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REVIEW: PART OF A SPECIAL ISSUE ON PLANT MATING SYSTEMS

Mating system shifts on the trailing edge

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• *Background* The trailing edges of species ranges are becoming a subject of increasing interest as the environment changes due to global warming. Trailing edge populations are likely to face extinction because of a decline in numbers and an inability to evolve new adaptations with sufficient speed. Discussions of character change in the trailing edge have focused on physiological, exomorphic and phenological traits. The mating pattern within populations has not been part of the discourse, in spite of the fact that the mating pattern may affect the ability of populations to respond to environmental change and to maintain their sizes. In this paper, the case is made that a substantial increase in self-fertilization rates may occur via plastic responses to stress.
• *Scope and Conclusions* Small populations on the trailing edge are especially vulnerable to environmental change because of inadequate levels of cross-fertilization. Evidence is presented that a deficiency of cross-seed production is due to inadequate pollinator services and a paucity of self-incompatibility alleles within populations. Evidence also is presented that if plants are self-compatible, self-fertilization may compensate in part for this deficiency through a stress-induced increase in levels of self-compatibility and stress-induced alterations in floral morphology that elevate self-pollination. Whereas increased self-fertility may afford populations the time to adapt to their changing environments, it can be concluded that increased selfing is not a panacea for the ills of environmental change, because it will lead to substantial reductions in genetic diversity, which may render adaptation unlikely.

Key words: Environmental change, mating system, phenotypic plasticity, self-fertilization, self-pollination, trailing edge.

INTRODUCTION

The globe is experiencing a warming trend that is unparalleled in recent history (IPCC, 2007). Bioclimatic envelop models, which are based on the observation that species are niche conservative (Prinzing *et al.*, 2001; Ackerly, 2003; Wiens and Graham, 2005), indicate that global warming will be accompanied by major displacement in species' ranges, with species spreading into higher latitudes or elevations (Ohlemüller *et al.*, 2006; Jump and Peñuelas, 2005; Thuiller *et al.*, 2008; Jump *et al.*, 2009). Indeed, changes in distributions have already begun.

Distributional changes are brought about by boundary expansion on the leading edge of a range and contraction on the trailing or rear edge of a range. The trailing edge is characterized by negative growth in population size, a reduction in population number and an increase in interpopulation distances (Hampe and Petit, 2005). If the environment continues to deteriorate, all populations in a region will be extirpated, and the trailing edge will shift in the direction of species expansion. If the rate of global warming is as forecasted, theoretical treatments indicate that most populations on the trailing edge will be unable to adapt to a deteriorating environment, and that they will go extinct (Lynch and Lande, 1993; Bürger and Lynch, 1995; Lynch, 1996). The position of the trailing edge changes in concert with systematic environmental alteration as opposed to 'standard' edges that are not moving in a given direction over time.

As the globe warms, populations at and near the trailing edge will be under strong pressure to adapt to new climatic conditions, especially reduced precipitation (Ackerly, 2003; Jump *et al.*, 2009). In response, edge populations may evolve physiological, morphological and life history attributes which better attune them to arid environments.

Discussions of character change in the trailing edge have focused on physiological, exomorphic and phenological traits (Davis and Shaw, 2001; Ackerly, 2003; Hampe and Petit, 2005; Jump *et al.*, 2009). The mating pattern within populations has not been part of the discourse, in spite of the fact that the mating pattern may affect the ability of populations to respond to environmental change and to maintain their sizes. The purpose of this paper is to highlight how the level of self-fertilization may increase at and near the retracting boundary of self-compatible plant species as a result of environment-induced changes within flowers and plants as a whole, a decline in the level of cross-pollination, and selection for greater self-fertility. Heightened self-fertility has important implications for population survival during environmental change because it provides a measure of reproductive assurance. This paper complements a recent discussion by Eckert *et al.* (2010) on plant mating-system change in response to anthropogenic habitat modification.

