
Trait Transitions in Explicit Ecological and Genomic Contexts: Plant Mating Systems as Case Studies

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Abstract

Plants are astonishingly diverse in how they reproduce sexually, and the study of plant mating systems provides some of the most compelling cases of parallel and independent evolutionary transitions. In this chapter, we review how the massive amount of genomic data being produced is allowing long-standing predictions from ecological and evolutionary theory to be put to test. After a review of theoretical predictions about the importance of considering the genomic architecture of the mating system, we focus on a set of recent discoveries on how the mating system is controlled in a variety of model and non-model species. In parallel, genomic approaches have revealed the complex interaction between the evolution of genes controlling mating systems and genome evolution, both genome-wide and in the mating system control region. In several cases, major transitions in the mating system can be clearly associated with important ecological changes, hence illuminating an important interplay between ecological and genomic approaches. We also list a number of major unsolved questions that remain for the field, and highlight foreseeable conceptual developments that are likely to play a major role in our understanding of how plant mating systems evolve in Nature.

Keywords

Selfing • Outcrossing • Self-incompatibility • Hermaphroditism • Dioecy • Gynodioecy • Androdioecy • Convergent evolution

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2.1 Plant Mating Systems as Models to Study Evolutionary Transitions

Evolutionary transitions are discrete changes to biological traits that spread to replace ancestral conditions. A fascinating issue in evolutionary

biology is to understand why replicated character state transitions occur among unrelated lineages and whether this may indicate either similar selective mechanisms and functional convergence or similar genomic constraints. A powerful way to address these questions is to study model systems in which the nature of selective processes can be clearly identified. The study of mating systems (the suite of traits affecting mating patterns among sexually reproducing individuals) is a particularly relevant field of investigation to address this issue because of their astonishing diversity, especially in plants, and the many parallel and independent transitions that have been described. This general definition of mating systems collectively refers to all mechanisms that affect who in a species is having sex with whom (Billiard et al. 2011), and includes the prevalence of *selfing* versus *outcrossing*, the occurrence of distinct classes of interbreeding individuals such as genders (male, females and hermaphrodites), mating types in fungi and algae and *self-incompatibility* phenotypes. Mating systems crucially matter from a genetic perspective because they control the way genes are transmitted from one generation to the next (mechanism of inheritance) and hence determine genome diversity and organization, as well as the potential for adaptive or non-adaptive evolution. Mating systems also matter from an ecological perspective because they determine the quantity and quality of propagules available for dispersal and hence metapopulation dynamics, including the capacity to colonize new habitat patches. They also directly impact key interspecific interactions such as the types of resources transferred between plants and their pollinators. Putting aside transitions from sexual to asexual reproduction (reviewed in Glémin and Galtier 2012), our review will focus on two specific types of transitions: (1) that between allogamy (where fertilization occurs between distinct individuals) and autogamy (where offspring are produced by self-fertilization) and (2) that between *hermaphroditism* (where all individuals in a species belong to the same (co)sexual phenotype) and dioecy (where individuals belong

to two separate sexual phenotypes, males and females) and their possible intermediate steps.

Phylogenetic mapping of mating system variation across Angiosperms has revealed that the different transitions occur at strikingly contrasted rates. For instance, heterostyly, which is a common form of heteromorphic *self-incompatibility*, has evolved at least 23 times independently within Angiosperm families (Lloyd and Webb 1992), and some authors have even suggested that heterostyly may have evolved as a derived trait within some genera (Graham and Barrett 2004). The rate of loss of heterostyly has not been quantitatively estimated, but homostylous species derived from heterostylous ancestors are common, suggesting that this reverse transition is also frequent (Barrett and Shore 2008). Homomorphic *self-incompatibility* is associated with no obvious morphological differences among *self-incompatibility* (SI) phenotypes, and so data on its phylogenetic distribution are more difficult to obtain. Still, homomorphic SI has been documented in at least 94 different families, and the detailed molecular analyses that have been conducted in five families (Brassicaceae, Papaveraceae, Rosaceae, Plantaginaceae, and Solanaceae) revealed three completely distinct molecular modes of action (Takayama and Isogai 2005), strongly suggesting that they represent as many independent emergences. The reverse transition, i.e. the loss of SI and ensuing shift to autogamy, has been considered as the most prevalent transition in plant evolution (Stebbins 1974). In Solanaceae, Goldberg et al. (2010) estimated that the rate of transition to *selfing* was as high as 0.55 transitions per lineage per million years, and Igic et al. (2008) estimated that this rate of loss was nearly 70 times higher than the rate of gain. Even more drastically, the data suggest that the asymmetry is so strong that the loss can be considered as irreversible within this family. *Dioecy* occurs in about 5–10 % of all species, but is present in half of Angiosperm families and probably appeared from hermaphroditic ancestors many times independently (Renner and Ricklefs 1995).

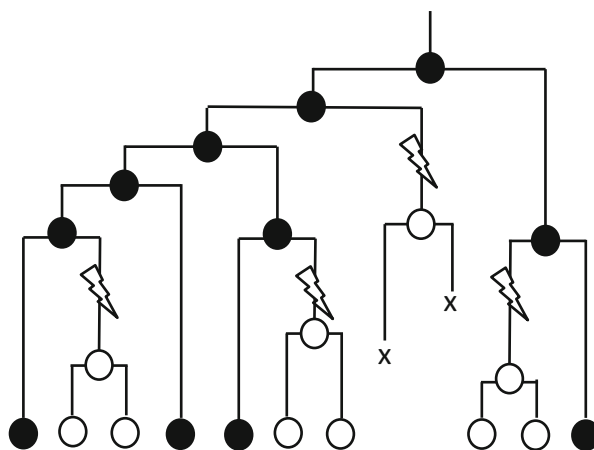


Fig. 2.1 The relative abundance of plant mating systems depends on the transition rates among mating systems as well as on their impact on rates of species diversification. The exhaustive phylogeny of a clade is represented, including extinct taxa, together with current and ancestral states of a trait related to the mating system (e.g. nodes with *black dots* correspond to self-incompatible, SI, species and those with *white dots* correspond to self-compatible, SC, species). Transitions between mating sys-

tem traits are indicated with the symbol ⚡ (here only transitions from SI to SC were observed). In this clade, the currently most abundant mating system is SC, which is due to a high rate of transition to SC and a high rate of speciation of SC lineages. However, most ancestral nodes are SI, which may suggest that SC taxa are short-lived and have higher rates of extinction (see text and see Goldberg et al. 2010)

Within the Asteraceae, *dioecy* seems to have been derived from *hermaphroditism* at least 5–9 times independently, while the reverse transition from *dioecy* back to *hermaphroditism* seems to have occurred only 0–2 times independently (Torices et al. 2011). With an estimated 133 transitions between *hermaphroditism* and *dioecy*, Bryophytes exhibit remarkable lability in sexual systems, and again the transition rate from *hermaphroditism* to *dioecy* was twice as high as the reverse transition (McDaniel et al. 2013). Overall, beside the great disparity in the rates of transitions, a striking feature is that most of them seem to be asymmetrical or even unidirectional.

This observation raises the question of the ecological and evolutionary factors influencing the rates of transitions between mating systems. Beside extrinsic (adaptive) causes such as Fisher's transmission advantage (Fisher 1941), the strength, genomic architecture and lability of *inbreeding depression* and ecological correlates associated with shifts of the mating system, intrinsic causes have also been invoked such as molecular constraints, possibly making some transition routes more likely than others.

In addition, the distribution of plant mating systems in extant species also depends on their impact on the relative evolutionary success of plant lineages. A key step in quantifying relative evolutionary success has been brought recently by methodological innovation in phylogenetic methods allowing to quantify the relative net diversification rate of lineages with contrasting life history traits, in particular allowing estimation of the relative rates of speciation and extinction (Maddison et al. 2007; FitzJohn 2010; Stadler 2011, Fig. 2.1). These approaches have been used for instance to determine the relative success of self-incompatible versus self-compatible lineages in Solanaceae (Goldberg et al. 2010; Goldberg and Igic 2012), of hermaphrodite versus dioecious mosses (McDaniel et al. 2013) or diploid versus polyploid lineages (Mayrose et al. 2010). Getting quantitative estimates, for instance for the relative rates of extinction of lineages with different mating systems, stimulates further theoretical studies to understand the causes of such differences. One important challenge is to develop models that link demographic processes

(species extinction) with population genetic features (e.g. *inbreeding depression*, probability of fixation of adaptive mutations).

Plant mating systems have been a focus of intensive research in evolutionary biology for nearly 150 years, since Darwin's seminal contribution on orchids (Darwin 1876, 1877), including aspects of theoretical analysis, phylogeny, ecology, and genetics. In parallel, major progress have been made on how mating systems are controlled at the genomic and physiological levels. In this chapter, we review how these two fronts of advances are beginning to merge, highlighting in particular how a detailed understanding of the genomic architecture of plant mating systems is providing important insight into the relative importance of extrinsic vs. intrinsic causes of plant mating system transitions and how these transitions affect the evolutionary success of plant lineages. We first focus on theoretical predictions regarding the consequences of several aspects of the genomic architecture of the mating system itself and that of *inbreeding depression* on the rates of transition between mating systems. We then review a set of recent empirical studies that identified mutations having caused mating system transitions in model and non-model species, and confront the nature of these causal mutations with theoretical predictions. Finally, we review another set of recent studies that demonstrate that mating system transitions are associated with major shifts in the patterns of genome organization and evolution, both genome-wide and in the regions involved in mating system determination.

2.2 Genomic Architecture and Plant Mating Systems Transitions: What Does Theory Predict?

In 1977, Lloyd suggested that the end product of evolution generally does not depend on how traits are determined genetically, and thus proposed that phenotypic models should be largely sufficient to investigate trait evolution in a given ecological context. He recognized, however, that

phenotypic models are not sufficient if one wants to predict the speed of evolution or the influence of other evolutionary forces, especially drift and mutations, whence taking into account genetic and genomic details into models might be important. Interestingly, Lloyd (1975, 1977) relied heavily on the example of mating system evolution to illustrate his purpose, and argued that the outcome of mating system evolution only depends on how fitness through male and female reproduction is maximized, without regard for how it is controlled at the genomic level. Recent theoretical models of mating system transitions in plants have strongly challenged this view, showing that the genetic and genomic details are indeed important, in two ways: the genetic determination of the mating system itself and the genetic architecture of *inbreeding depression*. In this section, we will assess the importance of these two points from a theoretical point of view, especially regarding the issue of variability of transitions rates in plant mating systems.

2.2.1 Transitions Between Outcrossing and Selfing: The Example of Homomorphic Gametophytic Self-Incompatibility in Angiosperms

The genetic determination model for homomorphic SI in Angiosperms is generally assumed to be bipartite: two linked non-homologous genes at a single locus, the S-locus, respectively coding for the pollen and pistil parts of the SI response (Fig. 2.2; note that alternative models with more than one locus are more appropriate in some groups such as the Poaceae). This explicit genetic architecture has dramatic consequences regarding theoretical expectations of when and how SI should be gained and lost.

Loss of SI. Whether a mutation making individuals self-compatible invades and eventually goes to fixation, leading to a loss of SI, mainly depends on five parameters: allelic diversity at the S-locus, the level of *inbreeding depression*, the extent of

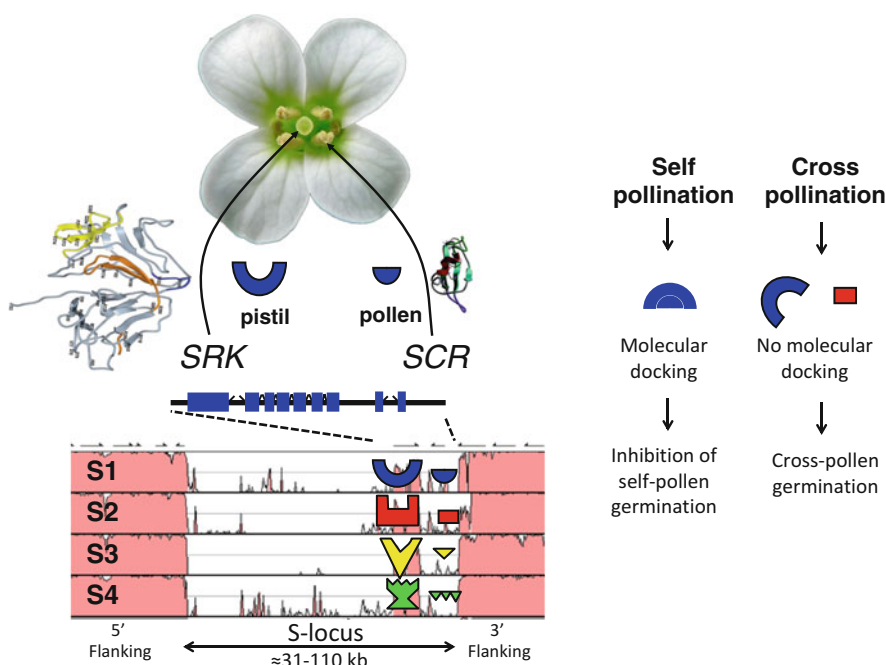


Fig. 2.2 Self-incompatibility in the Brassicaceae at a glance. SI specificity in the Brassicaceae is controlled by two tightly linked genes, *SCR* and *SRK* expressed in anther tapetum and in stigmatic papilla, respectively, that function as a molecular lock-and-key mechanism. When produced by the same S-haplotype (following either self-pollination or cross-pollination by an individual expressing the same S-haplotype), the cognate *SCR* and *SRK* proteins physically interact and activate a downstream signalling cascade (including the *ARC1* gene and several others) that disrupts proper pollen hydration, ultimately preventing fertilization. Upon cross-pollination by an individual expressing a different S-haplotype, the two pro-

teins do not physically interact, allowing fertilization to proceed. The genomic region containing the various lock-and-key combinations of *SCR* and *SRK* (represented by distinct shapes and colours) is characterized by extreme sequence divergence, as shown by the complete lack of sequence identity in a region of ca. 31–110 kb (conservation plots at the *bottom*; size varies across the different S-haplotypes, Goubet et al. 2012) (3D models of *SCR* and the extracellular domain of *SRK* are reprinted from Chookajorn et al. (2003) and Naithani et al. (2007) respectively, published with kind permission of © National Academy of Sciences, U.S.A. 2003 and 2007. All Rights Reserved)

self-pollination, the level of *pollen limitation* and that of *pollen discounting*. In brief, the invasion of a self-compatible mutation is favoured when *selfing* is high and efficient (i.e. if *inbreeding depression* is low and *pollen limitation* is high), and if the pollen received through outcrossing is also efficient (i.e. if allelic diversity and *pollen discounting* are low). Four different mutational events can be thought of, that all would result in a self-compatible mutant: the mutation can affect the pollen part, the pistil part, both parts at once, or a modifier locus unlinked to the S-locus (e.g. a gene involved in the biochemical processes underlying the SI response). For a given set of parameter values, the conditions under which the

mutation invades and becomes fixed were shown to depend on the type of mutations (Charlesworth and Charlesworth 1979; Uyenoyama et al. 2001; Porcher and Lande 2005b). First, the conditions for the invasion of a mutation affecting both pollen and pistil parts are less limited than for the other mutation types, especially regarding *inbreeding depression*. This is because such a mutation benefits from the transmission through both male and female functions. Second, if *pollen limitation* is relatively low, a mutation affecting the pollen part only is more likely to invade than if affecting the pistil part only, because self-compatible pollen benefits both from *selfing* and from outcrossing with all individuals in

the population, while a self-compatible pistil is favoured only by *selfing*. Last, a mutation affecting an unlinked modifier gene is less likely to invade, especially regarding *inbreeding depression*, because individuals bearing this mutation have the same fitness as *selfing* individuals in a self-compatible population. In short, all things being equal and regarding only selection strength, the mutational event causing the loss of SI would be expected to affect most probably both pollen and pistil genes, followed by a mutation affecting the pollen gene only, a mutation affecting the pistil part only, and finally affecting an unlinked modifier gene.

