

cutaneous denervation of the hindpaw in the cat. *J. Neurophysiol.* 94, 2911–2927.

11. Georgopoulos, A.P., and Grillner, S. (1989). Visuomotor coordination in reaching and locomotion. *Science* 245, 1209–1210.
12. Bjursten, L.M., Norrsell, K., and Norrsell, U. (1976). Behavioural repertory of cats without

cerebral cortex from infancy. *Exp. Brain Res.* 25, 115–130.

13. Grillner, S., and Wallén, P. (2004). Innate versus learned movements—a false dichotomy? *Prog. Brain Res.* 143, 3–12.
14. Stephenson-Jones, M., Samuelsson, E., Ericsson, J., Robertson, B., and Grillner, S.

(2011). Evolutionary conservation of the basal ganglia as a common vertebrate mechanism for action selection. *Curr. Biol.* 21, 1081–1091.

15. Li, N., Chen, T.W., Guo, Z.V., Gerfen, C.R., and Svoboda, K.A. (2015). A motor cortex circuit for motor planning and movement. *Nature* 519, 51–56.

## Plant Mating Systems: Female Sterility in the Driver's Seat

John R. Pannell\* and Marie Voillemot

Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

\*Correspondence: [john.pannell@unil.ch](mailto:john.pannell@unil.ch)

<http://dx.doi.org/10.1016/j.cub.2015.04.044>

Violation of Mendel's Law of Segregation by selfish X chromosomes that favour their own transmission is known for a number of organisms. Now, a new study reveals sex-ratio distortion favouring males and explains previously puzzling sex ratios in a Mediterranean shrub.

Plants display a bewildering range of reproductive systems and strategies to promote fitness through male and female functions [1]. The nomenclature that has been coined to refer to these systems is enough to turn most people away immediately — for example 'heterodichogamy may reduce geitonogamy in entomophilous phanerophytes'. This is a pity, because the basic ideas in the field are relatively simple, and some of the peculiarities of plant mating can provide wonderful illustrations of general principles in genetics and evolution. The sexual system termed 'gynodioecy' is one such example, which even first-year introductions to evolutionary biology might profitably use as a way to explain the importance of gene-level thinking for understanding adaptations and the genetic conflicts that can limit them. A gynodioecious population is just a hermaphrodite population in which some individuals express male-sterility mutations and thus fail to produce pollen. Such populations effectively comprise hermaphrodites and females.

Why should gynodioecy evolve in a well-functioning hermaphroditic

population? There are a number of reasons for this, including benefits of inbreeding avoidance [2,3], but perhaps the most important cause for the success of male sterility mutations has nothing to do with the benefits they might have for the individuals expressing them. Rather, a mutation causing male sterility can spread due to selfish benefits that it alone enjoys, at the expense of the plant carrying it [3]. Male sterility mutations causing gynodioecy very often occur in genes of the mitochondrial genome, which in most flowering plants are transmitted to progeny only through ovules and not through pollen [4,5]. Consequently, these genes have no evolutionary interest at all in the production of pollen, which, from their 'point of view', represents a waste of resources that might otherwise be used to produce more ovules and seeds — this is similar to the advantage gained by male-killing elements in animal species that are transmitted only maternally [5–7]. A male-sterility mutation will spread in a population if the reduction in pollen production by individuals expressing it allows even an incremental increase in seed production. Given that pollen represents an expensive investment, this is often the case. The result is often

a population with a frequency of females in excess of 50% [3] — a strategy that is demonstrably suboptimal from the point of view of autosomal genes that are transmitted by both ovules and pollen. In gynodioecious populations, autosomes are known to 'fight back' against male sterility by restoring fertility, leading to complex sex-ratio dynamics (e.g., [8,9]).

