry, watershed management and sustained natural forest resource management. Few have considered the conservation of beneficial animals such as pollinators.

The multiple use of tree plantations should be included in any planting scheme. Selecting highly nectariferous tree species or those that allow nectariferous undergrowth brings additional income sources (beekeeping or native pollinator management) until the tree crop can be harvested. Therefore, higher diversity contributes to the sustainability of future crops and a higher quality of environmental conditions in general. Wise planning of multiple uses can help avoid loss of income and may instead become an attractive alternative.

Successional growth (second-growth habitat): While forests provide a large diversity of resources to nectar and pollen-feeding animals, this need is also met by certain savannahs and successional re-growth of fields and forests. The latter, in some tropical areas, can sometimes produce more nectar than mature forests. They also form an essential part of natural and "mature" ecosystems, harbouring many animal species and forming essential habitats for many pollinators and other beneficial insects.

Traditional slash-and-burn agriculture continuously creates areas of successional growth. If small enough and not too dense, these plots might maintain the desired pollinator species. In regions adhering only to slash and burn agriculture, there should be no pollinator shortages. This is due to the lack of vast monocultures. The principle of cutting only small areas and letting them regenerate, or replanting them with forest species, might be practised even in larger forest plantations. The same may be true in intermediate forest-agriculture zones or some park boundary zones where restricted exploitation is permitted. Forest edges provide a narrower, yet similar, habitat that should not be neglected. A rich flora and beneficial fauna can be maintained through minimal maintenance such as periodic cutting and selective clearing. Fallow fields in crop rotation or land regeneration (dunes, strip mines or eroded soils), like field boundaries, may be left to the natural succession of plant growth. They can also be planted with nectariferous, soil-improving species or receive minimum management, such as no-tillage, additional seeding and periodic cutting, to maintain successional growth at a preferred stage.

Nectar plants cultivated to benefit pollinators: Under most circumstances it is not common practice or economically feasible to plant crops solely for the purpose of providing nectar to pollinators. The value of honey or the resulting colony population of pollinators is always considered negligible in comparison to the value of the planted crop or the planting cost. For well-planned land use this may still be true in immediately recoverable monetary terms. But over the long term, the gap between planting costs and benefits from honey harvests, better pollination, increased natural pest control, lower fertilizer needs and other secondary benefits will become narrower. Eventually, such planting costs may become negligible

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[6] Please see the first edition of this publication, entitled *Pollination of Cultivated Plants in the Tropics* (1995), available online: books.google.com/books?isbn=9251036594

in comparison to all other benefits (when these are properly appreciated).

Pollinator populations can be enhanced through proper selection of flower species for their flowering times. This approach has been advocated for the maintenance of bumblebees in England, where they are very important pollinators. Thus early-flowering species serve to augment social bee populations or increase solitary bee populations or next year's population. Late-flowering species may increase the number of reproductive bees for the following season or year. Methods for studying the requirements and the preferred food plants of bumblebees on a countrywide scale were developed for England. Accordingly, groups of school children and volunteers were organized to make many of the basic observations. This worthwhile and affordable effort proved educational for the participants, increasing their environmental awareness, and was also very useful for researchers and farmers.

Abundance of attractive alternative food sources may in some cases reduce the efficiency of artificial and natural pollinator populations, if flowering occurs simultaneously with crop flowering. It is important to test, whenever possible, whether controlling such competing flora will decrease the following year's pollinator populations more than it will increase this year's pollination efficiency. This assessment should take into account alternative choices in pollinator species, crop varieties or timing of planting and pollinator introduction.

Cover crops: The practice of crop rotation enables the planting of cover crops during the fallow period. While the soil is recuperating the cover crop may provide flowers to pollinators needed in neighbouring fields. Self-seeding plants such as *Mellilotus* or other nitrogen-fixing legumes enrich the soil and may also provide a commercial honey crop, very rich fodder to livestock and/or "green manure". A combination of *Mellilotus* varieties can provide flowers over six months even on poor soils (at <40 °C). Some of these varieties have developed in Argentina for extreme subtropical climates.

Some problems do arise, similar to those stemming from highly nectariferous successional growth or forests. Attractive nectar-producing, non-crop flowers can compete with crop flowers for pollinators. In the case of natural pollinators, planting schedules and flowering periods must be synchronized as much as possible. The same problem with artificially enhanced pollinator populations can also be solved by placing colonies directly in the middle of the crop area, by providing more pollinators than are usually recommended, and/or by introducing the pollinator populations at a time when already 20 percent to 30 percent of crop flowers have opened. In extreme cases, competing floral resources may have to be temporarily reduced or eliminated during the crop flowering period.

3.2.4 Crop selection

It may be possible (as seen for many crops) to select additional varieties that do not require external pollination agents such as insects. Those varieties that continue to require pollinating insects, however, need to be made more attractive to pollinators (see Section 19.1). This means that more attention needs to be paid to flowering times and duration, nectar secretion and/or pollen attractiveness.

More emphasis on indigenous crops will reduce the need for exotic pollinators such as *Apis mellifera* in most of the world. Certain pollinators may prove less difficult to manage and propagate than imported honey bees, under local conditions. For example, it is generally well appreciated that *Apis cerana* is superior to *Apis mellifera* in much of the Asian tropics, due to better resistance to natural enemies and greater tolerance of environmental and resource conditions.[7]

The planting of *Mellilotus* in Northern Argentina, in a crop rotation system alternating with the cultivation of rice and cattle grazing, shows promise for profitable honey production (Krell, pers. obs.). A study by Accorti (1992) for Italy also demonstrates

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[7] For more information see Section 2.5.4 in *Pollination of Cultivated Plants in the Tropics* (1995): books.google.com/books?isbn=9251036594

substantial savings in fertilizer expenses and petroleum resources for honey production under improved environmental conditions, rather than using sugar from sugar beets to feed the bee colonies. Further studies on similar subjects will likely show that conversion to environmentally "friendlier" cultivation methods can ultimately be more profitable. Maintaining wild pollinators and sustaining imported ones requires careful selection of crop and non-crop (cover crop) species.

Good management practices include cover crops and perennial crop varieties. Timber species should be selected among other criteria for their high nectar secretion. Unfortunately, this subject has not been sufficiently considered in the past, nor been given due importance by plant breeders. This is particularly relevant in forest plantations where harvest and therefore income are realized many years after the initial investment, as nectariferous species can provide a "balancing income" (cash flow) and provide for natural as well as managed pollinator species. The selection of nectariferous tree crops is relatively easy because many, if not most, tropical tree species are naturally good producers of nectar. Their indiscriminate cutting also drastically reduces the nectar sources available to all pollinator species, not just honey bees.

The creation or conservation of large wildlands for honey production can have strong secondary effects on pollinator availability in distant agricultural areas. This is demonstrated by an example from Sri Lanka. After the disappearance of most of the natural forest suitable for honey production, rubber plantations (*Hevea brasiliensis*) have become the principal sites for beekeeping. Recent improvements in bee management techniques are only now starting to permit beekeeping on a larger semi-commercial scale. However, the new varieties of rubber slowly replacing those of old plantations are said to produce little or no nectar. If this proves true, the developing beekeeping industry will have no future. The need for moveable pollinator populations is also simultaneously growing, in part due to the same environmental degradation, deforestation and increased pesticide use. They are needed for increasing seed production requirements and exotic cash crops such as gherkins (i.e. pickling cucumbers). Thus, eliminating profitable beekeeping on a commercial scale also eliminates manageable pollinator populations. The latter can only be made available in sufficient numbers through migratory beekeeping (i.e. moving hives into areas where pollinator enhancement is required). In effect, the selection of the new rubber variety might restrict agricultural cultivation possibilities in parts of the country far removed from rubber-growing areas. This example demonstrates the far-reaching consequences a slight change in cultivar or crop can have on the agricultural productivity of apparently unrelated, distant regions.

3.2.5 Pesticides

Aside from habitat destruction, the application of pesticides in large quantities and over large areas is the primary reason that wild pollinator populations have been reduced or completely destroyed. Large aerial applications over hundreds of thousands of hectares of Central American and African tropical forests to control the Mediterranean fruit fly, tsetse fly and malaria mosquito have undoubtedly had an impact on the pollinator fauna. Documentation of agricultural chemical effects, however, is incomplete (see Chapter 20 for recent evaluations regarding bees and beneficial insects). Farm applications are more frequent and widespread, also covering very large areas. Agricultural pesticides are often misapplied and have highly toxic effects on local animals (see Chapter 4).

Along the northwest coast of Sri Lanka, pesticides may have led to a production loss involving cucumber cultivation. Initial production during the first and second year was fairly high. During the third and fourth year production strongly declined, and after five years had dropped to only 30 percent of the first year's output, despite increased fertilizer and pesticide use. During the same period more land was cleared in the dry forest zone and pesticides were applied, including by other farmers. The cucumbers are now deformed and of uneven growth – a clear indication of insufficient pollination. Unfortunately there is little that can be done. Together with increased pesticide use, the habitat was destroyed which otherwise could have allowed the re-establishment of honey bee colonies. Years of replanting will be necessary before the native pollinator population can increase its numbers.

Over the last decades, pesticides have become more potent, and only recently more specific. The broader a spectrum of pest species a pesticide potentially controls, the more devastating its effect will be on the total fauna, both pests and beneficial species alike. Its longevity in the environment and application timing and methods may further contribute to its destructiveness.

Although many broad-spectrum pesticides have been banned from the markets of industrialized countries for health and environmental safety reasons, many if not most of them are still being used in tropical and subtropical countries. Low levels of farmer and consumer education and strong political and economic interests permit the continued use of these often cheaper but more dangerous toxins. The newer, sometimes less toxic or more specific pesticides are usually much more expensive and therefore less accessible to the rural poor.[8]

Integrated pest management methods that will reduce pesticide use require very disciplined and well-educated farmers with more technical assistance than is available in most rural areas. Organic farming without the use of artificial or toxic chemicals requires traditional methods and even more education with new crops or at least a different kind of education than that commonly taught.

3.2.6 Cultivation practices

Studies of pollinator distribution in crop fields seem to indicate very limited foraging ranges of honey bees in situations with many more flowers than foragers. Similarly unsaturated conditions would occur with low natural pollinator populations or exceedingly large surfaces planted with one crop. If the overabundance of food (nectar) cannot be exploited, pollinators will concentrate on the areas closest to their natural habitat or nest. Uneven or incomplete pollination is often the result. Smaller field sizes and shapes following the contours of forest edges are therefore very important for pollination with "unenhanced" or natural pollinator populations.

Intercropping, or the planting of different crops in alternating rows or mixed rows, breaks up the uniform surfaces, reduces the overabundance of one food source and thus increases fruit set across the field. Although the number of plants to produce a crop is lower, production per plant is increased and the mixture of crops maintains or improves farmer income. Intercropping may also reduce relative production costs due to lessened pesticide and fertilizer requirements.

The most pressing change to be made to preserve natural pollinator populations is the adoption of less toxic and more balanced cultivation practices. Many of the alternatives have already been mentioned, such as reduced and more focused pesticide application (within integrated pest management programmes where pesticide-free cultivation is impossible), selection of more resistant locally adapted or indigenous crops, a larger variety of crops, multicropping systems, crop rotation, less tillage and more manuring. Last but not least, the soil must be monitored and taken care of as a highly complex living organism – a concept firmly established in many traditional cultures, but utterly disregarded by most of this century's agricultural development.

Initially, some of the suggested changes may result in lower yields than those heralded by the so-called "green revolution", but over the short term they save foreign exchange (pesticides and fertilizers) and farmer's lives (poisoning), and over

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[8] See the IPM PRIME database (https://ipmprime.org/pesticides/Home#), the Xerces Society for lists on known toxicity of pesticides to bees and other pollinators. University-based IPM extension agencies are among the most valuable of the numerous available online resources.

the long term they preserve and likely increase yields for the future and reduce health costs, due to healthier food and water. The modern meaning of the "green revolution" is no longer equated with "highest output of biomass by any available means", but instead with the healthiest, least destructive, sufficient output of food.

3.2.7 Conclusion

To solve pollination-related problems in general, the easiest solution would be to switch to crop varieties that do not need pollinators, or to pollinator species that are easily manipulated and multiplied, such as some honey bees. This quick fix, often demanding a large investment, may be the remedy for some circumstances, but is unlikely to provide a long-term or sustainable solution. Fundamentally, it does not address the need for hybrid seed production, or for outcrossing in the many plant species that must be cross-pollinated to produce seed or fruit. Unless sufficient natural, non-cultivated flora are available, even the ubiquitous Western honey bee cannot provide the solution to pollination needs. Only a few highly specialized pollinator species with relatively short life spans, such as the alfalfa leaf cutter bee, may be maintained with one or a few crop species alone.

The next most efficient change would be to increase natural pollinator populations through reduced pesticide use. Alternative cultivation methods, conservation and selective planting will further increase natural pollinator populations and improve environmental conditions, as well as reduce farming costs.

Knowing the requirements, deficiencies and the costs, certain pollinator-limited crops may simply be poor choices for the economics of a given area. This is particularly true for some exotic or export crops which have to meet very specific standards of fruit shape or quality. Taken into account early enough, these conditions can prevent disappointing results, failed projects and farmers' losses.

For any sustainable and affordable solution to succeed, less destructive cultivation methods are necessary. Conservation efforts and sound agricultural practices are central to this goal. Creation or preservation of diverse environments, not only in national parks, is also required. This is true to the same extent for natural and managed pollinator populations.

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Part II

APPLIED POLLINATION:

BASIC APPROACHES

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Chapter 4

INTEGRATING POLLINATOR HEALTH INTO TREE FRUIT IPM: A CASE STUDY OF PENNSYLVANIA APPLE PRODUCTION

D.J. Biddinger, E.G. Rajotte and N.K. Joshi

4.1 IPM AND THE RECENT POLLINATOR CRISIS

Integrated Pest Management (IPM) is a longstanding, science-based, decision-making process whose ecological roots lie in the use of multiple biological, cultural, physical and chemical tactics to protect crops in a way that minimizes economic, health and environmental risks. IPM is a management philosophy that can address any pest complex (insect, disease, weed, vertebrate, etc.) and can be adapted to any agricultural production goals including conventional, sustainable and organic. In addition, IPM for a given crop can evolve to meet new production demands such as pesticide use reduction, incorporation of ecosystem services and food safety [1]. As in the case of pollinators, IPM can be adjusted to protect pollinator health, just as it is adjusted to protect other beneficial organisms such as predators and parasitoids of pests. Indeed, growers understand the IPM paradigm, which means that pollinator protection, as a part of IPM, can profit from an already trusted line of reasoning.

Similarly, while it is evident to IPM practitioners that long-term reliance on a single pesticide or biological control agent is not sustainable, reliance on a single pollinator such as the Western hive honey bee (*Apis mellifera L.*) is also unsustainable and less obvious. Honey bees are still the most valuable pollinator in temperate tree fruit crops, because they are well understood, relatively easy to maintain, mobile in large numbers and able to rapidly communicate the locations of new food sources [2]. However, it is well known that honey bees are not the best pollinators for all crops [3, 4]. They are generalist foragers easily distracted from target crops like cucurbits, pears and apples by other flowering plant species such as dandelions (*Taraxacum sp*.) and other more sugar-rich nectar sources. In addition, honey bee populations have declined in recent years to the point that total reliance on them for pollination is increasingly risky. Since 2006, North American beekeepers have lost approximately one-third to one-half of honey bee colonies mostly due to Colony Collapse Disorder (CCD) [5]. Those losses compounded losses caused by: (i) the introduction of two parasitic mite species; (ii) viral, fungal and bacterial diseases; (iii) pesticide poisoning; (iv) hybridization with the Africanized variety of honey bee; (v) economic threats from loss of honey bee price supports and global honey competition, and (vi) agricultural intensification of monocultures to maximize yields, which have removed much of the adjacent flowering and nesting resources [6]. Despite increased need for pollination services for crops such as the US$2 billion almond industry, honey bee colonies had already declined by over 40 percent in the United States since 1947 [7], even before the emergence of CCD. The importation of honey bees from outside the United States to meet demand for pollination began in 2005, however this solution carries substantial risks, as it greatly increases the chance of introducing new pests and pathogens to all domestic bee species. Fruit growers in the eastern United States have been exploring the free services of native and various other "pollen bees" (see below) to supplement or replace the honey bee for pollination, at a recommended rate of two hives per acre for apple pollination.

The challenge is integration across two dimensions: integrating pollen bees into crop production pollination strategies (usually formulated by horticulturalists and apiarists) and integrating all pollinators into IPM crop protection programmes, which often include pesticide use, developed by plant protection specialists in entomology and plant pathology in a format that growers can implement. As an illustration of this double integration, this chapter uses a case study of apple production in the eastern United States, specifically southern Pennsylvania, where small to medium-sized orchards nestle in the rolling Appalachian mountains among a patchwork of forest land and diverse agriculture. Unlike larger orchards (with apple blocks > 4 ha), Pennsylvania orchards, with their high perimeter-to-area ratios, are exposed to diverse habitats, and most apple flowers are no more than a few hundred metres from an orchard edge.

4.2 THE IMPORTANCE OF POLLINATORS IN APPLE PRODUCTION

All apple cultivars require cross-pollination to ensure the production of commercial crops for the fresh market, where the size and shape of the fruit are considered just as important as yield. Small, deformed apples are considered to be of lesser value and are destined for the processing and juice market, at a fraction of the price of high-quality fresh market apples. Therefore, maximizing fruit set is not as important in apple as it is for crops like almond, tart cherry and blueberry, where commercial yields require 75 percent or more of blossoms to set [8]. In contrast, apple only requires 2–8 percent of the flowers at bloom to set fruit, with excess fruit chemically thinned soon after bloom to concentrate the tree's resources on producing fewer but larger fruit, and to prevent a biennial cropping (alternate bearing, see Glossary) – a tendency of most apple cultivars [8]. The bloom period of apple lasts only seven to ten days, on average, and occurs in the early spring, well before most crops other than tree fruit. The weather during apple bloom is often cool, wet and windy, with only short windows of optimal honey bee foraging weather, but the period is functionally longer for more cold-tolerant pollen bees such as *Osmia* and *Bombus* species.

4.2.1 Non-honey bee pollinators that provide insurance for sustainable apple pollination

The prevailing perception is that domesticated honey bees are necessary for a successful apple crop. However, many apple producers in Pennsylvania and New York have stopped relying on honey bees over at least the last ten years, with no reported economic loss. Instead, adequate pollination services are provided by other bee species that occur naturally in the surrounding landscape. Reliance on wild pollinators is quite common in the two states: a 2011 survey showed that 51 percent of Pennsylvania growers never rent honey bees for apple pollination [9], as is the case for the majority of smaller apple growers in New York [10]. Moving from direct augmentation of honey bees to promoting existing populations of wild pollinators avoids the expense of renting honey bee hives, and is therefore of great interest to many growers, especially in the face of the tripling of rental rates since 2006, driven by variable honey bee hive availability and production costs.[1] The growing dependence on wild pollinators means that management of orchards, field edges and natural areas to ensure nesting habitat, adequate forage and protection from pesticides have become important issues to ensure sustainable fruit pollination in the eastern United States.

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[1] As of 2014, the rental rate had reached US$100/hive.

Increased reliance on non-honey bee pollinators faces its own challenges. Multiple pollinator species are necessary to provide the biological insurance for sustainable pollination in many crops, but in many situations oversimplification of agricultural landscapes has eliminated the alternate food sources and nesting sites necessary to sustain those wild pollinators. Near total reliance on the honey bee in the past has also resulted in a lack of knowledge regarding which wild pollinators are regionally available for a specific crop, how effective they may be, how far they fly, and their requirements for additional floral and nesting resources. There are, however, 3 500 non-*Apis* bee species in the United States that also function as important pollinators of most specialty crops [11]. They include the many species of bumblebees and what are often referred to as solitary bees. These bees are also known as "pollen bees" because their main value, in relation to people, is not the production of honey, but the collection and transfer of pollen for the fertilization of plants [12]. Pollen bees are critical components of food webs associated with wildlife habitats of all types in North America, and were present long before the introduction of honey bees by Europeans. The value of pollen bees as pollinators is conservatively estimated at US$3 billion annually for US agriculture [11]. Because of the popular focus on honey bees, the services of pollen bees frequently go unrecognized (see Part IV), and their value for agriculture and especially for unmanaged ecosystems is probably much higher than estimated. For most bee species, the paucity of long-term population data and our incomplete knowledge of even basic taxonomy, life history and ecology make assessing their value and possible declines in some regions very difficult [11]. Recent research on eastern US tree fruit production has shown that many species of wild and managed pollen bees can supplement honey bees for pollination and in some situations replace them.

4.2.2 Pollinator diversity during apple bloom

Wild pollinators consist of a variety of species in a given area, each with its own life history traits, flower preferences and crop pollination usefulness. The early spring bloom of tree fruits such as plum, peach, pear, cherry and apple, importantly, means that only bees that overwinter as adults are available for tree fruit pollination. They include the univoltine species of *Andrena*, *Colletes* and *Osmia*, but also the multivoltine *Augochlora*, *Bombus*, *Ceratina*, *Halictus*, *Lasioglossum*, *Osmia* and *Xylocopa* [13].

At fruit tree bloom, the multivoltine species are typically present in much lower number (or only as queens in the case of *Bombus*), as they initiate nests that will give rise to greatly increased population sizes in the summer and autumn generations. Net collection surveys undertaken by the authors since 2007 have found 52 bee species and seven syrphid fly species pollinating apple (Table 4.1).

Out of the 371 known species of bees in Pennsylvania [14], over 180 occur in orchards during the spring growing season. Since at least some wild pollinators such as *Osmia* are up to 80 times more effective in pollinating apple than the honey bee on a per bee basis, orchards pollinated mostly by pollen bees may have noticeably lower bee abundance than orchards stocked with honey bee hives. Orchards pollinated mostly by pollen bees do not literally "hum" with bee activity since many of the bees, with the exception of *Anthophora* and *Bombus,* are relatively quiet during flight, and fewer are active at a given time. Adult syrphid activity during bloom is much lower than that of pollen bees in most cases, and it seems to be more dependent on pesticide input against aphids. This occurs because the syrphid larvae feed on aphids and then overwinter in the orchards after a flare up of aphid pests the previous summer.

Table 4.1
LIST OF POLLINATING BEES AND SYRPHID FLIES FOUND VISITING APPLE BLOSSOMS IN PENNSYLVANIA FRUIT-GROWING REGIONS

FAMILY – ANDRENIDAE
Andrena bisalicis Viereck
Andrena bradleyi Viereck
Andrena canadensis Dalla Torre
Andrena carlini Cockerell
Andrena commoda Smith
Andrena crataegi Robertson
Andrena cressonii Robertson
Andrena daekei Viereck
Andrena dunning Cockerell
Andrena erythronii Robertson
Andrena heraclei Robertson
Andrena hilaris Smith
Andrena ilicis Mitchell
Andrena imitatrix Cresson
Andrena macoupinensis Robertson
Andrena nasonii Robertson
Andrena nuda Robertson
Andrena perplexa Smith
Andrena pruni Robertson
Andrena robertsonii Dalla Torre
Andrena rugosa Robertson
Andrena vicina Smith
Andrena wilkella (Kirby)
Andrena ziziaeformis Cockerell

FAMILY – MEGACHILIDAE
Osmia bucephala Cresson
Osmia cornifrons (Radoszkowski)
Osmia lignaria Say
Osmia pumila Cresson
Osmia taurus Smith

FAMILY – APIDAE
Anthophora abrupta Say
Apis mellifera L.
Bombus bimaculatus Cresson
Bombus griseocollis (DeGeer)
Bombus impatiens Cresson
Bombus perplexus Cresson
Bombus vagans Smith
Ceratina dupla Say
Ceratina calcarata Robertson
Nomada lehighensis Cockerell
Nomada ovata Robertson
Xylocopa virginica (L.)

FAMILY – HALICTIDAE
Augochlora pura (Say)
Augochloropsis metallica (F.)
Halictus confusus Smith
Halictus rubicundus (Christ)
Lasioglossum acuminatum McGinley
Lasioglossum admirandum (Sandhouse)
Lasioglossum pilosum (Smith)
Lasioglossum quebecense (Crawford)
Lasioglossum truncatum (Robertson)
Lasioglossum versans (Lovell)

FAMILY – SYRPHIDAE
Allograpta obliqua (Say)
Eristalis tenax (L.)
Eristalis dimidiata Wiedemann
Eupeodes americanus (Wiedemann)
Platycheirus immarginatus (Zetterstedt)
Syrphus rectus Osten
Syrphus torvus Osten
Toxomerus geminatus (Say)
Toxomerus marginatus (Say)

Source: Biddinger, Rajotte and Joshi

4.2.3 Roles of landscape and floristic diversity in support of apple orchard pollinators

Perhaps the most important factor that determines the reliability of wild pollinators is habitat suitability, both in the orchard and in the surrounding countryside. Orchards in the major fruit-producing region of Adams County, Pennsylvania, where most of the field studies were centred, are typical of those found in the eastern Appalachian Mountains. They have steep, well-drained soils located in a landscape matrix of approximately 8 percent fruit orchards, 24 percent arable and pasture land, 9 percent developed area and 56 percent forests [15]. The region has a humid continental climate, with an average yearly rainfall of 112 cm, average summer temperatures ranging from 16 °C to 28 °C, and winter temperatures of -5 °C to 5 °C [16]. The size of individual orchard blocks averages about 2–4 ha in size and blocks often border undeveloped scrub, forest or fence rows. In these Pennsylvania apple orchards, floristic diversity was documented in orchard, forest and forest edge habitats surrounding commercial apple, in order to explore the correlation between plant diversity and orchard pollinator communities. The result was a surprisingly diverse plant community with the forest edge/orchard border the most species rich, supporting 169 out of 228 plant species recorded in the survey. Plant species richness and evenness in the orchard and forest edge habitats, and plant community evenness in the forest habitat, were significant predictors of bee species richness and abundance in the orchard. In addition, plant species richness and evenness in the forest edge habitat were significantly correlated with bee community composition in the orchard. The results show that local plant communities in crop and non-crop habitats close to orchards play an important role in provisioning wild apple pollinators [17].

Figure 4.1

A PEACH ORCHARD IN SPRING AND A BUMBLEBEE VISITING AN APPLE BLOOM, IN PENNSYLVANIA STATE, USA

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Apples and peaches only need 2–8 percent of the bloom to set fruit, and thus are chemically or hand thinned to obtain fruit but of commercial size

The response of pollinator richness and abundance to floral resource availability, and the effects of local factors such as field management, within-field plant diversity and field margin plant diversity, have been well documented [17–20]. Given the value of local access to floristic diversity, supplementation of plant communities in agricultural landscapes is an important conservation strategy for pollinator communities. Managing non-cropped field edges, hedgerows, roadsides, meadows and semi-natural grasslands in agricultural landscapes for increased floral diversity has been widely studied and recommended for pollinator conservation. However, selection of plants with similar bloom phenology and attractiveness to pollinators of the crop being pollinated could cause competition for resources and should be avoided.

Many plants attractive to pollinators are also attractive to beneficial predators and parasitoids of pests for the same reasons (pollen and nectar sources), but should be considered for their potential to harbour potential insect and disease pests of the adjacent crop. One example in Pennsylvania was the consideration of Eastern Redbud (*Cercis canadensis*) for provisioning services to flower visitors. While attractive to many early season pollinator species, it has a bloom period that often overlaps apple and could compete with apple bloom for pollinators. It is also a legume whose seed pods provide an attractive food source for a major pest of apples, the Brown Marmorated Stink Bug (*Halyomorpha halys*). After screening many different species of plants for attractiveness to pollinators and beneficial insects for several seasons, however, the study also found that clustered mountain mint (*Pycnanthemum muticum*), which blooms after apple and is very attractive to many species of pollinators, is also attractive to the crabronid wasp, *Bycertes quadrifasciata,* and a syrphid fly, *Trichopoda pennipes*, both of which are effective native predators or parasitoids of the Brown Marmorated Stink Bug [21].

4.3 IPM, PESTICIDES AND POLLINATORS IN APPLE

Integrated pest management (IPM) for apple production in the eastern United States is quite complex. During the growing season, more than a dozen major insect and mite pests [22, 23], eight to ten fungal and bacterial diseases, and several vertebrate pests can attack the fruit and the trees [22]. Many of the pests attack simultaneously. In the case of weed management, not only can weeds compete with apple trees for nutrients, water and pollinators, but some weeds are alternate hosts for plant diseases or the nematodes that cause them. Over the last 50 years, IPM in Pennsylvania tree fruit has developed into an efficient and profitable combination of host plant resistance, biological control, sophisticated pest monitoring, and pest predictions based on mathematical models and weather data, as well as highly time and economic threshold-specific pesticide applications [22]. Each management tactic was developed through university research programmes, and fruit growers were taught how to implement those practices through a comprehensive extension education programme. Integral to IPM in apples is the potential to modify the IPM programme to protect living IPM tools (biological control agents), such as predatory mites, parasitoids and other general predators [24–28]. It is this IPM experience that will allow further modification of the programme to protect pollinators, while maintaining protection from pests.

The cause of the recent decline of honey bees and other pollinators is multifactorial and may include crop pesticides, bee disease, parasites, pesticide use in hives, lack of forage and transportation stress. Many suspect that pesticides play a major role in the decline, which has given rise to a call to ban a group of insecticides known as the neonicotinoids. Pesticide applications may include multiple types of insecticides, fungicides, bactericides, herbicides, surfactants and others. All have their own toxicity profiles and affect various insect species including bees. They may also have unexpected consequences when used in combination, which is common in apple production in the eastern United States. Researchers are just beginning to understand the chemicals and combinations as they affect pollinators [29–33].

The neonicotinoids were developed and marketed in response to the Food Quality Protection Act of 1996 [34], which mandated the elimination from the market of pesticides such as organophosphates and carbamates that have unacceptable human toxicity. In addition to improved human safety, neonicotinoid insecticides have also proven to be safer to most beneficial insects other than bees and allow the biological control of important apple pests such as San Jose scale, woolly apple aphid, European red mite, leafminers and leafhoppers, to name a few [22]. The situation is even more complicated because not all neonicotinoid active ingredients are equally toxic to bees [35]. Even the toxicity of the same neonicotinoid active ingredient may vary in its toxicity to different species of bees or become more toxic when used in combination with certain fungicides [29]. Eliminating neonicotinoids could necessitate the use of less effective alternative pesticides, which could increase production costs by more than US$100 per acre due to secondary pest flare ups, and could also aggravate nascent pest resistance problems. The use – or non-use – of neonicotinoid insecticides to manage pests in apples through an IPM approach has multiple benefits and costs.

The first step in properly examining the role of pesticides in bee health is to understand the actual field exposure that bees encounter. Most studies that examine pesticide impact on pollinators consider only short-term acute contact exposure to adult bees, because those are the most easily conducted bioassays. The experience of this study showed that, when testing new experimental pesticides for apple pests and beneficial insects, lab assays in general are poor predictors of field performance [36, 37], but are at least a starting point for understanding pesticide toxicity. In conducting such bioassays, however, many studies use technical pesticide dissolved in acetone to standardize the assays with those that are conducted by EPA (US Environmental Protection Agency) for honey bees. These studies have the benefit of minimizing potential differences in readings from solvents and inert products that often vary between manufacturers of the same pesticide active ingredient. *However, they also have a major limitation because the acetone moves the pesticide directly into the insect haemolymph and thereby denies the insect cuticle its potential as a major barrier to pesticide exposure*. A recent study [29] found that active insecticide ingredients tested on the honey bee using the formulated product dissolved in water were 100 times less lethal than indicated, compared to published studies using the technical product in acetone [35].

Insecticides, however, are not applied during the short apple bloom; so direct contact of surface insecticide residues on bees is not likely to be an important route of exposure. Contact exposure to residues from pre-bloom sprays is also unlikely since bees do not walk on foliage. They normally contact only the inner portion of the apple flower, which was protected from pre-bloom applications. Fungicides, however, are heavily applied during bloom and are discussed below. The mostly likely route of pesticide exposure to bees in tree fruit is through the ingestion of contaminated pollen and nectar from the application of systemic insecticide and fungicide applied before bloom. Ingestion bioassays on bees are much more difficult to conduct than contact assays and are mostly absent for bees other than the honey bee and some *Bombus* species. Determining levels of pesticide in the nectar and pollen under field conditions is the first critical step in determining the exposure level of bees subjected to low doses in multiple flower visits over time. The preliminary studies showed a neonicotinoid insecticide such as thiamethoxam, sprayed at the pink bud stage of apple at a typical 100 ppm field rate, is reduced by translocation in the plant tissues. Five days after application at 25 percent bloom, only 1–4 ppb is present in the nectar and pollen [38]. Determining the amount of nectar or pollen consumed daily by various bees in comparison to their body weight is the next step in determining an aggregate dose for each bee as it visits many flowers each day and ingests a relatively low dose of pesticide at each flower. Unfortunately, such consumption rates are lacking in studies for bees other than the honey bee. Likewise, the long-term acute mortality of solitary or non-*Apis* bee larvae through ingestion of contaminated pollen is a major exposure pathway that needs further investigation for multiple species.

A shortcoming of the regulatory process in the United States is that pollinator pesticide susceptibility is determined using the honey bee as a proxy for all pollinator species. Honey bee susceptibility is not an accurate predictor for wild bees such as mason bees (*Osmia*) [29], leafcutter bees or bumblebees. Furthermore, susceptibility varies by bee species and pesticide [39]. For example, one recent trial conducted for this study showed that the Japanese orchard bee was 26 times less susceptible to imidacloprid contact than the honey bee, but 12 times more susceptible to acetamiprid [29]. Both products are neonicotinoids.

4.4 PESTICIDE RECOMMENDATIONS IN APPLE IPM TO PROTECT POLLINATORS

An important advantage of the IPM approach is that pest management practices can be adjusted to accommodate new factors. Just as apple IPM adjusted to meet food safety regulations resulting from the Food Quality Protection Act (FQPA), IPM can be adjusted to protect pollinators. In the United States, land-grant universities are responsible for applied research and extension education in support of local and regional agriculture. Growers look to land-grant universities for recommendations including the latest management knowledge and newest technology. Like many other cropping systems, present tree fruit IPM recommendations for pollinators are based on minimizing pesticide impact on the European honey bee, rather than protecting wild pollinators whose value to crop pollination was often thought to be minimal and was therefore ignored. IPM recommendations for honey bees in eastern US tree fruit have often been fairly straightforward: (i) do not spray insecticides during bloom or when hives are present in the orchards; (ii) if you have to spray fungicides during bloom, spray at night or in the early morning when honey bees are not foraging; and (iii) restrictions are lifted when the honey bee hives are removed. The timing of hive removal was nominally at petal fall when flowers were no longer supposed to be present, but in practice, many hives were removed earlier when a significant portion of apple bloom was still present and wild bees were still visiting flowers. The bees were therefore exposed to more biocides or harmful products. Exceptions to the ban on insecticide application during bloom included *Bacillus thuriengensis* products or insect growth regulator insecticides specific to Lepidoptera (IGRs), such as tebufenozide, methoxyfenozide and renaxypyr for tortricid leafroller pests, which were best controlled at bloom. Those applications were thought to be pest specific and safe to bees [33].

Additional restrictions were placed on systemic insecticides when honey bee hives were placed in orchards, of which neonicotinoids are only the latest additions to a list of systemic products from multiple pesticide classes. Systemic insecticides are often regarded as IPM friendly, as the pesticides are absorbed into the plant tissues where they are accessible only to plant feeders and not beneficial predators and parasitoids [40]. The problem with systemic pesticides is potential movement into the nectar and pollen, with the result that pre-bloom sprays could also be toxic to honey bees foraging during bloom. Beginning with the registration of imidacloprid in the mid-1990s, the neonicotinoid class of insecticides mostly replaced organophosphate and carbamate insecticides, which were phased out largely due to human health and environmental impact issues [28].

The six different neonicotinoid compounds currently registered in the United States for tree fruit are much safer products to humans, less impactful on the environment, are key components in the control of pesticide-resistant pests, and have helped to promote biological control of several pests in tree fruit IPM systems. While neonicotinoids have harmed bees in some agricultural systems [41, 42], the compounds can be integrated into agriculture in many cases to preserve their beneficial aspects as long as steps are taken to minimize their impact on non-target organisms such as pollinators and other beneficial insects. A complete ban of this pesticide class, especially in the short term, may result in: (i) a reversion to older, more toxic compounds which they were intended to replace; (ii) a switch to broad spectrum pyrethroid sprays, which would destroy existing IPM programmes by eliminating most biological control agents; or (iii) complete loss of control over pests such as the rosy apple aphid (*Dysaphis plantaginea*), which is resistant to organophosphate, carbamate and pyrethroids, and for which no alternative control methods (including biological control) exist. For example, two neonicotinoids, acetamiprid and thiacloprid, which are much less systemic than the others and much safer to bees, are recommended by Penn State University [22] for the pre-bloom control of rosy apple aphid, because these compounds do not significantly translocate into the flowers (D.J. Biddinger, unpublished data).

In the past, insecticides that affected pollinators had their use curtailed or modified through Penn State recommendations and extension education. The organophosphate, chlorpyrifos, which is not systemic but has a high vapour pressure that effectively fumigates orchards for several days after application, is restricted for several weeks prior to bloom. Off-label applications made closer to bloom have been responsible for widespread kills of both honey bee colonies and managed *Osmia* species (D.J. Biddinger, pers. obs.). Micro-encapsulated formulations such as methyl parathion were formulated in time-release beads of approximately the same size as pollen grains; these are easily picked up by foraging bees from ground cover plants such as dandelion, which are exposed to sprays before apple bloom but which honey bees also visit during the apple bloom. Those formulations are now restricted. The chitin inhibitor insect growth regulator (IGR) insecticide novaluron was also restricted around tree fruit bloom period because of the potential for sterility and developmental effects from sub-lethal doses, demonstrated in pests [43] and conceivable for bees. Novaluron applied during bloom in almonds has sublethal effects on *Osmia* reproduction and honey bees [44].

At present, six different neonicotinoid compounds are currently registered in the United States for tree fruit. While neonicotinoids have harmed bees in some agricultural systems [41, 42], the experience of the authors has been that these compounds can be integrated into agriculture in many cases to preserve their beneficial aspects, as long as steps are taken to minimize their impact on non-target organisms such as pollinators and other beneficial insects. In particular, this class of pesticides was found to be beneficial, as they can be used in existing IPM programmes in ways that do not eliminate most biological control agents.

4.5 FUNGICIDES

Fungicides, long thought to be relatively harmless to pollinators and therefore safe to spray during bloom, are now indicted as potential pollinator threats [45, 46], resulting in public calls for their elimination from use. This is a complicated problem and solutions rely on understanding the detailed relationships among chemicals, pollinators and pest management needs. It is not prudent to treat the topic with broad statements, such as "no fungicides should be sprayed during bloom", as the matter requires more detailed study.

The purpose of fungicide sprays applied during bloom is to protect plants from diseases that can infect future fruit. Thus, fungicide sprays during bloom can decrease or negate the need for fungicides later in the season. The period from just prior to bloom to just after petal fall are critical times during the disease cycles of pathogens such as apple scab, botrytis, powdery mildew, cherry leaf spot, brown rot and cedar apple rust. Such major disease problems, if left untreated during this time, devastate the apple crop, while diseases such as fire blight can cause the decline and eventual death of trees. In the case of apple scab, controlling the early season form, called primary scab, which attacks foliage mostly until just after bloom, prevents the buildup of secondary scab, which attacks the fruit during summer. Efforts to control secondary scab require three to four times more fungicide sprays (and cost) than stopping the disease in the form of primary scab. A practice long utilized to minimize fungicide residues on the fruit is therefore being questioned. In such cases, what is a grower or field researcher to do?

It might help to understand why this shift in thinking came about, especially since fungicides were previously thought quite safe for bees. For decades, growers have known not to apply most insecticides during bloom, with the exception of very few examples with unique modes of action mentioned above. Most fungicides when applied alone still appear safe, but it is now feared that the combination of some fungicides with a neonicotinoid may synergize its toxicity [47, 29] and possibly that of insecticides such as the pyrethroids [48]. The fungicides of most concern are a widely used class known as the ergosterol biosynthesis inhibitor fungicides (e.g. myclobutanil, fenbuconazole), commonly known as DMIs (DeMethylation Inhibitors). DMI fungicides are also systemic, as with neonicotinoid insecticides, and can also be found in nectar and pollen after pre-bloom sprays (D.J. Biddinger, unpublished data). Their systemic activity is one reason that fungicides are effective for some major apple diseases. The single lab study [47] that caused this controversy, which used technical neonicotinoid product dissolved in acetone, found synergism of 105 to 1 141-fold for honey bees from contact with acetamiprid and thiacloprid when mixed with two different DMI fungicides. It is less well known that the study did not find synergism of other neonicotinoid insecticides with DMI fungicides, and field studies using the formulated product of both acetamprid and a DMI fungicide show no synergism.

In a recent study [29], the authors tested formulated product acetamiprid and imidacloprid with field rates of formulated DMI fungicide in water. Laboratory studies on both honey bees and *Osmia cornifrons* reveal synergism barely significant at a fivefold level with acetamiprid, and insignificant for imidacloprid. The results agree with a field trial that also found no field effects when formulated product of both the insecticide and fungicide were used [49]. Until alternative research shows otherwise, the authors of this study consider almost all fungicides, with the exception of the older type fungicides captan, chlorothalinil and mancozeb, safe even in combinations [22, 33, 50, 51]. The older type compounds are contact fungicides with some insecticidal properties that can affect larval development through chronic exposure during nectar and pollen feeding [51, 52]. Penn State University recommends reduced rates of such fungicide application during bloom. Additionally, sulfur and lime sulfur, used heavily in organic apple production in the eastern United States, are restricted during bloom because the odour is repellent to bees for up to 48 hours, depending on application rate and formulation [53, 54].

4.6 IPM RECOMMENDATIONS FOR CONSERVING WILD POLLEN BEES FOR TREE FRUIT POLLINATION

Most pesticide restrictions and recommendations concerning pollinators are implemented primarily as a means to protect honey bees. However, the dozens of other important, wild pollinator species also have unique pesticide vulnerabilities. Information on pesticide effects on non-honey bees is for the most part lacking, but certain groups such as the megachilids, *Megachile rotundata* and *Osmia* spp., appear to be less susceptible on average than the honey bee [29, 39]. Recent bioassays on honey bees and *Osmia cornifrons* show that pesticide susceptibility or tolerance varies within each species and also varies among pesticides within the same pesticide class, such as acetamiprid and imidacloprid [29].

Looking beyond the issue of pesticides, a variety of other farm practices need to be employed to encourage wild pollinators. Perhaps the most important IPM aspect to conserving wild pollinators in Pennsylvania apple orchards – where in many cases they are the primary pollinators – is recognizing that this service is provided by a combination of species that may have many different nesting and floral resource needs, currently met by the adjacent non-crop landscape, in which bee diversity increases with plant diversity. A hedgerow of pine trees will not significantly aid pollinators, but a hedgerow of many flowering trees, shrubs and wild flowers will help to maintain a diverse bee community [55]. Most pollen bees other than *Bombus* do not fly more than a few hundred metres from their natal habitat, so plans for removal of a fence row or woodlot should consider the effect it might have on pollinators. Unlike honey bees, which can be moved in and out of orchards, pollen bees are susceptible to harsh pesticides in the orchard and from drift into adjacent nesting and foraging habitats over a longer period. Border sprays of insecticides to habitats adjacent to orchards for Brown Marmorated Stink Bug control in the mid-Atlantic states are most likely hurting wild pollinators more than the pest. Pesticides applied to other crop species later in the season can also affect some wild bees of importance to apple, such as *Bombus*.

4.7 THE INSTITUTIONALIZATION OF POLLINATOR HEALTH PROTECTION

Recognition of honey bee decline and a rising reliance on wild, pollen bees is gradually forming part of public policy, providing increased funding for research and education on this topic. The US Food, Conservation, and Energy Act of 2008 (otherwise known as the Farm Bill) acknowledged the great importance of pollen bees for agriculture by providing funding for farmers to increase and protect pollinator habitats on farmland. Farmers are encouraged to seed strips of wildflowers along their property to encourage bee visitation to their crops, or to leave part of their property fallow to increase pollinator habitats [55, 56]. Farmer encouragement can extend to conservation payments by the USDA

Natural Resources Conservation Service (NRCS), which underwrite pollinator-friendly farm practices. Thus far, little is known about the efficacy of wildflower strips in increasing fruit yield, or how far plantings need to be spaced in relation to crop species in order to maximize crop pollination. If pollen bees do not forage for long distances and nest along the borders of orchards, then apple flowers in the interior of large apple blocks may be pollen limited without the help of longer-range honey bees [57–59]. If this is the case, honey bee hives should be placed in the centres of those larger blocks of orchards rather than along the borders, or additional nesting sites and food sources in the pollinator strips should be placed in the centre of large orchards. It does not appear that pollen bees are nesting within the orchard itself due to pesticides and lack of nesting sites, and are thus mostly coming from the borders [38]. Data from this study indicate that foraging ranges of some of the most important solitary bees are < 100 m in distance from nesting sites in an adjacent habitat [57, 58]. Even visits by longer-ranged honey bees and bumblebees decline within 200 m from a wooded habitat.

Some state that the present pollinator crisis is based mainly on honey bee declines. However, in addition to honey bee protection, there is a need to encourage and make use of the myriad other pollinator species, and by properly adjusting crop IPM practices, to protect all pollinator species.

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Chapter 5

A NATIVE GROUND-NESTING BEE (*NOMIA MELANDERI*) SUSTAINABLY MANAGED TO POLLINATE ALFALFA ACROSS AN INTENSIVELY AGRICULTURAL LANDSCAPE

J.H. Cane

5.1 INTRODUCTION

The primary challenge for agricultural pollination is to provide sufficient numbers of bees to match the vast blooms put forth by extensive crop monocultures. Exemplars for the magnitude of flower production per hectare include almonds (2 million) [1], cranberries (6–50 million) [2, 3] and, most dramatically, alfalfa (120–500 million) [4, 5]. For these and many other crops, the majority of flowers must be visited at least once by a bee for commercial yields of fruit or seed. For most zoophilous crops, the honey bee (*Apis mellifera* L.) remains the dominant pollinator, as reviewed in Free (1993) [6]. Honey bees prevail partly because of their foraging versatility, but mostly because each colony, housed in a mobile hive, can cheaply and reliably field tens of thousands of pollinating foragers on demand. But why are honey bees needed at all?

Many crops are more effectively pollinated by one or more species of non-Apis bees [7, 8], including diverse ground-nesting species [9]. Ground-nesters often dominate regional wild bee faunas; for instance, 85 percent of eastern North America's bee species nest underground [10]. However, ground-nesting bees are not generally used in management of crop pollination for reasons of crop rotation and because nest sites cannot be readily prepared and colonized. A prominent exception is the alkali bee, *Nomia melanderi* Cockerell, a native to the arid desert basins of western North America. The bee is a floral generalist, but is valued as the most effective alfalfa pollinator [11]. It nests gregariously in moist basin soils bearing salty surfaces [12]. Small (1 cubic foot) soil cubes cut or cored from dense nesting aggregations are used to populate newly prepared nesting sites amid alfalfa seed fields [13]. In most growing areas in the western United States, however, its use has been supplanted by managed populations of an adventive Eurasian cavity-nesting bee, the alfalfa leafcutting bee, *Megachile rotundata* Fabricius (Megachilidae). Managed populations of *M. rotundata* are dwindling on US alfalfa seed farms, however, so growers annually replenish their stocks with billions of nest cells bought from Canadian producers [14]. As frequent replenishment of *N. melanderi* stocks is impractical, growers must manage populations in a sustainable manner to benefit from this effective pollinator.

Over the past half-century, alfalfa seed farmers have met with variable success in managing alkali bees. The most suitable sites for alkali bee nest beds possess silty soils with good hydraulic conductivity, moist subsoils and a surface free of vegetation that is periodically sealed with salt (typically NaCl) [15]. Larval predators can be problematic, particularly bombyliid flies [16] and oil beetles [17]. Like other bees, alkali bees are susceptible to sundry insecticides [12], which if misapplied or mistimed can decimate their populations [18]. Otherwise, factors driving the population dynamics of these and other ground-nesting bees are rarely documented.

No species of solitary (non-social) bee has been exhaustively surveyed at the landscape scale, owing to the simple challenge posed by locating every nest. Spatially or temporally extensive surveys of bees report counts of individuals caught while visiting flowers or passively trapped, reviewed in Williams *et al.* (2001) [19]. Neither measure enables calculation of the total numbers of bees residing in an area. The goal of this eight-year study was to survey and document population trends for the entire meta-population of alkali bees nesting across an arid, irrigated 240 km^2 agricultural landscape in Washington state.

5.2 DESCRIPTION OF SURVEY METHODOLOGIES

5.2.1 Nesting aggregations

Past and present nesting beds of alkali bees were surveyed and measured in the Touchet Valley west of Walla Walla, Washington state, an alfalfa seed-growing region since about 1950. Nesting beds there are sub-irrigated naturally, or subsurface water is distributed using moats or buried perforated pipes. The 56 currently or recently populated nesting beds were found through grower accounts and aerial photographs (courtesy of the National Resource Conservation Service). The white salt surfaces of nesting beds contrast with the dark foliage of adjacent alfalfa (Figure 5.1). Ages of some older nesting beds were known by growers or obtained from old field research records. The surface area of each nesting bed was measured by planimeter on the aerial photographs, and confirmed or validated on the ground, especially those nesting beds that were expanded or renovated by growers during this study.

Figure 5.1

AERIAL PHOTOGRAPH OF A 3-KM WIDE PORTION OF THE TOUCHET VALLEY

Aerial photo showing growing alfalfa seed fields (dark) and alkali bee nesting beds (pale polygons indicated with white arrows). The lack of hedgerows, fallow fields or uncultivated land illustrates the valley's agricultural intensity

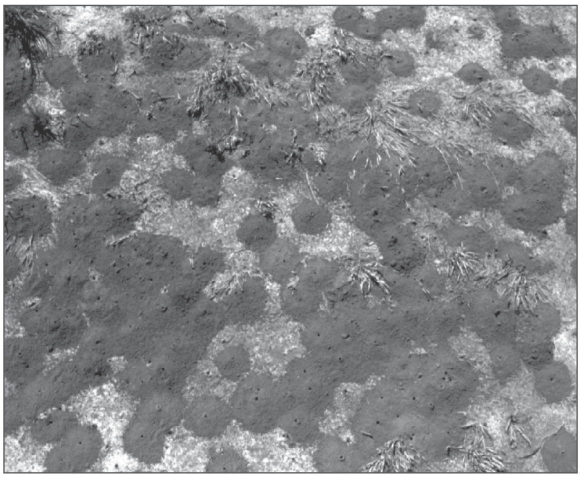
Source: J. H. Cane, the present study

5.2.2 Population measurement

Nesting densities were surveyed annually in late June during peak alfalfa bloom after nests had been initiated. A female typically makes one nest [20]. Depending on aggregation size, 10 to 20 quadrats (measuring 1 m^2) were placed at random coordinates on the surface of every aggregation. All holes within each quadrat were counted, including those with excavated soil heaps (tumuli) and those with emergence holes (Figure 5.2), as pollen-laden females were commonly seen returning to emergence holes [21]. The reliability of the randomized quadrat method was checked by the same two persons counting nesting holes for three replicated sets of ten quadrats each, on one small nesting bed. These were compared using a two-way analysis of variance (ANOVA) of survey taker by quadrat set. No other ground-nesting bee or wasp nested abundantly amid active *Nomia* aggregations. Average hole density per aggregation was multiplied by the measured area of the nesting aggregation to estimate the sum of holes per nesting bed. Counts of holes were converted to nest counts using observed frequencies of occupation (see below). The average annual rate of nest density change was estimated as the slope of a linear regression fitted to the valley's annual grand average of nesting densities.

Figure 5.2

SURFACE OF NESTING BED SHOWING NEW NESTS WITH SOIL HEAPS (TUMULI) AS WELL AS EMERGENCE HOLES OFTEN REUSED FOR NESTING



Source: J. H. Cane, the present study

5.2.3 Nest hole utilization

Videography was used in 2003 to verify the proportions of counted holes in actual use by nesting female alkali bees. On mornings of good nesting activity, a video camera was set to vertically view a marked 0.25 m^2 rectangle of aggregation surface bearing discernable holes, which were then counted. The view was filmed for 90 min and later replayed, counting every hole that a resident bee either departed or entered. Dubious brief entries were rare and not counted. In all, five aggregations were thus filmed, for a grand average of the fraction of holes in use. Each aggregation's annual total count of holes was multiplied by this average fraction of holes in use to estimate the total numbers of alkali bee nests per each aggregation.

5.3 SURVEY RESULTS

5.3.1 Nest hole utilization

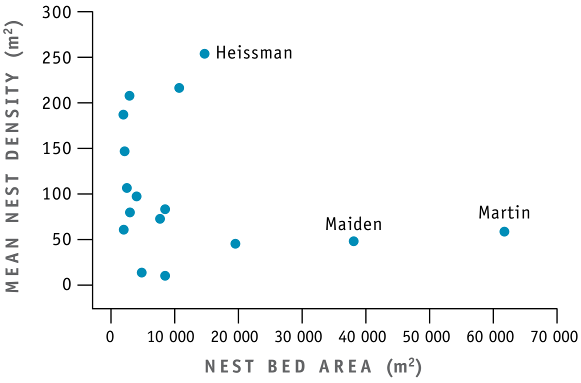
Many holes without tumuli were nonetheless active *Nomia* nests. The average morning foraging trip lasted 52 ± 20 min (N = 92), so filming for 90 min should have revealed nest occupancy. Of the 139 holes (23–31/nest site) observed, 92 were in use (66 percent overall, 55–83 percent/aggregation). Therefore, all hole counts in quadrats were multiplied by two-thirds to arrive at an estimate of active nests in each aggregation.

5.3.2 Population variability

Measured nesting densities varied widely within and between individual nesting aggregations. This variation was not an artefact; repeated surveys of the same nesting bed yielded nest density estimates that were within 20 percent of each other and statistically equivalent ($P > 0.9$). Active nesting beds ranged by more than 100-fold in surface area from 405 m^2 to 61 600 m^2. Valley wide, 20 ha was dedicated to active alkali bee nesting beds, or about 0.6 percent of the area planted to seed alfalfa. Even at the populous Heismann bed, average density in the quadrats (256 nests/m^2) was less than the greatest nest density measured there (713 nests/m^2). If all nest beds were so populous, the valley's extant aggregations would have 60 million nests. All nest beds were therefore big enough to accommodate more population growth (Figure 5.3).

Figure 5.3

RELATIONSHIP BETWEEN NESTING DENSITY AND NEST BED SIZE FOR ALKALI BEES IN THE TOUCHET VALLEY IN 2006



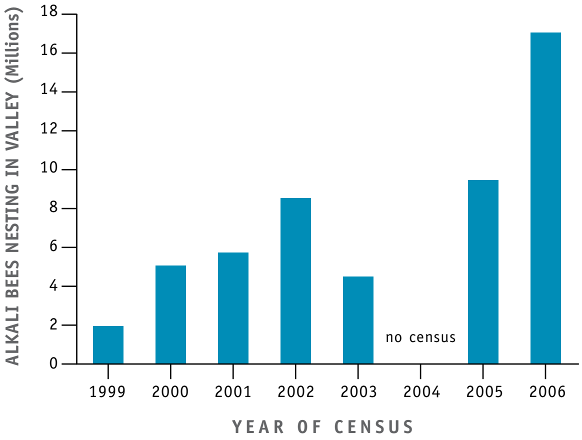
Source: J. H. Cane, the present study

5.3.3 Aggregation and meta-population growth

Alkali bee populations multiplied dramatically between 1999 and 2006. Over eight years, valley wide populations grew ninefold to 16.7 million females (Figure 5.4). Growers expanded and improved two large and ultimately populous nesting beds (Martin and Maiden beds; Figure 5.5, nos. 47 and 48; Figure 5.3) adding 8 ha of suitable nesting habitat (the large Heismann bed was not expanded). In general, populations multiplied through denser nesting on existing nest beds, adding an average of eight nests/m^2 annually ($r2 = 0.77$, slope = 8 ± 2 nests, $t = 4.1$, $P \leq 0.01$) (Figure 5.6).

Figure 5.4

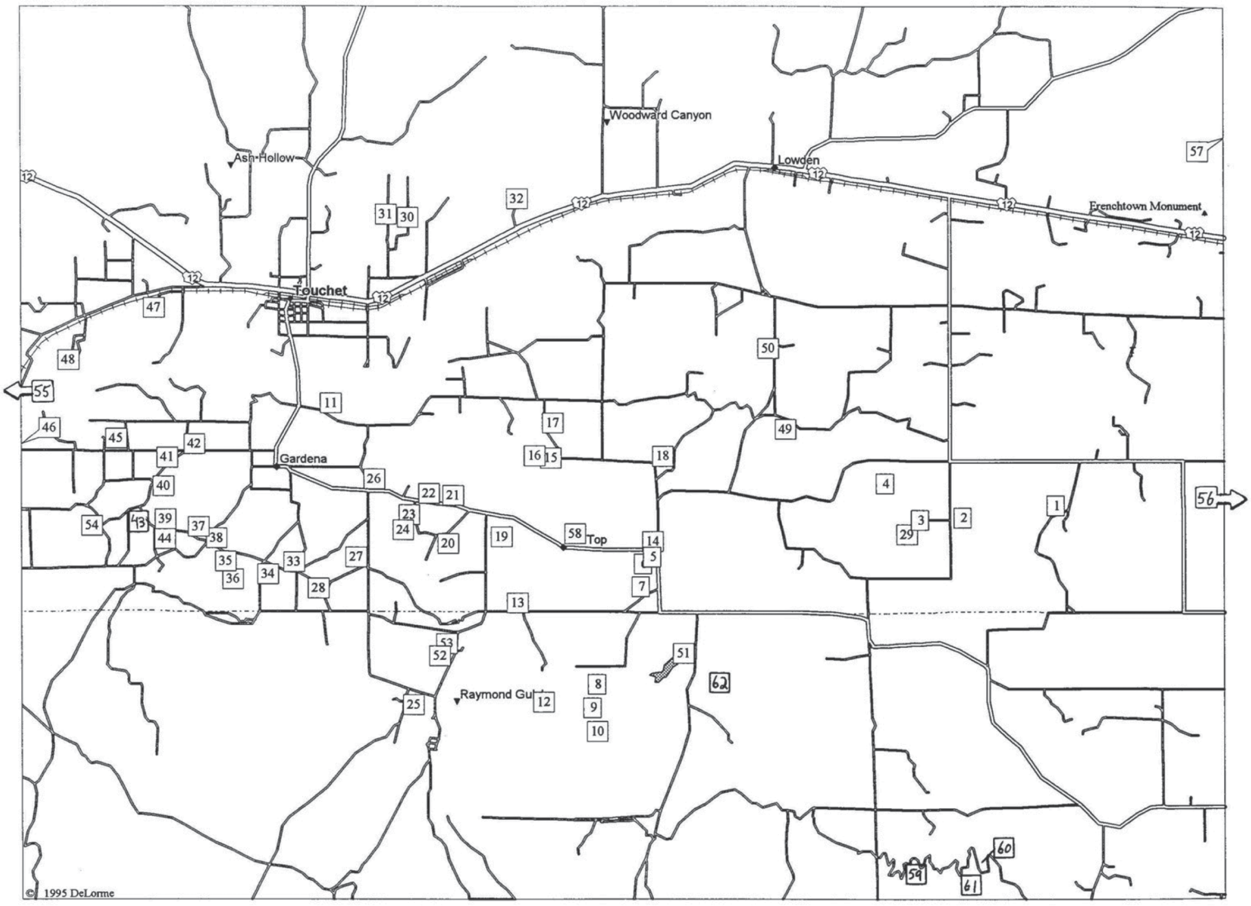
SUM OF ALKALI BEES NESTING ANNUALLY IN THE TOUCHET VALLEY OF SOUTHEASTERN WASHINGTON



Source: J. H. Cane, the present study

Figure 5.5

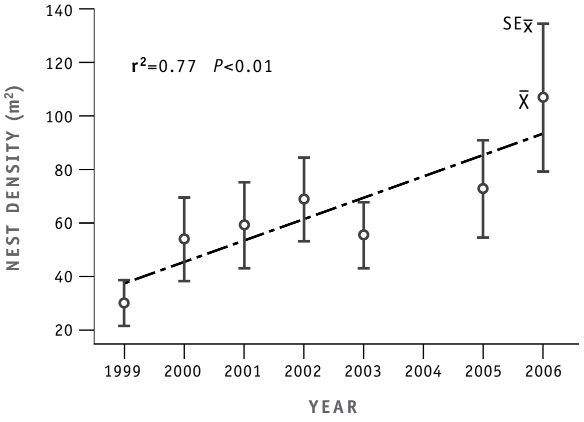
MAP OF NUMBERED NESTING BEDS SURVEYED DURING THIS STUDY



Nest bed numbers 46, 55, 56 and 57 are beyond the map boundaries. The image is 13 km wide

Source: J. H. Cane, the present study

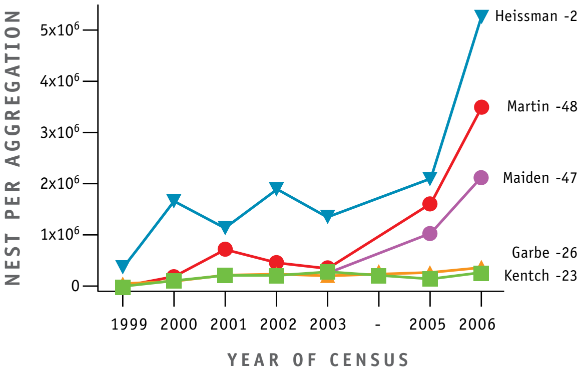
Figure 5.6
VALLEY-WIDE INCREASE IN AVERAGE ANNUAL NESTING DENSITIES OF ALKALI BEES IN THE TOUCHET VALLEY



Shown here are the annual grand means and their standard errors, calculated from the mean densities for the 24 most populous surveyed beds. The linear regression is fitted to the eight annual grand means

Source: J. H. Cane, the present study

Figure 5.7
POPULATION GROWTH OF FIVE REPRESENTATIVE ALKALI BEE NESTING BEDS SURVEYED ANNUALLY IN THE TOUCHET VALLEY



Names are those used by local growers, and nest bed nos. are taken from Figure 5.5

Source: J. H. Cane, the present study

5.3.4 Subsurface moisture and aggregation growth

Most nesting beds received supplemental sub-irrigation. In one case, a grower tripled the surface area of one nesting bed with ample natural soil moisture (Maiden bed) to 3.8 ha over the eight-year survey period; it ultimately became home to 9 percent of the valley's alkali bees (Figure 5.7). Prior to surface salting and weed removal, nesting there was exceedingly sparse (0.2 nests/m^2). Eight years later, the population had swollen to 39 nests/m^2 (Figure 5.3). Within nesting beds, the densest nesting accompanied moist but not wet soils (average tensiometer readings of 21 ± 9 kilopascals (kPa), whereas sparsely populated areas of nesting beds were invariably drier (tensiometer readings of 29 ± 9 kPa) (Cane, unpublished data for 28 nesting beds) [22]. Adequate nest bed moisture is essential; growers who ceased sub-irrigating practices lost their *Nomia* populations on four large nesting beds.

5.4 DISCUSSION

Population sizes of alkali bees nesting in the Touchet Valley ultimately surpassed those reported for any other non-social bee in the world. This is true for both individual nesting aggregations (5.3 million at the Heismann bed) and collectively for the 16.7 million alkali bees nesting in the valley. Previously, the largest bee meta-population was found spread along 7 km of riverbank in the Russian Federation, where *Dasypoda plumipes* and several co-nesting species were informally estimated to collectively comprise 12 million bees [23]. Estimates for populous individual aggregations of other ground-nesting bees include: 28 000 nesting *Andrena postomias* [24], 80 000 nesting *Mesoxaea texana* [25], 155 000 *Dieunomia triangulifera* [26], 180 000 *Anthophora edwardsii* (A. Washburn, unpublished data) and 423 000 *Centris caesalpiniae* [27].

Longevities of some of these alkali bee-nesting aggregations exceed all previous records for bees, verified by the following cases and evidence. A wild alkali bee-nesting site near Preston, Idaho noted by

G.E. Bohart in 1971 remained populous 34 years later. In the Touchet Valley, several managed nest beds have been continuously populated for 50 years. For example, the artificially sub-irrigated "Sutherland" bed (Figure 5.5, no. 23) was one of 104 sampled in 1958 as part of a nest soil survey (unpublished report by W.H. Weaver et al.). From 1973–1977, the bed was producing 80–186 alkali bee progeny/ft^3 [15]. Thirty years later, from 2000 to 2006, its population doubled to 250 000 nests. Another managed nest bed (Figure 5.5, no. 19) was built in the 1950s by the current grower's father, and today has 300 000 nesting bees. Other now populous nesting sites (e.g. Maiden and Martin nest beds, Figures 5.5 and 5.7) have also existed for decades, and were formerly populous. During the 1980s and early 1990s, they fell into disuse or were buried under sandy flood sediments. During the last eight years, site renovations fostered dramatic population recoveries (184-fold and 89-fold growth) (Figure 5.7). The Heissman nesting bed was started in 1973 with 11 ft3 soil cores transplanted from natural aggregation no. 55 (Figure 5.5). From reported prepupal densities that year [15], the aggregation began with only about 550 females. Thirty-three generations later, their descendants number 5.3 million nesting females, achievable through population doubling every two years, although actual growth is more sporadic (Figure 5.7). The remarkable longevity and growth of nesting aggregations of the alkali bee is without published precedent, but such persistence may be more common than is known for bees that nest gregariously.

Most bee-nesting aggregations are studied for a few years and are considered ephemeral. Scattered reports of long-lived nesting aggregations include: 20 years for *Panurginus polytrichus* [28], 22 years for *Trachusa byssina* (as *T. serratulae*) [29], 22–35 years for *Dieunomia triangulifera* [26] (and Michener, unpublished data), and 37 years for *Lasioglossum malachurum* (Stöckhert, cited in [30]). Nesting sites of *Trachusa perdita* and *T. gummifera* were found to be still populous when revisited after 24–27 years (Thorp, unpublished data). The paucity of such multidecadal records may reflect a failure to seek such data, rather than the rarity of the phenomenon. Nesting aggregations may decline with shifting habitat attributes that alter nesting suitability, such as shading from forest succession [31] or changing land use, rather than the intrinsic brevity of gregarious nesting itself.

Why have managed alkali bees flourished in this valley when insecticides were implicated in the demise of managed alkali bees introduced to California [18]? Several factors seem important. First, the primary crop in the Touchet Valley has been and continues to be seed alfalfa, an acceptable and timely floral resource for alkali bees. The valley produces an estimated 1 trillion alfalfa flowers annually, but periodic floral resource dearth can constrain population growth. The 2002–2003 decline in alkali bee populations (Figure 5.4) followed shrinkage in acreage planted. The valley's rotational crops (wheat, field peas and chickpeas) do not feed bees, but neither are they sprayed with insecticides during alfalfa bloom. Hence, at midsummer and within an alkali bee's substantial flight range (5–10 km^2) [32], the valley's alkali bees are unlikely to contact any broad-spectrum insecticide. For alfalfa seed crops, Touchet growers conscientiously scout fields for pests such as *Lygus* bugs, aphids and seed weevils, using economic damage thresholds to guide their spray decisions. Growers typically anticipate and suppress threatening pest problems using one or more insecticides before or after bloom. The permitted pesticide repertoire includes eight herbicides and defoliants, and 11 insecticides (e.g. chlorpyrifos, dimethoate, naled) all applied from the ground to minimize drift. If pests threaten during bloom, only one broad spectrum but short-lived insecticide (Dibrom) can be safely used [12]. Otherwise, growers choose a narrow spectrum insecticide that is safe for bees. Nonetheless, in the early 1990s, some nesting populations in the western end of the valley crashed dramatically. Most growers implicate either use of a new broad-spectrum insecticide, metasystox, applied during bloom, or a brief period of potato growing, a crop demanding frequent insecticide use. Metasystox, although safe for bees after 8 hours once dried on the foliage [15], remains lethal on dewy foliage. Growers ceased using metasystox during bloom, with the result that this episode was the last extensive die-off of alkali bees in the valley. Paradoxically, extensive monocultures of seed alfalfa with little or no alternative bloom, coupled with conscientious use of conventional insecticides, have been compatible with fostering populations of this wide-ranging polylectic bee.

Among ground-nesting bees, the alkali bee's unusual suite of attributes may uniquely favour its intensive large-scale management. Alkali bees nest gregariously and densely, yet females can navigate unerringly to the entrances of their individual nests (J.H. Cane, unpublished data). The single annual generation of managed alkali bees in Washington coincides with alfalfa bloom. Hence, the lack of alternative bloom during the remainder of the growing season is irrelevant, in contrast with the needs of social or multivoltine bees. In addition, the parasite/predator problems are amenable to control. Furthermore, the alkali bee's nesting habits allow artificial colonization of new sites. The silty damp nesting soils and shallow nests of alkali bees facilitate coring into soil blocks of manageable size (ca. 40 kg), each containing hundreds of durable prepupae. Thousands of cores are used to initiate a newly prepared nesting bed. Many other ground-nesting bees known to be effective crop pollinators [9] nest more deeply, or in hard clays or friable sands that cannot be cut and moved.

The genus *Nomia* is unusual among bees for generally lacking specific cleptoparasitic bees [33]. Only *Nomada suavis* Cresson attacks the alkali bee, albeit rarely if at all [34, 15]. Many ground-nesting bees commonly host specific cleptoparasites whose numbers can multiply and deplete their host's nesting aggregations [35, 36]. The alkali bee's freedom from cleptoparasites is enigmatic. It may be partially explained by the Nomiinae having evolved no cleptoparasitic lineages, because cleptoparasites of many groups parasitize their relatives [33].

The alkali bee does host several significant larval parasitoids, however. An oil beetle (*Meloe niger* Kirby; Meloidae) infested 4–31 percent of alkali bee nest cells in the Touchet Valley from 1973 to 1976, before control by pitfall trapping [17]. Bee flies (Bombyliidae) can parasitize substantial numbers of ground-nesting bees, sometimes causing population declines [37, 38]. Larvae of the bee fly *Heterostylum robustum* (Osten Sacken) kill mature alkali bee larvae, with early reports associating 90 percent parasitism by *H. robustum* with decimated large alkali bee nesting aggregations [16]. From 1965 to 1977 among Touchet Valley nesting aggregations, *H. robustum* parasitism accounted for 0–18 percent of sampled nest cell mortality [15]. Its impact on alkali bees has diminished further recently, a survey of six states finding only 3 percent parasitism by *H. robustum* (R. Rust, unpublished data). The insignificance of these parasites in today's managed alkali bee-nesting aggregations is puzzling, given that their fecundity far exceeds that of their hosts [16, 17, 39].