Gain of SI. The reverse transition, i.e. that from a self-compatible to a self-incompatible population seems difficult for at least two reasons. First because it implies the independent evolution of pollen and pistil SI genes, and second because it requires a very high level of *inbreeding depression*. Yet, the very existence of the many independent transitions observed in Angiosperms (Takayama and Isogai 2005) demonstrates that conditions should exist under which such events can occur. The appearance of a functional SI system can be decomposed in two evolutionary steps. First, two genes should appear at the S-locus, expressed in pollen and pistil, respectively, which recognize each other and prevent fertilization when recognition occurs. Second, the S-locus diversifies and becomes fully functional, excluding self-compatible genotypes. Little is known theoretically about the first step (appearance of a SI haplotype), but the conditions under which a self-compatible genotype can be maintained in polymorphism with functional SI alleles have been studied. The maintenance of polymorphism is important since it is necessary for the evolution of new SI haplotypes and thus the evolution towards a fully functional SI system (Uyenoyama et al. 2001). Several models have shown that a self-compatible haplotype can be maintained in polymorphism with SI alleles, but under restricted conditions, except when the number of SI alleles is low (Charlesworth and Charlesworth 1979; Porcher and Lande 2005b). Interestingly, polymorphism is easier to main-

tain when self-compatible haplotypes are due to mutation in the pollen part than in the pistil part (Uyenoyama et al. 2001; Gervais et al. 2011). This implies the simple prediction that most probably the diversification of the S-locus occurs sequentially by the appearance of new SI specificities at the pollen gene.

2.2.2 Transitions Between Dioecy and Hermaphroditism

Two main hypotheses have been proposed to understand the transitions between *hermaphroditism* and *dioecy*, i.e. separate sexes in a population, namely the resource allocation theory and the two-steps evolution hypothesis. These hypothesis mostly differ by the nature and genetic architecture of the mutations that cause the transition. Under both scenarios, *inbreeding depression* plays an important role since it decreases the fitness of hermaphrodites and thus makes more difficult the invasion of hermaphrodites into populations that already have separate sexes, or conversely facilitates the invasion of male or female individuals into hermaphroditic populations.

The resource allocation theory (Charnov 1982). This theory states that fitness through female and male reproduction can vary and thus differential resource allocation between the sexes can be favoured or disfavoured by natural selection. It is based on two key assumptions. First, there must be a fitness trade-off between male and female functions, i.e. a good pollen producer cannot also be a good ovule provider, and vice-versa. No clear empirical evidence for the occurrence of such trade-off has been demonstrated, although there are several reports of negative genetic correlations between investment in male and female functions in hermaphrodites (reviewed in Ashman 2003). Second, because it is based on models of evolutionary stable strategies (ESS), this theory explicitly assumes that the relative investment in male and female functions varies as the result of mutations that each has a small phenotypic effect. To the best of our knowledge, no empirical

study has tried to identify the genetic architecture of this trait, which would allow testing this basic prediction in the flowering plants.

The two steps hypothesis. It is generally considered that it is impossible for a single mutation to cause the evolution of *dioecy* (Charlesworth and Charlesworth 2010a) because a single mutation entirely abolishing both the male and the female functions at once would lead to fully sterile individuals, and because it is difficult to imagine a single mutation that would sterilize the male function in some individuals and the female function in some others. Hence, the “two steps hypothesis” posits that the transitions from *hermaphroditism* to *dioecy* are caused by two successive evolutionary steps: the invasion and spread of a male-sterility mutation followed by a female-sterility mutation, in either order (Charlesworth and Charlesworth 2010a). The backward transition from *dioecy* to *hermaphroditism* can also be caused by two evolutionary steps restoring male and female fertilities, respectively. Since it is generally thought that the ancestral mating system in Angiosperms is *hermaphroditism*, we will focus on the transition towards *dioecy* (analogous predictions can easily be made for the backward transition). Two pathways can be considered, depending on whether the first mutation causes male or female sterility. If the first mutation causes male sterility, then transient populations are composed of hermaphroditic and female individuals, a mating system that is called *gynodioecy*. If the first mutation causes female sterility, then hermaphroditic and male individuals will coexist in transient populations, a mating system that is called *androdioecy*. Following this scenario, *androdioecy* and *gynodioecy* are seen as necessary intermediates. A male or female sterility mutation can invade a population if it increases female or male fitness, respectively, of the unisexual individuals, i.e. a female sterility mutation must increase male fitness while a male sterility mutation must increase female fitness. The advantage of the sterility mutation to one sex must more than compensate the loss in fitness to the other sex,

which is possible only if plants are able to reallocate resources.

The genetic architecture of male and female sterility mutations critically matters for which pathway is most likely to occur. In most Angiosperms, mitochondria and chloroplasts are transmitted by female gametes only, while the nuclear genome is typically transmitted via both male and female gametes, hence creating a sexual asymmetry in the transmission of the two genomes. Accordingly, *gynodioecy* can be controlled by male sterility mutations that are either nuclear or cytoplasmic (Dufaÿ and Billard 2012), although the relative proportion of species with nuclear or cytoplasmic *gynodioecy* is not known. In contrast, only nuclear *androdioecy* is known so far. The conditions for the invasion and maintenance of nuclear mutations are identical regardless of whether they affect the male or female functions: the fitness of the sex that remains fertile must be at least twice that of the hermaphrodites. The case of cytoplasmic mutations, however, is strikingly different and involves a classical example of genomic conflict. Because cytoplasmic mutations affecting the male function would not suffer from any reduction in fitness (the cytoplasm is maternally transmitted), cytoplasmic *gynodioecy* can arise as soon as the fitness of females gets somewhat higher than that of hermaphrodites, which is a less stringent condition than that expected for nuclear *gynodioecy* (Charlesworth and Charlesworth 2010a). The evolutionary stability of cytoplasmic *gynodioecy*, however, is more difficult to account for. Indeed, fixation of a male sterility mutation would lead to a population composed of female individuals only, which would go extinct by lack of pollen for fertilization. Hence, the sex-ratio bias would create strong selective advantage for any mutation in the nuclear genome able to restore male fertility. If both the cytoplasmic male sterility mutation and the nuclear restorers of male fertility become fixed in the population, the population goes back to *hermaphroditism*. In contrast, the two mutations can stably (or cyclically) segregate in the population, leading to evolutionarily stable *gynodioecy* (Gouyon et al.

1991). Overall, because the general conditions for the emergence and maintenance are generally less stringent for *gynodioecy* than for *androdioecy*, theoretical models predict that under the two-steps hypothesis, the first step leading to *dioecy* should be through *gynodioecy*, most likely through a male sterility mutation occurring in the cytoplasmic genome.

Once *gynodioecy* or *androdioecy* has evolved, *dioecy* may then result from the fixation of mutations that decrease resource allocation to the still fertile sex in hermaphrodites. Interestingly, the latter mutations are only expected to invade the population if they are in complete linkage disequilibrium with the initial mutation causing either *gynodioecy* or *androdioecy*. In fact, recombination would produce offspring with both sterility mutations in their genome, which would therefore be fully sterile. Recombination is therefore expected to be extremely low between male and female sterility mutations, involving genes that were either initially adjacent or have become adjacent through translocation. From a genomic point of view, we might therefore expect the evolution of genomic regions determining maleness and femaleness, that may eventually evolve into *bona fide* sexual chromosomes.

Other routes: via monoecy, subdioecy or distyly. Few models have investigated the evolution from *hermaphroditism* to *dioecy* by these alternative evolutionary pathways, even though they are supported by empirical evidence (reviewed in Pannell and Verdu 2006). *Monoecious* populations are composed of hermaphroditic individuals but with separate male and female flowers. It has been suggested that a transition from monoecy to *dioecy* might be possible simply by the successive fixation of small effects mutations changing the ratio between male and female flowers within individuals (Charlesworth and Charlesworth 1978; Lloyd 1980). This pathway is related to the resource allocation theory (see above) but here the genes underlying the transition are suggested to be the ones controlling the number of flowers of a given sex. Subdioecy refers to populations that regularly contain imperfectly sexually differentiated individuals of either or both sexes,

in addition to strictly unisexual individuals. Ross (1982) analyzed a population genetic model assuming two genes affecting pollen and ovules production, and assuming a resource allocation trade-off. The model makes the important prediction that evolution towards subdioecy is easier when the underlying genes are genetically linked, which makes a readily testable hypothesis for genomic investigation. Distyly has been suggested as another possible pathway for the transition between *hermaphroditism* to *dioecy*. Specifically, if the two morphs differ in how efficiently they export pollen, for instance because physical contact of the pollinator body with anthers is more important in one morph than in the other, mutations further increasing male reproduction at the cost of female reproduction in the morph that is already better at exporting pollen would become fixed. In response, mutations increasing female reproduction at the cost of male reproduction in the other morph would also become fixed, eventually leading to fully specialized male and female individuals derived from the two morphotypes (Lloyd 1979). A prediction of this model is that such mutations are expected to appear in linkage with the locus determining the morphotypes.

2.2.3 Importance of the Genomic Architecture of Inbreeding Depression

Inbreeding depression is believed to be one the most important evolutionary forces in the evolution of mating systems for at least two reasons. First, it decreases Fisher's "automatic" transmission advantage, whereby *selfing* genes are transmitted 50 % more efficiently to the progeny than genes preventing *selfing* (Fisher 1941). Second, *inbreeding depression* potentially decreases the fitness of hermaphrodite individuals, which is the only category of individuals able to self, leaving male or female individuals relatively unaffected (the highest possible level of inbreeding is obtained when a hermaphrodite reproduces by *selfing*). Accordingly, most models of mating system evolution take *inbreeding depression* into account. Although the issue was

highly controversial in the 1970s, it is now widely accepted that *inbreeding depression* is mainly due to the expression of mutations that are deleterious and at least partially recessive: in inbred individuals, such mutations are more often homozygous and thus expressed than in outbred individuals (Charlesworth and Charlesworth 1987). A difficulty then appears: deleterious mutations, once expressed in homozygous individuals, can be eliminated by natural selection, a process that is called purging. The purging of deleterious mutations is more efficient in inbred, especially *selfing*, populations. The consequence of purging is that *inbreeding depression* is expected to be lower in *selfing* than in outcrossing populations (Roze and Rousset 2004). Theoretical investigations that explicitly modeled *inbreeding depression* and purging showed that the maintenance of outcrossing is possible only under stringent conditions (e.g. Porcher and Lande 2005a), the maintenance of SI especially being difficult (Porcher and Lande 2005b). In fact, purging is efficient in selfers mostly when selection is strong (deleterious mutations have large effect and are not too recessive), while *inbreeding depression* can remain high in the case of mildly deleterious and recessive mutations (Charlesworth and Willis 2009), especially if deleterious mutations appear at multiple loci and if there is epistasis. It has therefore been proposed that during the transition from outcrossing to *selfing*, deleterious mutations causing *inbreeding depression* should be purged, making the reverse transition (back to outcrossing) less likely to occur. Based on the dynamics of *inbreeding depression* caused by recessive deleterious mutations, theory therefore predicts that transitions from outcrossing to *selfing* should be unidirectional.

Two other processes can however permit the maintenance of high *inbreeding depression* even in *selfing* populations. The first process is overdominance, whereby heterozygotes are more fit than homozygotes, allowing polymorphism (and thus *inbreeding depression*) to be maintained. The second process is associative overdominance where there is strong linkage between deleterious mutations, in particular in genomic regions with low recombination. In

such case, some haplotypes can accumulate a different suite of linked deleterious mutations from that accumulated by other haplotypes. It has been suggested that non-recombining mating system control regions, such as the S-locus or heteromorphic sex chromosomes, can accumulate such different suites of linked deleterious mutations, which have been called the “sheltered load” (Uyenoyama 2003). Few models have analyzed the importance of such phenomena on the evolution of mating systems. Charlesworth and Charlesworth (1990) showed that outcrossing may be more easily maintained when *inbreeding depression* is due to loci at which heterozygotes are advantaged. Porcher and Lande (2005b) showed that the existence of a sheltered load can facilitate the maintenance of SI. To our knowledge, no model has investigated the case of the transition between *hermaphroditism* and *dioecy*. While this clearly highlights the central importance of *inbreeding depression*, very little is known empirically about its key parameters, i.e. the distribution of the effects of deleterious mutations and of their dominance coefficient (see Sect. 2.5).

