BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Promoting pollination and pollinators in farming

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Contents

Introduction

It has been reported that up to 95% of all flowering plants require the services of other organisms to move pollen from male to female flower parts during the pollination process. These organisms, including bees, are collectively known as pollinators. However, in light of the growing evidence of global declines in pollinator species, the management, ecology and conservation of wild and managed pollinators is a subject of growing importance and research activity.

This volume reviews the wealth of research on our current understanding of existing pollination processes and their importance to our global ecosystems. The book considers how pollinators interact with plants, as well as the major threats to pollinator species, including climate change, diseases and pesticide exposure. The book is split into three parts: Part 1 chapters focus on understanding pollinators and pollination, focusing specifically on their role in agriculture, the role and application of olfaction and the use of wind pollination in crop plants. Chapters in Part 2 examine the various threats to pollinators, such as the impact of climate change, disease, the use of neonicotinoid insecticides and pesticides as well as the impact of alien bees on native ones. Part 3 chapters review promoting pollinators and pollination, focusing specifically on the role of habitat conservation and restoration, the alteration of crop management practices and the use of ecological network approaches. Chapters also highlight best management practices for pollinator protection, focusing specifically on US apple production and the use of entomovectoring technology.

Part 1 Understanding pollinators and pollination

The first chapter of this volume provides an overview of what pollination is and the role of pollinators in agriculture. Chapter 1 begins by discussing the basics of pollination and goes on to discuss pollinators and their diversity. The chapter moves on to review the ecology and evolution of floral traits, focusing specifically on the origins of flowering plants and their relationship with pollinators, floral traits and the ecology of pollination as well as the co-evolution of plants and pollinators. A section on domestication and its impact on plant-pollinator relationships is also provided, which is then followed by an analysis of how pollinators impact agriculture and how pollinators are present in modern agriculture practices.

The next chapter examines the role and application of olfaction in crop plant-pollinator interactions. Chapter 2 introduces the background and theory underpinning the use of odours by insects in pollinators. It discusses how flowers produce odours and highlights issues specific to crops such as selective breeding. It then explores current technologies and case studies in which natural or synthetic odours on or near the crop, and the interaction with insects, influences visitation, pollination success and yield.

Chapter 3 reviews the role of wind pollination in crop plants. This chapter reflects on the early transition from wind-pollinated species (especially Poaceae) into crop species and the current state of wind-pollination in agricultural pollination networks. It then provides a short review of the evolution and biomechanics of wind pollination to establish why humans moved away from open pollination. A more deep exploration of the relative importance (or lack thereof) in crops such Zea, Triticum, Oryza, and Secale follows, as does a focus on the extant risk of heterospecific pollen transfer to wind-pollinated weeds. The chapter also discusses the role of anthropogenic climate change on wind-pollinated crops and the future and relative importance of wind-pollination in widespread and niche crops. The chapter ends with a case study of how one might create a 'win-win' in terms of conservation and restoration of natural habitats to promote wind-pollination in farming.

Part 2 Threats to pollinators

Part 2 opens with a chapter that focuses on assessing the impacts of climate change on pollinators. Chapter 4 first presents an overview of observed and predicted impacts of climate change on pollinators, focusing on elements such as rising temperatures, loss of habitat, temporal and spatial mismatches between plants and pollinators and extreme events. The chapter also highlights the effect climate change has on pollinator cues, factors that may mediate species' responses, including synergisms with other threatening processes. A section emphasising the importance of understanding climate change impacts on pollinators is also provided, which is then followed by a section presenting a number of ways in which we can help pollinators face the challenge of climate change.

Chapter 5 looks at the impact of diseases on pollinators. The chapter first provides an analysis of various honey bee diseases, focusing specifically on ectoparasitic mites, viruses, fungi, bacteria, trypanosomes and common pests such as the small hive beetle and wax moths. It also discusses how disease impact on honey bee colonies and pollination can be measured. A section on the poorly known wild bee diseases is also provided, discussing the major known pests and pathogens of both bumble bees and other solitary bee species. The chapter reviews disease transmission, spillover and spillback in all three pollinator taxa as well as some of the current methods and approaches for controlling pests and pathogens.