Decades of intensive farming in the Touchet Valley (Figure 5.1) have largely eliminated its native flora and bee communities (Cane, unpublished data). The native alkali bee has persisted and proliferated, however, owing to active stewardship by alfalfa seed growers that favours bee multiplication while minimizing natural and agricultural mortality factors. Growers foster bee reproduction by creating and maintaining large and suitable nesting sites, and adjust crop rotations to retain ample alfalfa bloom within the alkali bee's flight range. Growers protect population gains of their alkali bees from the potential capacity of larval parasitoids and predators to multiply faster than their hosts. During alfalfa bloom, growers also conscientiously eschew insecticide applications of known risk to bees. These practices, combined with serendipitous attributes of the alkali bee and the locale, have led to the most populous and long-lived individual nesting aggregations and landscape scale meta-populations ever recorded for a native bee. Whether or not this success can be repeated with other valuable native pollinators remains to be seen.

5.5 CONCLUSION

The world's only intensively managed ground-nesting bee, the alkali bee (*Nomia melanderi* Cockerell), has been used for > 50 years as an effective pollinator of alfalfa (*Medicago sativa* L.) grown for seed in the western United States. Across a 240-km^2 watershed in Washington state, the 24 most populous of 56 nest sites found were surveyed annually for nesting bees over an eight-year period. Alkali bees multiplied ninefold to 17 million females, the largest reported meta-population of non-social bees. Several sites have remained populous for an unprecedented 50 years. The most populous nesting bed (1.5 ha) grew to 5.3 million nesting females (median = 278 nests/m^2), the largest bee nesting aggregation ever recorded. This first exhaustive landscape level survey for any non-social bee reveals that even amid intensive conventional agriculture, a native bee can sustainably multiply to vast numbers, its nesting aggregations persisting for decades.

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Chapter 6

BUCKWHEAT POLLINATION IN A COMPLEX TEMPERATE LANDSCAPE

H. Taki

6.1 INTRODUCTION

Cropping practices that now dominate agricultural landscapes typically have short fallow periods, high inputs of capital and labour, and heavy use of pesticides and chemical fertilizers. This is the process of intensive farming agriculture. In contrast, many crop species produced by a diversity of traditional agriculture practices require lower external inputs per unit land area. Landscapes under this form of agriculture are widespread and support large rural human populations. Although urbanization is proceeding apace throughout the world, many millions of people live and work in rural mosaic landscapes where they practise smallholder agriculture. There are more than 500 million small landholders globally, with the majority living in Asia [1].[2] Smallholder farming is sometimes set in biodiversity rich landscapes (see Chapter 7).

This section presents the general floral biology of buckwheat (*Fagopyrum esculentum*) and the cultivation practices used to produce it. It focuses in particular on pollination mechanisms of this crop at landscape scale. Small fields were used as model sites to study buckwheat pollination biology in a complex temperate landscape located on the northeastern coast of Honshu (Hitachiota, Ibaraki Prefecture) in Japan. Small landholders grow the buckwheat cultivar "Hitachiakisoba" in a predominantly forested region (Figure 6.1). The complex landscape comprises a mosaic of agricultural fields embedded in semi-natural lands and natural forests. Buckwheat produced in the region is consumed within the prefecture. Sowing is normally completed during August and harvesting takes place in October. No fertilizers, pesticides or other agrochemicals are used in the buckwheat fields.

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[2] More recent figures are available at www.fao.org/fileadmin/user_upload/iyff/photos/large_FAO-Infographic-IYFF14-en_jpeg.jpg and in FAO. 2014. *State of Food and Agriculture*. Rome.

Figure 6.1
BUCKWHEAT FIELDS IN THE MOUNTAINOUS ENVIRONS OF HITACHIOTA, IBARAKI PREFECTURE, JAPAN

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Figure 6.2
BUCKWHEAT PIN TYPE (UP) AND THRUM TYPE (BOTTOM) FLOWERS

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Pin flowers have long styles that project beyond the short stamens; thrum flowers have long stamens that extend beyond the short styles

6.2 BUCKWHEAT PLANTS AND FLOWERS

Fagopyrum esculentum, often known as common buckwheat, is an annual, herbaceous crop that likely originated in southern China [2]. Buckwheat is a member of the angiosperm family Polygonaceae, commonly known as the knotweed family or smartweed/buckwheat family, which includes the Eurasian genus *Fagopyrum*, the North American *Eriogonum* and *Fallopia*, a genus native to temperate and subtropical regions of the northern hemisphere. Species in all three genera are referred to as wild buckwheat. Common buckwheat has been widely cultivated for centuries in North America, South America and Eurasia to provide food for both humans and livestock [3]. *Fagopyrum esculentum* has several congeners including the related "Tartary buckwheat" (*F. tataricum*), cultivated for grain in Asia [2, 4, 5]. Buckwheat grows relatively rapidly, producing seeds in about six weeks, then ripening in 10 to 11 weeks when plants reach 75 to 125 cm in height.

Buckwheat is self-incompatible and has hermaphrodite white or pink flowers arranged in racemes or cymes. The flowers are distylous (Figure 6.2), and the pin morph has a long style projecting beyond the short stamens, while the thrum morph has long stamens projecting beyond the short style. The two flower morphs generally occur in approximately equal proportions in single populations [6, 7]. Each flower has only one ovule [8]. Average gynoecium lengths of pin and thrum flowers are 2.6 and 1.4 mm, respectively, and the respective stamen lengths are 1.7 and 2.5 mm [9]. Individual plants produce numerous inflorescences over a period of about 25 to 30 days. Each flower is open and receptive for pollination for approximately one day [10]. The flower secretes nectar at the base of the ovary.

In warm climates, buckwheat can be cultivated by sowing late in the year, with flowers forming in cooler weather. Flowers provide pollen and nectar to populations of natural enemies, such as parasitoid wasps, which control pests on other crop species [11, 12]. Studies of buckwheat pollen availability and frequencies of flower visits by insects indicate that pollination activity is highest during the morning [9, 13, 14]. In addition to supporting populations of biological control agents, a cover of buckwheat suppresses or reduces weeds and improves soil condition [15].

6.3 BUCKWHEAT AS A FOOD

Cultivated *F. esculentum* is the most economically important buckwheat species globally, and production is on the increase worldwide. Buckwheat was cultivated frequently in North America during the eighteenth and nineteenth centuries. Since then, the Russian Federation has become the world's largest producer (796 551 tonnes annually) [16]. By 2012, annual production in China had expanded to 700 000 tonnes, followed by Ukraine (238 700), Poland (84,421), the United States (82 000), Brazil (60 000), Kazakhstan (48 000), Japan (44 600), Lithuania (30 600) and the United Republic of Tanzania (10 000) [16]. Buckwheat is produced by many small landholders in Asian countries. For example, on Honshu Island, Japan, the crop local smallholders typically grow the crop on land not agriculturally suitable for paddy rice [17]. In 2007, Japan imported 71 000 tonnes of buckwheat, which amounted to 70 percent of total consumption in the country [18].

Common buckwheat is a culturally important foodstuff in Japan; it is used for flour in soba noodles, which are in high demand throughout the country. During 1986–2007, the land area in Japan planted with common buckwheat increased from about 19 600 ha to 46 100 ha [18]. In addition to its short production cycle, buckwheat has the advantage of growing well on low fertility or acidic soils, although those should be well drained. Excessive fertilization, particularly with nitrogen, may reduce yields. Thus, buckwheat is often grown late in the year after a different crop species has been harvested. It is also raised in climates with short growing seasons.

Although buckwheat cannot be classified among the cereals, which are members of the grass family Poaceae, the seeds in the achene fruits are generally considered cereals because of similarities in their use [3]. Many "nutraceutical" compounds occur in the seeds and other plant organs of buckwheat. Experiments with animal models and with humans demonstrate that buckwheat flour may reduce incidence of diabetes, obesity, hypertension, hypercholesterolemia and constipation [19, 20]. Furthermore, buckwheat is an important raw material in foodstuffs because it contains polyphenols, including the flavonoids rutin, orientin, vitexin, quercetin, isovitexin and isoorientin [19, 20]. Among such antioxidant components, rutin is considered to have the greatest health-promoting properties. Rutin is anti-inflammatory, anti-carcinogenic [21] and effective in preventing capillary apoplexy and retinal hemorrhage [22]. Importantly, noodles contain much less rutin (78 mg/kg) than does dark buckwheat flour (218 mg/kg) [23], which in turn contains less than buckwheat leaf flour (~2 700 mg/kg). The rutin contents of raw and precooked groats (hulled kernels of grains) are 230 mg/kg and 88 mg/kg, respectively [23].

Each achene fruit of buckwheat has a single seed with a hard external hull that protects the starchy white endosperm used to make buckwheat flour. The seed coat is green or tan and can darken the buckwheat flour because seed hulls are blackish and some portion of them may be included in the flour. Buckwheat groats are commonly eaten in Asia and Europe. Pancakes made from the flour are consumed in several countries, and buckwheat noodles are a key traditional component in the cuisines of some Asian countries [24]. Soba noodles are still customarily eaten on New Year's Eve in most regions of Japan. There is also a tradition of sharing noodles with new neighbours in Japan, although this custom is becoming rare. In addition to the production of cereal staples, buckwheat is important for the honey industry, with the resulting dark honey possessing a strong, distinctive taste.

6.4 POLLINATION STUDIES OF BUCKWHEAT

Crop pollination by animals is of particular importance for food production [25–27]. Crop species that are *dioecious* (male and female functions on different individual plants) or heterostylous (e.g. buckwheat) only set seeds and fruits after pollen has been transferred between flowers, usually by an animal of different plant individuals of the same species [28]. The nectar and pollen of buckwheat attract diverse insects including Hymenoptera, Diptera, Coleoptera and Lepidoptera [29–33]. Pollination is occasionally anemophilous (by wind) over short distances [34], but insects are the main pollinators of buckwheat. Honey bees (*Apis* spp.) are reportedly dominant flower visitors in many parts of the world and are likely principal pollinators of buckwheat [9, 17, 31, 33, 35–37]. However, diverse potential pollinating species besides honey bees also visit the flowers [13, 29–33, 38, 39].

The buckwheat pollinator fauna has been studied within islands of the Japanese archipelago. On the northern island of Hokkaido, the bumblebees *Bombus ardens* and *B. hypocrita* are principal visitor species (75.4 percent of total visitors collected on flowers), and more than 96 percent of captured individuals have buckwheat pollen attached to their body surface [38]. Another study on Honshu reports more than 70 species of flower-visiting beetles, butterflies, flies, ants, bees and other Hymenoptera. About 43 percent of individuals captured on buckwheat are wild, while managed and wild honeybees belonging to the species *Apis cerana* and *A. mellifera* comprise the other 57 percent [39].

The aim of this study in the environs of Hitachiota, Ibaraki Prefecture, Honshu was to improve understanding of the effects of diverse pollinator species (paying special attention to insects smaller than honey bees) on seed set in buckwheat. Although such insects may have a body surface area too small to carry substantial pollen loads between pin and thrum flowers, they do visit the flowers and consume pollen and nectar. The authors tested the hypothesis that, during those feeding activities, small insects transfer pollen from the short anthers of buckwheat pin flowers to the short styles of thrum flowers, thereby contributing to seed set in thrum flowers. In many distylous plant species, the contrasting anther positions of pin and thrum flowers ensure that pollen grains from the two different flower types are carried on different body parts of the animal pollinators, which results in outcrossing pollen transfer between morphs [40]. This mechanism has been corroborated in a number of plant species [41]. For example, bumblebees pollinating *Primula sieboldii*, a distylous herb, carry pin and thrum pollen on different parts of their mouthparts [42]. Likewise, butterflies visiting flowers of the distylous herb *Pentanisia prunelloides* (Rubiaceae) carry the pollen from short-styled and long-styled flowers on their heads and proboscides, respectively [43]. Although pollination of distylous plants is sometimes performed by a single species carrying pollen attached to different body parts, in the case of buckwheat, pollination occurs via diverse animals [44].

6.4.1 Pollination bagging experiments

In the experiment conducted in the environs of Hitachiota [39], flowers were covered with wide-mesh bags to exclude honey bees and larger insects, and subsequent seed sets were counted in control (unbagged) and bagged (1 × 1 mm mesh) treatments. Controls permitted pollination by wind and diverse insects. Furthermore, a relatively large mesh size (4.5 × 4.5 mm) in bagged treatments permitted pollination both by wind and small arthropods, but not by larger insects. The coarse mesh was expected to exclude most large potential insect pollinators from the buckwheat flowers, including honey bees [45]. Seed set was compared between pin and thrum flower morphs in bagged treatments and controls. Bagging with fine mesh (1 × 1 mm) greatly reduced seed set in both pin and thrum flowers. Bagging with coarse mesh (4.5 × 4.5 mm) greatly reduced seed set in only pin flowers, where small insects including ants, bees, wasps and flies carried pin-morph pollen. Those smaller insects transferred pollen from the short stamens of pin flowers to the short pistils of thrum flowers, allowing normal seed set in thrum flowers. Thus, even insects smaller than honey bees have the potential to maintain at least half the observed yield of buckwheat grain.

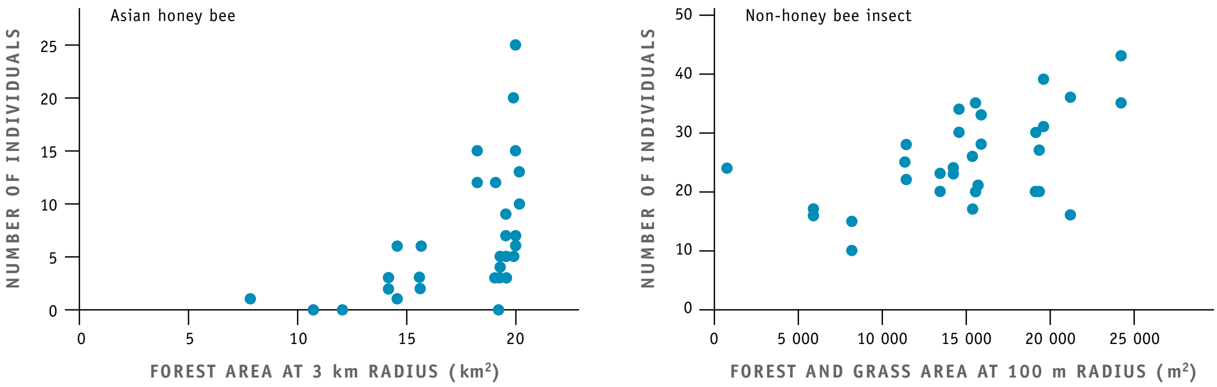
6.4.2 Buckwheat pollination success and pollinator flight range

In the same Hitachiota study region, a different study was performed to explore multiple spatial effects on buckwheat with a special focus on pollinator abundance and pollination success. The two-year study was located in an area where pollinators include a managed honey bee (*A. mellifera*), a native honey bee (*A. cerana*) and various wild insects [17]. While *Apis mellifera* is a domesticated, managed honey bee in Japan, wild populations of *A. mellifera* have not been reported there [46], likely because of colony predation by the giant hornet *Vespa mandarinia*. While the indigenous *A. cerana* has a unique thermal defence against this hornet, *A. mellifera* is quickly overwhelmed by its attacks [47]. *Apis cerana* nests in tree cavities, thus most natural nesting sites are found in forests [46, 48]. In addition to *Apis* spp., solitary bees, ants, flies, butterflies and beetles were included in the study [39]. The authors of the study expected the habitats of these species to be found in semi-natural to natural ecosystems, such as the forests and grasslands surrounding buckwheat fields.

The premise was that landscape factors affect the behaviour of individual pollinator groups differently, leading to interactions across a range of spatial scales. *Apis* and other pollinating insects most likely differ in dispersal (flight and orientation) abilities and would therefore respond differently to diverse landscape factors according to spatial scale. To test this, 1 206 insects including 192 *A. mellifera*, 205 *A. cerana*, and 809 others (72 Coleoptera, 372 Diptera, 318 Hymenoptera and 47 Lepidoptera) were collected, and correlations between different landscape factors were analysed across different spatial scales for pollinator abundance or pollination success. The abundance of *A. mellifera* is correlated with distance from managed hives, but that of *A. cerana* and other native insects in buckwheat fields is significantly correlated with the area of forest cover within a 3 km radius of cultivated buckwheat and the area of forest and grassland cover within a 100 m radius (Figure 6.3).

Figure 6.3

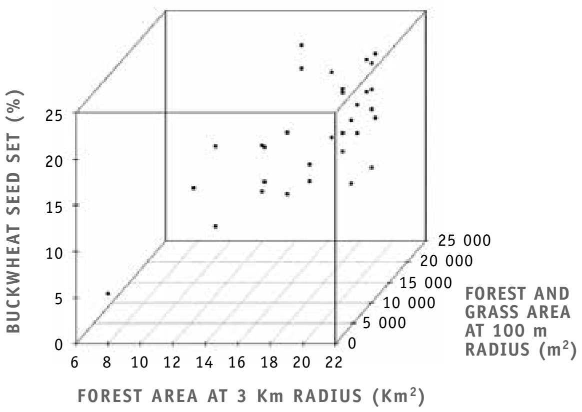
RELATIONSHIPS BETWEEN AREAS OF FOREST AND GRASSLAND COVER SURROUNDING BUCKWHEAT (*FAGOPYRUM ESCULENTUM*) FIELDS AND THE ABUNDANCES OF ASIAN HONEY BEES (*APIS CERANA*) AND NON-HONEY BEE INSECTS



Source: H. Taki

Figure 6.4

RELATIONSHIPS BETWEEN SEED SET IN BUCKWHEAT (*FAGOPYRUM ESCULENTUM*) AND AREAS OF FOREST AND GRASSLAND COVER SURROUNDING CROP FIELDS



Source: H. Taki

However, only the two landscape factors associated with the abundance of *A. cerana* and other wild insects show significant positive correlations with buckwheat seed set (Figure 6.4).

In the buckwheat system of Hitachiota, the wild native species *A. cerana* is the primary pollinator, followed in importance by other insects. *Apis cerana* tends to nest in the tree cavities that occur in mature and old growth forests. High densities of this bee species would be promoted by the conservation of suitable forest trees (with an appropriate age structure and abundance of potential nest cavities) across spatial scales of several kilometres. Non-honey bee insect pollinators of buckwheat include diverse species whose abundances are related to areas of forests and grasslands across much smaller spatial scales. A local-scale conservation and management may be more appropriate for those insects. Even newly created semi-natural lands can provide important habitat for some pollinators, while mature forests may provide limited nest and food resources for some non-honey bee insects [49]. Finally, of course, it is also possible to manage domestic *A. mellifera* populations for buckwheat pollination. A "saturation pollination" procedure with large numbers of colonies may be necessary to ensure that *A. mellifera* visits focal crops [35].

Diverse organisms operate at different spatial scales and therefore ecosystem services provided by different organisms incorporate multiple scales. The observations for this study demonstrate that the *A. cerana* abundance response operates at landscape scales of several kilometres, while the response of non-honey bee insects takes place at a much smaller scale. Both scales also significantly correlate with the pollination success of buckwheat. At times when buckwheat is not flowering in cultivated fields, natural and semi-natural lands – such as forests and grasslands surrounding the fields – provide nesting and food resources for pollinators [50]. Unexpectedly, neither distance from hives nor *A. mellifera* abundance correlates with the pollination success of buckwheat, even though colonies of *A. mellifera* visit nearby flowers most heavily. A study in New York state [14], suggests that buckwheat is pollinated primarily by *A. mellifera* there, but its behaviour is not well adapted to the crop, and the data from the present study suggest it is an ineffective pollinator.

6.4.3 Buckwheat pollination and landscape matrix quality

Another study conducted on buckwheat pollinators in the environs of Hitachiota examines the quality of the landscape matrix surrounding buckwheat fields, and how that may affect pollinator abundance in crop fields [51]. *Apis cerana* was the target pollinator species, while conifer plantations and natural broadleaf forests surrounding the buckwheat fields formed the matrix. The study postulates that the abundance of *A. cerana* in buckwheat fields is more strongly correlated (positively) with the area of surrounding natural forests than with the area of surrounding conifer plantations. The landscape contains agricultural fields (buckwheat fields, rice paddies, orchards and tea plantations) surrounded by semi-natural to natural tracts with cedar plantations or deciduous forest. The original dominant canopy species in the forest is deciduous broadleaf konara oak (*Quercus serrata*), mizunara oak (*Quercus crispula*) and Japanese beech (*Fagus crenata*), while conifer plantations contain Japanese cedar (*Cryptomeria japonica*) and Japanese cypress (*Chamaecyparis obtusa*). The abundance of *A. cerana* was measured over three years. Their number related significantly to the area of natural forest on a 1 500 m spatial scale, but not to the area of the plantation forest.

Thus, forest composition in tracts that surround agricultural fields influences the densities of *A. cerana* on buckwheat flowers. Pollinator foraging range varies with species and spatial scales across landscape factors [52, 53]. The study in the environs of Hitachiota demonstrates that abundance of *A. cerana* in buckwheat fields is strongly correlated with natural forest area within a 1500 m radius of the fields [51]. *Apis cerana*, a wild and native honey bee species in the study region, nests in cavities of tree species found mainly in forested lands [46], and uses floral resources of diverse trees, shrubs and herbs for food [54]. Nest and food resources are less common in tree plantations of *C. japonica* and *C. obtusa* than in natural stands. Such plantation forests, consisting of one or two tree species, are typically grown as close-aged monocultures and are intensively managed. Therefore, managed trees of those two species would not provide the kinds of cavities preferred as nesting sites by wild honey bees, the main pollinators of buckwheat.

6.5 CONCLUSION

Fagopyrum esculentum is a self-incompatible species that is strongly dependent on its animal pollinators. The flowers are distylous; the pin morph has a long style projecting beyond the short stamens, and the thrum morph has long stamens projecting beyond the short style. The Russian Federation, China and Ukraine currently produce the most buckwheat – their aggregate annual production now exceeds 1.7×10^6 t [16]. In addition to industrial-scale agriculture, many small landholders grow buckwheat within mosaic landscapes across Asia. The authors' study of buckwheat pollination in a complex temperate landscape demonstrates that the system may be managed by conserving natural or semi-natural areas near farms as habitat for pollinators. Such a conservation strategy would maintain adequate pollinator densities across landscapes, which would in turn contribute to the stabilization of crop pollination systems [55].

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Chapter 7

SMALLHOLDER POLLINATION PERSPECTIVES

7.1 EXPERIENCES PROMOTING POLLINATION TECHNOLOGY AMONG SMALLHOLDER FARMERS IN KENYA, THROUGH FARMER FIELD SCHOOLS

M. Kasina

7.1.1 Introduction and initial results

Kenya is a largely agricultural economy where 80 percent of producers are small-scale farmers. While the majority of crops grown (55 percent) do not require animal-mediated pollination, those that do contribute about 65 percent of the country's agricultural GDP. Despite the availability of such statistical data, little has been done to manage pollinators in agriculture, due mostly to a lack of reports and advice on how to implement pollinator management. Suitable programmes focusing on pollinators and validating their importance were therefore necessary.

Over the past ten years, a publicity and information drive on the role pollination plays in enhancing crop yields in Kenya has increased interest in pollinators and their management. Although enlightenment of the public and farmers about pollinators and pollination can be achieved through the media, hands-on demonstrations about the value of pollination play a vital role.

There is a general perception that bees, both in species and number, have declined over recent years. Farmers interviewed across the country have noted reduced bee activity in their farmlands [1]. These observations match reports from recent monitoring exercises in the country [2]. To halt any further loss, practitioners favour pollinator conservation within agricultural landscapes, compared to the conventional approach to conservation (i.e. solely within protected areas) [3].

Farmers nonetheless continue practices that are not friendly to pollinators, such as improper use of pesticides, unfavourable soil amendments including the application of inorganic fertilizers and flood irrigation without consideration of soil-nesting pollinator needs, and land clearance. These practices all constitute major threats to the presence of pollinator in farmland. Mitigation, through educating farmers about different pollinators and the benefits of pollinators for their livelihood, is both desirable and essential.

Farmer Field Schools (FFS) educate farmers about topical sustainable agriculture issues, based upon a growth cycle [4] (e.g. a crop season). They are highly participatory and include hands-on analysis and decision-making (on the part of farmers) during training sessions and implementation. Since the late 1980s, the Food and Agriculture Organization of the United Nations (FAO) has used this approach to disseminate sustainable agricultural practices to farmers [5]. It relies extensively on the training and facilitation skills of Trainers of Trainers (ToTs), who usually undergo training themselves on how to implement an FFS or have relevant experience in this field. In addition, facilitators must have mastered the main areas of expertise [6], in particular agricultural practices proposed for testing by farmers. The success of an FFS relies on the following elements [7]:

- group members that have a common interest regardless of whether the group existed previously or has just formed;
- field plots where farmers can meet and carry out their observations;
- facilitators to guide farmers in the practice of a given subject;
- a curriculum to be followed during the season-long training that takes into consideration all aspects of the target subject;
- a programme leader who heads the larger programme to which the FFS activity is anchored and provides guidance for facilitators/ToTs to ensure the FFS proceeds satisfactorily;
- financial support to ensure successful implementation of the FFS activities.

The FFS approach is geared towards influencing the behaviour of target farmers and their perception of a given subject, with a view to ensuring gains from farming in practice. Dissemination of sustainable agricultural practice to non-FFS farmers through farmer-to-farmer contacts is encouraged.

Previous FFS activities in Kenya since the introduction of this approach in 1995 have proved successful [8, 9]. The wide range of topics covered includes integrated pest management, optimizing crop production, soil fertility management, and livestock nutrition and health, as well as a broad look at human health learning. FFS can clearly be modelled to resolve various identified problems.

The model was chosen specifically to transmit knowledge of pollination to Kenyan smallholder farmers, who represent the main growers and owners of the majority of the agricultural land. Influencing their perception about pollinators and pollination may result in pollinator conservation within agricultural land, thus contributing to improved food security and stable livelihoods in those systems. Although farmer-to-farmer dissemination of learned knowledge from FFS is low [4], benefits can be shared as a result of farmers changing their farming practices, with other farmers observing the results directly and implementing the necessary changes. In addition, since pollinators constitute a "public good", enabling graduate FFS farmers to share ways of managing them helps to ensure they play a sufficient role in their agro-ecosystem. This was the first step to disseminating the pollination message through national agricultural farming systems, and the first attempt to utilize an FFS approach.

7.1.2 Field studies

The FFS activities were carried out on farmland neighbouring North Kakamega forest, the northeast Mt. Kenya forest reserve, and east, north and west Kilimambogo forest during 2012 to 2014. The Kenya Pollination Project identified these areas as STEP (*study, train, evaluate, promote*) sites. The three sites share similar characteristics:

- the existence of natural habitats bordering the sites, which could play a role in pollination services for farmland;
- the availability of many small-scale farmers;
- the presence to varying degrees of small-scale farming systems, ranging from farmers practising no intensification (minimal input) to those more agriculturally sophisticated (with high input use and mechanization, even in small land holdings). In terms of human activity, however, there is a high

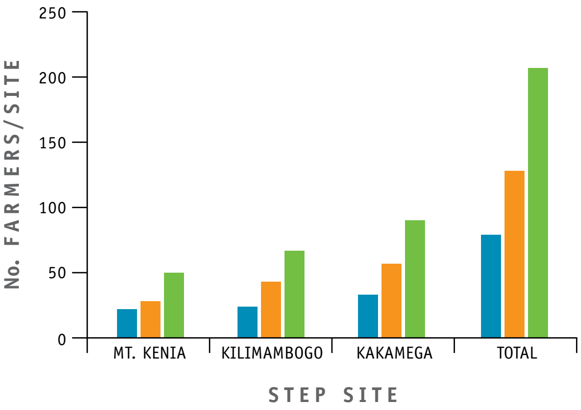
level of diversity. Farmers at the Mt. Kenya site have the highest level of agricultural intensification and are very commercially oriented. Kakamega has the best agricultural lands and relatively high rainfall, but farming is not intensive, with most cultivated land under sugar cane. At Kilimambogo, rainfall is meagre and subsistence farming on semi-arid farm operations is the norm.

Training approach: Four groups were identified at each site through the government extension department. Each group professed an interest in learning about pollination technology, and identified one person to be trained as a ToT. Likewise, field extension officers were identified within the sites for ToT training. All the trainees underwent a one-week training/refresher course on implementing FFS and all aspects of crop production, including pollination information. They then returned to their farms and implemented FFS across three cycles, based upon their identified crops. The first cycle focused on delivering a message to farmers enabling them to understand flower visitors and pollination. The second cycle was dedicated to pollination in crop production and economic benefit, and the third cycle focused on understanding best practices that enhance pollinators in cropland. Data collection was based on group discussion and individual farmer reflection on a given topic. Other information collected related to the demography of the group and the experiences of the ToTs and facilitators, based on a given issue discussed in a workshop.

Results: FFS group characteristics and demography: About 210 farmers participated in the FFS activities carried out across two cycles, 2012–2013 and 2013–2014. The number of female participants in each group was higher than the number of males across all three STEP sites, a characteristic found not only in Kenya, but also in other parts of the world (Figure 7.1) [4]. The generally held opinion that it is beneficial to include more men in FFS activities, because they are the main decision-makers for most farming activities, was not found to be relevant in the case of the field studies. A baseline study demonstrated that households in the study sites have no preference regarding the selection of trainee household member, and both household head and spouse discuss and make decisions regarding farm activities on an equal basis [1].

Figure 7.1

FARMERS WHO PARTICIPATED IN THE FFS ON POLLINATION TECHNOLOGY IN KENYA, 2012–2014



Source: M. Kasina

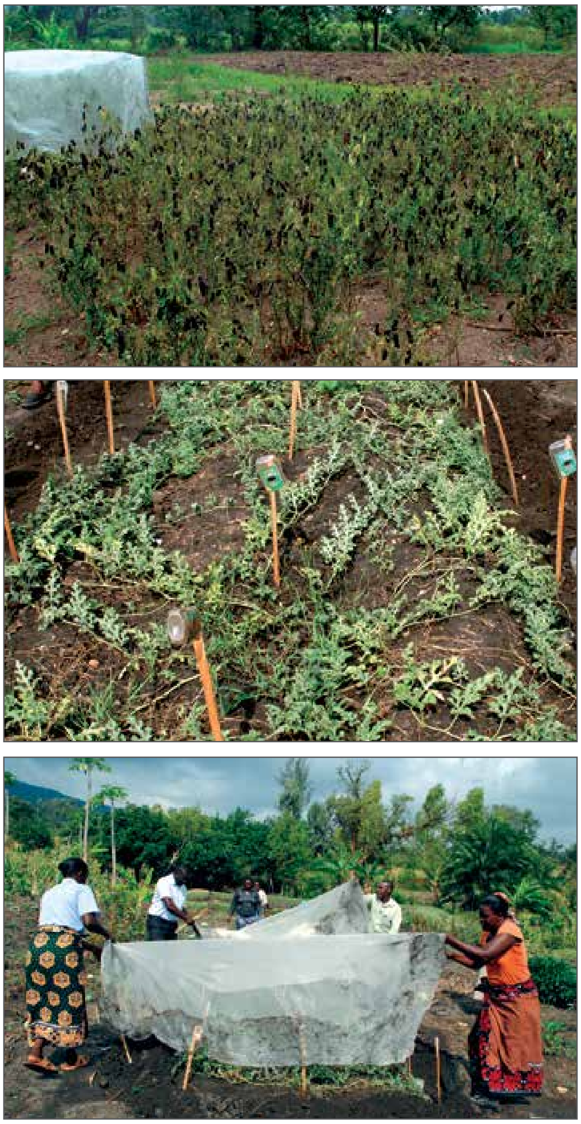
Farmers selected different crops depending on the STEP site (Table 7.1). However, crops belonging to the *Cucurbita* family were included as part of demonstration plots for purposes of comparison with farmer-identified crops. This was because most pumpkins will not fruit without pollination, because they have male and female flowers in different parts of the plant, and thus require a pollinator to transfer the pollen (Section 7.2). Those finally chosen were pumpkin (Mt. Kenya and Kakamega) and watermelon (Kilimambogo), based on farmer preference. Other crops chosen included dry common beans, French beans, peas (var. mangetout) and canola (at the Mt. Kenya STEP site), and spider plant and *Crotalaria* (at the Kakamega STEP site, Figure 7.2, see also [10]). The main reasons given for the choice of crop were that they were commonly grown in the area, that there was a ready market for the crop, and that farmers had considerable experience in their cultivation.

Table 7.1
CHOICE OF CROPS BY THE FFS GROUPS AT THE THREE STEP SITES

CROP	No. STEP SITES	No. GROUPS
Common beans (*Phaseolus vulgaris*)	1	2
Pumpkin (*Cucurbita melo*)	2	5
Canola (*Brassica napus*)	1	1
Mange tout (*Pisum sativum*)	1	1
French beans (*Phaseolus vulgaris*)	1	1
Spider plant (*Cleome gynandra*)	1	4
Crotalaria (*Crotalaria* sp.)	1	4
Watermelon (*Citrullus lanatus*)	1	4

Source: M. Kasina

Figure 7.2
CROTALARIA POLLINATION TRIAL BY MSALABA HORTICULTURE FFS GROUP (KAKAMEGA) AND A PLOT BY MAKANDARA FFS GROUP (KILIMAMBOGO) SHOWING NO WATERMELON FRUITS FORMED COMPARED TO OPEN POLLINATED PLANTS, AND SHOWING EXPERIMENTAL COVERING OF FLOWERS TO EXCLUDE POLLINATORS AND RECORD THE RESULT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Baseline knowledge and farmer understanding of pollinators and degree of pollination: A guidance document was prepared before the start of the FFS cycle and was used by the ToTs and site teams to assist implementation. First, baseline information was collected to ascertain the level of knowledge farmers possessed regarding pollinators and pollination. Findings from surveys targeting all households (not necessarily those participating in the FFS activities) showed that farmers understood flower visitors but could not relate flower visitation to crop yields. Moreover, even though they understood pollination, it was not perceived as a vital input of crop production. Farmers did not manage the blooming period of their crops, even though they acknowledged that without flowers there might be no gain from the crops. Farmers could also not comprehend (as mentioned above) how pollination improves crop yields. At the Mt. Kenya STEP site, one of the groups recruited a secondary school in the vicinity for the purpose of disseminating knowledge to teachers. Students and teachers were able to define pollination (following a discussion with facilitators) but could not comprehend its role in crop production. The school later started an agriculture club to facilitate learning by students and teachers about pollinators and their effects on crop yield. The club went on to produce poems and a play to explain the role of pollinators to the general public.

PLAY 1, CHORAL VERSE
BATTLE OF POLLINATORS

GROUP 1: STARTING	GROUP 2: RESPONDING
The drums beat The trumpet cries The harp strings The music Of competition. We will applaud The winner And boo The loser!	I say We the Bees Are the kings Of pollination! We are fuzzy We carry electrostatic charge – Weee! Ever heard of that? It's our pollen basket – Our hind legs!
Impressed, Ladies and gentlemen? Is there anything To impress anyone there? We the family of flies – Hover flies, drone flies Are large, bulky and hairy, And the shiny – Nothing to compare With the violent clan Of warlord Bees!	Mmm! Can flies surely compare? With our nectar-hunting ways? We professionally move From flower to flower Collecting nectar Which we convert Into honey For us For you If you are lucky We don't get you!
Ooh! How we wish He only knew – Only knew How our cousin Just for example – For example only Mimic – Ever heard of that? – Mimic pheromones – Pheromones of aphids – Aphids of all things! In order to attract them For pollination	Who doesn't know.... It's public knowledge Undisputable truth That we The family of bees International Are the only recognized Commercial pollinating agents We live in commercial hives, In the bellies of huge trees In holes underground In rock cavities Surely, The bee Is The superpower of pollination!
Do we need argue any further? Do we? Who can't note Who can't see us Everywhere As we dance *Sakata* Over every flower None-selectively Pollinating, pollinating With our multi-coloured Dresses Who can't recognize We are homeless In service!	You are great The flies!
You are great, The bees!	**All** We are all great In pollination.

Reproduced here with permission from Nyarigino Secondary School, Laikipia County, Kenya.

PLAY 2, SOLO VERSE
HAIL POLLINATORS

I want to sing a song,
To the creator of the universe,
For his wisdom,
And blessings.

When I look,
Behind me,
In front of me,
All around me,
I marvel,
All the things He created.

This beautiful flower,
That delights my eyes,
Do you see,
How it smiles,
How it gestures,
In anticipation,
Of a pollinator!
Like a love,
Waiting for her beloved.

Imagine if pollinators,
Were not there,
Where would your
Vegetables
Your *Githeri*, your beans
Your tomatoes, your fruits
Come from?

Imagine – Just imagine
If we killed all pollinators –
The bees, the moths, the butterflies
The wasps, the birds and all:

Imagine – Just imagine
Going to town, your market place
To call a professional artificial pollinator
And you meet him
Or her

Rollicking in his or her
Swivel chair
And you knocked at the mahogany or glass door
Cautiously, in awe
But in urgent need
Of pollination services
Come right in!
Help yourself to the daily paper
As I finish
Some assignments here.

As you dejectedly, boringly, pretentiously
Read the forced paper
You cursed – in your heart
At the arrogance
Of the businessman
That held you at ransom
In time, money and opportunity!

Hail! Hail, Pollinators
May the Earth
Give more of you –
You selfless servants
Of human existence!

PLAY 3
THE MEETING

An open ground, grassy:
The Honey Bee flies onto the stage blowing a trumpet. He looks agitated, anxious and disturbed.

HONEY BEE (*Talking to himself*): I thought they think the way I think! Can't they see? Can't they? (Blows the trumpet) Comrades! Comrade pollinators! Hurry up! Gather here immediately.

WASP: (*Straightening his wings and scratching his leg*): We are here, comrade Bee – The whole family of wasps. What's up?

BEE: (*Agitated*) What's up? Just because your house is in Man's house, you think you are special!
(Enter the Beetle rolling a ball of dung)

BEETLE: We are here, comrade.

BEE: (*Disinterestedly*) Just sit and wait. (*Agitated*) And stop that game!
(*A large group of flies enter the stage, sniffing here and there*).

BEE: Could you sit down, butterflies.

BUTTERFLY: Where do we sit? We may mess our flowery dresses!

BEE: You are thinking of dresses? Of beauty when you are not sure of your life tomorrow? Foolish!

ANT: Don't step on us! Just because we live underground and don't fly does not mean we are not pollinators.

BAT: (*Standing up*) Comrade Bee, I doubt if this meeting has not been invaded by spies of man. I have seen Monkey here. Surely, is monkey seriously, a pollinator? We are worried!

BIRD: I understand your fears, comrade Bat. We are also here. I can see comrade Ant and lizard a bit nervous. I want to assure them of their security. Monkey is one of us, incidentally!
(Ant, Moth, lizard and Butterfly huddle together, terrified – mistrusting Bird's assurance of security).

BEE: (*Flying threateningly towards bird*) Please be warned: do not salivate about any of these comrades.

WASP: Comrade Bee. Please tell us why you called us. I and Beetle can help you in matters of security. We will sting anyone who messes this meeting.

ANT, MOTH, BUTTERFLY AND LIZARD (*in unison*): Yes, security! We trust Wasp!

BEE: (*Climbing onto a rostrum*) Ladies and gentlemen. This is an urgent meeting. If you look around, you will note that the population of each of your families has declined. There is danger of our extinction from the face of the Earth.

BUTTERFLY: It's true! My sister, the Hoverfly is dead; my cousin Carrion fly is dead. They were all poisoned by man.

ANT: What about us! We are now Internally Displaced Pollinators! Man has destroyed our houses using tractors!

BIRD: Comrades! You don't know what you are talking about! In my family only, only a few of us are alive – and by the sheer grace of God! Man has invented one deadly poisonous poison after another.

WASP: (*Contemplatively*) Man is ignorant, comrades! We help pollinate his crops yet he kills us recklessly.

MONKEY: The other day I went to look for tomatoes in his farm. Men, I was hungry. I gobbled one, two, three ... Before I could turn and say "weee" I was in Intensive Care Unit on top of a tree. Vomiting! The tomatoes had been sprayed that very morning!

BEE: Comrades, no one can understand the mind of man! No one!
Take me, for example, I give him priceless honey yet when harvesting the same delicacy, he has to spray the hive with insecticides and kill a whole family of us.

BIRD: Though he thinks he has the technology, he doesn't reason that it cost him nothing when we pollinate his crops.

LIZARD: I feel for you, Bird and Bee. The way you do that pollination daily and diligently. One would think you are paid by man! Can't you try going on strike one day? Like what the teachers did the other day?

ANT: I would join you in singing "solidarity forever"!
(*All join in singing, happily*). Solidarity forever, solidarity forever x2
For the union makes us strong!
(*They applause themselves*) Wonderful! Wonderful!

WASP: I suggest we call Man and clarify to him that unless he understands our role in sustaining his food security, he is soon going to commit suicide himself. (*All laugh*) Sure! Killing us is suicide for him!

ALL: Agreed! Man must now understand the importance of pollinators. He must conserve us or perish.

Experiences in strengthening pollination knowledge: Past FFS activities largely depended on farmer experience for the problem being addressed. For example, most farmers have direct experience of pest and disease control, soil fertility management, or failing crop yields due to failed technology, such as seed and varietal choice. However, target farmers had no experience of the importance of pollination for crop production or of the concept of a "pollination deficit" among their crops. The choice of crop was tricky, because farmers choose their preferred crops in line with FFS guidance; however, the selected crops were not known to fully depend on pollinators to set fruit or seeds. For farmers to appreciate the pollinator factor, it was suggested that additional crops of Cucurbitaceae be included in the demonstrations, to which farmers agreed. Since the ToTs and facilitators had not conducted a demonstration on the role of pollination in crop production, this constituted a learning experience for them too, thereby putting theory into practice.

In the first FFS, farmers chose to test both the effect of pollination and soil "amendments" (comparing inorganic fertilizer to farm yard manure) on crop yields. The farmers focused more on soil amendments, with which they were familiar. By the end of the cycle, awareness of pollinators and pollination had increased, but the farmers could not conceptualize the value of pollination in terms of overall crop production. The second FFS was thus designed to only test pollination value and thus aid farmers gain firsthand experience.

Experiences in strengthening pollination value: Since farmers easily adopt technology that has the potential to increase their income, pollination and its valuation was deemed an important discovery for farmers. That involved comparing yields of plants denied open pollination (via netting or isolation from the outside) with those allowed open visitation by pollinators. Facilitators and ToTs experienced some anxiety regarding the outcome of the trial, as this was new territory for them. However, the pollination outcomes during the cycle proved consistent with the expected training and exposure protocol.

Public response to pollination information at agricultural shows and field days: During field days and agricultural shows, it became apparent that most people were aware of bees as pollinators, but did not conceive of pollination as an important agricultural input; and that all participants knew about honey bees, but regarded other species not as bees, but as flower pests. After understanding the value of pollinators, people requested advice on how to acquire bees for pollination purposes. This response demonstrates that greater exposure to the role of pollination in agriculture increased demand and receptiveness toward methods that enhance pollinator presence. Another major challenge highlighted by public participation concerns the use of pesticides during flowering periods. Participants noted that flower pests such as thrips and flower beetles can defoliate flowers and constitute the main reason for the application of sprays. With more interaction, it was noted that spray application at flowering is just prophylactic, and farmers use it fearing flower abortion, whether pests are present or not. Therefore, it is important to present strategies for different crops at flowering and to advise on best management options that consider the protection of pollinators. The following can be recommended:

- Follow carefully the instructions on pesticide labels regarding personal safety. In a different study, it was found that farmers did not prioritize their safety or that of applicants. It is essential to take adequate precautions when applying pesticides.
- Some pesticides have greater toxicity levels for bees. Farmers should avoid spraying these varieties on flowering crops and plants.
- Close attention should be paid to the directions on use and rates of application provided on pesticide labels. These can reduce the effects on pollinators. Spray when it is not windy to avoid high spray drift.
- The study showed that bees visit crops at different times of the day. Spray applications should be times accordingly. For example, bees forage before 07:00 hours at Kakamega and Kilimambogo, but start about 09:00 hours on the northeastern side of

Mt. Kenya where it is considerably cooler. Likewise, there are very few foragers after 15:00 hours at all three locations.

- Seed treatment with pesticide ensures minimal use of pest control products at the initial stages of crop growth, and can drastically reduce spray application. While it constitutes a major contributor to pollinator poisoning in developed countries (see Chapters 4 and 16), the mode of application in Kenya does not produce dust particles that may impact pollinators. However, systemic pesticides are known to transfer to the flowering parts, and may impact pollinators through this route.
- Farmers with an apiary should locate downwind to avoid pesticide drift into the apiary. In addition, the area will need a woodlot to act as a barrier against spray drift.
- Practice other pest management approaches. Pesticides are not a panacea for the challenges of pests. Effective pest management requires the use of a wide range of tools to combat pests, many of which are designed to be cost-effective. For example, farmers can control caterpillars by collecting and squashing them when their population is low. They can also use smoke for aphids, soap sprays for plant-sucking insects, preserve natural enemies and introduce more (these are available on the Kenyan market), perform crop rotation to reduce soil borne diseases and early pests, and use trap crops to attract or repel pests from the crop.

Experiences in handling groups: At the start of FFS, group members were enthusiastic about expected activities and gains by the end of the crop cycle. However, some members departed during the FFS activities. Challenges encountered in handling groups include:

- *High, undefined expectations regarding the possible financial or material gains from the project.* This was the principal challenge, with most farmers later stating that they received handouts in the form of cash or non-cash items during all projects in which they participated. This factor reduced farmer interest in the project. It was "undefined" because it did not form part of the recruitment exercise and only surfaced informally. This constraining factor was managed by educating farmers to accept that the gain of knowledge is more beneficial than material gain.
- *Commitment by the farmers to participate in the classes.* Most groups existed before the project, with specific interests such as financial mobilization and seeking project support. They met regularly but at fairly large intervals (once a month). The FFS activities required weekly meetings, which made farmers change their normal meeting schedules.

  This constraining factor was managed by ensuring farmers gain knowledge each time they have a meeting. Focusing on a wide range of different topics, such as crop management, rather than just pollinators, increased farmer interest. Key topic leaders were also invited once in a while to ensure farmer participation. At Kilimambogo, farmers devised a weekly merry-go-round (a form of social support system) that benefited only those present at each meeting, which also increased participation.
- *Sharing of pollination messages outside the group members.* Farmers were not keen to share learned information with other farmers. They noted that doing so benefits those farmers who are not willing to form or be part of a group, do not spent time in group meetings and thus would encourage others to desist from meeting with other farmers.

  This constraining factor was managed through the development of beekeeping and bee management aspects. Farmers were informed that engaging their neighbours in pollinator management would ensure that pollinators are protected wherever they go. Otherwise, implementation of pollinator-friendly practices could be undermined by the lack of similar practices among their neighbours, with the possibility of negative effects on pollinators. It was emphasized that sharing information at the village level results in mutual gain. In addition, farmers were informed that, as pioneers of pollination management, they would gain more respect by sharing information.

- *Funding for FFS activities*. While the project catered to major activities including management of demonstration plots, farmers were also involved in other external projects. For example, an exchange programme was needed to understand how farmers at other STEP sites are learning. Farmers also needed investment to support other newly instituted farm activities, such as water management.

  This constraining factor was managed by advising farmers to seek support from other projects or activities, and to make contributions to support identified members during exchange visits. In the absence of funds for farmer exchange visits, exchange visits by site managers enabled farmers to receive testimonials from other STEP sites.

Managing such challenges allowed the groups to focus on the lessons of the FFS, which resulted in greater gain among the farmers, as elaborated below.

Major farmer learning/knowledge impact: The FFS studies allowed farmers to accumulate knowledge on pollinators as well as other crop management factors. Based on the knowledge evaluation across all groups at all STEP sites, the following is known:

- All farmers can differentiate bees from crop pests.
- Farmers can identify different bee and pollinator species.
- Farmers recognize efficient pollinators of the focus crop, as well as all bees visiting the crop:
  - *Crotalaria*: leafcutter (*Megachile* spp.) bees, carpenter (*Xylocopa*) bees
  - Spider plant (*Cleome*): hawk moths
  - Beans: carpenter bees and frequently honey bees
  - Pumpkin: honey bees
  - Canola: honey bees
  - Watermelon: honey bees.
- Key farmer discoveries include:
  - knowledge of pollinators and what they do, and understanding that flower visitors are not destructors of crop flowers, as earlier thought;
  - knowledge of pollination, with farmers recognizing that without sufficient pollination, yields are greatly diminished and for some crops, no yields are obtained;
  - food resources for pollinators are mainly nectar and pollen, and having those all year round ensures pollinator presence in the farmland;
  - incomes from pollinators, ascertained by linking crop yields with pollinator work and calculating the amount that comes from pollination provision (i.e. the pollinators):
    - watermelon and pumpkin: 100 percent income from pollinators
    - spider plant and canola: high yield losses (more than 60 percent) as a result of insufficient pollination [thus potential yield gain by > 150 percent]
    - beans: yield reduction by more than 40 percent as a result of insufficient pollination [thus potential yield gain by > 66 percent];
  - major changes in farming behaviour, with farmers who participated in the FFS activities becoming more aware of the environment, ecosystem and best approaches for sustainable agriculture. They talked less of using synthetic pesticides and were challenged on how to protect their crops from pests while protecting bees and other pollinators;
  - other learning apart from pollination:
    - farmers were exposed to ways of delivering research questions on pollination (e.g. comparing yields from bagged and unbagged flowers)
    - pest management that considers protection of pollinators, cultural practices and wise use of pesticides when it is possible to avoid pollinator contact/poisoning
    - increased knowledge of crop and farm management, record keeping and other farm activities.

AESA (Agro-ecosystem assessment): This is the backbone of the learning process employed for the FFS approach. Farmers were able to fill AESA forms at every meeting event. This activity enhanced their skills on the different components of training.

7.1.3 Conclusion and recommendations

FFS activities on understanding pollinators, pollination and the economic gains of pollination service were well received and proved successful. The next planned FFS activities include pollinator management to train farmers and expose them to best practices, though participants have been exposed to aspects of these areas during previous FFS activities. In addition, a co-funded project with the Marin Community Foundation (MCF) focuses on the use of a hedgerow system at the STEP sites, as well as other activities to manage pollinators, particularly bees (see also Section 7.3). The project results will enhance delivery of pollination management packages to other farmers, who were unable to carry out studies on the use of hedgerows to enhance pollinators on the farm.

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7.2 POLLINATION SERVICES AND MELON IN FAMILY FARMING AREAS, NORTHEASTERN BRAZIL

L.H.P Kiill, M.F. Ribeiro, K.M.M. Siqueira and E.M.S. Silva

7.2.1 Introduction

The lack of pollinators is considered a limiting factor for the productivity of many crops worldwide [1], especially given the expansion of agricultural areas. In addition, absence of information about pollinators and factors involved in the efficiency of "ecosystem services" hinders the successful use of those services. Several agricultural inputs and practices that play an important role in current production systems have highly negative effects on the diversity, abundance and use of pollinators, the most severe of which come from the improper use of pesticides [2].

Recent studies performed in Brazil [3] demonstrate the economic value of pollinators, and indicate that a considerable increase in production occurs when the crop is visited by pollinating bees, even for self-pollinating species. In the case of melon (*Cucumis Melo L.,* Cucurbitaceae), production in general depends on the introduction of honey bee colonies [4], as the areas cultivated are usually devoid of pollinators or have very few present. This chapter presents the author's experience with small producers of melon in northeastern Brazil, specifically in Petrolina, Pernambuco and Juazeiro, Bahia. It examines the obstacles encountered and highlights some measures that could enhance pollination services for cultivation.

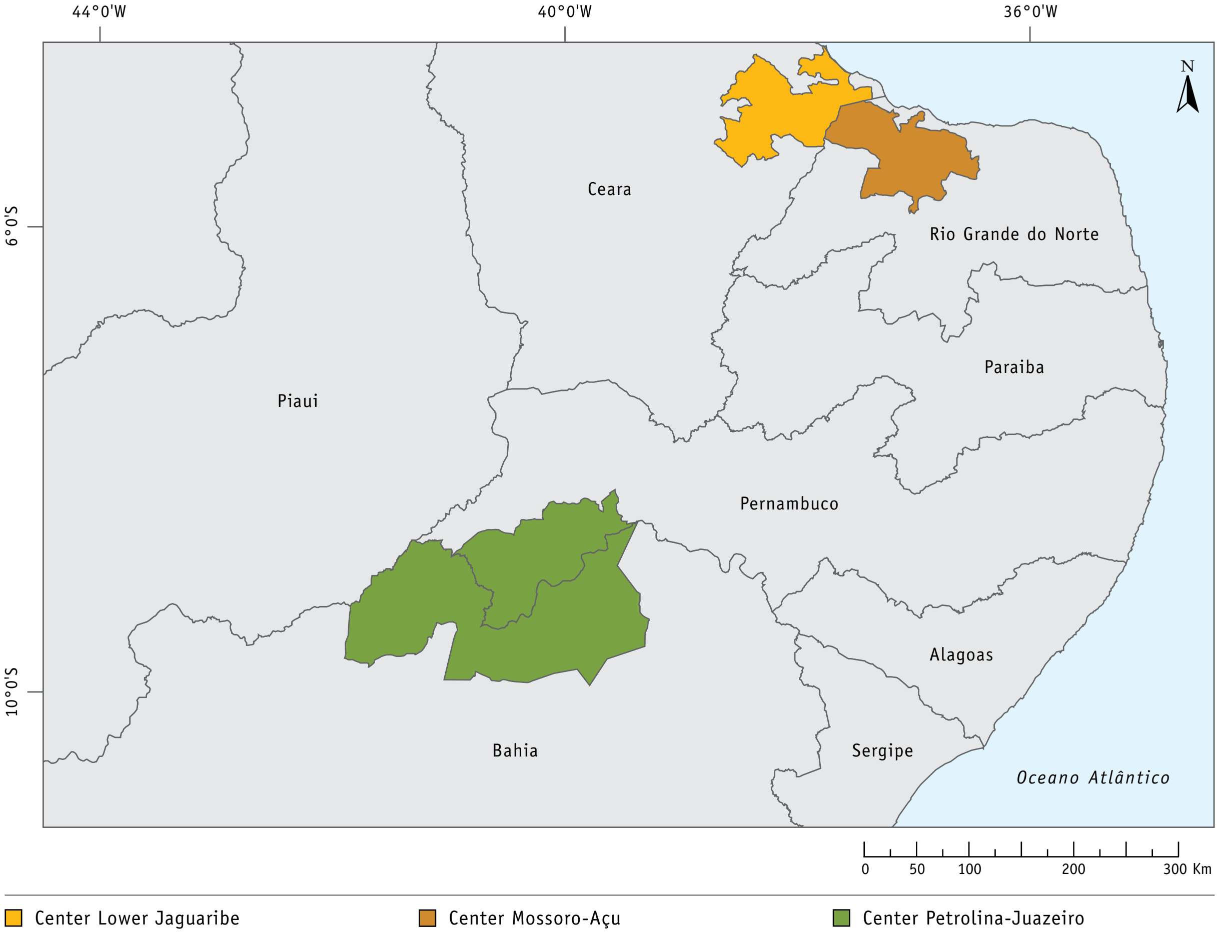
7.2.2 Cultivation expansion

Melon (*Cucumis melo* L.) is an ancient crop that perhaps originated in tropical Africa, spreading thereafter to India and Asia [5]. Other theories regarding the origin of this species suggest it radiated outwards in primary and secondary waves from India [6], Arabia and South Asia [7], and China [8]. The introduction of melon to Brazil occurred with European immigrants. Melon cultivation developed in Rio Grande do Sul, which remained the largest producer until the end of the 1960s. Further expansion of melon culture took place only after 1970, when important production centres emerged in the states of São Paulo (southeast region), Pará (northern region) and the middle lower São Francisco River basin, mainly in Petrolina, Pernambuco and Juazeiro, Bahia, in the northeast. By 1992, the northeast region accounted for 84 percent of Brazil's production [9, 10], with Rio Grande do Norte the largest producer.

Current production centres: As of 2011, Brazilian melon production had reached 499 330 tonnes [11], 93 percent of which came from the northeast. The main producers in the region are the centres of Mossoró and Açu, Rio Grande do Norte, Lower Jaguaribe, Ceará, and Petrolina, Pernambuco, and Juazeiro in Bahia state (Figure 7.3) [12]. In general, the production centres of Mossoró and Açu, Rio Grande do Norte and Lower Jaguaribe and Ceará depend on monocultures and account for 80.59 percent of national production and 100 percent of exports [12, 13]. These regions are characterized by large and medium-sized companies with modern technologies, irrigation equipment, packaging, fruit classification, and high productivity and quality, along with substantial competitiveness in domestic and foreign markets [14].

The growing areas are free of the South American curcubit fruit fly *Anastrepha grandis*, and have characteristic patterns of high solar insolation, low rainfall (except January to May) and low humidity, which enable melon production during almost the entire year [15]. The addition of certain adopted procedures, such as the use of agro-textiles (non-woven fabrics), have further optimized regional production systems (Figure 7.4). This approach has proven very convenient for integrated management of pests and viral diseases [16]. A soil cover of thick plastic reduces surface water evaporation and temperature fluctuation, and prevents direct contact of fruit with the soil. By decreasing direct moisture and injuries to the peel, postharvest diseases and invasive plants are better controlled [17, 18]. Colonies of Africanized *Apis mellifera* are also introduced to improve pollination [19].

Figure 7.3
THREE MAIN CENTRES OF MELON PRODUCTION IN NORTHEASTERN BRAZIL



Adapted from: GIS Laboratory at EMBRAPA Tropic Semiarid Geographic Coordinates Systems Datum SIRGAS 2000

In the production centres of Petrolina, Pernambuco state and Juazeiro, Bahia state, farmers and small rural entrepreneurs in the irrigated perimeters are responsible for most of the planting. They possess moderate to few financial resources and grow melon mainly between February and April, with their product intended for the domestic market [20]. Farm size averages about 6 ha, with one permanent workman and temporary labour. Although melon is predominant, more than one crop (e.g. tomato, watermelon, sweet pepper) is common, with the crop area varying according to current market value [21]. In such areas, mechanized activities require the rental of agricultural machinery and implements [21], and water from the São Francisco River. Some plantations are equipped with furrow or drip irrigation, with use of plastic covers (Figure 7.5) where mainly yellow melon or "piel de sapo" melon are grown. Honey bee hives are seldom moved into the flowering melon fields.

Among crop varieties, the most marketed types in Brazil are *Yellow*® Honey Dew, *Piel de sapo*®, *Charentais*®, *Cantaloupe*® and *Galia*®. The first three belong to the botanical group "Inodorus", and are hardy during transportation and odourless, with a long shelf life. Charentais and cantaloupe melons are aromatic, have a high content of soluble solids and a short post-harvest life [22].

Figure 7.4

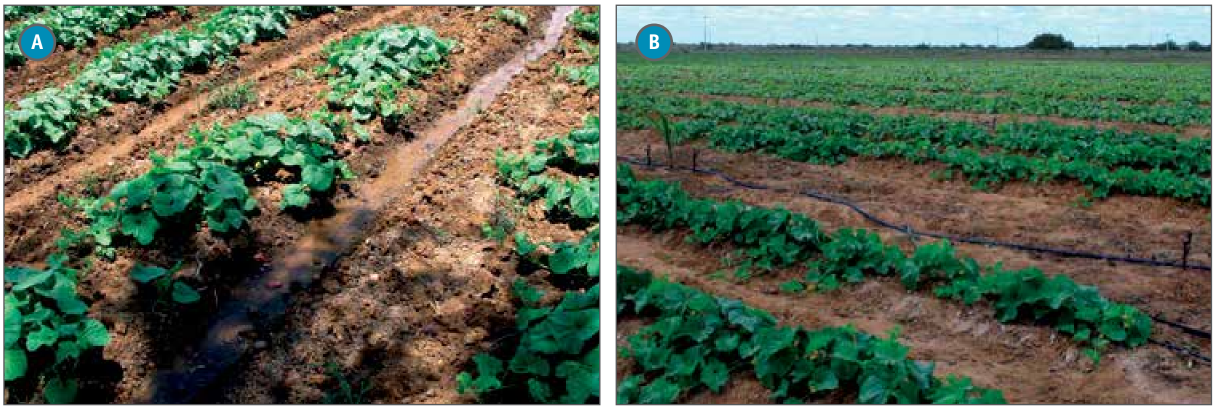
APPLIED TECHNIQUES FOR OPTIMIZATION OF CROP SYSTEMS IN CULTIVATION CENTRES OF MOSSORÓ AND AÇU, AND RIO GRANDE DO NORTE, AND LOWER JAGUARIBE AND CEARÁ

(a) area covered with fabric, (b) area with the cover removed, and (c) area with honey bee hives near the melon crop

Source: L.H.P Kiill, M.F. Ribeiro, K.M.M. Siqueira and E.M.S. Silva

Figure 7.5

MELON CROP AREAS IN PETROLINA, PERNAMBUCO AND JUAZEIRO, BAHIA



a) with irrigation by ditch, and (b) drip irrigation (plastic cover removed)

Source: L.H.P Kiill, M.F. Ribeiro, K.M.M. Siqueira and E.M.S. Silva

7.2.3 Pollination ecology

Most melon cultivars are andromonoecious, presenting male and hermaphrodite flowers together [23]. The flowering period starts 25 to 30 days after planting, depending on the variety, cultivar and climatic conditions. The anthesis of male flowers precedes that of hermaphrodites by two to five days, and more male than hermaphrodite flowers are produced. A study conducted in Ceará State reports a sex ratio for male:hermaphrodite ranging from 1:6.1 to 1:11.3 for seven hybrids, with an average of 20.5 days of male flower anthesis and 10.7 days for hermaphrodite flowers [24]. Conversely, in Juazeiro-Bahia the sex ratio for two hybrids of the yellow variety is 1:16 and 1:19, with an average of 22.7 and 19.6 days for the male flowers and 16 to 20 for the hermaphrodite flowers [25].

Floral anthesis occurs in the early morning between 05:00 and 05:30 hours, with no difference between flower types, and with stigma receptivity coincident with anthesis or flower opening [26]. The hermaphrodite flowers are larger than the male ones (Figure 7.6), regardless of the hybrid variety, with the largest differences related to flower height [27]. Melon hybrids have different flower morphologies, possibly resulting in pollinator behaviour that favours hermaphrodite flowers. In hybrids, hermaphrodite flowers seem more visible and have a larger surface, thus increasing visual signal and facilitating the landing of floral visitors [27].

Figure 7.6
MELON MALE FLOWER (LEFT) AND HERMAPHRODITE FLOWER (RIGHT), SHOWING SIZE DIFFERENCE

Source: L.H.P Kiill, M.F. Ribeiro, K.M.M. Siqueira and E.M.S. Silva

Anther dehiscence occurs towards the outside of the flower, not the central portion near the stigma surface. In this way, even viable pollen grains that might otherwise germinate on the stigma of their own flower lie at the base of the corolla, with no possibility of contact with the stigma [28]. This characteristic reinforces the need for outcrossing pollinators to transfer pollen from anther to stigma. Generally, flower lifespan is about 12 hours, and from 15.00 hours petals begin to wilt and lose colour, with no difference between melon or flower varieties.

Nectar is produced by both flower types, but hermaphrodite flowers produce larger amounts. Measurement of nectar volume performed at different times documents a range of 5 028–8 700 µL (microlitres) for hermaphrodite flowers, and 1 851–3 850 µL for male flowers. The difference may explain the higher attraction of hermaphrodite flowers for pollinators [25, 27].

As to reproductive strategy, melon does not develop fruit by parthenocarpy or by self-pollination; it requires pollen transfer by animals [26]. Studies conducted in the Ceará on manual cross-pollination and open pollination (by bees) resulted in 98.3 percent and 75.7 percent fruit set (not necessarily mature fruit, only initiation), respectively [29]. However, the authors reported 100 percent abortion of fruit when flowers self-pollinate in *Yellow*® and *Piel de Sapo*® melon, but confirm fruit development using manual pollination, thus indicating that both types are self-compatible [30]. These results emphasize the importance of insect vectors for pollen transfer between flowers and plants.

In this context, studies on melon pollination in the region of Mossoró (Rio Grande do Norte) record the presence of bees, flies, butterflies and ant visitors of melon flowers [31]. According to observed insect behaviour patterns and frequency of visits, the authors conclude that the presence of Africanized honey bees (feral hybrid *Apis mellifera scutellata*) is essential for proper fruit production. Moreover, they observe that bee visits are more frequent in the morning, and note the presence of up to two individuals visiting a flower simultaneously.

In the same region, the present authors recorded bees, butterflies and flies as visitors of melon flowers (*Yellow*®, *Cantaloupe*® and *Galia*®) [30]. The visitation pattern of *A. mellifera* in dry or rainy season differs notably with regard to the frequency of bee visits. In relation to peak visitation, differences occur in different types of melon. For *Yellow*® and *Cantaloupe*®, most visits occur in the morning, while for *Galia*® the peak is between 14:00 and 15:00 hours during the rainy season, and between 10:00 and 11:00 hours during the dry season. In general, irrespective of melon type, hermaphrodite flowers are visited more than male flowers, and pollen foraging is more frequent in the morning, while visits for nectar collection occur throughout the day.

Studies performed in Ceará on bee foraging behaviour at *Yellow*® melon found that visits are concentrated in the morning, with more intense pollen collection, and without a preference for flower type [32]. The authors also commented that bees display flower fidelity in melon, visiting many flowers uninterruptedly.

Observations made at Mossoró in Rio Grande do Norte state, Pacajus, Ceará, Petrolina in Pernambuco state and Juazeiro in Bahia state, found that 12 insect species visit the flowers including bees, wasps, flies, butterflies and beetles [30]. Bees account for 58 percent of the total species, among which *A. mellifera* and *Xylocopa grisescens* visit all types of melon. The fly *Palpada vinetorum* (Syrphidae) occurs on three melon varieties, although at low frequencies. Additional floral visitors occur sporadically.

Studies in Juazeiro, Bahia, report that *A. mellifera* is a more frequent visitor in the morning and collects pollen mainly from 07:00 to 11:00 hours [25]. In Petrolina, Pernambuco, a comparison of the three melon cultivars showed different visitation peaks for *A. mellifera* on flowers of *Yellow*®, *Cantaloupe*® and *Piel de Sapo*® melons, from 11:00 to 12:00 hours, 10:00 to 11:00 hours and 15:00 to 16:00 hours, respectively [27]. With regard to the foraged floral resource, the authors mention that nectar collection is constant throughout the day, while pollen collection occurs largely in the morning. As for the flower type, hermaphrodite flowers usually receive more visits in *Yellow*® and *Piel de Sapo*® cultivars, while the opposite is found for *Cantaloupe*® when flowering.

7.2.4 Pollination service in family farming areas

As already stated, melon depends on pollinators to achieve adequate fruit set, yield, fruit quantity and quality [29, 33]. That melons often depend on honey bees for pollination is well recognized [34–41]. Various authors observe differences in the quantity and quality of fruit produced by natural cross-pollination related to honey bee foraging [42].

Studies on visitors of melon flowers come from various countries, with an almost exclusive record of *A. mellifera* as the main pollinator [26, 39, 43–46]. Three or four colonies/ha are recommended in areas where there is a pollination deficit [46–48]. In Brazil, honey bee colonies are employed for melon pollination in all monoculture centres of Mossoró and Açu, Rio Grande do Norte state, and Lower Jaguaribe and Ceará, with colony use ranging from two to four hives/ha, depending on other factors, such as the general abundance of insects and native plants in bloom [19]. Nevertheless, the same has not been observed in Petrolina, Pernambuco and Juazeiro, Bahia, where few farmers introduce honey bee hives. This may be related primarily to lack of knowledge regarding the importance of pollination for melon cultivation, with farmers still relying on natural pollinators in remnants of native vegetation (Caatinga). However, the expansion of agriculture and irrigated areas are hindering pollination services, with more malformed fruits and/or low fruit set each year.

The recommended use of managed pollinators now consists of one beehive for each 3 000 plants, depending on the density of planting. In commercial melon areas, yield increases by 40 percent when using this density, and fruit quality and financial gains are augmented [30]. However, the procedure should be executed with caution, given the proximity of crop areas and the potential risk of accidents generated in the area by honey bee colonies (some of which are explosively aggressive) (Figure 7.4c). It should also be noted that if such hive introduction increases pollination services to melon and other fruits (guava, coconut, lemon), it may also have negative impacts, such as the displacement of pollinators or pollen theft (removal without pollination) on a large scale, which can affect plant reproduction of both crops and native plants. A similar situation exists for plots of yellow passion fruit, which may be visited but not pollinated by honey bees [49].

Taking into account the above-mentioned issues, the addition of hives may not always advisable due to maintenance and other costs. As previously noted, most properties cover 6 ha, with 100 percent of the area used for cultivation (Figure 7.7a), thus a continuous presence of hives on the site is not feasible. In such cases, the renting of colonies for just the flowering period is probably the best strategy. Another advantage is that transport and maintenance remain the responsibility of the beekeeper.

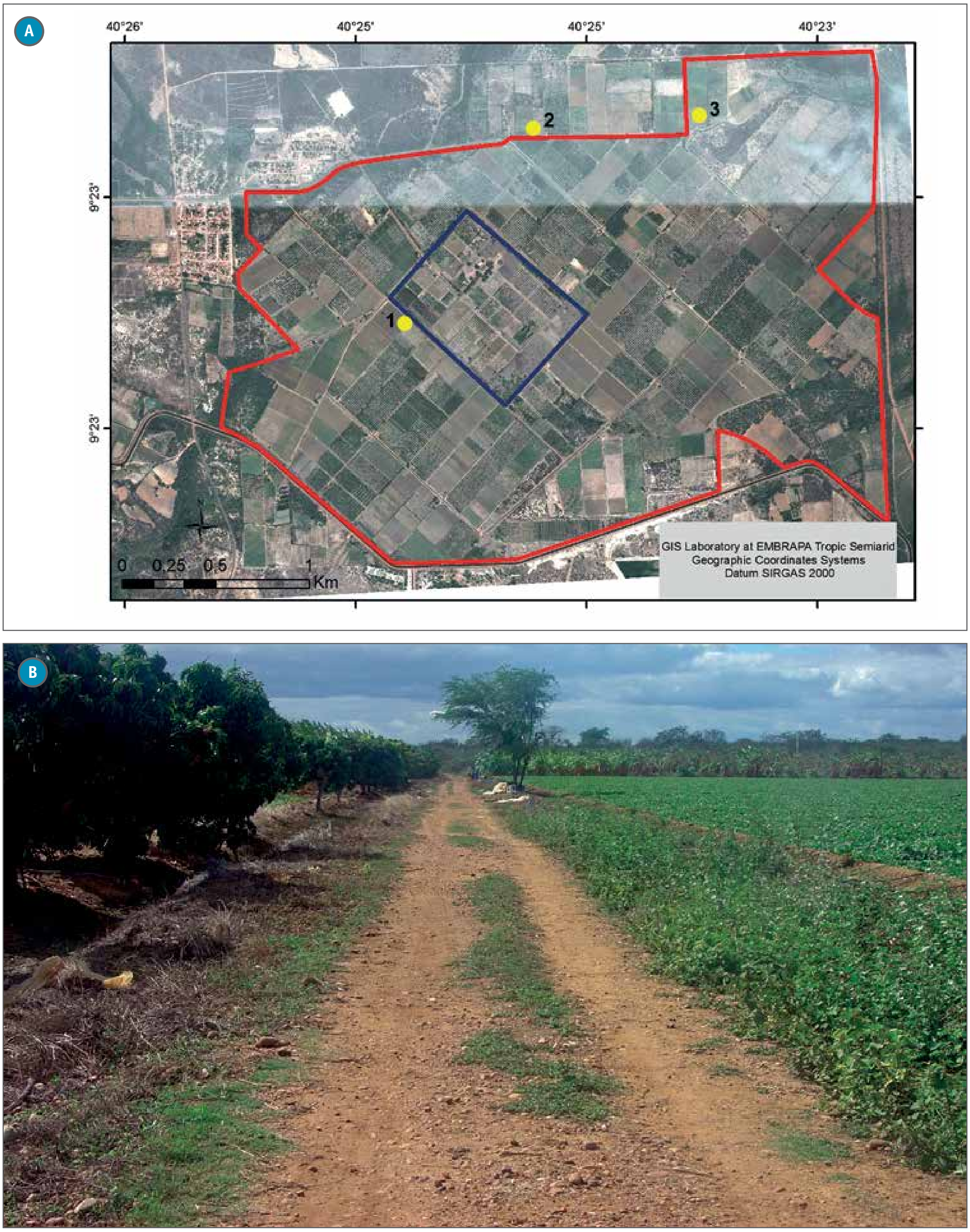
The introduction of hives in the cultivated field should be performed at the beginning of flowering, around the twentieth day after sowing or the sixth day from the initiation of flowering. Thus, colonies will be settled by the time the greatest numbers of hermaphrodite flowers are open, around the tenth day after flowering begins.

