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REPRODUCTIVE BIOLOGY OF THREE FERN SPECIES MAY CONTRIBUTE TO DIFFERENTIAL COLONIZATION SUCCESS IN POST-AGRICULTURAL FORESTS[1]

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Because selfing enables a single individual to reproduce in a new location, the ability to self-fertilize should enhance plants' capacity for colonization. This study examined whether selfing ability correlated with successful migration in three fern species, *Dryopteris carthusiana*, *Dryopteris intermedia*, and *Polystichum acrostichoides*, which vary in their ability to colonize forests on abandoned agricultural lands in central New York, USA. *Polystichum acrostichoides* is much more frequent in forests that were never cleared for agriculture, *D. carthusiana* is more frequent in forests that developed on former fields, and *D. intermedia* is equally frequent in the two forest types. To test the hypothesis that better-colonizing species and post-agricultural forest populations have greater selfing ability, I assessed the sporophyte production of gametophytes grown in isolation and in pairs of varying relatedness. *Dryopteris carthusiana* had the highest reproductive success and selfing ability and *P. acrostichoides* the lowest. These results support the hypothesis that selfing may facilitate colonization in these species. They also exemplify the general pattern that polyploid fern species have higher rates of self-fertilization than related diploids, as the allotetraploid *D. carthusiana* had greater selfing ability than both diploid species.

Key words: Baker's Law; Dryopteridaceae; genetic load; inbreeding depression; land-use history; New York; polyploidy; self-fertilization.

Understanding how life history traits relate to colonizing ability can reveal the processes underlying natural patterns of plant distribution and help to predict species' responses to human introduction, extirpation, and habitat alteration. Because better colonizers are more likely to become invasive, more apt to survive habitat fragmentation, and quicker to recover after restoration, identifying traits that promote plant migration can aid efforts to preserve biological diversity in human-modified habitats. One trait long thought to facilitate colonization is the ability to self-fertilize (Lloyd, 1980). Darwin (1876) discussed the suggestion that hermaphroditic and monoecious plants should spread more easily than dioecious species because a single individual could found a reproductive population. On the same principle, Baker (1955, 1967) proposed that self-compatibility should facilitate long-distance dispersal, an idea Stebbins (1957) called "Baker's Law." In fact, self-fertilization would be favored not only in migration across long distances, but in any landscape with frequent local colonization and extinction (Pannell and Barrett, 1998).

Despite the logical appeal and theoretical support of this hypothesis, however, it remains unclear how often range expansions and establishment events actually depend on selfing. Most of the empirical evidence for Baker's Law comes from large-scale, biogeographic patterns, such as the prevalence of self-compatible species in island floras (Carlquist, 1974; McMullen, 1987; Webb and Kelly, 1993; Anderson et al., 2001). In many cases, selfing taxa occur at the range margins of outcrossing sister taxa (Solbrig and Rollins, 1977; Wyatt, 1986; Barrett and Shore, 1987; Barrett et al., 1989; Moeller and Geber, 2005). These patterns suggest an association between selfing and historical colonization, but few studies have directly measured both selfing ability and colonization success during ongoing migrations. For example, species introductions have allowed for comparisons of selfing abilities among congeners of varying invasiveness (Gerlach and Rice, 2003) and between established and recently colonized populations (Schueller, 2004).

Like the spread of invasives, the recolonization of restored habitats by native species provides an ideal opportunity to study the role of selfing in contemporary colonization. Among the most common restored habitats worldwide are forests on abandoned agricultural lands (Williams, 1989; Ball, 2001). Even hundreds of years after reforestation, herbaceous forest species vary widely in their ability to recolonize post-agricultural sites (reviewed by Flinn and Vellend, 2005). While several studies have explored relationships between migration rates and life history traits, especially those associated with dispersal (Matlack, 1994; Verheyen et al., 2003), none have examined how plant mating systems may affect the recolonization of post-agricultural forests.

Here I use a post-agricultural landscape in central New York to investigate whether selfing ability may contribute to the differential colonization success of three fern species. Ferns and other homosporous plants are particularly interesting in this context because their mating systems potentially include outcrossing, between gametophytes from different sporophytes; intergametophytic selfing, between gametophytes from the same sporophyte, which is analogous to selfing in seed plants; and intragametophytic selfing, between gametes from the same gametophyte, which has no analog in seed plants and yields fully homozygous progeny (Klekowski, 1969). Though all homosporous plants have the potential to produce bisexual

