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NEWS AND VIEWS

PERSPECTIVE

Disassortative mating and the maintenance of sexual polymorphism in painted maple

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Since Darwin's pioneering research on plant reproductive biology (e.g. Darwin 1877), understanding the mechanisms maintaining the diverse sexual strategies of plants has remained an important challenge for evolutionary biologists. In some species, populations are sexually polymorphic and contain two or more mating morphs (sex phenotypes). Differences in morphology or phenology among the morphs influence patterns of non-random mating. In these populations, negative frequency-dependent selection arising from disassortative (intermorph) mating is usually required for the evolutionary maintenance of sexual polymorphism, but few studies have demonstrated the required patterns of non-random mating. In the current issue of *Molecular Ecology*, Shang *et al.* (2012) make an important contribution to our understanding of how disassortative mating influences sex phenotype ratios in *Acer pictum* subsp. *mono* (painted maple), a heterodichogamous, deciduous tree of eastern China. They monitored sex expression in 97 adults and used paternity analysis of open-pollinated seed to examine disassortative mating among three sex phenotypes. Using a deterministic 'pollen transfer' model, Shang *et al.* present convincing evidence that differences in the degree of disassortative mating in progeny arrays of the sex phenotypes can explain their uneven frequencies in the adult population. This study provides a useful example of how the deployment of genetic markers, demographic monitoring and modelling can be integrated to investigate the maintenance of sexual diversity in plants.

Keywords: *Acer*, dichogamy, heterodichogamy, paternity analysis, plants, sexual polymorphism

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Shang *et al.* focus on a species with a complex and relatively uncommon sexual strategy known as heterodichogamy. Dichogamy is the temporal separation of male and female function and is a common adaptation in plants to reduce inbreeding and self-interference (Lloyd & Webb 1986). However, populations of heterodichogamous species are polymorphic for dichogamy and often contain equal frequencies of protandrous and protogynous morphs that differ in the timing of female and male sex function (Bai *et al.* 2007; Gleiser *et al.* 2008; Kikuchi *et al.* 2009). Significantly, in *Acer pictum* an additional phenotype occurs that cycles through male, female and then male sex function (duodichogamy) within each flowering season.

Heterodichogamy is phylogenetically dispersed and is reported from 12 families and 18 genera of flowering plants (Renner 2001; Endress & Lorence 2004); however, it is especially well represented in maples—*Acer* (Renner *et al.* 2007). In *A. pictum*, plants are monoecious (separate male and female flowers), but individuals belong predominantly to one of three sex phenotypes described above (and see Fig. 1). The reciprocal and synchronous nature of flowering in heterodichogamous populations has led to the suggestion that these polymorphisms are maintained because they reduce selfing and in so doing promote intermorph (disassortative) mating (Gleeson 1982). Few studies have examined the mechanisms maintaining more complex forms of heterodichogamy, such as the presence of three morphs as in *A. pictum*, and this led the authors to investigate the factors responsible for the maintenance of this complex sexual polymorphism.

To confirm the identity of sex phenotypes and their relative frequencies, Shang *et al.* monitored the sex expression of 97 adult trees over 4 years in their study population. This revealed morph ratios biased towards the duodichogamous sex phenotype (Fig. 2). To investigate the patterns of disassortative mating, Shang *et al.* used microsatellite markers and paternity analysis of open-pollinated seed to characterize pollen transfer rates within and between the sex phenotypes. The observed patterns were then compared to those expected given the frequencies of sex phenotypes and the distance among individuals. By using likelihood models to estimate the decline in paternity with distance, Shang *et al.* ensured that the spatial context of individuals, as well as the ratios of the sex phenotypes, was accounted for in the estimation of expected mating patterns. Their results supported the prediction of predominately disassortative mating among the three mating morphs (Fig. 2; see Table 2 and Fig. 2 in Shang *et al.* 2012) and confirmed earlier findings in other *Acer* species, with mostly protandrous and protogynous sex phenotypes, in which high levels of disassortative mating have also been found (Gleiser *et al.* 2008; Kikuchi *et al.* 2009).