7.2.5 Conclusion

In the region studied, issues relating to pollination services remain little known among farmers and technicians, who are largely ignorant of the importance of pollinators for fruit production in general, and seldom bother to keep them at cultivation sites. Raising their awareness is therefore a key objective, so as to enable the adoption of other crop management practices that benefit pollinators, especially for melon cultivation. The dissemination of knowledge to increase awareness and local safety standards is imperative to minimize the risk of accidents, especially given the density of crops and the number of hives needed to ensure full pollination. The issue deserves special attention because if these rules are not obeyed and accidents do occur, the use of colonies in hives will become untenable and melon production in the region will suffer. Farmers, beekeepers, assistant technicians and others involved must be receive clear instruction and be made aware of the importance of complying with safety standards.

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

Figure 7.7
(A) SATELLITE IMAGE OF THE IRRIGATED PERIMETER OF MANDACARU (IN RED), IN JUAZEIRO, WITH PLOT 65 (NUMBER 3), AND (B) PARTIAL VIEW OF THE CROP AREA SHOWING THE SURROUNDINGS AND PROXIMITY BETWEEN CROP AREAS



Source: L.H.P Kiill, M.F. Ribeiro, K.M.M. Siqueira and E.M.S. Silva

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7.3 POLLINATION IN SOME KENYAN SMALLHOLDER CROPS

D.J. Martins

7.3.1 Hawkmoth and skipper butterfly pollination of papaya

Breeding system and fruit characteristics: Papaya is a fully dioecious plant species in which male (pollen bearing) and female (fruit bearing) flowers are generally found on separate plants. Papaya trees in cultivation are thus considered either "male" or "female". However, while the pistillate (female) flowers account for the majority of marketable fruit, the hermaphroditic, staminate flowers can self to produce smaller fruit that ripens less readily, but can be cooked and eaten. Cross-pollination of the pistillate flowers produces much more fruit and of higher quality. In papaya, the floral production of fragrance and floral visitor activity are highest after dusk and before 20:00 hours. Such a pattern indicates a moth pollination syndrome [2].

On individual trees, the male flowers are produced in larger numbers than female flowers, whether the tree's flowers are male, female or bisexual. They are produced in small bunches on short panicles originating from the trunk, between the leaf bases. Female flowers are borne on short stalks from the tree trunk, among the leaves. The fruit hangs down as it develops with ripe fruit generally located below the leaves. As a rule, only the male flowers offer rewards to pollinators in most of the Kenyan farms observed. This system is thought to form part of the "deceit pollination" phenomenon, in which female flowers benefit from the cues advertised to pollinators by male flowers [1].

This section presents information on papaya pollination in Kenya based upon work at two sites between 2003 and 2006 (the Kerio Valley and Machakos) [3, 4], with additional observations of floral visitors and pollen transport made at other Kenyan sites with smallholder farms growing papaya.

Field studies and pollinators: Moths such as hawkmoths and skipper butterflies are of great importance to papaya. Farmers who are dependent on the production and sale of this fruit crop need to understand, manage or conserve these species. The diversity and foraging patterns of these insects were assessed through direct observation (for general details on methods please see the sections on coriander and passion fruit, below). Additionally, for papaya, hawkmoths were observed after dusk using a dimmed flashlight (by placing masking tape over the glass). The time of each hawkmoth visit was recorded, along with the number of flowers visited and the identity of the visitor. Visitation data were recorded in 1 min intervals. Flowers were watched from about 18:00 hours until 20–30 mins after visitation by the last hawkmoth. Dark-coloured clothing was worn during observations and movement was limited so as not to startle the hawkmoths. Prior experience and the limited number of species at both sites [6] allowed for easy identification of the hawkmoths feeding at flowers [5]. Visitors that visited both male and female flowers were checked for pollen loads using the fuchsin gel method [7].

Dioecious papaya on smallholder farms in Kenya appears to require pollination to set fruit, in line with previous studies [8, 9]. Pollination is carried out by primarily crepuscular/nocturnal hawkmoths (Sphingidae) and skipper butterflies (Hesperiidae) (Table 7.2 and Figure 7.8).

Both groups of pollinators observed on papaya in Kenya are fast-flying, large and highly mobile insects. This makes them good pollinators. Pollination is effected primarily in an hour or so after dusk. This fairly narrow window of time allows hawkmoths to visit both male and female flowers, as they are able to quickly cover the distances between trees and plantations.

Table 7.2

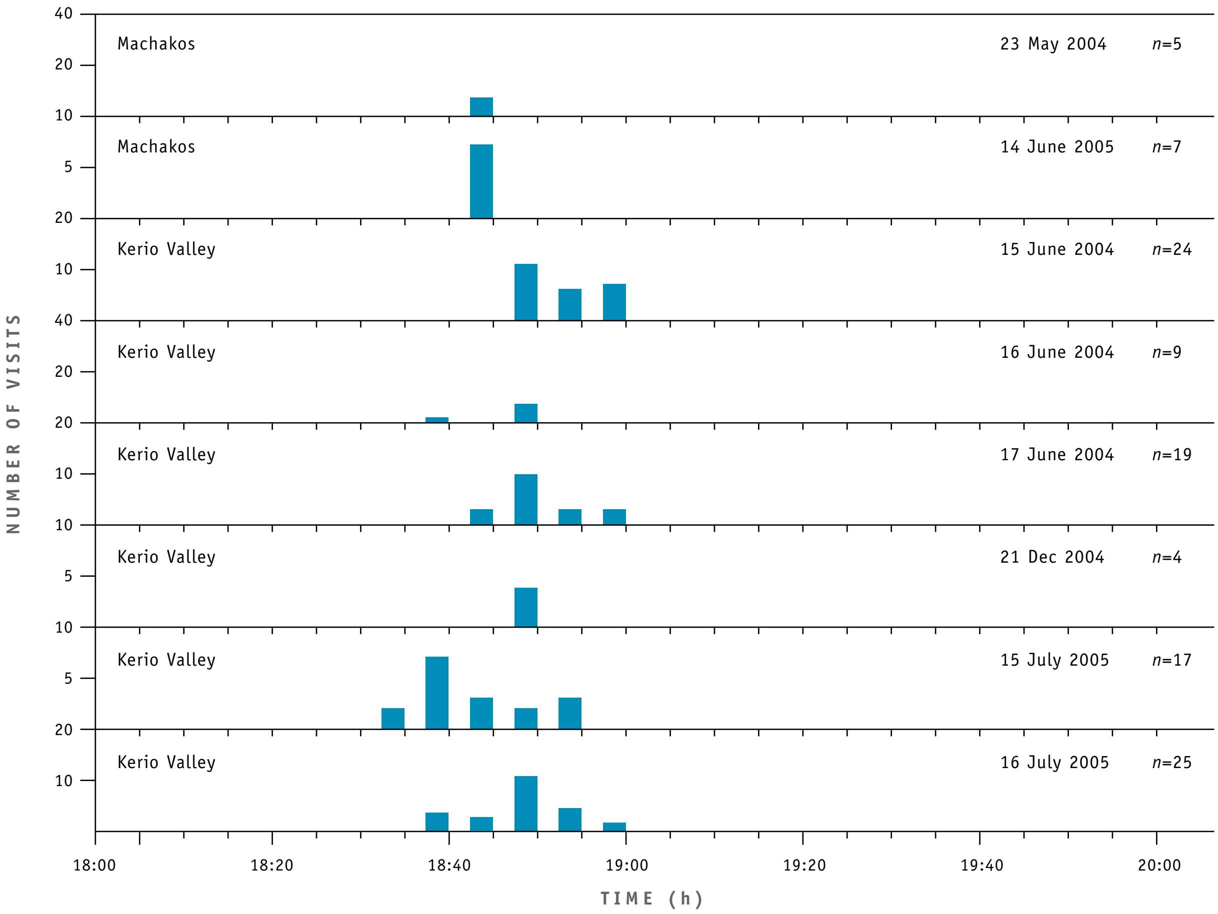
PAPAYA POLLINATOR DIVERSITY, DISPERSAL AND POLLEN TRANSPORT IN KENYA

VISITOR	VISITS: MALE FLOWERS, FEMALE FLOWERS, BOTH	DISPERSAL SCORE (SD)	POLLEN TRANSPORT
Blue bottle flies (Calliphoridae)	Female only	N/A	N/A
Fruit flies (*Didacus* sp.)	Female only	N/A	N/A
Apis mellifera	Male only	N/A	Low
Coeliades pisistratus (Hesperiidae)	Both male/female	1.3 (± 0.48)	High
Coeliades forestan (Hesperiidae)	Both male/female	1.4 (± 0.52)	High
Hippotion celerio (Sphingidae)	Both male/female	1.2 (± 0.42)	High
Agrius convolvuli (Sphingidae)	Both male/female	1.11 (± 0.31)	High
Daphnis nerii (Sphingidae)	Both male/female	1.3 (± 0.48)	High
Nephele comma (Sphingidae)	Both male/female	1.1 (± 0.32)	High
Sphingomorpha chlorea (Noctuidae)	Both male/female (uncommon)	2.2 (± 0.63)	High

Source: D.J. Martins

Figure 7.8

TOTAL HAWKMOTH VISITATION TO PAPAYA FOR REPRESENTATIVE EVENINGS FROM MACHAKOS AND KERIO VALLEY IN KENYA



Source: Reproduced with permission from Martins and Johnson, 2009 [4]

Habitat and pollination landscape: Based on two sites, a comparison was made of habitat types and quality to determine if they affected pollination and fruit set. Two main landscape features relate to hawkmoth availability: alternative nectar sources among wildflowers and availability of larval food plants. Such forage plants also serve as diurnal resting places for hawkmoths, which need sites for shelter during the day. The importance of hedgerows and natural vegetation adjacent to farms is thus useful for moths as well as other pollinators.

The main components of biodiversity contributing alternative resources to pollinators on papaya farming are various species of indigenous plants. Because farms are located along streams, the large trees growing in the riparian area constitute an important component of the agrobiodiversity on and around the farms. Large stands of *Acacia* trees are also protected around the farms and are used seasonally as a source of pods, fed to livestock and traded in the adjacent highlands.

Traditionally, the livestock enclosures and homesteads of the region, known as *bomas,* are encircled with a thorny fence or hedgerow to keep livestock in and deter predators at night. These hedgerows are often overgrown and covered by creepers including several *Ipomoea* species (Convolvulaceae) and *Cissus quadrangularis* (Vitaceae). The maintenance of thorny hedgerows in the settled small-scale farms alongside large numbers of free-ranging livestock is one of the main practices contributing to persistence of hawkmoths around the farms. Both *Ipomoea* and *Cissus quadrangularis* are larval host plants for *Agrius convolvuli* and *Hippotion osiris* – two of the more common hawkmoth pollinators of papaya.

Farmer knowledge and practices: Farmers in the Kerio Valley possessed varying levels of knowledge regarding the subject of papaya pollination. Some educated farmers were aware of the necessity for pollination, while others were unaware of the process. However, on most farms, "unproductive" male papaya trees are maintained, often because the farmer is imitating the practice of other farmers – and since larger farms with several male trees are more productive, this sets an example for smaller scale farms. At least some trees without fruit are necessary to ensure the availability of pollen, which can only be provided by a male, and therefore, fruitless tree.

The main practices carried out on smallholder farms in Kenya in relation to papaya pollination include:

- the maintenance of male trees on farms;
- the protection and encouragement of alternative nectar sources for pollinators;
- planting of larval food plants in hedgerows;
- protection of trees in surrounding bush and woodland areas.

Conclusion: The Kerio Valley is a high biodiversity area [10], where surrounding non-farm vegetation is rich in resources for pollinators. This is composed primarily of *Acacia tortilis* in woodland areas and a diverse bush vegetation of trees and shrubs in drier areas, including several species that flower at different times of year and provide nectar resources to hawkmoths outside farms. To adequately conserve pollination services for papaya (and many other crops), the pollinators need larval host/breeding sites, wild sources of nectar, and protection from exposure to pesticides and other chemicals. Existing land management strategies could be harnessed to incorporate pollinator conservation strategies. For example, fallow communal land is a widespread feature of subsistence farming in rural Kenya and such areas tend to be used to graze livestock. Accordingly, there is a strong community incentive to conserve areas of natural vegetation close to small-scale farms, which also afford pollinator habitats for moths and butterflies that pollinate papaya.

7.3.2 Honey bee pollination of irrigated dry season passion fruit

Fruit pollination on small farms in Kenya: A comparison of different local fruit produce demonstrates why passion fruit is rapidly gaining popularity in rural Kenya [11]. The fruit is sold for cash, used in the production of juice and exported [12]. Demand is high and farmers producing passion fruit have a ready market for their produce. This has led to the year-round cultivation of passion fruit in many small-scale farming areas.

The Kerio Valley constitutes a large extension of the Great Rift Valley system. Most of the passion fruit farming sites are located on the valley edges close to the western wall of the valley, from Iten and Tambach, running north and south for a few kilometres. Altitude in the valley ranges from 900 m in the Lake Kamnarok basin to over 2 300 m in adjacent highlands. Passion fruit is cultivated in all these areas, but appears to be most productive at around 2 000 m.

Rainfall is highly variable and patchy, and is strongly linked to an altitudinal gradient, with steep highland areas receiving more rain than the arid bushland and acacia woodland that dominate the valley floor and lower slopes. The mean annual temperature ranges from 14 °C in the highlands to 24 °C in the semi-arid lowlands. Annual rainfall in lower areas of the valley rarely reaches more than 400 mm, so long-term cultivation requires irrigation from streams originating in the highlands.

Farms are typically small, rarely more than 4 acres (< 2 ha), and are generally managed by one extended family. Women perform most of the day-to-day cultivating and weeding, while men tend livestock and prepare land before the rainy season. Seasonal crops include maize, beans and millets, as well as small orchards of mango, citrus, banana and papaya that are gathered locally for sale in towns and cities.

Table 7.3 shows the crop calendars for the three main pollinator-dependent fruit at this site: passionfruit, mango and papaya.

Table 7.4 shows the values of crops. The contributions of these three fruit crops to household income still needs to be studied. There are marked differences between the values at the site compared to commercial markets.

Pollination during dry season: The goal of this study was to look at the pollination of passion fruit outside of the principal growing, flowering and insect activity season in Kerio Valley. All observations were carried out at a small-scale highland farming system near the town of Iten on the western edge of the Kerio Valley in Marakwet County, Rift Valley Province, Kenya, where passion fruit is cultivated and harvested throughout the year. The main question asked was: "What insects are responsible for pollinating passionfruit in the dry season, given the extremely seasonal nature of this area and the importance of the crop for farmer income/household nutrition in the dry season?"

Table 7.3

CROP POLLINATION CALENDAR FOR MANGO, PAPAYA AND PASSION FRUIT, KERIO VALLEY, KENYA

CROP	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL MONTHS
Mango					X	X		X	X		X		5–6
Papaya	X			X	X	X	X	X	X	X	X	X	~ 10
Passion Fruit	X		X	X	X	X	X	X	X	X	X	X	~ 11

Source: D.J. Martins

Table 7.4

CROP VALUES ALONG THE VALUE CHAIN FOR MANGO, PAPAYA AND PASSION FRUIT, KERIO VALLEY, KENYA

CROP	VALUE AT HOUSEHOLD (KSHS)	VALUE AT HOUSEHOLD (USD)	VALUE AT MARKET (KSHS)	VALUE AT MARKET (USD)	UNIT
Mango	10	0.125	50–70	0.625–0.875	1 mango
Papaya	30	0.375	70–120	0.875–1.50	1 papaya
Passion fruit	35	0.438	100–200	1.25–2.5	1 kg

Notes: values as of December 2013. KShs = Kenya Shillings.

Source: D.J. Martins

Plants established by seedlings within small-scale farms were monitored, and individual plants were used as the unit for observation with a single flower used for collecting finer scale visitation data. Observations and experiments were carried out in December 2013 and January 2014 during flowering of plants in the dry season. To determine the potential pollinating role of flower visitors, flowers on ten separate plants on separate vines were bagged at the bud stage to exclude pollinators.

The study plants were randomly selected from among different patches. Observations were carried out from morning at around 07:00 hours until 17:00 hours over 30 days. This diurnal observation time period corresponds with the main activity patterns of the generalist flower-visiting diurnal insects in the dryland habitat [13, 14] and floral anthesis, based on pilot observations made at the beginning of the study. Plants were observed from a short distance (~ 1 m) so as not to disturb the visitors. The identity of visitors, duration of visits and movement between individual flower heads were recorded. The flower-visitation pattern and data analyses were conducted using Excel and "R" software.

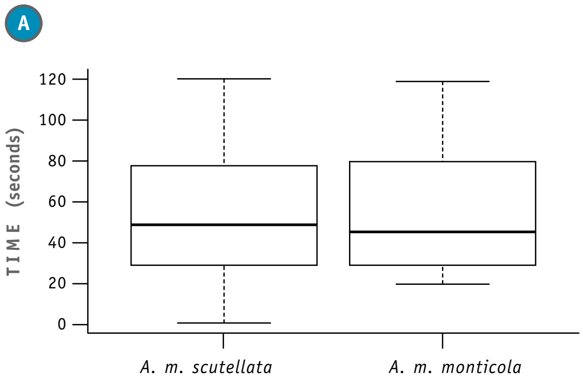
A small number of flower visitors were also captured by netting near flowers. These were checked for pollen load using the fuschine gel method [7]. Pollinators were scored for transport of pollen (high or low). High pollen carriers were those with > 100 grains of pollen observed on the slide, while low carriers were those with < 20 pollen grains.

Movement by pollinators was also recorded, with movement between patches scored on a scale of 1 to 3 (1 = disperses regularly between patches, 2 = limited dispersal and 3 = no dispersal). Pollinators were not captured on the flowers under study to avoid influencing recorded visitation rates. Pollinator visitation rates were also measured by following individual pollinators for ca. 5 to 10 minutes and counting the total number of flowers visited before the pollinator left the individual plant or patch under observation.

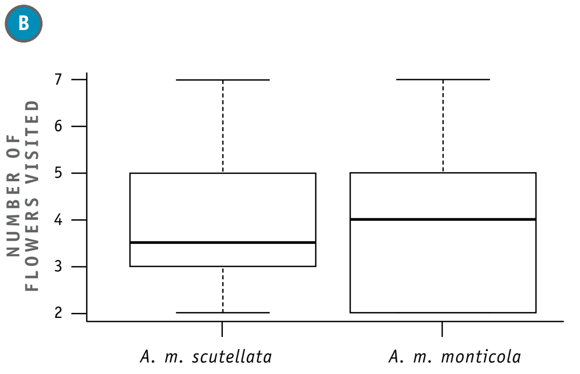
Pollination by two local honey bees: As with previous reviews of crop pollination [8, 9, 14–21], passion fruit was found to be dependent on pollinators and was visited/pollinated by two different subspecies of honey bees at this site (the common honey bee, *Apis mellifera scutellata* and the mountain honey bee *Apis mellifera monticola*) (Figure 7.9). In contrast with previous studies and observations made in other parts of East Africa, carpenter bees (*Xylocopa* spp.) were not observed among flower visitors. As this was the dry season, passion fruit was cultivated using irrigation. At other times of year, carpenter bees are more common and visit crops in this region.

Figure 7.9

(A) MEAN DURATION OF TWO HONEY BEE SUBSPECIES VISITS TO FLOWERING PASSION FRUIT AT ITEN, KERIO VALLEY, KENYA (B) MEAN NUMBER OF FLOWERS VISITED BY HONEY BEE SUBSPECIES ON PASSION FRUIT AT ITEN, KERIO VALLEY, KENYA



Note: Data from December 2013 to January 2014.



Note: Data from December 2013 to January 2014.

Source: D.J. Martins

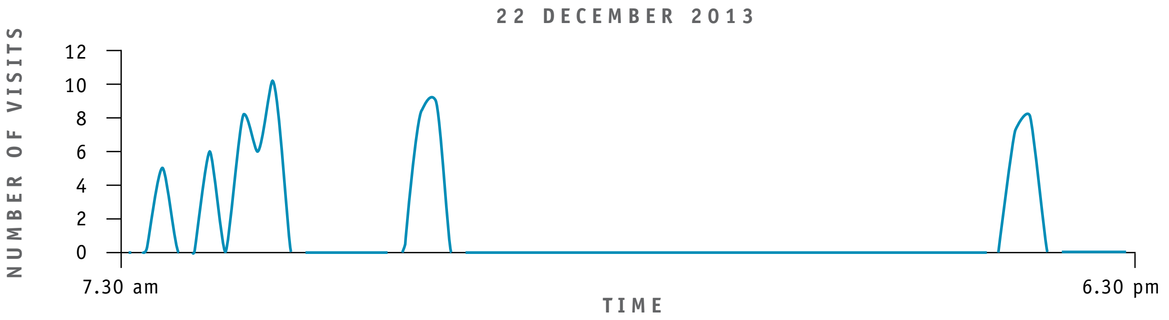
Honey bee visits to the flowers averaged just under a minute (Figure 7.9), and both pollen and nectar were collected by the bees. Visitation over time was concentrated in the morning, with a second smaller peak in the afternoon (Figure 7.10). This pattern is consistent with dry season foraging observations of honey bees in East Africa. Both honey bee subspecies visited on average four flowers during a foraging trip in the early morning hours, before leaving the plant being observed (Figure 7.9b).

In terms of fruit set, this study proved consistent with previous work showing that passion fruit benefits from pollinators [22, 23] because no bagged flowers set fruit. The behaviour and interactions among honey bees appear to influence successful pollination of passion fruit. While not directly quantified, honey bees made contact with the stigma of the flowers more frequently when more than one individual (typically two or three) were foraging on the flowers (see Figure 7.9b). This outcome needs to be studied in detail because of the implications for future managed pollination of the crop.

Conclusion: Understanding how pollinators perform across different growing seasons is important in small-scale farming systems undergoing intensification. This study found that honey bees can serve as pollinators of passion fruit, and underscores the importance of bee diversity in pollination [24, 25]. The two different honey bee subspecies visiting passion fruit originate

Figure 7.10

VISITATION RATES OF BEES TO A SINGLE FLOWERING PASSION FRUIT PLANT AT ITEN, KERIO VALLEY, KENYA ON 22 DECEMBER 2013



Note: Counts of pollinators made at 10-minute intervals.

Source: D.J. Martins

Table 7.5

DISPERSAL AND POLLEN TRANSPORT SCORES FOR HONEY BEES AT PASSION FRUIT

VISITOR	NUMBER OF RECORDS	DISPERSAL SCORE (SD)	POLLEN TRANSPORT
A. m. scutellata	42	1.24 (± 0.43)	High
A. m. monticola	18	1.22 (± 0.42)	High

Source: D.J. Martins

from both managed and wild honey bee colonies at the site. The mountain honey bees are likely to have arrived in this area from the higher altitude areas of the Cherangani Hills; thus it may be important to protect pollinator habitats at a landscape level.

7.3.3 Native insect and bee pollination of coriander

Crops from "dhania" in mixed farming systems: Coriander (*Coriandrum sativum,* Apiaceae), also commonly known as cilantro, is an important spice crop widely cultivated in the tropics of the Old World. In East Africa, coriander is commonly known as "dhania" in Swahili. Coriander is cultivated both for sale as a fresh herb, as well as for its seeds, which are sold as a seasoning/spice either whole or processed into a powder. Coriander in Kenya is grown primarily by small-scale farmers in mixed farming systems. It is widely cultivated in almost all regions of the country and provides small-scale farmers with both income and herbs for household use. All coriander cultivation is performed by sowing seeds, periodically harvesting fresh leaves and stems, and then eventually harvesting seeds.

Coriander is popular in Asian cuisine, the Middle East, Horn of Africa/Eastern Africa, North Africa and the Mediterranean. Globally, coriander is considered an important commercial spice/seed and production is estimated annually at 600 000 tonnes, mostly within Asia [26]. However, such trade statistics frequently overlook small-scale production, consumption and use at local level. Coriander is growing in popularity and its consumption is increasing, especially due to its association with health benefits both as an antioxidant and as a means to improve insulin function [27, 28].

Field studies on pollination: Previous studies of coriander pollination have been performed primarily in South Asia and demonstrate the role of bees (including honey bees) and other insect pollinators in augmenting seed set [29–33] along with yield and quality [34, 35]. A study in the Assiut area of Egypt finds both wild bees and honey bees involved in coriander pollination [36]. Therefore, coriander represents an example of a pollinator-dependent crop in which seeds resulting from pollination are not only sown but also consumed and traded. As a fast-growing annual, the seed is essential for small-scale farmers to cultivate coriander. The aim of this study was to document the floral visitors and pollination system of coriander in Turkana. The main questions were: "What pollinator taxa visit the flowers and what are their patterns of visitation, pollen dispersal and efficacy as pollinators?"

All observations of coriander were carried out in a small-scale riverine farming system around the Turkana Basin Institute at Nachekichok, South Turkwel (03°08' N, 35°52' E) in Turkana County, Rift Valley Province, northern Kenya. Patches of plants established by direct seeding were monitored and used as the unit for observation with a single umbelliferous flowering head being used for collecting finer scale visitation data. Observations and experiments were carried out in March 2012 during flowering. To determine the potential pollinating role of flower visitors, flowering heads on ten plants in separate patches were bagged at the bud stage to exclude pollinators.

The study plants were randomly selected within different patches. Observations were carried out from approximately 08:00 hours to 17:00 hours over ten days during March 2012. This observation time period corresponds with generalist flower-visiting diurnal insects in the dryland habitat [13, 14] and peaks during floral anthesis, based on pilot observations made at the beginning of the study. Plants were observed from a short distance (2 or 3 m) so as not to disturb the visitors. The identity of visitors, duration of visits and movement between individual flower heads were recorded. A small number of flower visitors were also captured by netting near flowers. These were checked for pollen load using the fuschine gel method [7]. Pollinators were scored for transport of pollen (high or low). High pollen carriers were those with > 100 grains of pollen observed on the slide, while low were those with < 20 pollen grains. Data analyses were conducted using Excel and "R" software.

Movement by pollinators was also studied. Movement between patches was scored on a scale of 1 to 3 (1 = disperses regularly between patches, 2 = limited dispersal and 3 = no dispersal). Pollinators were not captured on flowers to avoid influencing recorded visitation rates. Pollinator visitation rates were also measured by following individual pollinators for approximately 5 to 10 min and counting the total number of flowers visited before the pollinator left the patch or area.

Visitor and pollinator diversity: Not surprisingly [8, 9], coriander depends on pollinators and was visited/pollinated by a number of different insects in Turkana (Figures 7.12). Three different bee genera (*Amegilla, Ceratina* and *Hypotrigona*), wasps (primarily cuckoo wasps, Chrysididae, but also a small number of unidentified spp.) and lycaenid butterflies are abundant. The most abundant visitor, the bee *Ceratina*, comprised 65 percent of all insect visitors, followed by small stingless bees, *Hypotrigona* (12.6 percent), wasps (10.8 percent), *Amegilla* (10.2 percent) and lycaenid butterflies (1.2 percent). The most effective pollen disperser between different individual plants is evidently *Ceratina*, followed by *Amegilla, Hypotrigona* and wasps. Lycaenid butterflies are poor dispersers (Table 7.6). The three bee genera have high pollen transport scores, while neither wasps nor lycaenid butterflies carry much pollen. Because bees are hairier and better adapted to transport pollen, and also contact anthers, they likely pollinate coriander at this site.

Table 7.6

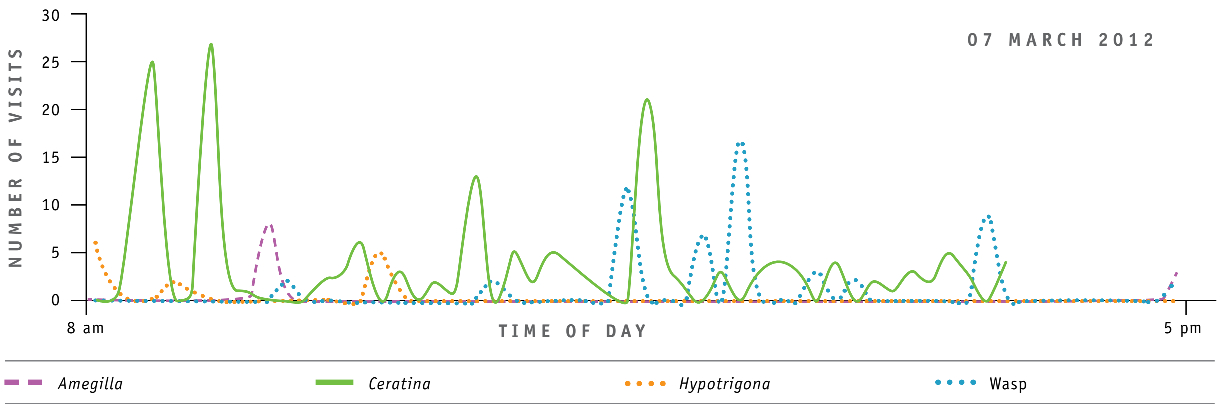
POLLINATOR DISPERSAL SCORES AMONG INDIVIDUAL FLOWERING PLANTS, FROM 663 OBSERVATIONS MADE OVER TWO DAYS IN MARCH 2012

VISITOR	NUMBER OF RECORDS	DISPERSAL SCORE (SD)	POLLEN TRANSPORT
Amegilla	68	1.2 (±0.58)	High
Ceratina	431	1.18 (±0.38)	High
Hypotrigona	84	1.39 (±0.49)	High
Wasp	72	1.82 (±0.95)	Low
Butterfly	8	2.38 (±0.74)	Low

Source: D.J. Martins

Figure 7.11

VISITATION RATES OF INSECTS TO A SINGLE FLOWERING UNIT (ONE UMBEL) OF CORIANDER AT SOUTH TURKWEL, TURKANA, KENYA ON 7 MARCH 2012



Notes: Data from observations made in March 2012. Counts of pollinators made at 10-minute intervals during the observation period.

Source: D.J. Martins

The patterns of insect visitation to flowers indicate that bees and wasps spend less time in a single patch (45 seconds to 1 min) than butterflies (~ 4 mins) (Figures 7.13). This indicates that bees acquire pollen as they rapidly move around the patch, which may contribute to their highly effective role in cross-pollination.

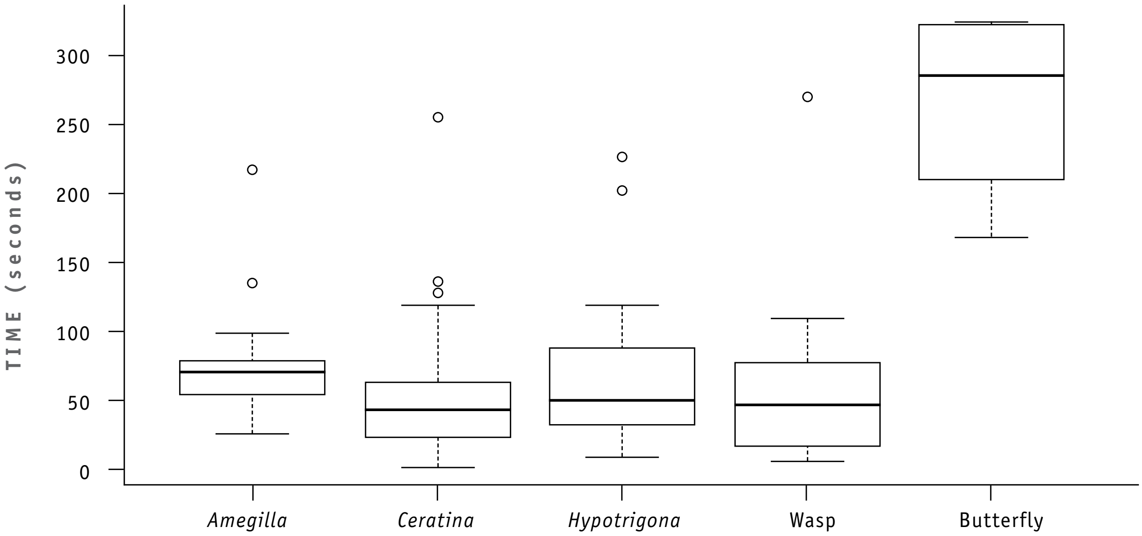
Conclusion: The observation that bagged flowers produce very little seed, in agreement with all past studies of coriander (and also dill), indicates that the plant depends on insects for pollination and also outcrossing. Pollinator visitation patterns over a whole day of observation also supports the conclusion that pollination services are associated with diversity of pollinators (Figure 7.14). As can be seen here, different pollinators visit at different times of day, with *Amegilla* for example, more active in the morning and evening, and *Ceratina, Hypotrigona* and wasps active throughout the day. Having different species of pollinators available is important for a fast-growing, synchronously flowering crop like coriander, as different seasons and weather conditions will mean that different insects may well serve as pollinators.

It is clear from a wide range of studies that wild bees are important crop pollinators, and this holds true in the case of coriander in northern Kenya. Although the suite of bee species pollinating this crop was not very large, it often varies from site to site. For example, a recent study of coriander pollination in the Mitidja area of Algeria found both honey bees (*Apis mellifera*) and six different species of wild bees (*Andrena*) serving as pollinators [36].

Because many farmers also save coriander seeds both for consumption and replanting, the role of pollinators is essential not just for production, but also for continuity of the crop and the lives and livelihoods of small-scale farmers.

Figure 7.12

MEAN DURATION OF DIFFERENT POLLINATOR TAXA VISITS TO A SINGLE PATCH OF FLOWERING CORIANDER AT SOUTH TURKWEL, TURKANA, KENYA

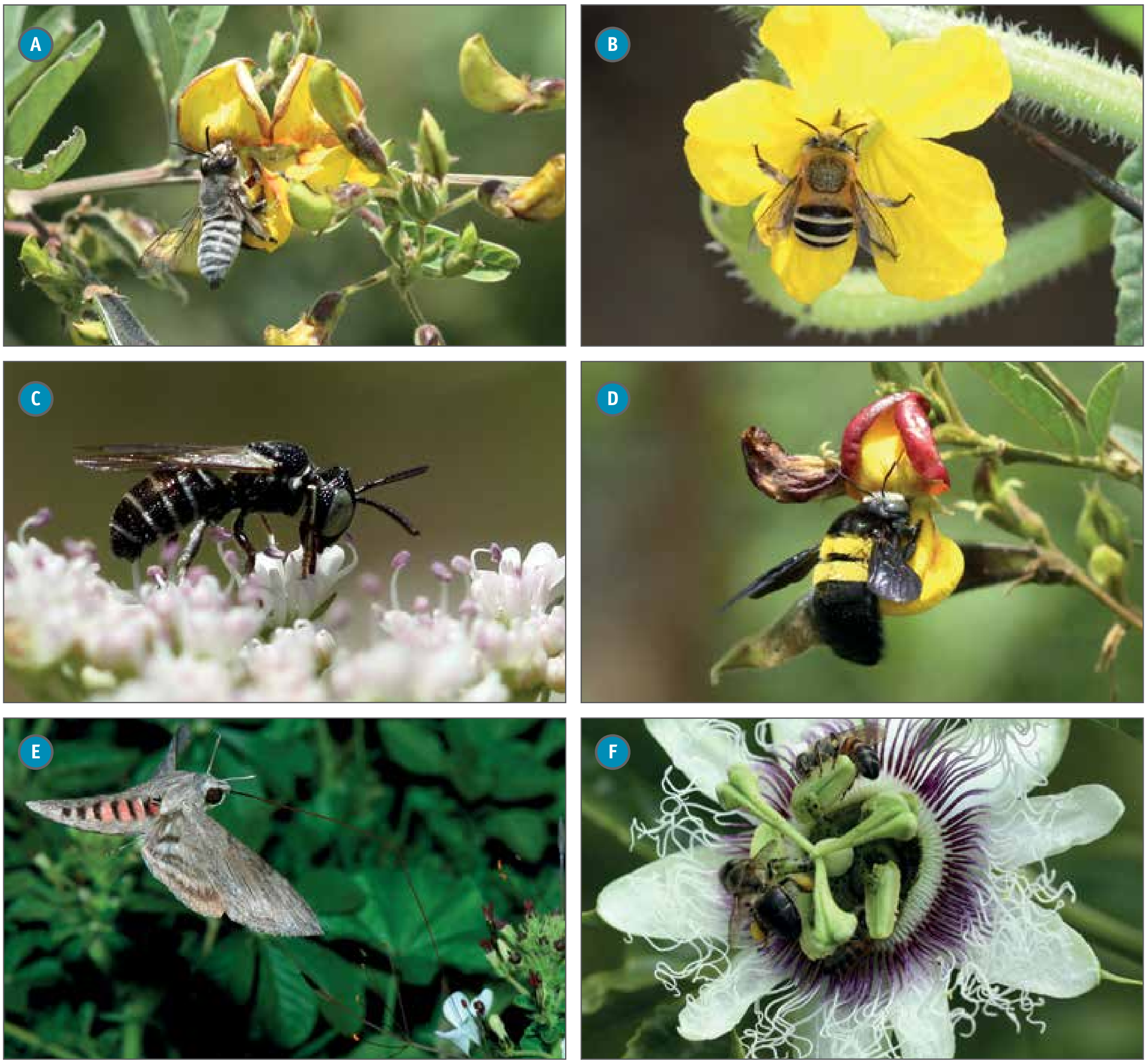


Note: Data from observations made in March 2012.

Source: D.J. Martins

Figure 7.13

POLLINATORS VISITING FLOWERS ON KENYAN FARMS: (A) *MEGACHILE* ON PEA FLOWER; (B) *AMEGILLA* ON WATERMELON FLOWER; (C) *CERATINA* VISITING CORIANDER; (D) *XYLOCOPA* ON PEA; (E) HAWKMOTH VISITING GYNANDROPSIS; AND (F) TWO SUBSPECIES OF *APIS MELLIFERA* VISITING PASSION FRUIT FLOWER



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7.3.4 Native bee pollination of eggplant

Eggplant (*Solanum melongena,* Solanaceae), also known as aubergine, is an important crop widely cultivated in the tropics of the Old World. In East Africa, eggplants are commonly known as brinjals or "bringania" in Swahili. Eggplant in Kenya is grown primarily by small-scale farmers in mixed farming systems situated in a wide range of climatic zones, ranging from coastal and dryland areas to highlands. Eggplant provides small-scale farmers, especially women farmers, with both income and food for household use. Eggplant cultivation is performed by sowing seeds or transplanted seedlings and then harvesting the fruits from the same plants over a relatively long period typically lasting several months.

Eggplants are thought to have originated in Asia and were domesticated there, primarily in India [38, 39]. They are popular in Africa, Asia, the Middle

East and the Mediterranean. Globally, eggplant is considered an important commercial species with production estimated at ~ 2 000 000 tonnes annually, mostly within Asia [40].

Field studies on pollination: Previous studies of eggplant pollination clearly demonstrate the role of bees in fruit production. Being a solanaceous species, pollinators are essential as eggplant is "buzz-pollinated" [41]. Studies in greenhouses, tunnels and open pollination systems have revealed the dependence of eggplant on pollinators [42–45], while a detailed study in southern Kenya showed that eggplants benefit from wild bee pollinators able to manipulate and "buzz" the flowers releasing pollen [46]. Thus, eggplant is an example of a pollinator-dependent crop where an absence of pollinators results in zero to very low yield.

As a long-lived, semi-perennial plant, eggplant's pollinators are essential for small-scale farmers to cultivate the crop. The aim of this study was to document floral visitors and the pollination system of eggplants in Turkana. The main questions were: "What pollinator taxa visit the flowers and what are their patterns of visitation, pollen transfer and efficacy as pollinators?"

All observations of eggplant were carried out in a small-scale riverine farming system around the Turkana Basin Institute at Nachekichok, South Turkwel (03°08' N, 35°52' E) in Turkana County, Rift Valley Province, northern Kenya. Patches of plants established by direct seeding were monitored and used as the unit for observation, with a single flowering plant being used for collecting finer-scale visitation data. Observations and experiments were carried out in March 2012. To determine the potential pollinating role of flower visitors, flowering heads on ten plants in separate patches were bagged at the bud stage to exclude pollinators.

The study plants were randomly selected within different patches. Observations were carried out from morning at approximately 08:00 hours to 17:00 hours over 20 days during March 2012. This observation time period corresponds with generalist flower-visiting diurnal insects in the dryland habitat [13, 14] based on pilot observations made at the beginning of the study. Plants were observed from a short distance (2 or 3 min), so as not to disturb the visitors. The identity of visitors, duration of visits and movement between individual flower heads were recorded. A small number of flower visitors were also captured by netting near flowers. These were checked for pollen load using the fuschine gel method [7]. Additional methods follow those used for the preceding studies of coriander in Turkana and passion fruit in the Kerio Valley.

Figure 7.14

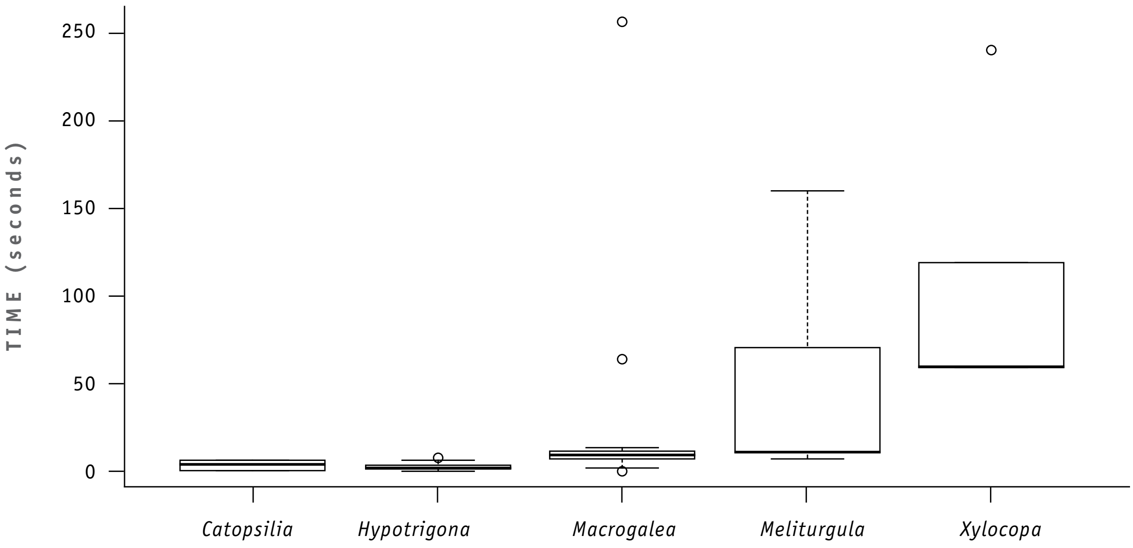
EGGPLANT FRUIT HARVEST AND POLLINATORS AT FLOWER: *HYPOTRIGONA* AND *APIS MELLIFERA*

Visitor and pollinator diversity: Consistent with other studies [41, 43–46], eggplant depends on pollinators and is visited/pollinated by a number of different insects in Turkana. Four different bee genera (*Hypotrigona, Xylocopa, Macrogalea* and *Meliturgula,* see Figure 7.16) and a very small number of pierid butterflies (all one species, *Catopsilia florella*) visit the flowers. Bagged flowers result in zero fruit set. The most abundant visitors, the carpenter bees, *Xylocopa* spp. account for 43 percent of all flower visits, followed by *Macrogalea* (29.1 percent), *Meliturgula* (13.1 percent) small stingless bees, *Hypotrigona* sp. (12.7 percent) and the butterfly *Catopsilia florella* (1.3 percent) out of a total of 671 visits recorded over five days. The most effective pollen dispersers are three native bee species, but not the tiny stingless bee *Hypotrigona* or butterfly, which are poor pollen dispersers (Table 7.6). The small stingless bees perch on flowers, where they gather pollen previously released by other bee visits. Observations of the butterflies suggest they visit particularly "showy" flowers, find no nectar and then immediately depart. Only three bees (not stingless bees) are likely good pollen dispersers (Table 7.6). The three larger bee species (*Macrogalea, Meliturgula* and *Xylocopa*) "buzz" flowers to release pollen, while moving frequently between different individual plants and transporting large amounts of non-scopal pollen. They can therefore be considered the main pollinators of eggplant at this site.

The patterns of insect visitation to flowers indicate that butterflies and small stingless bees spend on average less time on a single plant (just a few seconds) than *Macrogalea* (20 seconds), *Meliturgula* (30 seconds) and *Xylocopa* (50 seconds), but note there are outliers (Figure 7.16). This indicates that the larger bees acquire pollen from flowers by spending more time buzzing, then moving around the flower scraping up the pollen that has been released. Observations of pollinator activity over a whole day further indicate that bees are the primary pollinators of eggplant at this site, as they visit across time. The difference in visitation patterns between the two days should be noted (Figure 7.17).

Figure 7.15

MEAN DURATION OF DIFFERENT POLLINATOR TAXA VISITS TO A PATCH OF FLOWERING EGGPLANT AT SOUTH TURKWEL, TURKANA, KENYA

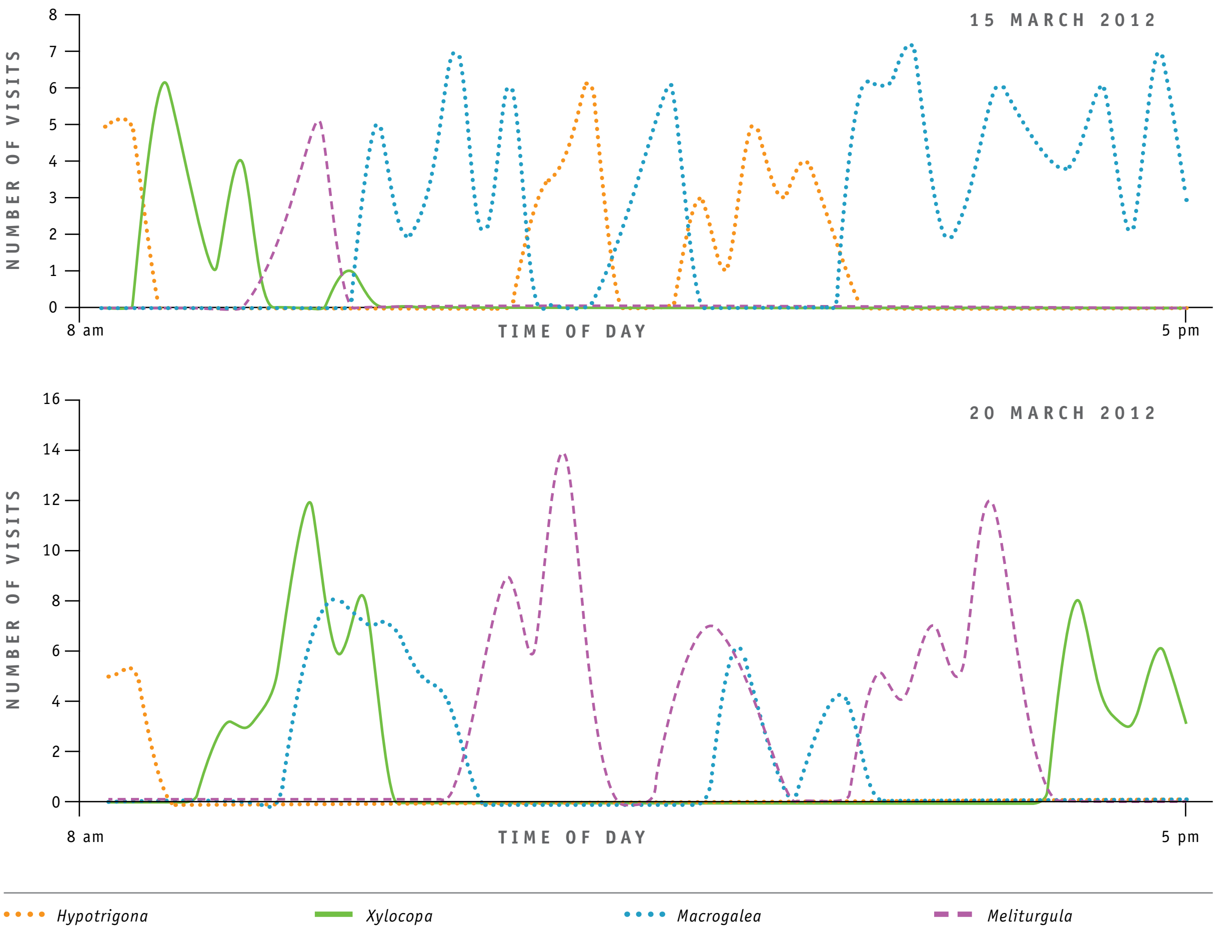


Note: Data from observations made in March 2012.

Source: D.J. Martins

Figure 7.16

VISITATION RATES OF INSECTS TO A SINGLE FLOWERING PATCH OF EGGPLANT AT SOUTH TURKWEL, TURKANA, KENYA ON 15 AND 20 MARCH 2012



Note: Counts of pollinators made at 10-minute intervals during the observation period.

Source: D.J. Martins

Conclusion: The observation that bagged eggplant flowers produce no fruit indicates that the plant depends on bees for pollination and also outcrossing. Pollinator visitation patterns over a whole day of observation reveal a diversity of pollinators (Figure 7.17). The different pollinators visit at different times of day, with *Xylocopa* spp. more active in the morning and evening, and *Macrogalea* and *Meliturgula* active throughout the day. Having different species of pollinators available is undoubtedly important for a semi-perennial crop such as eggplant, where yields are continuous over several months once the plants have reached maturity. Notably, *Macrogalea* may be considered for development as a managed pollinator species for utilization in greenhouses and intensive horticulture.

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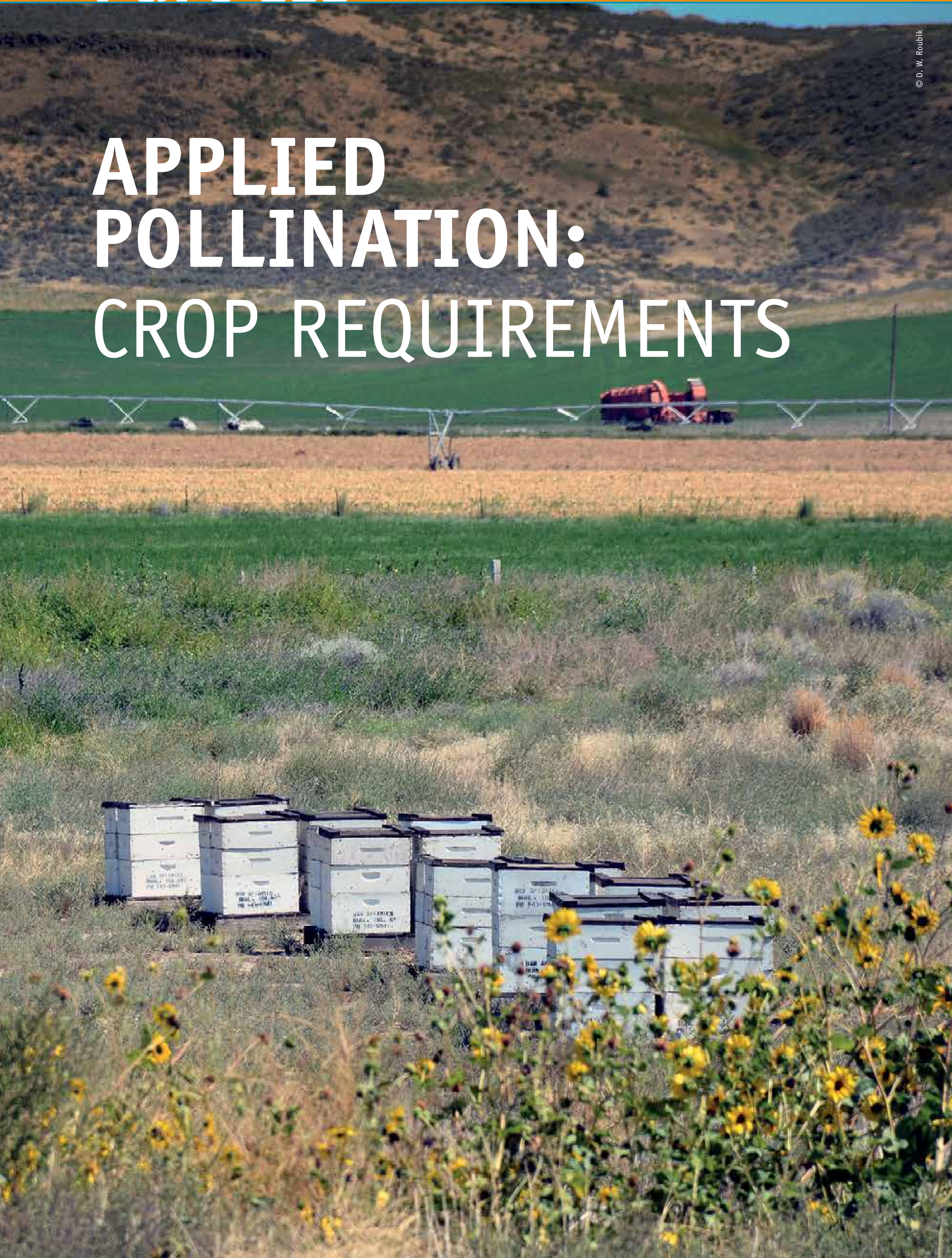
Part III

APPLIED POLLINATION: CROP REQUIREMENTS



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Chapter 8

APPLIED POLLINATION IN TEMPERATE AND SUBTROPICAL AREAS

R.P. Macfarlane

In 1995, R.P. Macfarlane made an effort to review temperate zone crops known to be pollinated by bees. While the text drew on available information worldwide, the primary focus was New Zealand farms. For this edition, new sections on berries and onion seed production have been added. The crop groups summarized in this chapter focus on major temperate crops, which are also grown in cooler regions within the tropics. The plant families include those of crop, weed and indigenous (native) plants. Shrubs, vines, herbs and trees are covered. These species flower from spring to autumn, and their flowering period is short to fairly long. The groups represent the variation in floral structure and breeding system found in crops pollinated primarily by insects or having a mixture of wind/insect and bird/insect pollination. Crops from less-specialized plant families, which are often suited to general pollinators, are considered first. Crops that are not well pollinated by honey bees are reviewed in more detail to illustrate the subtleties often involved. More detailed information comparisons regarding the following pollination notes are given in the selected crop studies presented in section 9.3.

Accounts of crop pollination in temperate climates are provided elsewhere by Delaplane *et al*. [1], Delaplane and Mayer [2], Mader *et al*. [3] and McGregor [4] for North America and Europe; Batra [5], Kapil and Jain [6], Ahmad [7] and Dafni [8] for the Indian subcontinent and the Middle East; Free [9] and Abrol for the world [10]; and Crane and Walker [11], Purseglove [12, 13] and Roubik [14]. Resources available online include publications by Free [9], Roubik [14] and Mader *et al.* [14], as well as notes by various authors accessible at www.pollinator.ca/bestpractices. The general references to this chapter include illustrations of flower morphology, valuable bibliographies and accounts of some regional pollinators, their effectiveness and the need to control insecticide use on crops. In addition, Hartman *et al.* provide basic agronomic notes on such crops, including fruit thinning or alternate bearing in kiwi fruit, peach, nectarine, plum, pear, apple, mandarin and olive trees [15].

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8.1 ERICACEAE

(4 250 species, 124 genera)

J.H Cane

8.1.1 Cranberry and lingonberry

The American cranberry (*Vaccinium macrocarpon* – Ericaceae) grows wild in the northeastern United States and adjacent Canadian maritime provinces [1]. Lingonberry (*V. vitis-idaea*) is circumpolar in distribution [2]. Both species are prostrate, long-lived, rhizomatous evergreens that grow as woody trailing stems or sub-shrubs. Populations of the berries form tangled clonal mats on sandy, acidic, often-peaty soils that have shallow water tables. The tart red fruits of both species are sources of dietary vitamin C, long eaten by native peoples. Crews of northern sailing ships were provisioned with cranberries to prevent scurvy. Berries were stowed onboard in 100 lb barrels, a common measure still used today.

The preparation of bogs or "beds" to grow cranberries was first commercialized 150 years ago, in New Jersey [1]. It remains an exacting and expensive practice. Today, 94 percent of the world's cultivated cranberries are grown in the United States (370 000 metric tonnes) and Canada (126 000 tonnes), mostly on smallholdings (averaging 20 ha) in Wisconsin, Massachusetts, Quebec, New Jersey and Washington. In Chile, the annual harvest is 20 000 tonnes, while several European countries produce smaller amounts. Most varieties are simple wild selections [3], but in recent decades cross-breeding has yielded superior cultivars. World production continues to increase, with the majority of lingonberry production coming from wild harvests in Finland, Germany, Sweden, and Newfoundland, Canada (36 000 metric tonnes), although commercial cultivation is increasing.

8.1.2 Floral biology of cranberry

The white flowers of cranberry are borne on short (5–8 cm) upright stems above the mat of vegetation. Plants typically produce many upright shoots with 4–7 flowers each, for an estimated density of 40–50 million flowers per cultivated hectare [4, 5]. Flowering occurs around or soon after midsummer. Each pendant flower bears four strap-like recessed petals and a narrow staminal column, surrounding a central pistil, and resembling a peeled banana. The style elongates such that when the stigma becomes moist and receptive, it extends beyond the tips of the anthers. Cranberry flowers are hermaphroditic. Pollen is shed through paired pores at tubular tips of the anthers, with about 7 000 tetrads per flower – four grains comprise a tetrad [6]. As with other Ericaceae, cranberries are unusual among buzz-pollinated flowers because they also secrete nectar between the anther bases. Nectar production varies somewhat by cultivar, ranging between 300–450 microgram of sugar in a 1–2 microlitre droplet (about 23 percent dissolved solids before evaporation), and it is unresponsive to soil fertility [7].

8.1.3 Pollination of cranberry

Individual plants (and clones) of cranberry are self-fertile, but manifest some inbreeding depression [8]. The flowers are not self-pollinating. Even physical jostling of the flowers, for example by wind, yields only a few small fruit [9]. Ripe berries contain up to 35 tiny black seeds – about one seed for every pollen tetrad deposited on a stigma. Pollen tetrads mostly germinate to produce three to four pollen tubes, but there is attrition in the style before tubes reach the ovaries [10]. Fruiting, berry size and seed set are decelerating curvilinear functions of stigmatic pollen load [11]. Fruit set is maximized at just eight seeds.

8.1.4 Pollinators of cranberries

Bees always probe cranberry flowers for nectar. Some foragers will audibly sonicate or buzz the staminal column, the resulting vibration ejecting pollen onto bees as they hang from the pendant flower. Wild worker bumblebees (*Bombus*) are very effective cranberry pollinators, typically delivering sufficient pollen to set a large fruit on the first visit [11]. They are often the most numerous group among the native bees at farmed cranberries, joined by diverse species of non-social ground-nesting *Andrena* and several species of *Osmia, Megachile, Melitta americana* and halictid bees

[12–14]. Wild bees may be sufficient for pollination at many smaller bogs, but are too sparse for pollination on larger bogs. On one Chilean farm, bumblebees did not visit cranberry at all (Cane, unpublished). The ground-nesting leaf-cutting bee *Megachile addenda* is often abundant in cranberry bogs of Massachusetts, USA [14]. In New Jersey, USA, this bee was found nesting in a large but short-lived aggregation in the sandy soil of a production bed [6]. In that setting, it regularly collected cranberry pollen to provision its brood cells, accomplished by stroking the cranberry flower's anthers with its legs. *Megachile addenda* is an effective cranberry pollinator, producing a calculated 1 400 cranberries per foraging day [6]. This polylectic bee was not previously identified on cranberry blooms. The smaller-bodied alfalfa leaf-cutting bee, another floral generalist, was tried as a managed pollinator, but only took nectar at cranberry flowers and proved a poor pollinator [15]. In contrast, the more specialized visitor of other *Vaccinium* flowers, *Osmia ribifloris*, demonstrated promise for managed pollination [16] and effectively pollinates blueberries [17]. When tried as a cranberry pollinator, however, females proved unable to learn how to work the flowers for pollen, and thus fail to either pollinate flowers or nest near the plants (Cane, unpublished).

For more than 70 years, migratory beekeepers have been contracted to pollinate cranberries on larger farms [4], at stocking rates of four hives per hectare. Honey bees are satisfactory cranberry pollinators, provided that the weather during bloom is favourably warm for their activity (often true in New Jersey, less so in cooler Wisconsin and Washington, USA). On one Chilean cranberry farm, workers from small colonies delivered adequate stigmatic pollen loads for full fruit set (Cane, unpublished). Individual legitimate visits by honey bees to virgin flowers often deposit the eight tetrads on floral stigmas that are needed to maximize fruit set [11]. Most honey bees take only the meagre nectar from cranberry flowers, sometimes thieving nectar by probing between the anther bases without making stigmatic contact [18]. Some pollen is transferred during legitimate nectar foraging, but better pollinators are found among a small contingent of a colony's workers, which actively extract pollen by drumming the anthers with their forelegs, thereby releasing the pollen [19]. Such pollen-foraging honey bees produce a fruit set 63 percent greater than that produced by nectar foragers [20]. More cranberry pollen-foragers are fielded by stronger colonies with abundant brood or colonies with pollen traps placed on their hives, as well as honey bee genotypes bred to horde pollen [20]. Surprisingly, supplemental feeding with sugar syrup does not result in a greater proportion of pollen foragers [20]. The use of large colonies is the only practical means of maximizing honey bee pollination of cranberries.

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8.1.5 Blueberry

Blueberries are *Vaccinium* that produce a tender palatable fruit without large bony seeds. Commercial blueberries are derived from species in the section Cyanococcus, of eastern North America. They are divisible into northern and southern highbush, varieties of *V. corymbosum* that differ in their winter chill requirements, rabbiteye (*V. ashei*) and the lowbush blueberry (*V. angustifolium*). Cultivated highbush and rabbit eye blueberries are derived from a narrow germ plasm base [1] subjected to complex breeding programmes involving polyploids, multispecies crosses and hybridization – all of which are natural tendencies in the section [2]. Plants are propagated vegetatively through cuttings or tissue culture. Modern breeding and commercial cultivation practices can be traced back to just a century ago, and to the comprehensive pioneering studies of Frederick Coville [3]. Lowbush blueberry is a peculiar crop, as it is not planted. Instead, existing wild blueberry "barrens" in Maine and eastern Canada maritimes are extended and encouraged through burning and herbicide and fertilizer application.

Canada and the United States produced three-quarters of the world's commercial blueberries in 2014 (109 000 and 258 000 metric tonnes, respectively (the United States Agriculture Statistics Service[1]/FAOSTAT, 2014 data); these nations are also the primary consumers. Chile has recently become a major producer and exporter (90 000 tonnes – Chilean Blueberry Committee data). Lesser amounts (< 2 percent the world market) are grown in Germany, Mexico, Poland and other countries. As of 2014, bearing acreage was about 100 000 ha worldwide, double the area of eight years ago, and half of that in North America (Cane, unpublished).

8.1.6 Floral biology of blueberries

The inflorescences of blueberries are corymbose. Clusters of five to seven buds give rise in spring to white flowers with fused corollas ranging in shape from urceolate to cylindrical. Large bushes of three *V. ashei* cultivars produce 9 000 to 11 000 flowers each (Cane, unpublished). The flowers are hermaphroditic; a column of stamens surrounds the central, usually exserted pistil. Pollen is shed through paired pores that terminate in the tubular tips of the anthers, which potentially eject 13 400 + 2 000 tetrads per flower for *V. ashei* "Tifblue" (Cane, unpublished). Like other Ericaceae, blueberries are unusual among buzz-pollinated flowers because nectar is also secreted in the flowers – basally, between the anther bases. Nectar production varies by cultivar and the blueberry species. Two widespread older cultivars of *V. corymbosum* average 5.7–7.7 microlitres of nectar (25–60 percent sugar), depending on time of day and the weather [4], comparable to cultivars of several *V. ashei* cultivars (Cane, unpublished). Cultivated blueberries offer much more nectar per flower than cranberries (see sections 8.1.1–8.1.4).

8.1.7 Pollination of blueberry

Blueberries require bee visitation for full pollination, however mechanical jostling of flowers produces small to modest yields, depending on the cultivar [5]. Individuals (and clones) vary in self-fertility [6]. Outcrossing augments fruit production in blueberries, not because they possess genetic self-incompatibility (e.g. S-alleles), but due to inbreeding depression, which is evident as post-zygotic abortion of selfed seeds [7, 8]. Inbreeding depression is pronounced in wild populations, which include clonal mats of lowbush blueberries and the earlier wild selections of northern highbush plants. Rabbiteye blueberries are often self-fruitful [9]. Some newer cultivars of northern highbush (e.g. "Duke") are popular because they are fruitful when grown in a clonal monoculture. Self-fertility has been improved for some complex hybrid cultivars of highbush blueberries [10].

8.1.8 Pollinators of blueberries

Bees always search in blueberry flowers for nectar. Foragers of most species audibly sonicate or buzz the staminal column; the vibration then jets pollen

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[1] See www.nass.usda.gov

onto them as they hang from the pendant flower. Wild queen bumblebees (*Bombus*) are very effective blueberry pollinators, and deliver sufficient pollen to set a large fruit on the first visit [11, 12]. Bumblebees can be numerous on flowers of cultivated blueberries [13–16], but their numbers are ultimately limited because queens are active during the spring blueberry bloom, while workers are active later in the season. Commercially produced and shipped bumblebee colonies have been tried. Ten of these per hectare yield marginally more lowbush blueberries than 7.5 honey bee hives per hectare [17], but they remain expensive.

Several native non-social bees native to the eastern United States are specialists for blueberries and can be numerous in cultivated blueberries, including *Colletes validus* [14, 18] and several common species of *Andrena*, such as *A. carolina, A. bradleyi* and *A. hilaris* [13, 14, 19, 20]. These are ground-nesting, as is another blueberry specialist, the southeastern blueberry bee, *Habropoda laboriosa* [21]. This bee is an effective [9, 22] and valuable [23] blueberry pollinator, which is widespread and often abundant at southern highbush and rabbiteye blueberry orchards across the southeastern United States [14]. Wild bees such as *H. laboriosa* are sufficiently numerous in many smaller orchards where *Vaccinium* grow wild (e.g. southeastern United States) to provide full pollination [14], but they become too sparse on larger farms [15], so additional managed bees are desirable.

A Japanese ground-nesting solitary bee, *Anthophora pilipes*, was introduced to the United States to pollinate blueberries [24], however it is not commercially managed. *Osmia* bees do not sonicate blueberry flowers, but instead insert their forelegs into flowers to stroke the anthers, which precludes nectaring [25]. Cavity-nesting *O. ribifloris* is native to the western United States. It can be managed [25] as an effective blueberry pollinator [26], showing good floral fidelity to *Vaccinium* [27], but has limited site fidelity for re-nesting (Cane, pers. obs.). Another managed *Osmia,* the transcontinental generalist *O. lignaria*, was no better at pollinating blueberries than honey bees [28]. A versatile floral generalist, the alfalfa leaf-cutting bee, *Megachile rotundata*, can be a satisfactory pollinator of lowbush blueberries [11, 29], but stocks must be replenished annually as it is a summer bee whose progeny need hot weather to develop. For other growing regions (e.g. northwestern United States) and countries (e.g. Chile, Poland), little is known or reported about floral guilds of blueberry bees other than bumblebees.

Honey bees continue to be favoured as managed bees to help pollinate blueberries, both in North America, and on other continents where native *Vaccinium* (and so their pollinator faunas) are absent, or are being cultivated far away from wild *Vaccinium* relatives and their bees (e.g. Australia, Chile, New Zealand, South Africa). Stocking densities of four populous hives/ha result in good yields on northern highbush [30]. Flowers of southern highbush must receive five or more honey bee visits to maximize pollination and berry weight, which increases with seed content [31]. Rabbiteye blueberries have the deepest corollas with the narrowest apertures [32]. For some widely used cultivars (e.g. "Tifblue"), these are deeper than the length of a honey bee's tongue [14]. As a consequence, honey bees are keen to use robbery holes commonly cut in corollar bases by carpenter bees, especially *Xylocopa virginica* at rabbiteye blueberries – with mixed consequences for subsequent fruiting [33, 34]. This example illustrates the unintended pollination consequences of breeding programmes that overlook pollinator preferences and mode of access to floral rewards.

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8.2 BRASSICACEAE (FORMERLY CRUCIFERAE)

(3 200 species, 380 genera)

Eight of the 40 *Brassica* species are cultivated as crops: toria, mustard, cabbage, rape, cauliflower, turnip, rocket cress and radish. However, the dwarf honey bee, *Apis florae*, is unable to pollinate flowers of cruciferous crops. *Apis cerana* could well behave like the Western honey bee by removing nectar from some crops without contacting the anthers and stigma, thus acting as a nectar thief.

8.2.1 Swede rape, *Brassica napus* and turnip, B. *campestris*

These crucifers are grown mainly for oil seed but the former is used as a greenfodder crop for livestock. Over 60 percent of the rape oil crop is grown in Asia and the Indian subcontinent in temperate and subtropical areas. The main rape-growing countries are China, India, Bangladesh and to a lesser extent Brazil, Colombia and Ethiopia. Rape flowers provide an important source of honey in Argentina, Bangladesh, China, Japan, Pakistan and Taiwan, but honey yields are a modest 7–14 kg per hectare.

Swede rape is self-fertile, but produces a greater weight of seed from longer pods containing more seeds, chiefly as a result of pollinator visits. Seed set and yield are poor in glasshouses that rely on self-pollination, and seed viability is better with cross-pollination. Flowers of winter rape (sown in autumn) remain open and can be pollinated for one to three days. Spring rape flowers can be pollinated during one or two days. Winter crops flower for about six weeks in late spring, and spring crops bloom in early summer in temperate zones but during the cool season (late autumn to early spring) in the Punjab. Rape is a useful source of nectar for honey bees. Some pollen is also gathered from crops but is discarded by 40.0–95.5 percent of foragers, and deliberate pollen collecting is rare.

