



## Pollination and plant reproductive biology

The reproductive biology and pollination of plants has been a traditional subject of naturalists' interest, and of both professional and lay people throughout the centuries. The pioneering work of Kölreuter (1761–1766), and particularly Sprengel (1793), provided detailed information on reproductive processes of plants, especially fertilisation through pollination. With admirable detail, accuracy and lucidity, Sprengel described floral adaptations in many flowering species. He concluded from his observations that flowers have these traits to attract insects for pollination. Later, this information was further used by Darwin to provide evidence for some of his theories about the effects of inbreeding (1876), the role of animals and plants in promoting reciprocal adaptations, which are viewed as typical cases of co-evolution (1862), and the effect of morphological adaptations of plants to promote outbreeding (1877). Thus, any historical account of plant reproductive biology, even the shortest, should mention the seminal works of Darwin (Pannell 2009), which included fine examples of his experimental and deductive approach. Later, *The Origin of Species* and Darwin's work on pollination and flowers encouraged other naturalists to study the reproductive biology of plants and the relationship between flowers and pollinators. Due to increasing specialisation of researchers and the development of new methods, research on plant reproductive biology was divided in two separate disciplines: floral and pollination biology, and population and quantitative genetics. During most of 20th century, these two aspects generally remained separate, despite the great insight provided by the Modern Synthesis on adaptation of traits, and the excellent opportunities provided by plants to explore these processes. However, noteworthy exceptions were the broad interests of Stebbins (1970, 1974) and Grant (1949), spanning genetics, ecology and systematics of plants.

Pollination biology, which was first developed over many decades as a descriptive field, was plagued by anecdotal information about the role of specific pollinators on the reproductive success of particular plant species. From his observations, Sprengel (1793) came to the conclusion that flowers have adaptations in order to attract insects for pollination. This tradition was followed by Delpino (1873–1874) when describing pollination syndromes, *i.e.* the suites of morphological, chemical and other traits that were viewed as the result of adaptation to specific pollinators and thus might indicate the actual pollinators of a species. This view was updated and refined by Faegri & van der Pijl (1966), and was more recently subjected to

new consideration and debate (Waser *et al.* 1996; Fenster *et al.* 2004; Ollerton *et al.* 2009). Currently, pollination syndromes are only viewed as a possible clue from which to start investigations on floral biology of a particular system. However, the question always remains as to whether the current pollinators are the same or functionally similar to those in ancestors of the species, which would have been selected for a particular flower phenotype. Since biological interactions, such as pollination, generally do not fossilise (but see Ramírez *et al.* 2007; Compton *et al.* 2010), we rely on comparative methods performed across clades to infer the ancestral pollinators.

Nevertheless, reproductive biology of plants remained essential for the inception of genetics, both in the gardens where Mendel grew his pea plants, and later in the very early 20<sup>th</sup> century when his work was rediscovered by plant geneticists. By this time, plant geneticists frequently used specific reproductive systems of plants, such as heterostyly, to examine the genetic basis of traits, as Mendel did with pea seed polymorphism. By developing specific approaches for exploring continuous traits, quantitative genetic methods elucidated their selection basis and spread into populations and species. Similarly, chromosomal studies demonstrated specific aspects of the physiology of plant reproduction, where hybridisation and polyploidy are extremely relevant processes. In general, these studies did not take into account the ecology of plant reproduction, namely pollination, dispersal and plant demography, although the abovementioned seminal works of Stebbins and Grant were noteworthy and influential keystones, when considering pollination.

With the onset of the development of modern molecular techniques for depicting genetic variation in populations, a new era that merged ecological and genetic approaches to study the adaptive significance of reproductive traits of plants started at the end of the last millennium (Barrett *et al.* 1992). These being traits such as the form of the perianth, type of fruit, flowering period or length and number of reproductive seasons, among others. Most of these studies take advantage of wide neutral genetic variation to trace the success of reproductive strategies of plants at population or individual level, including the female and male components (Morgan & Conner 2001). These new approaches were comprehensively summarised in the work of Morgan & Schoen (1997). More recently, there are indications that some genome-wide markers are not as neutral as formerly envisaged, and in fact have been used to show that variation in floral traits across populations should have a

selective basis, although the mechanism is still poorly understood (Herrera & Bazaga 2008). Increased effort is now being devoted to ascertaining the genetic basis of plant reproductive traits with continuous variations (e.g. pollinator attractiveness: Schemske & Bradshaw 1999; Whittall *et al.* 2006).

