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Sexual dimorphism in flowering plants

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Abstract

Among dioecious flowering plants, females and males often differ in a range of morphological, physiological, and life-history traits. This is referred to as sexual dimorphism, and understanding why it occurs is a central question in evolutionary biology. Our review documents a range of sexually dimorphic traits in angiosperm species, discusses their ecological consequences, and details the genetic and evolutionary processes that drive divergence between female and male phenotypes. We consider why sexual dimorphism in plants is generally less well developed than in many animal groups, and also the importance of sexual and natural selection in contributing to differences between the sexes. Many sexually dimorphic characters, including both vegetative and flowering traits, are associated with differences in the costs of reproduction, which are usually greater in females, particularly in longer-lived species. These differences can influence the frequency and distribution of females and males across resource gradients and within heterogeneous environments, causing niche differences and the spatial segregation of the sexes. The interplay between sex-specific adaptation and the breakdown of between-sex genetic correlations allows for the independent evolution of female and male traits, and this is influenced in some species by the presence of sex chromosomes. We conclude by providing suggestions for future work on sexual dimorphism in plants, including investigations of the ecological and genetic basis of intraspecific variation, and genetic mapping and expression studies aimed at understanding the genetic architecture of sexually dimorphic trait variation.

Key words: Costs of reproduction, dioecy, flowering plants, niche differentiation, sex chromosomes, sexual antagonism, sexual dimorphism, sexual selection.

Introduction

The majority (~90%) of flowering plants exhibit hermaphroditic sex expression, with individuals functioning as both female and male parents. More rarely, populations are reproductively subdivided into two sexes (females and males), a condition known as dioecy. Although the incidence of dioecy is relatively uncommon (~6–7%; Renner and Ricklefs, 1995), it is reported in close to half of all angiosperm families (Heilbut, 2000) and may have originated on at least 100 occasions from hermaphroditic ancestors (Charlesworth, 2002). There has been considerable interest since Darwin's (1877) early work on understanding why dioecy occurs in plants, and the selective mechanisms responsible for its origin and maintenance (reviewed in Charlesworth, 1999). The origin of separate sexes is commonly associated with the evolution of sexual dimorphism, and this has occurred to varying

degrees in many dioecious plants (Correns, 1928; Lloyd and Webb, 1977; Geber *et al.*, 1999). The goal of this article is to review the nature of sexual dimorphism in angiosperms, discuss how and why it arises, and consider its ecological and evolutionary consequences.

Sexual dimorphism describes differences between the sexes in primary and secondary sex characters. The former relate directly to male (androecium) and female (gynoecium) sexual organs, and the latter to differences between the sexes in structures other than sex organs themselves, including any aspect of morphology or physiology. The term gender dimorphism is sometimes used in the plant literature synonymously with sexual dimorphism, but we restrict its usage here to refer to populations in which there are distinct genders (females, males, or hermaphrodites)

that differ in their relative contribution to fitness as pollen or seed parents. This perspective follows the concept of gender developed by David Lloyd, in which the functional gender of a plant refers to the relative contribution to fitness an individual makes from maternal versus paternal investment (Lloyd, 1979; Lloyd and Bawa, 1984). For a more extended discussion of these terms and their usage, see Sakai and Weller (1999). The important issue for the purpose of this review is that once dioecy evolves from gender monomorphism, the sexual morphs have different roles and are usually selected to diverge in their characteristics, resulting in sexual dimorphism.

Darwin (1871) described many striking examples in which females and males of animal species differ dramatically in morphology, coloration, size, and behavior. He proposed that sexual selection resulting from variation among individuals in mating success could explain the evolution of sexual dimorphism, and distinguished two fundamentally different types: intrasexual competition among individuals of one sex for mates, and intersexual selection or ‘mate choice’ resulting from the preferences of one sex for traits of the other. In most instances, the former involves males and the latter females. This difference was later explained by Bateman’s principle (Bateman 1948), which states that male reproductive success will be most often limited by the availability of mating partners, whereas female reproductive success is more likely to be limited by the availability of resources. This should result in greater variance in male than female mating success. A vast literature now exists on the concepts and measurement of sexual selection (reviewed in Andersson, 1994; Shuster and Wade, 2003), and this topic is a dynamic area in modern evolutionary and behavioural ecology.

Darwin (1871) largely neglected the possibility that sexual selection might also operate in plants. This may have been because of their non-sentient habit, primarily hermaphroditic sexual condition, and less conspicuous sexual dimorphism in dioecious species. Now it is generally appreciated, although not without some controversy, that the concepts of sexual selection and Bateman’s principle can be applied to flowering plants, regardless of their particular sexual system (reviewed in Charlesworth *et al.*, 1987; Arnold, 1994; Wilson *et al.*, 1994; Delph and Ashman, 2006; Moore and Pannell, 2011). This advance has helped to explain various facets of pollination and mating biology, particularly the function of reproductive traits (Willson, 1979; Willson and Burley, 1983; Bell, 1985; Queller, 1987; Harder and Barrett, 1996; Moore and Pannell, 2011). An important question that arises is the extent to which sexual selection rather than other forms of natural selection (e.g. viability and fecundity selection) can explain the patterns of sexual dimorphism in dioecious species. The different reproductive requirements of females and males cause sex-specific selection pressures on traits that influence viability and fertility, and both natural and sexual selection could influence the adaptive evolution of such traits. We address these issues below.

Despite growing interest in sexual dimorphism in flowering plants, there are still many unresolved issues concerning the genetic architecture and evolution of trait differences between the sexes. A fundamental question that arises when considering the genetic basis of sexually dimorphic traits is the extent to which shared genetic control of traits constrains the evolution

of sexual dimorphism. Understanding how different genetic architectures influence evolutionary trajectories of phenotypic change in the sexes is important for inferring how dimorphism evolves and is maintained, and also for understanding adaptive evolution more generally (Lande, 1980). Recent interest in sexual dimorphism has focused on the constraints and conflicts that arise when the evolutionary interests of females and males diverge. An important result from these studies is that the independent evolution of the sexes is often constrained by high intersexual genetic correlations (Poissant *et al.*, 2010). Most of this work has been conducted on animals (e.g. Bonduriansky and Rowe, 2005; Chenoweth *et al.*, 2010), although several studies have explored the genetics of sexual dimorphism in plant species (reviewed in Meagher, 1999; and, more recently, Ashman, 2003; McDaniel, 2005; Steven *et al.*, 2007; Delph *et al.*, 2010, 2011). We review these studies and consider their implications for understanding how and why sexual dimorphism evolves.

Theory indicates that the divergence of traits in females or males is facilitated by the presence of sex chromosomes, as these are the only genomic regions that differ between the sexes (Rice, 1984; Mank, 2009). Because genes on sex chromosomes spend different amounts of evolutionary time in females and males, they are expected to obtain fitness benefits disproportionately through one sex or the other. Indeed, there is evidence that genes involved in sex-specific adaptation have non-random genomic distributions and are located on the sex chromosomes (Gibson *et al.*, 2002; Zhou and Bachtrog, 2012). Moreover, because of the selective benefit of linkage between genes involved in sex determination and those involved in sex-specific functions, it is expected that genes with sexually antagonistic effects (i.e. beneficial in one sex but deleterious in the other) should be over-represented on the sex chromosomes (Rice, 1984; Charlesworth *et al.*, 2005). We consider the evidence for this and review recent progress in understanding the relationships between sex chromosomes and the evolution of sexual dimorphism.