ENVIRONMENT-ENHANCED SELF-FERTILIZATION

Environments that deviate from those to which a species is well-adapted may affect the penchant for selfing through their influence on the self-incompatibility (S) locus (Levin,

1996; Good-Avila *et al.*, 2008). The level of self-fertility in weakly self-fertile (pseudo-compatible) species may be elevated when plants are exposed to reduced light intensities [e.g. *Oenothera organensis* (Emerson, 1940) and *Petunia hybrida* (Flaschenreim and Ascher, 1980)]. High temperatures also may heighten self-fertility [e.g. *Lilium longiflorum* (Ascher and Peloquin, 1970), *Brassica oleracea* (Johnson, 1971), *Lycopersicon peruvianum* (Hogenboom, 1972), *Petunia hybrida* (Takahashi, 1973), *Cichorium sativum* (Eenick, 1981) and *Convolvulus arvensis* (Westwood *et al.*, 1997)]. Even exposure to saline spray may increase the level of pseudo-self-compatibility [e.g. *Brassica napus* (Fu *et al.*, 1992) and *Senecio squalidus* (Hiscock, 2000)].

Self-fertility in inhospitable environments also may be increased in some species through a change in flower development. One common alteration is a reduction in stigma–anther separation [reduced herkogamy; e.g. *Lycopersicon esculentum* (Rick *et al.*, 1977), *Datura wrightii* (Elle and Hare, 2002), *Arabidopsis thaliana* (Brock and Weinig, 2007), *Mimulus guttatus* (van Kleunen, 2007) and *Eichhornia paniculata* (Vallejo-Marin and Barrett, 2009)], which results in higher levels of self-pollination. The reduction in herkogamy is mediated by a reduction in flower size, which is a common response to harsh growing conditions [e.g. *Polemonium viscosum* (Galen, 2000), *Epilobium angustifolium* (Carroll *et al.*, 2001) and *Rosemarinus officinalis* (Herrera, 2005)]. In some species, reduced flower size in marginal habitats is due to accelerated floral growth rate [e.g. *Clarkia xantiana* (Runions and Geber, 2000; Mazer *et al.*, 2004). Even herbivory may increase anther–stigma proximity and increase the level of autogamy (cf. Penet *et al.*, 2009).

Some species regularly produce cleistogamic flowers (diminutive and automatically self-pollinating) in addition to chasmogamic (showy and cross-pollinating) flowers. The proportion of cleistogamic flowers and the level of self-fertilization may increase when their habitats are deficient in light, moisture or nutrients (Le Corff, 1993). In *Impatiens capensis*, even herbivory may increase the proportion of cleistogamic flowers (Steets and Ashman, 2004).The proportion of flowers that are cleistogamic typically is a function of plant size, as demonstrated in *Mimulus nasutus* (Diaz and Macnair, 1998).

INCREASED SELFING DUE TO INADEQUATE POLLEN RECEIPT

The level of pollen exchange among members of a population is a function of population size. As populations in the trailing edge shrink in response to ever increasing climatic stress, they become less desirable resources for pollinators, and cross-pollination levels decline [e.g. *Dianthus deltoides* (Jennersten, 1988), *Banksia goodii* (Lamont *et al.*, 1993), *Nepeta cataria* (Sih and Baltus, 1987), *Brassica kaber* (Kunin, 1997), *Clarkia xantiana* (Moeller and Geber, 2005) and *Lupinus perennis* (Bernhardt *et al.*, 2008)]. Cross-pollination levels in wind-pollinated species are also dependent on population size [e.g. *Pinus ponderosa* (Farris and Mitton, 1984), *Plantago coronopus* (Wolff *et al.*, 1988), *Pinus sylvestris* (Robledo-Arnuncio *et al.*, 2004) and *Paris quadrifolia* (Jacquemym and Brys, 2008)]. If plants are self-incompatible, their reproductive success is negatively correlated with population size, whereas if plants are self-compatible the loss of cross-seed production is mitigated to some degree by an increase in self-seed production (Aizen *et al.*, 2002; Wilcock and Neiland, 2002; Aizen and Feinsinger, 2003).