2.2.4 Long-Term Evolutionary Consequences of Mating System Transitions

Why and when should selfing be an evolutionary dead-end? A long-standing debate regarding the transition between *selfing* and outcrossing is whether the mating system affects the diversification rates of species, i.e. whether extinction and speciation rates depend on the mating system of a species. In fact, based on the distribution of *selfing* species in phylogenies, which are more frequent at the leaves of phylogenetic trees (Fig. 2.1), it has been suggested that *selfing* should be an evolutionary dead-end (Stebbins 1974). Two evolutionary processes have been proposed (Takebayashi and Morrell 2001). First, *selfing* and outcrossing species may differ in the rate at which they accumulate deleterious mutations. Indeed, the effective population size of *selfing*

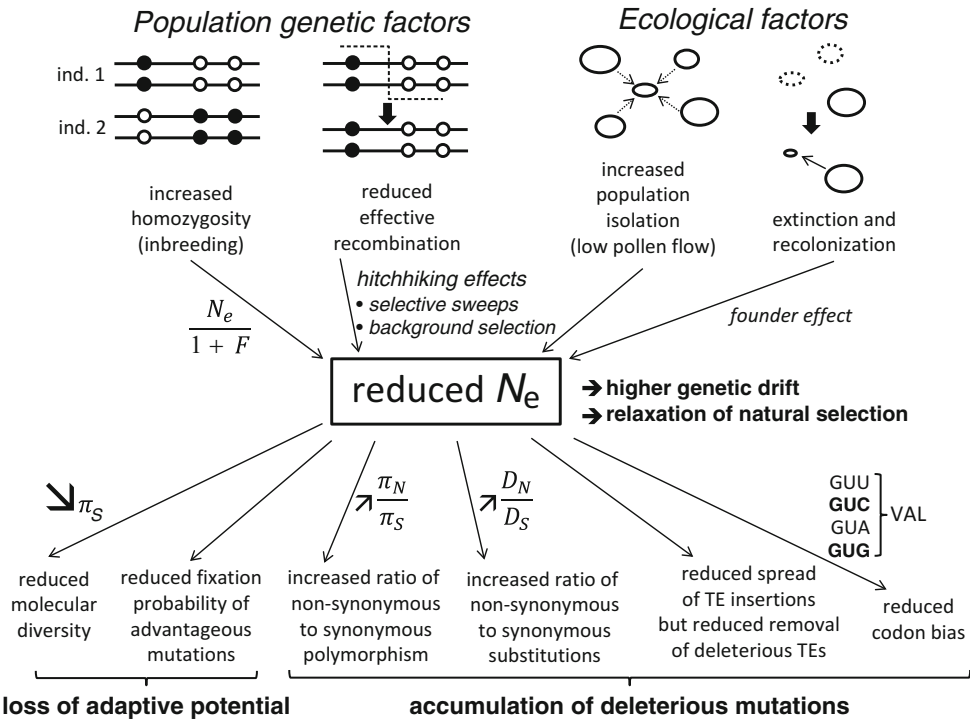


Fig. 2.3 Genomic effects and evolutionary consequences of a transition from outcrossing to selfing in plant populations. Population genetic factors and ecological factors combine to increase the importance of genetic drift as opposed to natural selection. These population genetic processes impact genome features and thereby may induce

a loss of adaptive potential and an accumulation of deleterious mutations. F , inbreeding coefficient; π_N and π_S , non-synonymous and synonymous nucleotide diversity, respectively; D_N and D_S , among-species non-synonymous and synonymous substitutions, respectively

populations is expected to be considerably lower than that of outcrossing populations (Fig. 2.3) because the number of independent sampling of gametes is reduced (Nordborg 2000) and because effective recombination rate is decreased, which increases the effect of hitchhiking, leading to large selective sweeps (Kaplan et al. 1989) and intense background selection (e.g. Charlesworth et al. 1995). The decrease of both effective population size and effective recombination rate decreases the efficacy of selection and thus the fixation of advantageous mutations as well as the elimination of deleterious mutations. Second, *selfing* and outcrossing species may also differ in how they adapt to changing environments. Two opposing processes should be taken into account, which makes it difficult to determine whether *selfing* or outcrossing is the most favourable (Glémin and Ronfort 2013). On the one hand, the

rate at which advantageous mutations enter the population is high when there is much standing variation, which is expected to be the case in outcrossers. On the other hand, the rate at which advantageous mutations are fixed is expected to be higher in selfers. This is however modulated by the genetic architecture of the beneficial mutations, i.e. whether beneficial mutations are dominant or recessive, and by the speed and strength of the environmental changes. Finally, even though the accumulation of deleterious mutations can lead to extinction of populations in the case of obligate selfers (Lynch et al. 1995b), a slight outcrossing rate is generally sufficient to purge deleterious mutations and keep population viability unaffected (Charlesworth et al. 1993). Overall, the outcome of these opposing forces may be that *selfing* species would have a lower adaptive potential rather than a higher accumu-

lation of deleterious mutations than outcrossers (Glémin and Ronfort 2013).

Dioecy and genomic changes: the evolution of sexual chromosomes. As explained above, the transition from *hermaphroditism* to *dioecy* is expected to occur by the successive fixation of male-sterility and female-sterility mutations. If the male-sterility mutation is recessive and the female-sterility is dominant, the heterozygous individuals at these loci will be males, while the homozygous individuals will be females. This would lead to the evolution of a proto-X and proto-Y genomic region determining the sex of individuals. Any mutation that has a sexually antagonistic effect, i.e. a positive effect on female (or male) and a negative effect on male (or female) fitness will become fixed if it is closely linked to the proto-X and proto-Y regions. Such a genomic region with no recombination is expected to evolve because of several processes. Deleterious mutations can accumulate because of Muller's Ratchet, due to hitchhiking by beneficial mutations and because of a reduced effective size of sexual chromosomes (Charlesworth 2002a). This process will lead to genetic degeneration and decrease in gene content of the Y chromosome (Bachtrog 2008). Finally, it has recently been suggested that there can be a turn-over of sexual chromosomes: the male determination on the Y chromosome moves to an autosomal chromosome which in turn evolves into a neo-Y chromosome (van Doorn and Kirkpatrick 2007). Hence, the evolution towards separate sexes is expected to have major consequences on the evolution of a whole chromosome and involves large genomic reorganisation.

2.3 Causes of Mating System Transitions: What Have We Learned from Molecular Genomic Approaches?

A series of recent advances in molecular genetic analyses have pinpointed the causal mutations for major shifts in the mating system of several

plant species and provided key insight about the mutational constraints involved.

2.3.1 Mutations to the Pollen Component of SI and the Extent of Pollen Limitation

Causal mutations for the transition from outcrossing to *selfing* have been identified in a handful of species. SI in the Brassicaceae is controlled by a molecular lock-and-key mechanism involving a transmembrane receptor protein deposited on the stigma surface (SRK, the "pistil part") and a small ligand protein deposited on the pollen coat (SCR, the "pollen part", Fig. 2.2). These two genes largely differ in size, SCR being a much smaller protein than SRK (respectively 83 vs. 432 aa on average in *Arabidopsis*, Goubet et al. 2012). Taking these figures at face value, the size of the mutational target would be predicted to differ between them, with more opportunities for the *SRK* gene to be knocked down by random mutation than *SCR*. In line with this simple expectation, the breakdown of SI in several domesticated *Brassica* cultivars was caused by female – disabling mutations (Tsuchimatsu et al. 2012). In sharp contrast, Tsuchimatsu et al. (2010) demonstrated that mutations in the pollen component (*SCR*) were responsible for the loss of SI in several natural *A. thaliana* accessions where *SRK* was intact and fully functional, as well as in *A. kamchatia* (Tsuchimatsu et al. 2012). Similarly, self-compatibility in *Capsella* also maps to the S-locus (Nasrallah et al. 2007; Slotte et al. 2012), and the fact that *SRK* appears to have retained a full-length coding region in some *C. rubella* accessions suggests that a mutation in the male component might have driven the loss of SI in this species (Guo et al. 2009). In *Leavenworthia alabamica*, controlled crosses and molecular analyses demonstrated that the self-compatibility observed in some populations also probably originated from the loss of function of the male component, *SCR* (Busch et al. 2011; Chantha et al. 2013). Hence, currently

available empirical evidence suggests that evolution of self-compatibility in wild Brassicaceae species tends to be driven by mutations in the male rather than in the female component. This contrast between natural and artificial selection is enlightening, because population genetics theory (Uyenoyama et al. 2001) predicts that natural selection should favour more strongly mutations disabling the pollen gene than those disabling the stigma gene (see Sect. 2.2.1). Indeed, this asymmetry in the direction of evolution rests on the key assumption that only male reproduction is limited by the SI mechanism, all ovules being ultimately fertilized, i.e. the amount of pollen available for fertilization is considered infinite and *pollen limitation* is absent. Hence, while *pollen limitation* seems to be frequent in natural populations (Busch and Schoen 2008), the fact that natural selection mostly favours male mutations tells us that the intensity of *pollen limitation* is weak in many ecological situations, or at least not strong enough to oppose the (apparently) higher rate of spontaneous mutation of the female component due to a wider mutational target. Clearly then, these observations provide a clear link between conclusions that can be made from genomic analyses and the underlying ecological conditions.

Interestingly, the genetic architecture of pollen SI specificity differs across species. In particular, Kubo et al. (2010) reported that in some Solanaceae species, pollen specificity for a given S-haplotype is determined by a series of tandemly duplicated pollen genes acting in a coordinated manner, each with a specific spectrum of anti-toxin activity against the full repertoire of S-RNase proteins they may encounter in pistils from other individuals of the species. Beside the mystery of how such an exquisitely co-evolved mechanism may have arisen and diversified, the multiplicity of pollen-S genes may potentially increase the size of the mutational target, leading to the prediction that these Solanaceae species may be even more prone to mating system shifts through the pollen component than species in which the pollen component is encoded by a single gene.

2.3.2 Transition to *Selfing*: Coupled to or Uncoupled from Speciation?

Genomic analyses of polymorphism have provided some important insights into the demographic context of the transition from outcrossing to *selfing* in two model species (Fig. 2.4). In *A. thaliana*, transgenic complementation experiments showed that a pair of functional *SRK-SCR* genes from *A. lyrata* was sufficient to largely rescue (albeit not fully) the SI phenotype. Hence, the signalling cascade downstream of *SCR* and *SRK* has remained largely intact in several accessions (Nasrallah et al. 2002, 2004; Boggs et al. 2009; Tsuchimatsu et al. 2010, but see Indriolo et al. 2012). This observation has two major implications: (1) the transition to *selfing* must have been recent, otherwise random mutations would have disrupted this signalling cascade if it has no other function and (2) it must have involved mutations at either *SCR* or *SRK* or both. Bechsgaard et al. (2006) identified in *A. lyrata* and *A. halleri* functional orthologs of the three *SRK* haplogroups that are still segregating in *A. thaliana*, but found no evidence for an acceleration of non-synonymous evolution along *A. thaliana* branches. Since *SRK* is currently pseudo-geneized in most *A. thaliana* accessions, this suggests that the loss of function of *SRK* must have been sufficiently recent that the relaxation of functional constraint could not be detected. Following this line of reasoning, Bechsgaard et al. (2006) concluded that the loss of function of *SRK* could not have occurred earlier than 413,000 years ago, while *A. thaliana* became separated from its close relatives *A. lyrata* and *A. halleri* about 5,000,000 years ago (Al-Shehbaz and O’Kane 2002 but see Beilstein et al. 2010). In other words, the currently highly *selfing* *A. thaliana* would have outcrossed for most of its evolutionary history. A second set of results, however, pointed to a more ancient transition to *selfing*. First, population genetics simulations showed that the genome-wide pattern of linkage disequilibrium (LD) decay with physical distance in *A. thaliana* is not compatible with such a

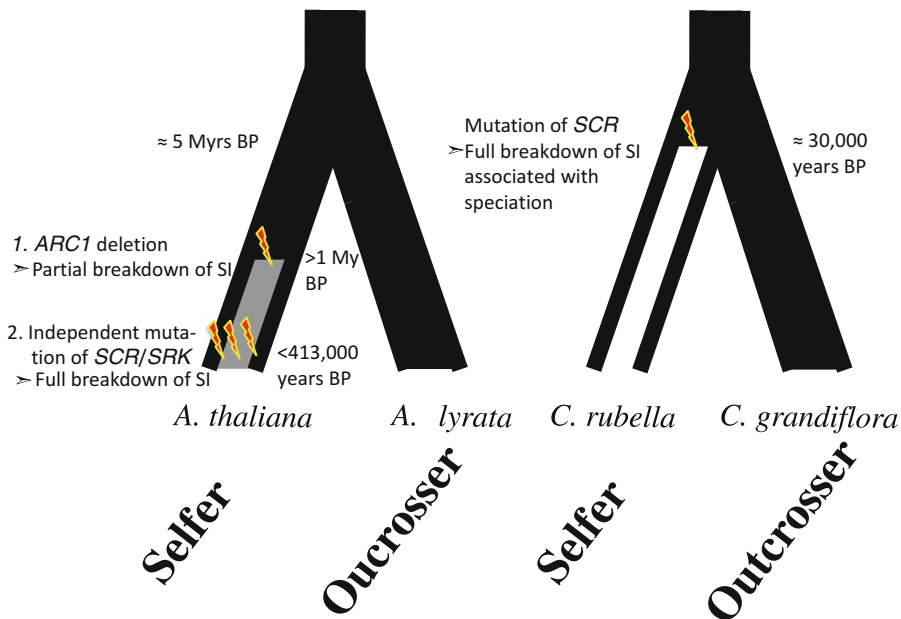


Fig. 2.4 Transition to selfing: coupled to or uncoupled from speciation? In *Arabidopsis*, the shift to autogamy in *A. thaliana* seems to be much more recent than speciation from the outcrosser *A. lyrata* (which occurred about 5,000,000 years ago). In *A. thaliana*, *SRK* became a pseudogene recently, no earlier than 413,000 years ago (Bechsgaard et al. 2006), possibly through three distinct causal mutations (Shimizu et al. 2008; Boggs et al. 2009). However, the pattern of LD decay along chromosomes suggests that *A. thaliana* became a selfer much more anciently, possibly 1,000,000 years ago. A possible solution to this paradox has been suggested by the recent discovery