We begin by documenting traits that distinguish female and male plants in the context of life history, including vegetative and reproductive characters and patterns of resource allocation. We highlight contrasts between life histories since they provide insight into how differences in the timing and costs of reproduction influence other aspects of dimorphism. We next consider the ecology of sexual dimorphism and the extent to which differences between females and males influence their distribution and frequency across environmental gradients. A particular focus of this section involves evaluating evidence for niche partitioning of the sexes and whether they respond differently to environmental stress. We then review what is known about the genetic architecture of sexual dimorphism and how this might influence divergence of traits in females and males. Insights from the genetics of sexual dimorphism are used to address the question of why plants generally exhibit less exaggerated dimorphism compared with animals. We also evaluate the role that sex chromosomes play in the evolution of sexual dimorphism and consider whether they have a disproportionate number of genes involved in sex-specific functions. We conclude by identifying several topics that would benefit from future study.

Traits distinguishing the sexes in dioecious populations

In contrast to many animal groups, the sex of an individual cannot usually be determined in plants before flowering (but see [García and Antor, 1995](#)) without sex-specific genetic markers (e.g. [Eppley et al., 1998](#); [Stehlik and Barrett, 2005](#); [Shelton, 2010](#)). As a result, more information is available for differences between the sexes in reproductive features than for vegetative traits. Nevertheless, the sexes can differ prior to reproduction in a range of characters, although these differences are rarely sufficiently obvious for females and males to be reliably distinguished solely on the basis of these traits.

There are few reports of differences between the sexes at the seed or seedling stage. In *Rumex nivalis*, male seeds are heavier and germinate earlier than female seeds, but overall levels of germination do not differ between the sexes ([Stehlik and Barrett, 2005](#)). Male seeds are also heavier than female seeds in *Spinacia oleracea* ([Freeman et al., 1994](#)). Sexual dimorphism in dormancy and survivorship occurs in *Silene latifolia* ([Purrington and Schmitt, 1995](#)), and environment-dependent differences between the sexes have been reported in seed germination in *Distichlis spicata* ([Eppley, 2001](#)). In contrast, there are numerous reports of differences in the size, morphology (e.g. leaf shape, stem characteristics), growth rate, and physiology of the sexes that are manifested during the vegetative phase of growth (reviewed in [Lloyd and Webb, 1977](#); [Dawson and Geber, 1999](#)). Sexual dimorphism in these traits is associated with contrasting strategies of the sexes, particularly in growth and reproductive expenditure.

Vegetative traits

In long-lived species, males often exceed females in vigour, shoot size, and their capacity for clonal propagation, although exceptions do occur (e.g. *Populus tremuloides*; [Sakai and Burris, 1985](#)). Repeated bouts of maternal investment in fruits and seeds can lead to higher rates of mortality in females (e.g. [Allen and Antos, 1993](#)) and may also exacerbate death by herbivory and disease (e.g. [Ward, 2007](#)). Reproductive costs result in physiological trade-offs in resource distributions, and these can influence future vegetative growth and reproduction. Females are expected to show stronger trade-offs with other life-history traits because of their typically higher investment in reproduction ([Delph and Meagher, 1995](#); table 1 in [Delph, 1999](#)), although this is not necessarily always expressed through higher somatic costs, because various compensatory mechanisms can offset differences between the sexes in the costs of reproduction (see table 2 in [Delph, 1999](#)). Moreover, in some wind-pollinated plants, male reproductive costs may match or exceed those of females because of the high investment in nitrogen-rich pollen ([Delph et al., 1993](#); [Harris and Pannell, 2008](#)). Determining the appropriate resource currencies is a major challenge for evaluating reproductive expenditure in dioecious plants.

A recent study by [Van Drunen and Dorken \(2012\)](#) of the clonal aquatic *Sagittaria latifolia* detected a 1:1 trade-off between biomass investment in female function and clonal reproduction

(ramet and corm production). In contrast, male investment had no apparent effect on the production of ramets and corms. Instead, the nitrogen content of corms was considerably lower than for females, indicating that the type of trade-off between the two reproductive modes differs between the sexes. In females, the trade-off thus involves the quantity of clonal propagules produced, whereas in males it appears to involve their quality. This study is informative because it highlights the fact that life-history trade-offs can involve different resource currencies in females and males (and see [Sánchez-Vilas and Pannell, 2011](#)), and also because it demonstrates that resource-based trade-offs are manifested not only at the ramet level, at which most studies of trade-offs have been performed in clonal plants, but also at the genet level, which is more relevant to fitness.

A particularly striking example of how the costs of reproduction influence sexual dimorphism involves differences between the sexes in plant architecture in *Leucadendron* ([Fig. 1](#)). This genus of fire-adapted shrubs endemic to the fynbos of the Cape region of South Africa exhibits variation in the degree of serotiny (cones that release their seeds after fire), and also in

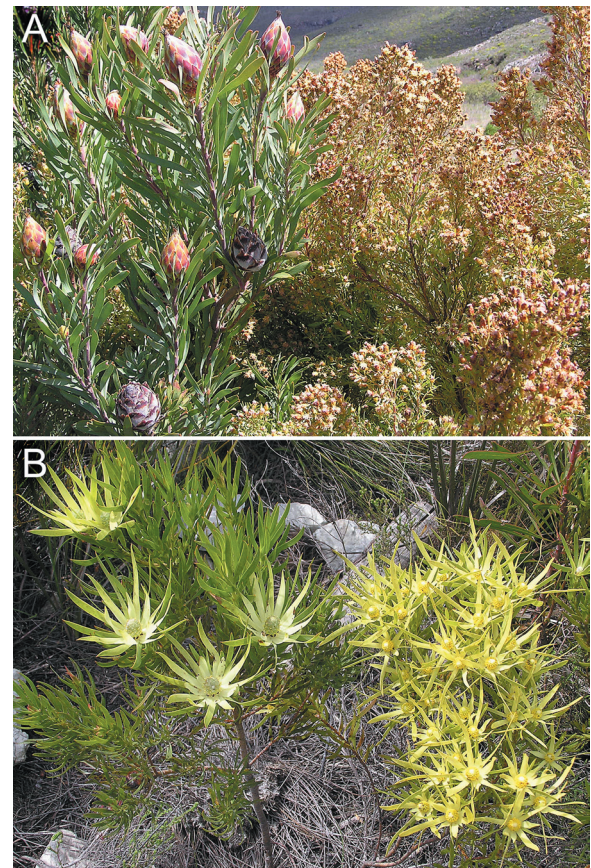


Fig. 1. Sexual dimorphism in *Leucadendron* (Proteaceae). (A) *Leucadendron rubrum*, a wind-pollinated species with striking sexual dimorphism in vegetative and reproductive traits. The female is on the left and the male is on the right. (B) *Leucadendron xanthocomus*, an insect-pollinated species in which males (right) exhibit much larger floral displays than females (left), and this can lead to viability selection against males with the largest displays.