Pollinator service per flower is not simply a function of plant numbers. It is also dependent on the number of flowers per plant, a trait that is plastic. Pollinators 'count' numbers of flowers, not just numbers of plants. Flower number is proportional to plant biomass, and biomass is sensitive to the environment (Weiner *et al.*, 2009). Accordingly, annuals growing in relatively inhospitable conditions will produce fewer flowers and seeds per plant than the same number of plants in a benign environment (Pigliucci, 2001; Reekie and Bazzaz, 2005; Bonser and Aarsen, 2009; Weiner *et al.*, 2009). Correlatively, perennials subjected to unfavorable conditions will produce fewer flowers and seeds per year and/or flower and seed less frequently than they would under favorable circumstances (Tyler, 2001; Pfeiffer *et al.*, 2006; Crone *et al.*, 2009; Jacquemyn *et al.*, 2010).

Populations with small numbers of plants and few flowers per plant also will experience reduced seed-set because pollinators tend to be less flower-constant (i.e. they will be less likely to sequentially visit a given species) in them, thereby depositing less conspecific pollen on stigmas during a given foraging bout than they would in large populations (Goulson *et al.*, 1997; Goulson and Wright, 1998; Gegear and Laverty, 2005). As conspecific pollen loads decline, heterospecific pollen loads are apt to increase, and may create a physical barrier to the contact of conspecific pollen with the stigma, (Waser, 1978; Kohn and Waser, 1985; Waser and Fugate, 1986), cause stigma closure (Waser and Fugate, 1986; Morales and Traveset, 2008), stylar clogging (Shore and Barrett, 1984; Galen and Gregory, 1989) or allelopathic inhibition of conspecific pollen (Sukhada and Jayachandra, 1980; Thomson *et al.*, 1981; Murphy and Aarsen, 1995). Inadequate receipt or placement of conspecific pollen leads to reduced seed-set (Ashman *et al.*, 2004; Steffan-Dewenter *et al.*, 2006). Species exploiting specialist pollinators may be affected more than those using generalist pollinators (Aigner, 2006; Steffan-Dewenter *et al.*, 2006). Inadequate pollen receipt may be the most prominent cause of reproductive impairment in marginal populations (Aguilar *et al.*, 2006).

Populations on the trailing edge may experience a reduction in cross-pollination if environmental change alters the phenological relationships of plants and their pollinators, as already appears to be happening (Memmott *et al.*, 2007; Hegland *et al.*, 2009). A reduction in cross-pollination will also accrue if environmental change is accompanied by a change in pollinator fauna (Gómez *et al.*, 2010), or by a regional decline in pollinator species diversity and pollinator population size (Potts *et al.*, 2010). Even annual change in climatic conditions may have significant effects on plant–pollinator relationships (Alarcón *et al.*, 2008; Dupont *et al.*, 2009).

In small populations, the amount of potentially effective cross- pollen may be limited by a paucity of different alleles at the self-incompatibility (S) locus, which translates into a paucity of potential mates (Byers and Meagher, 1992; Young *et al.*, 2000; Willi and Fischer, 2005; Glémin *et al.*, 2008).

If plants share S-alleles, crosses between them will either be unsuccessful or only partially successful (de Nettancourt, 2001). Accordingly, a higher proportion of crosses in small populations are apt to yield no or few seeds than crosses in large populations where numerous S-alleles are likely to be present. A small population of *Brassica insularis* may have as few as three S-alleles versus up to 30 S-alleles in large populations (Glémin *et al.*, 2005). Small populations of *Senecio squalidis* may have between two and six S-alleles (Brennan *et al.*, 2006), and small populations of *Carthamus flavescens* may have only six to eight such alleles (Imbrie and Knowles, 1971; Imbrie *et al.*, 1972).

An increase in self-seed production at the expense of cross-seed production is reflected in lower outcrossing rates (*t*) in small populations. This relationship is well illustrated in a recent meta-analysis of 22 studies involving populations of different sizes in 27 species (Eckert *et al.*, 2010). The result is consistent with that from another large meta-analysis which showed that the inbreeding coefficient of progeny tended to be higher in small populations than in large ones of the same species (Aguilar *et al.*, 2008). This meta-analysis also showed that genetic diversity and heterozygosity were more prone to decline in small populations.