Insects are the principal pollinators of *Brassica*, in particular bees, however wind also contributes to pollination but shaking the plants. The yellow rape flowers are mostly pollinated by insects, although two beetle pests only carried about 10 percent of the pollen of honey bees and bumblebees. In the case of spring rape, some honey bees take nectar without pollinating the flowers. As temperatures increase, the honey bee flower visitation rate increases and the number of flowers visited per plant decline, likely resulting in an improvement in cross-pollination. Pollen collection reaches its peak in the morning, therefore effective pollination may barely exceed ten hours even on a fine day. During this period, each honey bee should visit 5 000–8 000 flowers. The giant honey bee *Apis dorsata* is an effective pollinator and increased yields have been reported when hives of *A. cerana* were introduced to crops. A hive density of 2–6/ha is recommended for pollination.

In Europe, *Bombus* is a consistent pollinator of rape flowers. In India, the solitary bee *Andrena leaena* is a reliable pollinator. Frequent visitors in India and Pakistan include *Apis florea*, which is not an effective pollinator, and *Andrena ilerda,* which may nest in rape fields. Other common visitors include *Halictus*, two more *Andrena*, and less often *Amegilla, Anthophora, Ceratina, Colletes, Lasioglossum, Nomada, Nomia, Nomioides, Pithitis smaragdula, Sphecodes, Thyreus* and *Xylocopa*.

8.3 ROSACEAE

(3 500 species, 120 genera)

Crops in the rose family have open flowers with stamens near the stigma. Each flower can usually be pollinated by generalist insect visitors. Flowering is intense and virtually completed in two to three weeks. Pollination is most frequent on the first day of flowering. Almond (*Prunus dulcis*) flowers first in early spring, then peaches and nectarine (*Pr. persica*), apricot (*Pr. armenica*), plum (*Pr. domesticus*), Japanese plum (*Pr. salicina*), sweet cherry (*Pr. avium*), tart cherry (*Pr. cerasus*), followed by European pear (*Pyrus communis*), nashi pear (*Py. serotina*) and finally apple (*Malus domestica*).

Daytime temperatures are critical for pollinator activity on almonds and less important for apples that flower a month later. Peaches, nectarines and apples will be unevenly shaped with inadequate pollination. Seed size is small and fruits elongate in poorly pollinated pears, and part of the apple core will lack pips if not pollinated. Almonds, apricots and peaches have single flower buds, while apples, cherries, pears and plums contain multiple flowers in each bud, giving them two to ten times the density of flowers. Information is scarce on flower density, although fruit set has been discussed (usually based on the proportion of multiple-flower buds that make fruit), which renders all data on fruit set difficult to interpret. Most orchards are planted with 100 to 400 trees/ha, while intensively trellised multi-tier apple and dwarf pear orchards can have up to 1 150 trees/ha.

8.3.1 Almonds, *Prunus dulcis*

Almond flowers decline in receptivity during the three days they may remain open. Almond has early, mid and late-flowering varieties, but most flowering occurs in the month that winter turns to spring. A profitable crop depends on cross-pollination of most flowers and 20 percent to 40 percent of flowers usually set fruit (but see Chapter 4).

The white flowers of almond are relatively attractive to honey bees and open when honey bee colonies are at about their smallest size during the season, with weather often restricting foraging to one to three hours per day. Nectar collectors rarely contact the stigma as they perch on the petal and probe nectaries between the bases of the stamens. About 150–200 honey bees/tree or five to ten strong hives/ha are recommended to allow honey bees to investigate more flowers and perform cross-pollination services more frequently. California produces over three-quarters of the almonds in the world, however there are not enough honey bee colonies to completely satisfy the need for pollinators.

In the United States, the mason bee, *Osmia lignaria*, has been used experimentally in almond orchards, while the orange orchard bee, *O. cornuta*, has been introduced for the pollination of almonds. *Osmia cornuta* is being used commercially for almond pollination in Spain, where 60–80 percent of the pollen collected by the bees comes from the fruit trees. In Kashmir, the temperature threshold for foraging on almond is 8 °C for *Apis cerana* and *Xylocopa fenestrata*. In New Zealand, the queens of *Bombus terrestris* freely use almond flowers. Flowering occurs mostly before nesting begins, therefore queens are the main visitors and nectar is the primary resource they seek. Pollinating *Lasioglossum* need both sunny conditions and 13.5 °C for flight.

8.3.2 Peaches and nectarines

Peaches and nectarines, like apples, need winter chilling, which restricts them to temperate and subtropical climates. Over 35 percent of all peaches and nectarines are produced in China (FAOSTAT, 2013 data).

Most peach varieties are self-fertile, but "Hale", "Marsan", "June Elberta", "Hallberta", "Candoka", "Chinese cling", "Almarand", "Crawford" and "Giant" require cross-pollination. The pink peach flowers are receptive for three days. Wind can dislodge pollen and set fruit. In the field, bees and other visitors contribute to pollination, but show little evidence of improving yields or fruit quality. Fruit set with honey bees can be twice that of bagged flowers. The use of 0.2–2.5 hives/ha is recommended for pollination.

In Japan, *Osmia cornifrons* is used for peach pollination; in Korea, *Megachile* are common wild pollinators; and in northern India, *Apis dorsata* is the most common honey bee and begins visiting the flowers about an hour earlier than imported *A. mellifera*. Flies remain active on flowers in overcast and rainy weather, unlike the honey bees.

8.3.3 Plums and cherries

China produces over 34 percent of the world's plums, while Turkey, Russia, Ukraine, Poland, Serbia and Hungary produce 68 percent of the sour cherries – Chile, Iran and Italy, Turkey, and the United States account for 50 percent of the other cherry varieties (FAO data, 2013). "Stella" is the only one of 30 common sweet cherry cultivars that does not need another variety to serve as a pollinizer. Tart cherries are largely self-pollinating, but can yield twice the crop with cross-pollination. Their flowers have a low sugar concentration.

Yearly fluctuations of 200–400 percent in plum yields have been reported in New Zealand and the United States. The factors resulting in such variation are considered to be low availability of pollinizing trees and degree of pollination and fruit formation. In the case of European plums, "Greengage", about half the purple to blue prune plums, and some "Yellow Egg" and "Lombard" (red to pink plums) do not require another variety for pollination. In all, 19 of the 30 main commercial varieties require a pollinizer to set fruit. Self-fertile plum varieties usually have 20 to 23 stamens on each white flower, while self-sterile varieties have 24 to 32 stamens. Fruit set with pollinating honey bees can be six times that of bagged flowers, thus plums are more responsive to pollinating bees than peaches.

Honey bees are effective pollinators of plums and cherries. In Australia, where there are few additional pollinators, fruit set reaches 36 percent when 7 to 21 honey bees are present at one time on the flowers of each tree. Between 1.3 and 5.0, and 2.5 colonies/ha are recommended for pollination of cherry and European plum, respectively. In northern India, *Apis cerana* forages longer each day than the imported honey bee, *A. mellifera*, on both plum and apples. A density of 2.5 honey bee colonies/ha is recommended for pollination in Europe.

The ornamental trees and shrubs, kowhai (*Sophora microphylla*), *Grevillea* and *Hakea saligna* are more attractive nectar sources for honey bees and bumblebees, while the pollen of *Brassica* and gorse compete with plums for honey bee use. In the United States and England, honey bees favour cherry pollen, but kale can be a competing pollen source.

The horn-faced bee, *Osmia cornifrons*, is used commercially for pollination of plums in Japan and is being introduced to the United States. In France, cherries and plums are favoured pollen sources for the mason bee, *Osmia cornuta*, which is also used to a limited extent in Former Yugoslavia and Spain for pollination of fruit orchards. *Osmia cornuta* forages at lower temperatures than the honey bee, and over smaller distances. *Andrena varians* is well synchronized with cherry and plum flowering, often collecting over 90 percent of its pollen from flowers. In northern Thailand, *A. florea, Trigona*[2] and *A. cerana* are the main bee visitors to plum flowers. Bumblebees that emerge early in the season and have relatively short tongues – *B. terrestris, B. lucorum, B. terricola* and *B. bimaculatus* – are the main species found on plums. Growers especially value their contribution to pollination in seasons with adverse weather during flowering. Cherries are among the favoured flowers for the first of the longer-tongued bumblebee species (e.g. *B. hortorum*) that emerge in spring.

8.3.4 Pears

China produces 41 percent of the world's pears. Each white pear flower sheds pollen for two to seven days and each tree flowers for about seven days. Adequate crops require 2–6 percent of the flowers to set fruit, and a 12-tonne yield/ha is possible. Most pear varieties need pollinizers, but under ideal conditions, "Bartlett", "Comice" and "Hardy" will set heavy crops of seedless pears. The use of two to five hives per hectare is recommended for pollination in Europe. During the ten days of flowering, 80 hours of temperatures higher than 16 °C are needed to ensure high levels of pollination with *Apis mellifera*. In the western United States, occasional failures of pear crops are attributed to poor weather conditions for honey bee foraging.

Pear flowers have plenty of pollen, but the sugar concentration of the nectar is as low as 8–10 percent, less than half that of cherries or apples. Thus, pear flowers are often relatively unattractive to bee visitors and may be visited mostly by flies. Honey bees prefer adjacent apple and sweet cherry trees, white mustard (*Brassica alba*) and chickweed (*Stellaria*), ground cover and hawthorn hedges (*Crataegeus*) to pear flowers.

At 1 300 m elevation in northern Thailand, *Trigona* [see footnote], *A.* florea and *A. cerana* are the main

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[2] *Trigona* now consists of several large genera, including *Lepidotrigona* and *Tetragonula* in the Old World, while *Trigona* is strictly Neotropical (Ed.).

bee visitors of pear flowers, while the hover fly, *Eristalis cerealis*, is a main visitor in Korea (along with non-wild honey bees). Hover fly abundance on flowers were found to decline by two-thirds when temperatures fell from 19 ° to 17 °C, and no flies were present at 16 °C.

Figure 8.1
PEAR AND PEACH FLOWERS AND FRUIT (SECTIONS) – ROSACEAE *PRUNUS AND PYRUS*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. reprinted by permission
[in original 1995 book published by FAO and edited by D. W. Roubik]

8.3.5 Apples

Apples are a major fruit crop in temperate and, to a lesser extent, subtropical regions. Globally, 33 percent of production comes from China, 3 percent from the United States, and 1 percent each from Argentina, Brazil, Chile, France and India, (FAOSTAT data, 2013). The flowers are an important source of honey, with reported crops of 20–40 kg/ha.

The most important commercial apple cultivars need pollen from another cultivar to set fruit. However, "Johnathan", "Rome beauty", "Oldenberg", "Wealthy", "Golden delicious", "Newton", "Grimes", "York", "Red gold" and "Yellow transparent" will set fruit in large blocks from their own pollen, or may even be parthenocarpic (i.e. developed without fertilization; see Glossary). Some varieties, with the possible exception of "Yellow transparent", produce heavier crops with cross-pollination.

Most of the honey bees that visit apple flowers are nectar collectors in North America and Europe. Nectar-collecting workers are effective pollinators of apple flowers except "Delicious" varieties that have gaps in the stamen ring. Honey bees work from the side around the bases of those apple flowers, while standing on the petals. Apparently the percentage of "side-working" honey bees increases as the season progresses, after most flowers have already been cross-pollinated. Individual honey bees tend to continue visiting the same foraging area, which discourages cross-pollination. Pollen-collecting honey bees, which effect fruit set better than nectar or nectar-and-pollen collectors, are in a minority unless nectar is unattractive or unavailable. In orchards with about 130 000 flowers/ha, around 200 pollinating honey bees/ha were needed to set 5 percent of apple flowers. However, it was estimated that only one in six honey bee visits resulted in the maturation of a fruit. The necessary re-visitation could double the numbers of pollinator visits required. This explains why 2.5 hives/ha, which can provide 2 400 pollinating honey bees in a hectare at any one time, are needed for pollination. In the western United States, 20 honey bee visits/tree/minute are recommended for pollination, and 1–5 hives/ha are recommended for pollination in Europe.

In the United States, oak (*Quercus*) and dandelion (*Taraxacum officinale*) can provide important pollen for honey bees while apple is flowering. Dandelion can be a temporary floral source, because it is used for nectar in cool conditions, when apple flowers are unattractive. Pollen from dandelion is collected rather earlier (mainly in the morning) than apple pollen, but very few honey bees collecting pollen from dandelion switch to collecting apple pollen. Mowing dandelion to concentrate pollen collectors on the apple flowers during the earlier part of flowering, when most fruit is set, would seem to be justified. Gorse (*Ulex europeaus*) at the start of flowering and horse chestnut (*Aesculus*) near the end of flowering can be competing pollen sources.

Three species of mason bee, *Osmia cornifrons* (from Japan), *O. lignaria* (from North America) and *O. cornuta* (from Europe), are valued apple and fruit tree pollinators. All are used commercially in Japan and the United States. One bee can pollinate and cause 2 450 flowers a day to set fruit, resulting in 50–60 percent fruit set within 50–100 m of their nests. Moreover, 84 percent of the brood cells in nests of *O. lignaria* come from apple pollen. In France, apple pollen is less common in bee nests, while plum and cherry accounts for 47–87 percent of pollen stores in nests. Competing pollen sources for *O. cornuta* are *Salix* and *Brassica*.

The bumblebees that emerge earliest in spring predominate on apple flowers. In Europe, these are *B. terrestris, B. lucorum and B. pratorum*; in North America, *B. terricola, B. occidentalis, B. affinis* and *B. impatiens;* in northern India two species of *Bombus*, and there are presumably others in China, Japan and the Republic of Korea. Bumblebees do not "side work" the flowers and visit them two or three times faster than nectar-collecting honey bees. Bumblebees also forage under cooler conditions, but the effect this has on the daily pollination of apples, compared to honey bees, has apparently not been recorded.

In England, *Andrena varians* used more apple pollen (usually over 80 percent) than seven other bees of this genus, while *A. albicans* is the most common flower visitor in Germany. As with honey bees, these bees are less active in cooler conditions and visit flowers at about half the rate of *A. mellifera*, making up for their slowness by consistently pollinating each visited flower and carrying more viable pollen. Flies (mainly hover and blowflies) also visit apple flowers, demonstrated wherever the pollinating guild has been thoroughly investigated. Studies in England and Canada show flies carry about 10 percent of the pollen carried by bees on their bodies. Flies may act as poor supplementary pollinators in the absence of bees, as the author has observed on Chatham Island.

8.4 MALVACEAE

(2 300 species, 200 genera)

Cotton varieties are the major malvaceous crop, utilizing four of the 32 *Gossypium* species. Kenaf (*Hibiscus cannabinus*) and okra (*H. esculentus*), like cotton, have large flowers and extrafloral nectaries. Honey bees appear unlikely to be efficient pollinators of kenaf and okra.

8.4.1 Upland, Asiatic tree cotton, *Gossypium hirsutum, G. arboreum*

About 20 percent of cotton is grown in China and the Indian subcontinent, 12 percent in Africa and 10 percent in South America. Other major cotton growing countries are Pakistan and Uzbekistan (3 percent, 7 percent), and Brazil, Australia and Turkey (3 percent each; FAOSTAT 2014). Cotton has also been a minor source of honey in El Salvador and Senegal, producing 30–90 kg/ha.

Cotton is self-fertile but benefits from cross-pollination by insects. Flowers last one day and begin to wilt in mid-afternoon. Each flower has one floral and four extrafloral nectaries. Nectar secretion is best at 25–35 °C; extrafloral nectaries secrete for several days and are difficult for small bees to use until the flower withers. The stigma protrudes 2.5 mm beyond the stamens.

Honey bees forage from extrafloral nectaries, which contain concentrated nectar (see section 8.6.1), until they are drained, leaving as few as 6 percent of bees visiting the floral nectaries. Boll retention (fruit set) on Asian cotton flowers visited by honey bees averages 57–62 percent, 50 percent for solitary bees of similar size and 30 percent for self-pollinated flowers. In the United States, the highest yields are obtained when one honey bee is present per each 100 flowers. In addition, a 500 percent increase in yield of hybrid seed cotton occurs with 16 honey bee colonies/ha (compared to no honey bee hives present). Honey bees usually prefer nectar from male-sterile (pollen-less) flowers. In Europe, 0.5–12.5 colonies/ha are recommended for pollination.

In India and Pakistan, *Apis dorsata, Xylocopa, Anthophora confusa, A. quadrifasciata, Megachile monticola* and scoliid wasps are the main pollinators of cotton flowers. The flowers are also visited by *Apis florea*, which may be a less effective pollinator due to its smaller size, and *Andrena ilerda, Coelioxys, Halictus, Nomada, Nomia, Pithitis smaragdula* and *Xylocopa*. In Egypt, *Xylocopa pubescens* and *Scolia*, and in North America, the solitary bees *Melissodes* and scoliid wasps *Elis plumipes,* consistently visit the floral nectaries, where their bodies become dusted with pollen.

Bumblebees and probably carpenter bees are considerably more effective pollinators than other bees, because they usually visit the floral nectary and touch both the stamens and stigma during foraging. In the United States, a bumblebee averages 1.2 flower visits/plant and in 9 hours potentially visits 1 700–2 750 flowers.

8.5 LINACEAE

(250 species, 12 genera)

8.5.1 Linseed or flax, *Linum usitatissimum*

The plants are grown for oil and linseed fibre. Most linseed production occurs in Asia and the Middle East, as follows: Russian Federation 14 percent, China 12 percent, Kazakhstan 11 percent and India 5 percent. The next highest production regions are the United States (6 percent) and Ethiopia (3 percent) (FAOSTAT, 2014).

The crops flower in summer for several weeks, but the peak occurs after the first week. A crop can produce dense flowers with plant density up to 400/m^{2}. In most cultivars the anthers are level with the stigma, but some have a lower or higher stigma. Linseed is self-fertile and self-pollinated. Cross-pollination occurs in at least 5–6 percent of cases, notably in varieties with the longest stigmas and the larger flowering cultivars.

Cage studies with honey bees in the England, Germany and the United States do not register increased yields, unlike Egyptian and Russian studies that include open plots and mention 22–43 percent increases in seed weight using pollinating honey bees. These different results could be due partly to different cultivars. Honey bees visit linseed most intensively in the morning for both nectar and pollen. Most workers stand on the petals, which are prone to dropping off, and probe the flower from the top. Some workers cling to the stalk and probe between petals, but may still cause selfing as they shake the flower. Linseed is a major honey source in Mozambique and an important pollen source in Egypt. It constitutes a medium honey and pollen source in Argentina and Mexico, where crops may yield a modest 2–12 kg/ha of honey.

The short and medium-tongued generalists *B. terrestris, B. lucorum, B. lapidarius and B. ruderarius* in Europe or New Zealand are the most common visitors. In Eygpt, the bees *Andrena pseudoorulata, Andrena* spp., *Xylocopa aestuans, Chalicodoma secula, Tetralonia* and *Anthophora*, and the wasps *Cryptocheilus discolor, Philanthus abdelkar, Polistes gallica*,and *Vespa orientalis* visit the flowers, as do butterflies, flies and beetles.

8.6 LILIACEAE

(1 200 species, 90 genera)

8.6.1 Onion, *Allium cepa*, shallot, *A. ascalonicum*, spring onions, *A. fistulosum*, leek, *A. porrum*, garlic, *A. sativum*, chives, *A. schoenoprasum*

Onion is produced throughout the world, with the above species used for food. Garlic and shallot seldom flower, being propagated vegetatively.

The best seed yields of onion can reach up to 1 500 kg/ha, but yields of 500–700 kg are more common (see section 8.6.2). Each flowerhead bears 50–2 000 flowers, and the pollen is shed in the first 24–36 hours, before the stigma is receptive. Cross-pollination is only needed for plants used in hybrid seed production. Up to 94 percent of the flowers produce seeds. In the United States, honey bees are considered essential for the pollination of hybrid crops, but the erratic use of onion flowers by bees has made it necessary to stock them at exceptionally high numbers – from 10 to 30 colonies/ha.

Onion is pollinated by bees and generalist flower-visiting insects, notably flies, with 267 species recorded from crops in the midwestern United States. Shallot flowers can be quite attractive to honey bees and bumblebees. In India, *Apis dorsata, A. florea* and *Tetragonula iridipennis* were the most common visitors to onion flowers, with *Tetragonula* working the flowers at about half the rate of honey bees.

8.6.2 Onion hybrid seed pollination in South Africa

M. Brand

The onion (*Allium cepa* L.) is entomophilous; plants have 200–600 small white florets carried in umbels on one or two elongated scapes, 1–2 m high. The florets are cup-shaped and have fully exposed reproductive parts, thereby representing a generalized pollination syndrome. Florets produce copious nectar in shallow nectaries, which attracts diverse and abundant insect visitors [1–8]. Each floret has the potential to produce six seeds from three carpels, with two ovules each. Although the onion is self-compatible, self-pollination is naturally limited because individual onion florets are protandrous – anthers dehisce before stigmas become receptive [9]. Self-pollination is prevented when hybrid seed is produced with F_1 hybrid parental lines, where male-sterile plants that do not produce pollen are cross-pollinated with male fertile plants that do [3]. Certain authors [10] report that airborne pollen is responsible for approximately 11 percent of the pollination of open pollinated onion hybrid flowers. The production of onion hybrid seed is therefore largely dependent on insect pollinator activity to ensure cross-pollination, seed set and profitable seed yields [11–13].

When anthers of the male-fertile florets dehisce, all pollen is shed within two to three days, mostly on the first day [11]. The stigma of the onion floret stays receptive for about three days, after which time receptivity gradually decreases until it ceases entirely after six to seven days [14]. Consequently, pollen needs to be transported on the day of anthesis for optimal germination potential, while viable pollen has to reach the stigma within the first three days of receptivity. When thousands of onion hybrid umbels come into flowering, an abundance of pollinators is needed to ensure extensive and continuous crop pollination during the entire blooming period [15].

Onion hybrid seed crops in South Africa flower from late October through November and are planted in the semi-arid climates of the Klein Karoo and southern Karoo regions in the Western Cape (Figure 8.2). Climatic conditions are optimal as they provide low humidity and mild, cool temperatures during the initial growth phase, followed by increased temperatures that induce flowering and support insect activity [16]. Such conditions occur within the Succulent Karoo biome, a recognized global biodiversity hotspot [17] hosting high levels of biodiversity and endemism.

The Klein Karoo is an oblong region covering about 23 500 km^2 [18] that takes the form of an extended valley stretching from east to west between two mountain ranges parallel to the South African south coast, the Langeberg-Outeniqua mountain range in the south and the Witteberg-Swartberg mountain range in the north. The Klein Karoo valley has nutrient rich loamy to clayey soils and receives 100–300 mm of rain annually [19]. The southern Karoo is a more arid region stretching northward from the Witteberg-Swartberg mountain range and has shallow, weakly developed alkaline soils [20]. It is characterized by extreme temperatures and unpredictable, highly variable annual rainfall of approximately 170 mm [20, 21].

Figure 8.2

ONION FIELD CULTIVATED FOR SEED AND NEARBY IRRIGATED FIELD IN THE KAROO, SOUTH AFRICA

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Commercial seed production: The seed industry in South Africa is well established and essentially run by the private sector [22]. Horticultural seed production (vegetable seeds) accounted for 21 percent of the South African seed market in 2000 [23]. The value of the domestic onion seed market during 2010 to 2011 was an estimated US$ 21.8 million. Seeds of F1 hybrid vegetable varieties are mainly imported from international companies, while the country is particularly self-sufficient in terms of the ownership of plant breeders' rights and varieties of most other crop species [23]. A total of 116 tonnes of onion hybrid seed was produced in South Africa during 2010 to 2011[3]. Strict quality controls and regulations apply to ensure that seed growers produce the required quantity as well as quality of onion hybrid seed. Since 1990, government financial assistance and assurance of stable producer prices has gradually declined to very low levels [22, 23]. Therefore, there is strong motivation to produce successful crops. In the case of onion hybrid varieties, South African seed companies commonly act as intermediaries between international breeders and local farmers, who multiply the hybrid seed through renewable contracts.

The onion seed cycle and pollinators: Onion seed production has a two-year cycle consisting of two phases: the seed-to-bulb phase and the bulb-to-seed phase. Therefore, two growing seasons occur from seed to seed, because no flowering occurs when the bulbs grow during the first year. Onion is a highly cross-pollinated crop and cross-pollination between cultivars is common [24]. Thus isolation between different cultivars is required during flowering to prevent genetic contamination by foreign pollen. Recommended isolation distances range between 0.8 km and 5.0 km, depending on the cultivar [24]. Alternatively, different localities can be dedicated for the production of certain cultivars [25]. Within a single crop, male fertile and male sterile rows are commonly planted at ratios of 1:3. In semi-arid places where onion seed crops are produced, "fertigation" is a common practice and water is administered through drip, sprinkle or flood irrigation systems, combined with fertilizer. Onion hybrid seed is a specialist crop that occupies relatively little ground, and unit expansion is of low priority [26].

Apis mellifera is the only managed pollinator used to pollinate onion hybrid seed crops worldwide, despite the fact that it is often not attracted to onion flowers [27, 28]localized foraging activity near their hives (mean flight distance = 266 m. This is possibly due to the high potassium ion content in the nectar [29, 30], and necessitates intensive managed hive-stocking densities of about ten hives per hectare [1, 3, 11, 24, 31], which is high in comparison to other vegetable seed crops [32]. In addition, honey bees forage selectively between male-fertile and male-sterile umbels within onion hybrid seed crops, usually foraging in higher numbers on male-fertile rows than on male-sterile rows [3, 11, 31, 33–35]. Such observations suggest discriminating behaviour by honey bees when visiting male fertile and male sterile umbels, which may be linked to honey bees adapting their foraging behaviour to lines offering more rewarding and attractive floral resources (sensu Waddington [36]).

In South Africa, the Cape honey bee (*Apis mellifera capensis* Esch.) is endemic to the Cape Floristic Region [37], where onion hybrid seeds are produced, and it forms part of the wild pollinator community. *Apis m. capensis* also populates managed beehives used by commercial beekeepers for crop pollination and honey production. Therefore, the pollination services already provided by wild honey bees cannot be distinguished from those of the rented managed honey bees. Some farmers rely considerably on wild honey bees for pollination and recognize the valuable and cost-effective ecosystem service they provide. These farmers usually use lower stocking densities of managed hives and deploy more managed honey bee colonies only when needed. Some farmers even provide unconventional, artificial nesting sites close to the crops for wild honey bee colonies. For example, one farmer buries 50-gallon metal drums near the crops,

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[3] The figures presented here are taken from www.sansor.org

thus providing domiciles free from poaching and predators for wild honey bee colonies. These colonies are not regarded as managed because honey is not harvested from them.

The majority of managed honey bee colonies for onion hybrid seed pollination reside permanently on farms and are owned and managed by local beekeepers. Such resident hives are moved into desired places during crop flowering periods, with managed colonies only occasionally sourced from outside the Klein Karoo for pollination purposes. This practice was reinforced with discovery of the highly infectious American Foul Brood disease in managed colonies during the first quarter of 2009, resulting in efforts to prevent the disease from spreading [38, 39]. Because of the arid conditions prevalent in the southern Karoo, which cannot sustain large numbers of honey bees all year, managed honey bee colonies are mostly externally sourced for onion hybrid seed production.

Recent field studies: Research conducted on 18 blooming onion hybrid seed crops during 2009 and 2010 aimed to determine the extent of pollination services from insects in natural habitats near crops, and assessed honey bee behaviour on the parental lines. Many insects visited the onion flowers on all crops investigated, regardless of natural habitat availability. It is important to note that the proximity of natural or semi-natural habitat is generally relatively close to cultivated crops in semi-arid production regions, because crops are mostly cultivated in alluvial terraces along water courses, which provide access to richer soils and irrigation water [21, 40, 41]. Some bee and wasp species are abundant along water courses because they use water for nest-building purposes [40]. The remaining land is largely unsuitable for cultivation and mainly used for livestock grazing, which is considered to be the single most important threat to biodiversity conservation in the region [42, 43].

Crop management practices, specifically weed and disease control and irrigation methods, significantly alter flower visitor assemblages. Crops with unhealthy plants are often overgrown with weed species that offer alternative floral resources during onion flowering periods. Unhealthy crops host more diverse insect assemblages, consisting mostly of numerous fly species attracted to diseased and rotting onion plants.

The unhealthy crops also happen to be situated in more cultivated areas, where closer proximity of ostrich camps – one of the main farming practices in the region – encourages a greater diversity of carrion fly species. The methods used for irrigation purposes often determine the availability of water to various insect species, thereby likely determining insect assemblages found within crops [35, 40, 44].

Based on high visitation frequencies and substantial loads of onion pollen on their bodies, honey bees (managed and wild) have the highest probable pollinator value of onion hybrid flowers. Honey bee visitation significantly increases the yield of onion hybrid seed, while anthophile diversity and non-*Apis* visitation has no effect on seed yield (M. Brand, unpublished data). The origin of the honey bee foragers was not determined since managed hives were present on all the examined crops; yet no relationship exists between honey bee visitations and managed hive density or natural habitat availability. However, there is a significant correlation between the total amount of rainfall received by the production regions and honey bee visitation frequency, underlining the importance of secondary factors caused by rainfall, such as wild flower abundance and soil moisture. A positive correlation between honey bee visitation and the diversity of hand-sampled insects on onion flowers indicates that onion varietal attractiveness and/or pollinator population size may determine overall insect visitation. Rainfall variability may also however, influence secondary factors such as soil moisture and water quality that have a direct impact on seed yield [45].

Weather and foraging honey bee behaviour: Another important factor that may influence honey bee visitation is the timing of rainy periods. As already mentioned, climates of arid and semi-arid regions are usually characterized by extreme temperatures and great variability in both the timing and amount of rainfall [46]. For this reason, succulent Karoo vegetation responds well to rain and the flowering period of wild plants is governed by the timing of rainfall [18]. Early rains lead to early flowering, but late rains cause the veld to flower later; this may coincide with flowering of the onion hybrid seed crops, which usually takes place from late October until late November. Natural vegetation in flower during this time is likely to compete for visitors with the blooming onion crops. This factor gains further importance because hybrid onion is relatively unattractive to honey bees [29, 30, 47].

Studies of honey bee behaviour and foraging patterns on onion flowers demonstrate a noticeable preference for the male fertile lines of onion hybrid seed crops investigated here. Nevertheless, honey bees on male sterile flowers account for 66 percent of the number of honey bee foragers on male fertile umbels. Male fertile flowers offer larger volumes of less concentrated nectar, and also pollen for brood rearing, which probably attracts more honey bees than the male sterile lines. Honey bees forage within parental lines rather than move among lines, while very few inter-species interactions are recorded; thus, bees tend to continue seeking a given flower type. Other foragers are so scarce that their presence seems to matter little.

A significant difference in onion flower scent profiles is found between the parental lines. Odour is a strong foraging cue used by honey bees to associate scent and nectar source. The difference in scent between the parental lines apparently encourages selective foraging through floral constancy. When honey bees evaluate a floral scent by hovering in front of the flowers of the opposite parent, contact with the floral reproductive parts is minimal, thereby limiting pollination. Therefore, hybrid onion breeding programmes should attempt to take such parental line differences into account when selecting for favourable production traits. The selection for more similar traits might lessen honey bee discrimination between parental lines [48].

Conclusion: Successful onion hybrid seed production in South Africa is largely dependent on honey bee visitation, and considerable pollination services are derived from wild honey bee colonies where managed hive-stocking densities are low. South African farmers can mostly gain satisfactory benefits from well-managed natural habitats near their crops. The succulent Karoo landscape has the capacity to support large populations of wild honey bees that can offer abundant pollination ecosystem services during favourable climatic conditions. Most farming practices are subject to environmental conditions favouring successful production. However, dependence of hybrid onion seed on insect pollination increases reliance on abundant wild honey bees, which may be attracted away from the crops by local flowers. Nonetheless, this apparent conflict in ecosystem services can be mitigated effectively by the use of managed honey bee colonies.

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8.7 APIACEAE (UMBELLIFERAE)

(3 000 species, 300 genera)

The flowers of Apiaceae have extensive flat platforms and shallow flowers that allow insect visitors to walk, thereby economizing on energy expended when not much nectar is available. Apiaceae include nine species of vegetables, herbs and spices: anise (*Pimpinella anisum*), cerelac or celery (*Apium graveolens*), chervil (*Anthriscus cerefolium*), coriander (*Coriandrum sativum*), dill (*Anethum graveolens*), fennel (*Foeniculum vulgare*), parsley (*Petroselium crispidum*), parsnip (*Pastinaca sativa*) and carrots (*Daucus carota*), which are the most important cosmopolitan species. The seed crops that are processed and then sold to growers depend heavily on insect pollination.

8.7.1 Carrot, *Daucus carota*

Carrot is the most important cultivated umbellifer species and must be cross-pollinated. Its flowers are mainly used for pollen by honey bees. The crops are in flower for about four weeks, and each white flower remains open at least a few days, with flowering within a flowerhead lasting for up to seven days. The flowers have the reputation of being a good honey source but quantification of yield is difficult, due to the limited areas cultivated for seed production.

Carrot seed crops are pollinated mainly by honey bees, with no stocking rates calculated thus far. Pollen-collecting bees of male-sterile lines carry about 10 percent of the pollen compared to nectar collectors on male-fertile flowers.

Figure 8.3

CARROT FIELD IN THE KAROO, CULTIVATED FOR SEED CROP

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Maximum seed production is achieved with ten honey bees per square metre. Pollination increases yield and evenness of seed size. In India, yields in open-pollinated flowers have reached 200–500 percent of those in caged plots. In the United States, 860 kg seed/ha has been produced using honey bees within caged plots.

In Egypt, *Anthophora* are abundant as the honey bee on carrot flowers. In the United States, 334 insect species visit flowers, the most important of which are bees (*Andrena, Halictus, Chloralictus, Colletes*), sphecid, vespid, pompilid and ichneumonid wasps (*Cerceria, Lindenius, Nyssa, Philanthus, Sceliphron*), and syrphid, bombyliid, sarcophagid, stratiomyid and tachinid flies (*Syritta, Tubifera, Eulalia, Stratiomys*). Gnats and midges also help pollinate carrot flowers.

8.8 MYRTACEAE
(3 000 species, 140 genera)

8.8.1 Eucalypts

Over 523 species of gum trees (*Eucalyptus*) exist in Australia and Indonesia. While birds alone are not the exclusive pollinators of eucalypts, they contribute to the pollination of about half the species, and are the main pollinators of perhaps 2 percent. Nearly 200 species are grown on 3.4 million ha elsewhere, from highland temperate to tropical climates in Africa, the Indian subcontinent, and North and South North America, primarily for timber and firewood with added value as windbreaks, shade, erosion control, livestock fodder and bee forage, depending on the species. Insect visitors to the open brush-cup flowers include honey bees, stingless bees, solitary bees and birds. At least 20 species are recognized as important sources of nectar or pollen for honey bees. A number of eucalypts are recommended for planting as bee forage in the tropics and subtropics in Africa, India, the Middle East and South America. This suggests that honey bees visit their flowers freely, but the degree to which the honey bee pollinates these flowers is still unknown.

Honey bees, stingless bees and other bees are believed to be effective pollinators of species with smaller flowers, such as *Eucalyptus melliodora*. Birds and some of the larger bees are likely to play a more important role in the pollination of gum species *E. ficifolia, E. casophylla, E. cosmophylla, E. macrocarpa, E. sideroxylon* and *E. leucoxylon*, which have larger red or yellow flowers, and those with little scent and large nectar volumes.

8.8.2 Clove, guava and allspice

Clove (*Syzygium aromaticum*), guava (*Psidium guajava*) and allspice (*Pimenta dioica*) are shrubs or trees with yellow to white flowers. Bees and other insects visit clove and guava flowers, which are slightly smaller and lack the red colour of *Acca* (formerly *Feijoa*, see below). This implies that bees and other insect visitors are probably more effective pollinators for clove and guava than for feijoas and the large gum flowers. The larger flowers of allspice could limit the effectiveness of some insect visitors. Such predictions need to be verified by more definitive studies on the pollination of these crops, which have received only minimal attention to date.

8.8.3 Feijoa, *Acca sellowiana*

Feijoa comes from southern Brazil and Uruguay, where bumblebees, carpenter bees and birds, among others, visit the flowers. Feijoa flowers in the early summer. The stigma of each flower protrudes by about 9 mm from the ring of stamens. With cross-pollination, 88 percent of the flowers set fruit, 2.5 times the level for self-pollinated flowers. The fruit and pulp weight of cross-pollinated flowers amounts to 200–300 percent that of selfed flowers, and fruit maturity is reduced by 6 percent (ten days) in the "Apollo" cultivar.

In Italy, Japan, New Zealand and the United States, larger insect visitors that can at least intermittently transfer pollen include honey bees, *Polistes* wasps, bumblebees and carpenter bees. Smaller halictid bees, ants and longhorn beetles may just collect pollen or chew the petals without accomplishing pollination. The larger blackbirds (*Turdus merula*) and mynahs (*Acriodtheres tristis*) approach the flower from the top, consume the red petals and deposit five to ten times as much pollen on the stigma as honey bees. After one visit, 30 percent to 50 percent of flowers form fruit. However, blackbirds apparently tend to work the margins of crops from shelter belts near their nests, because significantly less fruit is set in the middle of larger blocks (0.5–0.7 ha) of feijoa. The smaller silver eye (*Zosterops lateralis*) approaches from below, seldom touches the stigma and deposits only 25 percent as much pollen on the stigma as honey bees. This is not enough to initiate fruit formation. In the United States, mockingbirds (*Mimus polyglottis*) visit the flowers, but their effectiveness for pollination has not been investigated. In two orchards and an enclosure where birds did not visit the flowers, 0 percent and 3 percent set fruit, compared to 25–34 percent for hand pollination. Honey bees approach the flower from the correct angle, but typically visit older flowers with available pollen where the stigma is no longer receptive. Honey bees visit an average of 13 flowers per plant (about ten times more than blackbirds) before moving to the next one, and none of the flowers visited formed fruit. Thus, in effect, honey bees tend to act as pollen thieves for this crop.

Acca flowers are unattractive to honey bees compared to surrounding clovers, *Eucalyptus*, *Verbascum*, *Rubus* and *Citrus*. The same is true for bumblebees with sunflower, white clover and lucerne. Carpenter bees and queen bumblebees are more effective pollinators than honey bees, providing they visit younger flowers, because these bees should more readily contact the stigma. Stocking orchards of Feijoa with honey bees has little to recommend it unless more effective pollinators are scarce.

8.9 ACTINIDIACEAE
(360 species, 3 genera)

8.9.1 Kiwi fruit, *Actinidia deliciosa*

The kiwi fruit is one of at least 60 *Actinidia* species from China, Japan, the Republic of Korea and Taiwan. Kiwi fruit is now widely grown in subtropical and milder temperate regions, but does require some winter chilling. A kiwi fruit orchard flowers for 10–18 days at the end of spring, when each male flower sheds pollen for two to three days after opening. Female flowers remain attractive to bees for five of the seven to nine days they can remain receptive. Kiwi fruit presents distinctive pollination features compared to most other crops. Flowers are pollinated by a combination of insects and wind, as are chestnuts (*Castanea*) certain willows (*Salix*) used for windbreaks and erosion control, and grapes (*Vitis*).

Male and female kiwi fruit flowers grow on separate vines, there is no nectar and female flowers have unviable pollen. Female flowers have 30–40 stigmas but are so large that even bumblebee queens may forage for pollen around the stamens with little contact of the stigma. About 200 seeds are needed for the fruit to form. Preferred fruit weigh 93–110 g and contain 900–1 400 seeds.

In New Zealand, an average of five honey bee hives per hectare are introduced to kiwi fruit orchards. However, rain may reduce pollen collection to less than 30 percent of normal levels. In Italy and New Zealand, kiwi fruit accounted for 5–26 percent of pollen collected by introduced honey bee colonies, but the percentage of kiwi fruit pollen nearly doubled when colonies were fed sugar syrup. The main competing pollens were strawberry and white clover, honey suckle, *Citrus*, *Brassica*, poppy, onion, asparagus and, towards the end of flowering, vipers bugloss.

Out of kiwi fruit flowers exposed to a single visit by honey bees, 26 percent produce a minimum-sized (72 g) commercial fruit, and 14 percent produce a size considered a preferred fruit. This implies that at least four visits to a female flower are needed to produce a high proportion of export-quality fruit. Most kiwi fruit pollen at commercial stocking rates is gathered by midday. Therefore, most honey bees forage for 3.0–4.5 hours daily on kiwi fruit, potentially visiting 740–1 120 flowers. Kiwi fruit orchards have around 500 females flowers per vine. An estimated two or three honey bees per two female vines are needed to effect adequate pollination, as already shown in initial studies on fruit formation and bee densities per vine.

Bumblebees, particularly the larger queens, are about 10–15 times more effective as pollinators than honey bees. Ferguson and Pusch (1991) found that bumblebees deposit seven times more viable pollen than honey bees (per visit) and that yields rise when bumblebee numbers increase on the flowers. The working rate and ability to forage under cooler conditions means that queens, in particular, can visit about twice as many flowers per day as the honey bees, provided that pollen is not depleted. In addition, alternative flowers are less important competitors for their visits. Bumblebees are used to a limited extent commercially for kiwi fruit pollination in New Zealand and are being used for pollination of kiwi fruit in Europe.

Kiwi fruit flowers are an attractive pollen source for diurnal and nocturnal insects, as shown by the over 150 species found on flowers among the small floral visitor fauna native to New Zealand. Hoverflies (*Syrphidae*) and solitary ground-nesting bees, *Leioproctus* are the other common, larger and active flower visitors. The flies carry only 10 percent of the amount of pollen carried by solitary bees on their bodies. In China, bumblebees and apparently carpenter and megachilid bees, in addition to honey bees, forage on the flowers. In wild kiwi fruit populations, wind may well act as a background pollinating agent, ensuring fruit set on all plants but those most remote from a male vine. Insects, primarily social and solitary bees, carry pollen to the more remote female plants.

8.10 VITACEAE (700 species, 12 genera)

8.10.1 Grapes, *Vitis* spp.

Grapes are among the most important fruit crops with over 8 000 named cultivars, the most important of which by far is *V. vinifera*. *Vitis rotundifolia* (muscadine), a native to North America, is distinctive in having non-functional stamens and requiring outcrossing, while seedless grapes are produced using plant hormone application. The European grape, *V. vinifera*, is generally bred to be self-fertile (self-pollinating). Grapes are often thought to be wind-pollinated, but their dependence on wind-pollination has not been investigated as thoroughly as kiwi fruit and other species. Grape flowers are generally unattractive to bees and other flower-visiting insects, produce little nectar and, despite their extensive production, are not a significant nectar source for honey bees anywhere in the world. The recommended number of beehives for pollination is 2–5 hives/2 ha.

China is the largest producer, accounting for 17 percent of total production, followed by Italy, Spain, the United States (12 percent each), France (8 percent) and Turkey (6 percent; FAOSTAT, 2013).

8.11 FABACEAE (LEGUMINOSAE) (19 000 species, 630 genera)

For human food, the common bean of American origin, *Phaseolus vulgaris*, and the broad or fava bean of the Old World, *Vicia faba*, are undoubtedly the most important. For food and a variety of other products, *Glycine max*, or soybean, is also extremely important. The latter, however, includes varieties unaffected by pollinator visits or not visited, and some that produce 20 percent more seeds and pods when flowers are visited by bees (Free, 1993). *Phaseolus* species are considered by FAO to represent all "dry beans", although *Phaseolus* is consumed both cooked and fresh. However, several other genera can be included in this group, such as *Vigna, Vicia, Cajanus, Canavalia, Arachis, Cicer* and *Mucuna*.

World production (FAOSTAT 2014) reflects habitat conversion to soybean in drier regions, with Argentina and Brazil accounting for almost half of the total (16 percent and 27 percent, respectively), followed by 1–4 percent among China, Paraguay, India, Canada and the United States. For "dry beans", the greatest producer is India (16 percent), followed by Myanmar (14 percent), Brazil (13 percent) Mexico and the United States (5 percent each), and Tanzania and China (4 percent each). Total tonnes produced in 2014 were recorded at 2.61 x 10^{7}.

The four legume crops chosen for review below are herbs that produce both pollen and nectar for insect visitors. Available summaries on pollination, the structure and response of the flowers to visitors and their importance as nectar sources for honey bees, taken together, demonstrate that honey bees are satisfactory pollinators of trefoils (*Lotus, Lespedeza*), sweet clovers (*Melilotus*) and sanfoin (*Onobrychis vicifolia*). Analysis of European and Canadian pollen collected by *Bombus*, direct observations of eight legume species in Denmark, and the author's observations in Canada and New Zealand show that short-tongued *B. teirrestris, B. lucorum* and *B. terricola* include *Lotus* as a favoured pollen and nectar source. Sweet clover is also a favoured nectar source. Conversely, the longer-tongued bumblebees of Europe and North America favour some of the vetch species (*Vicia*) and everlasting peas (*Lathyrus*).

In the tropical and subtropical savannahs and deserts of South America and the United States, bee species with generalized food sources form a common group of insect visitors on leguminous trees. This applies at least to the mesquites, algarroba and tamarugo (*Prosopis*), to nectar-bearing wattle (*Acacia*) in Africa, the Americas, Asia and Australia, and tamarind (*Tamarindus indica*). Information on honey bee forage in Australia and other parts of the world shows that some of the widespread *Acacia* mainly yield pollen and little or no nectar from the flowers. Other regionally important multiple-purpose, livestock forage, timber and erosion-control trees or shrubs include the genera *Albizia, Cassia* (now *Senna* in large part), *Ceratonia, Cordeauxia, Dalbergia, Desmodium, Enterolobium, Gleditsia, Intsia, Leucaena, Mimosa, Pterocarpus, Samanea, Schizolobium, Sesbania, Tipuana* or the creepers or shrubs *Phaseolus*. Attempts at cultivation have been made with most of these genera, but *Instia, Schizolobium, Enterolobium, Tipuana and Samanea* have barely gone beyond local trials, despite their rapid growth and valuable wood. Of the cultivated plants, sissoo *Dalbergia sissoo* (India and Pakistan), honey locust, *Gleditsia tricanthos* (Pakistan, South Africa) bracatinga (*Mimosa scabrella*, Brazil), roundleaved bloodwood (*Pterocarpus rotundifolius*, Mozambique, South Africa) and tipa (*Tipuana tipa*, Bolivia) are rated as important honey sources. Thus, they are likely to be visited often by honey bees. Central American studies of pollination on *Cassia* and *Cochlospermum* (Cochlospermaceae) show that tree legumes include pollen-rich flowers that are buzz pollinated by *Centris* and *Xylocopa*. The principles derived from pollination of temperate legumes seem to have the greatest potential application for studies of tree crops in the tropics, which require substantial research to place them on a par with herbaceous species.

Figure 8.4

TAMARIND – *TAMARINDUS*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 205. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

Figure 8.5

HALICTID BEE BUZZ-POLLINATING AND *XYLOCOPA* ROBBING NECTAR AT LEGUME FLOWERS

Source: J.M. F. Camargo original drawings, reprinted by permission of artist and publisher. Presented in: G. Gottsberger, J. M. F. Camargo, I. Silberbauer-Gottsberger. 1988. Bot. Jahrb. Syst. 109:459-500. [from original 1995 FAO book]

Figure 8.6
CAESALPINIACEOUS LEGUME - *CASSIA*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 184. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

Figure 8.7
MIMOSACEAOUS LEGUME – *MIMOSA*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

8.11.1 White clover, *Trifolium repens*.

This herb is mainly used in temperate regions, but grows well in subtropical climates. White clover is of particular value in well-stocked pastures, where its underground stolons enable it to survive repeated heavy grazing. White clover and other legumes have high digestibility and protein for grazers. White clover also has a high capacity to increase soil nitrogen levels. Crops can produce 320–520 million flowers/ha.

Observations on white clover in fields on Chatham Island, New Zealand, show that seed is not formed in the absence of honey bees, bumblebees or solitary bee pollinators, which confirms studies in cages. White clover flowers from late spring until autumn, depending on when it is grazed. White clover is an important honey source in Argentina, China, Colombia, Ecuador, and parts of Brazil, and a minor source in Algeria, the Azores and Lebanon. Crops usually produce 100–200 kg honey/ha.

White clover flowers are 3–4 mm deep and can be pollinated readily by honey bees and short-tongued bees. Seed yields of *T. repens* can be increased by 200–300 percent when crops are stocked with honey bees. Abundance of all pollinating bees is low on white clover flowers at less than 18 °C, because nectar secretion ceases at about this temperature. Honey bees are normally effective in white clover pollination. No benefit may accrue from having more than 1.2 honey bees/m^2, unless the crop flowers profusely (i.e. 430 million flowers/ha). In this case, 5.6–6.0 honey bees/m^2 may be needed. Under field conditions, 2.5–3.0 honey bees/1 000 flowers can cause seed-set of 85–95 percent. One to three colonies/ha are recommended. Usually there is little need to use other pollinators. However, alternative pollinators can provide backup pollination under adverse weather on smaller crops, and in pastures under-stocked with honey bees (less than one hive per 500 ha). European and New Zealand studies show that other pollinators include *B. terrestris, B. lucorum, B. lapidarius, Melitta leporina, Anthidium punctatum* and presumably *Andrena ovulata, A. labialis, Eucera longicornis* and *E. clypeata*. *Bombus lucorum* and *B. terrestris* are useful for pollination of breeding lines in screen cages.

8.11.2 Berseem, Egyptian clover, *Trifolium alexandrium*

This forage crop is used particularly in drier and warmer climates. Berseem clover is important in northern Africa, India, the Middle East and Pakistan. Crops flower for several weeks in summer; the flower is 7–8 mm deep and may remain receptive for 10–12 days. The flowerheads can set over 70 seeds/head and crops can produce up to 600 kg/ha of seed. Comparisons of caged and open plots demonstrate the need for cross-pollination. Berseem crops are visited avidly for nectar and pollen by honey bees. Berseem clover is rated as an important source for honey in the Ganges, Indus and Nile plains, and pollen trapping in the Nile valley confirms the importance off Berseem as a pollen source. For maximum seed-set, 2–4 honey bees/m^2 are deemed adequate. In India, *Apis dorsata* and *A. cerana* are the commonest visitors, but the small honey bee *A. florea* only visits the flowers when berseem nectar is plentiful. The crop does not have a significantly higher flower density than white clover and presents no problems for honey bee pollination. One to three colonies/ha should provide satisfactory pollination.

In Eygpt, an alkali bee, *Nomia unidentata*, includes berseem clover in its food sources, while *Chalicodoma mucorea, Osmia latrielli* and *Andrena ovulata* are considered valuable pollinators. *Anthidium, Andrena, Osmia* and *Xylocopa* visit the flowers and probably have sufficiently long tongues to effect pollination. This should be verified, because the behaviour of these pollinators and *Halictus* on the crop has not been studied.

8.11.3 Lucerne, alfalfa, *Medicago sativa*

This highly productive leguminous hay and pastoral crop is more drought resistant than the clovers. The mauve to yellow-streaked flowers have corollas about 4 mm deep and flower during summer. Crops may produce 0.1 to 0.2 million flowers/m^2 over the four to six-week flowering period. Under favourable conditions, lucerne is an attractive nectar source for bees and yields 100–200 kg honey/ha. Lucerne is a major honey source in Argentina, China, Mexico and Mozambique, but is a poor pollen source.

Solitary bees regularly trip the flowers and at least 13 genera have efficient pollinators. The alfalfa leafcutter bee *Megachile rotundata* has become the leading pollinator on the American continent, but is much less important in Europe, India, the Middle East and the Russian Federation. The threshold for flight is around 18 °C and the alfalfa leafcutter bee only forages freely over 20 °C, with periods of cool weather restricting its effectiveness. In Canada, New Zealand and the United States, use of the leafcutter bee has increased seed yields of lucerne from 500–1 000 percent to 500–1 200 kg/ha. Alfalfa leafcutter bees were also introduced to South America, but inadequate steps were taken to screen out natural enemies from stocks imported from North America. The alkali bee of the United States, *Nomia melanderi*, forages under lower temperatures and stronger winds than the lucerne leafcutter bee. However, the special "beds" needed for nesting in the ground restrict pollinator placement within crops, compared to the lucerne leafcutter bee. Bee abundance of 5 000–6 000/ha tripped around 50 percent of flowers and yielded 700–1 150 kg/ha. Introductions have succeeded in producing naturalized populations but limited management options in New Zealand. The alkali bee could be of value in lucerne pollination in parts of Africa, southwestern Europe, northern India, and South America. Diseases and parasites are relatively scarce among the lucerne leafcutter bee and the alkali bee in New Zealand.

Tripping rates of 50–100 percent and faster flower visitation mean that many of the solitary bees and bumblebees are 40 to over 100 times more effective (per bee) than honey bees in lucerne pollination, even without taking a longer working day into account. In North America, unmanaged and effective solitary bee pollinators of lucerne include *Anthophora, Osmia, Megachile, Hoplitis, Andrena prunorum, A. wilkella* and *Calliopsis andreniformis*. The major pollinating bees in Europe, the Middle East and the southern Russian Federation are *Rhophites canus, Osmia latreillei, Melitta leporina, Melitturga clavicornis, Megachile* spp. (short adult activity periods), *Eucera longicornis, E. clypeata, E. cinerea* (medium adult activity periods), and *Andrena flavipes* and *A. ovulata* (two adult generations and long activity).

Important alternative pollen sources for solitary bees, *Eucera, Melitturga, Melitta, Andrena labialis* and *A. ovulata* include white clover, red clover, lotus and vetch in France, while notable alternative pollen sources for *A. flavipes* are St. John's wort, Hypericum and Asteraceae (including sunflower). In the Czech Republic, farming of *Rhophites canus* relies on securing food supplies and protecting ground-nesting sites. Initial management studies on *Osmia latreillei* have been carried out in Israel.

European *Anthophora parietina* can be partially managed at nesting sites as a general legume seed pollinator, and in Egypt the mason bee, *Chalicodoma mucorea* or *Megachile mucorea* is a potentially famable species for hotter climates. Medium and shorter-tongued bumblebees are generally more effective pollinators of lucerne because they trip flowers more consistently and prefer lucerne more than longer-tongued species. In India, *Megachile nana* and *M. flavipes* are used for pollination. Similarly, in South Africa, *Xylocopa* and *Megachile gratiosa* have been tested as potential lucerne pollinators. In Argentina, *Megachile pallefacta, Xylocopa ordinaria, X. splendidula, Melissodes nigroaenea* and possibly *Bombus robustus* are effective pollinators of lucerne, as are colletid bees in Chile. In contrast, nectar-collecting honey bees and shorter-tongued bumblebee species are largely ineffective pollinators. These bees learn rapidly to insert their tongue through the side of the flower and only trip the pollinating mechanism accidentally. Consequently, they trip as little as 0.2–5.0 percent of flowers, although the percentages are higher in hot dry regions. In New Zealand, where pollination relies largely on honey bees, potential lucerne yield seed production under ideal conditions is 1 500–2 000 kg/ha, but reaches only 75 kg/ha on average without control of mirid bugs.

Few pollen-foraging bees visit lucerne, due to the small amount of pollen produced per flower. The pollen of other crops such as mustard, *Brassica nigra*, is often more attractive to honey bees. Hence, honey bees are only moderately effective as pollinators on large crops in Mediterranean climates, where very little alternative pollen is available. Conversely, the removal of nectar by honey bees from crops largely served by leafcutter and alkali bees, may reduce the propagation of these bees and thus perhaps also reduce seed yields.

8.11.4 Field, faba, tick or horse beans, *Vicia faba*

Field, faba, tick or horse beans are an important global "pulse" crop. The beans originated in Asia and remain a staple food in Arab countries. China accounts for over half of total production, while Egypt and Ethiopia combined produce about 5 percent of world supply. Brazil, Mexico, Morocco and Tunisia each produce about 1 percent. In 1981, Chinese yields amounted to 40 percent of global production, while Ethiopian and Brazilian yields (358 kg/ha) averaged 11–25 percent of the best European producing countries (3 200 kg/ha). Yields with pollinating bees may reach 4 520 kg/ha.

Faba bean is a legume crop that relies both on selfing and outbreeding. It forms seed readily without a pollinating bee, provided it comes from cross-pollinated seeds. However, plants from self-pollinated seeds form virtually no seed unless the flowers are cross-pollinated. Crops produce 20–80 plants/m^2, 50–80 flowers/plant and 13.5 million flowers/ha at peak flowering. Flowers can be pollinated for up to six days and pollen up to five days old will fertilize ovules. Flowers start to open at 12 °C and only open freely above 13 °C. The extrafloral nectaries are found on the underside of the stipules, and often have dark spots. In England, 8–20 percent of flowers on more productive crops form seed pods. Cross-pollination allows for setting of pods lower on the stem, accelerates setting and pod maturation, and reduces the duration of crop flowering and harvesting losses. Selfing increases plant losses in winter-sown crops. Outcrossing of 30–40 percent (out of a range of 4–54 percent) apparently represents an equilibrium, while selfing increases on later flowers further up the stem. The randomness of cross-bred seeds within pods suggests that cross-pollinating bees visit 67 percent of the flowers in England.

Some shorter-tongued bumblebee species of the subgenus *Bombus*, carpenter bees and apparently some ant species (at least *Cataglyphis bicolor*) make holes at the base of the broad bean to rob nectar. Nectar-collecting honey bees make use of these holes and, therefore, do not pollinate the flowers. Honey bees visit the extrafloral nectaries before any flowers open and continue to use extrafloral nectaries more intensively as flowering progresses. Honey bees collecting pollen visit the new flowers mainly between 13:00 and 16:00 hours, as they open. Pollen collection can decline after peak flowering. The daily percentage of bean pollen collected in honey bee hives near the crop varies depending on competing crops and inherent colony preference for bean pollen, with an average of about 20 percent (out of a range of 1–88 percent). In the Nile valley, broad bean is a primary pollen source for honey bees, suggesting the presence of appreciable numbers of effective pollinating workers on the crop. *Brassica napus* is an important competing pollen source for honey bees.

Low temperature during bean flowering can restrict both foraging by honey bees and the formation of seed in the early flowering crops of temperate zones. In England, crops covering up to 2 ha are considered to have sufficient wild pollinators, but crossing decreases with larger crops of 12–32 ha. Larger crops may require two to five honey bee colonies per hectare for pollination. In addition, cross-pollination at field margins can be almost twice the level within the field. Stocking with honey bees can therefore improve yield distribution within the crop. Experience in Australia suggests that crops may not need stocking with extra honey bees in areas with moderate temperatures and cool, dry winters, because the flowers open in late winter and early spring when honey bees must search for pollen. Milder temperatures also allow honey bees to be more effective pollinators. Longer-tongued bumblebees, *B. ruderatus, B. hortorum, B. subterraneaus, B. distinguendus, B. pascuorum, B. sylvarum, B. lapidarius* (in Europe), *B. borealis, B. griseocollis, B. vagans* (in North America) and solitary bees visit the front of the flower and pollinate, regardless of whether the bean flower has a hole at the base. The latter three European species and *B. rufocinctus* may sometimes use the hole at the base of the corolla. *Bombus ruderatus* is the only species that extends to Mediterranean climates in northwest Africa and subtropical climates in southern Europe and northern New Zealand.

The longest-tongued bumblebees visit the flowers about 2.5 times faster compared to pollinating honey bees, while other bumblebees visit about two times faster. For example, *Bombus hortorum* can visit about 1 800 flowers in a six-hour day. Using this figure, one longer-tongued *Bombus* or three to four pollen-collecting honey bees per square metre (given the likely shorter working day of honey bees) should fully pollinate a crop with 13.5 million open flowers/ha. However, this estimate needs to be verified under field conditions. The majority of the 13 or more bumblebee species of the subgenus *Fervidobombus* from Central and South America and the subgenera *Thoracicobombus* and *Megabombus* from Asia to the Middle East have tongues long enough to permit effective pollination of faba bean. Queens of *B. lucorum* and *B. terrestris* have long tongues, thus need not resort to piercing the bean flowers at the beginning of flowering, and even shorter-tongued species can be effective pollinators. Bumblebees forage at temperatures as low as 10 °C, however temperatures above 15 °C and no more than light winds favour foraging and nectar secretion.

In Egypt, long-tongued *Anthophora senescens* and *A. aegyptiaca* are common pollinators. The crop is also visited by *Andrena ovulata, Osmia submicans* and *Tetralonia lanuginosa*. Related solitary bees in France pollinate the flowers only slightly faster than honey bees. Male carpenter bees, *Xylocopa aestuans*, make a hole at the base of the flower to obtain nectar, but are not effective pollinators of faba bean.

8.11.5 Red clover, *Trifolium pratense*

Red clover is a perennial legume with high yield in temperate to subtropical climates that have a reasonably dependable annual rainfall above 600 mm. Red clover is mainly used for cattle forage and as a component in dairy pastures. It averages 100–120 flowers per flowerhead (raceme). Each flower has a slender tube measuring 8 mm to 10 mm long depending on whether the variety is diploid (shorter) or tetraploid (longer). Average to excellent crops produce 2–4 million flowering racemes/ha during the peak of flowering. Consequently, 3 600–7 200 flowers/m^2 need pollinating each day. If crops are not cut or grazed, they flower in early summer for a longer period (about 8–10 weeks) than those used to produce seeds for fodder (4–8 weeks flowering). Crops that begin flowering about midsummer normally have a higher intensity of peak flowering, more easily determined optimal harvesting and a better potential for high seed yields. Fully pollinated diploid crops can form seed on 80–90 percent of the flowers. At best, tetraploids tend to form seed on 70–80 percent of the flowers, due to ovule abortion. Diploid crops yield seed more reliably because the flowers can be pollinated more satisfactorily by honey bees and lucerne leafcutter bees, which can reach the nectar in the shorter diploid flowers.

Most temperate regions have shorter-tongued bumblebees of the subgenera *Bombus* or *Mendacibombus*, which bite a hole at the base of the flower to reach the nectar. There are no shorter-tongued bumblebees of these subgenera in highland regions of Africa or Central and South America, or the subtropical highlands in southwestern India. However, carpenter bees (*Xylocopa*) and wasps (*Ropalidia*) also make holes in flowers. Thus, red clover flowers are probably vulnerable to nectar robbing in highland areas of continental African, Asia Australia and India. The actions of nectar-robbing bees can be readily observed. The head of the bee is obscured among the flowers as it uses the hole, making no contact with the stamens or stigma. These holes are also used by nectar-collecting honey bees.

All longer-tongued bumblebees and pollen-collecting, shorter-tongued bumblebees forage from the front or top of the flower and make contact with the stamens and stigma. The whole body can be seen. The most effective bumblebee pollinators of red clover with the longest tongues, are found in 8 of about 30 *Bombus* subgenera as follows:

- *Megabombus: hortorum, ruderatus, argillaceus* (Europe to Asia);
- *Fervidobombus: fervidus, pennsylvanicus, dahlbomi* (North or South America);
- *Thoracobombus: pascorum, sylvarum, pseudobaibalensis* (Europe to Japan);
- *Diversobombus: diversus, montivagus* (East Asia);
- *Subterranobomus: subterraneus, borealis, distinguendis, appositus* (Holarctic);
- *Bombias: nevadensis, auricomus* (North America),
- *Seperatobombus: griseocollis, morrisoni* (North America);
- *Pyrobombus: vagans, ardens* (Holarctic, but only species with the longer tongues are effective in red clover pollination).

Species such as *B. dahlbomi* and *B. subterraneus*, which start colonies late in the season, tend to form small colonies. They become abundant only during part of the red clover flowering season.

At the start of flowering, 80–100 percent of honey bee foragers usually collect pollen from red clover. During main flowering, however, only 5–11 percent of honey bees and shorter-tongued bumblebees pollinate the crop. The difference in one study was due to an influx of nectar-collecting honey bees from adjacent white clover crops, as well as weeds that stop flowering as red clover comes into flower. Honey bees visit an average of 12 flowers/min – less than half the rate of longer-tongued species. Honey bee foraging on red clover declines below 25 °C and ceases altogether at 16–17 °C. Persistent low temperatures reduce honey bee foraging to 5.6 hours/day, compared to 10 hours for bumblebees. The cumulative effect is such that longer-tongued bumblebees visit about four times more flowers per day than honey bees. In the field, seed formation improves until bee numbers reach levels at which they pollinate each flower during a day. A predictive model estimates that 2 000–4 000 longer-tongued bumblebees/ha (or their equivalent) can pollinate the average and best crops at peak flowering. The model estimates that the usual combined honey and bumblebee populations may only pollinate up to one-third of the flower crop.

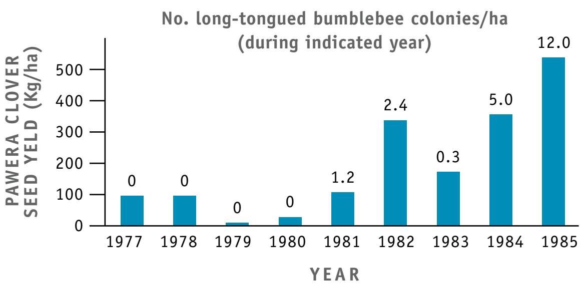
Crops that flower in early summer can arrive too early to assist colony development of late-season emerging bumblebees. Such crops receive competition for honey bees from lotus or white clover. Box gum trees and thistles (*Cirsium, Carduus*) act as complementary flowers for honey bees pollinating red clover, because honey bees mainly use these flowers for nectar. In the Murray basin, Australia, seed yields of up to 300 kg/ha are achieved on a tetraploid red clover where box gums are common and no bumblebees or carpenter bees exist. Detailed studies on lucerne and red clover crops in New Zealand also show that lucerne is a complementary crop for pollination of red clover by honey bees. Foxglove (*Digitalis*) may be a competing floral source for bumblebees during the early part of red clover flowering, but should probably not be removed near red clover crops, as this "competitor" is often used by longer-tongued bumblebees as a vital food source for colonies before most commercial crops are in flower.

Honey bee hives contain about 500–1 000 times more bees than colonies of longer-tongued bumblebees. Usually, 4–10 hives of honey bees/ha are recommended for red clover pollination. Studies on the same farm demonstrate that introducing up to 12 colonies of *Bombus horturum* and *B. ruderatus*/ha can result in an up to fivefold increase in seed yield. *Bombus hortorum* colonies are on average 50 percent larger than those of *B. ruderatus*. Estimated yields of between 500 kg to over 600 kg/ha can be obtained when only 5–10 colonies of *B. hortorum* are used per hectare (see Figure 8.9). Yields of 1 850 kg/ha have been achieved in Washington state, USA.

Bumblebee colonies mainly comprising *B. hortorum* have been commercially supplied to red clover growers in New Zealand. This process began in 1982 with hives occupied by queens in suburban sites with a favourable sequence of food supplies. It is also technically possible to rear some of the longer-tongued species. However, a colony of less than half that of *B. terrestris*, which is used for tomato pollination (producing poorer revenue returns compared to glasshouse crops) has so far resulted in acceptable pollination levels, thus inhibiting the development of a major supply of bumblebee colonies for red clover. The best prospects seem to result from the development of a farming system for suitable bumblebee species, especially in regions that lack the main colony enemies – *Psithyrus, Melittobia acasta, Vitula* and *Aphomia sociella*, all of which are difficult to control (see Chapter 11).

Figure 8.8

NUMBER OF LONG-TONGUED BUMBLEBEE COLONIES/HA (DURING INDICATED YEAR)



Source: R. P. Macfarlane.

Most regions are home to some effective solitary bee pollinators of red clover. They include *Osmia coerulescens* in Europe and the United States, *Xylocopa* in China and the Middle East, *Eucera socialis* in Japan, *Osmia bruneri, Melissodes* and *Tetralonia* in North America, and *Centris chilensis* and *Anthophora* in South America. The lucerne leafcutter bee can increase seed yields on diploid red clovers from 291 kg to 410 kg/ha.

8.12 ASTERACEAE (COMPOSITAE)

(20 000 species, 1 100 genera)

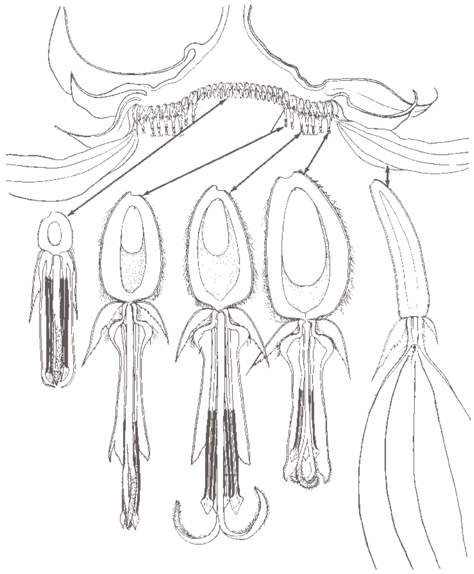
In Asteraceae crops, the close association of the tubular florets and outer ray florets make the inflorescence more conspicuous to bees, wasps, beetles, flies and moths that visit the flowers. Hummingbirds are among the visitors to some composite species often found in Neotropical highlands and páramo (alpine tundra ecosystems). The nectar of composites, unlike that of Apiaceae, is protected from rain by its position in the small, tubular florets. The weedy *Artemesia*, *Ambrosia* and *Xanthium* are wind pollinated, but Bathurst burr (*X. spinoosum*) provides a small amount of nectar and pollen for honey bees. The sunflower, *Helianthus annuus*, is the most extensively grown composite. Other Asteraceae crops such as artichoke (*Cynara scolymus*), chicory (*Chicorum intybus*), endive (*Chicorum endiva*) and lettuce (*Lactuca sativa*) produce smaller flowerheads in summer, allowing for more movement with fewer visits per head and, thus, better cross-pollination than with sunflowers.

8.12.1 Sunflower, *Helianthus annuus*

Sunflowers are grown in the temperate zone and subtropical and highland tropical South America, Asia, India and Africa. The major producers of sunflower are China, India, South Africa, Sudan and Turkey. Sunflower was first cultivated in northern Mexico and the western United States, and was grown mainly for oil, but also used for livestock feed and human food. It now forms part of the biodiesel industry.

Sunflower has 1 000–2 000 flowers/flowerhead, 100 000 flowerheads and 2–40 million flowers/ha. Each head flowers for 6–10 days. Stigmas may remain

Figure 8.9
SUNFLOWER – *HELIANTHUS* (SECTION OF FLOWERHEAD)



Source: S. E. McGregor. 1976. Insect pollination of cultivated plants. Agriculture Handbook No. 496. United States Department of Agriculture. Washington, D. C.

receptive for up to 14 days, but receptivity declines each day. A crop flowers for three to five weeks in summer to early autumn, and at least 70–90 percent of the flowers can form seed. In the United States, mainly male-sterile, apomictic sunflower varieties are used, even though male-fertile varieties can be more productive. Pollen and nectar are produced only during the male phase of the central disc florets.

The diversity of flower visitors to sunflower and its importance as a source of honey in parts of Africa, South America and the Indian subcontinent constitute evidence that sunflower is a relatively attractive flowering crop for bees. Higher levels of nectar lower the efficiency of individual pollinators because they spend more time on each head and floret. The major producing states in the United States have introduced 8-10 percent of the recommended 2.5 honey bee colonies/ha for maximum pollination. A linear model predicts that seed oil content would increase by 10 percent with 15 honey bees per 100 heads. Honey bees seldom collect pollen from sunflower and often clean and discard sunflower pollen from their bodies. A total of five to six honey bee visits/flower are needed to achieve maximum seed formation. At least five honey bees/flowerhead are needed for average yields (1 500 kg/ha).