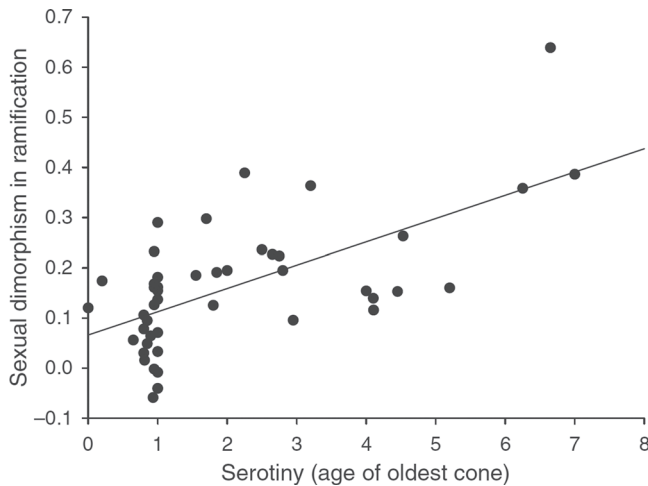


Fig. 2. The relationship between sexual dimorphism in ramification (branching) and the age of the oldest cone, an index of the degree of serotiny in *Leucadendron*. Each point is a different species. After Harris and Pannell 2010; 98, 509-515, with permission from John Wiley and Sons.

sexual dimorphism for leaf and branching traits, with males typically possessing more branches and smaller and more abundant leaves than females (Midgley, 2010). Harris and Pannell (2010) conducted a comparative analysis of 49 species and found that the degree of serotiny was strongly associated with the degree of sexual dimorphism: females in species with well-developed serotiny were less highly branched (showed less ramification) than males (Fig. 2). These findings suggest that the reproductive burden of maintaining cones over years in females involves a significant physiological cost and that this in turn influences patterns of growth in females in ways not experienced by males. This reproductive cost in females has also been invoked to account for the occurrence of Rensch's rule, the evolutionary allometry of size dimorphism (Rensch, 1960), in three lineages of New Zealand plants in which sexual size dimorphism decreases with body size when females are the larger sex, but increases when males are larger (Kavanagh *et al.*, 2011; and see Obeso, 2002).

In contrast to long-lived species, females are often larger than males in short-lived polycarpic and monocarpic species (Lloyd and Webb, 1977; Delph, 1999; Obeso, 2002), although this difference can depend on when during the life history comparisons are made. Dynamic patterns of sex-specific growth and resource allocation are particularly evident in short-lived dioecious plants, highlighting the importance of making comparisons at various life cycle stages. For example, in the short-lived perennial *Silene latifolia*, allocation patterns to vegetative growth are similar between the sexes prior to flowering, although there is evidence of sexual dimorphism in gene expression long before this occurs (Zluvova *et al.*, 2010). Once reproduction commences, however, dimorphism develops rapidly, with females growing larger and living longer than males, which produce up to 16 times as many flowers (reviewed in Delph, 1999). This difference is consistent with the idea that there are contrasting sex-specific optima for traits affecting longevity (e.g. Delph and Herlihy, 2012),

and this can favour a 'live fast, die young' strategy in males (Bonduriansky *et al.*, 2008). This strategy seems likely in other dioecious plants in which males senesce earlier than females.

Experimental studies involving the manipulation of reproductive expenditure (by bud removal) and nitrogen resources provide insight on the causes of size dimorphism in annual *Mercurialis annua*, a species in which males have less biomass than females (Harris and Pannell, 2008). The two sexes differed in allocation patterns, with males investing proportionately more in root growth, presumably to provide nitrogen for pollen production, thus restricting above-ground vegetative growth, and females investing more in producing photosynthetic leaves capable of supplying carbon for fruits and seeds. The timing of resource deployment and the relative versus absolute differences in the sizes of below- versus above-ground sources and sinks that supply different resources can thus explain the observed patterns of size dimorphism (and see Sánchez-Vilas and Pannell, 2011). Sex-specific allocation patterns in *M. annua* vary temporally and also respond to environmental heterogeneity. Hesse and Pannell (2011) found that the sexes differentially adjusted their reproductive allocation in response to resource availability and plant competition. In particular, males reduced their reproductive expenditure when grown in poor soils, whereas females increased theirs, especially when competing with other females. However, there was relatively little effect of resources on the degree of size dimorphism so that the relative size disparities were maintained across environmental treatments and over time.

In wind-pollinated annual *Rumex hastatulus*, height dimorphism changes predictably during the life cycle, with males taller than females at flowering and the reverse pattern occurring during seed maturation (Pickup and Barrett, 2012). In this species, both pollen and seeds are wind dispersed, and the temporal changes in plant height during the life cycle seem likely to be adaptive and are matched to optimize both pollen and seed dispersal functions temporally, for which there is a premium on height for maximizing propagule dispersal distance by wind.

Reproductive traits

There are numerous examples of sexual dimorphism in reproductive traits of dioecious species, and these have been well summarized in the reviews of Delph (1999) and Eckhart (1999). Sex-specific differences include flowering phenology and periodicity (e.g. Thomas and LaFrankie, 1993), bud abortion (Abe 2002), flower size (e.g. Delph *et al.*, 1996), flower number per plant (Delph *et al.*, 2005), floral longevity (e.g. Primack, 1985), nutrient content of flowers (e.g. Carroll and Delph, 1996), nectar production (e.g. Bawa and Opler, 1975), floral fragrances (Ashman, 2009), floral defence against herbivory (e.g. Corneslissen and Stirling, 2005), and various inflorescence characteristics including total flower number (e.g. Barrett, 1992), daily display size (e.g. Yakimowski *et al.*, 2011), and inflorescence architecture (e.g. Rourke, 1989). In animal-pollinated species, these differences can have important consequences for pollinator visitation, competition for mates, and the evolution of sexual dimorphism (Vaughton and Ramsey, 1998; Ashman, 2000; Case and Barrett, 2004; Glaettli and Barrett, 2008). There are obviously constraints on how different the reproductive traits

of females and males in animal-pollinated species can become; too much divergence could interfere with mating success if pollinators are more attracted to one sex than the other, or if the sexes attract different pollinators. Such constraints are absent from wind-pollinated plants, and the contrasting biophysical requirements for pollen dispersal and pollen capture have led to striking cases of sexual dimorphism in plant architecture and flower production in some species (e.g. *Leucadendron rubrum*; Fig. 1A). In some cases, the direction of difference between females and males is quite consistent (e.g. in long-lived species, males commonly flower at a younger age and more often than females; Delph, 1999), whereas for other traits this is not the case (e.g. flower size; Delph *et al.*, 1996). Below we discuss recent examples that were not available when earlier reviews were conducted, and we consider hypotheses to account for the patterns observed.

A common observation in long-lived dioecious plants is that males flower more regularly than females (Lloyd and Webb, 1977; Bawa *et al.*, 1982; Nicotra, 1998). This pattern is generally interpreted as resulting from greater female than male reproductive expenditure (e.g. Ågren, 1988; Queenborough *et al.*, 2007). However, the extent to which variation in environmental factors might also influence patterns of flowering in the sexes of dioecious species is less well understood. A recent study of sexual differences in year-to-year flowering in *Lindera triloba*, a multistemmed understory shrub of temperate forests in Japan, provides useful insights in this regard (Matsushita *et al.*, 2011). The authors monitored sunshine hours and flowering patterns of the sexes over five consecutive years at both the ramet and genet level. Flowering fluctuated annually and was positively correlated with the number of sunshine hours during the preceding summer. Although, as expected, annual flowering intensity was greater in males than females, interannual variation in ramet flowering and inflorescence production was also more pronounced in males, with ramets more sensitive to light conditions and the growth status and size of the genets to which they belonged. This observation suggests that the extent of modular integration of ramets within genets differs between the sexes. Evidence from girdling experiments indicated that female ramets are capable of earlier physiological independence than male ramets (Isogimi *et al.*, 2011). As yet the physiological mechanisms by which ramet flowering between the sexes may be differently coordinated is unclear, but this issue could be investigated by tracing patterns of carbon translocation using ^{13}C labelling (e.g. Ida *et al.*, 2012).

