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Note:

How can an understanding of plant-pollinator interactions contribute to global food security?

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Abstract

Pollination of crops by animals is an essential part of global food production, but evidence suggests that wild pollinator populations may be declining while a number of problems are besetting managed honey bee colonies. Animal-pollinated crops grown today, bred in an environment where pollination was less likely to limit fruit set, are often suboptimal in attracting and sustaining their pollinator populations. Research into plant-pollinator interactions is often conducted in a curiosity-driven, ecological framework, but may inform breeding and biotechnological approaches to enhance pollinator attraction and crop yield. In this article we review key topics in current plant-pollinator research that have potential roles in future crop breeding for enhanced global food security.

1. Introduction

Pollination of crops by insects and vertebrates is an essential part of global food production. Recent reports have estimated that 35% of global crop yield depends on the activity of animal pollinators [1]. Yet, at the same time, evidence has started to accumulate that wild pollinator populations may be declining, while a number of different biotic and abiotic problems are besetting managed honey bee colonies [2]. In light of these two statements it is clear that pollination biology has a large, and increasingly urgent, role to play in protecting and maintaining global food supply. Crop breeding programmes select for agronomic traits such as yield or disease resistance [3]. Therefore, it is highly likely that insect-pollinated crops grown today, bred in an environment where pollinators were more abundant and pollination was less likely to limit fruit set, are suboptimal in terms of their floral traits with respect to attracting and sustaining their pollinator populations. Our aim in this article is to review a range of aspects of plant-pollinator research that have potential utility for crop breeders, and to highlight areas of the field where increased research effort might yield important agronomic improvements.

2. Pollinators and crop production

While wind-pollinated cereals still account for the majority of calories produced worldwide for human consumption, crop dependence on animal pollinators is increasing, and at a greater rate than honey bee colony production [4]. Around 75 % of the 115 highest producing crops worldwide benefit from greater yields when pollinated by animals, mainly bees [1] (Figure 1), with brazil nut, watermelon, cantaloupe, *Cucurbita* spp., cocoa, and vanilla the most pollinator-dependent of these [5]. Pollinators can also improve the quality of crops [6] and the nutritional value of pollinator dependent crops is perhaps even more important than their economic value. Pollinator-dependent crop production of vital micronutrients accounts for a large proportion of total production in many areas; for example the reliance on pollinators for vitamin A is close to 50% in Thailand [7].

Research over the past few decades has documented declines in both wild pollinator populations and the abundance and health of managed honey bee hives. These two issues are largely separate, though have become conflated in the popular media [8]. “Colony collapse disorder”, parasites such as varroa, and, more recently, neonicotinoid pesticides have all been implicated in the reduction of the number of honey bee hives at a regional level, particularly in Europe and North America [9-11]. In contrast, the loss of diversity and abundance of wild pollinators such as social bumblebees, solitary bees, hoverflies, wasps and butterflies has mainly been attributed to changes in land use and reduction in the area of habitat available for foraging and life cycle completion, [12-14] a process, which in the UK at least, has deep historical roots [15**].

The relative importance of honey bees and wild pollinators for agriculture depends upon both the crop and local management practices; in the UK and parts of the USA it is thought that wild pollinators are responsible for the large majority of crop pollination [16,17]. Wild bees have also been shown to improve fruit set in a wide variety of crop systems, independent of the abundance of honey bees [18**]. This implies that future habitat conservation efforts, particularly at a landscape scale, could provide both immediate and long-term benefits to agriculture in the form of locally enhanced crop production and insurance against fluctuations in wild pollinator abundance. Examples of such efforts are enhanced agri-environmental schemes on farms and appropriate restoration of post-industrial areas, including landfill sites [19,20]. There is some evidence that conservation programmes in northern Europe may have slowed the rate of decline of some pollinators, but more research is required to substantiate this trend [15**,21**].