by Indriolo et al. (2012) that the downstream signalling pathway is actually not fully intact in *A. thaliana*, lacking the *ARC1* gene. Fixation of this deletion may have caused an intermediate period of mixed mating system (in grey), followed by more recent full breakdown of SI and ensuing shift to autogamy (in white). In *Capsella* in contrast, the breakdown of SI is due to the recent fixation of a single S-haplotype whose pollen part is non-functional. Speciation is also extremely recent (30–50,000 years ago, Guo et al. 2009), suggesting that the two events were coupled. Note the sharply different time scales of speciation in the two genera

recent transition to *selfing*, but more closely resembles that predicted at equilibrium in an ancient selfer, which would have selfed for at least 1,000,000 years (Tang et al. 2007). Second, Indriolo et al. (2012) recently showed that *A. thaliana* was fixed for a deletion in one of the genes of the downstream signalling cascade of the SI response (*ARC1*). Hence, contrary to previous claims, this cascade is not fully intact in *A. thaliana*. When inactivated in *A. lyrata*, the *ARC1* gene leads to partial breakdown of SI, possibly suggesting that fixation of this deletion in *A. thaliana* may have led to a mixed mating system for some time, before *SRK* became a pseudogene. Interestingly, Tantikanjana et al. (2009) suggested that at least in one mutant *A. thaliana* background *SRK* has a dual role, jointly controlling both the SI response and pistil exertion, hence possibly accounting for

the delay with which *SRK* became a pseudogene even after its downstream SI signalling cascade started to decay. Overall, the data in *A. thaliana* therefore seem to be consistent with a two-steps scenario (Fig. 2.4), whereby an early (>1 Myrs) mutation in *ARC1* slightly decreased the strength of SI, while the SI system was fully inactivated only recently as *SRK* became a pseudogene, possibly through independent causal mutations (Shimizu et al. 2008; Boggs et al. 2009). In *Capsella* in contrast, Guo et al. (2009), reported that the time at which *SRK* became a pseudogene in *C. rubella* was largely consistent with the time of the split from the closely related outcrosser *C. grandiflora* (Foxe et al. 2009; St Onge et al. 2011), suggesting that, contrary to *Arabidopsis*, the transition to *selfing* in *Capsella* was coupled with speciation (Fig. 2.4). Interestingly, a recent

phylogenetic analysis (Goldberg and Igic 2012) suggests that the loss of SI in Solanaceae seems to occur largely by the cladogenetic mode (whereby the shift to *selfing* is associated with speciation, like in *Capsella*) rather than by the alternative anagenetic mode (whereby the transition to *selfing* occurs through fixation of self-compatible mutants in a species that is already isolated, like in *Arabidopsis*). It will now be interesting to extend this kind of analysis to other groups and to assess the generality of this conclusion.

2.3.3 The *Selfing* Syndrome: Neutral Degeneration or Selection for More Efficient Selfing?

While the loss of SI, at least partial, is a prerequisite step towards the evolution of *selfing*, it does not necessarily imply that *selfing* will predominate in the self-compatible lineage. In fact, most *selfing* species exhibit a “*selfing* syndrome”, a characteristic suite of traits, including reduction in size of floral organs, reduced flower opening, shorter physical distance between anthers and stigmas, and reduced temporal separation between male and female maturity. They also typically produce less pollen, and invest relatively more in ovule production, all features that are collectively believed to promote selfing (Darwin 1876; Ornduff 1969). Fishman et al. (2002) showed that the basis of phenotypic floral divergence between the large-flowered outcrosser *Mimulus guttatus* and the small-flowered selfer *M. nasutus* was highly polygenic, involving a large number of small-effect QTLs. Two recent studies in the species pair formed by *C. rubella* (a selfer) and its close outcrossing relative *C. grandiflora* also reported numerous strong QTLs for floral morphology, some of which overlapped across the traits measured (Sicard et al. 2011; Slotte et al. 2012). In an elegant backcrossing experiment, Sicard et al. (2011) introgressed the non-functional S-locus of the selfer *C. rubella* into the genomic background of the outcrosser *C. grandiflora*, resulting in a plant whose floral morphology closely resembled that of the outcrosser but was fully self-compatible. Inter-

estingly, these plants selfed autonomously only about half as efficiently as native *C. rubella* plants, hence demonstrating experimentally that the traits associated with the selfing syndrome do indeed provide more efficient self-pollination in *C. rubella*. Slotte et al. (2012) provided further evidence for the adaptive significance of the selfing syndrome, by comparing the direction of QTL effects. Most of them (86 %) were in the direction expected from phenotypic differences between the two species, an observation consistent with directional selection having favoured the evolution of the selfing syndrome in *C. rubella*. Moreover, while *C. rubella* has low genomic diversity overall as compared to *C. grandiflora*, the QTL regions exhibit an even more extreme reduction in diversity and an excess of fixed differences relative to shared polymorphism than other genomic regions in *C. rubella*. This observation suggests that QTL regions may have been the targets of recent selective sweeps, hence again supporting the notion that natural selection for efficient self-pollination rather than neutral processes have driven evolution of the *selfing* syndrome.

2.3.4 Genomic Constraints on How SI May Arise in the First Place

While it is relatively straightforward to imagine how gene-disruptive mutations can lead to the loss of SI in a species, the primary evolution of SI in a plant family is a more difficult issue to address empirically. Yet, a recent ground-breaking study (de Graaf et al. 2012) reported that the genes controlling SI in *Papaver* (*PrpS* and *PrsS*, controlling the pollen and pistil specificity, respectively) were able to function normally when transformed into *A. thaliana* and result in pollen inhibition in this species. This result is spectacular because *Papaver* and *Arabidopsis* became separated ca. 140,000,000 years ago, and also because SI in outcrossing *Arabidopsis* species involves completely different molecular mechanisms. This strongly suggests that SI in Papaveraceae functions through a very general signalling pathway that is highly conserved across

Angiosperms rather than through a specific set of genes that would function solely in SI. Hence, the evolution of SI in *Papaver* only had to involve recruitment of the two recognition proteins, with minimal constraint on the pre-existence of the downstream signalling cascade. Accordingly, a meta-analysis by Ferrer and Good (2012) reported that at least 22 Angiosperm families with SI were polymorphic in the type of SI mechanism, hence suggesting the possibility of multiple origins of SI in different species even within a given family, i.e. at a very short phylogenetic scale. While the genomic basis of most of these SI mechanisms is currently unknown (having been elucidated at the molecular level in only five families), it will be exciting to learn whether distinct genes have been recruited to control SI in each of these species, or whether some genes or gene families are more prone to serve as SI genes. A recent study in *Leavenworthia alabamica* does indeed suggest that the SI recognition function may have been transferred secondarily from *SCR-SRK* to a distinct pair of highly linked genes that belong to the same two gene families but are at a different genomic location (Chantha et al. 2013). Another recent study in *Senecio* provided evidence for yet another mechanism contributing to the lability of mating systems. Indeed, Kim et al. (2008) reported that a cluster of regulatory genes promoting flower asymmetry in the inflorescence (the proportion of disc- vs. ray-florets) had been transferred by introgression from the diploid *S. squalidus* into the tetraploid *S. vulgaris*, leading to an increase in the rate of outcrossing. These results highlight how a complex trait such as SI may be regained during evolution either by recruitment of paralogous genes or by horizontal gene transfer.

2.3.5 Gender Transitions

Data on the molecular events that provoked gender transitions (from *hermaphroditism* to *dioecy* for instance) are much more scarce. The best-studied system is that of *gynodioecy*, whereby female individuals are produced in a species as a consequence of the presence of

male-sterility mutations. In some species, male-sterility is encoded by cytoplasmic factors, and evolves as the result of a nuclear-cytoplasmic conflict (see Sect. 2.2.2). Male sterility mutations have been characterized at the molecular level in a handful of species only and were found to have different molecular natures, including novel gain-of-function chimeric genes resulting from intra-genomic recombination. Generally speaking however, the details of how these mutations function to ultimately lead to male sterility remain poorly known (Touzet 2012). Genes able to mask the action of male-sterility factors (coined “nuclear restorer genes”), have been cloned in petunia, radish and rice and found to generally belong to the pentatricopeptide (PPR) gene family, which is involved in organelle gene expression (Touzet and Budar 2004).

Across *monoecious* or *dioecious* plants, arrest of reproductive organs occurs at all stages of development with no apparent preference for a particular stage, although there is a clear tendency for the male and female organ abortions to occur at the same stage, raising the question of the mechanisms by which coordinated regulatory processes between male and female organs have evolved (Diggle et al. 2011). In the few species in which details of the molecular mechanisms controlling the production of unisexual flowers have been investigated, they were found to proceed through various alterations of developmental processes. In *dioecious Spinacia oleraceae* for example, where flowers are unisexual from inception, two floral organ identity homeotic genes of class B are differentially expressed between the sexes throughout flower development, and knocking them down in males results in the development of a functional gynoeceum, suggesting that they act as masculinizing genes. In maize, where gynoeceum abortion occurs later in development of male inflorescences (right after initiation), individual mutations in at least four distinct genes have been shown to cause the development of hermaphroditic instead of unisexual flowers (Acosta et al. 2009; Banks 2008), suggesting the involvement of many different pathways. Similarly in melon where flowers become unisexual after primordia initiation, *andromonoecious* lines

(in which individual plants carry both male and hermaphroditic flowers) are due to a single SNP in an ethylene biosynthesis enzyme expressed after carpel primordia have been initiated (Boualem et al. 2008), while the female flowers observed in some other lines (called gynodioecious) result from the insertion of a transposon that caused heritable epigenetic changes in the promoter of a transcription factor expressed early in flower development (Martin et al. 2009). Beside the fact that the detailed mechanisms by which these causal mutations ultimately lead to organ abortion are currently not known, these mutations have been observed in cultivars only and may therefore tell us little of which mutations may actually trigger mating system shifts in natural ecological settings. Yet, these studies do tell us that not many mutational steps are indeed required to shift gender distribution in a species. It will now be especially interesting to determine whether similar molecular mechanisms are also encountered in natural populations, and whether a small number of large-effect mutations (as in melon) or rather a large number of small-effect mutations are typically involved, thus providing insight into which of the proposed scenarios for this transition (see Sect. 2.2.2) is most frequent. While the small number of species in which detailed genetic and molecular mechanisms have been uncovered remain too small to make general statements at this point, it seems that species in which sex determination occurs early in development (before primordia initiation) could use the same specific organ identity/homeotic genes in a convergent manner, whereas species in which sex determination occurs later in development (after primordia initiation) could use a broader diversity of general developmental processes to achieve abortion of sexual organs (Diggle et al. 2011). It will be interesting to assess the generality of this prediction.

Two recent studies have suggested that the evolution of genders may interfere with other features of the mating system that are generally considered independently from one another. In a recent landmark paper, Saumitou-Laprade et al. (2010) demonstrated that the maintenance of *androdioecy* in *Phillyrea* can be explained by the existence of a novel as yet undescribed

SI system that restricts mate availability of hermaphrodites but does not function in males, hence offsetting the reproductive disadvantage that males face due to the loss of female function. Similarly, Ehlers and Schierup (2008) showed that breakdown of SI is more likely to occur in gynodioecious species, whereas in turn the breakdown of SI tends to promote stability of gynodioecious populations. These two studies clearly demonstrate the fact that different aspects of the mating system do interact strongly (*androdioecy* or *gynodioecy* and SI), and therefore highlight the importance of considering them jointly.

2.4 Genomic Consequences of Mating Systems Transitions: Genome-Wide Effects and Local Effects on the Mating System Control Region

While the data required to quantify the population genomic effects of mating system transitions has long remained a technical challenge, the increasing availability of polymorphism data at the whole genome level within and between closely related species with contrasted mating systems now allows more accurate estimates of how mating system transitions impact genome organization and evolution. In this section, we review the recent literature and explore the genomic consequences of mating system transitions at two levels, first looking at genome-wide patterns (Table 2.1); second looking at the patterns of molecular evolution in the genomic regions involved in mating system determination.

2.4.1 Genome-Wide Effects of Transitions from Outcrossing to Selfing

Several population genetic and ecological factors combine to cause a strong expected reduction in effective population size in association with the transition from outcrossing to *selfing*

Table 2.1 Empirical tests of predictions about the genomic consequences of a transition from outcrossing to selfing in plant populations. Studies performed using genome wide data are underlined

Predicted consequence of transition from outcrossing to selfing	Prediction confirmed	Prediction tested but not confirmed
Reduced level of molecular diversity	Roselius et al. (2005) – <i>Solanum</i> Modliszewski and Willis (2012) – <i>Mimulus</i> Pettengil and Moeller (2011) – <i>Clarkia</i> Ross-Ibarra et al. (2008)/Nordborg et al. (2005) – <i>Arabidopsis</i> St Onge et al. (2011) – <i>Capsella</i> Ness et al. (2010) – <i>Eichhornia</i>	
Reduced ratio of non-synonymous to synonymous polymorphism within species	Glémin et al. (2006) – meta-analysis Slotte et al. (2010) – <i>Arabidopsis</i> Slotte et al. (2013) – <i>Capsella</i>	
Reduced ratio of non-synonymous to synonymous substitution among species		Wright et al. (2002) – <i>Arabidopsis</i> Haudry et al. (2007) – <i>Triticeae</i> Escobar et al. (2010) – <i>Triticeae</i>
Reduced bias in synonymous codon usage	Qiu et al. (2011) – <i>Arabidopsis</i> and <i>Capsella</i> Haudry et al. (2008) – <i>Triticeae</i>	
Reduced level of transposition of transposable elements	Morgan (2001) – meta-analysis Tam et al. (2007) – <i>Solanum</i> de la Chaux et al. (2012) – <i>Arabidopsis</i>	
Reduced selection efficacy against transposed elements	Wright et al. (2001) – <i>Arabidopsis</i> Lockton and Gaut (2010) – <i>Arabidopsis</i>	

(summarized in Fig. 2.3, Sect. 2.2.4). Briefly, this reduction is expected to cause a decrease in genome-wide levels of polymorphism within *selfing* taxa, but is also expected to impact genome-wide patterns of molecular evolution (e.g. relative abundance of non-synonymous versus synonymous polymorphisms or substitutions; patterns of codon usage; dynamics of selfish elements) as a consequence of a reduction in the efficacy of positive (adaptive) and negative (purifying) directional selection in *selfing* taxa (reviewed by Wright et al. 2008; Glémin and Galtier 2012).