Comparative studies of animal-pollinated dioecious species indicate that they commonly possess flowers that are less showy than outcrossing hermaphrodites, with small flowers that are often white, pale yellow, or green in colour (Charlesworth, 1993; Renner and Ricklefs, 1995; Vamosi *et al.*, 2003). Nevertheless, the aggregation of these flowers can result in large floral displays that often show sexual dimorphism in floral and inflorescence traits. Following Bateman's principle, floral and inflorescence traits that increase pollinator attraction would be expected to evolve under stronger pollinator-mediated selection in male than in female plants. This leads to the prediction that large floral displays evolve primarily to increase male fertility and is based on the assumption that male outcrossed siring success increases with more pollinator visits, with only a few visits required to maximize

female fertility. However, there is now evidence for widespread pollen limitation of seed production in flowering plants (e.g. Burd, 1994; Larson and Barrett, 2000; Ashman *et al.*, 2004), indicating that the assumption that male but not female fertility is limited by access to mates is not always true. Indeed, there is evidence that the strength of selection on attractive traits can increase with greater pollen limitation of seed set (Ashman and Morgan, 2004), and that this may lead to the evolution of diverse reproductive adaptations (Harder and Aizen, 2010). These findings, and the recent appreciation of the context-dependent nature of selection on floral traits, suggest that determining the relative importance of both natural and sexual selection will be critical for explaining patterns of sexually dimorphic trait variation.

A recent experimental study of *Silene latifolia* by Delph and Herlihy (2012) exposes the complexity of selection on flower size and number. In this species, a flower size/number trade-off occurs within each sex, and floral traits are genetically correlated with leaf physiology (Delph *et al.*, 2005). The authors used experimental arrays composed of selection lines of small- versus large-flowered plants to increase the phenotypic variation on which selection acts. Because they measured both pollen production and siring success (with genetic markers), they were able to distinguish fecundity selection from sexual selection in males. In females, they found evidence for both fecundity and viability selection favouring large-flowered plants but no evidence for sexual selection. In contrast, sexual selection favoured small flowered and early flowering males, but viability selection opposed this and instead favoured large-flowered males, thus producing a 'tug-of-war' between the two forms of selection. An important conclusion from this study is that the relative importance and direction of the different forms of selection can be highly dependent on environmental conditions. In its native Europe, *S. latifolia* occurs over a wide geographical range, experiencing widely different levels of precipitation, and this may contribute to the considerable variation among populations in flower size and number.

Sexual selection is most obvious in animals when it favours the evolution of extravagant male displays that enhance mating success at the expense of reduced viability. The larger floral displays of males in many animal-pollinated dioecious species are usually interpreted as resulting from male-male competition for mates, but few cases are known where this is associated with the reduced survival of male plants as a result of viability selection (but see Delph and Herlihy, 2012). A striking example involves *Leucadendron xanthocomus* (Fig. 1B) in which males can produce up to 20 times more flowers than females. Bond and Maze (1999) found that the number of insect visits to male plants increased linearly with floral display size, but that increasing display size was associated with a higher probability of plant death. In contrast, the seed set and survival of females was not associated with display size. The ultimate cause of death in male plants appears to be the high maintenance cost of the abundant yellow non-photosynthetic display leaves (Fig. 1B) that attract pollinators, but which cause considerable shading of photosynthetic leaves.

More recently, Hemborg and Bond (2005) have proposed that the striking sexual dimorphism in *L. xanthocomus* has been promoted by the activities of its pollinator, a nitulid beetle (*Pria*

cinerascens), which depends entirely on the species for egg-laying sites and food for adults and larvae. Based on field observations and manipulative experiments, they proposed that the different resources available from the two sexes have driven the evolution of sexual dimorphism. Males provide food and egg-laying sites, whereas the nectarless females, because of the particular cup-shaped morphology of their flower heads, provide only shelter for the beetles from rain, which is frequent during flowering. This idea involving ‘specialized female rewards’ is novel as it challenges the assumption that ‘rewardless’ females necessarily function only by deceit. Future work on this system should determine whether the number of insect visits to male plants is positively associated with male siring success, as assumed. Phenotypic selection analysis would also be useful to investigate the extent to which mating success and viability in males are counterbalanced to produce the optimal display size.

The key functional component of floral display size is the number of flowers in anthesis on a given day, rather than total flower production, as only the former should determine pollinator attraction and mating success (Harder and Barrett, 1996). In common with most dioecious species, flower size and the total number of flowers per inflorescence in *Sagittaria latifolia* is greater in males than in females; however, daily display size is larger in females (Fig. 3, 4; Yakimowski *et al.*, 2011). This difference results from the more synchronized opening of flowers within female inflorescences, in contrast to males (Fig. 4C, D). The cause of this difference in flowering strategy probably resides in the different reproductive roles of females and males. More protracted flowering in males is likely to have been shaped by sexual selection to increase the number and variety of mating partners. This pattern of flowering serves to restrict the diminishing returns commonly associated with male function by presenting pollen gradually over time and maximizing the number

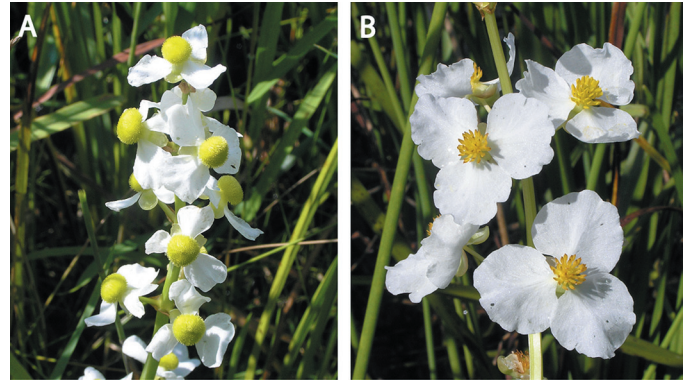


Fig. 3. Sexual dimorphism in flower size and daily display size in *Sagittaria latifolia* (Alismataceae). The female is on the left and the male on the right. After Yakimowski *et al.* (2011); 108, 765–776, with permission from Oxford University Press.

of different insect visitors that participate in cross-pollination (Lloyd, 1984; Harder and Thomson, 1989). A study of siring success in mating arrays of *S. latifolia* supports this hypothesis as male fertility increased linearly with flower production in a manner that is consistent with a linear gain curve (Perry and Dorken, 2011). In females, the larger daily floral displays may function to compensate for the smaller size of female flowers, and also for the absence of pollen as a reward. More work is needed on the sex-specific flowering schedules of dioecious plants, as these determine not only the scope for sexual selection but also the intensity of frequency-dependent selection. Also, the wide variation among populations of *S. latifolia* in the degree of sexual dimorphism (Fig. 4) raises questions regarding the relative importance of ecological and genetic factors in governing this variation.