3. Plant-pollinator interaction research with implications for food security

a. Crops as a resource for pollinators

Insect-pollinated crops can provide a substantial nutritional resource to pollinator communities, which may help maintain their populations over generations. Mass flowering crops such as oilseed rape/canola (*Brassica napus*) are of particular interest in this respect as they provide a bonanza of food for pollinators [22]. However, because this reward is transient, the benefits to pollinators have been found to be species specific and dependent on timing [23-26*]. Phenological matching of crop flowering and pollinator activity could result in a two-fold benefit, improving the reproductive potential of pollinators and promoting more efficient pollination of crops both in current and subsequent years.

In the example of oilseed rape, key lifecycle stages of the red mason bee *Osmia bicornis* (a solitary bee) occur concurrently with flowering, leading to increased reproductive success for the bees [25,26*]. Contrastingly, for bumblebees (*Bombus* spp.), while the temporary increase in resources that early flowering oilseed rape provides may help colony founding [22,24,27], a lack of food later in the season can lead to this not translating into an increase in the number of queens and males [24]. This can be resolved by complementing early flowering crops with late flowering crops in adjacent fields, or strips of semi-natural flower-rich vegetation, ensuring a stable foraging supply over a longer period [28,29]. An alternative approach would be to coordinate crop flowering with key life cycle stages for pollinators, by breeding for different flowering times as appropriate. In crops such as oilseed rape and the field bean (*Vicia faba*) QTLs for both flowering time and duration have been identified and the molecular basis of these traits is well defined [30-32].

b. Exploiting multiple pollinators

The ability of flowering plants to utilize multiple pollinators can be beneficial in ensuring fruit set. The majority of flowering plants engage in flexible relationships with their pollinators that are variable within populations, and over both time and space [33]. This variability can be at the level of species within broad taxonomic/functional groups (e.g. use of different large bee species) or use of pollinators from very different groups (e.g. bees and birds, or butterflies and bees). Much of this flexibility depends upon the local ecological context in which a plant finds itself [33-35].

This also applies to most crop plants, where the effective pollinators will be determined by the plant's floral biology and the locality, season and year in which it is planted. For example, in manipulative caged plant experiments it was shown that various bumblebees are the main pollinators of field beans, with honey bees (*Apis mellifera*) and red mason bees playing a secondary role; in contrast the same groups plus hoverflies (*Episyrphus balteatus*) are equally good at pollinating oilseed rape [36]. Under field conditions, the importance of these different groups will depend upon their visitation rate to flowers, which is largely determined by their abundance, which will fluctuate over time and space. These findings probably apply to the majority of crops grown worldwide as most are relatively generalised in their interactions with local and managed pollinators.

Looking at which floral traits change in response to different groups of pollinators over the course of evolution may provide insights into which traits would be useful to target in breeding programmes to improve pollinator visitation. If a floral trait changes repeatedly in a phylogenetic context it is available for selection to target. However, if a floral trait is fixed, either no genetic variability is present, or else the trait is constrained by its developmental or functional basis. For example, flower colour is a trait with astonishing lability over evolutionary time and the potential to discriminate between pollinator types. Multiple evolutionary shifts from hummingbird to moth pollination in *Aquilegia* have been associated with independent losses of anthocyanin production [37]. The molecular basis of many such shifts is attributable to changes in the transcription factors that regulate the pigment synthetic pathway (reviewed by [38]), and similar changes can cause variations in the pattern of floral pigment, generating spots, veins and other nectar guides that are differentially used by different pollinators [39,40*,41]. However changing a single trait such as flower colour alone is unlikely to affect the type and diversity of pollinators to a crop because it must be backed up by a change in the quality or quantity of the reward being offered, and its accessibility to particular pollinators.

c. Attracting more of whatever pollinators there are

From the pollinator's perspective, it may be a floral trait's utility as an indicator of reward rather than its inherent attractiveness that is most important (e.g. [42,43**]). The importance of honest signals for foraging decisions of bees was recently demonstrated by Knauer and Schiestl [43**] who showed that bumblebees specifically selected for a volatile signal which correlated with floral reward in *Brassica rapa*. Floral scent may be particularly useful for pollinators as an honest trait [44], although the most honest traits are those physically linked to the reward itself [45].