Therefore, it is not surprising that the new assemblages of studies now appear in botanical and evolutionary journals and consider together ecological, physiological and genetic aspects of plant reproduction, while pollination still receives most attention. The papers in this special issue of *Plant Biology* examine the reproductive biology of different plants and ask how interactions of certain pollinators with plants and their behaviour on flowers influence the morphology of reproductive organs or the flowering phenology, and how this can influence fruit and seed production in relation to the whole reproductive cycle. Several papers in this special issue of *Plant Biology* study the reproductive biology and pollination ecology of certain groups of plants in order to compare the effectiveness of specific flower visitors as pollinators and to find morphological adaptations of flowers that guarantee optimal fertilisation. Albeit not comprehensive, this collection of papers provides wide coverage of topics developed under the umbrella of current plant reproductive biology.

Plants offer some unique flower designs, which have been used by evolutionary biologists to test hypotheses on the evolution of outbreeding and disassortative mating. One such mechanism is heterostyly, where two or three morphs co-exist in a population and mating occurs preferentially between the morphs rather than within them because of the reciprocal position of their sex organs. **Ferero *et al.* (2011)** analysed to what extent these polymorphisms are truly reciprocal and are accompanied by other reciprocal traits. They report wide variations within *Lithodora s.l.* (Boraginaceae) that are correlated with integrated floral morphology, probably as a result of selection for the precise location of pollen on the pollinator body.

**Arceo-Gómez *et al.* (2011)** show that mirror-image flowers, another form of reciprocal style polymorphism, of *Chamaecrista chamaecristoides* (Fabaceae) are highly dependent of buzz pollinators. Vibration at the correct frequency is necessary not only for pollen release but also for pollen capture and deposition inside on the stigma. Furthermore, precise positioning of pollinators inside the flower guarantees successful pollination.

Plants often attract organisms that may potentially compromise reproductive fitness, such as nectar robbers. **Zhang *et al.* (2011)** found behavioural differences between male and female carpenter bees that visit *Glecho-ma longituba* (Lamiaceae) flowers. They discuss differences in food resource preference between male and female carpenter bees that may influence the evolution of floral design and reproductive success of *G. longituba*.

**Ortega-Baes *et al.* (2011)** used field experiments to analyse the reproductive biology of *Echinopsis terscheckii*, a columnar cactus with nocturnal flowers that is endemic

to the semi-arid regions of northwest Argentina. They found a generalised pollination system and observed that moths were the most effective pollinators and visited flowers frequently at night, whereas bees were the most frequent visitors during the day. In order to compare the effectiveness of birds and insects as pollinators, **Schmid *et al.* (2011)** studied the floral biology of the bromeliad *Aechmea nudicaulis* (L.) Grisebach (Bromeliaceae) in the biome of the Atlantic rain forest, southern Brazil. They found a bimodal pollination system, with many floral traits characteristic for ornithophily. While hummingbirds were the most efficient pollinators, bees were additional pollen vectors, and both groups of pollinators guaranteed successful reproduction in *A. nudicaulis*. In a further paper, **Vale *et al.* (2011)** characterise the breeding system in the nectarless orchid *Broughtonia lindenii*, with the aim of identifying factors that limit fruit production. They demonstrated pollinator dependence and found males of the bee *Melissodes leprieuri* were the main pollinators.

**Tal (2011)** investigated flowering phenological patterns in crowns of four temperate deciduous tree species. This paper asks whether there are spatio-temporal patterns in the development of flowering in trees, and how these might relate to reproductive processes. He found that early-flowering trees display a clear and consistent acropetalous and centrifugal flowering pattern, whereas this pattern is lacking in species that flower after leaf unfolding.