The next chapter focuses on how neonicotinoid insecticides affect bees and other pollinators. Chapter 6 discusses the wide range of research on how neonicotinoids affect both managed and wild bee populations in particular. It reviews levels of environmental contamination and how this affects topical and oral exposure routes. The chapter also addresses sublethal effects and briefly discusses the interaction of different stressors. It includes a number of case studies showing the negative effects of neonicotinoids on a range of bee species.

Moving on from Chapter 6, Chapter 7 examines the impact of pesticides on pollinators. The chapter begins by providing an overview of the origins of bee testing and risk assessment, then moves on to discuss the testing of pesticide effects in pollinators, drawing attention to species testing, testing methodologies and designs and guidelines and risk assessment guidance documents. The chapter also examines test method development and validation and highlights the principles of Good Laboratory Practice. A section on the ecotoxicological risk assessment for pollinators is included, which is then followed by an analysis of both the indirect and sublethal effects of pesticides. Risk mitigation and pesticide incident monitoring are also discussed.

The final chapter of Part 2 reviews the impact of alien bees on native ones. Chapter 8 explores the main impacts of alien bees on native bees through competition for food or nesting resources, interference, pathogen spillover and genetic contamination. Implications for native bee conservation are also discussed. In addition, in this chapter, a particular focus on the first alien bee that colonised Europe, *Megachile sculpturalis* is also emphasised. The chapter also highlights the main knowledge gaps and important trends for future research. Finally, avenues for managing alien bee species and preventing their introduction are provided.

Part 3 Promoting pollinators and pollination

Chapter 9 focuses on challenges and options in habitat restoration for solitary bees which account for 90% of bee species. As well as being important parts of local ecosystems, these species are pollinators of a wide range of crops such as alfalfa, tomato, eggplant and blueberries, cucurbit crops (such as pumpkin, squash and watermelon) as well as orchard crops such as almonds and cherries. The chapter looks at challenges facing habitat restoration and research on the effectiveness of existing restoration projects. The chapter also includes case studies on commercial management of Alkali bees, promoting stem or cavity-nesting bees and providing underground nesting boxes for bumblebees.

The next chapter of Part 2 draws attention to the alteration of crop management practices to promote pollinators. Chapter 10 begins by introducing the current approaches that are currently used when it comes to managing production space for pollinators within the context of various cropping systems, such as row crops, specialty crops, perennial orchards and perennial forage and pasture systems. The chapter then goes on to provide several case studies demonstrating these approaches, drawing specific attention to annual row and specialty crop systems as well as perennial orchard and forage systems. Assessing the efficacy of alternative agronomic practices is also discussed.

The subject of Chapter 11 is the use of ecological network approaches for promoting pollinators in agriculture. The chapter begins by describing the important and agriculturally relevant characteristics and structures in plant-pollinator networks. It then moves on to examine the use of ecological networks at the field, farm, landscape and national scale. The chapter also highlights the importance of filling in major gaps in pollinator networks. A section on embedding pollination within wider agroecosystem networks is also provided, which is followed by an analysis of the potential next steps for pollination network research.

Chapter 12 describes a set of pollinator best management practices (BMPs) for US apple production. It first provides an overview of apple orchard pollinators, drawing specific attention to ground nesting bees, mason bees, small carpenter bees and wild bumble bee queens. The chapter moves on to provide an overview of the various pests and diseases that can affect apple production. This is then followed by a section that highlights the potential hazards to pollinators from apple pest management practices. The chapter also examines best management practices to promote pollinators as well as the use of integrated pest and pollinator management and pesticide application to manage apple pests and diseases.

The final chapter of the book focuses on using pollinators to spread biocontrol agents via the use of entomovectoring technology. Chapter 13 first highlights the factors that are important for successful entomovectoring, such as the type of vector, the dispenser, the biocontrol agent product and biosafety. The chapter moves on to provide successful and failed attempts at using bumble bees as vectors for entomovectoring. This section is then followed by a case study that focuses on entomovectoring (also known as apivectoring) of microbial biological control agents by *Bombus* spp., especially *B. terrestris*, against grey mould *Botrytis cinerea* and other pests in strawberry production, drawing specific attention to the importance of tackling and controlling *Botrytis cinerea* infection in strawberries.

Acknowledgement

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- Cover image: A male hoary squash bee on staminate pumpkin flower. 2011. © Sheila Macleod Potter.

Chapter 1

What is pollination and what are pollinators in agriculture?