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gametophytes, most maintain outcrossing mating systems through several primary mechanisms (Haufler, 1987; Soltis and Soltis, 1992). Gametophytes may become unisexual by developing male and female function either exclusively or sequentially. In many species, mature female gametophytes enhance opportunities for outcrossing by releasing antheridiogen, a pheromone that stimulates spore germination and induces maleness in neighboring gametophytes (Näf, 1979). When gametophytes do undergo intragametophytic selfing, deleterious recessive alleles may hinder the survival of the completely homozygous sporophytes (Klekowski, 1969). Ferns' great capacity for dispersal via windblown spores presumably facilitates outcrossing by increasing mate availability in many habitats. In order to mate, however, two gametophytes must establish simultaneously within about 5–10 cm of one another, an unlikely event after long-distance dispersal (Peck et al., 1990; Schneller et al., 1990; Greer and McCarthy, 1997). Thus, selfing may be as important to colonization in ferns as in seed plants.

This study focuses on *Dryopteris carthusiana* (Villars) H. P. Fuchs, *Dryopteris intermedia* (Muhlenberg ex Willdenow) A. Gray, and *Polystichum acrostichoides* (Michaux) Schott (Dryopteridaceae), which are wintergreen, herbaceous perennials common in mesic, upland forests and native to eastern North America (Montgomery and Wagner, 1993; Wagner, 1993). The range of *D. carthusiana* also extends throughout Eurasia. Despite a similar capacity for long-distance dispersal via windblown spores (Flinn, 2006), these three species have contrasting distributions across forests that were never cleared for agriculture (i.e., primary forests) and forests that established on plowed fields 85–100 years ago (i.e., secondary forests, sensu Rackham, 1980; Peterken, 1981). In central New York, *P. acrostichoides* is among the herb species most restricted to primary forests, *D. intermedia* is equally frequent in the two forest types, and *D. carthusiana* is more frequent in secondary forests (Singleton et al., 2001; Flinn, 2006). I hypothesized that, if selfing facilitated colonization, then species that are more successful colonists should have greater selfing ability than species that are less successful colonists. Thus, I expected *D. carthusiana* to have greater selfing ability than *D. intermedia*, and *D. intermedia* to have greater selfing ability than *P. acrostichoides*. Another reason to predict a higher tolerance for inbreeding in *D. carthusiana* is that this species is tetraploid, whereas *D. intermedia* and *P. acrostichoides* are diploid (Montgomery and Wagner, 1993; Wagner, 1993), and the fixed heterozygosity of recent polyploids should reduce inbreeding depression (Stebbins, 1950; Lande and Schemske, 1985). In addition, if populations in secondary forests were recently founded through selfing, then plants from secondary forests should have greater selfing ability than plants from primary forests. To test these hypotheses, I conducted an experiment in which I grew gametophytes either in isolation or in pairs, allowing different levels of inbreeding, and compared rates of sporophyte production.

MATERIALS AND METHODS

Study sites—Spores for this experiment came from fern populations in three pairs of adjacent primary and secondary forests, located on mesic uplands in Tompkins County, New York, USA. The secondary forests were abandoned from agriculture 85–100 years ago, according to 1936–1938 aerial photographs. Field evidence showed they had been plowed, eliminating all native vegetation. In central New York, both the *Dryopteris* species and *Polystichum acrostichoides* occur in tree and shrub thickets on sites plowed 20–40 years before (Stover and Marks, 1998). Therefore, fern populations in the oldest secondary forests may have established as many as 80 years ago, whereas populations in primary forests could have continuously occupied the sites for hundreds of years.

Spore collection—To obtain spores, I collected fertile fronds of the three species between 30 June and 11 July 2003. Using transects to stratify samples across 1 ha, I took fronds from 20–30 plants of each species from each forest stand. The fronds were sealed in glassine envelopes and dried in ovens at 35°C for 1 wk to promote spore release.

Gametophyte culture—I sowed the spores on nutrient medium in 60 × 15 mm petri dishes by piercing the glassine envelopes with an insect pin, making holes just large enough to sift out spores without pieces of frond, indusia, or sporangia (D. R. Farrar, Iowa State University, personal communication). The medium contained Parker's macroelements and Thompson's microelements solidified with 1% agar (Klekowski, 1969). To minimize contamination, I autoclaved the medium at 121°C for 15 min and added the fungicide nystatin at 50 mg/L. The dishes were sealed with Parafilm (American National Can, Chicago, Illinois, USA) and placed in a growth chamber under 14 h light at 26°C and 10 h dark at 16°C.