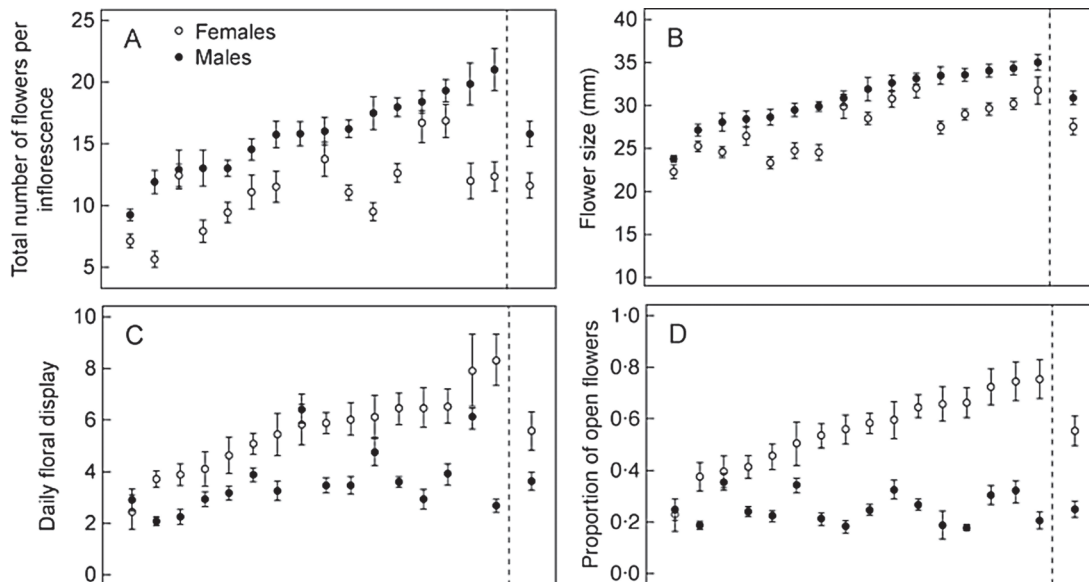


Fig. 4. Variation among populations of *Sagittaria latifolia* in the degree of sexual dimorphism in: (A) total number of flowers per inflorescence; (B) flower size; (C) number of flowers in anthesis per inflorescence per day (daily floral display); and (D) proportion of total flowers open per inflorescence per day. All values are means with standard errors; the right-hand panels for each trait provide the grand means. After Yakimowski *et al.* (2011); 108, 765–776, with permission from Oxford University Press.

There is a growing literature on the role of floral fragrance in pollinator attraction, raising the question of whether sexual dimorphism in floral scent occurs in dioecious species. Based on a survey of 33 gender-dimorphic species, [Ashman \(2009\)](#) found that in the majority of species male plants emitted more volatiles per flower than females, a result consistent with sexual selection. However, several alternative hypotheses also predict this outcome as well as other patterns (see table 2 in [Ashman 2009](#)). For example, higher volatile amounts in males could be a simple allometric consequence of larger flower size, but this cannot be the case in *Silene latifolia* because flowers in females are considerably larger than in males. [Waelti et al. \(2009\)](#) found that male plants emitted significantly larger amounts of scent and that naïve pollinating male moths preferred male over female flowers. Female moths showed no such preference, possibly because only female flowers are used for oviposition and are preferred sites for larval development. Future experimental studies on the chemical ecology of scent dimorphism seem likely to yield new insights into the pollination biology of dioecious plants.

Ecology of sexual dimorphism

The cases of sexual dimorphism described in the preceding section reflect contrasting functional roles for the sexes with implications for their frequency and distribution. In particular, differences in life history, physiology, and reproductive expenditure may influence the frequency of sexes across broad environmental gradients, resulting in geographical variation in sex ratios, and, at finer spatial scales, the occupation of different environmental niches in heterogeneous environments. In this section, we review evidence that sexual dimorphism can have ecological consequences, reinforcing, and perhaps also promoting, secondary sexual divergence. Our focus here is on the response of the sexes to abiotic factors and plant competition, although there are numerous other potential ecological consequences of sexual dimorphism. To mention one example, a recent meta-analysis of sex-biased herbivory ([Cornelissen and Stirling, 2005](#)) found that male plants exhibited significantly higher levels of herbivory than female plants (and see [Ågren et al., 1999](#)). This may have been because, in the species surveyed, males were generally larger but possessed lower concentrations of secondary compounds and other plant defences.

The sex ratios of dioecious populations commonly deviate from the equilibrium expectation of the 1:1 primary sex ratio predicted by Fisherian theory ([Delph, 1999](#); [de Jong and Klinkhamer, 2005](#); [Sinclair et al., 2012](#); [Field et al., in press](#)). A recent survey of flowering sex ratios among angiosperm families revealed that about half showed significant deviations from equality, with male bias almost twice as common as female bias ([Barrett et al., 2010](#)). The frequent occurrence of male-biased sex ratios is likely to be associated with the greater reproductive investment of females, as this commonly results in the earlier onset and more frequent flowering of males and the greater mortality of females ([Lloyd and Webb, 1977](#); [Delph, 1999](#), [Obeso, 2002](#)). This observation leads to the prediction

that long-lived dioecious species that experience repeated episodes of reproduction should be more likely to develop male-biased sex ratios. Such effects may be especially strong in species with a large maternal investment in costly fleshy fruits, a common correlate of dioecy ([Vamosi et al., 2003](#)). These predictions were recently confirmed in comparative analyses of the life-history correlates of dioecy, in which male-biased sex ratios were associated with woody growth forms and fleshy fruits ([Sinclair et al., 2012](#); [Field et al., in press](#)). Differences in the degree of sexual dimorphism in reproductive expenditure may therefore be influential in shaping patterns of sex ratio variation among angiosperm species.

Sexual dimorphism in the costs of reproduction may also be expected to influence sex ratio variation among populations of dioecious species, especially if they occupy a broad range of environmental conditions. Higher reproductive expenditure and/or greater sensitivity to stress in females should result in more male-biased sex ratios along gradients of resource availability and growing season length. There is some evidence from studies of sex ratios along environmental gradients to support this hypothesis (e.g. [Grant and Mitton, 1979](#); [Fox and Harrison, 1981](#); [Marques et al., 2002](#); [Pickering and Hill, 2002](#); [Li et al., 2007](#)). Growing season length may also differentially affect the sexes, especially in northern latitudes where a shorter growing season may limit opportunities for females to mature seed successfully. A latitudinal survey of sex ratios of *Sagittaria latifolia* in eastern North America (S.B. Yakimowski and S.C.H. Barrett, unpublished data) revealed patterns consistent with the hypothesis that females are more sensitive to conditions that limit their reproductive activities. Based on a survey of 116 populations at the northern range limit of this species, the authors found a significant decline in the frequency of females with increasing latitude. Because of the clonal nature of *S. latifolia*, it is unclear whether this result simply reflects a reduction in the flowering of female ramets at range limits, or whether genet sex ratios are also male biased.

Similar processes causing among-population variation in sex ratios can result in the segregation of sexes in spatially heterogeneous environments. Indeed, there is considerable evidence for the 'spatial segregation of the sexes' (SSS) in populations of dioecious plants, and in some cases the physiological mechanisms causing habitat segregation have been investigated (reviewed in [Dawson and Geber, 1999](#)). Spatial segregation of the sexes has been reported in >30 dioecious species from 20 families, and in the vast majority of cases male-biased sex ratios are reported in more stressful sites ([Bierzychudek and Eckhart, 1988](#); [Mercer and Eppley, 2010](#)). Extreme SSS could influence successful mating if the sexes become too spatially isolated, and there has been interest in the mechanisms causing habitat differentiation and why some species exhibit this phenomenon and not others.

A variety of adaptive and non-adaptive hypotheses have been proposed to explain SSS. Several seem unlikely [e.g. habitat selection, sex choice (gender diphasy), maternal control of sex ratio, and sex differential germination] as they are either unknown in plants, (e.g. habitat selection), or are of limited occurrence (e.g. gender diphasy) (see [Lloyd and Bawa, 1984](#)). Early work suggested that SSS results from niche partitioning

that has evolved as an adaptive response to reduce competition between the sexes (Freeman *et al.*, 1976; Onyekwelu and Harper, 1979; Cox, 1981). However, in a critique of this hypothesis, Bierzychudek and Eckhart (1988) proposed that SSS is more likely to be a simple non-adaptive outcome of differential mortality between the sexes as a result of sexual dimorphism in reproductive expenditure. Of course the occurrence of niche differences between the sexes does not necessarily indicate that intersexual competition is the cause of SSS. Thus, determining the nature of sex-specific competitive effects is crucial for understanding the ultimate causes of niche segregation of the sexes.