The maternal inheritance of male sterility provides one reason for its relatively high frequency in plants in comparison with its counterpart, female sterility, which obviously cannot be transmitted by maternally inherited genes. Female sterility due to autosomal genes could in principle spread in a population, but the conditions that might allow this are very stringent [2,10]. This is because the loss of a female function effectively halves the fitness of an outcrossing hermaphrodite, and it is unlikely that female-sterile plants could compensate for this loss by more than doubling their siring success, as would be required for their spread. 'Androdioecy', the occurrence of female-sterile individuals (i.e., males) in a population with hermaphrodites, is indeed extremely rare, and almost all of the few known



**Figure 1. *Phillyrea angustifolia*.**

(A) *P. angustifolia* growing in south-western Portugal, with close-ups of its axillary inflorescences (B) and its female-sterile and hermaphrodite flowers (C). Note the absence of a pistil between the anthers of the female-sterile flower (left) and its presence in the hermaphrodite flower (right). There are two classes of hermaphrodites,  $H_a$  and  $H_b$ , whereby individuals are cross compatible but cannot mate with members their own class (see text and Figure 2 for details). Photographs courtesy of Colin Hughes and John Baker.

cases of it appear to have evolved from dioecy, not hermaphroditism [11,12], and none of them has shown any evidence for the importance of selfish genes in the way that gynodioecy has. But a new study [13] of the Mediterranean shrub *Phillyrea angustifolia* (Figure 1), recently published in the journal *Evolution*, both confirms the evolution of androdioecy from hermaphroditism and provides tantalizing evidence for a type of selfish genetic element not previously known in any plant species, something akin to a Y chromosome ‘meiotic driver’.

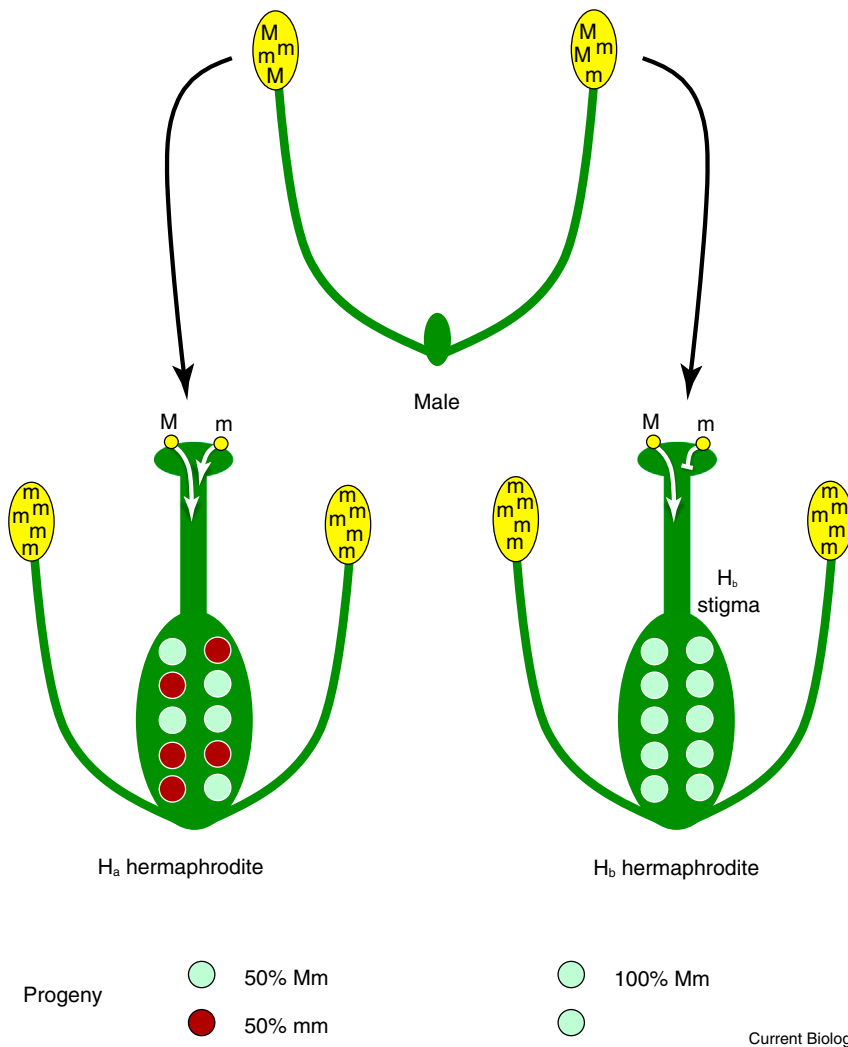
Previous work by the same team of scientists [14] found that *P. angustifolia* presents an unusual example of a diallelic self-incompatibility (SI) system that prevented hermaphrodites from mating with themselves and all other hermaphrodites with the same genotype at the incompatibility (S) locus, which amounts to half the potential seed producers in the population. Significantly, while this SI system compromises siring opportunities for hermaphrodites, the female-sterile plants could mate successfully with all hermaphrodites. This immediately gives the female sterility mutation the possibility of compensating