Experimental crosses—After 2 wk, I established crosses by transplanting gametophytes onto fresh medium with a dissecting microscope and a scalpel, placing pairs 1 cm apart. To compare reproductive success at four potential levels of inbreeding, gametophytes grew either in isolation, paired with another gametophyte from the same sporophyte, paired with a gametophyte from a different sporophyte in the same population, or paired with a gametophyte from a sporophyte in a different population at least 2 km away. Pairs were randomly matched within the appropriate pool. Isolated gametophytes could only reproduce through intragametophytic selfing, whereas paired gametophytes could either self-fertilize or outcross. The four inbreeding levels were crossed with the three species and the two forest types in a fully factorial design. Replicating the experiment across three sites and 20 plants per population therefore yielded 1440 crosses involving 2520 gametophytes. I maintained the cultures for 18 mo, watering gametophytes with an eyedropper to facilitate fertilization and examining them monthly for the presence of sporophytes.

Statistical analysis—I assessed the effects of inbreeding level, species, forest history, and their interactions on the likelihood of sporophyte production with maximum-likelihood analysis (PROC CATMOD in SAS; SAS Institute, Cary, North Carolina, USA). An additional factor accounted for site effects. I tested all possible two- and three-way interactions and dropped from the final model those not significant at $P < 0.05$. This analysis considered only the 953 gametophytes that survived to sexual maturity, at least 1 mo after transplanting. To make maximum use of the available information, the analysis included sporophyte production from each member of pairs.

RESULTS

Gametophytes had modest reproductive success overall. Of gametophytes that survived to sexual maturity, 39% formed sporophytes. The three species had significantly different rates of sporophyte production (Table 1). Across all treatments, *Dryopteris carthusiana* had the highest reproductive success, with 50% of gametophytes forming sporophytes; *Dryopteris intermedia* was intermediate, with 31%; and *Polystichum acrostichoides* had the lowest reproductive success, with 21%.

Sporophyte production did not differ consistently among the four potential levels of inbreeding (Table 1). However, the three species responded differently to the different inbreeding levels (Table 1, Fig. 1). *Dryopteris carthusiana* had high reproductive success across all levels of inbreeding. In fact, 63% of isolated gametophytes formed sporophytes in this species, a higher rate than when outcrossing was possible. Likewise, the

TABLE 1. Maximum-likelihood analysis of the effects of species, inbreeding level, forest history, and their interactions on sporophyte production for three fern species colonizing post-agricultural forests in central New York. An additional factor accounts for the three replicate sites.

Effect	df	Wald χ^2	P
Intercept	1	46.37	<0.0001
Site	2	45.16	<0.0001
Species	2	36.73	<0.0001
Inbreeding level	3	4.60	0.2037
Forest history	1	0.42	0.5155
Species × inbreeding level	6	27.00	0.0001
Species × forest history	2	9.42	0.0090
Likelihood ratio	50	86.14	0.0011

sporophyte production of *D. intermedia* was fairly consistent across inbreeding levels, ranging from 25–38%. For *P. acrostichoides*, by contrast, reproductive success increased dramatically as gametophytes had greater access to outcrossing. Only 11% of isolated gametophytes produced sporophytes via intragametophytic selfing, whereas 50% of crosses between different populations produced sporophytes.

Plants from primary and secondary forests did not differ consistently in rates of sporophyte production, nor did they perform differently across levels of inbreeding, as indicated by the lack of interaction between forest history and inbreeding level (Table 1). Rather, the effect of forest history varied among the three species (Table 1). *Dryopteris carthusiana* plants from primary and secondary forests had equally high rates of sporophyte production, near 50%. In *D. intermedia*, reproductive success was slightly higher among plants from secondary forests, 36%, than from primary forests, 27%. *Polystichum acrostichoides* showed the opposite trend, with the proportion of gametophytes forming sporophytes over twice as high among plants from primary forests as from secondary forests, 24% vs. 10%.

DISCUSSION

This experiment revealed differences among species in gametophyte reproductive biology that may have a strong influence on the colonization of post-agricultural forests by these ferns. The most successful colonist, *Dryopteris carthusiana*, had the greatest reproductive success overall, whereas the least successful colonist, *Polystichum acrostichoides*, had the lowest. In fact, *D. carthusiana* gametophytes were over twice as likely to form sporophytes as those of *P. acrostichoides*. Such consistently higher rates of sporophyte production could speed the colonization process and help explain the species' distributions. In addition, the species' responses to inbreeding were consistent with the hypothesis that selfing ability may facilitate colonization. The potential for self-fertilization was greater in *D. carthusiana* than in *D. intermedia*, and in *D. intermedia* than in *P. acrostichoides*.