Levels of molecular diversity. Levels of neutral nucleotide diversity are expected to depend on the product of the effective population size times the neutral mutation rate. If we assume that mutation rates are not impacted by the mating system, we expect a twofold or higher decrease in neutral polymorphisms (expressed with statistics such as π_S , the nucleotide diversity at synonymous sites) in *selfing* taxa (Charlesworth 2003). In a large survey comprising 105 Angiosperm species, Glémin et al. (2006) found overall evidence for higher values of π_S (measured at

the species level) in outcrossing as compared to *selfing* species with a twofold difference. Similar results but with more striking differences in π_S were generally obtained in studies focusing on narrower phylogenetic groups but with larger genome sampling: 12-fold difference between three outcrossing and two *selfing* species of tomato wild relatives (14 nuclear genes, Roselius et al. 2005); sixfold difference between the outcrosser *Mimulus guttatus* and the selfer *M. nasutus* (six genes, Modliszewski and Willis 2012); fivefold difference between the outcrosser *Clarkia xantiana* ssp *xantiana* and the selfer *C. xantiana* ssp *parviflora* (eight loci, Pettengill and Moeller 2011); threefold difference between the outcrosser *Arabidopsis lyrata* (77 genes, Ross-Ibarra et al. 2008) and the selfer *A. thaliana* (876 genes, Nordborg et al. 2005); but only twofold difference between the outcrosser *Capsella grandiflora* and the selfer *C. rubella* (16 genes, St Onge et al. 2011), and between outcrossing and *selfing* populations of *Eichhornia paniculata* (ten loci, Ness et al. 2010). Overall these results indicate that population genetic factors (inbreeding,

genetic hitchhiking, background selection) are probably not sufficient to explain the observed reduction in neutral diversity in some *selfing* taxa. This discrepancy is thought to be related to additional differences in ecology or demographic history between selfers and outcrosser. Selfing taxa may indeed experience strong bottlenecks at the time of speciation when evolving from outcrossing ancestors (Modliszewski and Willis 2012) and/or frequent founder effects in relation to their higher colonization potential (Baker 1955; Schoen and Brown 1991), and these events will not be compensated by genetic exchange among populations or closely related species as gene flow through pollen is highly reduced in *selfing* taxa (Ingvarsson 2002).

Ratio of non-synonymous to synonymous polymorphism within species. Although neutral diversity is indeed lower in *selfing* taxa, an increase in the relative occurrence of non-synonymous (π_N) vs. synonymous (π_S) polymorphisms is expected as compared to outcrossing taxa (Charlesworth and Wright 2001). This is because selfers are less efficient in eliminating weakly deleterious mutations, corresponding to a large fraction of non-synonymous mutations, owing to their reduced effective population size (Glémin 2007). In the meta-analysis of Glémin et al. (2006), a significantly higher value of π_N/π_S was indeed observed for *selfing* taxa. With a dataset on 257 loci, Slotte et al. (2010) found evidence for a larger proportion of slightly deleterious non-synonymous mutations occurring in populations of the selfer *A. thaliana*, as compared to the outcrosser *Capsella grandiflora*. Hence, clear evidence for relaxed selection on weakly deleterious mutations in *selfing* species has been brought by recent genomic data. In addition, using whole genome data on 80 accessions from different populations of *A. thaliana*, Cao et al. (2011) showed that populations with lower effective population size experience greater relaxation of selection, suggesting strong heterogeneity among populations in the efficacy of selection in *selfing* species, which could have important ecological and evolutionary implications.

Ratio of non-synonymous to synonymous substitution among species. Differences in the efficacy of selection between *selfing* and outcrossing taxa should lead to higher rates of fixation of weakly deleterious alleles in selfers (Glémin 2007). This could be detected by comparing estimates of the ratio ω of non-synonymous to synonymous substitutions occurring in *selfing* versus outcrossing lineages in specific groups. In a comparison between the outcrosser *A. lyrata* and the selfer *A. thaliana* based on 23 genes, Wright et al. (2002) did not find evidence for higher fixation rates of non-synonymous mutations. Similar negative results were obtained by Haudry et al. (2008) in an analysis of two *selfing* and two outcrossing species of the tribe Triticeae (Poaceae) using data from 46 genes, and by Escobar et al. (2010) on 19 species of Triticeae using data from 27 genes. Although the datasets used in these studies are limited, the results suggest that the expected relaxation of selection in selfers is not so apparent in the long term and may not greatly influence substitution rates and genome evolution. However, a possible explanation for the discrepancy between results on polymorphisms and substitutions could be that the *selfing* taxa investigated have recently evolved (e.g. Bechsgaard et al. 2006), such that the time elapsed may have been too short to allow detecting significant effects on the fixation of mutations.

Codon usage. The relaxation of selection in selfers in association with reduced effective population size is also expected to alter patterns of codon usage in protein coding genes, as mutations towards non-optimal synonymous codons can be considered as slightly deleterious mutations subject to purifying selection (Marais et al. 2004). Using large datasets from two *selfing* species (*A. thaliana* and *C. rubella*) and their closely related outcrossing species (*A. lyrata* and *C. grandiflora*, respectively), Qiu et al. (2011) found clear evidence for a relaxed selection on synonymous codons in selfers as compared to their outcrossing relatives. Similar results, but with weaker statistical support, have been obtained by comparing two *selfing* with two outcrossing species in Triticeae (Haudry et al.

2008). A potential pitfall in these analyses is the confounding effect of GC-biased gene conversion (gBGC), which is a neutral process occurring during double-strand break recombination repair and leading to a bias towards G and C alleles, mimicking the effect of selection for optimal codons (Marais 2003). Indeed, gBGC is associated with recombination at heterozygous sites, but because of the low polymorphism found in *selfing* taxa, it is believed to be ineffective in selfers, while potentially important in outcrossers (Marais et al. 2004). In the study on two Brassicaceae genera (*Arabidopsis* and *Capsella*, that both contain *selfing* and outcrossing species), the effect of gBGC was tested using intron sequence data but no difference was detected between selfers and outcrossers (Qiu et al. 2011). In contrast, in the study on Triticeae, higher levels of gBGC were detected in outcrossing as compared to *selfing* taxa, and this potentially can impede the detection of relaxed selection on codon bias (Haudry et al. 2008).

Transposable elements dynamics. In equilibrium models of TE evolution, the number of copies in a given TE family results from a balance between the process of transposition leading to genomic spread of the family at the population level, and the selective removal of copies with deleterious effects. A transition from outcrossing to *selfing* is expected to have opposite effects on the processes of transposition and purging, so the net outcome is not straightforward to predict (Wright and Schoen 1999; Morgan 2001). Indeed, the high homozygosity occurring in selfers, and low rates of genetic exchange among individuals will cause a reduced spread of new TE insertions throughout the population, whereas the selective removal of weakly deleterious insertions will be either more or less effective in selfers depending on the level of dominance and nature of the deleterious effects (disruption of gene function vs. mediation of ectopic exchange between distinct chromosomes). Empirical results are still limited. Morgan (2001) reviewed studies on Ty1 copia-like elements for a number of species pairs and concluded that copy number is reduced overall in selfers as compared to outcrossers.

Tam et al. (2007), observed lower frequencies of insertion of copia-like elements in *selfing* as compared to outcrossing species of tomato wild relatives, but no differences in current copy numbers. In *Arabidopsis*, copy number for a vast majority of TE families was found to be lower in the selfer *A. thaliana* than in the outcrosser *A. lyrata* (de la Chaux et al. 2012), and the results suggest that the rate of transposition has recently decreased in *A. thaliana*, probably after the shift in mating system. Regarding the issue of selective removal of TE insertions, two studies reported that TE insertions segregate at higher frequencies in *A. thaliana*, as compared to *A. lyrata*, suggesting relaxation of selection against weakly deleterious mutations in the *selfing* lineage (Wright et al. 2001; Lockton and Gaut 2010).

Evolutionary consequences of genome-wide effects: is selfing an evolutionary dead end? Although the number of detailed empirical studies of the genome-wide effects of a transition to *selfing* is still scarce, and some results are controversial, a consensus can be found for two major consequences: a decrease in nucleotide polymorphism genome-wide, and a relative increase in frequency of mildly deleterious alleles in *selfing* populations. These empirical evidence are related to the two classical genetic threats associated with *selfing*, namely the loss of adaptive potential caused by a lack of standing variation (Stebbins 1957; Glémin and Ronfort 2013), and the accumulation of deleterious mutations, potentially leading to a “mutational meltdown” whereby deleterious alleles become fixed and contribute to population extinction (Lynch et al. 1995a; see Sect. 2.2.4 and Fig. 2.3). Altogether, these processes could cause an increase in the rate of extinction of *selfing* clades as compared to outcrossing clades, but this still needs to be demonstrated empirically. In this context, phylogenetic approaches involving estimation of differences in diversification rates in relation to mating system traits, or comparative analyses of rates of diversification in *selfing* versus outcrossing clades are interesting approaches to estimate indirectly the evolutionary consequences of mating system

transitions. Such approaches have recently shown very clear evidence for a reduction in evolutionary success of self-compatible clades in Angiosperms (as measured by the net diversification rate, i.e. speciation minus extinction rates; Goldberg et al. 2010; Goldberg and Igic 2012; Ferrer and Good 2012).

2.4.2 Genome-Wide Effects of Transitions from Hermaphroditism to Gynodioecy and/or Dioecy

In contrast to the evolution of *selfing*, a transition from *hermaphroditism* to *gynodioecy* and/or *dioecy* is not expected to cause major changes in population genetics processes affecting effective population size. If the hermaphroditic ancestor was partially reproducing by *selfing*, however, one could predict that the transition would lead to an increase in outcrossing level (Charlesworth and Charlesworth 1978), and thus to a (moderate) increase in effective population size in gynodioecious or dioecious taxa. In contrast, two types of ecological factors associated to the transition to *dioecy* could alter metapopulation dynamics, thereby causing a reduction in effective population size (Kafer et al. 2013): the “seed-shadow handicap”, i.e. the overall reduction in seed dispersal efficiency due to a lower proportion of seed-producing individuals (Heilbut et al. 2001) and a higher sensitivity to variation in pollinator abundance in animal-pollinated dioecious species as a consequence of sexual selection for increased pollinator attraction in males (Vamosi and Otto 2002). In contrast to studies on the effect of *selfing*, the empirical literature on genomic effects of the transition to *gynodioecy* or *dioecy* is strikingly scarce. In agreement with the predictions based on ecological factors, Kafer et al. (2013) found evidence for a reduction in the efficacy of selection (measured on patterns of nucleotide substitutions with the ratio ω) in dioecious species of the section *Melandrium* in the genus *Silene* (e.g. *S. latifolia*), as compared to a gynodioecious close relative (*S. vulgaris*). However they found no difference in a second

comparison involving the dioecious *S. otites* and the gynodioecious *S. nutans*. They suggest that the discrepancy could be explained by differences in the timescale of the two comparisons, with a much more recent evolution of *dioecy* in *S. otites* as compared to the *Melandrium* section, so that the time is too short for the evolution of genomic differences (Kafer et al. 2013). This suggestion is confirmed by another study that showed the occurrence of shared polymorphism at nuclear and mitochondrial genes between *S. otites* and *S. nutans*, and which observed similar levels of genetic diversity in both species (Lahiani et al. 2013). Finally, a comparison of transposable elements accumulation between the dioecious *S. latifolia* and the gynodioecious *S. vulgaris* showed a very striking accumulation of a *gypsy* retroelement in the former that could partially account for its much larger genome (Cegan et al. 2012).

2.4.3 Local Effects of Mating System Transitions on Genomic Regions Involved in Mating System Determination

Regions involved in mating system determination often show very different patterns of molecular evolution as compared to unlinked control regions. These are due to two major properties of such regions (Charlesworth 2006). First, they are generally subject to strong negative frequency-dependent selection on sex ratio or on mating type frequencies, due to the transmission advantage of the rarest sex or fecundity advantage of the rarest mating type/SI allele. Second, the recombination rate is frequently highly reduced in such regions. As a consequence, the different functional haplotypes at these regions are expected to show very strong nucleotide divergence, some of it being due to positive (diversifying) selection on the functional genes involved in mating, and some being due to a drift process intensified by long-term maintenance of the polymorphism and low effective population size of sets of gene copies of a given functional haplotype (Vekemans and Slatkin 1994; Charlesworth et al. 2005). The lack of recom-

bination in these regions is also expected to reduce the efficacy of selection and drive genetic degeneration over time causing accumulation of repetitive DNA and decrease in gene content (Charlesworth and Charlesworth 2000; Bachtrog 2008), as commonly found in non-recombining regions of Y chromosomes (Wang et al. 2012; Bergero et al. 2008). Transitions in mating systems may potentially have a large impact on patterns of molecular evolution in regions involved in mating system determination, as for instance the transition from *hermaphroditism* to *dioecy*, which causes the formation of neo sex chromosomes (Ming et al. 2011) and the breakdown of *self-incompatibility*, which may cause a loss of diversity at the S-locus and restoration of recombination (Guo et al. 2009). The transition that occurred within Chlorophyceae between isogamous (no differences in gamete sizes between mating types, as in *Chlamydomonas*) and anisogamous (e.g. *Volvox*) mating systems constitutes another striking example of a transition that had a major impact on the mating type locus region. Indeed, the mating type locus in the anisogamous *Volvox* was found to be homologous to that in the isogamous *Chlamydomonas*, but with a fivefold increase in size, due to inclusion of a higher number of genes (including some genes controlling gamete size) in association with a large inversion preventing intra-locus recombination (Ferris et al. 2010; Charlesworth and Charlesworth 2010b).