Surprisingly few studies have investigated sexual differences in competitive ability in dioecious species (reviewed in Ågren *et al.*, 1999; see Sánchez-Vilas *et al.*, 2011). Recent studies of the North American clonal salt marsh grass *Distichlis spicata* by Eppley and colleagues provide valuable clues on the role of competition in potentially contributing towards SSS. In this species, sex ratios vary widely within salt marshes, varying from female to male predominance along gradients of elevation and nutrients (Eppley *et al.*, 1998; Eppley, 2001). Sex-specific genetic markers confirmed that SSS is evident at the genet level and is not simply a result of sex-specific differences in the flowering of ramets. The availability of markers has also allowed juveniles to be sexed and used in competition and reciprocal transplant experiments (Eppley, 2006; Mercer and Eppley, 2010). These experiments have demonstrated that females are stronger competitors than males, at least in some environments, and that competition between females and males is significantly more intense than competition between plants of the same sex, an assumption of the niche-partitioning hypothesis. Collectively these results suggest that environment-dependent differences in competitive ability during the seedling stage help to maintain patterns of niche segregation in *D. spicata*. They also provide the best evidence to date for niche partitioning in dioecious plants. However, because these studies have only focused on competitive interactions among seedlings of *D. spicata*, it is not possible at this stage to rule out the contribution of sexual dimorphism in physiology and reproductive expenditure to the SSS. Indeed, it seems probable that both niche partitioning and features of sexual dimorphism play a role in this system.

Sexual dimorphism in physiology and reproduction can result in the sexes requiring different resources from the environment (e.g. Dudley, 2006; Harris and Pannell, 2008), a phenomenon known as the 'Jack Sprat effect' (Onyekwelu and Harper, 1979; Cox, 1981). The possibility that the sexes modify their ecological niches had not been considered in any detail until recently, especially with regard to future offspring performance. By growing plants of *M. annus* in soil previously occupied by females or males, Sánchez-Vilas and Pannell (2010) found that plants grown in soil in which females had previously grown were significantly smaller in terms of total biomass than those grown in soil previously occupied by males. As discussed earlier, in this species, females are larger than males and therefore they may have depleted more resources from the soil than males. This form of 'niche construction' may occur in other cases of sexual size dimorphism in dioecious plants.

Evolution and genetics of sexual dimorphism

When dioecy evolves from hermaphroditism, females and males are expected to diverge and specialize to their respective unisexual conditions. This is because hermaphroditic plants cannot be simultaneously optimized for both female and male function. Therefore, when separate sexes evolve, constraints to gender specialization are relieved and the establishment of unisexuality is expected to be associated with sex-specific adaptation, particularly in reproductive traits. However, when the sexes have different optimal values for such traits, a shared genetic architecture can constrain them from evolving toward their respective trait optima (Fig. 5). However, sexual dimorphism can still evolve when such trade-offs exist, and this can involve sex-limited gene expression and the breakdown of strong intersexual genetic correlations (Rhen, 2000). Such divergence is facilitated by both natural and sexual selection (Lande, 1980). Indeed, these are the primary evolutionary processes responsible for the evolution and maintenance of sexual dimorphism, and although non-adaptive processes including drift and mutation can affect genetic variability in sexual dimorphism, they cannot by themselves explain its persistence (Lande, 1981; Kirkpatrick, 1982). Rather, sexual dimorphism results from the interplay between sex-specific adaptation and the breakdown of genetic correlations that constrain the independent evolution of traits subject to asymmetric (sex-biased) selection in females and males (Lande, 1979, 1980). Thus, the rate and extent of evolutionary change in sexually dimorphic traits will be strongly influenced by their underlying genetic architecture and the patterns of genetic variation and covariation available to selection. In this section, we review

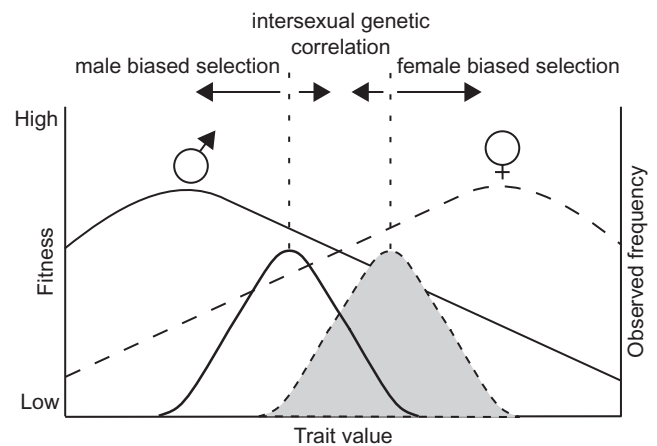


Fig. 5. A hypothetical scenario in which females (dashed lines) and males (solid lines) have different optima for the same trait, causing sex-biased selection (long arrows). A shared genetic architecture results in intersexual genetic correlations (r_{MF}) that constrain the independent divergence of females and males (short arrows) and cause their respective trait distributions (shaded curves) to be suboptimal. With $r_{MF} < 1$, conflict imposed by genetic constraint may be resolved through the evolution of sexual dimorphism (modified from Bedhome and Chippendale, 2008; pp. 185–194, with permission from Oxford University Press).

quantitative genetic approaches to the study of sexual dimorphism in dioecious plants (and see Geber, 1999; Meagher, 1999).

Quantitative genetic models

Consider two homologous traits, Z_f and Z_m , which affect fitness in both females and males. The standard expression for the change in the mean of a single trait, Z , is given by $\Delta\bar{Z} = R = h^2s$, where the response to selection (R) is equal to the trait's heritability (h^2) multiplied by the selection differential (s) for the trait, and s is the difference in the mean of the trait after (Z^*) and before (Z) selection. Heritability is given in the narrow sense as the proportion of phenotypic variance (V_p) attributable to additive genetic variance (V_A). This equation can be extended to predict the change in the means of two homologous traits in females and males, Z_f and Z_m , giving the following two expressions:

$$\Delta\bar{Z}_f = \frac{1}{2} \left(h_f^2 V_{p_f} i_f + h_f h_m r_{MF} V_{p_f} i_m \right)$$

$$\Delta\bar{Z}_m = \frac{1}{2} \left(h_m^2 V_{p_m} i_m + h_m h_f r_{MF} V_{p_m} i_f \right)$$

where the 1/2 accounts for the fact that autosomal traits receive equal contributions from each parent, h_f^2 and h_m^2 are the heritabilities for each sex, and i represents a standardized measure of sex-specific selection intensity. Of particular interest is the quantity r_{MF} , which describes the between-sex genetic correlation for traits Z_m and Z_f ; it is given by:

$$r_{MF} = \frac{\text{Cov}(M, F)}{\sqrt{V_{AM} V_{AF}}}$$

and determines the extent to which selection in one sex will cause a correlated response in the other: $r_{MF} = 1$ implies an exact correlated response.

Because between-sex genetic correlations constrain the independent evolution of female and male traits, a negative relationship has been predicted between the extent of sexual dimorphism and r_{MF} (Slatkin, 1984; Reeve and Fairbairn, 2001; Bonduriansky and Chenoweth, 2009). Studies of animal species report consistent negative relationships between r_{MF} and phenotypic sexual dimorphism (e.g. Bonduriansky and Rowe, 2005; Poissant *et al.*, 2008; Chenoweth *et al.*, 2010), and recent meta-analyses by Poissant *et al.* (2010) and Wyman (2012) suggest that this pattern holds for a variety of taxa. In contrast, there are few empirical estimates of r_{MF} in plants, and our understanding of the influence of genetic constraint on the evolution of sexual dimorphism is limited.