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1 Introduction

The Altamira cave system in northern Spain is renowned for the contemporary depictions of Paleolithic life that adorn its walls in vivid blacks, reds, and ochres. But tucked away from the main chamber's iconic herds of bison is an inconspicuous painting in an unassuming side chamber. It depicts a gangly human figure climbing a winding structure – most likely, a ladder. At the upper end of the ladder are four thick, overlapping arches nested within each other, surrounded by thin winged figures – the nest of a wild honey bee colony, and the bees themselves. This painting at Altamira, dated 13 500 years old, is a prehistoric account of beekeeping – the oldest one known to this day (Crane, 1999). Similar paintings depicting ladders, bees' nests, and bees are found in prehistoric art across the world: primarily in South Africa, but also in Australia, India, France, and Spain (Crane, 1986). They are a testament that even in the earliest chapters of human history, humankind has relied on the activities of pollinators.

Honey bees, their flower-visiting habits, and their industrious honey-making skills have undoubtedly been appreciated by the humans of the ancient world, appearing in Aristotle's *History of Animals*, Virgil's *Georgics*,

http://dx.doi.org/10.19103/AS.2022.0111.01

and the Old Testament. The Romans and Greeks were well aware of the importance of pollination in the production of date palms (*Ficus carica*); the polymath Theophrastus (c 371–287 BC) described the plant's 'male and female' flowers and the necessity of a 'union' between two flower types for the trees to bear fruit. But it was only much later, in the late seventeenth century, that Rudolf Jakob Camerarius (1665–1721) observed that male anthers and female stigmas were prerequisites to plant reproduction. His work was built upon by the investigations of several botanists, including Bradley (1731), Miller (1724), and Vaillant (1718); by the early eighteenth century, it was widely accepted that pollen, known as the *Farina Fecundens*, was the mode of sexual transmission of plants.

The work of Kölreuter (1733–1806) was fundamental in establishing the importance of insect vectors in the transport of pollen, the structure and mechanism of pollen, and the role of nectar in attracting pollinators. Sprengel (1750–1816) further examined the structure and function of flower parts, describing in detail a diversity of floral adaptations involved in attracting pollinators. Darwin's (1809–1882) publication of *The Origin of Species* and his studies on pollination mechanisms (notably his work with orchids) were followed by a surge of interest in pollination; this included Hermann Müller's (1829–1883) and Federico Delpino's (1868–1875) investigations into a myriad of plant–pollinator systems and Knuth's seminal Handbook of Flower Pollination series (Knuth 1906–1909). With the twentieth century came the advent of genetics, the discovery of DNA, and an explosion of interest in plant ecology. Such discoveries shifted the study of pollination toward understanding the molecular mechanisms, evolutionary history, and interspecies relationships that govern pollination. There are countless contributors to this recent era of pollination studies, in addition to others that were crucial in the discovery of pollination and its basic mechanisms. Their work is beyond the scope of this brief introduction; for further reading, Proctor (1996a) provides a comprehensive summary.

2 The basics of pollination

Pollination is a key first step in plant reproduction. But to understand pollination, one must first be familiar with how pollen is produced. Pertinent floral structures are shown in Fig. 1. The *corolla*, which is the shape and structure formed by a flower's petals, serves chiefly to attract pollinators. The *calyx* (or sepals) protects the flower in the bud and serves as a structural support for the corolla. The *androecium* (or *stamens*) are the male reproductive structures of flowers consisting of *anthers* that each rest atop a structural *filament*. The *gynoecium* is the collective female reproductive structure comprised of individual *stigmas* resting upon a *style* that connects to the *ovary*, where the flower's *ovules* reside.

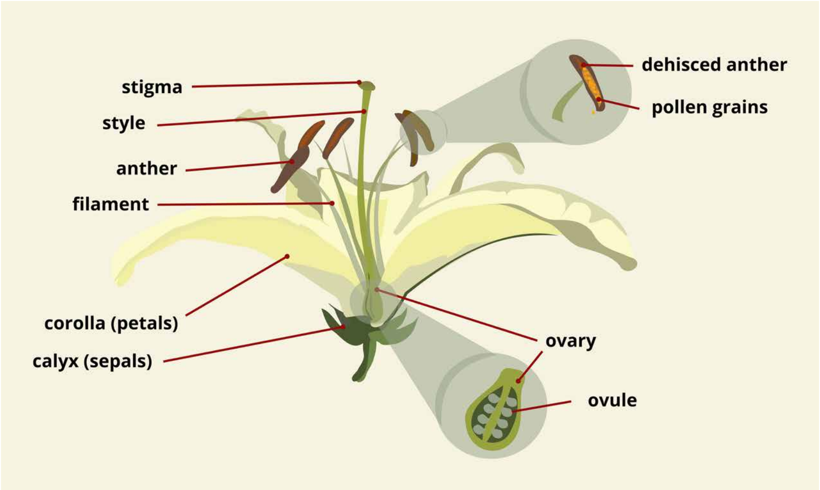

Figure 1 Cross-section of a mature flower and its components.