In order to successfully utilise floral traits for crop improvement, it is important to understand how they attract pollinators. Recent experiments with volatile cues have highlighted the complexity of their function. Experimentally augmenting floral scent increased pollinator attraction for *Hesperis matronalis* [46], but only with specific components of its floral bouquet. In contrast, a similar experiment with *Curcurbita pepo* had no effect on pollinators but increased visits from florivores [47]**.** Similar dynamics can occur with visual cues [48,49] for example the showy bracts of *Dalechampia scandens* are attractive to both pollinators and seed predators [48]. Balancing these potential costs of trade-offs from traits with multiple effects will be necessary for selecting appropriate crop breeding strategies [49].

d. Manipulating floral reward

Since pollinators often visit flowers to harvest nectar and pollen, breeding programmes that improve reward production, nutritive value or availability perhaps have the most potential to enhance pollination and fruit set of crops reliant on both wild and managed pollinator populations. The mean reward value of nectar encountered by a pollinator has been shown to be positively correlated with the proportion of flowers visited on a plant, the time spent on a flower, flower constancy, and the number of unrewarding flowers that will be visited before moving to a new patch [50-52]. These factors should enhance overall pollination rates of a crop but may also increase the proportion of self pollen received [52]. For crop systems such as the field bean, which benefit from both self and non-self pollen [53], this will not necessarily have a negative impact, but for others the optimum size of the reward to deliver maximum yields may need to be more carefully assessed.

Nectar is rarely just a simple sugar solution. Beside sugars, nectar can contain amino acids, nectarin proteins, volatile compounds, minerals, and secondary metabolites such as phenolics and alkaloids [54,55**,56 and references within]. The additives to the nectar listed above may have nutritive value, but some also have the potential to modify pollinator behaviour, or defend against microbes and nectar thieves. For example, the amino acids proline and phenylalanine act as phagostimulants, causing insects to visit more flowers than they would usually. Other compounds such as non-protein amino acids (reviewed by [57]) and caffeine [55**] also have the capability to increase the number of visits a flower receives.

Recent studies have identified transcription factors from the MYB family as regulators of nectar production in *Arabidopsis (AtMYB57)* and *Nicotiana* (*NtMYB305*) [58,59]. MYB305 has been shown to regulate nectarin production through *NECTARIN* genes [60] and starch accumulation during nectary development and thus the amount of nectar secreted [59]. Nectar secretion is also under the control of plant growth regulators jasmonic acid and auxin [58,61,62]. Downstream, the sugar transporter *AtSWEET9* is involved in the export of sugars into the nectary [63**]. This export is coupled with the hydrolysis of sucrose into glucose and fructose by *CELL WALL INVERTASE 4*, providing a sink for sucrose export and allowing sugars to accumulate [64]. One area worthy of more attention is how the ratio of sucrose:hexose in nectar is controlled and what consequences this has for the attractiveness of a crop to different pollinators.

For pollinators that obtain their nutrition solely from flowers, pollen is a vital source of nitrogen from which to rear offspring. As well as proteins and amino acids, pollen contains lipids, vitamins, and sometimes starch [65,66]. As the chemical composition of pollen varies between plant species [66], its nutritional value to pollinators will also differ. Experienced pollen foragers are able to determine the nutritional quality of pollen and preferentially choose those containing a greater content of essential amino acids leucine, isoleucine and valine [66,67]. Therefore, a potential route to increase pollinator visitation to crops could be to manipulate pollen quantity by altering the expression of pollen-specific nutrient transporters, such as amino acid transporters (eg. *AtLHT* genes, *NsAAP1*, *LeProT1;* reviewed by [68]) which have been identified in *Arabidopsis,* tobacco and tomato.