In the highlands of southern India, *Apis cerana, A. dorsata* and *A. florea* account for 85 percent of flower visitors on sunflowers. Approximately 9 percent of the 412 bee species that have been recorded visiting sunflower in the western United States restrict all pollen and nectar collection to sunflower. Yields of up to 4 960 kg/ha are achieved where solitary bees are the main pollinators, compared with the US average of 1 460 kg/ha. Less than 1 000 sunflower leafcutter bees, *Megachile pugnata*, per hectare are needed for sunflower pollination. Four solitary specialist pollinators average 1.02–0.24 million pollen grains on their bodies, compared to 0.06–0.002 million for non-specialist honey bee, bumblebee and solitary bee pollinators.

Specialist sunflower pollinators, *Melissodes agilis, Andrena helianthi, M. pugnata, Svastra* and *Diadasia*, are more active earlier in the day than the generalist pollinators *Apis, Bombus* and *Halictus*. *Megachile agilis* and *Andrena helianthi* can cause seed set 5–11 times higher per visit than the honey bee. Bagged flowerheads with as few as seven visits produce 540 seeds, compared to 240 seeds for heads receiving over 100 visits per day. Seed set declines as the season progresses. Specialist sunflower pollinators form a greater part of the pollinating guild. Specialist solitary species seem to displace generalist pollinators from sunflower to other flowers such as onion, carrot, red clover and white sweet clover.

In South Africa, the long-tongued *Tetralonia* and short-tongued *Lasioglossum* visit sunflowers, while maize, grasses, *Xanthium* and *Clematis* act as competing pollen sources for honey bees. In Spain, 31 bee species have been observed on sunflowers. In India, 21 genera of insects have been found on sunflowers, while in Pakistan, *Andrena fulvicrus, Ceratina viridissima, Xylocopa dissimilis, X. rufescens* and *X. fenestra* are the main pollinating bees. Sunflower is a favoured food source for *Bombus lucorum* and *B. terrestris*, both of which extend to northern Israel, northern Iraq and Kashmir, while *B. terrestris* extends to northwest Africa.

8.13 SOLANACEAE

(2 800 species, 80 genera)

Solanaceous crops such as tomato (*Solanum lycopersicon*), sweet pepper and chillies (*Capsicum annum* and *C. frutescens*), tobacco (*Nicotiana tabacum*), eggplant (*Solanum melongena*), potato (*S. tuberosum*) and tamarillo (*Cyphomandra betacea*) originated in the Americas. They mostly have pendulous flowers that produce no nectar for foraging bees. Bees visit the flowers to gather pollen, which has the highest protein and nitrogen content among pollen varieties (see Section 2.3.2). Honey bees do not "buzz" or "milk" the anthers of any of the flowering plants, and thus are ill adapted to extract the food offered to bees by Solanaceae. In the field, however, honey bees and bumblebees are among the most frequent insect visitors to crops. Other frequently recorded visitors at crops include the bee genera *Amegilla, Centris, Exomalopsis, Xylocopa, Caupolicana, Hylaeus, Ptiloglossa, Stenotritus, Augochloropsis, Lasioglossum, Nomia* and *Protoxaea*.

8.13.1 Tomatoes, *Solanum lycopersicum*

One-third of all tomatoes are grown in Asia and India, 17 percent in Africa, 6 percent in Central America and 6 percent in South America. The highest yields are obtained in Europe and Japan where tomatoes are grown hydroponically in glasshouses. The major producers in the tropics are Brazil, China, Egypt, India, Indonesia and Mexico (see section 9.3.4 and Chapter 11).

European and North American studies on tomatoes and potatoes grown hydroponically find that shorter or medium-tongued bumblebee, *B. terrestris* (subgenus *Bombus*), and *B. impatiens, B. ternarius* and *B. vosnesenskii* (subgenus *Pyrobombus*) – which are more generalized in their flower usage – are better pollinators than longer-tongued bumblebees. The last group depend more on flowers from a few plant families. Honey bees can be somewhat useful in pollination of glasshouse tomatoes in winter, but as soon as flowers become available outside the glasshouse, the honey bees forage there instead. As they cannot ordinarily collect the pollen and there is no nectar, they are not avid foragers on these or any other solanaceous crops. Mechanical vibration of anthers is expensive and tedious for human operators, who may miss or damage flowers or suffer from allergic reactions to the pollen. Progress with pollination by bumblebees can be monitored, because within an hour a brown ring appears on the stamens where the bee has held the anther in its mandibles while vibrating the flower (see section 19.2). Each bumblebee can set more than 96 percent of fruit, resulting in 105–120 percent heavier fruit on average than fruit set with honey bees. In glasshouses, about eight to ten colonies of bumblebees are used per crop hectare.

In the field, the following bumblebees and other bees pollinate tomato flowers, shown here by region:

- Peru: *Bombus funebris, Centris surinamensis, Xylocopa brasilianorum, Anthophora arequipensis, A. tricincta, Exomalopsis bruesi, Augochlora matucanensis, A. nigromarginata and Lonchopria;*
- North America: *Anthophora urbana, Augochloropsis ignita;*
- Puerto Rico: *Exomalopsis globosa;*
- Guadeloupe: *Exomalopsis.*

One pollen-collecting bee observed each minute caused 40 percent of flowers to set fruit in Peru, compared to 10 percent in California. In Guadeloupe, 67 percent of pollen gathered by *Exomalopsis* came from the solanaceous crops of tomato, eggplant and sweet pepper (see also Chapter 4 and sections 7.3 and 9.3.4).

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See also: www.pollinator.ca/bestpractices

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Chapter 9

APPLIED POLLINATION AND SELECTED STUDIES

9.1 APPLIED POLLINATION IN AMERICA

D.W. Roubik

Farmers of both North and South America are making increasing use of bees. Statistics[4] on the value of agricultural production (including both plants and animals) provide the basic facts: seven of the top-ranked 21 agricultural production commodities include those benefited by bees and other pollinators. For example, the productivity of some varieties of soybean and cotton increases by approximately 20 percent when pollinated by bees.

The soybean *Glycine*, the tomato *Solanum lycopersicum*, the almonds *Prunus dulcis* and *P. amygdalus*, and lucerne or rape seed *Brassica* are the top earners among animal-pollinated crops, substantially above those that follow, including apples *Malus*, strawberries *Fragaria* and certain *Citrus*. In Central America, the top performers are beans (*Phaseolus*) and African oil palm (*Elaeis*) at the top, followed by coconut (*Cocos*), cotton (*Gossypium*) and peanuts (*Arachis*). There are similarities between South America and North America, with the Andean, Chilean, Argentine and Patagonian areas representing temperate and subtropical climes. The remaining regions located within the Tropic of Capricorn and Tropic of Cancer region present an array of animal-pollinated crops similar to Central America and Mexico. Soybean is overwhelmingly the most valued crop in South America (2010 data), at 20 times that of the next most valuable pollinated crop – beans, followed by cotton, sunflower (*Helianthus*), oil palm, peanuts and coconut. All of these plants are pollinated by insects, in most cases by bees.

The above value data consider the net, not the gross, yield. Such a ranking reveals something approximately similar to relative sustainability in economic terms – meaning that the owner, society or land manager is likely to be able and willing to provide the input necessary to prolong and sustain production. Economic and environmental sustainability are obviously different – one depends heavily on outside input and the other does not. In terms of short-term interests, however, the most profitable scheme is most likely to be that which is maintained. Another way to examine such data is the amount of total production – meaning the gross yield and the total arable land dedicated to the crop – and the length of time that land has been used for agriculture (including cattle culture and dairy farming), with fertilizer and other forms of management. What might be expected

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[4] FAOSTAT (faostat3.fao.org), accessed February 2014

if crops were rotated or if the land were to be left fallow or used to facilitate the buildup of pollinator populations? For more information on these questions see the Preface and other chapters in this book.

9.1.1 OVERVIEW

Constant habitat alteration and African (or Africanized – they were at one time clearly a hybrid) honey bees have greatly modified pollination ecology in the Western Hemisphere and nearly all of tropical America during the past 20–50 years.[5] At the same time, former small farms have been absorbed into larger holdings and are now managed by businesses, with smallholders becoming urban citizens (see Part I). This trend, which has been quite pronounced over the past decade, integrates formerly cultivated land into potentially regenerating natural vegetation – whether forest, savannah or grassland.

Since 1975, in French Guiana, where there is essentially a natural habitat and no apiculture, Africanized and native bees have interacted and overlap broadly in range and food choice. This has not led to a steady decline of the latter, although the former, near towns, seem more abundant than ever. In much broader forest areas, occurrence of the Africanized honey bee is more sporadic and the bee is notably less abundant, although a 150-km trip by air into any remote area is liable to reveal early morning foraging by the Africanized bee on grasses and other open-habitat vegetation, next to the airstrip.

Prior to spread of the African honey bee from southern Brazil after 1956, perhaps 6 million hived colonies of European honey bees of the largely African species *Apis mellifera* were kept in the Neotropics. They were not normally deployed in pollination, but instead used in honey and wax production, or hive products such as pollen or royal jelly. Applied or managed pollination at the level of rented hives was uncommon. No large feral honey bee population existed independent of apiaries. The feral colonies of European origin were the result of "apiary fallout" and soon perished, either by predation or starvation, except in highly modified agro-ecosystems within the tropical highlands (approximately 700 to 2000 m in elevation). This remains the scenario at the time of writing (September 2014).

Until the 1980s, only a few places had a high density of managed honey bee colonies originally from Europe (one to ten colonies/km^2). These included parts of the Yucatán peninsula, El Salvador, and the subtropics of southern Brazil and northern Argentina. As a rule, honey bees were completely absent in the Amazon basin, and in humid or rainy tropical lowlands and mountains between Buenos Aires, Argentina, and Veracruz to Tampico, central Mexico. Today, *Apis mellifera* of European origin exist in temperate areas and some islands of the Americas, while those of African origin assimilated all apiary bees from Europe and are the only resident honey bees. The latter are clearly mostly African, not a hybrid intermediate in their behaviour or ecology, compared to the European honey bees.

Until recently, the Africanized honey bee and European *Apis mellifera* present since European colonial times were not important in the agricultural scheme in much of the Americas. In a summary of the known bee species in the Neotropics, Moure *et al.* (2013) place total bee species in the Neotropics near 6 000, with an estimated number of 3 700 in Brazil. In North America and the southern temperate zone of South America, approximately 5 000 bee species are present. But not all bees are equal, at least in agriculture. Honey-making bees consisting of *Bombus* and Meliponini number over 500 species, and there are also honey-making wasps such as *Brachygastra and Polybia*. Today, there are, conservatively, two to ten "wild" Africanized honey bee colonies/km^2, on average, covering an area of approximately 20 million km^2. This is at least ten times the number of European apiary colonies maintained in the American tropics and subtropics up until the 1970s. Virtually no European colonies remain, even though their range was less than 10 percent that of the current range of Africanized honey bees.

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[5] See Roubik (2009) for a summary of the advance and proliferation of the Africanized honey bee.

Figure 9.1
AFRICANIZED HONEY BEES ARE PRIMARILY USED FOR HONEY OR WAX AND ARE RARELY MANAGED FOR POLLINATION IN THE NEOTROPICS

Source: Photo in Chiriquí Province, Republic of Panama, courtesy of Eric Tourneret

In North America, fewer honey bees live in the wild than previously, due to mite parasites and pesticides (see Chapters 1, 4 and 16). However, the overall number of honey bees in the Americas has greatly increased. The majority (those in the tropics and subtropics) are a different "ecotype" from the original African subspecies, *Apis mellifera scutellata*, introduced in 1956. Most importantly, they are widespread, rather than isolated in apiaries, but seem most abundant in drier or subtropical agricultural areas where there are more people and buildings in which to make nests and fewer large predators of bee colonies.

Africanized bee immigrants *may* have caused the demise of some native bees, such as species of *Melipona*, which are honey-making meliponine bees similar in size to *Apis*. The floral specialists or "oligoleges" on rosids (a large order of flowering plants) are likely to have sustained a population decline due to honey bee competition. However, there are no long-term data to validate this assertion. Conversely, a 17-year study in the Yucatán peninsula and a 30-year study in French Guiana show little evidence of a decline in *Melipona*. In Yucatán, over-large meliponary size (intraspecific competition) and the abandonment of ancient husbandry techniques for this bee species have had a significant impact. However, in truly wild habitats, no obvious decline is apparent. In addition, the numbers of managed bee colonies are stable for nearly half of stingless beekeepers, and the presence of relatively more disturbed habitats, and presumably of honey bees in that environment, had little impact. The foraging native bees were able to rapidly decide which flowers to visit and to avoid competition with Africanized honey bees, thus partitioning floral resources with that invasive colonial bee.

The fact that so many cultivated plants used in tropical countries originated in the Neotropics[6] does not mean that their reproductive biology has been better studied there (see especially Purseglove's (1968, 1972) treatments of tropical crops). Applied pollination technology in tropical America is mostly devoted to exotic species grown there, such as canola (lucerne or rapeseed), coconut, coffee, citrus, cotton, mangoes, melons, watermelon, apples, peaches and cardamom. European honey bees have been used in tropical America for commercial pollination of nearly all those crops. However, they have been replaced by African and "Africanized" honey bees, even as managed pollinators (sections 7.2 and 9.3.7). Many Neotropical flower visitors still play a part in pollination, but have yet to receive recognition or, in most cases, adequate field study. The native crops, fortunately, still seem to have sufficient native pollinators to service them. At present, there is no urgent need to bolster propagation, seed set and fruit production of those indigenous species through management schemes or other means.

Many forest crops in the tropics come from America. Notable among them are the Brazil nut (*Bertholletia*) (see section 9.3.1), rubber (*Hevea*), Pejibaye palm or chonta dura (*Bactris*), kapok (*Ceiba*), vegetable ivory (*Phytelephas*), chicle (*Manilkara*), nanche, nance, or mirici (*Byrsonima*), hog plum (*Spondias*), prickly pear or nopal (*Opuntia*) and the piquis (*Caryocar*). As elsewhere in the tropics, native palms such as *Bactris, Acrocomia, Attalea, Astrocaryum, Ceroxylon, Chamaedora, Elaeis, Iriartea, Jessenia, Mauritia, Maximiliana, Oenocarpus, Orbygnia, Phytelephas, Scheelea* and *Syagrus* provide many useful products that are not exported. These are among the most valuable of all plants but infrequently produce cash crops or revenue (see also section 9.3.10). Their breeding systems often involve dioecy (males and the female fruit-bearing plants are separate) and the main pollinators are flies, beetles and bees. Honey bees and stingless bees may visit these plants in large number, but are often merely thieves. They never visit female inflorescences and therefore play no active role in pollination.

A few native Neotropical crops like pineapple (*Ananas*), and non-native crops such as banana (*Musa*), some mangoes (*Mangifera*), and certain oranges and tangerines (*Citrus*), have no pollination requirements. They propagate vegetatively and are parthenocarpic; however, most crops require pollinators. Native Neotropical crops grown on other continents are numerous. Among the most important are cacao, sunflower, passion fruit, chilli peppers, sisal, annatto, cashew, soursops, peanut, star apple, papaya, quinine, chayote, rubber, gourds and squash, tomato, guava, certain cotton, potato, sunflower, vanilla, sweet potato, cassava, tobacco, guayule, avocado, the common bean, pimento, mesquite, physic nut (*Jatropha curcas)* and jojoba.

None of these plants were dependent in any way on honey bees, because *Apis* was not present in tropical America until the late 1600s. Almost certainly, no *Apis* bees were widespread in tropical areas until the last half-century or so, since the release of *Apis mellifera scutellata* from South Africa in Brazil. Natural selection and evolution produced by interactions between plants and a flower visitor, such as honey bees, could result in only small changes to plants and their breeding system, floral morphology, nectar and pollen production, or other characteristics – if any – in such a short time.

Nonetheless, for native American plants, outcrossing by bees seems the most common mode of reproduction. This is not surprising considering that many more bee species live in the Neotropics than in other equatorial regions. Neotropical bees are estimated at > 4 000 species including > 500 that are perennial and social, and perhaps 100 more that are social, but not perennial. However, modes of crop reproduction vary widely and incorporate all pollinator groups, as indicated by the reports in this book. The pollination of major cultivated plants in the Neotropics is reviewed below, emphasizing the native species of flowering plants (see also Parts II and III).

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[6] See Roubik (1995), Appendix I.

9.1.2 Plant genera and pollination

***Agave* – sisal, henequen (Asparagaceae – Agavoideae):** *Agave sisaliana* and several other species are cultivated for fibre in Mexico and Central America where they originated, and also Africa, Asia and the Philippines, often for local use. Flowers are pollinated at night by bats including the genus *Leptonycteris*, but are also visited during the day and pollinated by larger bees such as *Xylocopa*, *Mesoxaea* and others. Individual flowers are hermaphrodite but pollen is shed before stigmas are receptive. Selfing within a flower does not occur, but selfing within inflorescences is possible because flowers open sequentially over a period of days. Individual inflorescences provide a significant level of pollen and nectar resources, thus introduced social bees such as *Apis* forage in large numbers.

***Anacardium* – cashew (Anacardiaceae):** *Anacardium occidentalae* is a small tree that produces a fruit with a swollen fruit stalk. The latter is roasted and exported as a nut crop extensively in Asia and the Neotropics, while the former is sold locally as an edible fruit. Cashew is insect-pollinated, but is not often visited by bees because of its tiny flowers and the miniscule amount of nectar it produces. However, bees appear to be the major pollinators, with additional pollination by flies. Flowers are both male and hermaphrodite, with the former shedding pollen earlier in the day. Self-compatibility and selfing have been shown, but cross-pollination greatly improves fruit production, and the breeding system favours outcrossing.

***Annona* and *Rollinia* – soursop and biribi (Annonaceae):** *Annona* and *Rollinia* are small trees that have hermaphrodite, pollen-only flowers in which the stigma is receptive well before anther dehiscence. Selfing is rare, flowers are self-compatible and outcrossing is the rule. Visitors and pollinators have seldom been observed but include beetles, especially the dynastine scarab, *Cyclocephala* and Chrysomelidae.

***Arachis* – peanut (Fabaceae):** *Arachis hypogaea* probably originated in Bolivia where 30 species exist. Being tetraploid, *Arachis* is not a wild species

Figure 9.2
CASHEW – *ANACARDIUM*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

Figure 9.3
BIRIBI – *ROLLINIA*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

and derived from crossing between diploid species. Cultivars of three groups are grown throughout the tropics and subtropics, with Asia surpassing Africa and America in production. Crops are ordinarily self-pollinating and self-fertile, but the original pollinators are thought to be xylocopine and megachilid bees. Indeed, some varieties are mechanically incapable of selfing, and the hermaphrodite flowers must be visited by an insect. Thrips serve as pollinators in parts of Africa, but the main cross-pollinators are bees of many different kinds.

Bertholletia (see section 9.3.1).

***Bixa* – annatto (Bixaceae):** *Bixa orellana* is a pollen-only flower originally from the lowlands of Ecuador and the eastern Andean slopes. The breeding system of this small tree has not been studied in detail, but self-compatibility with outcrossing by bees, primarily *Melipona*, has been studied in large accessions of several varieties in Costa Rica, in the wild in Ecuador and in Brazil (Roubik, unpublished data). Seeds are coated with a red-orange dye used by the food and cosmetics industries, which is exported by Brazil, East Africa, Ecuador, India, Jamaica, Panama and Peru. Flowers are visited heavily in the early morning by *Melipona,* especially *M. fallax, M. fuliginosa* and *M. titiana* in their respective regions, and are also pollinated by a variety of euglossines including *Eulaema* and *Euglossa*, as well as *Epicharis*, *Xylocopa* and small meliponines. Where those bees are absent, halictid bees such as *Augochlora* and *Pseudaugochloropsis*, visit the flowers. Honey bees do not find this flower attractive and seldom forage there.

***Cajanus* – pigeon pea, juandú (Fabaceae):** *Cajanus cajan* is a shrub that spread to Africa after domestication in southern India 3 500 years ago, and is now widely cultivated on a small scale in Africa, Asia, and subtropical and tropical America. Flowers are cleistogamous (spontaneously self-pollinating) before the flower opens, but are afterwards visited by bees and are outcrossed to a small extent.

Figure 9.4
ANNATTO – *BIXA*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 503. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

***Capsicum* – chilli pepper and green pepper (Solanaceae):** *Capsicum annuum* and *C. frutescens*, sometimes considered one species, are originally Neotropical. Mexico and Peru account for 2–4 percent of global production of dry chillies (sold as spice), while China and India account for 45 percent of world production. Several African and Asian countries – Bangladesh, Côte d'Ivoire, Egypt, Ethiopia, Ghana, Myanmar and Viet Nam – produce dry chillies on a scale similar to that of the above-mentioned Neotropical countries. China is by far the largest producer of fresh chiles at 33 percent, followed by Mexico and Turkey (5 percent each), then Indonesia, Spain and the United States (2–4 percent; FAOSTAT 2013). The flowers are hermaphrodite but stigma receptivity precedes anther dehiscence, thus favouring outcrossing. The stigma is beyond the reach of anthers, which makes selfing unlikely. The main pollinators are solitary bees such as the communally nesting *Exomalopsis*, as well as the social bees, *Bombus*. Pollen is also gathered by small stingless bees such as *Tetragonisca* and small halictids, although they are probably not effective pollinators. A large variety of Neotropical bees visit the flowers of *Capsicum*. The flowers produce nectar, but the anthers of *Capcisum*, like other Solanaceae, are poricidally dehiscent. Pollen is often the only reward to visitors of flowers with poricidally dehiscent anthers, and it is only collected effectively by certain kinds of bees, excluding honey bees. However, the nectar of the chilli flowers makes them attractive to honey bees, as well as flies, all of which pollinate.

***Carica* – papaya (Caricaceae):** *Carica papaya* is a small tree that may produce good crops for a few years. Fruit is consumed locally and is seldom sold at external markets. The two major producers are Brazil and India, which represent over half of global production. However, several countries account for 1–2 percent of production worldwide, including Bangladesh, China, Colombia, Cuba, Democratic Republic of Congo, Peru, Philippines, Thailand and Venezuela, while Dominican Republic and Mexico produce 6–7 percent of the annual papaya crop (FAOSTAT, 2013). Both male and hermaphrodite flowers are present, usually on different trees, and also at different times on the same plant. Some cultivars, such as "Solo" are gynodioecious, including some individuals that are strictly female. One male tree for every 25 females is recommended for adequate fruit set. The main pollinators are hawkmoths, *Hyles* and other species, but some hermaphrodite flowers readily self-pollinate, and apomixis cannot be ruled out for some cultivars. Nectar is provided only by male flowers, which are visited by sunbirds (Old World tropics), hummingbirds (Neotropics), bees, flies and hesperiid butterflies (*Perichares*). Only hawkmoths (Sphingidae) and butterflies have been observed consistently visiting both male and female flowers when stigmas are receptive (see section 7.3.1).

***Cinchona* – quinine (Rubiaceae):** The bark of *Cinchona* and its several cultivated South American species constitute a source of drugs used against malaria, fever and cardiac arrhythmias. Vegetatively propagated hybrids are cultivated mainly in Bolivia, Ecuador, India, Indonesia, Peru and Zaire. Flowers are hermaphrodite and dimorphic, having either protruding stamens or stigmas. Accordingly, they require cross-pollination, purportedly by flies, bees or butterflies.

***Citrullus* – watermelon (Cucurbitaceae):** *Citrullus lanatus* is native to Africa and is now widely cultivated in the Americas. Honey bee hives near crops improve fruit set. Flowers on a single vine are male or female, although some cultivars have hermaphrodite flowers that are self-fertile but not self-pollinating. Studies in India have found that honey bees and *Tetragonula*[7] frequently collect nectar and pollen at flowers. In Kenya, honey bees and *Lasioglossum* are effective pollinators (Njoroge and Ngumi, 2010).

***Citrus* – oranges, etc. (Rutaceae):** These small Asian trees are widely cultivated throughout tropical and subtropical America. To produce seeds, *citrus* requires a pollinator, however the same is not always true for fruit production. Agamospermy, the formation of embryos through asexual reproductive process without the formation of gametes (by gametogenesis) and the act of fertilization, is common. Breeding systems vary greatly between species. Endosperm may be initiated by fertilization and normal pollination, but shortly thereafter an apomictic embryo invades the embryo sac, outcompeting the sexually produced embryo. Flowers may be self-pollinating (see section 2.1). Citrus farmers in the Neotropics use honey bee colonies, now solely Africanized honey bees, within extensive plantations.

***Cocos* – coconut (Arecaceae):** This southeast Asian palm is visited heavily by honey bees and stingless bees, and even by day-flying moths (*Urania*) for its nectar. While the bees collect pollen, wasps and other insects also arrive and, along with bees, collect nectar. Separate male and female flowers are borne on the same inflorescence. Hives of honey bees are used

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[7] Not *Melipona*, as given in the older literature, as this genus does not exist in the Old World.

for pollination in plantations. Although pollinators increase fruit set, another major pollinating agent is wind, and selfing is insignificant.

Figure 9.5
COCONUT – *COCOS*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

***Coffea* – coffee (Rubiaceae):** *Coffea arabica* is one of nine originally African cultivated species (out of 60 species in the genus), and is the only tetraploid. It is probably, therefore, an artificially selected hybrid. All diploid species are self-sterile and require outcrossing, usually performed by bees and also by wind. Large Neotropical producers of *C. arabica* are Brazil and Colombia, while Costa Rica and Mexico are considerably smaller exporters. Viet Nam, with three annual harvests, is second to Brazil (FAOSTAT, 2013). Hives of honey bees are introduced into the extensive coffee plantation areas and are generally believed to improve yield. One hive each 100 m is recommended. However, flowers are hermaphrodite, self-fertile and autogamous. They may also be amphicarpic, which means that some flowers require visitation and outcrossing, while others do not. Studies on enhancement of production through cross-pollination by bees are fairly numerous, and insect visitors do in fact greatly enhance seed set and fruit maturation. Some plants are heterostylous. Many bee species and genera gather pollen or nectar at the flowers – mostly *Apis*, meliponines and halictines, but also euglossines, bombines and centridines.

***Cucumis* – melon and cucumber (Cucurbitaceae):** The fruits of *C. anguria* (Asian in origin) *C. melo* (African) and *C. sativus* (South Asian) are either cooked or eaten raw, and all but the first are cultivated worldwide in the tropics. Honey bee hives are introduced to improve yield, and bees in general are strongly attracted to the nectar and pollen of the flowers. Flowers are male or female, but some plants have hermaphrodite and male flowers. Plants are self-compatible but insect visitors are required, with honey bees the most common. One foraging honey bee for each ten hermaphrodite flowers is recommended to obtain full fruit set. Efficient pollination of cantaloupe and sweet melon in the Neotropics should require two to three honey bee colonies per hectare.

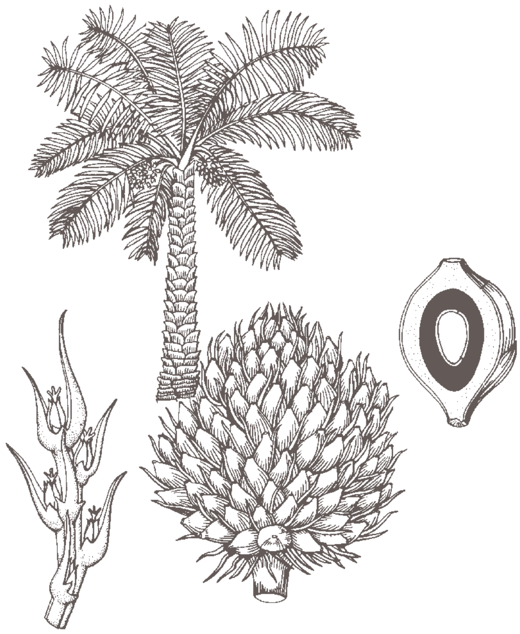
Figure 9.6
CUCUMBER – *CUCUMIS*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

***Cucurbita* – squash and gourds (Cucurbitaceae):** *Cucurbita pepo* and three other cultivated species out of a group of about 25 species, all Neotropical, originate from Mexico. The herbaceous running vines dispersed both north and south of their point of origin along with their 20 species of pollinators, solitary bees of the genera *Peponapis* and *Xenoglossa*. The flowers are male or female, and are apparently not self-compatible among flowers of one plant, therefore outcrossing by bees is required. Both large and small carpenter bees, *Xylocopa* and *Pithitis*, and *Apis*, among many other bee genera, also pollinate the flowers. Two to four hives of *A. mellifera* per hectare are used for pollination.

***Elaeis* – African oil palm (Arecaceae):** *Elaeis guineensis* is primarily a vegetable oil crop cultivated extensively in western Africa and southeast Asia, but is now planted in large areas in lowland Costa Rica, Colombia and Ecuador, sometimes near congeneric species native to America with which it produces fertile hybrids. Bees visit the male inflorescences to collect pollen and are not pollinators, while beetles of the families Curculionidae (*Elaeidobius*, several species) and Nitidulidae (*Mystrops*) visit both male and female flowers and are responsible for almost all fruit set (see section 9.3.10). The crop is harvested for biofuels (see section 9.3.9 on *Jatropha*).

Figure 9.7
OIL PALM – *ELAEIS*



Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

***Gossypium* – cotton (Malvaceae):** Neotropical *Gossypium hirsutum* and *G. barbadense* are the world's most extensively cultivated cottons among the 12 cultivated species and varieties, the oldest of which is African. Indigenous species are found throughout the tropics and subtropics. Both extrafloral and floral nectar attract pollinating bees, wasps and other insects. Flowers are largely self-pollinating and outcrossing is minimal, but it does improve yield (section 9.3.3). In tropical America, *Exomalopsis*, *Melissodes* and other solitary bees appear to be the most important native pollinators, but *Apis, Bombus, Xylocopa* and a few other insects also are pollinators.

***Helianthus* – sunflower (Asteraceae):** *Helianthus annuus* is native to the Americas and is exported largely from Argentina (5 percent of global production). However, it also grown worldwide with Ukraine and the Russian Federation accounting for 44 percent of production, followed by Romania, China, Bulgaria, Turkey, Hungary and France (4–5 percent; FAOSTAT, 2014). As with composite flowers in general, it is visited by a wide variety of native bees that may specialize in its pollen and nectar. As pollinators, the larger solitary bees and *Bombus* are undoubtedly the most important pollinators, but all *Apis* species visit flowers. The non-hybrid varieties can self-pollinate but benefit greatly from outcrossing by bees. *Helianthus* is also a biofuels crop, and is therefore not grown just for human consumption.

***Hevea* – rubber (Euphorbiaceae):** *Hevea brasiliensis* is the most important of all natural, commercial elastomers. Originating in the Brazilian Amazon, it is now distributed widely for commercial use in lowland equatorial wet forests. Flowers are either male or female, and self-pollination (strictly dependent on pollinators) within an inflorescence is approximately 10–20 percent as productive as cross-pollination. Flies of the genera

Dasyhela, Artrichopogan, Forcipomyia, Stilobezzia and *Culicoides* are the main pollinators. Some stingless bees collect pollen, both in the New World and the Old, but provide minimal pollination. *Apis* often fail to collect the pollen or visit only the extrafloral nectaries, and very seldom visit the female flowers. No species of *Apis* appears to be a reliable pollinator of this crop.

***Ipomoea* – sweet potato (Convolvulaceae):** *Ipomoea batatas* is widely cultivated, with thousands of cultivars among three cultivated species. Production is highest in Asia, followed by Africa and is lowest in tropical America, where the crops originated. Hermaphrodite flowers open in the evening and can be pollinated until early the following morning. Self-incompatibility and cross-incompatibility are known, and cross-pollination (perhaps including nocturnal pollinators) is needed for seed set. Some apparently obligate visitors of the genus in the Neotropics are *Melitoma* and *Ancylosceilis*, and *Melissodes* visit the flowers where the former, native bees are absent. Many other bees occasionally visit the flowers.

***Mangifera* – mango (Anacardiaceae):** *Mangifera indica* is among more than 60 Asian species, five others of which are cultivated commercially (see section 9.3.6). One or two fertile stamens occur on the hermaphrodite flowers, and male flowers have an aborted pistil. Stigmas are immediately receptive and self-pollination occurs, but only when visited by a pollinator or otherwise transported. As with *Citrus*, agamospermy is the rule, but endosperm tissue only results from pollination, regardless of whether the embryo is a clone of the female parent plant. Some cultivars, at least in Mexico, are often kept with hives of honey bees to ensure adequate fruit set. Flies and bees are the major pollinators, where pollinators are necessary, but visitors are rare on the flowers.

Figure 9.8
MANGO – *MANGIFERA*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

***Manihot* – cassava, yucca, manioc, tapioca (Euphorbiaceae):** *Manihot esculenta* is among 200 Neotropical species, and is grown throughout the tropics, but nowhere known in the wild. Africa is the largest producer, followed by Asia and then the Neotropics. Flowers are either male or female and outcrossing by bees is enforced by lack of synchrony in opening by male and female flowers on an inflorescence. *Trigona* and other small to medium-sized meliponine honey bees commonly collect nectar and pollen from the flowers.

***Nicotiana* – tobacco (Solanaceae):** *Nicotiana tobacum* (and probably the eight other cultivated species) is self-pollinating, but hummingbirds, butterflies, bees and other insects seeking its nectar cause outcrossing. Stigma and style lengths vary among cultivars, thus influencing the chances of selfing. Self-compatibility is likely prevalent, and cross-incompatibility has also been found. Pollen from the parent plant is at a disadvantage compared to that of other plants, which produce pollen tubes that grow much faster to reach the ovary. Some male-sterile varieties used for seed production require outcrossing, provided by *Bombus* and *Apis* among others.

Figure 9.9

YUCCA – *MANIHOT*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

Figure 9.10

TOBACCO – *NICOTIANA*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

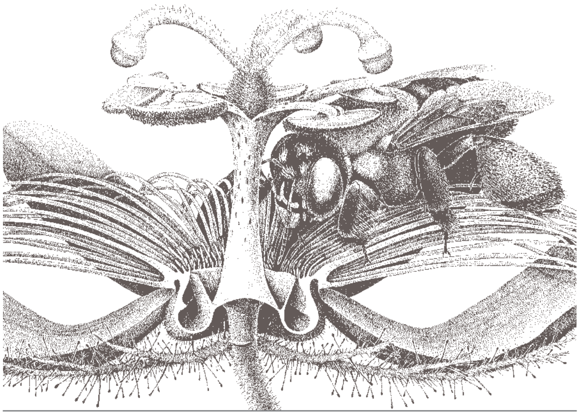
***Opuntia* – nopal, prickly pear (Cactaceae):** *Opuntia ficus-indica* is commercially cultivated in drier tropical areas and originated in Mexico. Some species, such as *O. aurantiaca,* are agamospermous. The main pollinators are probably birds and bees.

***Parthenium* – *guayule* (Asteraceae):** *Parthenium argentatum* originated in subtropical northern Mexico and is cultivated in the dry tropics as an elastomer crop. Both the rubber content of seeds and seed production increase with cross-pollination. The hermaphrodite flowers are self-incompatible, with *Apis* an adequate pollinator, although the most important native pollinating insects are unknown.

***Passiflora* – passion fruit (Passifloraceae):** *Passiflora edulis* is the most commercially successful of 500 species of climbing vines native to most of the mainland tropics, nearly all of which are Neotropical. *Passiflora edulis* var. *edulis* (purple granadilla) is grown in tropical highlands and the subtropics, while *P. edulis* var. *flavicarpa* (yellow granadilla) is better suited to lowlands (see also Chapters 15, 9.3.2). The large flowers are visited by a variety of bees and other insects, and also some hummingbirds and bananaquits. Larger bees that visit and consistently pollinate *Passiflora* in the Neotropics are *Xylocopa* and *Ptiloglossa* – *Xylocopa* is also the principal Asian pollinator. Very few flowers are autogamous, and self and cross-incompatibility within clones are common. Cross-pollination greatly improves fruit set and quality. Honey bee hives are sometimes used to enhance pollination, but management of *Xylocopa* is now a reality (see Chapter 15).

Figure 9.11

***CENTRIS* VISITING *PASSIFLORA* (SECTION)**



Source: J.M. F. Camargo original drawings, reprinted by permission of artist and publisher. Presented in: G. Gottsberger, J. M. F. Camargo, I. Silberbauer-Gottsberger. 1988. Bot. Jahrb. Syst. 109:459-500. [from original 1995 FAO book]

***Persea* – avocado (Lauraceae):** *Persea americana* is produced mainly in tropical America, where there are three main groups of cultivars. Mexican cultivars have smaller fruits and are adapted to poorer growing conditions; Guatemalan are larger with rough skin; and West Indian are the largest with smoother skin, but are much less resistant to cool temperatures. The largest share of world production comes from Central Mexico at 30 percent, with another 8 percent from Dominican Republic, and 2–6 percent (total 24 percent) from Brazil, Chile, Colombia, Peru, the United States and Venezuela. In Africa, Kenya accounts for 4 percent, and the top producer in Asia, Indonesia, represents 5 percent of global production (FAOSTAT, 2013). The hermaphrodite flowers exhibit two flowering schedules: the stigmas are receptive on the morning of the first day and shed pollen on the afternoon of the second, or the stigmas are receptive only on the afternoon of the first day and shed pollen on the morning of the second. Cultivars of both are needed to ensure pollination, even though the receptive periods and pollen availability overlap slightly for the two flower types. Cultivars vary from self-compatible to self-incompatible, but cross-pollination always improves production. Bees, bats, wasps and flies are pollinators in different parts of the world. *Geotrigona* (Meliponini) and *Trigona nigerrima* are the main pollinators in Mexico, Guatemala and areas of origin (Roubik, pers. obs.). Honey bee colonies are stocked at densities of two to three colonies per hectare to maximize fruit set.

***Phaseolus* – common bean (Fabaceae):** *Phaseolus vulgaris* is one of seven Neotropical bean species cultivated widely. Flowers self-pollinate upon opening but remain receptive and can be fertilized with pollen from other plants during eight hours. Búrquez and Sarukhán (1980) have conducted extensive studies of native pollinators. Many different bees can cross-pollinate the flowers (see Chapter 8.11 on dry beans).

***Sechium* – chayote (Cucurbitaceae):** *Sechium edule* is a perennial vine whose main product is the fruit, which is eaten cooked. Outcrossing is needed because the flowers are either male or female, with female flowers more attractive to visiting bees and wasps. Small bees are by far the most frequent visitors in Costa Rica and include primarily meliponines, genera *Trigona* and *Partamona*. Honey bees very seldom visit the flowers.

Figure 9.12
AVOCADO – *PERSEA*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

***Simmondsia* – jojoba (Simmondsiaceae):** *Simmondsia chinensis* is a native subtropical shrub of the southwestern United States, which is dioecious and produces seeds yielding wax and oil. The largest producers include Argentina, Australia, Brazil, Costa Rica, Israel, Mexico, Paraguay and the southwestern United States. The flowers are pollen resources for bees, and honey bees contribute to pollen dispersal by enhancing wind pollination when landing on flowers to forage.

***Solanum* – eggplant, tomato, potato and naranjilla (Solanaceae):** *Solanum* species have hermaphrodite or andromoneceous flowers, which produce pollen but no nectar. Several species from South America are extensively cultivated, with *Solanum quitoense* – lulo and narajilla – cultivated principally in the highlands of Costa Rica and Ecuador. The principal pollinators are *Bombus* and *Eulaema*, but few detailed studies have been made. Flowers are self-compatible but require visitation by buzz-collecting bees. *Solanum melongena* (eggplant) has hermaphrodite flowers displaying heterostyly, and some flowers are able to self-pollinate (see section 7.3.4). Certain cultivars are male-sterile, thus hybrids require bee outcrossing to produce seed. One genus of bee that effects outcrossing is *Exomalopsis*, while honey bees fail to buzz-collect pollen and find no nectar at flowers, making them poor pollinators. *Solanum tuberosum* (potato) is often self-pollinating, but self-incompatible and male-sterile cultivars are known. Seed production improves with outcrossing. Few bees find the amount of pollen offered per flower a sufficient award for cross-pollination, but tentative visits by *Bombus* and *Apis* have been observed. Tomato has dozens of native pollinators in the Neotropics, many of which belong to *Exomalopsis*, and greenhouses can utilize both *Bombus* and *Melipona* (see Chapter 8.13.1, and Chapters 11 and 13).

***Solanum* – tomato (Solanaceae):** *Solanum lycopersicum* (formerly *Lycopsersicon esculentum*) is one of six tomato species, all native to western South America and the Galápagos. Tomato is a pollen-only producing flower visited by bumblebees, the larger halictids and additional buzz-collecting bees of the Apidae family. Flowers are self-fertile and may self-pollinate through the action of wind or shaking, but cross-pollination is favoured by stigmatic receptivity before anthers dehisce. Parthenocarpic fruit is sometimes produced. *Solanum quitoense* (formerly *Cyphomandra quitoense*) – lulo or naranjilla – is pollinated by bumblebees in its native Andes.

***Theobroma* – cacao (Malvaceae-Grewioideae):** *Theobroma cacao* is a small tree among several species cultivated principally in Brazil, Malaysia and West Africa. Flowers are hermaphrodite, but selfing is impossible due to separation of anthers and stigma. Self-incompatiblity has also been shown. The principal pollinators are flies, *Lasioshelea* and *Forcipomyia* (Ceratapogonidae) (see Frimpong *et al.*, 2011).

Figure 9.13
SOLANACEAE NATIVE TO THE NEOTROPICS – TOMATO, CHILLI PEPPER AND EGGPLANT- *CAPSICUM* AND *SOLANUM*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

Figure 9.14
CACAO – *THEOBROMA*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

***Vanilla* – vanilla (Orchidaceae):** At least two of the crop species, *V. planifolia* and *V. pompona*, originated in southern Mexico and Central America, where the principal pollinator is the euglossine bee, *Eualema*, and in particular the smaller species *polychroma, speciosa, marcii* and *nigrita*. The pollen masses form a triangular wedge carried on the bee's scutellum, which is easily identified in the field. Only outcrossing produces fertile seed. The flowering schedule of this plant, at least in nature, is not well understood and does not occur yearly. References in the literature to *Melipona* as a primary pollinator are based either on incorrect identification or an aberrant occurrence. *Melipona* does occasionally visit the orchids *Maxillaria* and *Xylobium*, but far less than other stingless bee genera.

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9.2 APPLIED POLLINATION IN ASIA AND AFRICA

P.G. Kevan and J.K.S. Mbaya

The requirements for pollination of crop plants by insects worldwide are presented in several encyclopaedic volumes that summarize the state of knowledge on a crop-by-crop basis. These books by J.B. Free (1970 and second edition, 1993), S.E. McGregor (1976) and D.P. Abrol (2012) are indispensable as reference material both for the development of beekeeping and the roles of bees and other animals in pollination. What also emerges from these books is the current lack of knowledge about tropical and subtropical crops. Research on crop pollination in the tropics and on economically valuable plants in general is urgently needed to fill gaps in the available knowledge, to resolve confusing and conflicting studies, and to suggest ways of improving productivity by pollinator management, conservation and other means.

Out of over 1 330 cultivated plant species, the largest proportion originated from Asia and the Neotropics, in almost equal amounts (see Roubik, 1995, Appendix I). Africa provided half as many as either of these regions, the temperate zone provided a quarter as much, and Australia provided barely one-eighth of the number of cultivated plants originating from the Neotropics or tropical and subtropical Asia. Furthermore, over half of the world's economically significant tropical plants originated in areas where honey bee species occur naturally. Notably, the Neotropics, the South Pacific region and Australia originally lacked *Apis*.

Present working knowledge of pollination among tropical plants is limited, both in terms of regions where the plants originated and where they are grown today. Appendix I[8] of the first edition of this compendium (Roubik, 1995) shows that out of approximately 700 plant species for which some data are available or reasonable guesses can be made, 600 have some association with bees, thus 100 do not – as far as is known. Present knowledge concerning plant breeding systems and the relative pollination value of each of the flower visitors is even less complete.[9]

The following two sections discuss the pollination requirements of many economically important plants of the mainland tropics and subtropics in Asia and Africa. Some species of the highlands are also treated in Chapter 3.1. Each section groups native and important introduced plants – excluding ornamentals and many weeds – using a logical system based on experience in these regions.

9.2.1 Applied pollination in Asia – crop types

Crops are categorized in the manner used in Appendix I (Roubik, 1995), although not all the categories were deemed worthwhile for inclusion here. The cultivated plants, their breeding systems, and the pollinators used or depended upon for pollination are discussed in relation to: (i) fruits and nuts, (ii) vegetables, (iii) cereals, (iv) drug, beverage, condiment and spice plants, (v) oil crops, (vi) forage crops, (vii) timber trees and natural vegetation, and (viii) fibre plants and isoprenoids (rubber).

Fruit and nuts: Tropical and subtropical fruits are very diverse in Asia. The pollination requirements of many are at least partly understood, and many have been improved and have to some degree naturalized.

The situation is complex for *Citrus*. Mandarin oranges are dependent on, and greatly benefit from, cross-pollination. Pummelo should be inter-planted with other cultivars for cross-pollination and to allow fruit set to take place. Most oranges do not depend on insects for pollination but may benefit from it, mainly by producing seeds. Lime pollination has not been well studied, but cross-pollination may be beneficial. In the case of lemons, the data are conflicting, varying from statements about pollination by insects being

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[8] The data in this Appendix were assembled in 1993. This area has been further explored in subsequent years, but still requires much further investigation.

[9] Considerable progress has been made since this text was first published in 1995 (see Chapter 3).

completely unnecessary to outcrossing or facilitation by deposition of pollen being required. All of these crops may vary with the particular cultivar. Grapefruit does not require cross-pollination but can benefit from pollinators [see the studies by Chacoff, Aizen and Aschero (2008)], and citrus trees are excellent sources of nectar and pollen.

Apples (see also Section 8.3) generally require inter-plantings of varieties, along with cross-pollination by insects. Pear is similar but the nectar is watery, and bees therefore do not collect the pollen. Plums and prunes are mostly self-incompatible; they require insect pollination and offer good nectar and pollen forage for bees. Apricots are variable in their pollinator requirements depending on the variety or cultivar. Cherries cannot self-pollinate, but some are self-compatible, thus inter-plantings of varieties and the presence of bees for pollination are advised. Peach and nectarine pollination is not well studied, despite the economic importance of these crops. At least some varieties appear to set fruit using their own pollen, but cross-pollination by bees is needed for good crops. With the exception of pear, all the above Rosaceae provide good nectar and pollen plants for bees.

Avocado (*Persea americana*) is grown widely throughout Asia and is dependent on cross-pollination by insects. The situation is similar for *Carambola* or star fruit (*Averrhoa carambola*) and ilimbi (*A. bilimbi*), and for *Ziziphus* (*Z. jujuba*, jujube and *Z. mauritania*, ber). Formerly classified as *Nephelium*: *Litchi chinensis*, *N. lappaceum*, *Dimocarpus longan*, litchi or lychee, rambutan and longan are excellent honey plants and also depend on insect cross-pollination (see section 9.3.5). The mango (*Mangifera indica*) generally requires insects for pollination (section 9.3.6), but cross-pollination between cultivars is not required. Papaya (*Carica papaya*) has a complex breeding system of male, hermaphrodite (three types) and female flowers in which the best fruit results from cross-pollination. Bees are sometimes recommended as pollinators, and collect pollen from male and hermaphrodite flowers. The normal Neotropical pollinators, however, are hawkmoths (Martins and Johnson, 2009). Persimmon (*Diospyros kaki*) is dioecious, and some cultivars produce fruit without pollination, but most cannot. The flowers produce nectar and pollen used by bees. McGregor (1975) lists *Diospyros discolor*, the mabolo, as dependent on insects for pollination. Honey bees are the most important pollinators of phalsa (*Grewia asiatica*) in India. Loquats (*Eriobotrya japonica*) benefit from visitation by *Apis* and *Bombus* (introduced *B. terrestris*), and is minimally self-pollinating.

Durian (*Durio zibethinus*) is a native southeast Asian forest tree. It is cross-pollinated by bats but also visited by bees, as the flowers are an abundant source of nectar. Durian has a slimy consistency and an overpowering smell. Soursops and custard apples (*Annona*) have been studied only slightly in Asia, where, as in South America, they appear to be pollinated by beetles. The flowers have almost no nectar. The cherimoya (*A. cherimola*) of South America requires at least some cross-pollination. The following all probably benefit from insect pollination: breadfruit, jackfruit (*Artocarpus*), mombins or hogplums (*Spondias*),

Figure 9.15
LITCHI – *NEPHELIUM*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

jambus, jambolans and related plants (*Syzygium*), bignay (*Antidesma*), otaheite gooseberry and mirabolan (*Phyllanthus*), lingaro (*Eleagnus philippensis*), wampi (*Clausena lansium*), sapote relatives, star apple, sapodilla (*Manilkara achras*), and egg fruit (*Pouteria campechiana*), introduced from South America.

Green sapote (*Calocarpum viride*), Runeala plum (*Flacourtia cataphracta*), kei apple and kitembilla (*Dovyalis*) require insect pollination. Other Indian plum relatives (*Flacourtia*), mangosteens (*Garcinia*), mamey apple (*Mammea americana*) and guava (*Psidium*) benefit from cross-pollination by insects, but the extent of their dependence is not known. Bananas (*Musa*) in the wild are pollinated by vertebrates, whereas the cultivated plants set fruit parthenocarpically.

Among viney fruit plants, the Chinese gooseberry or kiwi fruit (*Actinidia deliciosa*) is dioecious and requires cross-pollination by pollen-collecting bees. Wild grape (*Vitis*) is similar, but the domestic grape (*V. vinifera*) can set fruit through selfing or wind-pollination. Bee pollination seems to increase fruit set in some varieties. Pollination in passion fruit (*Passiflora*) is complicated by the structure of the flower (sections 7.3 and 9.3.2), and requires cross-pollination. However, honey bees may not always accomplish this, with Carpenter bees (*Xylocopa*) seeming best suited to the task. The shrubby pomegranate (*Punica granatum*) has not been well studied, although the flowers produce only pollen. Pineapple (*Ananas sativus*) requires cross-pollination for seed to be produced, but this is undesirable for table fruit. Honey bees cannot reach the nectar, which is hidden at the base of the reddish tubular flowers that are pollinated by hummingbirds in South and Central America. Prickly pear cactus (*Opuntia*) flowers provide large amounts of pollen, however their pollination requirements are largely unknown.

From the foregoing, it is evident that there are weaknesses in current knowledge of fruit pollination in parts of Asia. Incomplete and conflicting reports need resolution, and various fruits such as dukus, jambus and others are mysteries, both in terms of pollination and their importance as bee plants.

Among the nut plants of Asia, cashew (*Anacardium occidentale*) is imported from the Neotropics, and constitutes an important cash crop, with India the world leader in production. Cross-pollination plays an important role and is apparently accomplished by small insects. Peanut (*Arachis hypogea*) flowers are visited by insects, including bees, which trip their flowers as they collect the pollen. These visits seem to have a beneficial effect in crop production. The almond (*Prunus dulcis*) is dependent on insects, primarily bees, for fruit set. Coconut and nutmeg are discussed below.

Vegetables: The fruit of many vegetable plants is not eaten, therefore production does not depend on insect pollination. However, insect cross-pollination plays an important role in obtaining the seeds of these plants, and their flowers are often excellent forage for bees. This list includes carrots (*Daucus carota*), cabbage, brocoli, cauliflower and other cole crops (*Brassica oleracea* and *B. pekinensis*), chicory (*Cichoriun intybus*), lettuce (*Lactuca sativa*), onions (*Allium*), raddish (*Raphanus sativus*), fennel or saunf (*Foeniculum vulgare*) and others. Sweet potato (*Ipomoea batatas*) and manioc or cassava (*Manihot esculenta*) are all good nectar plants, whose flowers are visited by many bee species, although their roles in pollination are not known. The plants are propagated by cuttings, but seeds are used in breeding programmes.

For vegetables where the fruit is eaten, pollination must be considered, as it often determines the size and "quality" of the fruit. The eggplant (*Solanum melongena*) is poorly studied for the most part, but requires pollination, for which bees can be used (see section 7.3.4). Two wild bees (a carpenter bee and a Macronomia) were shown to substantially contribute to eggplant yields in Kenya (Gemmill-Herren and Ochieng, 2008). Tomatoes (*Solanum lycopersicum*) are not automatically self-pollinating, but movement of the plant causes pollen to fall from the anthers onto the stigmas (see section 9.3.4). Thus, wind, insects or artificial vibration will bring about fruit set. Hot peppers (*Capsicum*) seem to bear fruit and seed in the same way as tomatoes, but do so better if cross-pollinated. The flowers of solanaceous crop plants (including potatoes, *Solanum tuberosum*, from which seeds are grown to produce seed-potatoes for plants) are not attractive to many bees, but would probably benefit from their foraging in terms of greater fruit quantity and quality. The cucurbit vegetables, pumpkins and squash (*Cucurbita*), cucumbers and gherkins (*Cucumis sativus*), balsam pear (*Mormodica charantia*), musk melon (*Cucumis melo*) (see Chapter 7.2), other watermelons (*Citrullus*) and gourds, including bottle gourd (*Lagenaria siceraria*), ash gourd (*Benincasa hispida*) and sponge gourd or luffa (*Luffa aegyptica*), all require pollinators for fruit set, for which bees are the principal pollinators. Okra (*Hibiscus esculentus*) is self-pollinating but is well visited by bees. The value of outcrossing has not been assessed.

In the case of periodic crops, semi-seasonal crops or pulses, cowpeas (*Vigna sinensis*) are highly attractive to bees. Pollination is best effected by large bees, rather than smaller bees or honey bees. Large bees such as *Xylocopa* (Apidae) or *Chalicodoma* (Megachilidae) are probably the chief pollinators of the horse bean (*Canavalia ensiformis*), at least in Indonesia, although this species and the sword bean (*C. gladiata*) are reported to be self-pollinating. Lentil (*Lens culinaris*), mung bean (*Phaseolus aureas*) and gram (*Cicer arietinum*) are thought to be self-pollinating. Horsegram (*Lablab niger*) requires pollination by insects. However, the pollination requirements of many leguminous crops are unknown, although the wild progenitors almost certainly all require insects, mostly bees. Soybean (*Glycine max*) is self-fertile, however bees bring benefits in terms of increased seed set and oil yields (see Morse and Calderone, 2000; Milfont *et al.*, 2013).

Figure 9.16
XYLOCOPA* VISITING *CANAVALIA

Source: J.M. F. Camargo original drawings, reprinted by permission of artist and publisher. Presented in: G. Gottsberger, J. M. F. Camargo, I. Silberbauer-Gottsberger. 1988. Bot. Jahrb. Syst. 109:459-500. [from original 1995 FAO book]

Cereals: Most cereals are independent of insects for pollination, as wind pollination prevails in the grasses. Maize (*Zea mays*), although a pollen source for bees, is wind pollinated. Many cereals do not reproduce by pollination; instead, the grain develops apomictically. Pearl millet (*Pennisetum typhoides*) may benefit from insect pollination, as bees are sometimes abundant when collecting pollen from the flowers.

Drug, beverage, condiment and spice plants: There is no comprehensive account of pollination needs among the wide variety of medicinal plants grown throughout Asia. Many are not economically prominent as yet, and are grown in small patches for specific uses. Poppy (*Papaver somniferum*) is grown for the illicit drug trade. It produces only pollen and is visited extensively by pollen foraging bees. The number of seeds produced is greater when pollinators are abundant. Hemp (*Cannabis sativa*) is wind pollinated, but bees visit the male flowers for pollen. Tobacco (*Nicotiana*) cross-pollination can be brought about by honey bees for hybrid seed production.

Coffee (*Coffea*) production can be considerably enhanced by augmented pollination with honey bees. *C. canephora* is obligately outcrossed and frequently wind pollinated, while *C. arabica* is self-compatible and autogamous. Coffee flowers are also a good source of nectar, although the honey is bitter and of no commercial value. Tea (*Camellia sinensis*) is not a good bee plant, and the small flowers are usually pollinated by flies. Cocoa (*Theobroma cacao*) is also pollinated by small flies (*Forcipomyia* of the family Ceratopogonidae), although some pollen-collecting bees (e.g. Meliponini and *Lasioglossum*) may also pollinate the small flowers.

Condiment and spice plants have been largely neglected in terms of their value for pollination or as bee plants. The crops of cardamom (*Elettaria cardamomum*) are much improved by honey bee visitation. Black pepper (*Piper nigrum*), however, remains an enigma; although visited faithfully by flies and bees, self-pollination, effected by rain, is still suggested as tenable. Coriander (*Coriandrum sativum*) (see section 7.3.3) is grown extensively in India and seems to benefit from cross-pollination by bees and other insects in Europe. Sesame (*Sesamum indicum*) is grown for its oil-rich seeds and is reportedly self-pollinating. Bees collect nectar and pollen from the flowers, but their importance in crop production has received only minimal study. In Egypt, the wide variety of flower visitors, mostly honey bees, has

Figure 9.17
SESAME – *SESAMUM*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

Figure 9.18
BLACK PEPPER – *PIPER NIGRUM*

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

substantially increased seed yield in open-pollinated plants (compared with those in cages). Vanilla grown in Asia is usually pollinated by hand. The mustards (*Brassica*) are variable in their pollination needs, but offer good bee forage and benefit from outcrossing.

Bee pollination of cloves (*Syzygium aromaticum*) requires outcrossing, although the clove of commerce is a flower bud. Bees probably play an important role in pollination, though other insects are involved and may be more significant in some areas. The same may be said of saffron (*Crocus sativus*), which is harvested for the floral stamens, but is nonetheless pollinated by bees. Nutmeg and mace are produced from *Myristica fragrans*. This plant is dioecious and so requires cross-pollination. How this is achieved is unknown, however, and small insects, bees and wind have all been suggested. Allspice (*Pimenta dioica*) is also dioecious and is pollinated effectively by honey bees in Jamaica (where neither is native). Cinnamon (*Cinamomum zeylanicum*) requires insect pollination.

Oil crops: The mustards, rapeseed and related *Brassica* are grown extensively for oilseed production in Asia. *Brassica campestris* is dependent on insects for pollination, and is an excellent source of pollen and nectar for bees. *Brassica juncea* is also more fruitful if bees are present. Niger (*Guizotia abyssinica*) is a good bee plant and seed yield is greater when beehives are placed in niger fields. Sunflower (*Helianthus annuus*) is grown in increasing amounts in Asia. Even though new self-compatible varieties are available, they benefit from cross-pollination and oil yields are greater. Self-incompatible varieties require insect pollination and bees are the primary agents. The flowers provide nectar of high quality and also pollen. Flax (*Linum usitatissum*) is grown for oil and fibre, and benefits from outcrossing by bees. Safflower (*Carthamus tinctorius*) is a good source of nectar and pollen for bees and yields more oil when cross-pollinated. The oil palm (*Elaeis guineensis*) is a very commercially successful oil-producing plant in tropical Asia (see also Chapter 9.3.10), and is pollinated effectively by weevils. While bees sometimes collect the pollen, it is not a good forage plant. The coconut (*Cocos nucifera*) is grown for its fruit, which provides food, drink, oil and fuel. Evidence is accumulating slowly that coconut production may be improved by augmented pollination by bees. Wind pollination is still apparently more significant, especially in plantations. The coconut

Figure 9.19
ROSE APPLE – *SYZYGIUM*

Source: L. H. Bailey. 1935. The standard cyclopedia of horticulture. New York: Macmillan.

Figure 9.20
CINNAMON – *CINNAMOMUM ZEYLANICUM*

Source: M. Casimiro Cavalcante

offers ample nectar and pollen to bees. Castor bean (*Ricinus communis*) has a mixed breeding system that favours geitonogamy via bee visitation and wind (see R.A. Rizzardo, *et al.*, 2012), and is pollinated by bees in Botswana.

Tung (*Aleurites fordii*) and tong (*A. montana*) are grown for their nuts, which when pressed yield oil used in varnishes, electrical insulators and protective coatings. *Aleurites fordii* may be dependent on insects for pollination, but this has not yet been confirmed.

Forage crops: Alfalfa (*Medicago sativa*) is grown in drier parts of tropical Asia. It requires insects for pollination, with honey bees and leafcutter bees the most effective pollinators. Kudzu (*Pueraria thunbergiana*) is pollinated by bees, and berseem (*Trifolium alexandrinum*) has a wide variety of pollinators on which it is dependent for seed set. Honey bees are effective pollinators in both cases.

Timber trees and natural vegetation: It is very difficult to obtain information on the pollination biology of highly valued timber trees of tropical and subtropical Asia. Chan and Appanah (1981) have discussed the role of thrips in pollination of dipterocarps and other trees in Malaysia, yet beetles also pollinate in Borneo (see Roubik, Sakai and Hamid Karim, 2005); and Appanah (1981) has made some generalizations on the role of bees in pollination in Malaysian primary forests. There are a few publications on the pollination of plants of the tropical forests (e.g. Appanah (1982), Bawa (1990, 1992), Faegri and van der Pijl (1979), Owens, Sornsathapornkul & Tangmitcharoen (1991), Panayotou and Ashton (1992)),[10] but in general this is a much neglected area of botany, and now forestry, since many formerly forested areas are being replanted with timber species. The value of forest trees in terms of honey and pollen harvests is well known.

With the continued large-scale cutting of tropical and subtropical forests in Asia, attention must be paid to "re-afforestation" programmes. To obtain seeds for re-afforestation, either by natural processes or with the assistance of human effort, the trees must be pollinated. If the trees are highly specific in their requirements for pollinators, and the pollinators finely attuned to the tree for their own reproduction, then over-cutting could produce a vicious cycle of decline in both the plant and pollinator. These issues are urgently in need of consideration. Honey bees or other managed pollinator groups may need to be incorporated in future plans to ameliorate foreseeable problems in such situations. In some cases, as with *Calliandra* introduced into Java, beekeeping projects have gone hand in hand with such programmes. Nevertheless, all too little is known of the reproductive biology of the most valued timber trees of forests.[11]

Fibre plants and rubber: The most important fibre plant is cotton (*Gossypium*), however, it is not thought to depend on insects for cross-pollination (although see section 9.3.3). In fact, cross-pollination has been considered detrimental, because the resultant seeds and progeny are not necessarily bred exclusively from the desired cultivar. Nevertheless, benefits do accrue from cross-fertilization including larger crops, more oil and hybrid vigour in progeny. Honey bees are used extensively in cotton fields where pure-line seed is not sought, making seed often "hybrid cotton". The flowers produce abundant pollen and nectar. Kapok (*Ceiba pentandra*) is a copious producer of nectar and excellent bee forage. In nature, bats are important pollinators, but the trees also seem to be self-fertile. Pollination of kenaf (*Hibiscus cannabinus*) is not fully understood but outcrossing by bees may be more important than now thought. Sunn (or sann) hemp (*Crotalaria juncea*) seems to require pollination by bees, at least for maximum fruit set, with carpenter bees (*Xylocopa*) playing a more valuable role than honey bees. *Cannabis sativa* is wind pollinated, but is used by bees for its pollen. Information on flax and coconut is given above.

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[10] See the General References in Roubik (1995) for more examples.

[11] See Roubik (1995), Appendix I.

Rubber (*Hevea brasiliensis*) is pollinated by insects, mostly Diptera (midges), however pollination does not contribute to the yield of the rubber sap, which is tapped from the tree trunk. Rubber is also an important honey plant in the tropics, as many bees forage for nectar from the extrafloral nectaries on the leaf petioles.

Conclusion: Many economically vital plants of tropical and subtropical Asia are "unknown" insofar as pollination requirements are concerned. Those listed are currently the most important and have received some attention, if only to indicate the lack of information about them. Certainly, of those economic plants for which documentation on breeding systems is available, the number requiring insect pollination is high. If to those are added the plants that certainly benefit from cross-pollination by insects, and those suspected of belonging in this category, only the cereals, bananas and seedless fruit remain outside the influence of pollinators. At the same time, most of the economic plants for which insect cross-pollination is at least beneficial are also useful to honey bees and other honey-making bees (stingless bees), which may also provide income to those who exploit these insects. Thus, beekeeping and agricultural productivity are as clearly interwoven in the tropics as they are in the temperate regions of the world.

9.2.2 Applied pollination in Africa – overview

The importance of pollination on the yield of most crops grown in temperate climates is known, at least partially, but relatively little information is available regarding the pollination of tropical crops. In Africa and other tropical regions, many studies on crop pollination are preliminary, mainly because of insufficient facilities. The geographic dimension and variety within Africa is also seldom appreciated, thus this section first outlines the general themes and then discusses the four basic regions of that continent.

The need to increase crop yield to meet the food requirements of growing populations all over the world is one of the most important problems in the tropics. In Africa, the pollination dependence of crops is expected to increase in tandem with food needs. In general, most African pollination studies have been made in response to specific production problems. For example, in East Africa, research on pollination was, and still is, closely tied to production problems arising in the export-oriented agriculture of pre-independence governments. Research has focused on commercial crops such as pyrethrum, coffee, cashew nut, sunflower and mangoes. Most post-independence research on agriculture has concentrated on improving production of the same commercial crops through breeding, but little study has been made of pollination of the improved crops.

Tree crops are common in the tropics and the improvement of any one by breeding is a long-term project. Short-term increases could possibly be secured by raising the density of pollinators around the crops. One way to increase pollinator abundance is through improvement of existing traditional apicultural practices. In some countries, however, priorities in apiculture development are dictated by production capacity, which is strongly affected by poverty, with research deferred to the future. Overall, beekeeping in Africa is slowly being improved through research, because the latter will not only provide honey and beeswax, but will also increase crop yield through pollination, all of which will raise farmer income (see also Chapters 2 and 3).

Pollinator behaviour and management: Insects recorded visiting flowers of crops are assumed to be pollinators. However, their real value as pollinators, or other types of visitors (Chapters 2 and 18), may not be known. Many species of insects and small animals visit flowers for nectar or pollen, or both, but few may be good pollinators. The most efficient pollinators carry plenty of pollen, brush against stigmata hence transferring pollen, visit several flowers of the same species in succession, and move frequently from flower to flower and plant to plant.

Pollination of few crops depends only on one or a few local insects. Most crops in Africa and elsewhere are visited by honey bees, whose pollen-carrying capacity and behaviour make them superior pollinators in many instances. Nevertheless, most races of African honey bees are very defensive. In part because of this behaviour, apiaries are located well away from areas of agricultural and other human activity. Colonies also abscond readily after disturbance during handling and transport, migrate during dry periods and swarm often. These features all decrease their value for pollination management, and their suitability for migratory beekeeping has been questioned. Moreover, in almost all of Africa, except some parts of South Africa, bees are kept in traditional log and other hives, and only more recently in top bar hives, which cannot be transported without comb breakage.

Apart from honey bees, very few other insects have been managed for crop pollination in most African countries (although see Chapters 11 and 13), partly because of a general lack of knowledge concerning the potential of wild insects as pollinators. Trials in rearing the Egyptian alkali bee (*Nomia unidentata*), for pollination of clover (*Trifolium alexandrinum*) have been performed in Egypt.

Farming systems and destruction of natural vegetation: Most farming in Africa consists of subsistence agriculture. Pollination problems rarely arise as there are sufficient wild insects living in the surrounding bush. The modernization of agriculture, however, has led to the clearing of large areas of natural vegetation, often to cultivate a single crop. Intensive cultivation frequently causes the destruction of plants that are beneficial as forage and the nesting sites of pollinators. As a result, there is a strong tendency for populations of pollinators to decrease, until they are too few for even minimum acceptable crop pollination. For example, in Kenya and Tanzania, subsistence agriculture left large areas of land fallow, which formerly provided ample sites for wild pollinators. Most of these have now been reduced. It is now apparent that the consequences of natural disasters such as drought can be aggravated by deforestation and unsuitable agricultural and pastoral practices. In addition, the increase in monoculture cropping results in flowering being concentrated over short periods, with a consequent need for larger pollinator populations for those short periods. However, no alternative forage is available outside of these flowering periods, resulting in times of floral dearth. In Africa, feeding bee colonies during periods of dearth is not generally practised. As a result, most colonies starve or emigrate from the crop area.

Enemies and poisoning of pollinators: Although many of the known bee diseases have not been reported in Africa, *Varroa* was identified in Tunisia in 1978 and *Nosema* in Libya and Egypt (1977) and South Africa (1972). The significance of bee diseases may not have been recognized as yet because most colonies of African honey bees inhabit wild nests or are kept in traditional hives that cannot be inspected readily. Moreover, farmers may not recognize the diseases. The largest threats to honey bee colonies in Africa at present are bee pests and predators. Several types of insects, spiders, birds and mammals (including human being) are recorded as enemies of bees in Africa. There are 17 species of African bee-eaters (*Merops* spp.) whose diet consists of 62–94 percent Hymenoptera. In the savannah areas of Kenya, Niger and Zimbabwe, honey bees make up as much as 96 percent of the diet of *Merops*. Colonies of bee-eaters can be as large as 25 000 individuals in Niger and an individual bird can eat up to 124 000 bees in a year. Such data provide an indication of the potential devastation brought about by birds. Other pests that can cause great damage to bee colonies include hive beetles (*Aethina tumida*) in South Africa, calliphorid fly larvae (*Pollenia*) in Egypt, predatory wasps (*Palarus latifrons*) in South Africa, the hornet *Vespa orientalis* in Egypt, and pirate wasps (*Philanthus triagulum*) in Egypt and Botswana.

In cases where insects are not direct pests to bees or crops, they may compete with honey bees for available nectar. Honey yields from *Eucalyptus grandis*, which form 80 percent of all *Eucalyptus* grown in South Africa, vary greatly, probably due in large part to infestation by *Drosophila flavohirta*, which may consume nectar and leave none to attract bees. In South Africa, *Eucalyptus* species produce nectar between midnight and sunrise. Ants forage at night and collect 42 percent of the nectar before honey bees start to forage. Sometimes, the types of crops adjacent to each other may lower pollination efficiency because of crop competition for available pollinators. One study reports that 40 percent to 46 percent of introduced bees visit an almond orchard, while 49 percent to 51 percent visit the adjacent pasture with *Aloe davyana* and *A. marlothii*. Thus, alternative sources of forage attract bees from the target crop. However, flowering of many crops in the tropics is staggered throughout much of the year, which means that critical resources for pollinators are available most of the time.

Continued use of insecticides alongside the increase in crop plantations accelerates loss of pollinators. Damage to honey bees differs according to many factors (see Chapter 20), including insecticide toxicity, methods and time of day of application, number of applications, proportion of foragers visiting treated crops, foraging behaviour of bees on the crop and drift of insecticide to the various sources of forage. Most poisonings occur when bees are collecting contaminated nectar, pollen and water. Insecticides imbibed with feed may be transported back to the colony where they poison both immature and adult bees. Several studies indicate that most insecticides used in agriculture are harmful to honey bees (see Chapters 4, 16 and 20). Spraying of crops, especially cotton, in Egypt, Kenya and Tanzania has made beekeeping impossible in cotton-growing areas. The insecticides most toxic to bees include phosparidon, BHC (lindane), Aminocarb, DDT, trichlorphon, Sevin (Carbaryl), Fenithion, Dimecron (Phosphamidon), Sumithion, Dicofol (Kelthane), Roxion, Toxaphene and Parathion, among others (see van der Valk & Koomen, 2013). All insecticides are toxic in nectar on the day of application and, thus, ordinarily should be applied at night (unless the bees are visiting bat-pollinated flowers). Residues on plant parts have shown that some insecticides, such as hostathion, persist for up to seven days on leaves. Toxicity of insecticides such as carbamates increases with temperature. It is advisable, therefore, to confine colonies in ventilated hives at the time of application.