The anthers are the site of pollen production. At maturity, the inner cells of the anther undergo meiosis to produce individual pollen grains. The outer layers of the anthers then split open, or *dehisce*, to release pollen. Appearing as a powdery, fine substance to the naked eye, pollen is made up of microscopic grains, each surrounded by an outer wall, or *exine*, that gives the grains their distinct shape and rigidity. The aid of a microscope will reveal that the pollen exines are covered in pores. An inner wall of cellulose and pectin, known as an *intine*, further protects the interior of the grain, which contains the gametes in the form of a *generative nucleus* and a supplemental *vegetative nucleus*.

Pollination is simply the transfer of pollen from the anthers of the androecium to the stigmas of the gynoecium. Following pollination is *fertilization*, which begins as the pollen grain attaches to the stigma, imbibes water, and *germinates* to form a pollen tube that penetrates the stigma's tissue and carves a path through the *style* to ovules in the *ovary*. The grain's vegetative nucleus moves through the newly formed tube, mediating the movement of the generative nucleus (Zhou and Meier, 2014), which has now divided into two separate male *gametes*. Upon arrival at the ovule, the vegetative nucleus dissolves, and one of the male gametes fuses with the egg to form a diploid embryo. The second male gamete fuses with a *diploid fusion nucleus* in the ovary, forming the endosperm that provides nutrients for the newly formed seed.

In angiosperms (flowering plants), most species bear hermaphrodite *perfect* flowers, containing both pollen-producing and ovule-bearing structures. An obvious consequence of this hermaphroditism is *autogamy*, the self-fertilization of a flower by its own pollen. Plants may also self-fertilize through *geitonogamy*, the fertilization of a flower by the pollen of another flower on the same plant. About 20% of angiosperms reproduce predominantly by self-fertilization (Barrett, 2003), and many plants reproduce through self-fertilization to some degree (Barrett, 2003; Goodwillie et al., 2005; Charlesworth, 2006; but see Lande and Schemske, 1985; Igić and Kohn, 2006). Self-fertilization grants the advantage of guaranteed reproduction, especially in environments where mates or pollinators are scarce (Kalisz et al., 2004; Aizen and Harder, 2007; reviewed in Busch and Delph, 2012).

The alternative reproductive strategy is *outcrossing*, fertilization with non-self-pollen. Darwin (1877) wrote that '[Nature] abhors perpetual self-fertilization'. Although inbreeding depression – the reduced survival and fertility of inbred offspring – is surprisingly uncommon in predominantly selfing plants (Husband and Schemske, 1996), self-fertilization is disadvantageous to outcrossing when considering gene flow, genetic variability, and diversification of plant lineages (Goldberg et al., 2010). Outcrossing plants employ mechanisms to minimize self-fertilization (Barrett, 2003). A common anti-selfing mechanism in plants is the spatial (*herkogamy*) and temporal (*dichogamy*) separation of pollen and stigma. In herkogamy, the anthers and stigma are physically separate, such that pollen cannot be passively transferred to the stigma. In dichogamy, the anthers mature asynchronously with the receptive period of the stigmas. Rather than relying on spatio-temporal separation, some plants separate anthers and stigmas into unisexual *imperfect flowers*, which can be a more effective mechanism to avoid self-fertilization. *Monoecious* plants bear both male and female imperfect flowers on the same plant (Fig. 2b); the plants are still hermaphroditic and may self-fertilize. Monoecious crops include corn, oil palms, and members of the Cucurbitaceae family (e.g. melons, pumpkins, cucumbers, and zucchini). *Dioecious* plants only bear flowers of one sex and must rely on a plant with opposite-sexed flowers to reproduce (Fig. 2c) – in this way, dioecy is the only mechanism that fully prevents self-fertilization. Dioecious crops are uncommon; some examples are asparagus, kiwi fruit, and hops. Finally, plants may prevent self-fertilization through *self-incompatibility*, a variety of biochemical barriers to the fertilization process. The mechanisms governing self-incompatibility vary widely across taxa; Glover (2014) provides a review. One mechanism of self-incompatibility is evident to many humans across the globe: the allergic response to pollen, commonly known as hay fever, is caused by self-incompatibility proteins that coat the pollen grain surfaces of some plant species (Proctor, 1996b).