It is a long-standing challenge to measure the paternal component of fitness in plants, particularly in hermaphroditic species. Seed mass is an important component of fitness, and it was thought that most of the variation in this trait came from the mother plant. However, the study of **de Jong *et al.* (2011)**, using fine experimental crosses from different accessions of the model organism *Arabidopsis thaliana*, shows that parents differentially sire seeds of different mass, although the causes of this remain obscure, as additive inheritance, typical of quantitative traits, was not found.

Sex allocation theory predicts that larger plant size may modify the balance in fitness gain in both genders, leading to uneven optimal male and female allocation (Charnov 1982). This reasoning has recently been applied to flowers (Méndez & Traveset 2003) and inflorescences (Méndez 2001) of plants producing one or a few flowers/inflorescences. **Torices & Méndez (2011)** studied sexual expression in relation to inflorescence size in the monoecious *Tussilago farfara* (Asteraceae). Interestingly, they found contrasting patterns of sex allocation in different populations.

**Faast *et al.* (2011)** found that small isolated populations of the rare orchid *Cladenia rigida* in southern Australia produce seeds with reduced viability, even though the number of fruits and seeds is similar to that of larger populations. Pollen limitation was discarded among possible causes of lower reproductive output. Instead, resource limitation and some selfing and biparental

inbreeding are proposed to play a role. These authors also provide indirect evidence for a causal effect of reduced seed viability on population decline, leading to a clear Allee effect. These results illustrate the need for checking viability when seeds are minute, as in orchids

Most flowering plants are hermaphroditic, and many are self-compatible, which is seen by evolutionary biologists as an opportunity to test the effects of inbreeding and outbreeding. **Gargano *et al.* (2011)** test the prediction that self-compatible plants show reduced effects of inbreeding depression. Selfing may purge genetic load associated with lethal recessive alleles that are expressed in homozygotes. The prediction was not fulfilled in the narrow endemic, self-compatible Italian *Dianthus guliae* (Caryophyllaceae), which showed reduced fitness after self-pollination in comparison with cross-pollination. After selfing, these effects were reduced, albeit still present in plants of the second generation.

**Alves-da-Silva *et al.* (2011)** examine the morphological and physiological requirements of embryos of the tropical climber *Aristolochia galeata* (Aristolochiaceae) in terms of growth and germination, and conclude that these traits may explain how this species thrives in woodlands of the Cerrado biome in Brazil. This climber delays growth through morpho-physiological dormancy, thus avoiding non-optimal conditions. However, in another species of the genus, the Mediterranean vine *Aristolochia baetica*, reproductive output seems to be limited at pre-dispersive stages (**Berjano *et al.* 2011**). Thus, fruit set is very low and probably limited by resource shortages rather than low quality or quantity of pollen supply to stigmas. This latter study contains data from several consecutive years, which is critical to ascertain patterns in highly variable climates, such as in the Mediterranean, and is usually not considered.

In addition to resource limitation, pre-dispersal seed ingestion by herbivores may also be an important cause of reproductive failure of plants. However, some of the seeds survive herbivore gut passage when parent plants are consumed and such seeds successfully disperse. Analysing a wide dataset with some phylogenetic control across species, **D'Hondt & Hoffmann (2011)** found that no single trait can predict the success of a seed germinating, and that probably dormancy-related traits have evolved, thus connecting seed dormancy and dispersal in dry-fruited plants.

Plant reproductive biology is usually studied from the perspective of a single component of the reproductive cycle. The evolution of single or sets of tightly interrelated traits (*e.g.* those in flowers or fruits) is well understood. However, the inter-relation of traits is in fact wider and affects the whole plant, determining its life history. A good example of this wide approach is that of **Dechamps *et al.* (2011)**, who examined the reproductive output and life-history variations in populations of *Thlaspi caerulescens* (Brassicaceae) subjected to edaphic (heavy metals) and water stress.