9.2.3 Pollination studies in African countries— by region[12]

Studies performed in Africa on crop pollination are grouped here into four regions: (i) North Africa, (ii) West Africa, (iii) East and Central Africa, and (iv) Southern Africa.

North Africa: The northernmost part of North Africa has a Mediterranean climate. Southwards, along the Tropic of Cancer, the region consists of Saharan desert. Most farming is conducted along rivers and where there are irrigation dams. In the dry parts, the area of cultivated land is being increased through reclamation of desert. Irrigation dams such as the Aswan dam in Egypt are thought to be vital for farming. The scarcity of wild pollinators in newly reclaimed lands is mainly a result of lack of wild flowering plants for supply of pollen and nectar. Consequently, crops on newly reclaimed areas suffer from lack of pollination. Colonies of *Apis mellifera* have been found suitable for establishment as pollinators of some crops in these areas. However, honey bees cannot pollinate all crops, so the introduction of wild bees, such as *Nomia, Andrena* and *Megachile*, is being attempted in Egypt. Eventually, established crops and the judicious use of pesticides should allow wild insects to become established, thereby improving pollination.

Preliminary studies identify over 30 species of crops that benefit from honey bee visits, although more work on their pollination requirements is needed. In terms of textile crops, the majority of studies have been carried out on cotton. Honey bees comprise 79.3 percent of all visitors to cotton in Egypt and 80 percent in Sudan. In Chad, 80–90 percent of cotton flowers are visited by honey bees, but although only 70 percent of hybrid capsules form, it seems sufficient for commercial production of hybrid cotton. Pollination of cotton by honey bees increases the weight of seed per boll, weight of cotton per plant and overall yield per plot. A positive correlation between temperature and numbers of honey bees

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[12] See also Chapters 7.1 and 7.3.

visiting cotton in Egypt exists – available nectar in cotton flowers increases with relative humidity and decreases with temperature, and plants contain no nectar at temperatures above 40 °C. Most bee visits occur from 12:00 to 14:00 hours, corresponding to peak nectar secretion and sugar concentration.

In Egypt, flax also benefits from pollination by wasps, field bugs, bees, beetles, flies and butterflies. Honey bees comprise 90 percent of all insect visitors and increase both the quality and quantity of the crop. Alfalfa (*Medicago sativa*) and Egyptian clover (*Trifolium alexandrinum*) are among the most important cultivated forage crops in North Africa that benefit from insect pollination. Alfalfa is visited by 37 species of Hymenoptera especially *Andrena ovutula, Chalicodoma flavipes, C. mucorea, Megachile submucida, Nomia* and other species of Halictidae, and *Apis mellifera*. The last bee species comprises up to 51 percent of individual pollinators in Egypt and up to 72 percent in the Sudan. *Chalicodoma mucorea* builds nests in mud houses, but trials in transferring to artificial nests have failed, as the adults do not withstand confinement and transportation. However, cells containing prepupae and pupae have been successfully transplanted into artificial cells punched in newly made mud bricks.

In Egypt, alfalfa flowers enclosed with honey bees give higher yields than those from which all insects are excluded. However, the yields are still not as high as those obtained from open-pollinated plots. The density of honey bees is higher in fields closer to hives than those 1.5 km away, whereas density of wild bees is higher on distant plots. This suggests that the wild and hive bees compete, and that colonies for pollination should be placed close to the crop. Egyptian clover is self-sterile and honey bees increase its yield. The crop is visited by Coleoptera and Diptera, halictid bees (especially *Nomia unidentata*) and honey bees. Honey bees make up 59.6 percent of the total insect visitors in Egypt and account for 82 percent of all pollinators in Sudan. On average, the number of seeds per head is 0.40, 1.21, 22.20 and 43.75, respectively, in plots protected from wind, screened against insects, open and caged with honey bees. For the same treatments, the percentage seed set is 0.65, 1.83, 33.80 and 65.87. The number of corresponding seedless heads is 82.86, 65.31, 2.80 and 0.40. As in alfalfa, there is a significant decrease in seed yield as distance from the apiary increases.

Bees and other insects are the principal pollinators of a variety of crops in North Africa. Among seed oil crops, sunflower in Sudan is pollinated by *Bombus* (introduced from Europe), *Nomia melanderi, Megachile rotundata, Halictus* and *A. mellifera*, with honey bees comprising 75 percent of all Hymenoptera. Although *Sesamum indicum* (sesame) is usually self-pollinated, insect pollination is important in increasing seed production. The most active insect visitors of sesame in Egypt are Diptera (Syrphidae), Coleoptera and *A. mellifera*, with bees accounting for 30 percent of all visits to flowers. In Egypt, peanut (*Arachis hypogaea*) is pollinated by Hymenoptera, especially Chrysididae, Halictidae, Sphecidae, Apidae and Megachilidae, as well as flies such as Syrphidae.

Date palms in Egypt are hand pollinated. Hand-pollinated palms achieved higher total soluble solids in fruit, the larger percentage of sugars and lower tannin contents than unpollinated ones.

A survey undertaken to identify important pollinators for beans (*Vicia faba*) in Egypt revealed that honey bees account for 77.3 percent of all insect visitors. Experiments in which honey bees are excluded reduced the yield by 2.8 percent, while enclosing the crop with honey bees increased it by 10.4 percent. In Sudan, the estimated percentage of buds of beans that drop before maturity is 86.7 percent for a local variety and 93.7 percent for an introduced one. Bud drop is appreciable both before and after fertilization. There are also indications that reduction in pod yield is associated with inadequate insect pollination. Pollination by honey bees and hand tripping of flowers increases pod set. Other studies in Egypt reveal that *Andrena, Halictus, Nomioides* and *A. mellifera* visit several other crops.

Honey bees represent 97.9 percent of Hymenoptera visitors to *Brassica oleracea*, 68 percent to *B. sinapis* and 67.7 percent to *Coriandrum sativum*. However, wild bees comprise 85.7 percent of visitors to *Cynodon* *dactylon,* 85 percent to *Raphanus sativus*, 76.9 percent to *Matricaria chamomilla* and 51.1 percent on *Daucus carota*. The main pollinators of onion are honey bees, whose visitation produces high seed set, weight of seed and yield per plant (see also sections 8.6.1 and 8.6.2). Although not much work has been undertaken on pollination of many other crops in North Africa, honey bees forage on borage (*Borago officinalis*), fennel (*Foeniculum vulgare*), dill (*Anethum graveoleus*) and squash (*Cucurbita*) in Egypt.

West Africa: This tropical to subtropical region is located on the west coast of Africa, south of the Sahara. Ndiaye (1976) has surveyed plants of Senegal visited by honey bees with a focus on investigating honey production, rather than pollination. Similarly, a few surveys of pollinators of various plants in Nigeria and Gabon have been initiated, with a view to preparing a reference collection of honey and pollen plants. Harris (1987) notes that cecidomyiids pollinate cocoa in West Africa. In Ghana, honey bees and *Xylocopa* increase yields and fruit quality of tomatoes (*Solanum lycopersicum*), peppers (*Capsicum frutescens*) and eggplants (*Solanum melongena*), which are partly self-incompatible and need cross-pollination for fruit set. Honey bees and hover flies constantly visit Rosaceae and pollinate *Prunus spinosa, Crataegus monogyna, Rosa canina* and *Rubus fruicosus* in Ghana. More recent studies have documented cocoa pollination dynamics in Ghana (Frimpong *et al*., 2011).

Preliminary studies of Locust bean tree (*Parkia biglobosa*) and butter tree (*Bytyrospermum parodoxum*) in Burkina Faso have shown that their fruit production is low, however it is unclear whether or not bees act as their pollinators. In Cameroon, oil palm (*Elais guineensis*) was originally thought to be wind pollinated, though Syed (1979) found evidence of visits by 12 species of insects. *Elaeidobius* and *Atheta* (Curculionidae) and Diptera make up the majority of oil palm pollinators in Cameroon and Côte d'Ivoire. Pollinator population varies in time and space depending on climatic conditions. From 80 percent to 85 percent of fruit bunches are pollinated during the wet season compared to 77 percent to 82 percent during the dry season. In West Africa, Baker finds that some plants are pollinated at night. He notes that moths (*Tegiticula*) pollinate Yucca and bats pollinate baobab (*Adansonia digitata*), kapok (*Ceiba pentadra*) and sausage tree (*Kigelia africana*).

East and Central Africa: This part of Africa comprises equatorial regions with scattered natural vegetation. In Tanzania, cashew nut (*Anarcardium occidentale),* coconut *(Cocos nucifera), Coffea arabica, Pyrethrum* and sunflower (*Helianthus annuus*) all benefit from bees. Accordingly, farmers have been encouraged to keep bees in plantations of those crops. Cashew nut flowers are visited by flies, ants and honey bees that transfer the sticky pollen to stigmas.

Coffee does not require insect pollination but is benefitted by pollinating insects. Coffee plants flower profusely for only a few days and bee colonies may be required for only a week. Flowering varies with altitude and so colonies can be used more than once by moving them from one altitudinal zone to another. In Kenya, bee abundance and seed set were found to be higher for organically grown coffee in Kiambu County, as compared to conventional farms using pesticides (Karanja *et al*., 2011). Tanzania has set research apiaries around coffee plantations in order to undertake further studies of pollination.

Preliminary studies on lucerne (*Medicago sativa*) in Tanzania revealed that honey bees tripped 53.6 percent of flowers they visited and increased seed production. Stingless bees such as *Meliponula* (*Axestotrigona*) *togoensis* are kept in modern hives in Tanzania, but no investigations have been attempted on crops that benefit from these bees. Stingless bees frequently visit coffee and other crops elsewhere (see Chapter 13).

Although improved techniques in beekeeping have been introduced on a large scale since the early 1970s in Kenya, commercial use of honey bees in pollination has been very limited. Pigeon pea (*Cajanus cajan*) has been found to increase outcrossing of two inbred lines by 25 percent to 94.5 percent when insects were used. In Kenya, the major insects found visiting pigeon pea included ten species of *Chalicodoma*, five of *Megachile*, five of *Xylocopa, Amegilla plumipes, Apis mellifera,* the butterfly *Lampides boeticus* and the parasitic apid *Thyreus*. Trials in Kenya showed that honey bees made up 86 percent and wild bees 33 percent of all insect visitors to sunflower. They also found that placing hives in pyrethrum fields improved seed yield and pyrethrin content. In Madagascar, honey bees visited *Grewia calvata, G. fancherei, Dombeya elliptica*, lalona (*Weinmamia bojeriana*), *Mimosa* and *Eucalyptus*, in addition to crops such as coffee, cocoa, vanilla, clove, basil, ylang-ylang and patchouli.

In Kenya, two wild bee species – a carpenter bee and a *Macronomia* species – were shown to substantively contribute to eggplant yields (Gemmill-Herren and Ochieng, 2008). Additionally, hawkmoths were identified as the key pollinators of papaya (Martins and Johnson, 2009). In both cases, the importance of conserving nearby wild or semi-natural habitat was shown to be important to maintaining levels of pollination service in Kenya.

Ficus sycomorus is chiefly found in riverside forests in East Africa and is pollinated by agaonid wasps, especially *Ceratosolen arbicus, C. galili* and *Sycophaga* sycomori. The ancient symbiosis between figs and agaonid wasps was first identified around Lake Magadi in Kenya (Galil and Eisikowitch, 1968).

East African work by Smith (1958) led to the compilation of an important reference work on honey plants and their distribution, flowering periods and identification of their pollen. Similar studies have been undertaken by Dale and Greenway (1961) in Kenya, and Lind and Tallantire (1962) in Uganda. Although none of these researchers studied pollination requirements for each plant, such studies are important as reference bases for further research.

Southern Africa: This region comprises mainly the South African Republic and adjoining countries. The Kalahari Desert is situated in the north along the Tropic of Capricorn, while in the south the climate tends towards the Mediterranean. Honey bees are important pollinators of subtropical crops in South Africa (see also Chapter 3), with annual yields from litchi, macadamia and other fruit or nut crops shown to be closely related to hive numbers in orchards. However, in many cases, there are no recommendations for commercial use of honey bee colonies in pollination. Before 1986, less than 5 percent of Transvaal beekeepers were involved in the pollination of subtropical crops, although colonies were transported to litchi, macadamia and mango orchards primarily to obtain honey. It has been estimated that 52 000 bee colonies are needed for pollination of apples, pears and plums in the Cape Province, but only 12 000 are employed at present. There is a great need for cooperation between beekeepers and growers of such crops to increase their production. In Transvaal, some beekeepers move honey bee colonies to crops such as kidney beans for pollination, and pay the growers a small fee or give them honey.

Nectar is produced by 17 cultivars of sunflower (*Helianthus annuus*) in South Africa. The process differs significantly, however, with honey bees and short-tongued Halictidae unable to reach all the nectar in certain cultivars. Commercial sunflower grown in cages excluding pollinators produced an average of 45 percent seed set compared to 73.5 percent seed set in open fields. Seed set increased to 72 percent with the introduction of honey bees to cages, to 76 percent with spotted maize beetles, to 44 percent with American bollworm larvae (*Heliothis armigera*) and to 38 percent with house flies.

Honey bees studied visiting *Citrus* did not collect its pollen, but instead landed on the flower petals to search for nectar without touching the stigmas. However, during takeoff, bees occasionally brushed the stigmas resulting in cross-pollination. Kiwi fruit (*Actinidia deliciosa*) can be pollinated by hand dusting methods using preserved and dry pollen, but is naturally pollinated by insects. Honey bees, placed in almond orchards close to a pasture with *Aloe*, collected 40–46 percent of almond pollen and 49–51 percent of aloe pollen, but there was no significant reduction in fruit set in almond. These results show that although alternative sources of forage can attract bees away from almonds, successful cross-pollination can still be achieved.

There are 127 species of *Aloe* in South Africa, but their value for beekeeping has not been determined. The floral morphology of *Aloe ferox* suggests it is pollinated by birds, but different bee species, especially *A. mellifera, Allodapula variegata* and *Lasioglossum,* formicine ants, chalcid wasps, syrphid flies and five species of birds have been observed to visit its flowers. One of the most common species is *Aloe marlothii*; honey bees collect its pollen and carpenter bees nest in the stems and may also effect pollination. Evidence has been found for hybridization between *Ficus nataliensis* and *F. thonningii* in Natal, where both species are pollinated by *Elizabethiella stuckenbergii*. In West and Central Africa, however, *Ficus natalensis* is pollinated by *Alfonsiella fimbriata*. The adults of *E. baijnathi* were attracted to *F. burtt-davyi*, but its attractiveness disappeared after pollination, indicating that some volatile compound was released before pollination but not afterwards. Agaonid wasps also pollinate other *Ficus* spp. The effect of *Pheidole megacephala* and *Polyrachis schistacea* (Formicidae) visiting fig trees reduced parasitism of pollinators by *Apocryptas guineensis* and seed predation by *Idarnes*. Insect pollinators have been reared from 70 species of *Ficus* and classification of the pollinators conforms with that of their host figs.

The common plants visited by bees, including growth type, flowering periods and usefulness to bees, have been studied in South Africa and Zimbabwe. These studies serve as a reference for the identification of African flora in future research.

9.2.4 Recommendations for future work

Although the preceding sections do not provide complete coverage of most crops in many countries, they clearly indicate the need for further information on pollination and the potential to increase crop yields and quality through use of pollinators. The primary means to achieve this will be the use of honey bees and wild bees. The following recommendations are made to harness this potential:

- In some countries, plant and insect collections are absent because fine taxonomic collections amassed in laboratories by colonial governments were removed from Africa following independence. Identification of native species, especially crops and their pollinators, should be encouraged.
- Crop breeding and pollination research should be integrated. In Kenya, studies have found that the highest-yielding cashew trees were the most attractive to honey bees. This suggests that it may be necessary later to select for high yield and attractiveness to bees in breeding programmes.
- Beekeepers, crop growers and state extension workers should be educated about crop pollination, especially through beekeeping programmes. The adult literacy level in most African countries has increased, with younger literate individuals increasingly becoming farmers. Written information is distributed in the form of simplified pamphlets, newsletters and booklets. Such booklets have been prepared in South Africa. Farmers can also benefit from radio and television broadcasts.
- Care should be exercised when importing plants and pollinators. For example, *Prosopis* (an arid climate shrub) has been introduced as a multipurpose forage crop in the dry parts of Kenya. However, such practices may be potentially hazardous, since introduced *P. juliflora* may achieve such rapid growth and dispersal that it attains pest status. Introduced species may also attract native pollinators away from native flora.
- There is a possibility that some Africanized honey bees (the naturalized honey bee of tropical America) are naturally less defensive, less excitable and less inclined to abscond and swarm. Selection for such desirable characteristics would allow beekeepers to practise migratory beekeeping for crops requiring pollination. This would also enable them to keep their bees in areas of high agricultural activity.
- To ensure a reliable source of managed and wild pollinators, a more comprehensive strategy for management of crop pollination is needed. This can be achieved by educating farmers and beekeepers about pollinators, their value, habitats and conservation. Pollinators should be protected from pests, predators and poisoning by insecticides.

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9.3 SELECTED STUDIES

9.3.1 Brazil nut in the Amazon

M. Maués, M.C. Cavalcante, A.C. dos Santos and C. Krug

Brazil nut natural history and uses: The Brazil nut, Pará nut or Paranuss, as it is known in the United States and Europe, is a native tree of the Amazon forest. A.J.A. Bonpland first identified the forest tree *Bertholletia excelsa* (Lecythidaceae) in 1808 as a species within a monospecific genus *Bertholletia* from the Lecythidaceae family, which occurs in non-flooded – "terra firme" – forest in Brazil, Bolivia, Colombia, the Guianas, Peru and Venezuela [1]. The tree produces particularly hard globose fruit varying from 11 cm to 16 cm in diameter and weighing 500 **g** to 1 500 g. Each bears 10 to 25 seeds approximately 3.5 cm to 5.0 cm long by 2 cm wide, with a distinctly triangular cross-section. Brazil nuts are protected by the hard case, and are readily harvested when the fruit falls many metres to the ground [1, 2]. Under natural conditions the nut is mostly consumed by the agouti (*Dasyprocta*), a caviomorphic rodent that eats seeds but also plays a major role in seed dispersal. Due to its habit of burying seeds in the forest for later consumption, where they are often forgotten, *B. excelsa* is dispersed and can regenerate [3, 4]. Some studies also suggest an anthropogenic influence on Brazil nut phytogeography [5].

Brazil nut is essentially a seed rather than a nut, but nomenclatural tradition prevails. The seeds sustain one of the most important extractive industries in the Neotropics. It is unique because they are harvested in natural forests and have been internationally traded for over 120 years by local people, thereby generating income in Brazil, Bolivia and Peru [6].

The commercial use of *B. excelsa* mainly involves the seeds, which are rich in oil, unsaturated fatty acid, sulfuric amino acid, phosphorous, potassium, iron, sodium, vitamin A, thiamine, riboflavin, niacin and Selenium [7]. The timber is extremely durable and one of the finest found among the many Amazonian tree species [8], although logging and trade of *B. excelsa* in natural forests is prohibited under law in Brazil [9].

Breeding system and seasonality: From October to January, Brazil nut trees display terminal panicles 14 cm to 45 cm long with an average of 0.76 (N = 182) flowers opening per day. Anthesis begins at night or after midnight, and full flower opening occurs from 01:00 a.m. to 05:30 a.m. The androecium of Neotropical Lecythidaceae is a peculiar structure and evidently evolved from an open and radially symmetrical form, such as in *Allantoma*, *Gustavia* and *Grias*, to the closed and zygomorphic structure composed of curved and concrescent staminodes in *Couratari*, *Corythophora*, *Coroupita*, *Escheweilera* and *Bertholletia* [10]. This type of androecium specialization is closely related to the pollination agents, as shown in the affinity of *B. excelsa* with medium to large-bodied native bees and long-tongued bees (orchid bees, tribe Euglossini). The nectar is produced at the staminode base, restricting the guild of pollinators to those capable of lifting the modified petal and the concrescent staminodes, then inserting the glossa far inside the floral chamber to reach the nectar [1, 11–13].

Bertholletia excelsa is predominantly an allogamous (outcrossing) plant, but apparently some self-compatibility exists, as observed in the initial fruit formation of selfed pistils from hand-pollination tests (geitonogamy) at two study sites [14, 15]. However, more reliable results come from cross-pollination and open-pollination tests [14]. Fruit abortion may indicate post-zygotic self-incompatibility, which deserves more detailed study. Evaluation of pollen tube growth in hand-pollinated pistils 48 hours after anthesis resulted in observations of pollen germination from all treatments (cleistogamous or automatic, self, cross and natural pollination), thus excluding sporophitic self-incompatibility (SSI) or pollen rejection at the stigmatic surface. Pollen tube growth from the top of the stigma down to the ovary predominates in cross-pollination, in comparison with geitonogamy and open-pollination treatments, thus providing little evidence for autogamy. This result raises the possibility that the incompatibility system in *B. excelsa* is ovarian or post-zygotic.

Brazil nut cultivation and pollination: The Brazil nut is a key non-timber forest product (NTFP) component in Extractivist Reserves (RESEX) in the Brazilian Amazon [16]. It is also a component of Agroforestry Systems (SAFs) and large-scale monocultures, such as those found in Pará and Amazonas States [17, 18]. Unfortunately, the idea prevails that Brazil nut plantations are not viable [19]. According to Soldán (2003), *B. excelsa* forms part of a complex and interconnected ecosystem, which may explain why all efforts to cultivate the tree outside the Amazon basin (e.g. Indonesia, Malaysia, Sri Lanka and the West Indies) have failed. In spite of this argument, Brazil nut has been raised in agroforestry systems and pure monoculture in the Brazilian Amazon since the 1980s, where there is high pollinator diversity [11, 14, 20]. Although few hard data have been published concerning fruit yield in silvicultural plots, Brazil nut growers complain of low production.

What is possibly leading to low fruit set? Natural Brazil nut populations in primary forest are densely aggregated in groups of 50 to 149 trees [21, 22], and fruit set ranges from 0 to 800 fruit per tree each year, with a mean of 66.2 [23], demonstrating very high variability. In a large-scale Brazil nut monoculture in the central Amazon region [24], annual production in 2007 registered 36.45 fruit/ha, resulting in 5.5 tonnes of nuts/ha, but the following year produced a fruit yield of 3 000 fruit/ha or 45 tonnes of nuts/ha. This pattern, generally called "alternate bearing" (see Glossary) is observed in natural stands [23].

Brazil nut plantations may obtain fewer benefits from pollinators, as observed in other crops [25] because of lower species richness and pollinator abundance in cultivated areas. This factor is correlated with larger distances from natural vegetation. The result is usually a pollination deficit caused by habitat modification [26]. Aside from the absence of pollinators or lower amounts of pollen transported by them [27], the potential drivers of pollination deficits are lack of compatible pollen for self-incompatible and dioecious species, and reduced pollen production and/or poor pollen quality due to plant genotype or phenotype and their interaction with nutrient status, water deficit or other growing conditions (see also Chapter 3.1). In a study of 41 crops worldwide [28], the diversity and abundance of wild insect pollinators proved to be declining in most agricultural landscapes, but the effect on crop yield is still uncertain. Pollen flow disruption due to inappropriate pollen transfer and insufficient pollen deposition by pollinators may be the main cause of a pollination deficit. The presence of wild pollinators in agroecosystems may also provide a complement to managed pollinators [27].

The main pollinators of the Brazil nut are bees of the genera *Bombus, Centris, Xylocopa, Eulaema* and *Epicharis*, both in natural populations and cultivated plots [11–14] (Table 9.1, Figure 9.22). *Xylocopa frontalis*, *Eulaema mocsaryi*, *Epicharis flava*, *Bombus transversalis*, *Centris ferruginea* and *Centris denudans* collect nectar and pollen while visiting the flowers, while *Eufriesea flaviventris* collects only pollen [14].

Pollinator-friendly practices for Brazil nut: In order to enhance natural populations of Brazil nut pollinators, best management practice should focus on compliance with the Brazilian Forest Code [29], which states that Amazonian properties shall use only 20 percent of the total area for any economic activity and/or buildings, leaving up to 80 percent as Legal Reserve and Permanent Preservation Areas (APPs). By preserving such natural habitats, pollinators, as well as predators, parasites and competitors that affect plants and their natural enemies or mutualists will be protected, and ecological services of pollination will provide seeds, fruit, vegetation and plant populations for other living things, including humankind. Farmers may adopt the following list of pollinator-friendly practices to support *on-farm* pollinator conservation (see also section 3.2):

- Be aware of pollinators present on the property and their nests (in order to protect nesting sites or related resources, such as dry wood, mud, water, resin, sand).
- Avoid pesticide use, particularly insecticides, giving preference to biological control or integrated pest management (IPM) practices, if necessary.
- Avoid the use of fire to clear non-cropping areas.

- Retain complementary flowering plants that are important for pollinator food and nesting requirements.
- Provide nesting sites for bees (old tree trunks, wood blocks, bamboo internodes, fence posts, and large trees) within the property.
- Maintain the connectivity of remnant native vegetation areas, in order to facilitate pollinator movement (ecological corridors).
- Disseminate the importance of pollinator-friendly agricultural practices and share experiences with other people.

Table 9.1

FLOWER VISITORS OF *BERTHOLLETIA EXCELSA* IN ITACOATIARA, AMAZONAS STATE*, TOMÉ-ASSU AND BELÉM, PARÁ STATE, BRAZIL

FAMILY	FLOWER VISITOR SPECIES	TYPE
Apidae	*Xylocopa (Neoxylocopa) frontalis* Olivier, 1789	EP
Apidae	*Xylocopa (Neoxylocopa) aurulenta* Fabricius, 1804	EP
Apidae	*Epicharis (Hoplepicharis) affinis* Smith, 1874	EP
Apidae	*Epicharis (Epicharana) flava* Friese, 1900	EP
Apidae	*Epicharis (Epicharana) conica* Smith, 1874	OP
Apidae	*Epicharis (Epicharana) rustica* Olivier, 1789	EP
Apidae	*Epicharis (Epicharis) umbraculata* Fabricius, 1804	EP
Apidae	*Epicharis (Parepicharis) zonata* Smith, 1854	EP
Apidae	*Epicharis sp.*	OP
Apidae	*Centris (Ptilotopus) americana* Klug, 1810	OP
Apidae	*Centris (Heterocentris) carrikeri* Cockerell, 1919	OP
Apidae	*Centris (Xanthemisia) ferruginea* Lepeletier, 1841	EP
Apidae	*Centris (Ptilotopus) denudans* Lepeletier, 1841	EP
Apidae	*Centris (Trachina) similis* Fabricius, 1804	EP
Apidae	*Centris sp.*	OP
Apidae	*Eulaema (Eulaema) meriana* Olivier, 1789	EP
Apidae	*Eulaema (Apeulaema) mocsaryi* Friese, 1899	EP
Apidae	*Eulaema (Apeulaema) cingulata* Fabricius, 1804	OP
Apidae	*Eulaema (Apeulaema) nigrita* Lepeletier, 1841	EP
Apidae	*Bombus (Fervidobombus) transversalis* Olivier, 1789	EP
Apidae	*Bombus (Fervidobombus) brevivillus*	EP
Apidae	*Eufriesea purpurata* Mocsàry, 1896	EP
Apidae	*Eufriesea flaviventris* Friese, 1899	EP
Apidae.	*Eufriesea* sp.	EP
Apidae	*Apis mellifera* Lepeletier, 1836	V
Apidae	*Frieseomelitta longipes* Smith, 1854	R
Apidae	*Melipona (Michmelia) lateralis* Erichson, 1848	V
Apidae	*Melipona (Michmelia) lateralis* Erichson, 1848	V
Apidae	*Trigona pallens* Fabricius, 1798	R
Apidae	*Frieseomelitta longipes* Smith, 1854	R
Megachilidae	*Megachile* sp.	PO

Notes: *Visitor list from [14]. EP = effective pollinator, OP = occasional pollinator, V = visitor, R = pollen robber or thief.

Source: M. Maués, M.C. Cavalcante, A.C. dos Santos and C. Krug

Figure 9.21

VISITORS AND POLLINATORS OF BRAZIL NUT - *BERTHOLLETIA EXCELSA* AT TWO CULTIVATED SYSTEMS, MONOCULTURES IN ITACOATIARA, AMAZONAS STATE AND AGROFORESTRY SYSTEMS IN TOMÉ-ASSU, PARÁ STATE, BRAZIL

(a) *Xylocopa frontalis* (♀); (b) *Bombus tranversalis* (♀); (c) *Centris americana* (♀); (d) *Centris denudans* (♀); (e) *Centris ferruginea* (♀); (f) *Epicharis zonata* (♀); (g) *Epicharis flava* (♀); (h) *Eufriesea flaviventris* (♀); (i) *Eufriesea purpurata* (♀); (j) *Eulaema bombiformis* (♀); (k) *Eulaema mocsaryi* (♀); and (l) *Eulaema cingulata* (♂)

Source: M. Casimiro Cavalcante

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9.3.2 Passion fruit in Colombia

R. Ospina-Torres, J. Jaramillo,
A. Rodriguez-C., M.M. Henao and
G. Nates-Parra

Colombia contains the greatest diversity of *Passiflora*, with recent studies identifying 170 species found mainly in the Andean region [1, 2]. At least 81 of these may have potential as edible fruit crops [3], but less than a dozen are cultivated and only two or three enter the agricultural industry. One is the yellow passion fruit (*Passiflora edulis* var. *flavicarpa*), whose commercial importance has motivated study [4]. The results of those studies clearly underscore the importance of wild bees [3, 5]. Because the self-incompatibility and floral morphology of the flower frequently require the pollination service of a large bee such as *Xylocopa* (Chapter 4.6), manual pollination is used in several regions of Brazil and Colombia. Furthermore, plant breeders are increasingly investigating self-compatible varieties. Two years ago, the authors began asking questions about floral biology and the role of bees in pollination of various *Passiflora* in Colombia, and relate here the status of this ongoing work.

Study methods: The species or varieties considered and localities (towns, followed by provinces or "departments") where fieldwork was conducted were: gulupa (*Passiflora edulis* var. *edulis*) and granadilla (*Passiflora liguralis*) in Buenavista (Boyacá); cholupa (*Passiflora maliformis*) in Rivera (Huila); and curuba (*Passiflora tripartita* var. *mollissima*) in Nuevo Colón (Boyacá). For each species a basic study of floral biology was made including a description of the floral cycle and its morpho-functional phases, development of the male and female fertile phases by testing pollen viability and stigma receptivity (formation of pollen tubes and fruit set), and monitoring of pollinator rewards – pollen and nectar. Additional study included experimental tests with selective bagging for each treatment, to clarify basic aspects of plant reproductive biology, particularly self-compatibility. The tests registered fruit formation with no fertilization (apomixis or agamospermy), manual self-pollination, self-pollination with no visitor, manual cross-pollination (xenogamy) and natural, open pollination. Finally, flower visitors were monitored and counted, then evaluated for pollination potential. Individual visits were further monitored by bagging a flower, removing the bag to permit a single visit, then replacing the bag.

Figure 9.22
PASSION FRUIT - *PASSIFLORA* FLOWER ON VINE, AND CROSS SECTION OF FRUIT AND SEEDS

Source: B. B. Simpson and M. Connor Ogorzaly. 1986. Economic Botany - plants in our world. New York: McGraw-Hill. page 116. reprinted by permission [in original 1995 book published by FAO and edited by D. W. Roubik]

Results – floral biology: Two of the four species were found to have a floral cycle of a day or less (Table 9.2). Cholupa (*P. maliformis*) has a relatively short cycle of 11 hours [6], and gulupa (*P. edulis*) has a cycle of 25 hours [7]. Furthermore, granadilla (*P. ligularis*) is open on average for 32 hours [8], while curuba (*P. tripartita* var. *mollissima*) displays wide variability, with flowers open between 36 hours and 72 hours [9]. The flowers of the first three species present a more or less synchronized flowering between bud opening and flower closing on the same day, while some flowers of curuba remain open until the next day or even longer, thus younger flowers overlap with older ones. It was also noted that the floral cycle of some curuba flowers can "stop" for several hours due to factors unknown. Because the flowering cycle varies in total duration among the four species, maximum stigmatic receptivity is expressed in terms of percentage of the total cycle (Table 9.2). Thus, curuba reaches maximum receptivity relatively early (14 percent of the cycle) [9], while somewhat later (30–40 percent) among the other species. Regarding the male structures, cholupa and gulupa have earlier anther dehiscence (2 percent) and the pollen is viable 3 to 4 hours after dehiscence [6, 7].

Nectar production is greater in cholupa (400 µL in the floral cycle) [6], but the nectar is relatively diluted, while gulupa, a species that produces less volume (122 µL), has a higher sugar concentration [7].

All species have highest concentrations at peak bloom.

Results – reproductive biology: Cholupa (*P. maliformis*) is completely self-incompatible, as with yellow passion fruit, while the others are self-compatible with manual pollination (Table 9.3). Gulupa (*P. edulis*) (33 percent) [7], and curuba (*P. tripartita* var. *mollissima*) (6.2 percent) [9] form fruit with no pollinator service, but have low fruit set compared with natural pollination (*P. edulis* 93 percent. *P. tripartita* 58 percent) [7, 9]. Interestingly, although they belong to the same taxonomic species, gulupa is self-compatible, while yellow passion fruit is not.

Table 9.2

FLORAL BIOLOGY TESTS FOR FOUR SPECIES OF *PASSIFLORA*

CROP/REFERENCE	ANTHESIS DURATION (HOURS)	PEAK STIGMATIC RECEPTIVITY (% HOURS)	PEAK POLLEN VIABILITY (% HOURS)	POLLEN DEHISCENCE (% HOURS)	NECTAR (UL)	SUGAR (MG/UL)*
P. edulis f. *edulis* [7]	25	40% (10 hours after anthesis)	14% (3.5 hours after anthesis)	2% (0.5 hours after anthesis)	122.1	1.0 – 35.3 – 32.1
P. ligularis [8]	32	32.3% (10.5 hours after anthesis)	–	–	3603.4	0.392 – 0.443 – 0.352
P. maliformis [6]	11	36.4% (4 hours after anthesis)	36.4% (4 hours after anthesis)	4.5% (0.5 hours after anthesis)	400	0.484 – 0.558 – 0.462
P. tripartita var. *mollissima* [9]	36	27.8% (10 hours after anthesis)	27.8% (10 hours after anthesis)	11.1% after anthesis)	272.6	0.92 – 19.50 – 26.67
	72	13.9% (10 hours after anthesis)	13.9% (10 hours after anthesis)	11.1% after anthesis)	272.6	0.92 – 19.50 – 26.67

Note: The sugar values are maximum for open, highest concentration in the cycle and in senescence.

Source: Ospina-Torres, *et al.* [present study]

Table 9.3

RESULTS OF REPRODUCTIVE BIOLOGY FOR FOUR SPECIES OF *PASSIFLORA* WITH DIFFERENT POLLINATION TREATMENTS

CROP/REFERENCE	TREATMENTS (% OF FRUIT SET)					
	XEN	AUT	GEI	APO	SPO	NAT
P. edulis f. *edulis* [7]	87	93	87	0	33	93
P. ligularis [8]	86.7	86.7	93.3	0	0	80
P. maliformis [6]	71.3	0	28.9	0	0	52.1
P. tripartita var. *mollissima* [9]	83.3	34.8	No data	17.2*	6.3	78.3

Notes: Fruit formed by apomixis are not viable in 10 days. XEN= Xenogamy, AUT= Autogamy, GEI= Geitonogamy, APO=Apomixis, SPO= Spontaneous selfing, NAT=Natural pollination.

Source: Ospina-Torres, *et al.*

Figure 9.23
THREE DIFFERENT BEES VISITING *PASSIFLORA*, EACH WITH DIFFERENT FORAGING AND POLLINATION METHODS. LEFT TO RIGHT: *AFRICANIZED APIS MELLIFERA*, *EULAEMA* AND *XYLOCOPA*

Source: Ospina-Torres, *et al.*

Results – visitors and pollinators: Using methods following Vaissiere *et al.* [10], and with some taxonomic results pending (Table 9.4), the assemblage of visitors, especially bees, was found to be more diverse at lower altitudes and warmer climates, especially for gulupa [11]. Both lowland and highland crops received numerous visits from Africanized honey bee (*Apis mellifera*), which accounted for over 74 percent of visits, making it the most recorded species, with the exception of a gulupa crop where it comprised less than 10 percent of visitors or was completely absent. Honey bees are medium-sized insects and their behaviour varies among the four *Passiflora*. The bees use several different methods to reach the floral nectaries. This is because their short tongue prevents them from achieving access in the normal manner and the nectaries are sometimes situated in a nectar chamber, which is difficult to access, despite not being located within a tubular corolla (Figure 9.24). In addition, they use perforations typically caused by *Diglossa* robber birds (in curuba) or other insects (in cholupa). Sometimes *A. mellifera* is unable to make contact with the reproductive structures of *Passiflora*, and a few honey bee visits are insufficient for effective pollination. However, honey bees do reach sufficient density and achieve higher visitation levels in extremely disturbed habitats or in poor weather, as in the curuba study area.

After honey bees, *Xylocopa* (carpenter bees, see Chapters 15 and 16) are the next most effective visitors. These and other large Apid bees, *Centris* and *Epicharis*, and large orchid bees *Eulaema* contact both anthers and the stigmatic surface of *Passiflora* flowers, sometimes achieving complete pollination with just one visit [8, 11]. Other wild bees of smaller size arrive, including stingless bees (Meliponini), and visit primarily lowland crops. However, their small size and the low frequency of visits diminish their pollination potential.

Other notable visitors include several species of hummingbird, which appear especially in the curuba and gulupa, but apparently do not pollinate. Although these heavy nectar users often exhibit territorial behaviour, for example by displacing larger bees such as *Xylocopa*, they have no contact with the reproductive structures of tubular flowers. For curuba, the hummingbirds act as secondary robbers and use perforations of *Diglossa* ("flowerpiercers", Thraupidae), which are common in the Colombian Andes.

It is important to note that the large hummingbird *Ensifera ensifera* [12], a native curuba pollinator, was not recorded in this study.

Table 9.4

VISITORS, ROBBERS OR THIEVES, AND POTENTIAL POLLINATORS OF FOUR SPECIES OF *PASSIFLORA*

CROP/ REFERENCE	HIGHER TAXON VISITOR	VISITOR SPECIES	FREQUENCY OF VISITS (%)	RESOURCE	CONTACT WITH SEXUAL STRUCTURES	TRANSPORT OF POLLEN	POTENTIAL POLLINATOR
Passiflora maliformis [14]	Apidae/Apini	*Apis mellifera*	87.5	N/P	Sometimes	Sometimes	Yes
	Apidae/ Xylocopini	*Xylocopa frontalis*	1.7	N	Yes	Yes	Yes
	Apidae/Centridini	*Centris flavifrons*	1.7	N	Yes	Yes	Yes
	Apidae/Centridini	*Centris insignis*	0.5	N	Yes	Yes	Yes
	Apidae/Centridini	*Epicharis* sp.	0.3	N	Yes	Yes	Yes
	Apidae/Centridini	*Centris obsoleta*	0.04	N	Yes	Yes	Yes
	Apidae/Centridini	*Centris vittata*	0.04	N	Sometimes	Sometimes	Occasional
	Apidae/Centridini	*Epicharis* sp.	0.04	N	Sometimes	Sometimes	Occasional
	Apidae/Eucerini	1 sp.	0.5	N	Sometimes	Sometimes	Occasional
	Apidae/ Euglossini	*Eulaema nigrita*	2.3	N/P	Yes	Yes	Yes
	Apidae/ Euglossini	*Eulaema cingulata*	1.3	N/P	Yes	Yes	Yes
	Apidae/ Euglossini	*Eulaema polychroma*	1.0	N/P	Yes	Yes	Yes
	Apidae/ Euglossini	*Euglossa variabilis*	0.04	N	Sometimes	Sometimes	Occasional
	Apidae/ Euglossini	*Euglossa sp.*	0.04	N	Sometimes	Sometimes	Occasional
	Halictidae/ Augochlorini	Morphospecies 1	0.2	N	No	No	No
	Halictidae/ Augochlorini	Morphospecies 2	0.04	N	No	No	No
	Apidae/ Meliponini	*Nannotrigona mellaria*	1.4	N/P	No	No	No
	Apidae/ Meliponini	*Trigonisca* sp.	1.14	N/P	No	No	No
	Apidae/ Meliponini	*Trigona fulviventris*	0.1	N/P	No	No	No
	Apidae/ Meliponini	*Scaptotrigona* sp.	0.04	N/P	No	No	No
	Apidae/ Meliponini	*Tetragona* sp.	0.04	N/P	No	No	No
	Coleoptera	Staphylinidae	No data	R/N	No	No	No
	Vespidae	Various species	No data	N	No	No	No*
	Trochilidae	Various species	No data	N	Sometimes	Sometimes	No data *
	Diptera	Drosophylidae	No data	R/N	No	No	No

CROP/ REFERENCE	HIGHER TAXON VISITOR	VISITOR SPECIES	FREQUENCY OF VISITS (%)	RESOURCE	CONTACT WITH SEXUAL STRUCTURES	TRANSPORT OF POLLEN	POTENTIAL POLLINATOR
Passiflora ligularis [13]	Apidae/ Apini	*Apis mellifera*	74.5	N/P	Yes	Yes	No
	Apidae/ Euglossini	*Eulaema* sp.	1.0	N	Yes	No data	No data
	Apidae/ Bombini	*Bombus atratus*	10.2	N	Yes	No data	Yes
	Apidae/ Xylocopini	*Xylocopa* sp. 1	6.3	N	Yes	No data	Yes
	Apidae/ Xylocopini	*Xylocopa* sp. 2	0.7	N	Yes	No data	Yes
	Apidae/ Eucerini	*Thygater* sp.	6.4	N	Sometimes	No data	No data
	Apidae/ Euglossini	*Eulaema bombiformis*	0.2	N	Sometimes	No data	Yes
	Apidae/ Centridini	*Epicharis sp.*	0.2	N	Yes	No data	Yes
	Trochilidae	1 sp.	0.7	N	No	No data	Yes

CROP/ REFERENCE	HIGHER TAXON VISITOR	VISITOR SPECIES	FREQUENCY OF VISITS (%)	RESOURCE	CONTACT WITH SEXUAL STRUCTURES	TRANSPORT OF POLLEN	POTENTIAL POLLINATOR
Passiflora tripartita var. *mollissima* [9]	Apidae/ Apini	*Apis mellifera*	85.2	N/P	Yes	No data	Yes
	Apidae/ Eucerini	*Thygater aethiops*	0.4	N/P	Yes	No data	Yes
	Apidae/ Xylocopini	*Xylocopa* sp.	1.5	N	No	No data	No
	Apidae/ Bombini	*Bombus atratus*	0.2	N	Yes	No data	No
	Halictidae/ Augochlorini	*Augochlora* sp.	0.3	N	No	No data	No
	Coleoptera	1 sp.	7.5	N/P	Yes	No data	Yes
	Vespidae	1 sp.	1.7	N	Yes	No data	Occasional
	Trochilidae	*Lesbia nuna*	0.8	N	No	No data	No
	Trochilidae	*Chlorostilbon gibsoni*	1.2	N	No	No data	No
	Trochilidae	*Coeligena prunellei*	0.6	N	No	No data	No
	Thraupidae	*Diglossa sittoides*	0.59	N	No	No data	No*

CROP/ REFERENCE	HIGHER TAXON VISITOR	VISITOR SPECIES	FREQUENCY OF VISITS (%)	RESOURCE	CONTACT WITH SEXUAL STRUCTURES	TRANSPORT OF POLLEN	POTENTIAL POLLINATOR
Passiflora edulis f. *edulis* [11]	Apidae/ Xylocopini	*Xylocopa frontalis/X. lachnea*	33	N	Yes	Yes	Yes
	Apidae/ Euglossini	*Eulaema cingulata*	1.7	N	Yes	No data	No data
	Apidae/ Bombini	*Bombus atratus*	No data	N	No data	No data	No data
	Apidae/ Centridini	*Epicharis* sp.	3.6	N	Yes	Yes	Yes
	Apidae/ Meliponini	*Frieseomelitta* sp.	0.8	N	No	No data	No data
	Apidae/ Meliponini	*Trigona fulviventris*	4	N	No	No data	No data
	Apidae/ Meliponini	*Tetragonisca angustula*	1.9	N	No	No data	No data
	Apidae/ Meliponini	*Trigona amalthea*	2.1	N	Sometimes	No data	No data
	Apidae/ Meliponini	*Paratrigona eutaniata*	1.3	N	No	No data	No data
	Apidae/ Meliponini	*Geotrigona* sp.	0.4	N	No data	No data	No data
	Apidae/ Apini	*Apis mellifera*	10	N/P	Yes	Sometimes	Yes
	Vespidae	1 sp.	No data	N	No data	No data	No data
	Diptera	Sciaridae	No data	N	No	No data	No data
	Diptera	*Dapsiops* sp.	No data	N	Sometimes	No data	No data
	Lepidoptera	Hesperiidae	0.4	N	No	No data	No data
	Trochiliformes	*Amazilia tzacatl*	41	N	Sometimes	Sometimes	Yes
	Trochiliformes	*Amazilia cyanifrons*	No data	N	Sometimes	Sometimes	Yes

Notes: primary or secondary nectar robbers. N/P = Nectar and Pollen; N = Nectar; P = Pollen; R/N = Refuge and Nectar.

Source: Ospina-Torres, *et al.*

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9.3.3 Bee pollination of cotton in Brazil

C.S.S. Pires, V.C. Pires and E.R. Sujii

Brazil's cotton is cultivated mainly in the mid-west, in large fields of 5 000 to 10 000 ha and with intensive use of insecticides and other agricultural input [1]. The region currently accounts for 70 percent of Brazilian cotton production [1]; the area planted for the 2012/2013 crop season covered 561 million ha and produced 2.3 million tonnes of fibre. In addition, cotton is also cultivated on small farms (0.5 to 5 ha) by smallholders in northeastern Brazil, with low levels of additional input. Cotton cultivation in the region constitutes a very important, and sometimes the only, income for such smallholders. Since 2005, "Embrapa Cotton" has run a programme in the northeastern region to produce organic cotton and increase production value in smallholdings. In these areas, cotton is grown using an organic approach, intercropping with food crops that form staple diets of local families [2].

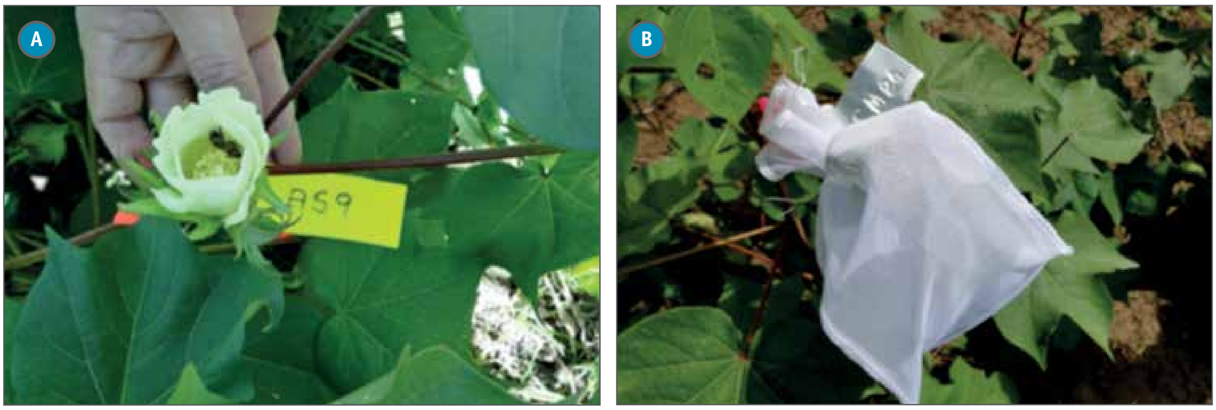
Bee assemblages visiting cotton flowers: The reproductive system of *Gossypium* – including *G. hirsutum* and *G. barbadense* native to the Neotropics, and *G. arboreum* and *G. herbaceum* native to the Old World tropics – may be considered both autogamous and allogamous [3, 4]. Cotton pollen, due to its relatively large size (81 μm to 143 μm) and stickiness, cannot be transported by wind. The flowers of cotton possess one floral and four extrafloral nectaries, and a shape and colour typical of entomophilous plants [3]. The main flower visitors are insects [5], and bees are the most important pollinators, both in Brazil [6–13] and in other parts of the world [3–4].

Visitors to cotton flowers include species of the five bee families that occur in Brazil. A total of 110 species are known from surveys conducted in the last ten years across different regions of the country on 11 varieties of cotton. The number may be higher, taking into account the likely existence of species new to science observed during sampling in the northeastern region (Pires, Pires and Sujii, unpublished data). Most species belong to the family Apidae (77 percent) and the subfamily Apinae, consisting of about 30 species, primarily feral Africanized *Apis mellifera* and native *Trigona spinipes*. The cotton production regions have distinct environmental conditions (e.g. upland savannah *cerrado* in the midwest and semi-desert *caatinga* in northeastern Brazil) and a very diverse and distinct wild bee fauna [13]. The similarity among bee assemblages is < 40 percent (Jaccard/Kulczynski similarity index).

Bee pollination of cotton: Although the cotton plant is autogamous and does not require pollinators, production increases considerably with a greater presence of bees in the crop area. Studies carried out by the authors over the last four years in Brazil demonstrate that, in general, bee visits to cotton flowers positively influence cotton productivity, but there is apparently no influence on fibre quality or seed vigour [13]. The positive results are more evident in areas where cotton is produced within an organic system and in combination with other crops where bee richness is high, compared to conventional production locations with low bee diversity and abundance. In the organic production area studied, flowers of the variety "Embrapa-BRS 1878H" open to visits by bees displayed a 14 percent increase in fibre weight, compared to flowers lacking bee visits (natural or "spontaneous" self-pollination), and a 17 percent increase in the number of seeds [13]. The high richness and abundance of bees on the organic farms, associated with management practices that favour pollinators, such as the use of small plantations near natural vegetation and without pesticides, likely contribute to the increased fibre weight and number of seeds (Figures 9.25 and 9.26). On the conventional farm, yield in flowers of the variety "Bayer-FM 910" open to bee visitation was similar to that of bagged flowers. Evidently, in this crop season the number of individuals observed visiting the cotton flowers (0.45 bees/hour) was inadequate to increase production. Another experiment with the same cotton variety on the same farm, in a different year, demonstrated the importance of native vegetation for maintenance of bee species richness, with production increasing concurrent with a greater number of bee species visiting cotton flowers. The productivity of cotton is also higher near vegetation, likely due in part to the greater richness of bees there. An indication of pollinator importance is that production potentially increases by 27 percent if bee richness includes at least four species on cotton flowers. The contribution of various species of bees together in pollination may be more important for cotton production than the contribution of a single species alone [13].

Figure 9.24

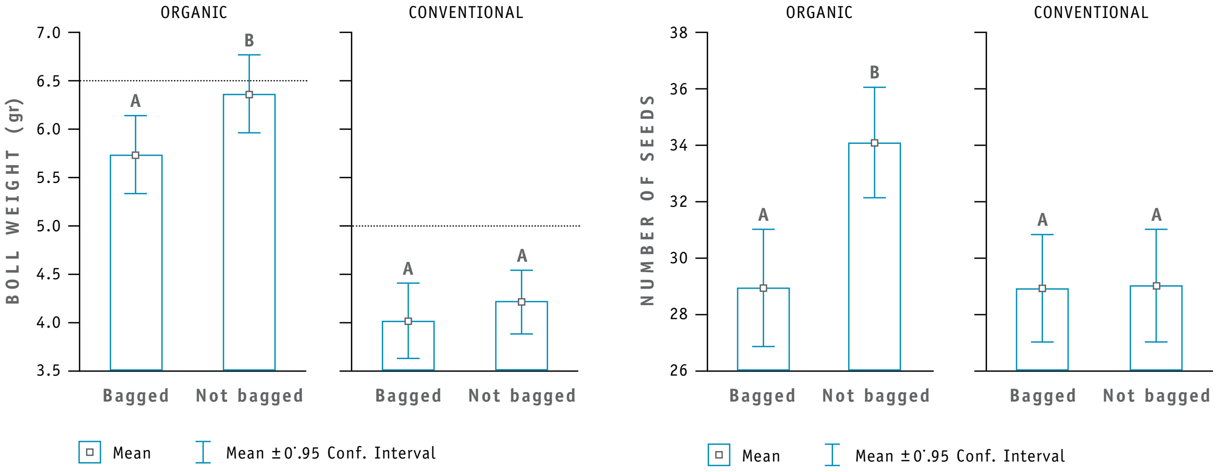
(A) COTTON FLOWERS OPEN TO BEE VISITS (NATURAL POLLINATION), AND (B) COTTON FLOWERS BAGGED TO PREVENT BEE VISITATION (SPONTANEOUS SELF POLLINATION)



Source: Pires *et al.*

Figure 9.25

BOLL WEIGHT OF FRUITS AND NUMBER OF SEEDS (MEAN NUMBER PER FRUIT) RESULTING FROM BAGGED COTTON FLOWERS (SELF-POLLINATION – BAGGED) AND COTTON FLOWERS OPEN TO BEE VISITATION (NATURAL POLLINATION – UNBAGGED), MEASURED IN AREAS OF ORGANIC (COTTON VARIETY = EMBRAPA – BRS 187 8H) AND CONVENTIONAL (COTTON VARIETY = BAYER – FM 910) PRODUCTION



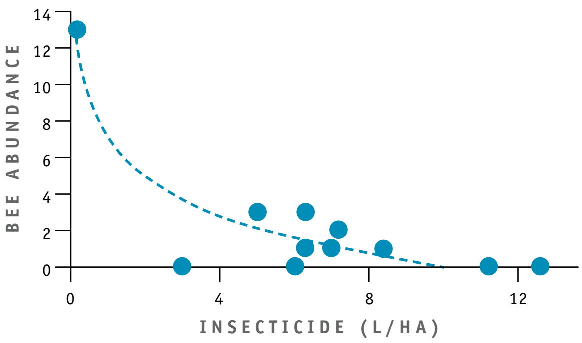
Note: Dotted line represents the mean value expected for boll weight for the tested variety. Different letters in the graphic represent significant differences between treatments based on Student's t test. Boll weight (organic area) t = -2.22; p = 0.03 and (conventional area) t = -0.73; p = 0.47. Number of seeds (organic area) t = -3.59; p < 0.01 and (conventional area) t = -0.09; p = 0.93.

Source: Pires *et al.*

Unlike organic cotton farm areas, conventional cotton production adopts a management strategy that does not favour bees. In addition to natural habitat loss, intense spraying for pest control affects bee communities. On a conventional cotton farm, a decrease in the abundance of wild bees is observed, including the wild Africanized *Apis mellifera*. This occurs with an increase in insecticide applied within a 15-day period prior to sampling bees on cotton flowers (Figure 9.26). It was not possible to establish whether the decrease in abundance is caused by the death of bees in the area or if the bees avoid the cotton areas when insecticide is present. The effects of insecticides on the bee community need to be investigated at a large scale or field level. In the laboratory, honey bees (*A. mellifera*) are killed by many pesticides, and when adult bees are in contact with the neonicotinoid group of insecticides, often used on cotton areas, they may suffer from memory loss and present abnormal foraging behaviour [14]. Additionally, the larvae, feeding in the nest on nectar and pollen contaminated with the insecticides, exhibit developmental problems and impaired mobility, decreasing their chance to reach adulthood [15].

Figure 9.26

ABUNDANCE OF WILD BEES AND FERAL *APIS MELLIFERA* ON COTTON FLOWERS (TOTAL NUMBER OF INDIVIDUALS/600 M^2) IN RELATION TO THE VOLUME OF INSECTICIDE (LITRES) APPLIED WITHIN THE 15-DAY INTERVAL BEFORE THE DATE OF SAMPLING FOR BEES



Note: Each point on the graph represents the total number of bees collected during 4 hours of sampling in a plot of 600 m^2.

Source: Pires *et al.*

Conclusion: The diversity and abundance of bee flower visitors play an important role in cotton pollination and in boosting production. Smallholders that cultivate cotton in an organic system can benefit from the high diversity of bees present in their area, with the authors' studies demonstrating an increase in cotton production. However, in large cotton production farms in Brazil, where crop plots are huge by any standards, and where environmental disturbance by chemical insecticides is frequent, low bee diversity and abundance are the rule. Accordingly, the farms do not benefit from bee pollination.

Despite the rich bee fauna observed on cotton and the large number of cotton varieties available on the market, the influence of bee pollination on commercial cotton production in Brazil remains poorly studied. Among 73 cotton varieties registered for use in the country [16], bee pollination has been studied only with five varieties. As expected, results are variable because of variation among cotton varieties, differences in crop management and differences in bee fauna between different sites. To date, the growers largely ignore the role of bee pollination in cotton production.

The benefits of bees for the cotton crop are real. The big challenge in cotton management is to coordinate pest control methods with "best" practices that favour pollinators (see Chapter 4). The first step is to value the service of pollinators, by educating farmers about the positive results provided by bees (see Chapter 7.1; see also Figure 9.3). Moreover, best practices or those that are "bee friendly" can be suggested, such as:

- maintenance of natural vegetation near the plantations;
- reduction in the number of insecticide applications in the crop areas via integrated pest management;
- avoiding insecticide application on fields when bees are most active.

Greater commercial value may be obtained when cotton is produced under pollinator friendly conditions.

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9.3.4 Tomato pollination in Brazil

M.C. Gaglianone, E.V. Franceschinelli, M.J.O. Campos, L. Freitas, C.M. Silva Neto, M.S. Deprá, M.A.S. Elias, L. Bergamini, P. Netto, B.G. Meyrelles, P.C. Montagnana, G.P. Patricio and L.A.O. Campos

Cultivated tomatoes (*Solanum lycopersicum*, Solanaceae) originated in western South America, where several wild species also occur [1, 2]. Now widespread throughout the world, the tomato has many different varieties derived from genetic improvement [3]. Tomato is a globally important food product and Brazil occupies ninth place in production terms [4]. The states of Goiás (GO), São Paulo (SP), Minas Gerais (MG) and Rio de Janeiro (RJ) are responsible for 70 percent of all Brazilian production, and produce average yields ranging from 66.5 to 84.2 tonnes/ha/year [5]. Most of the cultivated area takes the form of small parcels (up to 2 ha) in open field (see Figure 9.27, RJ, SP and GO), with production in greenhouses accounting for a smaller proportion (Figure 9.27, MG). Tomato crops are temporary and short-cycled, but depending on climate and rainfall patterns, are often obtained during more than one season. Currently, a major concern is intensive use of pesticides that can make the product dangerous for human consumption and threaten beneficial insects in the plantation, such as pollinators. For this reason, organic tomato production has been increasing in recent years.

Figure 9.27
VIEW OF CULTIVATED AREAS IN DIFFERENT STATES OF BRAZIL

Rio de Janeiro (RJ), Goiás (GO), São Paulo (SP) and Minas Gerais (MG)

Source: Gaglianone *et al.*

Plant and flower morphology: Tomatoes have a herbaceous/shrubby habit and reach up to 2 m in height. Plants produce mature fruits 90 to 120 days after seed germination, or 45 to 55 days after flowering. Tomato inflorescences are dichasial cymes, and the flowers are bisexual and actinomorphic. Petals, sepals and anthers vary in number from five to seven. Petals are yellow and fused at their bases (Figure 9.28). Stamens have large yellow anthers with poricidal dehiscence, which need vibration or "buzzing" for pollen to leave them. Anthers are fused to form a cone that surrounds the pistil, and the stigma is located slightly below the anther pores in most tomato varieties. Tomato flowers have no nectar.

Floral biology for tomatoes is similar among the cultivars in different regions of Brazil. Flowers open at around 06:30 hours and require approximately one hour to expose the reproductive structures. These are pendulous and the petals become deflexed in the afternoon when closure begins. Mean pollen production for the Italian variety grown in GO is 333.200 ± 299.500 grains per flower, with little availability during the first hour of anthesis, between 07:00 and 08:00 hours. Pollen availability reaches a peak around noon, when the highest flower visitation rate by insects occurs. Pollen viability is high (97 ± 12.6 percent) but varies somewhat during the day.

The stigma is apparently receptive during the entire anthesis period. Its position below the anther cone diverges from wild forms, where the stigma protrudes beyond the pores, thereby establishing a herkogamous floral morphology that avoids self-pollination. In contrast, the cultivated varieties – plants with stigmas below the anther openings – were selected to achieve self-pollination and therefore conserve artificially selected traits [6]. Nevertheless, the buzzing pollen-collection behaviour of bees improves pollination and productivity [7, 8], while the cultivated varieties can self-pollinate when the wind or other forces shake the flowers.

Breeding system: Cultivated tomato plants are self-compatible. However, because of the poricidal anther structure, vibration of the flowers is needed to release pollen grains. Thus, the only pollinators are certain bees that vibrate the anthers by holding them and shivering their flight muscles, in a process called "buzz pollination" [9]. Although wind shakes the flowers and can lead to self-pollination, vibration by buzzing bees results in the transfer of larger numbers of pollen grains to the stigma. On average, stigmas of open flowers receive 114 ± 68 more pollen grains than those of bagged flowers (data from GO). Data obtained in GO, RJ, MG and SP indicate that tomatoes from open (unbagged) flowers probably visited by pollinators are larger, heavier and have more seeds compared to those of bagged flowers (see Table 9.5), [7, 8, 10].

Figure 9.28
TOMATO (*SOLANUM LYCOPERSICUM*) FLOWERS

(a) deflexed petals and fused anthers; (b) extended petals and central cone of anthers; and (c) fruit in development

Source: Gaglianone *et al.*

Table 9.5
QUALITY OF TOMATO FRUITS OBTAINED FROM BAGGED AND OPEN (UNBAGGED) FLOWER TREATMENTS IN OPEN ORCHARDS AND GREENHOUSES IN BRAZILIAN STATES: GOIÁS (GO), RIO DE JANEIRO (RJ), MINAS GERAIS (MG) AND SÃO PAULO (SP)

AREAS (STATE)	TOMATO VARIETIES	TREATMENT	WEIGHT (g) (AVERAGE ± DP)	SEED NUMBER (AVERAGE ± DP)	FRUIT SIZE (mm) (AVERAGE ± DP)
GO	*Italian*	Open (natural pollination)	70.69 ± 20.40^a (n=31)	183.94 ± 46.34^a (n=36)	51.12 ± 5.43^a (n=27)
		Bagged (self-pollination)	47.06 ± 26.88^b (n=31)	59.63 ± 38.54^b (n=36)	46.59 ± 8.14^b (n=27)
RJ	*Salada*	Open (natural pollination)	99.1 ± 37.1^a (n=114)	166.2 ± 57.4^a (n=114)	NE
		Bagged (self-pollination)	95.6 ±30.6^a(n=102)	147.7 ± 56.4^b (n=102)	NE
SP	Cherry (*cereja*)	Open (natural pollination)	15.0 ± 7.9^a (n=16)	50.1 ± 16.5^a (n=16)	NE
		Bagged (self-pollination)	14.4 ±6.3^a (n=22)	36.5 ± 15.6^b (n=22)	NE
MG*	Chipano® (*cereja vermelho*)	Open (natural pollination)	17.6 ± 2.3 (n=15)	NE	NE
		Bagged (self-pollination)	14.3 ± 4.1 (n=15)	NE	NE
MG*	Sweet Gold® (*cereja amarelo*)	Open (natural pollination)	20.5 ± 2.6 ^{a} (n=15)	NE	NE
		Bagged (self-pollination)	13.8 ± 5.6 ^{b} (n=15)	NE	NE
MG	*Sophia*	Open (natural pollination)	110.9 ± 65 (n=39)	NE	NE
		Bagged (self-pollination)	65.8 ± 35.7 (n=33)	NE	NE
MG	*Aguamiel*	Open (natural pollination)	57.36 ± 27.6 (n=74)	NE	NE
		Bagged (self-pollination)	48.27 ± 24.7 (n=46)	NE	NE

Notes: NE = not evaluated; a,b = Different letters represent significant differences between treatments with the same variety.

Source: Gaglianone *et al.*

Pollinators: All flower visitors are bees. The higher the bee visitation to tomato flowers, the greater the fruit set [7, 8]. Given the role of bees in increasing pollination rate, evaluations were made in 68 tomato orchards in the states of GO, RJ, MG and SP to recognize and quantify more effective pollinators in the different regions (Table 9.6). Flower-visiting bees are females belonging to the families Apidae, Halictidae and Andrenidae (Table 9.7). The number of species visiting tomato flowers varies from 18 (SP) to 40 (RJ). The greatest similarity in the composition of species occurs between RJ and GO. *Exomalopsis analis* and *Oxaea flavescens* visit tomato flowers in the four selected study areas and 9 percent of all observed species occur in at least three of those states. Most species behave as buzz pollinators (Figure 9.29), while "non-buzzers" such as *Apis mellifera*, *Paratrigona lineata*, *Trigona spinipes* and *Dialictus* spp. are visitors but not pollinators. In total, 14 to 38 bee species display the potential to pollinate tomato flowers (Table 9.7). Their size varies from small (< 8mm, such as *Exomalopsis* spp.) to large bees (> 15 mm, such as *Xylocopa* spp.). Among the most common pollinators, *Exomalopsis* and *Augochloropsis* spp. represent 30.5 percent (SP) to 70.6 percent (GO) of all visitors listed. Bumblebees (*Bombus* spp.) are very frequent in MG (11.2 percent) and prominent mainly in SP (37.8 percent of visiting bees), whereas *Pseudaugochlora* occurs more frequently in GO (7 percent of all bees).

Table 9.6

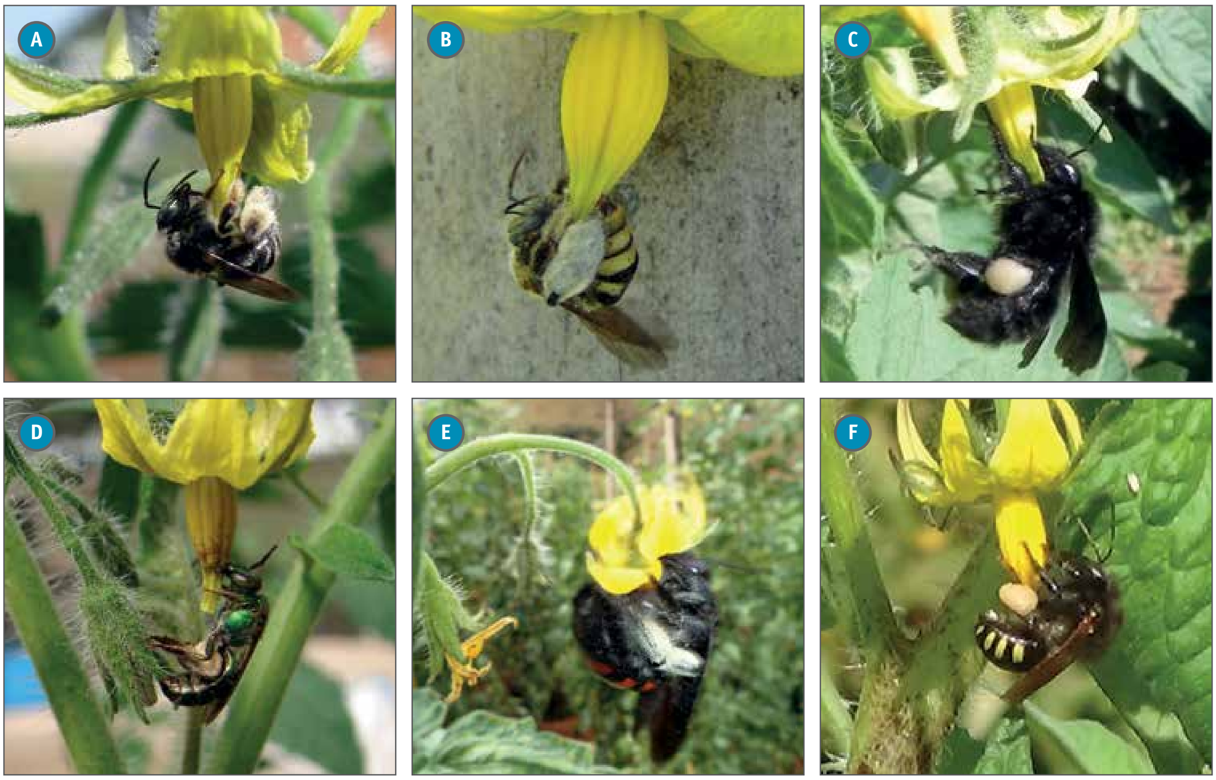
SAMPLING EFFORTS, SPECIES RICHNESS AND ABUNDANCE OF VISITORS AND POLLINATORS OF TOMATO FLOWERS IN BRAZIL

	RJ	GO	MG	SP
Number of orchards studied	36	14	12	06
Flowering events	April – August	March – June September – December	March – June September – December	March – June September – December
Sampling effort (hours)	162	52	120	384
Richness of visitors	40	32	20	18
Richness of pollinators	**38**	**26**	**16**	**14**
Abundance of visitors	1 729	303	1 085	90
Abundance of pollinators	**1 410**	**268**	**520**	**78**

Source: Gaglianone *et al.*

Figure 9.29

POLLINATORS OF TOMATO IN THE STUDIED AREAS: (A) *EXOMALOPSIS ANALIS,* (B) *EXOMALOPSIS AUROPILOSA*, (C) *BOMBUS MORIO*, (D) *AUGOCHLOROPSIS* SP., (E) *XYLOCOPA FRONTALIS* AND (F) *MELIPONA QUADRIFASCIATA*



Source: Gaglianone *et al.*

Table 9.7

RELATIVE ABUNDANCE OF BEES VISITING FLOWERS OF TOMATO (*SOLANUM LYCOPERSICUM*) IN OPEN ORCHARDS IN THE STATES OF RIO DE JANEIRO (RJ), GOIÁS (GO), SÃO PAULO (SP) AND MINAS GERAIS (MG), BRAZIL

		RJ	GO	SP	MG
APIDAE					
Apidae spp.			0.6% (3 spp.)		
Apis mellifera Linnaeus, 1758	NP	10%	0.3%		46.5%
Bombus morio (Swederus, 1787)	P	6.9%	0.3%	11.1%	
Bombus pauloensis Friese, 1913	P			26.6%	11.1%
Centris sp.	P				0.4%
Centris (Hemisiella) sp.	P		0.3%		
Centris aenea Lepeletier, 1841	P	0.4%	0.3%		
Centris fuscata Lepeletier, 1841	P	0.4%	0.6%		
Centris nitens Lepeletier, 1841	P	0.1%			
Centris tarsata Smith, 1874	P	0.2%	0.3%		
Centris terminata Smith, 1874	P	<0.1%			
Centris varia (Erichson, 1848)	P	0.2%			
Epicharis sp.	P		0.3%		
Euglossa spp.	P	0.9%			
Eulaema cingulata (Fabricius, 1804)	P	< 0.1%			
Eulaema nigrita Lepeletier, 1841	P	0.9%	2%		
Exomalopsis spp	P	2.1%	1.6%		
Exomalopsis analis Spinola, 1853	P	34.4%	39.3%	22.2%	15.3%
Exomalopsis auropilosa Spinola, 1853	P	15.9%	4.6%		5.9%
Exomalopsis elephantopodis Schrottky, 1909	P				1.5%
Exomalopsis fernandoi Moure, 1990	P				0.6%
Exomalopsis fulvofasciata Smith, 1879	P				1.4%
Exomalopsis minor Schrottky, 1910	P		1%		
Exomalopsis ypirangensis Schrottky, 1910	P				< 0.1%
Frieseomellita sp.	NP		0.3%		
Geotrigona subterranea (Friese, 1901)	NP		3%		
Melipona bicolor Lepeletier, 1836	P				0.8%
Melipona quadrifasciata quadrifasciata Lep., 1836	P	< 0.1%		2.2%	1.4%
Meliponini sp.	NP		0.3%		
Melissodes sp.	P				0.2%
Paratrigona lineata (Lepeletier, 1836)	NP		7%		
Paratrigona subnuda Moure, 1947	NP			10%	
Plebeia sp.	NP				0.6%
Tetragonisca angustula (Latreille, 1811)	NP		0.3%	1.1%	

		RJ	GO	SP	MG
Thygater sp.	P	< 0.1%			
Trigona hyalinata (Lepeletier, 1836)	NP				< 0.1%
Trigona spinipes (Fabricius, 1793)	NP	8.3%		1.1%	4.7%
Xylocopa spp	P				< 0.1%
Xylocopa artifex Smith, 1874	P			1.1%	
Xylocopa frontalis (Olivier, 1789)	P	0.4%			< 0.1%
Xylocopa muscaria (Fabricius, 1775)	P	1.9%			
Xylocopa nigrocincta Smith, 1854	P	1%			
Xylocopa ordinaria Smith, 1874	P	0.1%			
Xylocopa suspecta Moure & Camargo, 1988	P	0.7%		1.1%	
HALICTIDAE					
Augochlora spp	P	< 0.1%			1.9%
Augochloropsis callichroa (Cockerell, 1900)	P		1.3%		
Augochloropsis cupreola (Cockerell, 1900)	P			2.2%	
Augochloropsis electra (Smith, 1853)	P	< 0.1%		2.2%	
Augochloropsis cfr *patens* (Vachal, 1903)	P	0.9%			
Augochloropsis cfr *sparsilis* (Vachal, 1903)	P	0.7%			
Augochloropsis smithiana (Cockerell, 1900)	P	0.3%	2%		
Augochloropsis spp	P	6.8%	24% (5 spp.)	7.7%	5.4%
Dialictus spp.	NP		1%		
Halictidae spp.	P		2%		
Pseudaugochlora erythrogaster Michener 1954	P	0.8%			
Pseudaugochlora graminea (Fabricius, 1804)	P	2.3%			
Pseudaugochlora indistincta Almeida, 2008	P			1.1%	
Pseudaugochlora spp	P	0.4%	7.3% (2 spp.)		
ANDRENIDAE					
Anthrenoides meridionalis (Schrotty, 1906)	NP			1.1%	
Oxaea flavescens Klug, 1807	P	1.4%	0.3	1.1%	0.7%
Oxaea sp.	P			6.6%	
Psaenythia bergii Holmberg, 1884	P			1.1%	
Not identified					0.2%
Bees sampled		**1 729**	**303**	**90**	**1 085**
Richness of species		**40**	**32**	**18**	**20**

Note: P=potential pollinators (buzzing bees); NP = non-pollinators (non-buzzing bees).