Patterns of molecular evolution at the self-incompatibility locus before and after a breakdown of incompatibility. In analogy to the differences between sex chromosomes, comparative surveys of full sequences of the S-locus region in self-incompatible species of the *Arabidopsis* genus have revealed the following patterns: high variability in size and gene organization among functional haplotypes, a complete absence of sequence similarity in intergenic sequences, and strong accumulation of transposable elements (Guo et al. 2011; Goubet et al. 2012). Similar patterns have been observed at the S-locus of other species of Brassicaceae (*Brassica rapa*, Fukai et al. 2003; *B. oleracea*,

Fujimoto et al. 2006), or in other multiallelic SI systems (*Prunus mume*, Entani et al. 2003). In a sporophytic SI system, these features were found to be associated with the dominance level of the S-locus haplotypes, with for instance dominant S-locus haplotypes accumulating more transposable elements than recessive ones (Goubet et al. 2012), because of a reduction in the efficacy of selection in the former due to lower recombination in dominant haplotypes (Castric et al. 2010), and/or because of their lower population frequencies (Schierup et al. 1997). It was suggested that recessive S-locus haplotypes (which can recombine in individuals homozygous at the S-locus) are analogous to X-chromosomes (recombining in females), while dominant haplotypes (which are always present in S-locus heterozygotes) are analogous to Y-chromosomes (Goubet et al. 2012). After a transition from SI to a selfing mating system, two different outcomes have been observed in the S-locus region, probably depending on whether *selfing* arose in association with a speciation event. The breakdown of SI was found to be associated with a species-wide fixation of a self-compatible S-locus haplotype in the selfer *Capsella rubella*, where all S-locus haplotypes are highly similar and non-functional (Guo et al. 2009, Fig. 2.4, see Sect. 2.3.2), as well as in one of the *selfing* races within the species *Leavenworthia alabamica* (Busch et al. 2011). In contrast, maintenance of several divergent non-functional haplotypes at the S-locus region has been reported in *Arabidopsis thaliana*, although with strong geographic differences in their relative frequencies (Boggs et al. 2009; Shimizu et al. 2004, 2008; Tsuchimatsu et al. 2010). Similarly in *A. kamchatica*, a recent allopolyploid *selfing* species originating from two self-incompatible species (*A. lyrata* and *A. halleri*), five divergent non-functional haplotypes were found, three of them originating from the parent *A. halleri*, and the last two originating from *A. lyrata* (Tsuchimatsu et al. 2012). These differences are expected to have a major impact on patterns of molecular evolution in the S-locus region in these *selfing* taxa, as the presence or absence of haplotype divergence at the S-locus is

expected to influence levels of recombination in that region.

Evolution of Sex Chromosomes in Dioecious Species. A transition from *hermaphroditism* to *dioecy* is often accompanied by gradual build-up of a set of sex chromosomes carrying sex determination genes, with a progressive reduction in recombination in the heterogametic genotype and genetic degradation of the Y chromosome (Ming et al. 2011). In the first stage the male and female sterility loci are still recombining, allowing the formation of hermaphrodite individuals as in *Fragaria virginiana* (Spigler et al. 2008). The following stages correspond to suppression of recombination between the two sex-determining loci and progressively larger neighbouring regions, allowing an increasing number of Y-linked genes to degenerate and form a male-specific region on the nascent Y chromosome (Ming et al. 2011). This gradual process is believed to involve several subsequent inversions, as suggested by an observed correlation between synonymous divergence between the X and Y sequences of *Silene latifolia* and *S. diclinis* and genetic distance to the pseudo-autosomal region (Nicolas et al. 2005; Bergero et al. 2007). This pattern has been observed in mammalian sex chromosomes and has been termed “evolutionary strata” (Lahn and Page 1999). Although the two sex chromosomes are homomorphic in the first stages (e.g. *Carica papaya* Liu et al. 2004), genetic degradation associated with the extension of the non-recombining region causes the accumulation of transposable elements and duplicated segments in the male-specific region causing significant expansion of the Y chromosome, as found in *S. latifolia* (Bergero et al. 2008), which generates heteromorphic sex chromosomes. Another feature associated with genetic degradation is an overall trend of reduced expression of Y-linked alleles, as observed in *S. latifolia* (Muyle et al. 2012). Interestingly, the genes showing reduced expression of the Y-linked allele were found to have higher expression of the X-linked allele in males than in females, a phenomenon known as dosage compensation, and which has been found

in other male heterogametic systems in animals (Muyle et al. 2012). A next step in evolution of sex chromosomes is believed to be a progressive loss of non-functional sequences across the Y accompanied by shrinking of the Y chromosome (Ming et al. 2011), such as been found in *Cycas revoluta* (Segawa et al. 1971).

Evolution of mitochondrial genomes in gynodioecious species with cytoplasmic male sterility factors. Because of the complete linkage disequilibrium within the mitochondrial genome, as well as between the chloroplastic and mitochondrial genomes in most Angiosperms, selection on cytoplasmic male sterility factors in gynodioecious species is expected to affect both cytoplasmic genomes throughout their total length (Touzet 2012). Two alternative selective scenarios have been proposed for the maintenance of gender polymorphism in gynodioecious species with cytoplasmic male sterility: (1) the balancing selection scenario, where two or more mitochondrial haplotypes (either several functionally distinct male sterile haplotypes, or a mixture of male fertile and male sterile haplotypes) are maintained over the long term and experience cycles of frequency changes over time (Gouyon et al. 1991; Dufay et al. 2009); and (2) the epidemic dynamics scenario, where new male-sterilizing haplotypes are continually arising by mutation and sweep through the population (Frank 1989). As noted by Charlesworth (2002b), the two alternative scenarios will have different effects on cytoplasmic neutral-locus diversity. In the case of haplotypes being maintained over a long period of time through balancing selection, diversity is expected to be high because different neutral mutations would accumulate over time in different haplotypes (Stadler and Delph 2002), while under the epidemic dynamics scenario a lower diversity would be expected as new sterilizing cytoplasmic will sweep through populations (Ingvarsson and Taylor 2002). Diversity in *Silene* mitochondrial genomes was found to be higher in gynodioecious than in non-gynodioecious species, suggesting that the balancing selection scenario is more

likely (Touzet and Delph 2009; Charlesworth 2010). Moreover, phylogenetic analyses of three male sterilizing mitochondrial haplotypes and three fertile haplotypes in *Beta maritima* show high divergence between the male sterile and the fertile lineages, suggesting long-term maintenance of the polymorphism (Darracq et al. 2011). The latter study also shows that the male sterile lineage has experienced an increase in mutation rate in the mitochondrial genome, which could suggest either that the sterilizing phenotype is a consequence of the higher mutation rate, or that sterilizing mutations could have caused an increase in the production of cellular reactive oxygen species in the mitochondria causing an elevation of mutation rates (Touzet 2012).

2.5 Perspectives: Open Questions

Convergent and parallel mating system transitions: what is the importance of gene reuse? A first set of open issues highlighted in our review is whether independent mating system transitions have been caused by mutations at the same nucleotides, genes or gene networks, or whether they were caused by mutations on entirely different genes. Along the same line, a major question is whether these mutations were independent (i.e. de novo mutations in genetic “hotspots” of variation and phenotypic evolution), or whether different lineages acquired them by ancestral polymorphism or lateral gene transfer. These questions are central in evolution not only for mating systems transitions, but for phenotypic evolution in general (Martin and Orgogozo 2013) and has been debated for decades. Thanks to the advances of genomics, there are now dozens of documented cases of the same genes being used repeatedly for phenotypic evolution in eukaryotes and prokaryotes (reviewed in Martin and Orgogozo 2013), although these cases are generally limited to convergent evolution between a few lineages only, generally two, except in the case of experimental evolution of simple organisms. As we detailed in this review, the recent literature on plant mating

systems reported clear evidence for molecular parallelism between lineages, e.g. the pollen gene involved in the breakdown of SI, paralogous *SCR/SRK*-like genes recruited in *Leavenworthia*, PPR genes recruited as male fertility restorers in gynodioecious species. Since mating system transitions occurred in plants dozens of times independently, we argue that they are excellent biological systems to assess the evolutionary importance of gene reuse. A current limitation is the low number of model systems that have been described down to the molecular level. The intense research aimed at dissecting the putative supergene controlling morphological differences between morphotypes in heterostylous species makes this mating system particularly promising for the years to come, once the supergene will have been identified in different groups.

If gene reuse and genetic hotspots are confirmed in independent cases of mating system transitions in plants in many lineages, then a further question arises: why are some genes used more frequently for transitions than others? Several causes have been hypothesized, including variation among genes in (i) mutation rate, whereby genes that mutate more frequently are more prone to cause phenotypic evolution, (ii) mutation size, whereby genes at which single mutations have the largest selective advantage are favoured and (iii) level of pleiotropic effects, favouring the use of genes having lower cascading effect in the regulatory networks (reviewed in Martin and Orgogozo 2013).

Plant mating systems in a broader context. Our review highlighted several clear cases of correlated evolution between mating systems and other life history traits or specific genomic features. A second set of open questions in the field will thus now be to assess the generality of this phenomenon, explicitly considering the evolution of mating systems in their broader genomic context. First, recent theoretical and empirical advances challenged the notion that the various aspects of plant mating systems can be considered as evolving independently from one another. Specifically, SI and *gynodioecy* mutually tend to decrease the conditions of their maintenance

(Ehlers and Schierup 2008) and the maintenance of *androdioecy* is facilitated by the existence of a functional SI (Saumitou-Laprade et al. 2010; Husse et al. 2013). An open question is therefore whether the existence of SI in plants facilitates the transition from *hermaphroditism* to *dioecy*. The joint evolution of SI and gender differentiation might even be a general feature of plant evolution, since anisogamy in the green Algae *Volvox* evolved by the recruitment of mutations in the genomic region determining SI (Ferris et al. 2010). Second, while studies on the loss of SI in *C. rubella* and *A. thaliana* highlight very different evolutionary scenarios in these two model species, with an apparent co-occurrence of the shift in mating system with a speciation event in the history of *C. rubella* but not in *A. thaliana* (Fig. 2.4), the relative importance of these scenarios among flowering plants remains to be investigated, as well as a possible association between the evolutionary scenario and the outcome in terms of maintenance of polymorphism at the mating system control region. Further, the putative occurrence of a transient period of mixed mating in the scenario that is not associated with a speciation event should be addressed. Third, the extent of *inbreeding depression* and its evolutionary lability constitute key features that affect transitions in plant mating systems. These features of *inbreeding depression* depend on whether the mutations involved are deleterious or under balancing selection, whether they have small or large effects on fitness, whether they are recessive or dominant, and on their organization and genomic location (the relative importance of genome wide load vs. sheltered load). While these issues are crucial in order to better understand mating systems transition, very little is currently known, especially in natural plant populations. We believe that this is a very important priority for research in ecological genomics.

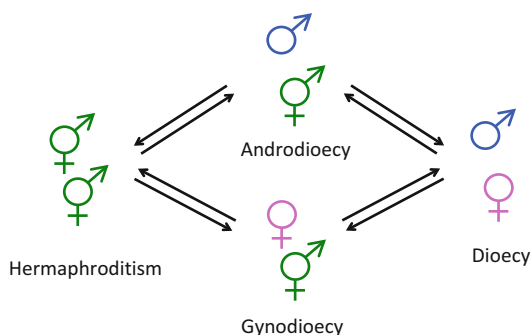
Plant mating systems and community ecology. Finally, while significant progress has been made in the field through genomic approaches, a major frontier will now be to place back mating system evolution in the ecological context of

interspecific interactions, especially at the community level. Thirty years ago, Charnov (1982) speculated that the evolution of *dioecy* might be affected by community-level laws, but this speculation can be extended to any transition in plant mating systems. For instance in plant species with different sexual morphs (heterostyly or *dioecy*), differential behaviour of pollinators on the sexual morphs (Case and Ashman 2009) would affect relative fitness of the latter and hence modify the evolution of genes involved in morphological differences between morphs. Furthermore, a decrease in pollinators abundance is expected to affect more drastically the demography of outcrossing than that of *selfing* species, hence favouring the evolution of higher *selfing* rates (Eckert et al. 2009). In turn, highly *selfing* species tend to offer less energy resources to their insect pollinators (such as nectar), which may further decrease pollinators abundance, eventually putting at risk population viability of both outcrossers and pollinators. How plant-pollinators interaction networks influence and are robust to the evolution of plant mating system transitions, and more generally how interspecific interactions at the community level affect the evolution of mating systems, their genomic architecture, and how in turn genomic features of mating systems affect the dynamics, stability and evolution of communities is an entire field open for investigation.

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Glossary

Hermaphroditism Hermaphroditism is the simultaneous coexistence of male and female reproductive organs on the same (co-sexual) individual (Fig. 2.1). Hermaphroditism is believed to be the ancestral state in Angiosperms, and the defining organ of Angiosperms (the flower) is itself a hermaphroditic organ, producing both pollen and ovules.



Selfing versus outcrossing A major consequence of hermaphroditism is the potential for self-fertilization, the most extreme form of inbreeding.

Self-incompatibility (SI) A genetic system promoting allogamy in many plants. There are two different types of SI, homomorphic and heteromorphic. In homomorphic SI, the different groups of mating partners differ by the type of recognition proteins they produce, but remain morphologically undistinguishable. In heteromorphic SI (e.g. heterostyly), the two (distyly) or three (tristyly) self- and within-morph incompatible mating groups typically differ by style length, anther height and pollen size.

Inbreeding depression Inbreeding depression is the decrease of fitness of offspring produced by inbred parents relatively to those produced by unrelated parents.

Pollen limitation A plant is pollen-limited if it does not receive enough pollen to fertilize all its ovules. Pollen limitation thus leads to a reduction in reproductive output through the female function.

Pollen discounting The loss of male reproduction in cross-fertilization due to the decrease of exported pollen, which occurs especially in autogamous species.

Gynodioecy (resp. androdioecy) Gynodioecy (resp. androdioecy) is a mating system whereby hermaphrodite individuals coexist with female (resp. male) individuals (Fig. 2.1).

Dioecy Dioecy is the separation of sexual functions in specialized (male and female) individuals (Fig. 2.1). Species in which some indi-

viduals with incomplete sexual specialization occur along with strictly unisexual individuals are termed **subdioecious**.

Monoecious Monoecious species are composed of hermaphrodites only, but in which male and female flowers are separated on each individual. In **gynomoecious** species, some individuals produce female-only flowers in variable proportion along with hermaphroditic flowers, while in **andromonoecious** species, some individuals produce male-only flowers along with hermaphroditic flowers.