## FUTURE RESEARCH

The study of plant–animal interactions has grown tremendously during recent decades, partly because of development of new methods (Thompson 2002). For example, molecular genetic tools and new analytical techniques are increasingly being used by plant ecologists and pollination biologists in order to answer questions concerning the causes and consequences of variations on reproductive success (Mitchell *et al.* 2009). However, many areas of pollination biology and plant reproductive biology are still poorly studied. Perhaps this is due to its less attractive nature, abiotic pollination has been comparatively less studied, yet it is of considerable importance in both taxonomy and ecology, particularly in relation to wind pollination (Culley *et al.* 2002). This type of pollination is mostly a derived condition from animal pollination, but there are many unanswered questions about the selective forces that promote this evolutionary shift (Friedman & Barrett 2008).

In most of the investigations into plant–animal relationships, species have been treated as binary, although the studied organisms are embedded in complex networks. These networks have provided insight into the complexity, community structure and evolutionary ecology of species' interactions (Bascompte *et al.* 2006; Vázquez *et al.* 2009). However, our understanding of the community context of pollination and floral evolution is still in its infancy (Geber & Möller 2006). Therefore, we must perform studies in which there are manipulations within communities and then evaluate functional and demographic responses. Since we know that results of such studies can be different in different populations (Torices & Méndez 2011), comparative approaches are necessary.

Anthropogenic changes to ecosystems, such as habitat fragmentation, agricultural intensification, urbanisation, pollution, pesticides and species' invasions can influence plant–pollinator interactions (see Mitchell *et al.* 2009 and references therein). Many studies have shown that variation in floral morphology affects pollination and reproductive success (Aizen & Vázquez 2006; Torices & Méndez 2011). However, few studies have investigated how different types of anthropogenic disturbance modify flower traits that have a function in pollinator attraction. Furthermore, it is increasingly evident that disturbance, particularly habitat fragmentation, leads to a disruption of reproductive performance of a species through interactions with pollinators, dispersers and predators (González-Varo *et al.* 2009, 2010; González-Varo 2010).

Climatic changes have the potential to act in concert with existing environmental alterations and can generate serious impacts for plant and pollinator networks (Yuan *et al.* 2009). For example, the info-chemical flow among organisms can be altered if abiotic factors cause significant changes in species pools, and also alter the timing of emissions of volatile organic compounds that function in pollinator attraction or plant defence. More investigations are needed to elucidate how insect-mediated pollination

might be altered during global climate change and how plant–plant communication could be affected by altered volatile terpenoid emissions.

Molecular genetic paternity analyses are needed to understand effects of selection on floral and other reproductive traits that incorporate lifetime male fitness (Conner 2006). Selection often acts differently through male rather than female fitness, therefore we need information to identify what floral trait values are adaptive and in what ways selection for male and female fitness conflict (Conner 2006). Few paternity studies have explored the role of ecological context, such as the effects of habitat fragmentation (Trapnell & Hamrick 2006) or the role of competitors and facilitators for pollination (Mitchell *et al.* 2009). It will be important to combine different methods in long-term field studies on the reproductive success of plants and the ecological genetics of flowers and fruits. Therefore, interdisciplinary collaborations are necessary, and geneticists, plant ecologists, zoologists and pollination and dispersal ecologists, as well as chemists and biochemists, should work in an integrative framework. Furthermore, we should use comparative approaches if we want to obtain more information on the evolution of reproductive traits. Some comparative studies devoted to plant reproductive traits have shown cases of convergence (Pérez *et al.* 2004; Waterman *et al.* 2009). In the few cases examined, shifts needed to achieve convergence seem to be more related to mutations in regulatory than in structural genes (Whittall *et al.* 2006). This underlines the strong need to further study the genetic and epigenetic machinery determining these traits, beyond model systems such as snapdragon (*Antirrhinum*). Knowledge of the genetic architecture and developmental constraints on traits will also help in determining why reproductive structures such as flowers and fruits are in general highly integrated and to what extent they are the result of adaptations or constraints (Armbruster *et al.* 2004).

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## CONFLICTS OF INTEREST

The authors have declared no potential conflicts.

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