These laboratory results agree with previous characterizations of the species' mating systems based on patterns of genetic variation in natural sporophyte populations. For example, populations of *D. carthusiana* had significant heterozygote deficiencies at polymorphic loci, suggesting high selfing rates (C. R. Werth, deceased, and C. H. Haufler, University of Kansas, unpublished data cited in Xiang et al., 2000). In contrast, *D. intermedia* appears to breed randomly, as indicated by genotype frequencies in accord with Hardy–Weinberg equilibrium (C. R. Werth, deceased, unpublished data cited in Xiang et al., 2000). Allozyme data demonstrated that *P. acrostichoides* and five other North American *Polystichum* species are highly outcrossing (Soltis and Soltis, 1990). In seven populations across the eastern United States, *P. acrostichoides* maintained high levels of genetic variation within populations, with inbreeding coefficients ranging from 0.007–0.084 and intragametophtyic selfing rates (estimated from genotype frequencies according to Holsinger, 1987) ranging from 0–12% (Soltis and Soltis, 1990; Soltis et al., 1990). The 11% intragametophytic selfing rate documented here for *P. acrostichoides* thus falls within the range of selfing rates estimated from natural populations.

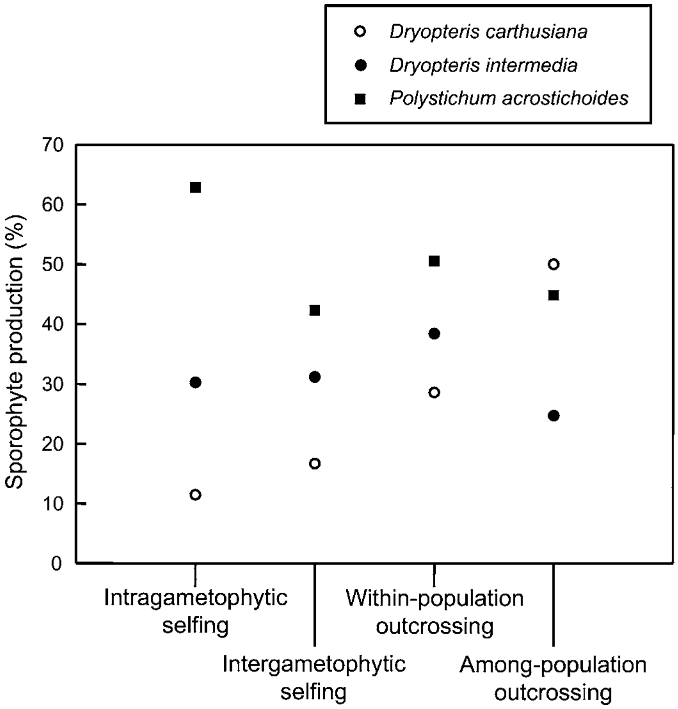

Fig. 1. Sporophyte production across four levels of inbreeding for three fern species: *Dryopteris carthusiana* (open circles), *D. intermedia* (closed circles), and *Polystichum acrostichoides* (squares). Ranging from high to low, the potential levels of inbreeding included intragametophytic selfing, intergametophytic selfing, within-population outcrossing, and among-population outcrossing (see Materials and Methods, *Experimental crosses*).

Previous studies of gametophyte ontogeny suggest that sex expression patterns may contribute to the reproductive outcomes observed in this experiment. Growing isolated *D. carthusiana* gametophytes on agar, Peck (1985) found that 86% were bisexual, indicating a high potential for self-fertilization. In denser laboratory cultures on soil (1–3 gametophytes cm^{-2}), both *D. carthusiana* and *D. intermedia* had mostly female gametophytes, 59–70%, with 17–27% male and 13–14% bisexual (Cousens, 1975). It is unknown whether *D. carthusiana* produces or responds to antheridiogen, but sex expression in *D. intermedia* can be influenced by this pheromone (C. R. Werth, deceased, unpublished data cited in Xiang et al., 2000). For *P. acrostichoides*, Greer and McCarthy (1997, 1999) reported that isolated gametophytes grown on soil invariably became female and remained unisexual, forming antheridia only on lobes separated from the meristem by necrosis. This pattern of sex expression, mediated by antheridiogen (Näf, 1979; Greer and McCarthy, 1997), would provide a mechanism to explain the species' highly outcrossing mating system.

The development of gametophytes in laboratory cultures, especially in isolation and on agar, may differ from growth patterns in denser populations and under field conditions (Rubin and Paolillo, 1983; Ranker and Houston, 2002). Likewise, the low overall reproductive success of gametophytes in this experiment, though comparable to rates seen in many other species (Peck et al., 1990), may reflect the cultural regime. In this case, however, the results of laboratory tests appear consistent with the available information from natural populations.