References

- Acosta IF, Laparra H, Romero SP, Schmelz E, Hamberg M, Mottinger JP, Moreno MA, Dellaporta SL (2009) Tasselseed1 is a lipoygenase affecting jasmonic acid signaling in sex determination of maize. *Science* 323:262–265
- Al-Shehbaz IA, O’Kane SLJ (2002) Taxonomy and phylogeny of *Arabidopsis* (Brassicaceae). In: Somerville CR, Meyerowitz EM (eds) *The Arabidopsis book*. American Society of Plant Biologists, Rockville
- Ashman TL (2003) Constraints on the evolution of males and sexual dimorphism: filed estimates of genetic architecture of reproductive traits in three populations of gynodioecious *Fragaria virginiana*. *Evolution* 57:2012–2025
- Bachtrog D (2008) The temporal dynamics of processes underlying Y chromosome degeneration. *Genetics* 179:1513–1525
- Baker HG (1955) Self-compatibility and establishment after “long-distance” dispersal. *Evolution* 9: 347–348
- Banks JA (2008) MicroRNA, sex determination and floral meristem determinacy in maize. *Genome Biol* 9:204
- Barrett SCH, Shore JS (2008) New insights on heterostyly: comparative biology, ecology and genetics. In: Franklin-Tong V (ed) *Self-incompatibility in flowering plants: evolution, diversity and mechanisms*. Springer-Verlag, Berlin, pp 3–32
- Bechsgaard JS, Castric V, Charlesworth D et al (2006) The transition to self-compatibility in *Arabidopsis thaliana* and evolution within S-haplotypes over 10 Myr. *Mol Biol Evol* 23:1741–1750
- Beilstein MA, Nagalingum NS, Clements MD et al (2010) Dated molecular phylogenies indicate a miocene origin for *Arabidopsis thaliana*. *Proc Natl Acad Sci* 107(43):18724–18728
- Bergero R, Forrest A, Kamau E, Charlesworth D (2007) Evolutionary strata on the X chromosomes of the dioecious plant *Silene latifolia*: evidence from new sex-linked genes. *Genetics* 175:1945–1954

- Bergero R, Forrest A, Charlesworth D (2008) Active miniature transposons from a plant genome and its nonrecombining Y chromosome. *Genetics* 178:1085–1092
- Billiard S, López-Villavicencio M et al (2011) Having sex, yes, but with whom? Inferences from fungi on the evolution of outcrossing and mating types. *Biol Rev* 86:421–442
- Boggs NA, Nasrallah JB, Nasrallah ME (2009) Independent S-locus mutations caused self-fertility in *Arabidopsis thaliana*. *PLoS Genet* 5:e1000426
- Boualem A, Fergany M, Fernandez R et al (2008) A conserved mutation in an ethylene biosynthesis enzyme leads to andromonoecy in melons. *Science* 321(5890):836–838
- Busch JW, Schoen DJ (2008) The evolution of self-incompatibility when mates are limiting. *Trends Plant Sci* 13:128–136
- Busch JW, Joly S, Schoen DJ (2011) Demographic signatures accompanying the evolution of selfing in *Leavenworthia alabamica*. *Mol Biol Evol* 28:1717–1729
- Cao J, Schneeberger K, Ossowski S et al (2011) Whole-genome sequencing of multiple *Arabidopsis thaliana* populations. *Nat Genet* 43:956–965
- Case AL, Ashman TL (2009) Resources and pollinators contribute to population sex ratio bias and pollen limitation in gynodioecious wild strawberry (*Fragaria virginiana*). *Oikos* 118:1250–1260
- Castric V, Bechsgaard J, Grenier S et al (2010) Molecular evolution within and between self-incompatibility specificities. *Mol Biol Evol* 27:11–20
- Cegan R, Vyskot B, Kejnovsky E et al (2012) Genomic diversity in two related plant species with and without sex chromosomes – *Silene latifolia* and *S. vulgaris*. *PLoS ONE* 7:e31898
- Chantha SC, Herman AC, Platts A, Vekemans X, Schoen DJ (2013) Secondary evolution of self-incompatibility in the mustard genus *Leavenworthia*. *PLoS Biol* 11(5):e1001560
- Charlesworth D (2002a) Plant sex determination and sex chromosomes. *Heredity* 88:94–101
- Charlesworth D (2002b) What maintains male-sterility factors in plant populations. *Heredity* 89:408–409
- Charlesworth D (2003) Effects of inbreeding on the genetic diversity of populations. *Phil Trans R Soc Lond B* 358:1051–1070
- Charlesworth D (2006) Balancing selection and its effects on sequences in nearby genome regions. *PLoS Genet* 2:e64
- Charlesworth D (2010) Don't forget the ancestral polymorphisms. *Heredity* 105:509–510
- Charlesworth B, Charlesworth D (1978) A model for the evolution of dioecy and gynodioecy. *Am Nat* 112:975–997
- Charlesworth D, Charlesworth B (1979) Evolution and breakdown of S-allele systems. *Heredity* 43:41–55
- Charlesworth D, Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Annu Rev Ecol Syst* 18:237–268
- Charlesworth D, Charlesworth B (1990) Inbreeding depression with heterozygote advantage and its effect on selection for modifiers changing the outcrossing rate. *Evolution* 44:870–888
- Charlesworth B, Charlesworth D (2000) The degeneration of Y chromosomes. *Phil Trans R Soc Lond B* 355:1563–1572
- Charlesworth B, Charlesworth D (2010a) Elements of evolutionary genetics. Roberts and Company Publishers, Greenwood Village
- Charlesworth D, Charlesworth B (2010b) Evolutionary biology: the origins of two sexes. *Current Biol* 20:R520
- Charlesworth D, Willis JH (2009) The genetics of inbreeding depression. *Nat Rev Genet* 10:783–796
- Charlesworth D, Wright SI (2001) Breeding systems and genome evolution. *Curr Opin Genet Dev* 11:685–690
- Charlesworth D, Morgan MT, Charlesworth B (1993) Mutation accumulation in finite outbreeding and inbreeding populations. *Genet Res* 61:39–56
- Charlesworth D, Charlesworth B, Morgan MT (1995) The pattern of neutral molecular variation under the background selection model. *Genetics* 141:1619–1632
- Charlesworth D, Vekemans X, Castric V, Glémin S (2005) Plant self-incompatibility systems: a molecular evolutionary perspective. *New Phytol* 168:61–69
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton
- Chookajorn T, Kachroo A, Ripoll DR, Clark AG, Nasrallah JB (2003) Specificity determinants and diversification of the Brassica self-incompatibility pollen ligand. *Proc Natl Acad Sci USA* 101:911–917
- Darracq A, Varré JS, Maréchal-Drouard L et al (2011) Structural and content diversity of mitochondrial genome in beet: a comparative genomic analysis. *Genome Biol Evol* 3:723–736
- Darwin C (1876) The effects of cross and self fertilisation in the vegetable kingdom. John Murray, London
- Darwin C (1877) The different forms of flowers on plants of the same species. John Murray, London
- de Graaf BH, Vatovec S, Juárez-Díaz JA, Chai L, Kooblall K, Wilkins KA, Zou H, Forbes T, Franklin FC, Franklin-Tong VE (2012) The *Papaver* self-incompatibility pollen S-determinant, PrpS, functions in *Arabidopsis thaliana*. *Curr Biol* 22(2):154–159
- de la Chaux N, Tsuchimatsu T, Shimizu KK, Wagner A (2012) The predominantly selfing plant *Arabidopsis thaliana* experienced a recent reduction in transposable element abundance compared to its outcrossing relative *Arabidopsis lyrata*. *Mob DNA* 3:2
- Diggle PK, Di Stilio VS, Gschwend AR, Golenberg EM, Moore RC, Russell JRW, Sinclair JP (2011) Multiple developmental processes underlie sex differentiation in angiosperms. *Trends Genet* 27(9):368–376
- Dufaÿ M, Billard E (2012) How much better are females? The occurrence of female advantage, its proximal causes and its variation within and among gynodioecious species. *Ann Bot* 109:505–519

- Dufay M, Cuguen J, Arnaud JF, Touzet P (2009) Sex ratio variation among gynodioecious populations of sea beet: can it be explained by frequency-dependent selection? *Evolution* 63:1483–1497
- Eckert CG, Ozimec B, Herlihy CR, Griffin CA, Routley MB (2009) Floral morphology mediates temporal variation in the mating system of a self-compatible plant. *Ecology* 90(6):1540–1548
- Ehlers BK, Schierup MH (2008) When gametophytic self-incompatibility meets gynodioecy. *Genet Res Camb* 90:27–35
- Entani T, Iwano M, Shiba H et al (2003) Comparative analysis of the self-incompatibility (S-) locus region of *Prunus mume*: identification of a pollen-expressed F-box gene with allelic diversity. *Genes Cells* 8: 203–213
- Escobar JS, Cenci A, Bolognini J et al (2010) An integrative test of the dead-end hypothesis of selfing evolution in *Triticeae* (Poaceae). *Evolution* 64:2855–2872
- Ferrer MM, Good SV (2012) Self-sterility in flowering plants: preventing self-fertilization increases family diversification rates. *Ann Bot* 110(3):535–553
- Ferris P, Olson B, Hoff PD et al (2010) Evolution of an expanded sex-determining locus in *Volvox*. *Science* 328:351–354
- Fisher RA (1941) Average excess and average effect of a gene substitution. *Ann Eugen* 11:53–63
- Fishman L, Kelly AJ, Willis JH (2002) Minor quantitative trait loci underlie floral traits associated with mating system divergence in *Mimulus*. *Evolution* 56(11):2138–2155
- FitzJohn RG (2010) Quantitative traits and diversification. *Syst Biol* 59:619–633
- Foxe JP, Slotte T, Stahl EA, Neuffer B, Hurkad H, Wright SI (2009) Recent speciation associated with the evolution of selfing in *Capsella*. *Proc Natl Acad Sci USA* 106(13):5241–5245
- Frank SA (1989) The evolutionary dynamics of cytoplasmic male-sterility. *Am Nat* 133:345–376
- Fujimoto R, Okazaki K, Fukai E, Kusaba M, Nishio T (2006) Comparison of the genome structure of the self-incompatibility (S) locus in inter-specific pairs of S haplotypes. *Genetics* 173:1157–1167
- Fukai E, Fujimoto R, Nishio T (2003) Genomic organization of the S core region and the S flanking regions of a class-II S haplotype in *Brassica rapa*. *Mol Gen Genomics* 269:361–369
- Gervais CE, Castaic V, Ressayre A, Billiard S (2011) Origin and diversification dynamics of self-incompatibility haplotypes. *Genetics* 188:625–636
- Glémin S (2007) Mating systems and the efficacy of selection at the molecular level. *Genetics* 177: 905–916
- Glémin S, Galtier N (2012) Genome evolution in outcrossing versus selfing versus asexual species. *Methods Mol Biol* 855:311–335
- Glémin S, Ronfort J (2013) Adaptation and maladaptation in selfing and outcrossing species: new mutations versus standing variation. *Evolution* 67:224–240
- Glémin S, Bazin E, Charlesworth D (2006) Impact of mating systems on patterns of sequence polymorphism in flowering plants. *Proc R Soc Land B* 273:3011–3019
- Goldberg EE, Iqic B (2012) Tempo and mode in plant breeding system evolution. *Evolution* 66:3701–3709
- Goldberg EE, Kohn JR, Lande R et al (2010) Species selection maintains self-incompatibility. *Science* 330:493–495
- Goubet PM, Bergès H, Bellec A et al (2012) Contrasted patterns of molecular evolution in dominant and recessive self-incompatibility haplotypes in *Arabidopsis*. *PLoS Genet* 8:e1002495
- Gouyon PH, Vichot F, Van Damme JMM (1991) Nuclear-cytoplasmic male sterility: single point equilibria versus limit cycles. *Am Nat* 137:498–514
- Graham SW, Barrett SCH (2004) Phylogenetic reconstruction of the evolution of stylar polymorphisms in *Narcissus* (Amaryllidaceae). *Am J Bot* 91: 1007–1021
- Guo YL, Bechsgaard JS, Slotte T, Neuffer B, Lascoux M, Weigel D, Schierup MH (2009) Recent speciation of *Capsella rubella* from *Capsella grandiflora*, associated with loss of self-incompatibility and an extreme bottleneck. *Proc Natl Acad Sci USA* 106(13): 5246–5251
- Guo Y, Zhao X, Lanz C, Weigel D (2011) Evolution of the S-locus region in *Arabidopsis thaliana* relatives. *Plant Physiol* 157:937–946
- Haudry A, Cenci A, Ravel C, Bataillon T, Brunel D, Poncet C, Hochu I, Poirier S, Santoni S, Glémin S, David J (2007) Grinding up wheat: a massive loss of nucleotide diversity since domestication. *Mol Biol Evol* 24:1506–1517
- Haudry A, Cenci A, Guilhaumon C et al (2008) Mating system and recombination affect molecular evolution in four *Triticeae* species. *Genet Res* 90:97–109
- Heilbut JC, Ilves KL, Otto SP (2001) The consequences of dioecy for seed dispersal: modeling the seed-shadow handicap. *Evolution* 55:880–888
- Husse L, Billiard S, Lepart J, Vernet P, Saumitou-Laprade P (2013) A one-locus model of androdioecy in a context with two homomorphic self-incompatibility groups: expected vs. observed male frequencies. *J Evol Biol* 26(6):1269–1280
- Iqic B, Lande R, Kohn JR (2008) Loss of self-incompatibility and its evolutionary consequences. *Int J Plant Sci* 169:93–104
- Indriolo E, Tharmapalan P, Wright SI, Goring DR (2012) The *ARC1* E3 Ligase gene is frequently deleted in self-compatible *Brassicaceae* species and has a conserved role in *Arabidopsis lyrata* self-pollen rejection. *Plant Cell* 24:4607–4620
- Ingvarsson PK (2002) A metapopulation perspective on genetic diversity and differentiation in partially self-fertilizing plants. *Evolution* 56:2368–2373
- Ingvarsson PK, Taylor DR (2002) Genealogical evidence for epidemics of selfish genes. *Proc Natl Acad Sci USA* 99:11265–11269