Pollination vectors transport pollen from anthers to stigmas. Pollen transfer can be achieved abiotically, through wind (anemophily) or water (hydrophily). The vast majority of abiotically pollinated plants are anemophilous (Ackerman, 2000), with nearly all gymnosperms (Faegri and van der Pijl, 1979) and 10% of all flowering plants transporting their pollen through the wind (Friedman

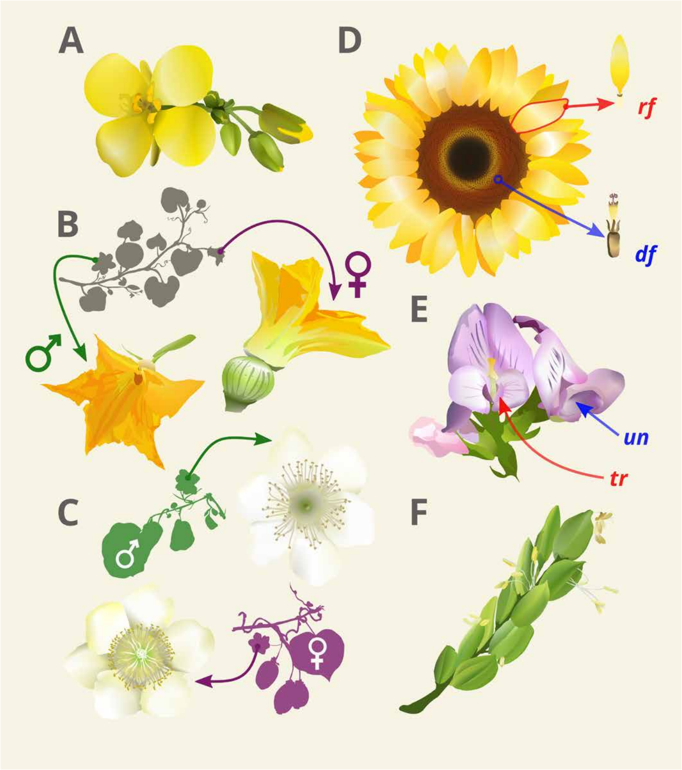

Figure 2 Floral traits and reproductive systems vary widely across plant taxa, including crop plants. (A) *Brassica napus*. The oilseed rape has bright, four-petalled flowers with four prominent anthers and two shorter anthers. Most other *Brassica* crops (e.g. kale, turnips, and bok choy) display similar four-petalled, yellow flowers. (B) *Cucurbita pepo*. Cucurbit crops, such as squash, pumpkin, melons, and cucumber, are monoecious. Individual plants produce both pollen-producing male flowers and stigma-bearing female flowers. On female flowers, the stigma and style connect to the developing fruit at the flower's base. (C) *Actinidia deliciosa*. Kiwifruit vines are dioecious, with male and female flowers occurring on separate plants. The male flowers bear numerous showy anthers. Prominently displayed in the centers of female flowers are fertile stigmas surrounded by a crown of sterile 'false anthers'. (D) The floral head, or *capitulum*, of a sunflower, *Helianthus annus*, is made up of many small ray florets (*rf*), with yellow petals surrounding a head of disk florets (*df*). Composite flower heads are characteristic in Asteraceae plants. (E) *Medicago sativa*. The complex flowers of alfalfa are wholly reliant on pollinators. The flowers' stigmas and anthers are sprung up inside two 'keel petals.' When a bee lands on the keel petal, it 'trips' the flower and the reproductive structures are explosively unfurled, releasing pollen. In the untripped flower (*un*), the intact keel petals enclose the reproductive structures. The exposed stigma and a remaining keel petal are visible on the tripped flower (*tr*). (F) *Oryza sativa*. Most major cereal crops, like rice shown here, are either self- or wind-pollinated. Characteristic of Poaceae plants: the inflorescence of rice bears dull, inconspicuous florets with many anthers.

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