A reduction in heterozygosity *per se* may increase the penchant for selfing in predominantly outcrossing plants. Increased selfing following inbreeding has been demonstrated in *Secale cereale* (Lundquist, 1960), *Agrostis tenuis* (Antonovics, 1968), *Nemesia strumosa* (Henny and Ascher, 1976), *Petunia integrifolia* (Dana and Ascher, 1985), *Senecio squalidus* (Hiscock, 2000), *Solanum caroliniense* (Mena-Ali *et al.*, 2008) and in *Phlox drummondii* (Levin, 1995).

EVOLUTIONARY LABILITY OF SELF-FERTILITY

As population size declines in response to climatic change, plants in the trailing edge that are more self-fertile than others are likely to be at a selective premium, because they will leave the most offspring, all else being equal. The penchant for selfing should then increase. This premise is based on the assumption that self-fertility is heritable. The responsiveness of self-fertility to selection is well illustrated in the numerous self-fertile domesticates that have been derived from nearly self-sterile wild progenitors (Rick, 1988). These include ornamentals (e.g. snapdragon, *Phlox* and petunia) and vegetable crops (e.g. tomatoes and cauliflower).

The evolutionary lability of self-fertility also is evident in results of selection experiments. Consider *Phlox drummondii*, where selection for increased autogamy was practiced for two generations (Bixby and Levin, 1996). During that period, autogamous seed-set in the predominantly outcrossing *P. drummondii* increased from 4 % to 56 % of the ovules in one population and from 22 % to 41 % in another. Two cycles of selection for increased self-fertility also were performed on the *P. drummondii* cultivar 'Salmon Beauty' in which autogamous seed-set increased from 40 % to 95 %.

Finally, the evolvability of the breeding system is evident in the shifts from outcrossing to facultative selfing during the colonization of heavy-metal substrates in *Thlaspi caerulescens*

(Dubois *et al.*, 2003), *Anthoxanthum odoratum* and *Agrostis tenuis* (Antonovics, 1968), and during the colonization of serpentine soils in *Lasthenia* (Rajakaruna, 2004) and *Mimulus* (Macnair and Gardiner, 1998). Evolvability also is illustrated in the many times that self-fertility has increased in ecologically marginal populations on the periphery of species' ranges [e.g. *Clarkia unguiculata* (Vasek, 1964), *Gilia achilleifolia* (Schoen, 1982), *Eichhornia paniculata* (Barrett *et al.*, 1989), *Arenaria uniflora* (Wyatt, 1988), *Nicotiana glauca* (Schueller, 2004), *Clarkia xantiana* (Moeller and Geber, 2005) and *Leavenworthia alabamica* (Busch, 2005)]. Floral morphology is also responsive to selection as shown in *Mimulus guttatus*, where populations that are pollen limited evolved reduced stigma–anther separation (Fenster and Ritland, 1994).

Although the genetic bases for shifts toward self-fertility have not been documented in the aforementioned species, the transit from self-sterility to self-fertility may result from loss of function mutations at the self-incompatibility locus (Igic *et al.*, 2008). If species already are facultative selfers, increased self-compatibility may arise from the suppression of S-gene activity by modifier genes (Levin, 1996; Good-Avila *et al.*, 2008).

DISCUSSION

An increase in the rate of self-fertilization in populations along or near the rear edges of species' ranges may occur in response to progressive climate change. This mating system shift could arise from environment-induced changes in pollen–pistil compatibility and/or flower architecture, a reduction in the level of cross-pollination in facultative selfers, and from the evolution of higher levels of self-fertility and within-flower self-pollination. Evolution may be based upon standing genetic variation or achieved through genetic assimilation, wherein phenotypes generated by plastic changes eventually are controlled by genetic change such that an inducing environment is not required (West-Eberhard, 2003; Pigliucci *et al.*, 2006; Crispo, 2008). Self-fertility also may increase first via the evolution of greater plasticity, and then be fixed by genetic assimilation (Lande, 2009).