- Käfer J, Talianov M, Bigot T et al (2013) Patterns of molecular evolution in dioecious and non-dioecious *Silene*. *J Evol Biol* 26:335–346
- Kaplan NL, Hudson RR, Langley CH (1989) The hitchhiking effect revisited. *Genetics* 123:887–899
- Kim M, Cui ML, Cubas P, Gillies A, Lee K, Chapman MA, Abbott RJ, Coen E (2008) Regulatory genes control a key morphological and ecological trait transferred between species. *Science* 322(5904):1116–1119
- Kubo K, Entani T, Takara A, Wang N, Fields AM, Hua Z, Toyoda M, Kawashima S, Ando T, Isogai A, Kao TH, Takayama S (2010) Collaborative non-self recognition system in S-RNase-based self-incompatibility. *Science* 330(6005):796–799
- Lahiani E, Dufay M, Castric V, Le Cadre S, Charlesworth D, Van Rossum F, Touzet P (2013) Disentangling the effects of mating systems and mutation rates on cytoplasmic diversity in gynodioecious *Silene nutans* and dioecious *Silene otites*. *Heredity* 111:157–164
- Lahn BT, Page DC (1999) Four evolutionary strata on the human X chromosome. *Science* 286:964–967
- Liu Z, Moore PH, Ma H et al (2004) A primitive Y chromosome in papaya marks incipient sex chromosome evolution. *Nature* 427:348–352
- Lloyd DG (1975) The maintenance of gynodioecy and androdioecy in angiosperms. *Genetica* 45:325–339
- Lloyd DG (1977) Genetic and phenotypic models of natural selection. *J Theor Biol* 69:543–560
- Lloyd DG (1979) Evolution towards dioecy in heterostylous populations. *Plant Syst Evol* 131:71–80
- Lloyd DG (1980) The distribution of gender in four angiosperm species illustrating two evolutionary pathways to dioecy. *Evolution* 34:123–134
- Lloyd DG, Webb CJ (1992) The evolution of heterostyly. In: Barrett SCH (ed) *Evolution and function of heterostyly*. Springer, Berlin/Heidelberg/New York, pp 151–178
- Lockton S, Gaut BS (2010) The evolution of transposable elements in natural populations of self-fertilizing *Arabidopsis thaliana* and its outcrossing relative *Arabidopsis lyrata*. *BMC Evol Biol* 10:10
- Lynch M, Conery J, Burger R (1995a) Mutation accumulation and the extinction of small populations. *Am Nat* 146:489–518
- Lynch M, Conery J, Burger R (1995b) Mutational meltdowns in sexual population. *Evolution* 49:1067–1080
- Maddison WP, Midford PE, Otto SP (2007) Estimating a binary character's effect on speciation and extinction. *Syst Biol* 56:701–710
- Marais G (2003) Biased gene conversion: implications for genome and sex evolution. *Trends Genet* 19:330–338
- Marais G, Charlesworth B, Wright SI (2004) Recombination and base composition: the case of the highly self-fertilizing plant *Arabidopsis thaliana*. *Genome Biol* 5:R45
- Martin A, Orgogozo V (2013) The loci of repeated evolution: a catalog of genetic hotspots of phenotypic variation. *Evolution* 67(5):1235–1250
- Martin A, Troadec C, Boualem A, Rajab M, Fernandez R, Morin H, Pitrat M, Dogimont C, Bendahmane A (2009) A transposon-induced epigenetic change leads to sex determination in melon. *Nature* 461(7267):1135–1138
- Mayrose I, Barker MS, Otto SP (2010) Probabilistic models of chromosome number evolution and the inference of polyploidy. *Syst Biol* 59:132–144
- McDaniel SF, Atwood J, Burleigh JG (2013) Recurrent evolution of dioecy in bryophytes. *Evolution* 67:567–572
- Ming R, Bendahmane A, Renner SS (2011) Sex chromosomes in land plants. *Annu Rev Plant Biol* 62:485–514
- Modliszewski JL, Willis JH (2012) Allotetraploid *Mimulus sookensis* are highly interfertile despite independent origins. *Mol Ecol* 21:5280–5298
- Morgan MT (2001) Transposable element number in mixed mating populations. *Genet Res* 77:261–275
- Muyle A, Zemp N, Deschamps C et al (2012) Rapid de novo evolution of X chromosome dosage compensation in *Silene latifolia*, a plant with young sex chromosomes. *PLoS Biol* 10:e1001308
- Naithani S, Chookajorn T, Ripoll DR, Nasrallah JB (2007) Structural modules for receptor dimerization in the S-locus receptor kinase extracellular domain. *Proc Natl Acad Sci USA* 104:12211–12216
- Nasrallah ME, Liu P, Nasrallah JB (2002) Generation of self-incompatible *Arabidopsis thaliana* by transfer of two S locus genes from *A. lyrata*. *Science* 297:247–249
- Nasrallah M, Liu P, Sherman-Broyles S, Boggs N, Nasrallah J (2004) Natural variation in expression of self-incompatibility in *Arabidopsis thaliana*: implications for the evolution of selfing. *Proc Natl Acad Sci USA* 101:16070–16074
- Nasrallah JB, Liu P, Sherman-Broyles S, Schmidt R, Nasrallah ME (2007) Epigenetic mechanisms for breakdown of self-incompatibility in interspecific hybrids. *Genetics* 175:1965–1973
- Ness RW, Wright SI, Barrett SCH (2010) Mating-system variation, demographic history and patterns of nucleotide diversity in the tristylous plant *Eichhornia paniculata*. *Genetics* 184:381–392
- Nicolas M, Marais G, Hykelova V et al (2005) A gradual process of recombination restriction in the evolutionary history of the sex chromosomes in dioecious plants. *PLoS Biol* 3:e4
- Nordborg M (2000) Linkage disequilibrium, gene trees and selfing: an ancestral recombination graph with partial self-fertilization. *Genetics* 154:923–929
- Nordborg M, Hu TT, Ishino Y et al (2005) The pattern of polymorphism in *Arabidopsis thaliana*. *PLoS Biol* 3:1289–1299
- Ornduff R (1969) Reproductive biology in relation to systematics. *Taxon* 18:121–133
- Pannell JR, Verdu M (2006) The evolution of gender specialization from dimorphic hermaphroditism: paths from heterodichogamy to gynodioecy and androdioecy. *Evolution* 60:660–673

- Pettengill JB, Moeller DA (2011) Tempo and mode of mating system evolution between incipient *Clarkia* species. *Evolution* 66:1210–1225
- Porcher E, Lande R (2005a) The evolution of self-fertilization and inbreeding depression under pollen discounting and pollen limitation. *J Evol Biol* 18: 497–508
- Porcher E, Lande R (2005b) Loss of gametophytic self-incompatibility with evolution of inbreeding depression. *Evolution* 59:46–60
- Qiu S, Zeng K, Slotte T et al (2011) Reduced efficacy of natural selection on codon usage bias in selfing *Arabidopsis* and *Capsella* species. *Genome Biol Evol* 3:868–880
- Renner SS, Ricklefs RE (1995) Dioecy and its correlates in the flowering plants. *Am J Bot* 82:596–606
- Roselius K, Stephan W, Stadler T (2005) The relationship of nucleotide polymorphism, recombination rate and selection in wild tomato species. *Genetics* 171: 753–763
- Ross MD (1982) Five evolutionary pathways to subdioecy. *Am Nat* 119:297–318
- Ross-Ibarra J, Wright SI, Foxe JP et al (2008) Patterns of polymorphism and demographic history in natural populations of *Arabidopsis lyrata*. *PLoS ONE* 3: e2411
- Roze D, Rousset F (2004) Joint effects of self-fertilization and population structure on the mutation load, inbreeding depression and heterosis. *Genetics* 167: 1001–1015
- Saumitou-Laprade P, Vernet P, Vassiliadis C, Hoareau Y, de Magny G, Dommée B, Lepart J (2010) A self-incompatibility system explains high male frequencies in an androdioecious plant. *Science* 327(5973):1648–1650
- Schierup MH, Vekemans X, Christiansen FB (1997) Evolutionary dynamics of sporophytic self-incompatibility alleles in plants. *Genetics* 147:835–846
- Schoen DJ, Brown AHD (1991) Intraspecific variation in population gene diversity and effective population size correlates with the mating system in plants. *Proc Natl Acad Sci USA* 88:4494–4497
- Segawa M, Kishi S, Tatuno S (1971) Sex chromosomes of *Cycas revoluta*. *Jpn J Genet* 46:33–39
- Shimizu KK, Cork JM, Caicedo AL et al (2004) Darwinian selection on a selfing locus. *Science* 306:2081–2084
- Shimizu KK, Shimizu-Inatsugi R, Tsuchimatsu T, Purugganan MD (2008) Independent origins of self-compatibility in *Arabidopsis thaliana*. *Mol Ecol* 17:704–714
- Sicard A, Stacey N, Hermann K, Dessoly J, Neuffer B, Bäurle I, Lenhard M (2011) Genetics, evolution, and adaptive significance of the selfing syndrome in the genus *Capsella*. *Plant Cell* 23(9):3156–3171
- Slotte T, Foxe JP, Hazzouri KM, Wright SI (2010) Genome-wide evidence for efficient positive and purifying selection in *Capsella grandiflora*, a plant species with a large effective population size. *Mol Biol Evol* 27:1813–1821
- Slotte T, Hazzouri KM, Stern D, Andolfatto P, Wright SI (2012) Genetic architecture and adaptive significance of the selfing syndrome in *Capsella*. *Evolution* 66(5):1360–1374
- Slotte T, Hazzouri KM, Ågren JA, Koenig D, Maumus F, Guo Y, Steige K, Platts AE, Escobar JS, Newman LK, Wang W, Mandakova T, Vello E, Smith SM, Steffen J, Takuno S, Brandvain Y, Coop G, Andolfatto P, Hu TT, Blanchette M, Clark RM, Quesseville H, Nordborg M, Gaut BS, Lysak MA, Jenkins J, Grimwood J, Prochnick S, Shu S, Rokhsar D, Schmutz J, Weigel D, Wright SI (2013) The *Capsella rubella* genome and the genomic consequences of rapid mating system evolution. *Nat Genet* 45:831–835
- Spigler RB, Lewers KS, Main DS, Ashman TL (2008) Genetic mapping of sex determination in a wild strawberry, *Fragaria virginiana*, reveals earliest form of sex chromosome. *Heredity* 101:507–517
- St Onge KR, Kallman T, Slotte T et al (2011) Contrasting demographic history and population structure in *Capsella rubella* and *Capsella grandiflora*, two closely related species with different mating systems. *Mol Ecol* 20:3306–3320
- Stadler T (2011) Inferring speciation and extinction processes from extant species data. *Proc Natl Acad Sci USA* 108:16145–16146
- Stadler T, Delph LF (2002) Ancient mitochondrial haplotypes and evidence for intragenic recombination in a gynodioecious plant. *Proc Natl Acad Sci USA* 99:11730–11735
- Stebbins GL (1957) Self fertilization and population variability in higher plants. *Am Nat* 91:337–354
- Stebbins GL (1974) Flowering plants: evolution above the species level. Harvard University Press, Cambridge
- Takayama S, Isogai A (2005) Self-incompatibility in plants. *Annu Rev Plant Biol* 56:467–489
- Takebayashi N, Morrell PL (2001) Is self-fertilization an evolutionary dead end? Revisiting an old hypothesis with genetic theories and a macroevolutionary approach. *Am J Bot* 88:1143–1150
- Tam SM, Causse M, Garchery C et al (2007) The distribution of copia-type retrotransposons and the evolutionary history of tomato and related wild species. *J Evol Biol* 20:1056–1072
- Tang C, Toomajian C, Sherman-Broyles S, Plagnol V, Guo YL et al (2007) The evolution of selfing in *Arabidopsis thaliana*. *Science* 317:1070–1072
- Tantikanjana T, Rizvi N, Nasrallah ME, Nasrallah JB (2009) A dual role for the S-locus receptor kinase in self-incompatibility and pistil development revealed by an *Arabidopsis rdr6* mutation. *Plant Cell* 21(9):2642–2654
- Torices R, Méndez M, Gomez MJ (2011) Where do monomorphic sexual systems fit in the evolution of dioecy? Insights from the largest family of angiosperms. *New Phytol* 190:234–248

- Touzet P (2012) Mitochondrial genome evolution and gynodioecy. In: Marechal-Drouard L (ed) *Advances in botanical research*, vol 63. Academic Press/Elsevier Science, London, pp 71–98
- Touzet P, Budar F (2004) Unveiling the molecular arms race between two conflicting genomes in cytoplasmic male sterility? *Trends Plant Sci* 9:568–570
- Touzet P, Delph LF (2009) The effect of breeding system on polymorphism in mitochondrial genes of *Silene*. *Genetics* 181:631–644
- Tsuchimatsu T, Suwabe K, Shimizu-Inatsugi R et al (2010) Evolution of self-compatibility in *Arabidopsis* by a mutation in the male specificity gene. *Nature* 464:1342–1346
- Tsuchimatsu T, Kaiser P, Yew C-L, Bachelier JB, Shimizu KK (2012) Recent loss of self-incompatibility by degradation of the male component in allotetraploid *Arabidopsis kamchatica*. *PLoS Genet* 8(7):e1002838
- Uyenoyama MK (2003) Genealogy-dependent variation in viability among self-incompatibility genotypes. *Theor Popul Biol* 63:281–293
- Uyenoyama M, Zhang Y, Newbigin E (2001) On the origin of self-incompatibility haplotypes: transition through self-compatible intermediates. *Genetics* 157:1805–1817
- Vamosi JC, Otto SP (2002) When looks can kill: the evolution of sexually dimorphic floral display and the extinction of dioecious plants. *Proc R Soc Lond B* 269:1187–1194
- van Doorn GS, Kirkpatrick M (2007) Turnover of sex chromosomes induced by sexual conflict. *Nature* 449:909–912
- Vekemans X, Slatkin M (1994) Gene and allelic genealogies at a gametophytic self-incompatibility locus. *Genetics* 137:1157–1165
- Wang J, Naa JK, Yub Q et al (2012) Sequencing papaya X and Y chromosomes reveals molecular basis of incipient sex chromosome evolution. *Proc Natl Acad Sci USA* 109:13710–13715
- Wright SI, Schoen DJ (1999) Transposon dynamics and the breeding system. *Genetica* 107:139–148
- Wright SI, Le QH, Schoen DJ, Bureau TE (2001) Population dynamics of an Ac-like transposable element in self- and crosspollinating *Arabidopsis*. *Genetics* 158:1279–1288
- Wright SI, Lauga B, Charlesworth D (2002) Rates and patterns of molecular evolution in inbred and outbred *Arabidopsis*. *Mol Biol Evol* 19:1407–1420
- Wright S, Ness RW, Foxe JP, Barrett SC (2008) Genomic consequences of outcrossing and selfing in plants. *Int J Plant Sci* 169:105–118