for lost seed production by handsome rewards in terms of siring success [14,15]. One might have thought that was the end of the story. But, motivated to explain why male frequencies in natural populations were higher than could be predicted by models accommodating the association between female sterility and SI [15], Billiard *et al.* [13] undertook a program of crosses to determine the siring potential of the males and hermaphrodites of the two different self-incompatibility classes in the populations. The results reported in their new paper indicate not only that males can sire progeny on both SI classes of hermaphrodites, as shown previously, but also that the progeny sired on mothers of one of the two classes were all male — giving the female-sterility mutation an additional large fitness benefit (Figure 2).

The mechanism causing the absence of hermaphrodite progeny in crosses between males and one of the SI classes of hermaphrodite of *P. angustifolia* is not yet known. Viewed in isolation, the result resembles Y chromosome ‘meiotic drive’, whereby Y chromosomes selfishly favour their own transmission over their X homologue [16]. Meiotic drive favouring X-chromosome transmission

is well known in a number of animal systems [16] and is known from at least one plant species, the dioecious species *Silene latifolia* [17]. In most of these cases, including *S. latifolia*, X chromosomes carried by some males are favoured during meiosis over the Y, so that the progeny they sire show female-biased sex ratios. But it is clear that the sex-ratio bias observed in *P. angustifolia* cannot be the result of a distortion of a fair meiosis (in which viable gametes are more likely to carry a Y than an X chromosome), because the same males whose progeny lacked hermaphrodites in crosses with one class of hermaphrodites sired substantial numbers of hermaphrodites in crosses with the other hermaphrodites. A more likely explanation, emphasised by Billiard *et al.* [13], is that the sex ratios observed in their crosses reflect an interaction between the sex-determining locus in *P. angustifolia* and the locus or loci governing self- and cross-incompatibility reactions (the S locus). On the one hand, pollen from males is able to overcome the incompatibility reaction in one class of hermaphrodites, whatever S allele it carries — so that all pollen from males is compatible with stigmas of those hermaphrodites. On the other hand, only pollen carrying the female-sterility mutation is compatible with the stigmas of the other class of hermaphrodites, and pollen grains not carrying it are rejected (Figure 2).

If the sex ratios reported by Billiard *et al.* [13] are the result of an interaction between sex determination and the self-incompatibility reaction, as seems likely, then the way self-incompatibility works in *P. angustifolia* is extraordinary. Crosses between hermaphrodites point to a diallelic sporophytic self-incompatibility system, whereby haploid pollen grains express the diploid self-incompatibility phenotype of their parent plant. With this system, which is well known from a large number of angiosperm species [18], pollen grains originating from a specific parent should either all be rejected or all be compatible with a particular stigma — as indeed seems to be the case for hermaphrodite x hermaphrodite crosses in



**Figure 2. Segregation distortion displayed by crosses in *Phillyrea angustifolia*.**

Males (female-sterile individuals) are heterozygous at the female-sterility locus, *Mm* (akin to a Y chromosome). They thus produce *M* and *m* pollen in equal proportions. Pollen of both haplotypes from males arriving on H<sub>b</sub> hermaphrodite stigmas can sire ovules, yielding a 1:1 ratio of males:hermaphrodites in the progeny. However, pollen lacking the female-sterility (*m*) allele is unable to sire ovules of H<sub>b</sub> hermaphrodites, so that all individuals in the progeny are male. (Note, it is not yet known whether *m*-bearing pollen tubes are arrested prior to fertilization, as suggested in the cartoon here, or whether *mm* progeny are aborted after fertilization by *m*-bearing pollen; this latter possibility would constitute a demographic cost to the population through reduced seed set.) Males carry alleles at a second locus that determines the compatibility class of their hermaphrodite progeny; there are therefore three possible male genotype classes (not shown in the simplified scheme here): two homozygote genotypes and a heterozygote genotype at the compatibility locus. It appears that the female-sterility allele (*M*) is capable of suppressing expression of alleles at compatibility (*S*) locus in the pollen of males, rendering male pollen grains compatible with both classes of hermaphrodites.