The species' contrasting mating systems also seem to support theoretical predictions about the evolutionary consequences of polyploidy. Polyploid species are expected to self-fertilize more often than diploids because genome duplication initially mitigates the effects of genetic load (Stebbins, 1950; Lande and Schemske, 1985). In the case study presented here, the allotetraploid *D. carthusiana* had a higher selfing rate than *D. intermedia*, one of its diploid progenitors (Walker, 1961), or *P. acrostichoides*, another closely related diploid. This example thus adds to the growing number of cases in which polyploid fern species tend to self-fertilize more than their diploid relatives (Hedrick, 1987; Masuyama and Watano, 1990; Soltis and Soltis, 2000; Chiou et al., 2002), though the relationship between polyploidy and inbreeding in seed plants remains much less clear (Husband and Schemske, 1997; Cook and Soltis, 1999; Mable, 2004; B. C. Barringer, Cornell University, unpublished manuscript).

Within species, I found no evidence for an association between the history of populations and their selfing ability. One plausible explanation for this result is that, contrary to the original hypothesis, the foundation of fern populations in post-agricultural forests did not involve elevated rates of self-fertilization. Because the post-agricultural forests in this study were adjacent to continuously forested areas, fern populations may have spread gradually across the land-use boundaries, remaining contiguous with areas of higher plant density that allowed for outcrossing. The proximity to source populations also makes the simultaneous arrival of multiple spores more likely. In fact, I have documented substantial spore banks in the soil of post-agricultural forests adjacent to but not containing sporophyte populations of these species (Flinn, 2006). Similar situations may be common in the region, as about 90% of the area in secondary forest is contiguous with older stands (Smith et al., 1993).

Alternatively, even if populations did establish through selfing, they may have grown sufficiently old and large that evidence of founder events involving selfing is no longer detectable. Rather, existing plants' selfing abilities could depend more strongly on mating patterns at current population densities than on a population bottleneck that may have occurred as many as 80 years ago. To obtain sufficient sample sizes for the experiment, I chose sites where all three species had population densities of at least 20 plants ha^{-1} in each forest stand. The effects of a founder event might be more evident at other sites in the region where population densities remain lower or in more isolated or more recently established populations. If in fact fern populations in forests of different history have similar selfing rates, the genetic consequences of post-agricultural forest colonization may be comparable to those seen for *Trillium grandiflorum* (Michx.) Salisb. in the same central New York landscape; primary and secondary forest populations did not differ in inbreeding coefficients or observed heterozygosity, though allelic richness and expected heterozygosity were slightly lower in secondary forests (Vellend, 2004). Describing patterns of genetic variation within and among fern populations would substantially improve our understanding of the role of selfing in the colonization of post-agricultural forests.

Several other studies have related mating systems to colonizing ability in ferns, at either the species or the population level. Based on studies of gametophyte development and reproduction, Holbrook-Walker and Lloyd (1973) and Lloyd (1974) suggested that Hawaiian fern species frequently found on newly formed lava flows, though primarily outcrossing, retained a greater ability to self-fertilize than species of late-successional habitats. In two species of Hawaiian *Sadleria* Kaulf., however, Ranker et al. (1996) later found that even populations on recent lava flows had genotype frequencies indicative of outcrossing and gametophytes with primarily unisexual development, antheridiogen systems, and very little ability to form sporophytes in isolation. Among three South Asian ferns, Singh and Roy (1977) found a greater capacity for self-fertilization in the more widely distributed, generalist species. Ranker et al. (2000) noted that the four fern species for which genetic evidence suggests a mixed mating system occupy both disturbed places and more stable habitats. A high capacity for self-fertilization may also have facilitated the spread of two invasive fern species in Florida (Lott et al., 2003).

While fewer studies have addressed mating-system variation among fern populations, Cousens (1979) found a higher incidence of bisexuality and a greater ability to self-fertilize in gametophytes from a disjunct population than from the central range of *Blechnum spicant* (L.) J. Sm. Similarly in *Asplenium platyneuron* (L.) Oakes, geographically disjunct, solitary plants on recent coal spoils had greater selfing ability than plants from dense populations in the center of the species' range (Crist and Farrar, 1983). Peck et al. (1990) contrasted the selfing and colonization abilities of *A. platyneuron* with *Adiantum pedatum* L., which had a very low rate of sporophyte formation by isolated gametophytes and had failed to colonize the coal spoils from adjacent populations for 50 years. Together with these studies, the patterns of fern reproductive biology documented here suggest that selfing ability may often be an important component of population establishment following long-distance dispersal.

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