Source: Gaglianone *et al.*

The frequency of visits varies throughout the day. In GO and RJ, the peak of bee visitation takes place from 10:00 to 12:00 hours. Bumblebees (*Bombus* spp.) arrive early in the morning, and their visitation rate peaks around 09:00 hours. Other large bees (*Xylocopa*, *Eulaema*, *Epicharis* and *Centris*) and Halictidae visit tomato flowers mostly between 9:00 and 13:00 hours in GO, while in RJ their activities are concentrated between 11:00 and 12:00 hours. Bees of the genus *Exomalopsis*, the most abundant pollinator in the tomato fields of three regions, begin visitation at around 09:00 hours, with a peak around 11:00 hours and a steep decline around noon.

Exomalopsis females hold the staminal cone with their mandibles and vibrate the anthers to release pollen grains. A bee works all around the staminal cone, buzzing repeatedly on different anthers. Periodically the bee stops buzzing and grooms itself, pushing pollen onto the scopae. *Exomalopsis analis* (Figure 9.29a) and *E. auropilosa* (Figure 9.29b) are the most common species of the genus in the study plots. Their nests are constructed in the soil, and attain depths of up to 1 m. Females within a nest seem to cooperate with cell provisioning and other behaviour, taking part in social interaction [11].

Bumblebees (*Bombus* spp, Figure 9.29c) are important pollinators of flowers with poricidal anthers [9, 12] and their role in enhancing tomato productivity is known from studies in other countries [13]. They are substantially more diverse in temperate climate countries, where they are reared and commercialized for pollination of crops, mainly tomato production [14]. Two bumblebees, *B. morio* and *B. pauloensis,* visit tomato flowers and have the highest abundance in the cooler climate of SP. In RJ, 34 percent of pollen grains in the scopae of *Bombus morio* captured near tomato plots belong to tomato flowers, indicating that this plant is an important source of pollen in the agroecosystem. *Bombus morio* and *B. pauloensis* have a Neotropical range [15] and are very common in many parts of Brazil [16]. They have primitively eusocial colonies, initiated by a single female or queen, and are not long lived [17]. Their nests, usually below ground, are constructed in cavities like the abandoned nests of rodents or termites, and also under clumps of grass [11].

Sweat bees (Halictidae, Figure 9.29d) correspond to 7.3 percent (MG) and to 35.9 percent (GO) of all visiting bees at tomato flowers. *Augochloropsis* and *Pseudaugochlora* seem important pollinators because of their ability to vibrate flowers and their high frequency of visits. They construct nests in bare soil in sunny locations, mostly in aggregations. Behaviour of *Augochloropsis* species varies from solitary to primitively eusocial [18, 19]. A possible facultative semi-social organization is known for *Pseudaugochlora* [20], where either one or a few females inhabit the nest with a division of labour in the latter, either related to oviposition or construction/provisioning.

Bees of the genus *Xylocopa* (Figure 9.29e), and *Epicharis*, *Centris* and *Eulaema* are not frequent visitors to tomato flowers, although they augment the richness of pollinators. Conversely, *Apis mellifera* displays relatively high frequency on tomato flowers in MG. However, observations for this study detected neither buzzing on flowers nor pollination of tomato, as previously reported [21].

Stingless bees of the genus *Melipona* (Figure 9.29f) are frequent visitors in SP and MG. Because of the management of these bees in hives, the introduction of nests in plantations, mainly in greenhouses [13, 22, 23], can benefit tomato flowers, as observed in experiments in MG. In open fields in MG, however, other pollen plants seem to be preferred and *Melipona* is not a frequent visitor to tomato flowers. Experiments reveal that tomato production in a greenhouse is enhanced by *Melipona quadrifasciata*, and the resulting fruit is heavier compared to fruit from self-pollination (Table 9.5). Other studies in Brazil present similar results [24].

Landscape and conservation considerations: Based on the close relationship between pollinator visitation and fruit set in tomato crops, it can be assumed that the decline of pollinators caused by loss of habitat leads to decreased rates of pollination. The influence of the landscape on the activity of pollinators was tested through two approaches: (a) monitoring the bee visits at different distances from a forest fragment and (b) analysing the relation between pollinator diversity in tomato crops and forest cover in the landscape.

For the first approach, bee visits to tomato flowers were monitored using indirect analysis of marks on the anther cone. Analysis of pollinator frequency in cultivated areas of SP revealed decreasing visits to flowers at increasing distances from forest fragments. The percentage of flowers without marks (small scars on anthers left by pollinating bees) increases with distance from a forest fragment. Moreover, the size of the visiting bees can be inferred by the type of mark on the anther cone, with a higher frequency of visits by pollinators of large and medium size occurring closer to the forest fragments. Overall, 25 percent of flowers closest to fragments have such anther scars, in comparison to 10 percent of flowers most distant from the fragment.

The second approach examined the relationship between forest cover and pollinator diversity in tomato crops. When comparing two landscapes in RJ, higher species richness was observed in crops near a large forest fragment compared to a landscape with less forest cover [25]. Furthermore, 90.9 percent and 87.6 percent of the estimated species in each landscape were captured, indicating that representative data were obtained.

In the GO study plots, spatial analysis highlighted the relationship between pollinator visitation rates and landscape variables, mainly the proportion of native vegetation cover at differing radii. Forest cover in a 1 km range is significant for *Exomalopsis* frequency, whereas native vegetation cover within 3 km correlates well with Augochlorini and *Bombus/Eulaema* visitation rates. Overall, the analysis indicated a consistent positive effect of native vegetation cover for those pollinator groups.

Similarly, additional studies have found that both richness and abundance of pollinators are strongly influenced by landscape composition [26, 27] (see also Chapter 6). Bee species traits such as ethology and body size can determine bee behaviour, resulting in different landscape effects for each species group. Small bees such as *Exomalopsis* and *Augochloropsis* have a foraging area that ranges from 250 m to 800 m, and they tend to live near cultivated fields. In contrast, larger bees such as *Bombus* have greater flight capacity and larger foraging areas [28]. In conclusion, the association of bees with native areas greatly influences pollination in open tomato fields, but the nature and magnitude of responses is highly dependent on plantation characteristics and the landscape in which they are found.

Furthermore, the occurrence of little known bee species in the studied regions, such as *Augochloropsis callichroa* and *Exomalopsis minor* in GO, underline the importance of correlations between agriculture, native pollinators and native vegetation.

Recommendations for the conservation and management of tomato pollinators: Tomato pollinators consist of bees that differ widely in their social and nesting behaviour. They range from solitary (most species encountered) to eusocial (Melipona), with a variety of social behaviour observed for *Exomalopsis, Augochloropsis* and *Bombus*. The data indicate a substantial richness of potential crop pollinators in the field, most of them ground-nesting bees. Bionomic characteristics of the bees, such as ground-nesting habits, make their individual management difficult; therefore, habitat management is crucial for pollinator conservation.

Some important pollinators, such as *Melipona* and *Bombus* species, use tree or ground-nesting cavities. The potential of those bees as pollinators for tomato is highlighted by several publications mentioned here, and confirmed by the results of this study in greenhouses with introduced *Melipona* nests.

Based on observations, the main recommendations for the conservation of tomato pollinators are as follows:

- Conserve the soil, prevent erosion and maintain land banks that are nesting sites of non-social bees.

- Encourage the rearing of stingless bees such as *Melipona* near cultivated areas, observing the native species in the region and specific characteristics such as food and climatic requirements.
- Preserve large trees which can shelter *Melipona* nests.
- Maintain forest and restore forest fragments near the crops, to permit an increase in the number of bee species and frequency of visitation to flowers.
- Limit the frequency of pesticide use and restrict it to periods of low bee activity (see Chapter 4).
- Maintain native flowering plants around the plantations, which serve as nectar sources for bees (since tomato flowers have no nectar).
- Evaluate local conditions for rearing native bumblebees for pollination.

Conclusion: Bees increase productivity and the quality of tomato fruit. Although the tomato produces fruit by self-pollination, bee visitation often increases the number and size of fruit and number of seeds. The diversity (composition, richness and abundance) of bee species visiting tomato flowers varies among regions, but species of *Exomalopsis*, *Augochloropsis* and *Bombus* are the most abundant visitors that potentially pollinate in any locality. All pollinators vibrate anther cones to gather pollen from tomato flowers – critical behaviour that enables the transfer of pollen between flowers. The bees are active on flowers throughout the flowering of tomato and peak in visitation at around 09:00 hours (bumblebees) and 11:00 to 12:00 hours (*Exomalopsis* and Augochlorini).

Landscape attributes influence pollinator abundance and therefore the rates of pollination. Those with greater forest cover have higher species richness and sustain a higher frequency of pollinators on flowers. Also, natural areas surrounding plantations host many bee species, and their preservation may improve productivity by maintaining native pollinator populations. The conservation of those areas, and restoration initiatives, should be encouraged.

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9.3.5 Pollination studies in rambutan (*Nephelium lappaceum*) in Soconusco, Chiapas, Mexico

M. Rincón-Rabanales, D.W. Roubik, L.I. Vargas-López, M.L. Adriano-Anaya, J.A. Vázquez-Ovando, I. Ovando-Medina, J. Grajales-Conesa and M. Salvador-Figueroa

Rambutan (*Nephelium lappaceum* L.; Sapindaceae) is found in the humid tropics, native to Indonesia and Malaysia, and is considered an underutilized fruit crop [1]. Rambutan and other crops such as lychees, durian, guavas and passion fruit are considered "minor tropical fruits" by FAO [2], because they are traded mostly at the regional level in smaller volumes. Their 15 million tonne annual total nonetheless accounts for 24 percent of total world tropical fruit production (data from 2000). The market share of rambutan is expanding most rapidly in Southeast Asia, namely Cambodia, Indonesia, Laos, Malaysia, the Philippines, Thailand and Viet Nam, as well as in Hawaii, the United States (Lahaina, Hilo and Kona), and in tropical America, particularly Costa Rica and Mexico (Soconusco region, Chiapas, Mexico) [3–4].

In Mexico, rambutan was introduced to the Soconusco region during 1950 to 1970 and currently covers 600 ha [4–5]. Pronounced phenotypic differences exist among plants, expressed by a prolonged bloom within the plantation and a high variability in ripe fruit colour (red, yellow and green). In addition, a new variety, "CERI61", has been developed (see below).

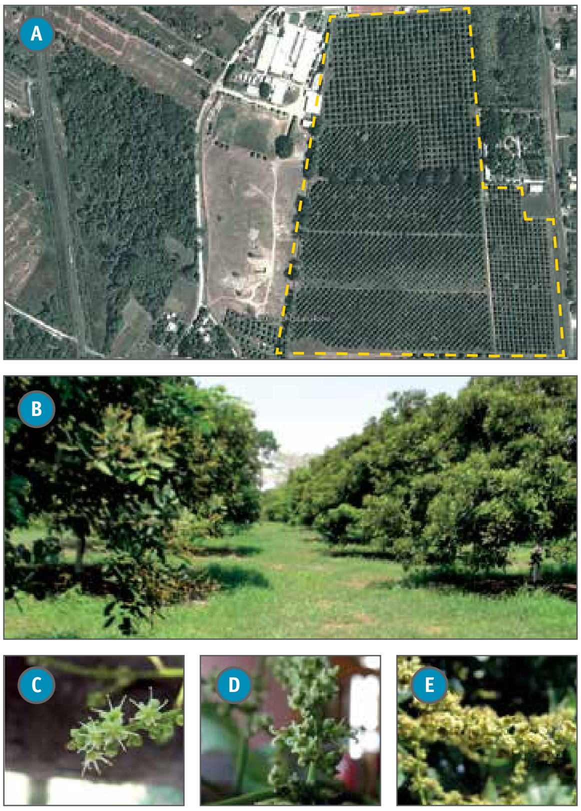
Today, there are three important cultivated areas in the Soconusco region:

Cacahoatan (14°59' N, 92°10' W, 480-600 m elev.). This area is undergoing a transformation from coffee to rambutan mixed with robusta coffee (*Coffea canephora*). Rambutan trees were initially used as shade trees for the coffee shrubs, but following the fall in coffee prices in 1990, rambutan became a new source of income. Once dedicated primarily to robusta coffee, today the San Alberto farm has 42 ha of rambutan mixed with coffee. The 2001 rambutan yield amounted to 2 500 kg. Another grower has about 100 trees, which yield almost 4 500 kg [4, 6].

Metapa de Domínguez (14°50' N, 92°11' W, 100 m elev.). Before rambutan was cultivated, land was planted with annual crops such as sorghum. The farm "El Herradero" covers > 30 ha, 7 ha of which is planted with rambutan (Figure 9.31 a, b). The 2000 harvest amounted to 3 500 kg, after which another 300 trees were planted, then 400 more trees in 2001, at which time the harvest reached 8 500 kg [4].

Figure 9.30

(A) THE "EL HERRADERO" RANCH LOCATED IN METAPA DE DOMINGUEZ, CHIAPAS IN THE SOCONUSCO REGION (AVERAGE ELEVATION 110 M), (B) RAMBUTAN ORCHARD, (C) MALE RAMBUTAN FLOWERS, (D) HERMAPHRODITE FLOWER, FUNCTIONALLY MALE, AND (E) HERMAPHRODITE FLOWER, FUNCTIONALLY FEMALE



Source: M. Rincón-Rabanales *et al.*

Huehuetan (15°01' N, 92°23' W, 50 m elev.). The "Chinita" farm covers 12 ha, with 10 ha planted with rambutan. From 1997 to 2001, 3 000 trees were planted. In 2001, production reached 3 tonnes ha^{-1} and by 2002 had risen to 7 tonnes ha^{-1} [4].

Because rambutan is an option for local farmers, from agro-entrepreneurs to small producers, and also agricultural traders in Soconusco, previous studies undertaken by the authors are summarized and interpreted here. Floral structure and fruit yield are emphasized and related to nectar, pollen dehiscence and viability, flower visitors and pollinator management using stingless bees (Meliponini, see Part IV) in a commercial orchard, which started up in 2000.

Floral biology: Rambutan is dioecious and about 50 percent of plants are male. The erect, widely branched inflorescences bear many flowers on shoot tips with pseudoterminal panicles. Flowers are either male, with only stamens well developed, or hermaphrodite – either basically female, with small indehiscent stamens and anthers, or male, with undeveloped stigmas [4, 7, 8]. The male flower is borne on male trees, which therefore bear no fruit, in approximately 30 cm clusters on terminal panicles that are greenish yellow and without petals (Figure 9.31c). There is no functional ovary and flowers on each panicle have five to seven stamens, with flowers approximately 5 mm wide and 2 mm long. There are hundreds to approximately 5 000 buds on a male panicle, with a mean average of about 3 000. At peak flowering up to 500 flowers open per day. Hermaphrodite flowers are borne on terminal panicles similar to those of male flowers. They have 1 766 ± 525 flowers at peak blooming, about 100 of which may open each day (Figure 9.31 d, e). The greenish yellow flowers are apetalous but the predominantly female flowers have a bilocular ovary beneath the bifid stigma. Six indehiscent stamens arise from the ovary base. All parts of the flower, except the yellow nectaries, are covered with fine pubescence. Flowers are approximately 5 mm long and 4 mm wide [7].

Floral nectar was sampled from panicles indirectly, using the foraging worker bees of *Scaptotrigona mexicana* on 5 March 2004. Nectar was extracted directly from the mouthparts of five bees into a 20 µL microcapillary tube, with samplings made between 08:00 hours and 14:00 hours throughout the orchard. The number of sampled bees holding no nectar was also recorded. Bees were scored for weight/weight sugar content in their foraged nectar using a handheld refractometer, and small samples were combined among bees, usually with five bees per aggregate sample.

Nectar production and bee foraging loads are maximal during 09:00 hours to 13:00 hours. The sugar concentration in nectar is 53.2 percent and does not change appreciably during the day (SD = 4.8, N = 100). Equal numbers of foragers carry either no nectar or have nectar loads, from 09:00 hours to 13:00 hours, while two to three times as many have no nectar loads before 09:00 hours and after 13:00 hours.

Flowering and pollination experiments: Flower visitors and the pollen they carry were recorded during four flowering periods (January and June 2001, 2002) for a new commercial variety of rambutan, CERI61 (Rosario Izapa experiment station, Mexican Institute of Forestry, Agriculture and Livestock Research, INIFAP) in an orchard of 1 000 trees covering 7 ha. The "El Herradero" ranch at Metapa de Dominguez, in addition to rambutan, has mango orchards and native secondary vegetation with *Ficus*, *Tabebuia rosea*, *Spondias mombin, S. purpurea, Cybistax donnell-smithii, Tecoma stans, Ceiba pentandra* and *Pachira aquatica* [9].

Flowering begins early in February and ends in April, peaks in March (46.9 percent – 48.7 percent total trees), and lasts effectively 30 ± 5 days. Hermaphrodite flowers account for > 95 percent but only 5 percent of the male flowers have pollen on stamens, which dehisce up to two days. To determine the effect of flower visitors, three experimental treatments were performed on ten trees with six marked panicles each. The T1 control treatment consisted of open pollination without manipulation (Figure 9.32a), T2 excluded all visitors with a 1 mm mesh bag placed over the panicle in bud stage (Figure 9.32b), and T3 induced pollination through the simultaneous placing of two cages over trees with buds in the same stage as T1 and T2 (Figure 9.32c). For the last treatment, two bee colonies were placed at opposite ends of the 16 x 16 x 4 m cage. The stingless bees (Meliponini) used in wooden hives were *Scaptotrigona mexicana* and *Tetragonisca angustula*, which have about 1 000 foragers per colony. For each pollination treatment, developing fruit were scored and final fruit were scored at commercial harvest. To estimate the proportion of flowers producing fruit, the total flowers in bagged panicles of ten trees were counted, producing a result of 1 776.5 ± 524.35.

Figure 9.31
(A) OPEN-POLLINATION TREATMENT, (B) BAGGED PANICLE OF RAMBUTAN, (C) *S. MEXICANA* HIVES IN ORCHARD WITH BEES VISITING RAMBUTAN PANICLES: (D) *S. MEXICANA*, (E) *HALICTUS HESPERUS*, AND (F) AFRICANIZED *A. MELLIFERA*

Source: M. Rincón-Rabanales *et al.*

Table 9.8
FRUIT PRODUCED IN THREE TREATMENTS ON RAMBUTAN, VARIETY CERI61: OPEN FLOWERS, INDUCED POLLINATION (BEE COLONIES PRESENTED IN CAGES) AND BAGGED FLOWERS WITH NO VISITORS, AT METAPA DE DOMÍNGUEZ, CHIAPAS, MEXICO

VARIABLE	INDUCED POLLINATION		OPEN POLLINATION		BAGGED FLOWERS	
	2001	2002	2001	2002	2001	2002
Fruit set	76.4 ± 27.2^{B}	71.4 ± 21.2^{B}	96.8 ± 37.7^{A}	110.1 ± 46.2^{A}	7.0 ± 8.0^{C}	5.6 ± 3.9^{C}
Mature fruit	21.2 ± 6.1^{A}	17.1 ± 6.5^{A}	22.8 ± 9.3 ^{A}	23.1 ± 7.9^{A}	1.8 ± 3.2 ^{B}	3.4 ± 3.3^{B}

Notes: All treatments included similar number of flowers (1804 ± 503 in 2001 and 1749 ± 545 in 2002; Tukey test, $p<0.05$). Data are means (and standard deviations) of ten biological replications. Cells with the same letter in a given row are not significantly different (Tukey test, $\alpha=0.01$).

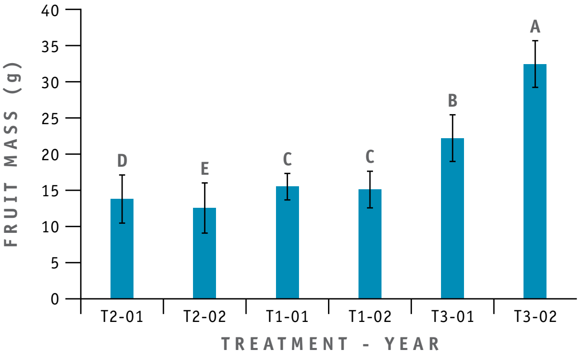
Source: M. Rincón-Rabanales *et al.*

Fruit yield from caged and open pollination: The results reveal a tenfold difference among the three treatments (ANOVA, $p < 0.001$). Although developing and mature fruit per flower are abundant and result from open pollination and selfing (caged pollination with bees) alike, the fruit from induced pollination in cages is more abundant (Duncan and Tukey tests, $p < 0.001$, Table 9.8), while there is little fruit when visitors are excluded.

Although proportions of flowers that produce mature fruit are equivalent in cages and with open pollination, the fruit mass, excluding seeds, is greater in the fruit of selfed flowers, as are seed mass and fruit length (Figure 9.33).

Many developing fruit drop during four weeks after flowering, with 50 percent lost. An additional 15 percent is lost by the seventh week. Up until fruit maturity at 11 weeks, little additional loss occurs. The average yield in this ranch increased with introduced stingless beehives (2000 to 2004), from 3.5 to 7 tonnes ha^{-1}. The results of the study agree with recent studies in Asia, where researchers found rambutan to be cross-pollinated and dependent on insects for pollination and fruit set [3]. The results also showed that bees are largely responsible for autogamy. In contrast, Kiew [10] states that rambutan is not bee pollinated but is parthenocarpic, because hermaphrodite flowers do not release pollen, and male individuals are not kept under cultivation. The Mexican cultivar "CERI61" is likely to differ in its pollination biology and genetics, compared to plants studied in Asia. Data from the study indicate that hermaphroditic flowers have viable pollen, which is often transferred by a pollinator to produce a fruit. Anthers were observed to dehisce with fully formed pollen grains. Pollen grains

Figure 9.32
MATURE FRUIT OF RAMBUTAN, VARIETY CERI61, YIELDED BY OPEN POLLINATION (T1), GEITONOGAMY [CAGED FLOWERS WITH BEES] (T3), OR POLLINATOR EXCLUSION (T2) DURING TWO YEARS IN CHIAPAS, MEXICO



Note: Columns with the same letters were not significantly different (Duncan test, $\alpha= 0.05$).

Source: M. Rincón-Rabanales *et al.*

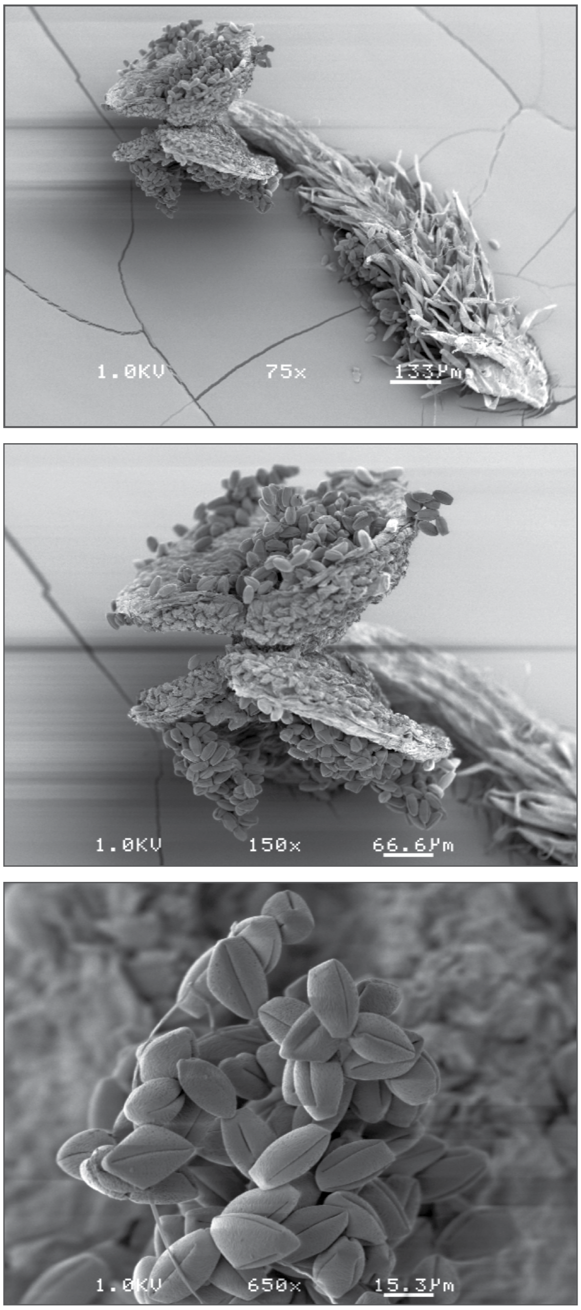
in a 20 percent sucrose solution germinate and grow normal tubes, indicating functionality (Figure 9.34).

Both geitonogamy and outcrossing are possible for rambutan, but there is no convincing evidence for apomixis or pollen-free seed development and parthenocarpic fruit production, because occasional "spontaneous" autogamy in a bagged inflorescence, which has viable pollen on anthers, cannot be discounted. Interestingly, the cage pollination treatment, which can only result in geitonogamy, produces significantly lower initial fruit set but equally abundant ripe fruit, compared to open pollination (Table 9.8), and much more and larger fruit than spontaneous selfing in the absence of pollinators, or possible parthenocarpy. Furthermore, flowers exposed to *S. mexicana* produce an average of 13 mature fruit per 1 000 flowers, while bagged flowers produce 1.5 mature fruit per 1 000 flowers. The bees presumably visit many flowers to obtain a nectar load and are known as group foragers [11]. Such small bees generally favour pollination of small, generalized flowers like rambutan [12, 13].

Diversity and abundance of pollinators on rambutan: Some insects are chiefly flower visitors and rarely pollinate [1, 14, 15], thus it is important to evaluate the real contribution of a flower visitor in pollination [1, 14]. Rambutan is visited by bees, flies, wasps, butterflies and ants [1, 14–18], some of which may pollinate flowers [1, 17–19]. The fly *Lucilia* sp. potentially pollinates rambutan [18], but does not carry pollen or mixed loads [19]. Conversely, calliphorid flies are abundant on rambutan flowers in India from 06:00 hours to 18:00 hours [15]. Fly abundance correlates with stigma receptivity and pollen availability, thus Calliphoridae may constitute pollinators there. However, even abundant flies [1, 16, 19], cannot be considered pollinators of rambutan without experimental study.

A study was undertaken to sample flower visitors intensively by placing a large net tent over an entire tree. The net mesh was 1 mm and the tent measured 3 m on each side. An individual flowering tree was covered, after which insects were collected in tubes containing ethyl acetate. Collections were made on different trees each hour, between 07:00 hours and 17:00 hours, every 15 days from February through March in 2001, and from February through April in 2002. The bees and other insects were identified by the authors.

Figure 9.33
ANTHERS OF *NEPHELIUM LAPPACEUM* FROM HERMAPHRODITE FLOWERS



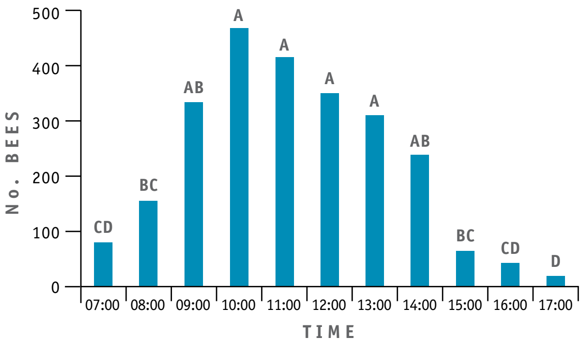
Up: stamen with open anther; middle and bottom: magnifications of anthers and pollen grains

Source: M. Rincón-Rabanales *et al.*

Among 28 186 individuals collected on the flowers, two bee families accounted for 97.1 percent of total insects: Apidae (*Tetragonisca, Trigona, Oxytrigona, Nannotrigona, Apis, Exomalopsis, Paratetrapedia* and *Scaptotrigona*), and Halictidae (*Halictus, Lasioglossum and Agapostemon*). They begin collecting both pollen and nectar but exclusively forage nectar after 10:00 hours (see Table 9.9, Figure 9.35). The potential pollinators carry only incomplete pollen loads. Pollen gathered almost completely consists of Asteraceae, Euphorbiaceae and a few other flowering plants common in the area. *Scaptotrigona mexicana* dominates flowers during the end of flowering and accounts for 81.64 percent of pollen collected by all bees. *Halictus hesperus*, a social but not a perennial bee, dominates flowers after most flowering occurs.

Figure 9.34

TOTAL BEES CAPTURED AT FLOWERS ON ENTIRE TREES (N = 12) COVERED WITH A COLLECTING TENT AT THE INDICATED TIMES. ANALYSIS OF DATA TRANSFORMED AS NATURAL LOGARITHM SHOWS COLUMNS WITH THE SAME LETTERS WERE NOT SIGNIFICANTLY DIFFERENT (DUNCAN TEST, A = 0.05)



Source: M. Rincón-Rabanales *et al.*

Table 9.9

RICHNESS AND ABUNDANCE (I) OF BEES COLLECTED DURING TWO FLOWERING PERIODS AT RAMBUTAN FLOWERS AT "EL HERRADERO" RANCH, CHIAPAS, MEXICO

BEE SPECIES	FEBRUARY	MARCH	APRIL	(I)	% REL
Apidae: Apinae					
Apis mellifera	3^{C}	1^{C}	1^{F}	5	0.02
Apidae: Apinae					
Scaptotrigona mexicana	2 840^{A}	4 819^{A}	2 063^{B}	9 722	34.49
S. pectoralis	58^{BC}	49^{BC}	16^{EF}	123	0.44
Tetragonisca angustula	659^{AB}	171^{BC}	23^{EF}	853	3.02
Nannotrigona pelilampoides	204^{BC}	48^{C}	105D^{EF}	357	1.27
Trigona fulviventris	21^{C}	21^{C}	12^{EF}	54	0.19
T. nigerrima	27^{C}	8^{C}	3^{F}	38	0.13
Oxitrigona mediorufa	43^{BC}	-	2^{F}	45	0.16
Apidae: Antophorinae					
Exomalopsis sp. 1	10^{C}	4^{C}	-	14	0.05
Paratetrapedia sp. 1	1^{C}	2^{C}	-	3	0.05
Halictidae					
Halictus hesperus	27^{C}	973^{AB}	13 675^{A}	14 675	52.07
Lasioglossum sp. 1	4^{C}	98B^{C}	1 409^{BC}	1511	5.36
Lasioglossum sp. 2	-	57^{BC}	5 55B^{CD}	612	2.17
Lasioglossum sp. 3	15^{C}	15^{C}	127^{CDE}	157	0.56
Agapostemon aff. *splendens*	7^{C}	5^{C}	4^{F}	16	0.06
Total of bees	3 919	6 271	17 995	28 185	100.00

Notes: Data were transformed for statistical analysis (ln). Data with the same letter are not significantly different (Duncan α = 0.05)

Source: M. Rincón-Rabanales *et al.*

Halictus builds nests in the ground near the orchard [20] and visits rambutan flowers. This seasonal, social bee is a significant visitor seen on the flowers and not merely flying up into the trap tent. Other studies find numerous social bees visiting rambutan [3].

Most *Scaptotrigona* carry very little nectar when sampled on flowers. *Apis mellifera scutellata* hybrids (Africanized honey bees), present on a few flowers (Figure 9.27), are not strongly attracted to rambutan, although its flowers occur in dense clusters on large panicles. The small floral nectar reward (evident by small or negligible nectar loads of *Scaptotrigona*), and non-aggressive competition between foragers that gradually deplete the nectar, or a combination of both, likely discourage this honey bee from greater visitation, despite the high sugar reward of > 50 percent by weight in nectar.

Pollinator management perspectives for rambutan orchards: The insignificant production of fruit in the absence of small bees indicates that this plant depends on bees for fruit set and retention. Mature fruit set after extensive fruit maturation periods, even in self-fertilizing plants, may be strongly visitor limited [21–23]. For example, the commercial yield of *Coffea arabica* increases by 56 percent when pollinators freely visit flowers, compared to autogamous, bagged flowers. As seen in coffee, many developing fruit are abscised by the variety of rambutan studied here, amounting to approximately 75 percent over a fruit maturation period of 111 days [24]. However, this is the first study (as far as the authors are aware) that shows selfing to gain greater maternal investment in fruit than outcrossing, and in a plant described as dioecious. In theory, selfing should help to purge lethal alleles [25] and in natural conditions, protogyny could offset the tendency of geitonogamy to monopolize maternal resources. The large proportion of aborted fruit suggests maternal discrimination based upon fruit genotype, with a bias for self-pollen.

Fruit abundance for commercial rambutan reaches 10 to 20 per panicle in Costa Rica [26], compared to 21 in the present study, while fruit number in Malaysia is lower [27, 28]. In the latter study and in Chiapas, fruit sizes were closely similar. The fact that the total yield (weight of individual fruit multiplied by fruit retained per flower) is highest from selfed flowers is of particular interest to rambutan producers. This implies that controlled production in greenhouses with pollinators can provide relatively high yields. The high yields at the Metapa orchard are over twice that of the leading producer (Thailand) of *Nephelium lappaceum* [29]. Thailand has approximately the same number and sizes of stingless bee species as Chiapas, but also possesses five honey bee species (D.W. Roubik, pers. obs.). In both hemispheres, adequate pollination service suggests further possible increases in productivity through pollinator management. Because of the number and availability of pollinators in the environment at the Chiapas site, primarily the stingless bees, orchard pollination is likely to be efficient.

The experience gained from study of the management of rambutan orchards demonstrates that *S. mexicana* is a useful commercial pollinator, largely due to the efforts of beekeepers and researchers in Soconusco, where *S. mexicana* is traditionally reared and kept in different meliponaries [30]. One noteworthy study with stingless bees and rambutan orchards was performed during 2003–2004, to test the effect of introducing different densities of *S. mexicana* colonies into orchards, and compare with open pollination with no bees introduced [31]. All treatments with bee visits (from managed hives or wild pollinators) set more fruit than bagged panicles, and the highest hive number introduced (eight hives) gave the greatest yield (Figure 9.35). Similarly, fruit quality parameters (weight and diameter of mature fruits) were greatest with the two highest hive densities.

Prospects for stingless bees in Mexico: Bees have substantial potential in agricultural practices [32–35]. In the world, an estimated 85 percent of all plant species that produce fruit and seeds depend on pollinator visits, and in Mexico in addition to Africanized *A. mellifera*, there is pollinator management with, *S. mexicana*, *S. pectoralis*, *S. hellwegeri*, *T. angustula*, *N. perilampoides*, *F. nigra*, *Plebeia frontalis*, *M. solani* and *M. beecheii*. One factor that limits the use of stingless bees as commercially managed pollinators is lack of knowledge of mass rearing techniques (see Chapter 13). For example, almost 70 percent of the stingless bee diversity of Mexico is present in Soconusco, but there are insufficient studies of conservation status [36–38] other than forage plant species and nest characteristics [39, 40]. Nonetheless, during the past 20 years stingless beekeeping continues to develop as an economic activity.

Over the last five years some stingless beekeepers are establishing partnerships to improve stingless bee mass rearing for *S. mexicana* (N = 700 hives), *M. beecheii* (N = 350 hives) and *T. angustula* (N = 200 hives). The goal, among agro-entrepreneurs in particular, is to trade and use these species as pollinators. With regard to rambutan crops, the El Herradero ranch, where Mr Alfonso Espino was a pioneer in providing stingless bees (eight hives per hectare = US$192 per hectare, per blossom period), has had the kind of success (during 2003 to 2009) documented in this section. *Scaptotrigona mexicana* colonies are rented at US$24, and colonies now sell for US$40 to US$100, between beekeepers and plantation owners. In conclusion, it is important that stingless beekeepers, farmers, researchers and authorities make an effort to promote programmes that conserve and protect wild pollinators in Soconusco, without using introduced bees of different geographic origin, to promote a sustainable agriculture for local communities.

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9.3.6 Mango

J. Hipólito, C. Pigozzo and B.F. Viana

Mangifera indica (Anacardiaceae) originated in South Asia, specifically in India, where more than 1 000 varieties are found, and has been cultivated for more than 4 000 years [1–3] (Figure 9.36). According to FAO [4], mango is cultivated in 102 countries, with 38.95 billion tonnes produced on 5.08 billion ha. In 2011, the greatest producer was India with 15.18 billion tonnes, corresponding to almost 59 percent of world production, followed by China (16 percent), Thailand (10 percent), Indonesia (8 percent) and Pakistan (7 percent). From 1990 to 2000, the area cultivated by mango increased by 42 percent, and total world production rose by 48 percent [5].

In 2004, Brazil accounted for the highest recorded global yield, producing 13.6 tonnes of fruit per hectare. Mango is grown in all physiographic regions of the country, in particular the southeast and northeast. It is grown in every state in the northeast, and is concentrated in irrigated semi-arid regions that provide excellent conditions for crop development and fruit quality. In 2000, mango cultivation in the northeastern region accounted for 51.7 percent of total Brazilian production, having increased by 105 percent between 1990 and 2000. The main cultivated areas are located in the states of Bahia, Pernambuco and Ceará, which contributed 39 percent, 18 percent and 12 percent, respectively, to production in the northeast [6].

Figure 9.35

***MANGIFERA INDICA* TREE IN FLOWER, TOMMY ATKINS VARIETY, SÃO FRANCISCO VALLEY, BAHIA, BRAZIL**

Source: Hipólito *et al.* [present study]

Currently, the most widely grown variety of mango is "Tommy Atkins". It accounts for the largest proportion of mango sold worldwide in terms of volume, mainly due to its intense colour, high yields and hardiness in transport over long distances. However, the risk of pests and diseases in commercial plantations using just one variety pose serious biological and economic threats. Diversification of commercial cultivars is therefore crucial to ensuring the long-term sustainability of Mango agribusiness [7].

Floral biology and pollination systems in Mango: the Tommy Atkins variety: The flowers of the Tommy Atkins variety of *Mangifera indica* are characterized by inflorescences known as a "determinate panicle". These vary in size, with length ranging from 10 cm to 42.5 cm and width from 6 cm to 57 cm. The number of flowers in inflorescences also varies ranging from 145 to 2 555. The inflorescences are heteromorphic (i.e. they have two flower types: staminate and "monocline"). Monocline or perfect flowers have a unilocular and uniovular ovary and stigma disposed laterally, as well as a single fertile stamen (some rare examples have two or three). The staminodes are at located the base and are sterile; there are usually five in number.

In general, monocline flowers represent 20 percent to 95 percent of those in an inflorescence. The staminate flowers are most often found at the lower part of the inflorescence (or at the base), while the same proportion of monocline and staminate flowers occur at the upper part (apex).

The flowers may have four to seven petals and sepals, with five being the most common number. The oval and lanceolate petals may be red, pink or yellow depending on their stage, which is indicative of the age of the flower (see Table 9.10 and Figure 9.37). The mean flower diameter is 7.8 mm and the depth is 5.3 mm. The plate-like flower has a simple morphology with nectar around the ovary. In staminate flowers, nectaries are located at the base of the petals, and in monoclines nectar is present as a film on the petals and ovaries.

The flower buds become flowers that pass through seven distinct stages in colour, petal position, and nectar and pollen availability (see Table 9.10 and Figure 9.37). Between anthesis and shrivelling, flowers remain available to visitors for 72 hours without closing. During this period the stigma remains receptive and anthers contain 71–250 viable pollen grains (mean 141, determined by staining in neutral red). Anthers contain as many as 920 grains [9]. Stigmatic receptivity and anthesis occur simultaneously.

Pollination systems: From pollination experiments conducted using bagged flowers prior to anthesis to compare spontaneous self-pollination (without manipulation of flowers), geitonogamy (flowers were manually pollinated with pollen from the same plant) and manual cross-pollination (flowers were manually pollinated with pollen from different plants on the crop), it was concluded that the flowers are self-compatible and that spontaneous self-pollination

Table 9.10
FLOWERING EVENT SEQUENCES IN *MANGIFERA INDICA* AT JUAZEIRO, BAHIA; TOMMY ATKINS VARIETY [8]

STAGE	HOUR*	EVENT
1		Flowers begin anthesis, petals yellow, anthers pink in colour
2	2–3 hours	Petals separate
3	5–7 hours	Petals in perpendicular position
4	24 hours	Petals completely separated
5	27 hours	Anthers change from pink to dark colour; pollen grains are exposed
6	32 hours	Distal ends of petals have pinkish colour
7	48 hours	Flowers almost red in colour (dark pink), dark anthers and stigma change from whitish to pink colour.

Note: *Related to time after anthesis, starting between 8:00 and 8:30 am.

Source: Sousa, Pigozzo and Viana, 2010.

occurs, as well as apparently apomixis (Agamospermy, or clonal pollen-free fruit and seed production). This suggests some degree of independence in relation to pollinators (in data related to initial fruit formation, i.e. ovule development). The rate of fruit set among treatments was not statistically different ($F = 0.940$, $\alpha = 0.452$), at least at the initial stage of fruit formation (final fruits are harvested after one month, approximately 110 days after the flower stage). As most fruit aborts near the final growth stage (i.e. mature fruit for exportation), *outcrossing* pollinators should decrease fruit abortion, because the presence of pollinators serves to increase mature fruit formation for harvest [10–12].

Wind and gravity also play a role in mango pollination. Anemophily experiments have demonstrated pollen flow between mango trees and between inflorescences through gravity [8]. However, pollination experiments associated with flower design suggest lower success from abiotic agents in mango pollination. Stigmas are exposed but present a very small receptive area, as often associated with flowers that are not wind pollinated.

Flower visitors and potential pollinators: Mango flowers produce a very sweet scent and attract many insects, which feed mainly on nectar. Pollen is produced in relatively small quantities and is used by few species [13].

In Juazeiro, Bahia, the predominant flower visitors are insects usually belonging to the following orders: Diptera (67 percent), Hymenoptera, Coleoptera or Lepidoptera (31 percent) [8]. The majority of visitors are small < 3 mm (82 percent), and are more frequent during the day than at night. Some flower visitors are predators that catch prey that gather nectar. The role of such predators is not well known, but they may act as pollinators and pest regulators. However, a high abundance may deter pollinators and cause pollination to decrease.

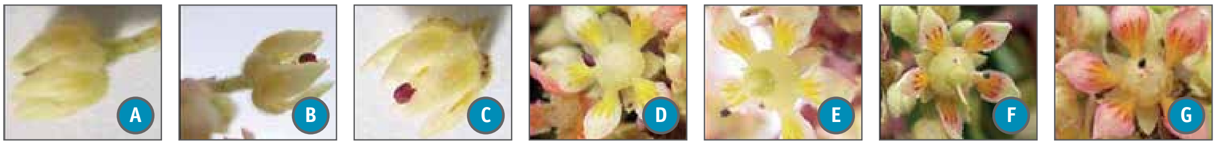
By observing the morphology of mango flowers, it can be inferred that the most effective pollinators are those able to feed in flowers, with the body close to the floral reproductive structures, and that receive pollen. Those too small to reach the floral reproductive structures are much less suitable as potential pollinators [13].

Judging from the characteristics of the mango flower and its visitors, pollinator families in Brazil include Calliphoridae, Chironomidae, Dolichopodidae, Milichidae, Muscidae, Otitidae, Sarcophagidae, Syrphidae, Tachinidae, Tephritidae and Tipulidae. These flies present the following morphological characteristics: (i) hairs on the venter, where there is contact with floral reproductive structures, (ii) dimensions compatible with flower size, and (iii) feeding structures for imbibing nectar (i.e. a broad tongue, suitable for collecting the nectar produced around the floral disks).

Certain bees can also pollinate mango. Among the potential pollinators observed at Juazeiro were meliponine bees – although their size is relatively small (body size 4–10 mm) – including *Plebeia* spp. and *Tetragonisca angustula*, which visit flowers at reproductive stages. The bees were seen foraging in mango flowers and contacting flower reproductive structures. Workers of the *Apis* genus are pollinators in other places [9, 10] (see also Chapter 14.1).

Figure 9.36

FLOWER STAGE IN MANGO FLOWERS



(a) flowers in anthesis; (b) petals begin to separate; (c) sepals perpendicular to the ovary; (d) one day after anthesis; (e) anthers open; (f) flowers change colour; and (g) flowers become darker and fully pink [8]

Source: Hipólito *et al.* [present study]

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9.3.7 Tropical apple production

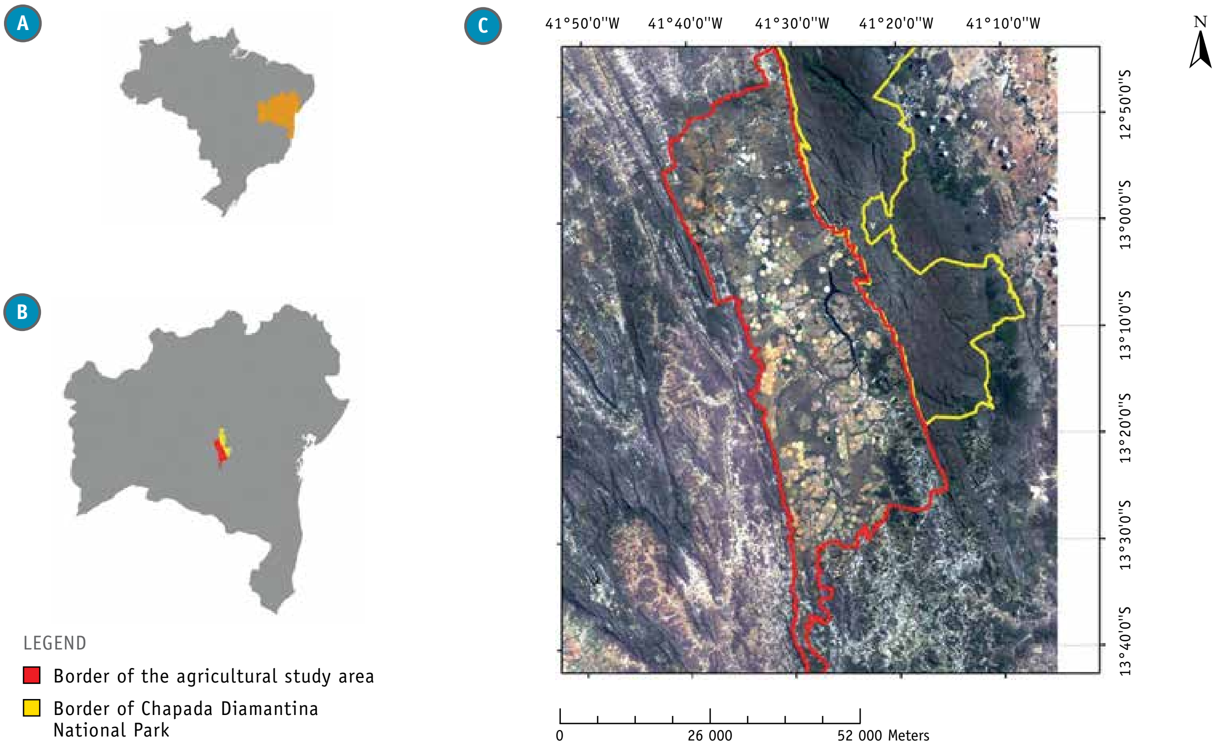
B.F. Viana and F.O. da Silva

In Brazil, apples of the "Gala" and "Fugi" cultivars account for 90 percent of the cultivated area, which is located mainly in subtropical conditions of low chilling [1]. New apple varieties that grow well in the warm weather conditions of tropical regions – under higher temperatures and fewer cool hours in a 24-hour cycle – are currently spreading throughout Brazil [1]. Noteworthy representatives are "Eva" ("Gala" x "Ana"), developed by the Agronomic Institute of Paraná – IAPAR 1999, and "Princess", developed by the Agricultural Research and Extension Company of Santa Catarina – EPAGRI 1986. These varieties are currently the most extensively cultivated apples in Minas Gerais state (in Piedade do Rio Grande), southeast Brazil [1], and also have considerable potential in northeast Brazil (Chapada Diamantina, Bahia state and Petrolina, Pernambuco state).

Bahia apples are produced in a 43 ha orchard by Bagisa Company for Agriculture and Commerce, South America (13º 24'50, 7" S, 41º 17 '7, 4" W), located in a region of irrigated agricultural land between the municipalities of Ibicoara and Mucugê, and bordered by Chapada Diamantina National Park (Figure 9.38). The dominant natural vegetation is arboreal savannah, including elements of high-altitude grasslands at an altitude of about 1 100 m. The mean annual temperature is 21 °C (range 16–26 °C). The rainy season lasts from November to March, and mean annual precipitation is 757 mm (data from Bagisa farm weather station).

Figure 9.37

LOCATION OF CHAPADA DIAMANTINA IN CENTRAL BAHIA, NORTHEASTERN BRAZIL



(A); and location of the apple study orchard in Chapada Diamantina (B). The right-hand, high-resolution (5 pixels m^{-1}) satellite image (SPOT) taken in September 2008 shows the study orchard near irrigated agriculture, located between the municipalities of Ibicoara (Mucugê) (190 000 ha, approximately 470 000 acres), and bordered by Chapada Diamantina National Park (C)

Source: B.F. Viana

Because apple varieties are genetically self-incompatible for pollination purposes, Eva and Princess (the "pollinizer") are raised together, so that the latter provides pollen to produce seeds and fruit. A ratio of more producing trees than pollinizer trees (e.g. 5 Eva: 1 Princess) is used, with donor pollen trees representing 15 percent to 20 percent of those within the orchard. Reducing the distance between varieties in an orchard improves pollen dispersal and pollination [2].

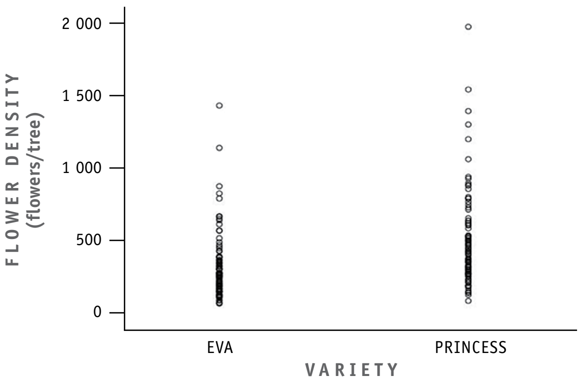
In Eva, the low requirement for cold weather – between 300 and 350 hours – to end dormancy and produce green branches contributes to the earlier ripening and larger size of the fruit [1]. Flowering is induced in June using synthetic hormones, so that trees bloom from early July to early August. Application consists of 12 L Dormex® (hydrogen cyanamide), 0.75 L Pyramex and 60 L Agrex oil mixed in 15 000 L water. During the flowering season, an interval of 8 to 10 days is allowed between successive applications, with the apple trees blooming for approximately 10 to 15 days.

Eva produces pollen grains of satisfactory quantity and germination capacity [3]. The pome-type fruits are red with yellow white streaks below, and are round in shape [1]. The features that make Princess a suitable pollinizer for Eva trees are pollen compatibility, a coinciding flowering period, the number of anthers per flower, the number of pollen grains per anther, and a higher pollen germination level and lower level of fruit production in comparison to the Eva variety [3]. In Chapada Diamantina, approximately 80 percent of flowers open between 10:00 hours and 14:00 hours, although some are open throughout the day (07:30–17:00 hours). Additionally, flower density is significantly greater in Princess than in Eva (Figure 9.39), although the number of flowers per individual tree producing fruit is greater in Eva (154 fruit/80 flowers) than in Princess (242 fruit/50 flowers).

Differences between varieties: The differences between the Eva and Princess varieties include inflorescence size, number of open flowers within inflorescences and floral form (Figure 9.40). In both varieties, each branch ends in a terminal umbel that lasts up to four days. The umbels from Eva and Princess trees bear five to six and three to six fully open flowers a day, respectively. Within each inflorescence, the central bud, called a "king blossom", opens first, while the others surrounding it bloom in an asynchronous fashion. Umbel size (length) ranges from 5 cm to 6 cm in Eva, while in Princess the size ranges from 4 cm to 5 cm. Eva and Princess floral forms share many morphological features and conform with varieties of *Malus domestica* [4, 5]. Regarding colour, the petals are pink, although the flowers of Princess are slightly darker pink than those of Eva. The petals change from dark pink (bud phase) to pale pink (old to senescent flowers). During the flower lifespan, the petals change position in relation to stamens and styles, so that flowers are bowl shaped in early opened flowers, but turn dish shaped once the petals are fully exposed. The exposed petals differ slightly in shape between Eva (4.6 ± 0.6 cm; N = 20) and Princess (5.3 ± 0.4 cm, N = 20; Figure 9.40). The five sepals and the receptacles are green and hairy, and petiole lengths vary from 0.5 cm in Princess to 1.5 cm in Eva. Due to the shorter petiole, inflorescences of Princess are composed of denser flowers.

Figure 9.38

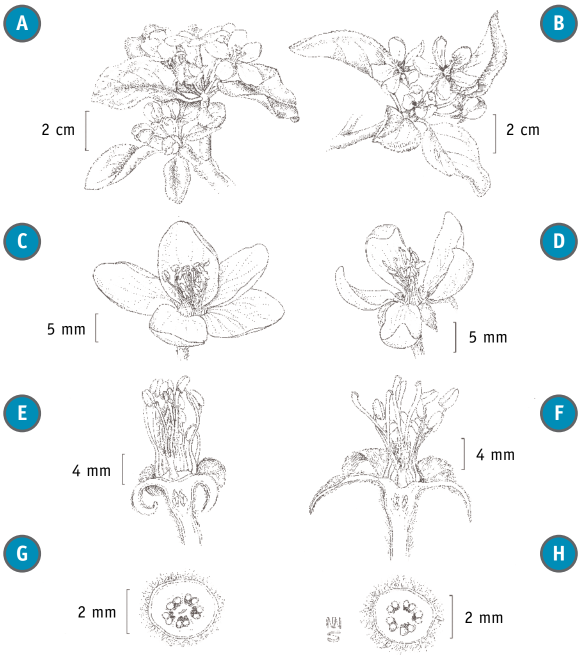
FLOWER DENSITY IN "EVA" AND "PRINCESS" APPLE VARIETIES IN ORCHARD AT CHAPADA DIAMANTINA, BAHIA, BRAZIL



Source: Viana and da Silva [present study]

Figure 9.39

SCHEMATIC REPRESENTATION OF INFLORESCENCE AND FLOWERS OF PRINCESS (LEFT) AND EVA (RIGHT) APPLE VARIETIES



(a, b) inflorescence; (c, d) fully open flowers; (e, f) stigmas and anthers with petals removed; and (g, h) transverse section, ovary

Source: drawing by Natanael Nascimento

Apple flowers are monoclinous and have 20 to 25 stamens, arranged in a circle surrounding the pistil; the filaments are white and anthers are yellow, with longitudinal dehiscence. Within a flower, anthers of longer stamens shed pollen before those of shorter ones. The flower is epigenous and the gynoecium inferior, with five locules in the ovary, each bearing two ovules, allowing the formation of ten seeds once maximum pollination is accomplished. The five styles have tricomes at the apical position and are fused at the base. Styles are longer than stamens in Eva, but are shorter in Princess (Figure 9.40). Apple flowers last for three days (including a senescent phase), and morphological and functional changes in androecium and gynoecium take place during full anthesis to the senescent phase. All five stigmatic surfaces are green in early open flowers and are 100 percent receptive, while pollen is 100 percent viable during the entire flower lifespan. Pollen is mostly removed within a 24-hour period, and after 48 hours nearly all pollen grains have been removed from anthers. During this period, the stigmatic surface is still receptive to viable pollen, and fertilization (between genetic varieties) can occur. The syncarpic ovary allows the pollen grains to reach ovules from any stigmatic surface position, which is frequently recorded in apple varieties [5]. In fertilized flowers, abscission of petals is coincident with enlargement of the receptacle, indicating the initial stage of fruit formation.

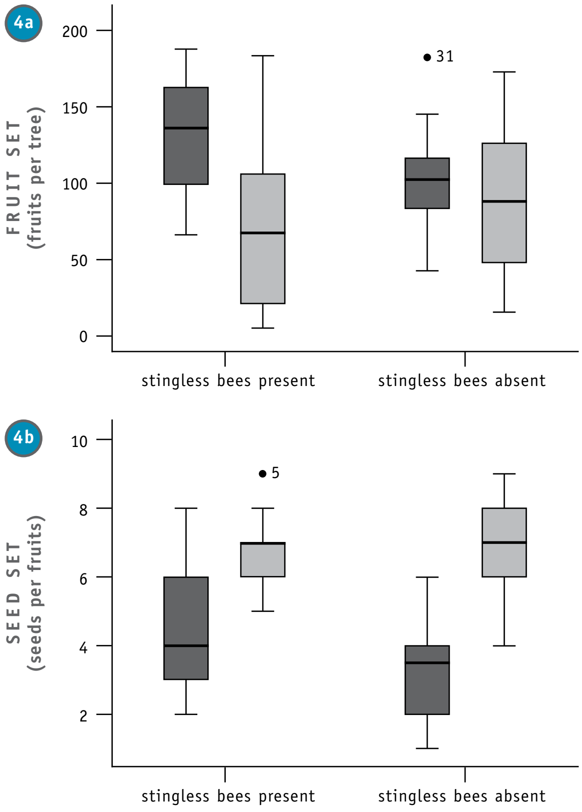
No remarkable difference was found in mean nectar volume (µL): (Eva: 1.38 ± 0.099 and Princess = 1.04 ± 0.13), mean nectar sugar concentration (percent) (Eva: 37.29 ± 2.88 and Princess: 38.33 ± 2.51) or in total sugar content (mg of sugar) (Eva: 0.61 and Princess: 0.46). Most nectar is produced and is available to visitors during the first 24 hours of anthesis, becoming scarce after 48 hours. In general, nectar content (mg of sugar) in the studied varieties fits the range recorded in other apple varieties [5].

Because of its self-incompatibility within clones or single varieties, apple relies on cross-pollination to produce seeds and fruit [6]. Failure in pollination results in low yields for farmers and can be related to many causes such as: plant condition (age and physiological state), production system (soil quality, water deficit, crop management) and pollinators (low density and richness leading to insufficient pollen quality and deposition on receptive stigmas, and weather conditions affecting the foraging behaviour of pollinators) (see section 3.1). In the studied orchard, pollinator limitation was the main cause of pollination deficit.

Pollination deficit: Among apples in Bahia state, such a deficit is indicated by significantly lower seed set obtained from naturally pollinated (mean = 4 seeds/fruit) compared to manually outcrossed fruit (mean = 8 seeds/fruit). This indicates a pollination deficit (section 3.1) in the apple orchard, reinforced by increased seed set from the experimental addition of pollinators. Apples from Eva trees set a mean of six seeds, while neither a greater number of honey bee hives (7 to 11 hives ha-1) nor the addition of pollen traps on hives (which tend to increase pollen collection trips [7]) produce general effects on seed set (Figure 9.41a). One possible explanation is that the density of seven honey bee hives ha-1 is already too high to detect any further effect of using a pollen trap. However, the addition of stingless bees (12 hives ha-1) with Africanized honey bees (7 hives ha-1) provides higher seed set and fruit production than the honey bees alone (Figure 9.41b).

Figure 9.40

FRUIT SET (4A) AND SEED SET (4B) COUNTED IN EVA (DARK GREY BAR) AND PRINCESS (LIGHT GREY BAR) TREES (N = 24 TREES FOR EACH TESTED DENSITY)



Data obtained in 2012 from three parcels densely populated with stingless bees (N = 12 colonies ha-1) and Africanized honey bees (7 hives ha-1 with pollen traps) simultaneously, and with Africanized honey bees alone (7 hives ha-1 with pollen traps)

Source: Viana and da Silva

Managed pollinators. Pollinators of apple flowers are mainly bees [5]. In Bahia, Africanized honey bees (hybrid *Apis mellifera scutellata*) are the most abundant and frequent pollinator. The honey bee hives were transported into the orchard at night during the peak of flowering and 24 hours prior to the start of the controlled density test. Within the parcels, hives were arranged at a distance of 10 m from the edge, separated from each other by a distance of 8 m in the treatments with 7 and 9 hives ha-1 and by a distance of 4 m in the treatments with 11 hives ha-1, and left there until the end of blooming season. Honey bee hives used for apple pollination are rented by farmers during blooming season and come from an apiary located in the municipality of Andaraí (112 km distant from the orchard). Because Africanized honey bees are defensive and sting often, workers are asked to avoid hives unless using a protective "beesuit" and do not handle the hives inside the orchard. There is a plum orchard nearby, which also benefited from the presence of the managed Africanized honey bees during the season. Few wild nests of Africanized honey bee are found because of the small amount of natural area.

Other free-living pollinating bees are sporadic in their appearance at apple flowers (e.g. Meliponini, Centridini, Xylocopini) or have unsuitable body size and/or behaviour on flowers. Africanized honey bees are effective pollinators when foraging for apple pollen, but not when foraging for nectar due to their side-working behaviour, which avoids stigma contact [8]. Visitation is improved in trees close to hives, which is important as more than three flower visits are needed to obtain four seeds per fruit.

A link has been found between yield and the introduction of pollinating bees, with yield increasing from 10 tonnes ha-1 to 27 tonnes ha-1 [9]. This figure, while significant, still represents only half the productivity of Eva in Minas Gerais state, which produces 40 tonnes ha-1 [10]. It is noteworthy that both orchards are of similar age and use the same production system. Although other factors such as apple variety traits [10] deserve investigation, pollinator abundance seems to be a major factor. In the Minas Gerais orchard, both amount and distance of natural areas from the crop are smaller than in those studied in Bahia. In Bahia, central pivot irrigation and intensive conventional farming leads to high input of pesticides and also to habitat loss. Currently, there is little natural habitat surrounding the apple orchard (23 percent in a radius of 2 km from the centre of the orchard). This may possibly explain why fewer free-living wild bees visit apple flowers at the orchard in Bahia. Moreover, *Melipona quadrifasciata anthidioides* and other meliponines no longer occur there. In certain plantations isolated from natural areas there are fewer insects visiting the target crop flowers and, consequently, fruiting decreases [11].

Conclusion: Eva and Princess are apple varieties that grow well in warm weather conditions such as those of southeastern Brazil, and also have considerable potential in the northeast. Eva provides the fruit and Princess acts as the pollinizer. Differences among varieties are noticeable in inflorescence size, number of open flowers within inflorescences and floral form. A pollination deficit in Bahia state is indicated by significantly lower seed set from natural open pollination (mean = 4 seeds/fruit) compared to manually outcrossed apple flowers (mean = 8 seeds/fruit). Africanized honey bee colonies used at 7 ha-1, with pollen traps on hives to increase bee pollen foraging, are currently the option used by apple producers. However, higher hive density produces no further increase in seed set. Honey bees and managed hives of the stingless bee *Melipona quadrifasciata anthidioides* together further increase yield from 10 tonnes ha-1 to 27 tonnes ha-1. Such observations argue for the adoption of pollinator-friendly practices that conserve native pollinators and develop native bee management.

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9.3.8 Canolaculture in southern Brazil

P. Nunes-Silva, S. Witter and B. Blochtein

The Brazilian Network for Canola Pollination was established in 2009 to study rapeseed pollination ecology in the main producing regions. The regions are all located in Rio Grande do Sul state. Esmeralda (28°03'13" S, 51°11'25" W) is a high *Araucaria* and forest remnant plateau of Serra do Nordeste situated at 960 m, with 76–83 percent relative humidity, a mean temperature of 14.4–16.8 °C and 1 412 to 2 162 mm mean annual rainfall. Estrela (29°30'07"S, 51°57'57"W) is a lower foothills region situated at 52 m, with relatively humidity of 75 percent, a mean temperature of 19.3 °C, mean annual rainfall of 1 547 mm, and subtropical forest. Guarani das Missões (28° 08' 52" S, 54° 24' 10" W) is located in the Missioneira ecoclimatic region at 175–425 m, with relative humidity of approximately 74 percent, a mean temperature of 18.8–19.6 °C, and open fields, natural forest patches and subtropical forest.

Floral and reproductive biology: Two canola oilseed rape (*Brassica napus*) cultivars are grown in these regions: "Hyola 420" at Esmeralda and "Hyola 61" at Estrela and Guarani das Missões. Anthesis of these rapeseed flowers occurs in three stages with some variation. The first occurs with buds closed and lasts three hours, but no nectar or pollen is presented and stigmas are not receptive. In the second phase, flowers are completely open and receptive, with pollen and nectar. The stage lasts four to six hours for Hyola 420 and 12–23 hours for Hyola 61. In the third stage, even though flowers are partially closed and senescence is evident, the stigma is still receptive, while nectar and pollen are no longer available. Hyola 61 has a 36-hour anthesis, while Hyola 420 exhibits a 12-hour anthesis. Other rapeseed cultivars (e.g. "CTC-4") have 32.5 ± 8.6 hours or a 48-hour anthesis, while anthesis lasts 72 hours for "Hyola 432".

During anthesis, the pistils grow and the stamens twist, positioning the dehiscent side of the anthers toward the flower's exterior [1], as reported in other studies [2, 3]. The staminal change may favour cross-pollination and limit autogamy, as the stigma is not receptive when anthers face inward [3]. However, this was not found in the present study and autogamy could occur with anthers facing inward (authors, unpublished data).

Rapeseed is self-compatible [4] and pod set via free visitation, xenogamy and autogamy confirms that Hyola 420 and Hyola 61 are also self-compatible. However, free visitation and xenogamy increase production, compared to autogamy, as measured by the number of pods formed. Free visitation increases production by 17 percent in Hyola 420 and approximately 30 percent in Hyola 61. For Hyola 432, a treatment allowing free visitation by insects (mainly *A. mellifera*) increases percentage pod set by 22 percent compared to autogamy [5].

Results vary according to production region, with increased quantity and quality of seeds produced under free visitation and xenogamy [6]. Among two sites with Hyola 61, seed weight is higher at Estrela under autogamy while Guarani das Missões seed weight increases with free visitation and xenogamy. One hypothesis to explain this difference is that less flower visitation occurs at Estrela, given that total visitation affects fruit production [7, 8]. Another possible cause is pollinator assemblage composition, because pollination benefit varies among species [9]. For the cultivars studied, Hyola 61 appears more dependent on insect pollination than Hyola 420 [1].

Pollinators and profitability in rapeseed: Rapeseed production is influenced by pollen vectors, such as wind, gravity and insects, in particular *Apis mellifera* [3, 10–13]. Despite being self-compatible and self-pollinated, rapeseed does not produce a great number of pods in the absence of pollinating insects [9]. Bees promote an increase not only in the amount of seeds produced, but also in the quality of the oil and thus, market value [5, 8, 10, 11]. An increase > 50 percent can result from the introduction of honey bee hives in rapeseed fields [9, 10, 12, 14].

In Brazil, although a relationship between the abundance of honey bees and seed production was not found in Rio Grande do Sul, this insect may be responsible for the majority of rapeseed pollination because it is the most abundant flower visitor [7, 10]. For rapeseed, native bees are effective pollinators [5, 8, 15].

Apiculture has grown in visibility on the Brazilian economic market due to increasing honey production and advances in pollination research. In addition, growers increasingly perceive the value of pollinators in agricultural areas, and may partner with beekeepers to increase yield. Because rapeseed is a winter crop – a period when there is a shortage of food for pollinators – it represents an alternative to feeding as a means to strengthen honey bee colonies. However, few partnerships have been established in Brazil, making it desirable to establish consortia, as all will benefit.

As the above studies make clear, the abundance and richness of insect pollinators in rapeseed flowers also varies with region, with the majority belonging to Hymenoptera and Diptera. In southern Brazil, canola fields have a low abundance of native bees, in contrast to the high abundance of honey bees [7]. The richness of native bees is also low, with 38 native species from the families of Colletidae, Andrenidae, Halictidae and Apidae, with Apidae and Halictidae the most abundant [6, 16]. Among Halictidae, *Pseudagapostemon tesselatus* is the most abundant species recorded in rapeseed fields of southern Brazil, among others of this family [8].