Delph *et al.* (2004a) reported that, in *S. latifolia*, the trait with the highest intersexual genetic correlations (petal-limb length) also exhibited the lowest levels of sexual dimorphism; however, this may, in part, be caused by petal-limb length not being highly correlated with flower number (Delph *et al.*, 2004a). Similarly, Ashman (2003) found that in gender-dimorphic *Fragaria virginiana*, a gynodioecious wild strawberry, flower number was the least sexually dimorphic trait and highly genetically correlated

between the sexes, suggesting a shared genetic architecture and constraint on the sex-specific divergence of this trait. Selection experiments in *S. latifolia* have also found that the between-sex genetic correlations for flower number were close to 1, and when this trait was selected in females it resulted in a significant and nearly equivalent change in both sexes (Meagher, 1999; Delph *et al.*, 2004b, 2010). The results of these studies provide evidence that genetic correlations can indeed cause coupled evolutionary responses in the sexes of dioecious plants.

Sexual dimorphism is prevalent among dioecious species, and this raises the question of how sexually dimorphic traits can diverge despite the constraints imposed by genetic correlations. One problem in conceptualizing the evolution of sexual dimorphism using the framework described by the univariate breeder's equation described above, is that the constraints imposed by r_{MF} are based on the assumption that genetic variances between the sexes are equivalent, whereas the available data suggest that this is often not the case (e.g. Cheverud *et al.*, 1985; Reeve and Fairbairn, 2001; Bonduriansky and Chenoweth, 2009; Poissant *et al.*, 2010). Furthermore, it ignores the fact that traits within each sex can be genetically correlated so that selection on a focal trait can cause a correlated response in a second trait, which may also be involved in sex-specific adaptation.

These problems are partially overcome by conceptualizing the evolution of sexual dimorphism using the framework developed by Lande (1980), who investigated the evolution of female and male traits using a modified version of the multivariate breeders equation and showed that the change in the mean of quantitative characters subject to sex-specific selection can be described by:

$$\Delta\bar{Z} = \frac{1}{2} \begin{pmatrix} \mathbf{G}_m & \mathbf{B} \\ \mathbf{B}^T & \mathbf{G}_f \end{pmatrix} \begin{pmatrix} \beta_m \\ \beta_f \end{pmatrix}$$

where \mathbf{G}_m and \mathbf{G}_f represent male and female genetic variance and covariance matrices, \mathbf{B} is the between-sex covariance matrix, and β_m and β_f are vectors of selection gradients for males and females. In this formulation, as in the univariate case, between-sex genetic covariance can constrain the independent evolution of traits in males and females, and \mathbf{B} can be thought of as the multivariate analogue of r_{MF} . When \mathbf{B} is similar to \mathbf{G} , little sex-specific divergence is possible.

An illuminating difference between the univariate and multivariate formulations is that because the matrix \mathbf{B} has both magnitude and direction, a positive between-sex genetic covariance can either increase or decrease the efficacy with which sexual dimorphism evolves depending on the orientation of \mathbf{B} with respect to \mathbf{G} . Thus, mechanisms that change the shape of either \mathbf{B} or \mathbf{G} can influence how dimorphism evolves, and moreover, the mode of selection (e.g. intersexual selection, natural selection) can affect the evolution of male and female traits by determining how selection gradients are specified for each sex. For example, sexual selection can alter male or female selection gradients by causing fitness to become a function of the distribution of phenotypes in the population (i.e. by causing fitness to become frequency dependent), and this can cause the sexes to respond asymmetrically to selection on traits that are correlated between them.

Studies that have used this multivariate framework for investigating the evolution of sexual dimorphism in animals have found that G matrices are often dimorphic (e.g. Rolff *et al.*, 2005; McGuigan and Blows, 2009; Lewis *et al.*, 2011; Gosden *et al.*, 2012), a pattern that seems to hold in several plant species as well (e.g. Ashman, 2003; Steven *et al.*, 2007; Campbell *et al.*, 2011). In *Silene latifolia*, Steven *et al.* (2007) estimated G matrices for females and males and found that although most traits were highly correlated, sex-specific G matrices differed in both magnitude and orientation, implying that even if the sexes were subject to similar selection regimes, they could exhibit different evolutionary responses. In wind-pollinated *Schiedea adamantis*, Campbell *et al.* (2011) reported significant between-sex differences in G matrices, which were probably due, in part, to lower genetic variation for flower number in females. These studies provide evidence against the assumption of equal female and male genetic variances and suggest that sex-specific responses to selection are often possible, even in the presence of intersexual genetic correlations. They also highlight how multivariate quantitative genetic approaches, which consider the interactions between intersexual covariances, sex-specific genetic variances, and selection gradients, can provide a more complete understanding of the evolution of sexual dimorphism.

Differences between plants and animals

Earlier reviews discussed quantitative genetic models in the context of sexual selection in animals and emphasized the need to consider three essential elements in conceptualizing the evolution of sexual dimorphism by sexual selection: female preference, mate choice, and the genetic correlation between them (Arnold, 1987; Bradbury and Andersson, 1987; Maynard Smith, 1991). In principle, there is no difficulty in applying these models to dioecious plants; however, there are important differences in the biology of plants and animals that may provide insights into why and how the evolution of sexual dimorphism differs between these groups. The extent to which mate choice operates in plants also warrants special consideration because of the indirect ways in which plants reproduce as a consequence of their immobility (Charlesworth *et al.*, 1987; Moore and Pannell, 2011). Indeed, the indirect nature of plant sexual interactions may be part of the explanation for why most plants show less extreme sexual dimorphism than animals.

Intersexual interaction in flowering plants is necessarily indirect and is mediated by the vectors of dispersal through which pollen is transferred and received (e.g. animals, wind, and water). This can cause the strength of the relationship between secondary sexual characters (e.g. flower size) and mating success to be reduced because of the uncertainties involved in pollen delivery and receipt, and this will reduce the strength of sexual selection (i.e. skew the shape of β_m of β_f) and result in a lower optimal trait value for the character in question. Further, because pollinators may often select for similar traits in both sexes, this should weaken the strength of between-sex disruptive selection and limit the divergence of attractive characters or floral rewards.

Opportunities for mate choice and male–female competitive interactions may still exist, however, and these could become more important once pollen grains are deposited on stigmas.

However, micro- and megagametophytes are necessarily dimorphic and so the effects of inter- or intrasexual selection at this stage might not be expected to cause secondary sexual dimorphism in traits expressed in sporophytes. Nevertheless, owing to significant overlap in gene expression between the sporophytic and gametophytic stages of the life cycle in plants (~60%; Mascarenhas, 1999), gametophytic selection may have direct effects on pollen characteristics and could indirectly influence the evolution of male sporophyte characters and, hence, sexual dimorphism. Thus, to the extent that mate choice occurs in plants, such male–female interactions must occur primarily in the post-pollination stage of the life cycle where the interaction may be less likely to produce exaggerated sexual dimorphism.

The typically weaker sexual dimorphism in plants than animals may also be explained by the recent evolutionary origins of dioecy in most lineages. When dioecy evolves from hermaphroditism and the sexes are initially monomorphic with respect to homologous characters, intersexual genetic correlations should be quite strong and could interfere with female and male trait divergence. Indeed, much of the genetic variation available for the evolution of sexual dimorphism is likely to have been initially shared by the sexes after the establishment of dioecy, and the recent origins of unisexuality in some lineages may mean that there has not been sufficient time for selection to break down intersexual genetic correlations. This hypothesis predicts a relationship between the degree of dimorphism and the age of dioecious lineages. As discussed earlier, other factors including the pollination system of dioecious species (e.g. animal versus wind pollination) may also influence the degree of morphological divergence, and comparative studies would be useful to investigate further the factors responsible for the patterns and degree of sexual dimorphism in plants.