Ultimately, when looking to increase crop yields through the enhancement of floral yields, there is still a lot of research on the genetic basis of the quantity and quality of floral reward produced to be done, which will allow a more targeted approach to crop breeding. Nectar is a much less costly reward for plants to produce in terms of nitrogen (and also in terms of gametes not available for reproduction) and may therefore hold most promise for improving pollinator visitation. However, in the context of trying to support pollinator populations by providing resources for reproduction it will also be important to consider whether crops provide a suitable pollen source to allow reproduction to occur.

e. Optimising efficiency of reward acquisition

The energetic reward provided by a plant can also be increased by reducing the costs incurred by a pollinator in obtaining it. The symmetry of a flower influences how easily a pollinator can acquire the reward by specifying the presence and position of landing platforms and occluded palates that require force to open. In *Antirrhinum majus* a transcriptional network comprising TCP and MYB family transcription factors has been shown to specify zygomorphy (bilateral symmetry) [69-72]. The mutants generated during these studies have provided insight into how pollinators forage to optimise their energy return. In wild type flowers bumblebees alight on the landing platform and generate sufficient force to open the palate and access the nectar, whereas other insects cannot; for example honey bees, which can only exert around a tenth of the force of bumblebees [73]. Mutants with all their petals ventralised are closed and inaccessible to pollinators (BJG, unpublished data). In contrast, mutants with all their petals dorsalised are open and readily accessible to a range of pollinators, including honey bees, but experience reduced visits by long-tongued bumblebees, likely as a result of nectar depletion by other foragers [74]. These extreme variants hint at the possibility of optimising floral symmetry and pollinator visitation using less extreme natural variation. In alfalfa it has been shown that the force required to open a flower is heritable and an easier to open flower is correlated with a greater rate of flower opening under field conditions [75].

At a finer scale, the shape of epidermal cells on the flower surface can influence the energetic efficiency of foraging. Whitney et al. [76] showed that *Bombus terrestris* foragers prefer flowers with conical epidermal cells to those with flat epidermal cells, but only when flowers were oriented vertically. Similarly, Alcorn et al. [77] found that flowers with conical epidermal cells were preferred when flowers were moving, but not when they were stationary. Conical epidermal cells enhance foraging efficiency by providing a surface into which the tarsal claws of bees can grip. Variation has been found within and between species in the extent and distribution of conical epidermal cells ([78]; EJB and BJG, unpublished), suggesting that this trait has potential as a breeding target for optimised pollinator attraction.

4. Conclusions

Although the various traits discussed above, and summarized in Figure 2, have potential as targets of crop breeding, there are surprisingly few published examples of research specifically analyzing or targeting yield through animal pollination. Perhaps the most extensive studies have been by Suso and colleagues, who have investigated how a number of floral traits affect outcrossing of the field bean (*Vicia faba*) [eg. 79,80*]. Traits such as standard petal dimensions, number of inflorescences, ovary length, and pollen content are all associated with changes in outcrossing level and by extension with animal pollination.

Much more work is needed to define how pollination biology can contribute to crop production, and it will also be important to consider the interaction between plant and pollinator in the wider context of the many other factors influencing pollinator numbers. However, as substantial variation appears to be present in a wide range of crops and floral traits [54,80*,81] - from the level of floral display right down to the size of reproductive structures – we are confident that there is great potential for additional research in this area to inform the breeding of higher yielding, more insect-friendly crops.

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Figure Legends

Figure 1. Crops and their pollinators. The pollinator shown is not necessarily the principal pollinator. **A** Sunflower with *Aglais io.* **B** Radish with beetle and fly pollinators. **C** Blueberry with *Bombus ternarius.* **D** Tomato with *Bombus terrestris.* **E** Apple with *Apis mellifera.* **F** Field bean with *Bombus hortorum.* **G** Coffee with *Apis mellifera.* **For image credits please refer to the Acknowledgements.**

Figure 2. Floral traits affecting pollinator visitation. The floral traits highlighted at the level of the crop, plant and flower may make useful targets for crop breeding programmes to enhance pollination rates.

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