Among Apidae, the richest guild is the Meliponini with eight species identified: *Trigona spinipes*, *Scaptotrigona bipunctata*, *Schwarziana quadripunctata*, *Mourella caerulea*, *Nannotrigona testaceicornis*, *Tetragonisca fiebrigi*, *Plebeia emerina* and *Plebeia nigriceps*. Among those species, *M. caerulea* (common name: bieira) and *S. bipunctata* (common name: tubuna) are more abundant in Esmeralda, and *T. fiebrigi* (common name: jataí) and *P. emerina* (common name: mirim emerina) are found in greater abundance in Guarani das Missões. When the bees visit rapeseed flowers pollination occurs because they touch both anther and stigma. The colonies of all species, with the exception of *M. caerulea*, which makes subterranean nests, can be bred in rational hives managed for pollination service. In fact, a comparison of the efficiency of *T. fiebrigi*, *P. emerina* and *A. mellifera* as pollinators of rapeseed flowers reveals that stingless bee species are as effective as honey bees and have potential for management. Biotic pollination as a whole is important for seed production in rapeseed, including the syrphid flies, which also contribute to rapeseed pollination [17, 18].

Bees and other insects that visit rapeseed flowers may be found in the natural areas (e.g. forest fragments) surrounding production fields, generally because the increasing distance between areas as well as their decreasing size leads to minimal flower visitation by non-*Apis* species (e.g. richness, abundance and visitation rates), crop pollination and yield [e.g. 19–21]. Furthermore, monoculture landscapes with little or no other habitat have a lower potential of rapeseed productivity than areas of diversified vegetation [21]. Bommarco *et al.* [11] verify that insects visiting rapeseed decrease within larger cultivated areas.

Likewise, in southern Brazil, an area within a field closer to forest fragments produces more seeds, and the resulting crops have higher economic value, highlighting the importance of natural areas for "Hyola 420" rapeseed [15]. This fact is clearly important in southern Brazil, which is largely homogeneous and dominated by agricultural fields with little natural habitat.

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9.3.9 Reproductive biology and pollinators of the multipurpose plant *Jatropha curcas* in Mesoamerica

M. Rincón-Rabanales, L.I. Vargas-López,
M.L. Adriano-Anaya, J.A. Vázquez-Ovando,
I. Ovando-Medina, J. Grajales-Conesa and M. Salvador-Figueroa

Jatropha curcas is a euphorb possibly native to Mexico and Central America [1, 2]. It is a multipurpose plant used for traditional medicine, biopesticide, land erosion control, living fences, lantern oil and soap making, and contains not only rich oil, but also toxic toxalbumin and jatrophin [3]. Moreover, in the last decade, it has been considered the most promising inedible (non-food) plant for biofuel production [4], thus many countries are establishing programmes for its commercial cultivation [5]. In the Mesoamerican region, where the greatest population-genetic diversity of *J. curcas* is found, several monocultures are being established, for example in Guatemala and Mexico (Chiapas and Michoacán states) [2, 6–9].

The establishment of new extensive crops requires knowledge of reproductive biology including flowering, phenological behaviour, sexual system, and fruit and seed production [10]. Research efforts aimed at acquiring this information are underway in several parts of the world. For example, in India, where the species is exotic, studies on floral biology and pollination ecology reveal that this monoecious and protandrous plant displays both geitonogamy and xenogamy, but also that self-pollination is the prevalent breeding system, which may explain the low genetic diversity in Asian germplasm. It is also possible that the environment affects the predominance of either geitonogamy or xenogamy [11–19]. In addition, there is a lack of knowledge about the pollinators of this plant. While it is accepted that *Apis mellifera* is an efficient pollinator for *J. curcas* [20, 21], other authors mention *A. cerana* [22] and ants [23] as the principal pollinators.

There is little available knowledge about the floral biology or pollination systems of *J. curcas* in Mesoamerica, its centre of origin and diversity, thus observational and experimental investigation must assess the floral biology and test the pollination efficiency of *A. mellifera* and other flower visitors. This chapter summarizes the authors' studies on *J. curcas* and its reproductive biology during five years under field conditions in southeastern tropical Mexico.

Floral biology and reproduction: Most of the studies were carried out within "living fences" of established *J. curcas* farm plots at Soconusco, Chiapas (14.5036 N, 92.1704 W) in southern Mexico. Based on their appearance (healthy and abundant foliage) and location (sunny areas), plants were selected on 600 m transects along ten-year-old living fences that undergo annual pruning.

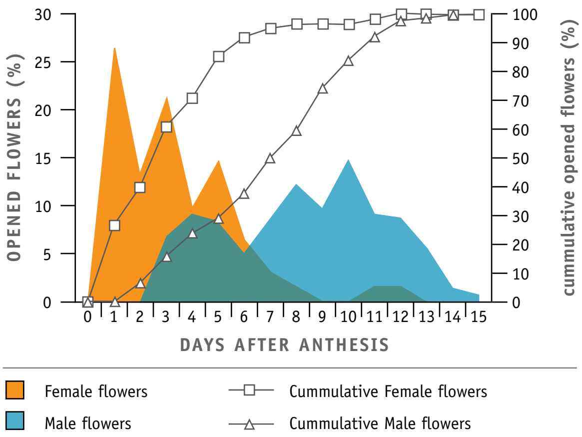
Floral phenology: Flowering and fruiting dynamics were studied in ten plants every 14 days during 2011. The plants have three flowering peaks (80 percent of total) in April, May and September, with three periods of peak fruiting in May, June and October. The studies systematically monitored: (i) the average number of inflorescences per primary branch in five plants, randomly selected (male and female flowers); (ii) the daily floral anthesis time and stigma receptivity for ten plants (30 days), in marked inflorescences (flower buds), at intervals of 10 min from 07:00 hours to 12:00 hours; and (iii) pollen and ovule production, estimated by collecting random inflorescences of ten plants with closed flowers, 20 female flowers and 20 male flowers . Pollen grains were extracted from male flowers and mounted in glycerinated gelatin on a slide, then quantified by stereomicroscope to determine the mean number of pollen grains per flower. In female flowers, the number of carpels and ovules per carpel were counted. The resulting data were used to estimate the pollen-to-ovule ratio.

The results indicate that *J. curcas* produces a mean of 1.25 inflorescences per branch, while female flowers per inflorescence average 2.2. The number of male flowers ranges from 35 to 198 flowers per inflorescence (mean: 106.7), and the proportion of female to male flowers is approximately 1:60. Pollen production by anthers ranges from 266 to 647 pollen grains (mean: 475.1), and production per flower ranges from 3 062 to 5 016 grains (mean: 4 224.4). The proportion of pollen grains per ovule was found to be 1 408:1. The male and female flowers open at 08:00 hours, with a maximum of open female flowers (64.29 percent) and male flowers (55.75 percent) at 09:00 hours, while the stigma is receptive from 10:00 to 12:00 hours.

Flowers open regularly over an average period of 15 days (Figure 9.42). Female flowers are the first to open and this process continues for eight days. Male flowers start opening two days after the female flowers, and continue for 13 days in the cycle, with the highest peak in days eight to ten.

Figure 9.41

OPENING DYNAMIC OF FEMALE AND MALE FLOWERS IN *JATROPHA CURCAS* IN THE SOCONUSCO REGION, CHIAPAS, MEXICO



Source: M. Rincón-Rabanales *et al.* [present study]

Some floral biology of *J. curcas* in the Mexican tropics, such as the proportion of male and female flowers (1:60), differs from other geographic areas. For example, Raju and Ezradanam [12] report that in India an inflorescence produces one to five female flowers and 25 to 93 male flowers (1:29). Additionally, Pinto *et al.* [24] found four to 12 female flowers and eight to 222 male flowers (1:20). This trait depends potentially upon genetics, geographic region, climate, nutrition, time and cultural practices, among other factors, which makes it a highly variable feature [13, 15, 24].

Pollen production per anther and per flower is higher in Chiapas than reported in other studies, such as Bhattacharya *et al.* [13], who found that each flower produces 1 617 pollen grains, with a pollen:ovule (P:O) ratio of 539:1. In this regard, Cruden [25] argues that the P:O ratio is as an indicator of the reproductive system. In the case of *J. curcas*, the P:O ratio is very high. The large amount of pollen could serve as a compensatory mechanism for pollen loss caused by the constant arrival of insect visitors to the inflorescences.

The opening of male and female flowers under the study conditions occured at 07:00 hours, which generally agrees with the findings of Raju and Ezradanam [12], who report that flowers open daily between 05:30 and 06:30 hours. Kaur *et al.* [18] report that male flowers open between 06:00 hours and 07:00 hours, while the female flowers open shortly thereafter (07:00–08:00 hours). The period of stigma receptivity (1–2 hours) is similar to that reported in India [13]. The opening pattern of flowers in the morning is related to the potential to attract insects, as the availability of resources (nectar and pollen) is significantly higher at this time of day.

Flowering of *J. curcas* in Chiapas occurs from March to November, somewhat consistent with Sukarin *et al.* [11], who reported two flowering peaks in May and November. Joker and Jepsen [26] observed flowering during the dry season and recorded two flowering peaks, although they mention that plants bloom throughout the year. Fruiting in the Chiapas study occured from April to December, contrary to the findings of Toral *et al.* [27], who observed fruit being produced in winter when the plant loses its leaves.

Breeding system: In order to understand the reproductive process, five pollination treatments were performed: (i) geitonogamy or artificial pollination with pollen from the same inflorescence (GEI); (ii) xenogamy (XEN) or artificial pollination with pollen from another plant; (iii) apomixis (APO), performed by removing the male flowers and placing non-toxic white glue (Resistol®, Mexico) on the stigma; and (iv) pollinator exclusion (ExP) and (v) open pollination (OpP). For each treatment, 20 inflorescences were used, one per plant, which were covered with tulle mesh bags of 1 mm mesh size, except in the case of OpP. Fertilization was checked 14 days after pollination and the number of mature fruits per treatment quantified at 55 days. The number of fruit and fruit quality were compared by ANOVA and a Tukey test ($\alpha = 0.05$).

Differences were found in the production and quality of fruit and seeds among the different reproductive modes ($p < 0.001$). The highest fruit set was obtained from open pollination (OpP: 86.3 ± 2.2) and xenogamy (XEN: 84.3 ± 6.3), which are statistically equal, followed by pollinator exclusion (ExP: 18.1 ± 7.2) and geitonogamy (GEI: 16.2 ± 7.3). In the apomixis treatment, five fruit were formed and four aborted ($n = 55$ female flowers). The single apomictic fruit had a high fresh weight but low seed weight, due to its thick endocarp.

Fruit reaches maturity substantially more in OpP and XEN treatments ($p < 0.001$). The choice of breeding mechanism also influences fruit and seed quality, with heavier and larger seeds resulting from OpP and XEN treatments ($p < 0.001$) (Table 9.11).

The highest level of fruit production (86.3 percent) occurs in open pollinated plants and xenogamy treatments (84.3 percent), consistent with the findings of other authors [10, 12, 13]. However, a lower fruit set (50–53 percent) is also reported in open pollinated flowers [14], consistent with pollinator limitation (Chapter 3.1). Regarding apomixis, a very low rate was found (2.5 percent), similar to the 5 percent reported by Santos *et al.* [28] in a semi-arid region in Brazil. In contrast, Bhattacharya *et al.* [13] and Kaur *et al.* [18] state that apomixis might be responsible for > 30 percent of fruit, while Chang-Wei *et al.* [15] report only a moderate effect of apomixis (12 percent).

Insect flower visitors and pollinators: Ten inflorescences (08:00 hours to 17:00 hours) were observed at intervals of 10 min, in order to register flower visitors, their time of arrival, the total time at each flower, the resource used (nectar or pollen), and movement among flowers of the same inflorescence and between inflorescences of the same or different plants. Insects visiting *J. curcas* flowers were collected on another living fence at a distance of 500 m from the study site, using entomological nets, between 06:00 hours and 18:00 hours. The bees (dissected head and thorax) were examined under a stereoscope and identified using the taxonomic keys of Ayala and Michener [29, 30]. The pollen of *J. curcas* on insects was identified by microscopy.

Insect visitors were classified as effective pollinators, occasional pollinators, accidental pollinators or pillagers using the following criteria: (i) number of individuals collected during different times of the day, (ii) recurrence and time of visit to male and female flowers, (iii) behaviour observed on flowers, and (iv) presence of *J. curcas* pollen (pure or mixed) on the body. The analysis included application of the Chi-square test.

Table 9.11

COMPARISON OF CHARACTERISTICS OF FRUITS AND SEEDS OBTAINED FROM DIFFERENT POLLINATION TREATMENTS IN *JATROPHA CURCAS* IN THE SOCONUSCO REGION, CHIAPAS, MEXICO

	OPP	XEN	GEI	EXP	APO*	F**	P
Fruits per inflorescence (n)	4.88^{a}	4.20^{a}	0.88^{b}	1.00^{b}	0.10^{c}	21.02	0.001
Fruit diameter (cm)	2.94^{a}	3.04^{a}	2.82^{ab}	2.64^{b}	2.9	2.98	0.035
Fruit length (cm)	3.29^{a}	3.26^{ab}	2.98^{bc}	2.85^{c}	3.1	4.73	0.004
Fruit fresh weight (g)	12.90^{a}	13.10^{a}	12.42^{a}	10.07^{b}	13.86	4.48	0.005
Seeds (n)	2.68^{a}	2.77^{a}	2.71^{a}	2.16^{b}	3.0	2.80	0.004
Seed fresh weight (g)	1.65^{a}	1.21^{b}	1.30^{b}	0.97^{c}	1.21	20.95	0.001

Notes: OpP: open pollination, XEN: xenogamy, GEI: geitonogamy, ExP: excluding pollinators, APO: apomixis.
*Due to the reduced number of fruits, the apomixis treatment was not included in most of the ANOVA tests.
**One-way ANOVA and Tukey tests were performed. Different superscripts letters in a row denote statistical differences.

Source: M. Rincón-Rabanales *et al.* [present study]

Diversity of insect visitors: Insect visitors to *J. curcas* include 36 species comprising four orders, 12 families and 16 genera (Table 9.12). Hymenoptera are the most diverse (75 percent of species) and dominant (72.6 percent total abundance), followed by Diptera (19.4 percent total species; dominance 26.3 percent).

Three types of pollinators were identified: (i) *accidental*, including the fly Tachinidae sp. 2, wasps, Vespidae sp. 1, Vespidae sp. 2, and one beetle species, Cerambycidae; (ii) *occasional*, comprising 14 species that include bees, ants and wasps; and (iii) *effective*, composed of nine species, bees and two fly species. The remaining insects are pillagers or nectar robbers (Table 9.12). Some pollinators carry *J. curcas* pollen alone or mixed with other pollen types: *Ageratum* aff. *houstonianum* (Mill.), *Acacia* aff. *cornigera* (L.) Willd., *Inga* sp., *Tridax* aff. *procumbens* (L.) and *Zea mays* (L.). Pollen from other species accounts for less than 10 percent of total loads (Table 9.13).

Table 9.12

POTENTIAL POLLINATORS OF *JATROPHA CURCAS* IN THE REGION OF SOCONUSCO, MEXICO

ORDER	FAMILY	GENUS	SPECIES	TYPE OF FORAGE	RELATIVE ABUNDANCE (%)	TYPE OF VISITOR
Hymenoptera	Apidae	*Apis*	*mellifera* L.	1, 2	1.1	OP
		Trigona	*fulviventris* Guérin	1, 2	7.3	EP
		Trigona	*fuscipennis* Friese	1, 2	1.1	EP
		Nannotrigona	*perilampoides* Cresson	1, 2	0.4	OP
		Scaptotrigona	*mexicana* Guérin-Meneville	1, 2	30.5	EP
		Tetragonisca	*angustula* Lepeletier	1, 2	7.3	EP
		Oxitrigona	*mediorufa* Cockerell	1	0.4	OP
		Melipona	*beecheii* Bennett	1, 2	0.4	OP
		Melipona	*solani* Cockerell	1, 2	0.4	OP
		Ceratina	*capitosa* Smith	1, 2	0.4	OP
		Triepeolus	sp. Robertson	1	0.4	PI
	Halictidae	*Agapostemon*	*nasutum* Smith	1, 2	7.3	EP
		Augochlora (*Augochlora*)	*quiriguensis* Cockerell	1, 2	0.7	OP
		Augochlora (*Oxystoglossella*)	*aurífera* Cockerell	1, 2	0.7	EP
		Augochlora (*Augochlora*)	*smaragdina* Friese	1, 2	0.4	OP
		Halictus (*Halictus*)	*ligatus* Say	1, 2	0.4	OP
		Halictus (*Seladonia*)	*Hesperus* Smith	1, 2	9.1	EP
		Lasioglossum (Dialictus)	sp. 1 Robertson	1, 2	0.4	OP
		Lasioglosum (Dialictus)	sp. 2 Robertson	1, 2	0.4	OP
	Formicidae	*Camponotus*	sp. 1 Mayr	1	0.4	OP, PI
		Crematogaster	sp. 1 Lund	1	0.4	OP, PI
	Sphecidae	–	sp. 2 Lund	1	0.4	OP, PI
	Sphecidae	–	sp. 1	1	0.4	PI
	Sphecidae	–	sp. 2	1	0.4	PI
	Vespidae	–	sp. 3	1	0.4	PI
	Vespidae	–	sp. 1	1	0.4	AP, PI
			sp. 2	1	0.7	AP, PI
Diptera	–	–	sp. 1	1	0.4	PI
	Syrphidae	–	sp. 1	1	7.3	EP
	Tachinidae	*Eristalis*	sp. 1	1	17.0	EP
	Tachinidae	–	sp. 2	1	0.4	AP, PI
	Syrphidae	–	sp. 1	1	0.4	PI
	Bombyliidae	–	sp. 1	1	0.4	PI
	Tephritidae	–	sp. 1	1	0.4	PI
Coleoptera	Cerambycidae	–	sp. 1	1	0.7	AP, PI
Hemiptera	Fulgoridae		sp. 1	1	0.4	PI

Note: AP: accidental pollinator, EP: efficient pollinator, PI: pillager, OP: occasional pollinator. 1 = nectar; 2 = pollen.

Source: M. Rincón-Rabanales *et al.*

Table 9.13

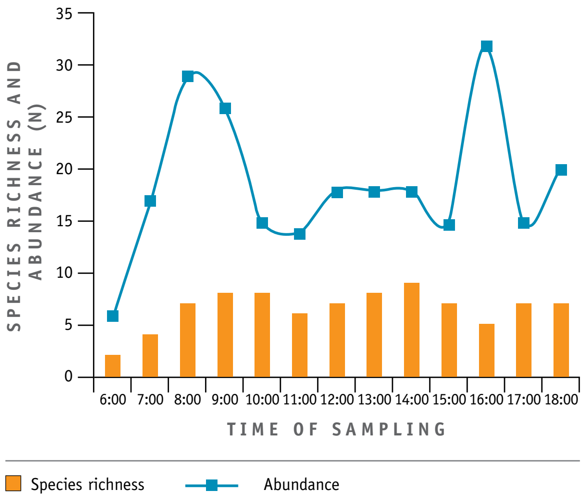
EFFECTIVE POLLINATORS OF *JATROPHA CURCAS* IN THE REGION OF SOCONUSCO, MEXICO

SPECIES	INDIVIDUALS COLLECTED (N)	TYPE OF POLLEN LOADS (%)		
		PURE LOADS	MIXED LOADS	WITHOUT LOADS
Scaptotrigona mexicana	84	65.5	20.2	14.3
Tetragonisca angustula	19	73.7	5.3	21.0
Trigona fulviventris	19	73.7	10.5	15.7
Trigona fuscipennis	3	100.0	–	–
Halictus hesperus	25	60.0	12.0	28.0
Agapostemon nasutum	19	36.9	10.5	52.6
Tachinidae sp. 1	49	63.3	2.0	34.7
Eristalis sp.	19	73.7	5.3	21.0
Apis mellifera	3	33.3	33.3	33.3

Source: M. Rincón-Rabanales *et al.*

Figure 9.42

DAILY DYNAMICS OF INSECTS VISITING *JATROPHA CURCAS* FLOWERS IN THE SOCONUSCO REGION, SOUTHERN MEXICO



Source: M. Rincón-Rabanales *et al.*

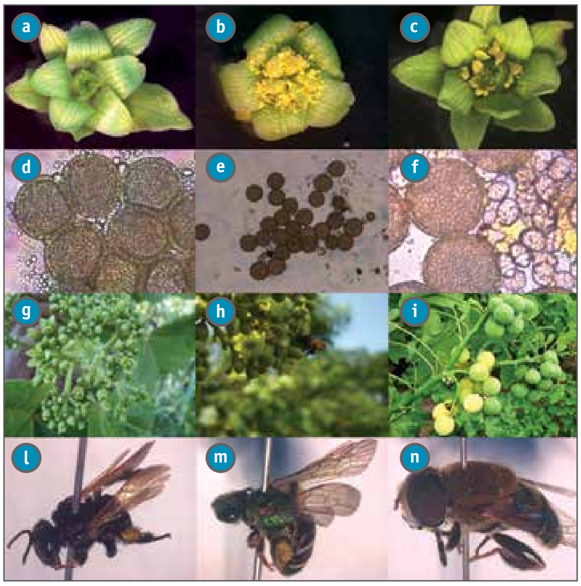
Insect flower visitation frequency: Insects visit *J. curcas* continuously from 06:00 hours until shortly after 18:00 hours, in a bimodal pattern (Figure 9.43). The main activity peaks occur when female flower nectar increases, from 07:00 to 09:00 hours. The greatest visitor richness of insects occurs during 09:00–10:00 hours, but peak visits take place at 16:00 hours (N = 32).

The most abundant insects were Hymenoptera and Diptera, as seen in previous studies in other areas [31]. Differences were found in the frequency and time of insect visits at female flowers ($\chi^2 = 21.78$, $p < 0.01$) and male flowers ($\chi 2 = 39.69$, $p < 0.01$). Insects observed in the marked panicles were *Scaptotrigona mexicana*, *Trigona fulviventris* (Guérin-Melènville), *T. fuscipennis* (Friese), *Agapostemon nasutus* (Smith), *Augochlora quiriguensis* (Cockerell), *Augochlora aurifera* (Cockerell), *Augochlora smaragdina* (Friese), *Halictus* (*Seladonia*) *hesperus* (Smith), Tachinidae sp. 1, *Eristalis* aff. *persa* (Williston), *Camponotus* (Mayr) and Vespidae sp. 1. Compared to other groups, bees visit more flowers (43.2 percent) and stay longer (38 percent). The second most important group is Diptera with 39.3 percent (frequency) and 31 percent (visit duration). The bees visit a larger number of female flowers (55.6 percent) than male flowers (46.4 percent). Both bees and flies spend more time visiting female flowers, while Vespidae sp. 1 prefer male flowers. Diptera forage exclusively on nectar, while bees collect both nectar and pollen.

Insect richness on flowers of *J. curcas* in the study area was substantially higher than in other geographic areas (Tables 9.12 and 9.13), with a high diversity and abundance of bees (19 species) and flies (nine species). The bees were small to medium in size (5–10 mm), and native stingless bees were the most diverse, abundant and compatible with the *J. curcas* flowers and breeding system. In contrast, most of the flies (7–14 mm body sizes and abundant hair) did not demonstrate effective pollinator behaviour. Two exceptions were *Eristalis* sp. and Tachinidae sp. 1, which visited male flowers frequently looking for fresh nectar and transported pure pollen stuck on their body for more than nine hours a day. They were observed visiting female flowers for nectar during the period of maximum stigma receptivity, facilitating xenogamy and geitonogamy, and were therefore classified as effective pollinators. The observations were consistent with studies by Raju and Ezradanam [12], who found that the Diptera *Chrysomya megacephala* (Fabricius) is an efficient pollinator that promotes xenogamy and geitonogamy. Conversely, Rianti *et al.* [17] report only *Eristalis tenax* (L.) as an infrequent visitor and not an effective pollinator for *J. curcas* in West Java.

Figure 9.43

***JATROPHA CURCAS* REPRODUCTIVE STRUCTURES AND ITS EFFICIENT POLLINATORS IN THE SOCONUSCO REGION, SOUTHERN MEXICO**



(a) female flower with receptive stigma; (b) male flower with dehiscent anthers; (c) hermaphrodite flower showing dehiscent anthers and receptive stigma; (d–e) *J. curcas* pollen grains recovered from loads of flower visitors; (f) *J. curcas* and *Inga* sp. mixed pollen recovered from flowers visitors; (g) inflorescence in the stage of flower buds; (h) female flower receiving the visit of *Trigona fulviventris*; (i) ripening fruits; and (j–l) *J. curcas* pollinators carrying pollen loads: stingless honey bee *Scaptotrigona mexicana* (j), the halictid *Agapostemon* sp. (k), the dipteran *Eristalis* aff. circe (l)

Source: M. Rincón-Rabanales *et al.*

The native stingless bees *S. mexicana*, *T. angustula*, *T. fulviventris* and *T. fuscipennis*, and the bees *H. hesperus* and *A. nasutus* are small (5–8 mm), with special structures for transporting pollen [32]. It is possible that these characteristics enable them to efficiently transport pollen to the stigma of *J. curcas*, as observed in other bee species [12, 13, 17, 33].

An effective pollinator of *J. curcas* is therefore one that: (i) visits several flowers during foraging [17], (ii) frequently shifts from one flower to another [17, 27], (iii) transports abundant pollen on its body, and (iv) touches some part of its body to the receptive stigma. In the present study, Africanized *A. mellifera* was scarce in relation to other pollinators (N = 3) and recorded only between 08:00 and 09:00 hours. One carried *J. curcas* pollen in great abundance on the head, venter and legs, while another transported pollen from different plant species. The results differed from other studies asserting that *A. mellifera* is a reliable pollinator of *J. curcas* [12–14, 16–18, 34]. Instead, the study classified this species as an occasional pollinator in the Mexican tropics, performing both geitonogamy and xenogamy.

Stingless bees, the main *Jatropha* pollinators observed, take advantage of a single source of food, such as with *Cocos nucifera* (L.), *Mangifera indica* (L.), *Carica papaya* (L.), *Citrus limon* (L.) and *Capsicum annuun* (L.) [35]. The study data revealed oligolectic or monolectic behaviour among meliponines, at least during the season studied (see also Chapter 14.3). Among these bees are *Scaptotrigona mexicana* and *Tetragonisca angustula*, which nest in trees, have moderate foraging ranges and make intensive use of available floral resources, and thus may pollinate extensive crops of *J. curcas*.

Conclusion: The genetic diversity of *J. curcas* is high in this Mesoamerican area and particularly in this region of Mexico. This may be due largely to the reliable pollination service provided by native stingless bees, and a strong protogyny in *J. curcas*, which leads to pollination by xenogamy and low prevalence of geitonogamy or selfing.

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9.3.10 African oil palm, *Elaeis guineensis*: pollination and weevils

P.G. Kevan

Oil palm is native to humid, tropical West Africa. It is one of the most important sources of vegetable oil, which is produced from the fruit and seeds, and has also become a major source of biodiesel (see Part 1). Oil palm is now grown in plantations in West Africa, Southeast Asia and tropical America. Despite its importance, the associated means of pollination was identified only in 1979, when the role played by insects, rather than wind, was proven.

The known, main natural pollinators of oil palm in Africa are three weevils (Coleoptera: Curculionidae) of the genus *Elaeidobius*. The one that has received the most attention is *E. kamerunicus*. This weevil was introduced from its native habitat in Central Africa to Malaysia in 1981, after careful quarantine and study of its potential to become a pest of non-target plants. It immediately became established and spread rapidly throughout the country's plantations, resulting in millions of dollars in profit to the industry. Prior to introduction of the weevil, pollination of oil palm was achieved by manually blowing pollen mixed with talc or another carrier/diluent onto the receptive female flowers.

To understand how beetles pollinate oil palm, it is necessary to examine the sexuality of the palm flowers. Oil palm has hermaphroditic flowers, but normally only reproduces through male or female function at any one time. The inflorescences may be either male or female: the male inflorescence consists of numerous long, fingerlike spikelets, each comprising thousands of pollen producing florets, while the bulky, female inflorescence consists of hundreds of densely packed florets, each of which consists of an egg-shaped ovary tipped by a trifid stigma measuring 0.5 cm across.

Weevils breed in the male inflorescences of the oil palm. While the spikelets are shedding their copious pollen, they are visited by female weevils. It is here that they become dusted with the pollen and lay their eggs. The female weevils and males that also visit the spikelets – presumably in search of mates – move from palm to palm, thus effecting outcrossing. During these movements they visit palms with female inflorescences. The reason for this is not fully understood, but the characteristic scent of the beetles, shared by the male inflorescences, is the main attractant.

The male spikelets remain on the inflorescences, attached to the palms and protected in the axils of the fronds, after they have expended their pollen. Their role in pollination has not yet finished, however, because the next generation of male and female weevil grubs grows and develops within them.

From the viewpoint of pollination management, the population of weevils is clearly significant. The density of male inflorescences relative to the density of female inflorescences is also important, as is the probability that a given weevil will transfer pollen between a male and female flower. It must also be remembered that male inflorescences do not contribute directly to oil yield in a plantation, but do occupy the place of female inflorescences on palms. The palms produce about eight to ten inflorescences per year, although the sex of the inflorescence is not constant throughout the entire year.

In order to maximize fruit and oil yield, plantation management must optimize the ratio and expression of male and female inflorescences to provide complete pollination of female inflorescences. That, in turn, requires that the population of weevils not drop below the threshold for complete pollination. Of course, absolutely complete pollination should not be expected (section 3.2).

Kevan and coworkers proposed "Pollinator Force" (see Figure 9.45) as a practical measure for monitoring pollinators for oil palm. To calculate the pollinator force, the following information is required:

- the density of male inflorescences or spikelets,
- the number of weevils emerging from those spikelets,
- the proportion of weevils not visiting male inflorescences which are shedding pollen,
- the proportion of weevils not visiting a receptive female inflorescence.

The values for the last two are unknown, and would require great research efforts to estimate. It can be assumed that the values would be low if the density of male spikelets were high. However, if they are too high at the expense of production of female inflorescences, then the crop yield will suffer. Unfortunately, the optimum ratio of palms in male phase to palms in female phase is not known, and the mechanisms within the palms that cause the production of inflorescences of one sex or the other are not completely understood.

In Malaysia, three decades after the introduction of *E. kamerunicus*, there has been no indication that the Pollinator Force has dropped below the critical level for economic harvesting. Some minor pests of weevils have been recorded (e.g. rats feeding at the grub-rich spikelets), and some low incidence of diseases. Nevertheless, weevil populations continue to be monitored in plantations in order to track potential pollination.

As oil palms continue to be improved through modern breeding and genetic techniques, the concept of pollinator force may become vital. It may be that with the development of lines of perennially female (oil-producing) palms that rarely enter the male phase, plantations will have to include pollinizer (male) palms (as with dates). The diminished gene pool within palm plantations, worldwide, will likely cause the pollinators to shift or become less attracted to flowers. There has been commercial interest in the development of hybrid oil palms, but pollination seems to be a problem. It may be that the weevil-attracting floral scents of the hybrid palms include a mixture of chemicals that are not recognized by the true pollinating species of either parent *Elaeis* spp.

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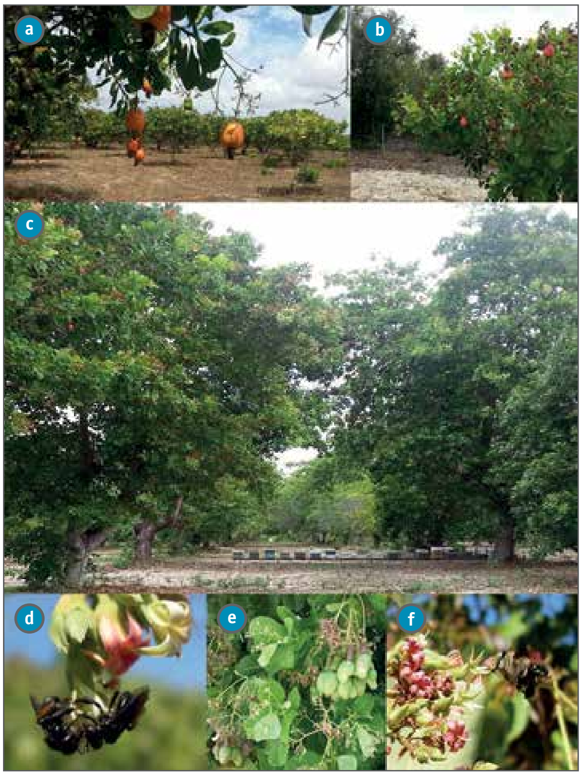
9.3.11 Cashew pollination: answering practical questions

B.M. Freitas

Cashew (*Anacardium occidentale* L.) is a tree that belongs to the Anacardiaceae. It is native to Brazil and cultivated mainly in tropical Central and South America, Africa and Asia. Exploited commercially for fruit that bears an edible kernel and highly prized industrial oil extracted from the nutshell, it is of value to the livelihood of local communities and many national economies (see Figure 9.44).

Figure 9.44

CASHEW (*ANACARDIUM OCCIDENTALE*) CULTIVATION AND ITS POLLINATORS



(a) the cashew fruit in an orchard of dwarf cashew trees; (b) pollination must take place within four hours after hermaphrodite flowers open, when plantation bordered by forest may attract pollinators; (c) *Apis mellifera* hives for pollination in an orchard of normal-sized cashew trees; (d) stingless bees visiting a cashew flower; (e) well-pollinated cashew tree bearing many fruitlets per panicle; (f) *Centris flavifrons* approaching a cashew flower

Source: B. M. Freitas [present study]

Global cashew nut production fluctuates considerably from year to year, and has ranged recently between 4.2 and 7.0 million tonnes of nuts per year from a harvested area of 4.7 million ha. Viet Nam, Nigeria, India, the Ivory Coast and Brazil are the world's largest producers and account for more than 80 percent of global cashew nut production [4].

The productivity of cashew orchards is often poor (200 to 893.5 kg nuts ha$^{-1)}$, despite a potential for higher yields (c.a. 1 300 kg nuts ha^{-1}). Several key factors seem important in this regard – from poor nutrition of plants and lack of soil management to irrigation and pest control – and the prevalence of orchards with old trees grown from seeds instead of selected, grafted and productive varieties [5–7]. However, recent advances in those areas have produced little or no benefit for the cashew yield.

Pollination seems to be the most important factor for increasing cashew yield. A high level of fruitlet abortion within days after pollination leads researchers to suspect inadequate or under pollination as a major cause of low cashew yields [8, 9]. Indeed, studies carried out on cashew pollination in the past 20 years find a significant pollination deficit and that insects, particularly bees, are the primary cashew pollinators [10–12]. The present section summarizes the currently available information and discusses the state of the art in cashew pollination. Based upon the literature and insights it offers, the text attempts to answer practical questions often posed by cashew growers on how to mitigate the pollination deficit in cashew crops, and thereby enhance nut yield.

Floral biology and pollination requirements: The cashew tree is andromonoecious, that is, it presents male and hermaphrodite (male and female) flowers in the same panicle. The proportion varies from one to 50 male flowers for each two hermaphrodite flowers, depending on the genetic stock and stage of blooming. The flowers have five white petals at anthesis, which change to pink by the end of the first day, and from pink to dark red over the next four days, before withering [13–16]. Nectar volume (0.31–1.10 µL), sugar concentration (14.0–19.9 percent) and amount of sugar (0.06–0.23 mg) per flower vary greatly according to genetic material, age and flower type [16]. Both types of flowers secrete nectar and have six to 10 short staminoids possessing mostly unviable (0–5 percent viability) pollen and one large stamen bearing highly viable (> 90 percent) pollen grains. The stamen produces about 800–1 000 pollen grains, but each staminoid has only 116–175 grains. In each, the pollen is covered with sticky and oily pollenkitt and cannot become airborne [9, 10, 16]. All those traits are associated with zoophily, not with wind pollination, as previously suggested by some studies [13, 17, 18]. Therefore, insects are necessary in cashew pollination.

The hermaphrodite flower has a style that takes the same position as the long stamen of male flowers, although its own stamen is shorter than its style. The ovary is superior and contains one ovule, and thus requires only one compatible pollen grain to set a fruit and seed. Male flowers have a rudimentary ovary that contains no ovule and cannot set fruit [15, 19].

The time of day that cashew flowers open and release pollen may vary among regions, but usually both kinds of flower open and dispense pollen in the morning. Male flowers open before hermaphrodite flowers and begin to release pollen as soon as the temperature reaches approximately 28 °C, normally early in the day. In Brazil and close to the equator, for instance, male flowers begin to open at 07:00 hours with 82 percent open by 10:00 hours, when the hermaphrodite flowers open. By 12:00 hours, all male flowers and 97 percent of hermaphrodite flowers are open and have released pollen [14, 16, 20].

The different times of opening for male and hermaphrodite flowers force pollinators to visit male flowers first, where they acquire pollen grains that they may transfer to the stigmas of hermaphrodite flowers later in the day. The pollination of hermaphroditic flowers is accomplished mainly during four hours, after which receptivity drops steeply. Although a few stigmas remain receptive for up to 48 hours after the flower opens, they represent less than 3 percent of the total. The viability of cashew pollen displays a similar pattern to that of stigma receptivity. Cashew pollen is highly viable at anther dehiscence, but viability drops quickly after four hours. Considering agronomic yield, cashew growers should thus consider the first four hours after the hermaphrodite flowers open as the critical period for pollination [19, 21]. The flower visitors within this timespan are the main cashew pollinators (see Figure 9.44b).

Flower visitors and potential pollinators: Not all flower visitors are pollinators. A number of insect species have been recorded visiting cashew inflorescences in agricultural habitats, particularly ants, bees, butterflies, flies, moths and wasps, and different studies have suggested one or the other are the effective pollinators [19, 22–25]. However, many such insects cannot be considered pollinators at all. Although they arrive at the cashew inflorescences or flowers, they do not necessarily touch the reproductive structures of the flower. For instance, ants including *Camponotus*, and most wasps, do not touch anthers and stigmas, and the butterfly *Aphrissa* does not discriminate between young flowers with fresh pollen and receptive stigmas, or the older flowers without viable pollen or receptive stigmas. The butterfly *Oanaus erippus* Cramer, and all nocturnal flower-visiting insects, visit flowers when pollen is no longer available and stigmas are unreceptive. Furthermore, some visitors do not show flower constancy to cashew flowers, but move frequently to other flower species (e.g. the butterfly *Euptoieta hegesra meridiania* Stichel) [9, 19].

Flies and moths may be major cashew pollinators, but this idea is based only on anecdotal observations of great numbers of individuals visiting cashew in certain localities, and no studies have demonstrated their effectiveness. In fact, considering the narrow pollination window of cashew, and fly behaviour on flowers, it seems unlikely that flies transfer much viable pollen between stamens and receptive stigmas. For moths, there is almost no available pollen, and no receptive stigmas when they visit the flowers in early evening – although they may still pollinate a few flowers. Therefore, seen in perspective, flies and moths may occasionally pollinate flowers and enhance yield but seem unlikely to act as principal cashew pollinators.

Most studies carried out on cashew pollination suggest that bees are the major pollinators [9, 10, 15, 21]. Bees usually are not only the most abundant flower visitors, but also exhibit foraging behaviour conducive to effective pollination. They display flower constancy, timing of visits coordinated with a hermaphrodite flower's anthesis, contact with anther and stigma in the same area of the body, systematic movement between young flowers, and a large number of cashew pollen grains on their bodies [9, 26]. In addition, bees forage on cashew flowers all day, including, most importantly, when flowers are producing fresh pollen and stigmas are most receptive for pollination. Social bees can also be present in great number. Thus, honeybees (*Apis mellifera*, *A. cerana*) have been used for pollination (see Figure 9.44c) and, recently, stingless bees have been recognized as important cashew pollinators (see Figure 9.44d) [12, 27, 28, 29].

Other flower visitors (solitary bees and other insects, or birds) may also be capable of pollinating cashew flowers, but their abundance in the orchard is low, thus they probably contribute little to the yield sought in commercial plantations, where an efficient and abundant pollinator is required [21, 30]. Nonetheless, recent studies with various crops, including cashew, suggest that such relatively scarce wild pollinators can play an essential role in improving crop pollination, because the sum of their services can be significant (see Figure 9.44e) [12, 31, 32] (see also section 3.1). Growers must try to ensure that cashew flowers receive adequate visits of managed bee colonies and also benefit from a diverse group of wild pollinators, in order to set the maximum number of fruit and maximize yield.

Cashew cultivation worldwide and its pollination perspective – orchards and establishment: Cashew orchards are predominantly grown from seeds collected or bought by farmers without much consideration of the value of selected varieties or cultivars [7]. As a consequence, the trees within a plantation have differing genetic constitution and differ substantially in traits such as plant height, fruit quality, drought and saline soil tolerance, or pest and disease resistance – all of which are important to agronomy [33]. Such variation in traits, related directly to pollination, including duration of tree blooming, proportion of male/hermaphrodite flowers, nectar volume, concentration and total sugar produced per flower, and so on, affect pollinator attraction to the plant, and pollination efficiency [15, 34–36] (see also Chapters 17 and 18). Usually, this is the reason why hundreds of bees may be observed visiting the flowers of a particular cashew tree, while its neighbour has few bees foraging. One tree may also bear many fruit and others almost none (see Figure 9.44e). Such differences result in uneven nut production among the trees of an orchard and between orchards grown in the same region. Even with the same horticultural practices, yield is often widely variable.

Cashew trees grown in plantations worldwide are tall, reaching up to 15 to 20 m in height and 10 to 20 m in width (see Figure 9.44c). Such a large size, besides taking a large area per plant and limiting the number of plants per orchard, demands large areas for plantations [33]. This factor also impedes horticultural practices such as pruning, foliar spraying, pest control and the prevention of diseases, as well as fruit selection. Hence, most cashew orchards are semi-extensive plantations where little or no agricultural practices are employed [15, 28]. Undoubtedly, the use of cashew strains, selected for agronomic traits, including tree size and pollination, would better suit cropping conditions and also attract pollinators to flowers, thus enhance pollination service and net yield per hectare or tree [11].

There have been initiatives to develop productive new cashew strains. An interesting outcome has been the selected clonal dwarf varieties of cashew developed by the Brazilian Agricultural Research Corporation (EMBRAPA). The dwarf varieties, besides being selected to comply with certain market demands, such as the size of the nut and its resistance to breaking during processing, or firmness and sweetness of the pulp, also fit desirable agronomic traits, such as higher yield potential and evenness in size and shape [37–39]. The tree size, 2–4 m tall and 7 m wide, is the main characteristic of the so-called dwarf tree, which allows cashew cultivation and application of all horticultural practices required at each crop stage (see Figure 9.44a).

As a result, the varieties are used in Brazil to establish new orchards, and to replace the canopy of old and unproductive orchards grown from seeds by grafting or simply replanting orchards with the new variety, now being sold to African and Asian countries [6, 7].

Nevertheless, the Brazilian dwarf varieties have a limitation: all strains derive from a single dwarf tree in the early 1970s, and different varieties were selected by inbreeding. Once a variety is established, all propagation is asexual, which results in clone plantlets to populate the orchards, invariably of a single dwarf cashew strain [33]. But because all trees within an orchard belong to the same variety, and are clones, any pollination carried out is technically a form of self-pollen, in which no mixing of different genetic material occurs other than through recombination during meiosis. Although most studies investigating cashew pollination requirements have assumed that cashew flowers set equally via self and cross-pollination [8, 9, 40], current research indicates partial self-incompatibility, which may vary from light to severe, depending on how close the trees are in their genetic composition [11, 41, 42].

Partial self incompatibility in cashew is late acting, as observed in other species of Anacardiaceae such as pistachio (*Pistacia vera* L.) [11]. Such late acting, self-incompatibility, instead of preventing pollen grains from germinating on the stigma or impeding their growth through the style, allows the pollen grains to germinate, and the pollen tube to reach the ovary [41, 42]. In cashew, this happens within 24 hours, but syngamy (fusion of gametes) is delayed for several days. During that period, phytohormones produced by the pollen tube make the ovary swell, and within seven days, after the petals wither, the ovary resembles a small fruitlet. However, no ovule fertilization has taken place, and if self-incompatibility prevents syngamy, no embryo will form inside the ovary. If syngamy occurs but the genetic material of the pollen grain is not compatible, the zygote formed will not develop into an embryo. Thus, in both situations, some nine to 15 days after pollination, when phytohormones produced by pollen tubes are no longer present, the ovary is aborted. If, however, the pollen grains are compatible with the ovary and gamete tissue, syngamy takes place, and the developing embryo resumes phytohormone production [11]. Continued phytohormone production results in fruit maturation and set. Thus, cashew bears a mixed mating system in which cross-pollination (xenogamy) prevails, due to partial self-incompatibility [11, 19, 41]. Such a relatively long period from pollination to fruit set explains the "abortion" of young fruitlets (really not fruit, but swollen ovaries) observed in cashew orchards, and also the fruit drop, usually associated with self-pollination. After that critical stage in early fruit development, fruit develops well and any further drop is not related to pollination, but probably to other causes such as pests or disease.

Therefore, in orchards of a single clonal dwarf cashew variety, all trees are genetically identical, and even though varieties have been selected for high nut productivity, partial self-incompatibility causes lower yield. Furthermore, the pollen viability of some dwarf varieties is as low as 33 percent, approximately one-third the viability of normal-sized cashew trees, probably due to the inbreeding process through which those varieties were developed [16, 33]. As a consequence, production by varieties expected to produce from 1,200 kg nut ha^{-1} (unirrigated) to 5,200 kg nut ha^{-1} (irrigated) barely reaches one-third of those figures [12, 37].

In orchards grown from local seeds, however, the trees are genetically diverse and the incidence of self-incompatible pollination mainly arises from geitonogamy, when pollen grains are transferred to stigmas within the same plant. Although the large size of the plants would favour geitonogamy, in most occasions self-pollen is prevented from fertilizing the ovule, which requires a compatible cross-pollen grain for fruit set [11, 41]. The excess of self-pollen transferred to stigmas may explain why loads of 33 pollen grains or more on an individual stigma are necessary to set a fruit, since cashew needs only one viable cross-pollen grain to fertilize the ovule [16, 21]. Prevalent geitonogamy may not interfere with adequate pollination and nut yield when outcrossing pollinators are present [41]. Therefore, even though plant selection, yield potential and horticultural care are lower in such orchards, for reasons previously explained, some nonetheless display good nut productivity due to conditions favouring adequate out-crossing pollination.

Recommended best practices to mitigate pollination deficit in cashew orchards: Cashew is highly dependent on animal pollination, thus growers should take measures to provide effective pollinators for orchards. Many cashew growers use honeybees (*Apis mellifera* and/or *A. cerana*) for cashew pollination [27, 28] (see Figure 9.46c). Nonetheless, investigations carried out with different crops suggest that native wild pollinators go beyond the pollination benefits provided by such colonies, whether in managed hives or, as now throughout Brazil, feral. The combination of honey bees with other feral bees seems necessary for maximizing crop pollination [31, 32]. Indeed, although honey bees can set cashew fruit and their large number per colony ensure that most flowers are visited, the presence and abundance of wild pollinators further enhances yield [12].

The landscape around and within farms affects the richness of species, abundance and pollination services provided by wild pollinators, and a recent study demonstrates that cashew plantations bordered by small forest fragments (ca. 5 ha) and located less than 1 km from forest of at least 100 ha produce significantly greater nut yield [12]. Large forest areas probably function as wild pollinator "reserves" for small forest fragments surrounding cashew plantations, from where pollinators forage on the cashew flowers. Plantations located more than 1 km from forest do not benefit from local wild pollinators because they are located beyond the normal flight range. Therefore, policies for conservation or restoration of forest areas close to already existing cashew plantations should be implemented (see Figure 9.44b).

Such measures should be implemented on a wide scale, considering the whole district, county, state or even the country. But the mere existence of pollinators close to plantations does not necessarily mean that they will visit the flowers in the cropped area. Farmers must adopt some pollinator-friendly practices to attract and to keep pollinators in the orchards, such as providing nesting sites, water sources, pollen and nectar-producing plant species when cashew is not blooming, and reduce or avoid ploughing and pesticide and herbicide spraying, which are becoming more frequent in agricultural areas that use dwarf strains of cashew. Additionally, many cashew orchards, worldwide, are set in semi-arid regions where rains are scant and trees bloom in months receiving no rain at all. Those plantations usually have no water sources and many pollinators cannot establish unless farmers provide water. In contrast, when cashew is not blooming, most pollinators tend to avoid orchards when searching for food. Thus, the presence of other plant species offering pollen, nectar and other resources in the area are essential to help maintain pollinators nearby, between cashew blooming periods. Tillage should be avoided because many cashew pollinators are ground-nesting bees, and this agricultural practice is extremely damaging for their populations. Finally, pesticide and herbicide spraying are known to be harmful to pollinating insects, with lethal and sub-lethal effects at the individual, colony and population levels [43].

Along with general pollinator-friendly practices, it is important to identify the species of wild cashew pollinators occurring in a region, because some have specific requirements that growers can meet to increase their presence in the area. For example, in Africa, stingless bees are implicated as important cashew pollinators [29]. Those bees have relatively short flight ranges and their presence on flowers in adequate numbers for successful pollination is observed only in orchards where they can nest within or around the plantation, or where hives are introduced for that purpose.

The growers, therefore, must introduce managed nests of the specific stingless bee species or provide adequate nesting sites in and surrounding the orchards (see Chapters 13 and 14).

Another example is oil-collecting bees. In Central and South America and Caribbean countries, some oil-collecting bees have proven to be excellent cashew pollinators, especially bees of the genus *Centris* (see Figure 9.44f). Although the adult bees visit and pollinate cashew flowers while foraging for nectar and pollen, female bees also need to visit oil-flower species to acquire oil, which is used as the energy source for their offspring [44]. Hence, lack of oil-flower species near cashew plantations may prevent large populations of *Centris* species from establishing and visiting flowers in the orchards [30]. Many *Centris* species are ground-nesting or nest in cavities in wood, and it has been demonstrated that lack of adequate nesting sites can impede population growth of such bees within an agricultural area [45]. In summary, cashew growers aiming to attract and maintain the bees should refrain from ploughing suitable areas for bee nest beds, should provide perforated wooden structures (often called "trap nests") as potential nest sites, and plant oil flower species inside or in the vicinity of the plantation. A good strategy could be to cultivate cashew trees in combination with another cash crop that is an oil flower species, such as acerola or West Indian cherry, *Malpighia emarginata* [30]. This approach may provide natural resources needed by bees, which in turn can produce higher yield in both cashew and acerola. In Ghana, nut yields of 1 250 kg/ha are related to high diversity and abundance of native bee pollinators, favoured by the cashew agro-ecosystem adopted there [29].

A virtual monoculture of the single dwarf variety represents the opposite of the above, but is likely to replace the semi-extensive cashew cultivation of low yield output in northeast Brazil. Certainly, the inbred origin and clonal multiplication of the varieties have a role in the low productivity thus far observed, but the main reason seems to be ignorance of the importance of cashew partial self-incompatibility, and the use of only one variety per orchard [11, 19]. In other crops where total or partial variety self-incompatibility are present, such as apple, *Malus domestica*, different varieties (termed "pollenizers") are planted within an orchard in order to ensure cross-pollination between plants belonging to distinct varieties and to maximize yield [15]. The same procedure should be adopted by cashew growers, using at least two dwarf varieties that experimental crossings show are compatible and favour cross pollination. Cashew breeders have been inter-crossing dwarf varieties since they first appeared and know which are compatible or incompatible [37, 46]. Combining such planned orchards with the pollinator-friendly practices presented above would significantly improve the amount and quality of pollination in cashew orchards, and permit higher yield.

Conclusions: Cashew requires insect pollination for fruit set and bees appear to be the major pollinators, although a rich and diverse guild of wild native floral visitors may play an essential role in maximizing nut yield. Most cashew plantations worldwide suffer low crop yields through inadequate pollination, either because agricultural practices reduce pollinator presence during flowering, or because the partially self-incompatible commercial strains are cultivated as single crops. To enhance crop yields, growers should adopt pollinator-friendly practices to improve the diversity and abundance of pollinators in the plantations themselves, which are extensive and also hold the potential, if properly managed, for maintaining local crop pollinators. In association with managed bee populations, such as honey bees or stingless bees, cashew horticulture may be significantly improved.

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GLOSSARY

A

Abiotic
not involving living things

Abortion
dropping of fertilized or unfertilized fruit from the mother plant

Achene
small, one-seeded fruit in which the thin walls are dry

Agamospermy
seed formation without sexual reproduction

Aggregate fruit
consisting of the many separate carpels of one flower

Allogamy
fertilization between pollen and ovules of different flowers

Alternate bearing
fruit bearing on a plant, which fluctuates from high to low in successive years (e.g. kiwi fruit and some apples)

Androdioecy
where male and hermaphrodite genets co-exist

Androecium
male unit or stamens, as a unit of flower

Andromonoecy/andromonecious
a hermaphrodite bears male and hermaphrodite flowers

Anemophily/anemophilous
wind-pollinated; plants that normally shed pollen carried by wind

Angiosperm
flowering plant – a major group of seed plants in which seeds develop within a closed ovary

Anther
part of the floral stamen that normally produces pollen

Anthesis
when flower is fully open and functional

Anthophilous
flower-loving – applied to an animal that can be a pollinator

Apogamety
autonomous development of a nucleus, apart from the egg nucleus into an embryo in an agamosperm

Apomixis/apomictic
non-sexual reproduction of a plant, including both forms in which no seeds are produced (vegetative reproduction) and those in which seeds are produced (agamospermy)

Apospory
elimination of spore formation from the life cycle with the formation of the gametophyte from vegetative tissues, usually the nucellus, not from spore

Archesporium
tissue within the nucellus of a young ovule that gives rise to the embryo sac mother cell, female meiosis and the embryo sac

Aril
network or covering of a seed from the point of seed attachment

Autogamy/autogamous
self-fertilizated (within a flower) without the need of a pollinator

Automixis
fusion of nuclei within the embryo sac

B

Berry
fleshy fruit with skin-like covering, having one to many seeds (but no stone), developed from a single pistil

Biocide
chemical that substantially debilitates or interrupts life cycle, reproduction or poisons a fungus, mite, insect, animal, plant or other living organism – includes miticide, acaricide, fungicide, herbicide, insecticide, germicide, bacteriacide, etc.

Bract
a small leaf or scalelike structure near the base of a flower

Brood parasite
organism feeding on and potentially killing a host organism in its egg, larval or pupal stage

Buzz pollination
pollen collection by a bee using bursts of wing muscle vibration while clinging to the anther— ejecting pollen from the anther apical pore, or shedding pollen from a normal anther

C

CCD
colony collapse disorder, reaction in honey bees to sublethal doses of imidacloprid and clothianidin neonicitinoid pesticide, resulting in dwindling colony size and death during winter; also refers to abrupt disappearance of most adult bees from hive, from multiple or unknown causes

Calyx
sepals or outer whorl of the perianth

Cantharophily/cantharophilous
pollination by beetles

Caprification
pollination of figs with certain tiny wasps (Agaonidae)

Capsule
dry, dehiscent seedpod from a flower with a compound pistil

Carpel
unit formed by ovary within a compound pistil

Catkin
spike or pendulous inflorescence made up of flowers of one sex

Certified seed
progeny of foundation, registered or certified seed, for example *Sweet Gold®* (a registered tomato cultivar) approved by official agency (see also "cultivar")

Chalaza
basal part of an ovule where it is attached to a stalk (funiculus)

Chalazogamy
entry of the pollen tube through the chalaza of the ovule

Chalkbrood
fungus *Ascosphaera* that infects and kills immature bees in open or closed brood cells (for honey bees, this is *A. apis*; *A. aggregata* attacks leafcutting bees)

Chasmogamous
having flowers in which pollination occurs while the flower is open

Chiropterophily/chiropterophilous
pollinated by bats

Cleistogamy/cleistogamous
having flowers that are self-fertilized without opening (opposite of chasmogamous)

Clone
one or more individuals obtained from a single parent by vegetative reproduction (i.e. clone plants are ramets that belong to the same genet)

Comb
bee nest component where eggs are hatched and develop into adults within brood cells; also cells where honey and pollen is stored in nests of *Apis* (honey bee species)

Corbicula/corbiculae
portion of the bee hind leg of certain Apidae on which pollen for brood is carried to the nest

Compatible
capable of producing fertile offspring between plants

Corolla
whole sheath of petals of a flower

Cross
union of different cultivars of the same species

Cross compatible
capable of being fertilized with pollen of a different variety

Cross pollination
pollination in which the pollen is transferred to another flower on a different plant of the same species

Crop fidelity
proportion of bees from a hive that forage only on the target crop

Cultivar
(similar to variety) international name for group of cultivated plants which, when reproduced sexually or asexually, retain their distinguishing characteristics (but are not necessarily a distinctive botanical species)

D

Deceit pollination
flowers offering no food or other reward receive pollinator visits by resembling rewarding flowers

Dehisce/dehiscence
opening of a seed pod or anther and release of contents

Dichogamy
floral condition in which male and female parts mature at different times, preventing self-pollination – in synchronous dichogamy the stamens and pistils reach maturity at different times in definite periods, as in the avocado, *Persea*

Dicliny
separation of sexes among flowers; not all genets in a population are hermaphroditic, such that males, females or both occur

Dioecy/dioecious
having separate sexes and two kinds of genets, such that stamens or male parts and pistils or female parts are on different plants.

Diploid
having a double set of chromosomes, usually one set from each parent

Diplospory
development of an apomictic embryo sac by mitosis or modified meioses of the archesporial cells

Drupe
succulent or fleshy fruit having one seed enclosed in stony endocarp

E

Elaiophore
floral oil-secreting gland

Embryo
rudimentary organism

Embryo sac
female gametophyte of flowering plants contained within ovule, developing from the surviving megaspore after female meiosis, and containing eight nuclei

Embryony
development of an embryo

Endocarp
inner layer of the pericarp

Endosperm
food reserve tissue in a seed, triploid in angiosperms, formed from a fertilizing sperm cell combining with the fused polar nuclei

Entomophily/entomophilous
pollination by insects

Ethephon
commercial horticultural product (2-chloroethyl phosphonic acid) that breaks down to release ethylene gas, which promotes uniform ripening in crops such as coffee, apples, figs, cherries, blueberries and pineapple

Ethylene
gas (C2H2) naturally produced by plants but sometimes applied commercially to induce flowering (pineapple) or increase production of female flowers (cucumber, pumpkin)

Exocarp
outermost layer of the fruit wall

Exserted
protruding beyond the margin of envelope or corolla

Exrareproductive nectary
("extrafloral nectary") a nectary on part of the plant outside of the flower

F

Female flower
one with a stigma and that bears fruit

Fertigation
irrigation with water combined with fertilizer

Fertile
capable of bearing fruit

Fertilization
union of male and female gametes to produce a zygote

Filament
hair-like element of stamen supporting the anther

Floral nectary (reproductive nectary)
nectary within a flower

Floret
one small flower

Flower
much shortened axis (the receptacle) bearing whorls of appendages concerned with reproduction – sepals, petals, stamens and carpels

Fruit
mature ovary with all its parts and adherents

G

Gamete
sexual cell

Geitonogamy
fertilization between pollen and ovules of different flowers on the same genet (plant)

Gametophyte
gamete-producing phase of algae, bryophytes and ferns, displaying alternation of generations; composed of haploid cells only

Genet
genetically individual plant, resulting from a single sexual fusion or zygote, and consisting of one to many ramets

Germination
development of plant from seed

Gynodioecy/gynodioecious
where female and hermaphrodite genets co-exist

Gynoecious
producing only or predominantly pistillate flowers

Gynoecium
female parts, or carpels, of a flower

Gynomonoecy/gynomonoecious
hermaphrodite bears both female and hermaphrodite flowers

H

Haploid
having a single set of chromosomes from a single parent; usually refers to a germ cell or gamete

Herkogamy/herkogamous
separation of anthers and stigma within a flower such that autogamy cannot occur in the absence of a pollinator

Hermaphrodite
(see perfect flower)

Heterogamy/heterogamous
a plant having two or more kinds of flowers

Heterostyly/heterostylous
a genetically determined condition in which stamens and styles come in two or three distinctive lengths, and individual flowers have stigmas and styles of different lengths – thus promoting crossing (e.g. distyly and tristyly)

Hive beetle
Aethina tumida (Nitidulidae), pest of stingless bees and honey bees which consumes brood and pollen in bee nests

Homogamy/homogamous
coincidence of anther dehiscence and stigma receptivity within a flower, so that autogamy is possible if herkogamy does not exist

Honey bee
bee that lives in a colony, has a queen, males and workers, and concentrates nectar, by evaporating water content, to make honey – normally 60-80% sugar; honey-making bees include the "honeybee" or honey bee *Apis* spp., stingless honey bees or stingless bees (Meliponini) and bumblebees, *Bombus* spp.

I

Indehiscent
not splitting open by its valves

Indeterminate
continuing to grow after flowering starts

Inflorescence
flower or group of flowers on a stem

Intersterile
failure to set fruit when flowers are crossed with pollen of certain other cultivars of the same species

L

Legume
one-celled fruit (pod) usually dehiscing down both sutures, and having the seed attached along a ventral suture

Locule
compartment or cell of ovary, anther or fruit

M

Male sterile
flowers lack stamens or viable pollen – commercially developed to increase outcrossing or fruit production by removing male function

Megaspore
in plant species producing two kinds of spores, spore-type that gives rise to female gametophyte

Meiosis
the reduction division of chromosomes, giving rise to two gametes, each with half the chromosomes of the parent cell

Melittophily/melittophilous
pollinated by bees

Mesocarp
the middle layer of pericarp or fruit wall

Micropyle
the pore or hole in the end of an egg through which sperm enters to fertilize the egg

Miticide/Acaracide
chemical biocide applied to rid plants or animals of mites (Acari)

Mitosis
the ordinary changes through which a cell nucleus passes during cell multiplication, producing daughter cells of chromosome number equal to the parent cell

Mixed inflorescence
branched inflorescence with both racemose and cymose components, as in grape and mango, in which the main inflorescence axis is racemose, and the small ultimate branches cymose

Monoecy/monoecious
having separate male and female flowers, but on the same plant

Multiple fruit
fruit consisting of the compressed fleshy fruitlets of the many flowers of a compact inflorescence in which the axis also becomes fleshy, as in pineapple, custard apple and *Monstera*

Myophily/myophilous
pollinated by flies

N

Nectar
sweet liquid produced in the nectary of plant, usually within a flower

Nectar guide
certain highly visible (to insects) ultraviolet-absorbing markings on a flower that guide or direct nectar feeders to nectar

Nectary
plant gland that secretes nectar

Neonicitinoid
neuro-active insecticide chemically similar to nicotine (tobacco plant), relatively harmless to mammals, although the most commonly used pesticide contains imidacloprid, which harms bee colonies (see "CCD")

Nosema
fungus parasite *Nosema* spp., with highly resistant spores, kills adult honey bees and other bees

Nucellus
central body of ovule containing the embryo-sac, which acts as a nurse to the archesporium

O

Oosphere
the unfertilized female gamete

Ornithophily/ornithophilous
pollinated by birds

Outcrossing
sexual reproduction between different genets, usually plants that are different individuals

Ovary
seedcase or part of the pistil, bearing ovules that develop into seed or fruit

Overbearing
excessive fruit production that damages the plant (breakage or mortality) or diminishes size and commercial quality of individual fruit

Ovule
structure that contains egg nucleus and develops into seed after fertilization of the egg cell within

P

Panicle
inflorescence with the main axis branched into an open racemose flower cluster

Papilionoceous
butterflylike, pealike flowers, with a large upper petal, two lateral wing petals, and two small united keel petals

Papillae
specialized epidermal cells of the stigma that receive the pollen grains

Parthenogenesis
production of new individuals from unfertilized egg cells

Parthenocarpy/parthenocarpic
development of a fruit without fertilization and therefore without seeds – as in navel orange, some figs, seedless grapes, pineapple and banana

Pedicel
stalk or stem of individual flower of inflorescence

Peduncle
primary flower stalk of an inflorescence

Perfect flower
bisexual or hermaphroditic; a flower having both stamens and pistil

Perianth
entire floral envelope including both corolla and calyx

Pericarp
ovary or fruit wall

Perisperm
storage tissue similar to the endosperm, but formed from the nucellus

Pesticide
chemical product used to remove unwanted plants, animals, fungi or other organisms (see also "biocide")

Petal
leaf or unit of a usually colored corolla or inner floral envelope

Petiole
leaf-stalk

Phorid fly
(Phoridae *Neohypocephala* and other genera) pest of stingless bees and honey bees, larvae consume brood and stored pollen, often killing colony

Pistil
normally central, seed-producing part of flower; usually consisting of ovary, style and stigma

Pistiilate
having pistils but no stamens

Placenta
surface or tissue part of ovary to which ovules become attached

Plant growth hormone
natural plant hormone used commercially to induce or improve seed and fruit production, including cytokinin, gibberellin, ethylene and auxin

Plant growth regulator
synthetic or natural plant hormone or non-nutrient chemical that influences growth and development, including 4-chlorophenoxy-acetic CID (4-CPA), similar to 2,4-D, used commercially to increase flowering and fruit set; another example is synthetic auxin naphthaleneacetic acid, used commercially to prevent fruit drop

Pollen
powdery grains produced by angiosperm anthers or microsporangia of gymnosperms, which contain the nucleus that fertilizes the oosphere to form a seed

Pollen robber
animal that damages the anther or its protective surrounding tissue to remove pollen, and does not contact the stigma

Pollen thief
animal that removes pollen without having contact with the stigma

Pollen tube
thin tubular outgrowth of pollen grain usually upon contact with stigma, and which penetrates style to ovary, permitting sperm nuclei to unite with egg cell

Pollenizer
plant source of compatible pollen for fertilizing receptive stigmas

Pollenkitt
outermost, pigmented oily layer of pollen grain

Pollinarium
in orchids and asclepiads, structure detached from the flower, bearing sacs of pollen grains, united to an adhesive disc that attaches to the pollinator

Pollinating
transferring pollen from anther to stigma

Pollination
placement of pollen on a stigma, the first step in fertilization

Pollination deficit
capacity for greater fruit and seed production (in a single season) with augmented pollination

Pollinator
animal that moves compatible pollen to a receptive stigma of the same plant species, such that fertilization and seed production can occur

Pod
monocarpellary fruit that dehisces down both sutures

Polyembryony
with more than one embryo in a fertilized ovule (e.g. mango)

Polygamy/polygamous
having both perfect (hermaphrodite) flowers and those of one sex (staminate or pistillate)

Polyembryonic
presence of more than one embryo in a fertilized ovule, formed adventitiously from the nucellus, for example mango (*Mangifera*)

Pome
fleshy fruit derived from several carpels, the receptacle and outer pericarp being fleshy, and the inner pericarp, papery

Poricidal
anther dehiscence occurs through an apical pore

Porogamy
entry of the pollen tube into the ovule via the micropyle

Proboscis/proboscides
tube-like or spongy feeding structure used by an insect to imbibe nectar or liquid

Protogynous-dichogamous
condition in which stigma receptivity precedes anther dehiscence within flower

Protandry/protandrous
flower in which anthers mature and release pollen before stigma is receptive

Protogyny/protogynous
flower in which the stigma is receptive before anthers release pollen

PSP
pollination service provider — a technical support service, soon to include more than *Megachile, Osmia, Tetragonula, Plebeia, Scaptotrigona, Apis, Melipona, Tetragonisca, Xylocopa* or *Trigonisca*

Psychophily/psychophilous
pollinated by butterflies and moths

R

Raceme
unbranched inflorescence

Ramet
physiologically independent individual (from one to many may compose a genet)

Receptacle
enlarged end of pedicel to which one or more flowers attached

Recruitment
behavioural process whereby foraging bee alerts/guides other workers of colony to field resource

Reproductives
among bees or social insects – males and queens (see also "workers")

Robbing
in pollination ecology, the destruction of at least part of a flower to obtain nectar, pollen or another resource

Roundup Ready™
glyphosate herbicide tolerant, usually applied to crops modified genetically by inserting a fish gene, making their seed produce plants tolerant of the specific herbicide

S

Scopa/scopae
portion of the body, usually rows of branched hairs on the abdomen or hindlegs, where female bees carry pollen for brood

Seed
fertilized and matured ovule or rudimentary plant, usually with [orchids have none- need symbiotic fungi...] food necessary for its germination

Self-compatible
a plant capable of being fertilized by pollen within its own group of flowers or genet

Self-fertile/self-fertilizing
a flower or floret capable of being fertilized by its own pollen

Selfing
fertilization of an ovule by a pollen grain of the same genet

Self pollinating
(autogamous) capable of placing its own pollen upon its own stigma; sometimes called "spontaneous pollination"

Self sterile
incapable of becoming fertilized by its own pollen

Semi compatibility
where two genets share some but not all gametophytic compatability traits, thus in some crosses some pollen grains can effect fertilization and others cannot

Sepal
the outermost part of flower, the parts of which form the calyx

Sessile
sitting, lacking a stalk or petiole

Sexual reproduction
reproduction through union of male and female gametes (as opposed to vegetative reproduction)

Social bee
a bee having females sharing a nest, either mutually tolerating the others or sharing a nesting site and material, with highly advanced or "eusocial behavior" involving a reproductive division of labour and overlap of generations (mother and daughter in the same nest)

Solitary bee
a bee completing its life cycle by emerging from a cell in a nest, then feeding and mating, after which the female constructs and provisions a new nest and produces brood there

Sonication
(see "buzz pollination")

Spadix
the fleshy axis of certain inflorescences, such as those of arum lilies, bearing the small flowers or florets

Spathe
a large bract enclosing the flower cluster

Spike
an inflorescence with elongated main axis and sessile flowers

Sporangium
a spore-producing organ

Sporophyte
the spore-producing, diploid phase of a species displaying alternation of generations

Stamen
the male part of a flower consisting of a filaments and anthers

Staminate
being entirely male, bearing only stamens

Staminode
an abortive stamen

Standard
a large upper petal of a papilionaceous legume flower

Stem
main axis of a plant

Sterile
barren, unfruitful, incapable of being fertilized

Stigma
receptive portion of the female sexual column

Style
part of the sexual column between the ovary and stigma

Syconium
multiple fruit of a fig in which the edible receptacle (flower axis) is hollow and lined on the inside with numerous fruitlets and seeds

T

Thievery
in pollination ecology, removal of a floral reward by an animal, where pollination does not follow as a result (as opposed to robbing)

Triocey
where co-existing genets are male only, female only, and hermaphrodite (complete polygamy)

Tripping
release of sexual column in legume flowers

Tuber
swollen end of an underground stem containing food reserves

U

Unisexual/imperfect flowers
flowers in which either stamens or pistils are functional, the non-functional member may be completely lacking

V

Varroa
mite genus responsible for parasitism of honey bee brood; genera *Varroa* and *Euvarroa* are similar

Vegetative reproduction
asexual reproduction (see apomixis)

Visitor
all animals visiting a flower, but not necessarily a pollinator which enhances plant reproduction

W

Worker
in social insects, individual that cannot mate or produce diploid (female) offspring

X

Xenogamy
fertilization between pollen and ovules between different genets

Z

Zoophily
pollinated by animals

Zygote
product of the two gametes or germ cells

THE POLLINATION OF CULTIVATED PLANTS

A COMPENDIUM FOR PRACTITIONERS

Volume 1

More than twenty years ago, the Food and Agriculture Organization of the United Nations contributed to the growing recognition of the role of pollination in agricultural production, with the publication of "The Pollination of Cultivated Plants in the Tropics". Since that time, the appreciation of pollinators has grown, alongside the realization that we stand to lose them. But our knowledge and understanding of crop pollination, pollinator biology, and best management practices has also expanded over this time.

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ISBN 978-92-5-130512-6

9 789251 305126
I9201EN/1/04.18