Both plastic and genetic responses may contribute to a range of phenotypic shifts in the trailing edge; and it may be difficult to partition causation among these responses (Jump and Peñuelas, 2005; Giennapp *et al.*, 2008). In the case of heightened selfing, plastic responses are apt to play a preeminent role early in the decline of populations, because phenotypic plasticity is immediate, while genetic change occurs across generations (Pulido and Berthold, 2004). However, over long time frames the capacity of populations to increase selfing via plasticity is much more limited than the ability of populations to increase selfing by genetic change (De Jong, 2005; Jump and Peñuelas, 2005).

Elevated levels of self-fertilization, whether based on the environment or genes, afford populations a measure of reproductive assurance (Kalisz and Vogler, 2003; Moeller and Geber, 2005; Goodwillie *et al.*, 2005; Eckert *et al.*, 2006; Busch and Schoen, 2008). Using models that included population dynamics, pollinator behaviour and self-fertilization, Morgan *et al.* (2005) showed that heighten levels of self-seed

production may negate a downward spiral to extinction that otherwise would be mandated by complete or substantial dependence on cross-pollination for seed production.

Reproductive assurance would promote population survival only if a gain in seed production is not outweighed by inbreeding depression, which is a likely correlate of selfing in outcrossing and predominantly outcrossing species (Lande and Schemske, 1985; Dudash and Fenster, 2000; Keller and Waller, 2002; Goodwillie *et al.*, 2005). The level of inbreeding depression in outcrossers is much greater than in selfers (Husband and Schemske, 1996). In many species, the magnitude of inbreeding depression is higher in stressful environments (Dudash, 1990; Johnston, 1992; Eckert and Barrett, 1994; Reed *et al.*, 2002; Armbruster and Reed, 2005). In general, higher levels of inbreeding depression substantially elevate the extinction risk of populations (O'Grady *et al.*, 2006; Vilas *et al.*, 2006; Wright *et al.*, 2008).

The balance between the effects of inbreeding depression and reproductive assurance varies among species, populations and environments. Selfing is advantageous under variable pollinator conditions in *Hibiscus trionum*, where inbreeding depression is high (Seed *et al.*, 2006), and in *Collinsia verna*, where inbreeding depression is low (Kalisz and Vogler, 2003). In *Aquilegia canadensis* (Herlihy and Eckert, 2002) and *Bulbine vagans* (Vaughton *et al.*, 2008), inbreeding depression erodes the magnitude of any benefit provided by reproductive assurance. The detrimental effect of inbreeding depression is the least when self-seed are not produced at the expense of cross-seed (Morgan *et al.*, 2005; Dornier *et al.*, 2008).

The relative effects of inbreeding depression and reproductive assurance may gradually shift in favour of the latter, if populations can purge their genetic load. This indeed has happened to various degrees in many plant populations (Byers and Waller, 1999; Crnokrak and Barrett, 2002; Reed *et al.*, 2003; Lienert and Fischer, 2004). Pujol *et al.* (2009) found that in *Mercurialis annua* inbreeding depression was depleted when the species passed through repeated bottlenecks during the process of range expansion. This reduction probably was achieved through the recurrent expression of, and selection against, deleterious recessive genes in small, inbred populations (Barrett and Charlesworth, 1991).

The pace of the decline in inbreeding depression depends on the environment (Biljsma *et al.*, 2000). The purging of deleterious alleles often proceeds faster during periods of environmental stress (cf. Swindell and Bouzat, 2006).

In addition to the removal of harmful genes, inbreeding depression in small populations may be reduced through immigration, i.e. when some seeds are sired by plants from extraneous sources and when some seeds are introduced from these sources (Sheridan and Karowe, 2000; Huford and Mazer, 2003; Willi and Fischer, 2005; Bossuyt, 2007). The exchange of genes between trailing edge populations may be quite beneficial in reducing inbreeding depression, because they are likely to be more genetically divergent than populations in the corpus of the species (Hampe and Petit, 2005). Note, however, that gene exchange between populations via pollen will be an inverse function of their selfing levels, because the greater the selfing level the lower will be the incidence of extraneous paternity.