*P. angustifolia*. But the apparent rejection by certain stigmas of X-bearing pollen and the compatibility of Y-bearing pollen produced by the same males points to a *gametophytic* self-incompatibility reaction, whereby pollen grains express their own self-incompatibility phenotype [18]. If this is the case, the combination of both sporophytic and gametophytic

expression of incompatibility is extremely unusual and demands a mechanistic explanation.

Future work will hopefully throw light on the mechanism responsible for the sex ratios observed in crosses between different genotypes of *P. angustifolia*. But whatever the underlying mechanism, phenomenologically the results of Billiard

*et al.* [13] can be interpreted as a striking example of the spread of an effectively selfish genetic element, in this case the female-sterility mutation (akin to a Y chromosome), favouring its own transmission. In this sense, the high frequencies of males co-occurring with hermaphrodites in populations of *P. angustifolia* as a result of a selfish female-sterility mutation mirrors the high frequencies of females in gynodioecious species expressing selfish cytoplasmic male-sterility mutations. Finally, we are moving towards a satisfying explanation for the spread and maintenance of female sterility from a hermaphroditic starting point in *P. angustifolia* — the only clear case of this phenomenon in plants to date.

#### REFERENCES

- Barrett, S.C.H. (2002). The evolution of plant sexual diversity. *Nat. Rev. Genet.* 3, 274–284.
- Charlesworth, D., and Charlesworth, B. (1978). A model for the evolution of dioecy and gynodioecy. *Am. Nat.* 112, 975–997.
- Bailey, M.F., and Delph, L.F. (2007). A field guide to models of sex-ratio evolution in gynodioecious species. *Oikos* 116, 1609–1617.
- Kaul, M.L.H. (1988). *Male Sterility in Higher Plants*. (Berlin: Springer Verlag).
- Lewis, D. (1941). Male sterility in natural populations of hermaphrodite plants. *New Phytol.* 40, 56–63.
- Hurst, L.D. (1991). The incidences and evolution of cytoplasmic male killers. *Proc. R. Soc. Lond. Biol. Sci.* 244, 91–99.
- Hamilton, W.D. (1967). Extraordinary sex ratios. *Science* 156, 477–488.
- Frank, S.A., and Barr, C.M. (2001). Spatial dynamics of cytoplasmic male sterility. In *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown, and J. Antonovics, eds. (Oxford: Blackwells), pp. 219–243.
- Dufay, M., and Pannell, J.R. (2010). The effect of pollen versus seed flow on the maintenance of nuclear-cytoplasmic gynodioecy. *Evolution* 64, 772–784.
- Lloyd, D.G. (1975). The maintenance of gynodioecy and androdioecy in angiosperms. *Genetica* 45, 325–339.
- Charlesworth, D. (1984). Androdioecy and the evolution of dioecy. *Biol. J. Linn. Soc.* 23, 333–348.
- Pannell, J.R. (2002). The evolution and maintenance of androdioecy. *Annu. Rev. Ecol. Syst.* 33, 397–425.

13. Billiard, S., Husse, L., Lepercq, P., Godé, C., Bourceaux, A., Lepart, J., Vernet, P., and Saumitou-Laprade, P. (2015). Selfish male-determining element favors the transition from hermaphroditism to androdioecy. *Evolution* **69**, 683–693.
14. Saumitou-Laprade, P., Vernet, P., Vassiliadis, C., Hoareau, Y., de Magny, G., Dommée, B., and Lepart, J. (2010). A self-incompatibility system explains high male frequencies in an androdioecious plant. *Science* **327**, 1648–1650.
15. Pannell, J.R., and Korbecka, G. (2010). Mating-system evolution: Rise of the irresistible males. *Curr. Biol.* **20**, 482–484.
16. Jaenike, J. (2001). Sex chromosome meiotic drive. *Annu. Rev. Ecol. Syst.* **32**, 25–49.
17. Taylor, D.R., and Ingvarsson, P.K. (2003). Common features of segregation distortion in plants and animals. *Genetica* **117**, 27–35.
18. Hiscock, S.J., and McInnis, S.M. (2003). The diversity of self-incompatibility systems in flowering plants. *Plant Biol.* **5**, 23–32.