Sex chromosomes and sexual dimorphism

The transition to dioecy has been associated with the evolution of sex chromosomes in some dioecious plant species (Charlesworth *et al.*, 2005), and theory suggests that they can facilitate the evolution of sexual dimorphism (Rice, 1984). This can occur by several mechanisms. One is through the influence of sex chromosomes on the genetic variance and covariance structures of females and males. The multivariate equation for the evolution of sexual dimorphism developed by Lande (1980) assumes that the genes involved in sexual dimorphism are linked to autosomes, but sex linkage can change the structure of female and male genetic variances because of the different number of sex-linked genes in each sex. For example, when the heterogametic sex (e.g. XY males or ZW females) contain only one allele per sex-linked locus (i.e. when they are hemizygous for genes on the sex chromosomes), it can express the genes regardless of dominance or recessivity, whereas the homogametic sex (e.g. XX females or ZZ males) contains two alleles for each sex-linked locus and can therefore be heterozygous or homozygous. It follows that the genetic variance contributed by sex-linked genes is asymmetric between the sexes and can be as much as 2-fold higher in XY males or ZW females (Lynch and Walsh, 1998). Such differences can translate into sex-specific responses to selection. Similarly, when genes linked to sex chromosomes or autosomes are sex

biased in expression, as might occur as a result of sex-specific selection, this can select for regulatory mechanisms that further limit expression levels in females or males (Ellegren and Parsch, 2007). In particular, when expression levels are simultaneously beneficial in one sex but deleterious in the other (i.e. sexually antagonistic), then, depending on the magnitude of gene expression and how deleterious their effects are, sex-limited expression can be selectively favoured to offset the negative fitness consequences of expressing these genes in both sexes.

Sex-linked genes with sexually antagonistic effects play an important role in theoretical models of plant sex chromosome evolution by causing selection against recombination between loci on newly evolving sex chromosomes (Charlesworth *et al.*, 2005). In addition, they play an important role in many aspects of sexual conflict theory (Armqvist and Rowe, 2005) and can be particularly important in contributing to sex-specific responses to selection because they decouple the genetic architecture of female and male traits, thus helping to resolve the conflict that arises when the sexes have different fitness optima but high intersexual genetic correlations.

Rice (1984) used a genetic model to investigate the relationship between sexual dimorphism and sex chromosomes, and predicted that genes with sexually antagonistic effects should be disproportionately located on sex chromosomes. His prediction stems from the conclusion that alleles of sex-linked genes can spread through dioecious populations even when the deleterious effects to one sex outweigh the benefits to the other. Subsequent theory on the evolution of sexual dimorphism through sexual selection has focused on this kind of sexual antagonism, but many of these models have assumed that traits under sexual selection are under the control of just one or a few genes, and often these genes are assumed to be located on the autosomes (Chapman *et al.*, 2003). Nonetheless, sexually dimorphic phenotypes are often associated with genes on the sex chromosomes because such genes have sex-biased transmission and genomic distributions.

The occurrence of sexual antagonism is of particular interest when it involves the X chromosome, as genes on this chromosome can preferentially evolve sex-biased fitness effects relative to autosomal genes (Rice, 1984). Imagine, for example, a sexually antagonistic mutation on an autosome that has a significant effect on the fitness of heterozygotes. When the fitness effects of such a mutation are positive in females and negative in males, the mutation can spread under positive selection only when the beneficial effects in females outweigh the deleterious effects in males (Vicoso and Charlesworth, 2006). However, if this mutation occurs on the X chromosome, its deleterious effects will only be expressed one-third of the time (i.e. in males) and hence the probability of such a mutation reaching fixation is greater when it occurs on an X chromosome than when it occurs on an autosome (Rice, 1984). It follows that the X chromosome can accumulate such female-benefit genes at a faster rate, and the 'feminization' of this chromosome might make it an evolutionary hot-spot for genes involved in sexual dimorphism (Gibson *et al.*, 2002).

Empirical work has attempted to determine whether sex chromosomes do indeed influence sexual dimorphism with an effect disproportionate to their size (reviewed in Mank, 2009).

In *Drosophila melanogaster*, there are reports that genes with sex-biased expression have non-random genomic distributions, with X chromosomes harbouring fewer genes with male-biased expression (Parisi *et al.*, 2003; but see Fitzpatrick, 2004). On the other hand, comparative studies in birds do not support an association between sex chromosomes and sexually selected dimorphic traits (Mank *et al.*, 2006). In plants, sexually dimorphic gene expression has been detected in both vegetative (Zluvova *et al.*, 2010) and floral (Muyle *et al.* 2012) characters in *Silene latifolia*, and there is evidence that some genes on the X chromosome of this species are male biased in their expression (Muyle *et al.*, 2012), suggesting that these genes may be involved in sexual antagonism. Genetic mapping in this species also suggests that genes in the recombining pseudoautosomal regions (PARs) may be involved in the evolution of sexually dimorphic and sexually antagonistic traits (Scotti and Delph, 2006; Delph *et al.*, 2010; Otto *et al.*, 2011). In particular, sex-specific quantitative trait loci map disproportionately to PARs, suggesting that in this species genes involved in sex-specific functions that recombine between sex chromosomes might have evolved sex-limited expression. There is still much work to do on the influence of sex-linked genes on sexual dimorphism, but recent evidence suggests that the presence of sex chromosomes can have important effects on sex-specific divergence and this can in turn influence the expression and distribution of genes underlying dimorphic traits.

Future studies

Our review has identified several topics that warrant further investigation. To conclude we highlight three research themes that we believe would be especially profitable in providing new insights on the evolution of sexual dimorphism in plants.

To our knowledge there have been no comparative studies of variation in plant sexual dimorphism. These could involve examining the ecological and life-history correlates of sexual dimorphism to address a range of unanswered questions. Does the degree and direction of sexual dimorphism differ between short- and long-lived dioecious species? Is dimorphism more strongly developed in species that occupy benign versus stressful environments? Do wind- versus animal-pollinated species differ in the extent of sexual dimorphism? Is dimorphism more strongly developed in older dioecious lineages? The increasing appearance of phylogenies of dioecious groups (e.g. Soza *et al.*, 2012) should enable these types of questions to be addressed.

Future microevolutionary investigations are needed on the extent of intraspecific variation in sexual dimorphism. Most studies of sexual differences have involved a limited sample of populations, and little is known about the patterns of geographical variation in sexual dimorphism, especially in species that occupy a wide range of environments. Where population differentiation in sexual dimorphism has been reported (e.g. Barrett, 1992; Kohorn, 1995), it has been at the phenotypic level, and it is not known if the differences simply represent plastic responses to local environmental conditions, or whether there is a significant genetic component to the observed differences among populations (Delph *et al.*, 2002; Delph and Bell, 2008). Identifying

genetic differentiation among populations in the degree of sexual dimorphism, and determining the local environmental conditions in which populations occur, could provide important insights into the relative importance of natural and sexual selection in shaping patterns of dimorphism.

Finally, there is a considerable amount of work to be done on understanding the genetic architecture of sexual dimorphism. Progress has been made in understanding the genes involved in the expression of dimorphic traits in a few model systems (e.g. Delph *et al.*, 2010), and the use of next-generation sequencing now enables such analyses in non-model organisms. Future studies would benefit both from quantitative genetic studies, which estimate the influence of sex-specific genetic variance and covariance structures, and from genetic mapping and gene expression experiments to investigate the role of sex-linked and sexually antagonistic genes in sexual dimorphism. Although we have emphasized the role of sex chromosomes in the evolution of sexual dimorphism, most dioecious species do not possess sex chromosomes and yet are sexually dimorphic. Future studies of the genetic architecture of sexual dimorphism in species without sex chromosomes would be valuable for understanding how rapidly sexual dimorphism can evolve in lineages where dioecy is of recent origin.

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