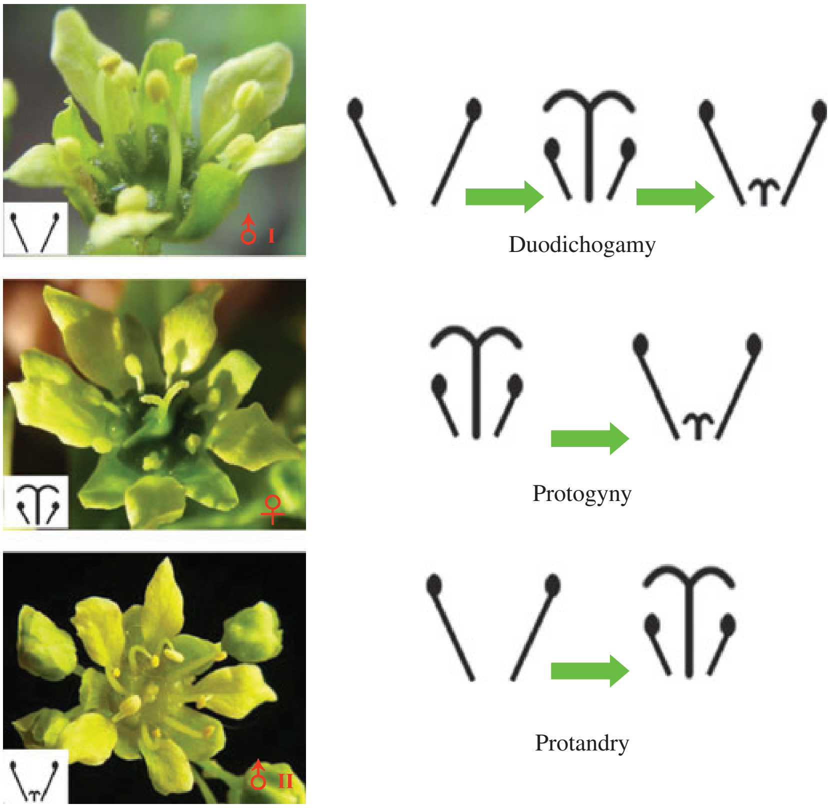

Fig. 1 In *Acer pictum* subsp. *mono*, populations consist of three sex phenotypes (right panel) that differ in the timing of male and female sex function within a given flowering season: duodichogamous (male—female—male), protogynous (female—male) and protandrous (male—female). Photographs (left panel) represent flowers of the three phases of the duodichogamous phenotype. Figure courtesy of Shang *et al*.

Equal morph or sex ratios (isoplethy) are predicted in many sexually polymorphic species as a result of negative frequency-dependent selection (Clarke *et al.* 1988). Why then are sex phenotype ratios in the population of *A. pictum* subsp. *mono* strongly biased towards the duodichogamous phenotype? Using a deterministic pollen transfer model of the mating process, Shang *et al.* provided evidence that the observed patterns of mating can explain the uneven morph ratios found in the adult population. Specifically, they demonstrated that this result is largely attributed to a higher degree of intramorph (assortative) mating among duodichogamous individuals than is evident for the other two sexual phenotypes (Fig. 2). In contrast to sexual polymorphisms like heterostyly, which usually possess strong physiological barriers to intramorph mating (Darwin 1877), species such as *A. pictum* subsp. *mono* are more vulnerable to a variety of environmental and demographic influences that influence the timing of sex function. This can influence the extent to which disassortative mating affects morph ratios. We therefore expect more frequent departures from the null expectation of isoplethy compared to sexual systems in which intramorph mating is precluded.

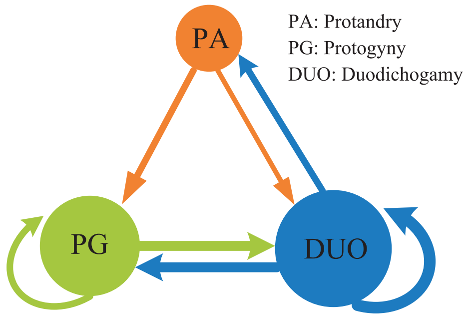

Fig. 2 Rates of intermorph and intramorph mating events among three sex phenotypes in a population of *Acer pictum* subsp. *mono*. Shang *et al.* used paternity analysis to reveal predominantly disassortative mating in the adult population. Circles are proportional to the frequency of the sex phenotype in the population, and the thickness of the arrows indicates the frequency of pollen transfer. Figure courtesy of Shang *et al*.