In spite of demographic and genetic obstacles, some populations of weakly self-compatible plants have survived contractions and given rise to predominantly selfing derivatives. This scenario is well illustrated in *Capsella*. Using comparative sequence information, Guo *et al.* (2009) and Foxe *et al.* (2009) estimated that the self-compatible *C. rubella* separated from the self-incompatible *C. grandiflora* from 20 000 to 50 000 thousand years ago, and that the breakdown of self-incompatibility occurred at about the same time. Nucleotide diversity patterns indicated that *C. rubella* has only one or two alleles at most loci, which suggests that the lineage probably experienced a pronounced contraction during its genesis. It is possible that *C. rubella* originated from a single individual. Selfing rates may increase rapidly in *Capsella* and in other members of the mustard family, where mutations in the *SCR* (male specificity) gene cause a breakdown in self-incompatibility (Nasrallah *et al.*, 2004, 2007; Boggs *et al.*, 2009; Guo *et al.*, 2009).

The transit through bottlenecks need not result in self-compatible genotypes replacing self-incompatible genotypes (Igic *et al.*, 2008). An initial shift toward self-compatibility may be reversed in part after populations expand. Self-compatibile genotypes are most likely to persist in species where populations are short-lived and colonization is frequent (Pannell and Barrett, 1998; Schoen and Busch, 2008). The association between population bottlenecks and increased selfing is best understood in relation to the colonization of marginal habitats or distant locales (e.g. Lloyd, 1992; Barrett, 2003; Barrett *et al.*, 2008; Busch, 2005; Pannell and Dorken, 2006; Moeller and Geber, 2005; Schoen and Busch, 2008).

The transition to higher levels of self-fertilization may buy trailing edge populations time to evolve adaptations suited to their new environmental conditions. This no doubt has happened in the past, because the trailing edge has been a source of evolutionary novelty and a focal point of speciation in some lineages (Davis and Shaw, 2001; Ackerly, 2003; Hampe and Petit, 2005). Adaptation in the trailing edge is most likely when a trailing edge becomes geographically stable (Hampe and Petit, 2005).

In conclusion, global environmental change will increasingly challenge the viability of populations along and near species' trailing edges. Populations are likely to undergo substantial contractions in their sizes. If genetic systems allow, rates of self-fertilization will increase. The latter will provide a measure of reproductive assurance, and thereby buffer populations against declines in reproductive output that normally accompany a reduction in cross-pollen receipt in small populations. Increased self-fertility may afford populations the time to adapt to their changing environments. However, increased selfing is not a panacea for the ills of environmental change, because it will lead to substantial reductions in genetic diversity, which may render adaptation in other traits unlikely (Charlesworth, 2003; Charlesworth and Wright, 2001). Thus, even if selfing levels are elevated, the demise of rear end populations is likely to be the norm, and the species range will usually retract.

Although framed within the context of range retraction, range fragmentation and population decline also may lead to heightened selfing in species' interiors. Regardless of the

context, a breeding system shift is a likely, but not necessary, outcome in self-compatible populations subject to deteriorating environments. Self-fertilization may increase by a few per cent or by many per cent depending on the environment, plasticity in floral traits, and on a populations' capacity for breeding system evolution. Breeding system shifts may occur in some populations, but not in others. Shifts may occur in some species, but not in others.

This paper lies in the realm of conjecture. We cannot know what may happen in the future. However, today is the future for species whose ranges began protracted movement thousands of years ago. Might not elevated levels of self-fertilization in contemporary geographically marginal populations be the selected product of systematic environmental change and range retraction? This possibility could be explored using climate envelop models, with which we may assess past species distributions (Hijmans and Graham, 2005; Nogués-Bravo, 2009). Biogeographic and ecological responses to environmental change are well documented for the past 10 000 to 20 000 years in many regions (Dawson *et al.*, 2011).

Elevated levels of selfing at or near geographical boundaries have been discussed in terms of range expansion into stressful environments or into habitats where pollinator service is inadequate (reviewed by Randle *et al.*, 2009). However, it is clear that expansion is not the only process favouring elevated selfing. In a changing world, reduced environmental hospitality will come to populations and groups thereof. They need not seek it out.

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