Shang *et al.* suggest a number of potential mechanisms that may explain the higher degree of assortative mating in the duodichogamous sex phenotype. These include the suggestion that because this sex phenotype passes through a male phase twice during each season, there may be more opportunities for selfing and intramorph mating. While this idea requires further testing, it may be difficult to disentangle from the fact that duodichogamous individuals in the adult population were also disproportionately represented and therefore would have had more opportunities to mate with one another.

Unfortunately, only ~50% of the sampled progeny in Shang *et al.*'s study could be assigned with confidence to paternal parents, implicating long-distance pollen dispersal from outside the population and mating with unknown partners. This is a common challenge in paternity analysis of natural populations (Jones *et al.* 2010) that requires more extensive genotyping of potential partners and knowledge of the nature of pollen dispersal in target species. New statistical approaches that assign pedigrees using both genotypic and phenotypic information can provide substantial improvements in paternity assignment (e.g. Hadfield *et al.* 2006). Moreover, the inclusion of information on the flowering phenology of individuals would almost certainly improve the accuracy of this type of analysis and enable testing of the role of flowering synchrony on male outcrossed siring success.

Shang *et al.* report an annual rate of transition among sexual phenotypes of 4.5%, with most switches between the duodichogamous and protandrous phenotypes, and virtually no transitions involving protogynous individuals. Similar patterns involving 'male inconstancy' were also reported by Sato (2002) and Gleiser *et al.* (2008) in *Acer japonicum* and *Acer opalus*, respectively. Sexual lability is a common feature of many sexually dimorphic plants (reviewed in Lloyd & Bawa 1984); however, most examples involve size-dependent modification in sex expression (e.g. Policansky 1981; Barrett *et al.* 1999), a factor that does not appear to be operating in *A. pictum* subsp. *mono* as measurements of tree diameter failed to reveal any differences among the three sex phenotypes in size. The extent to which sexual lability may contribute to the maintenance of heterodichogamy remains unclear although its occurrence may have implications for transitions to other sexual systems in *Acer*.

One challenge in the study of long-lived species in which sex expression changes over years is the accurate characterization of the lifetime sexual system of populations. However, Shang *et al.* argue that the low rates of sexual transitions over the 4 years of their study and the high levels of disassortative mating they document provide clear evidence of at least two functionally distinct mating morphs in *A. pictum.* Similar results involving high disassortative mating and low rates of sexual transitions have also been observed in *A. opalus* (Gleiser *et al.* 2008), suggesting that at least these two species are legitimately heterodichogamous. Although requiring considerable patience, it would be valuable to conduct controlled crosses among the the sex phenotypes of *A. pictum* to determine the genetic basis of the sexual polymorphism. This has been conducted in the English walnut (*Juglans regia*) and pecan (*Carya illinoensis*), which are also heterodichogamous, and in which protogyny vs. protandry appears to be controlled by a single locus with two alleles with protogyny dominant (Gleeson 1982; Thompson & Romberg 1985). The addition of genetic information as well as mating patterns to predictive models of morph ratio evolution may provide useful insights.

For those courageous enough to study long-lived plants with dynamic sex expression, *Acer* provides excellent opportunities for future investigations of the evolution and maintenance of sexual strategies. Unlike some taxa of trees in which there is relatively limited variation in sex expression and mating biology, among the 124 species of *Acer*, 13 are dioecious and the remaining monoecious species have diverse floral strategies including dichogamy, duodichogamy and heterodichogamy (Renner *et al.* 2007). The study by Shang *et al.* fills an important gap in our knowledge of the mating biology of heterodichogamous sexual systems by investigating the mechanisms governing the biased sex phenotype ratios that can occur when duodichogamous individuals enter the picture. Future work on this fascinating system could usefully include large-scale geographic surveys of sex phenotype frequencies to determine whether the duodichogamous phenotype commonly dominates in populations.

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