

TRANSIENT SI AND THE DYNAMICS OF SELF-INCOMPATIBILITY ALLELES: A SIMULATION MODEL AND EMPIRICAL TEST

Carol Goodwillie^{1,2}

¹Department of Biology, East Carolina University, Howell Science Complex, Greenville, North Carolina 27858

²E-mail: goodwilliec@ecu.edu

Received December 11, 2007

Accepted April 26, 2008

A stochastic computer simulation model was created to compare the combined effects of selection and genetic drift on the dynamics of *S*-alleles under full sporophytic self-incompatibility (SI) versus transient SI, a form of partial SI in which flowers become self-compatible as they age. *S*-alleles were lost more rapidly with transient than with full SI, as is expected with weakened frequency-dependent selection. Based on these results, equilibrium *S*-allele diversity is expected to be lower with partial SI for populations of comparable size and migration rates. Consistent with model results, a comparison of the proportion of incompatible crosses in full diallel experiments for a fully SI and a transiently SI species in the annual genus *Leptosiphon* suggests that *S*-allele diversity is lower in the partially SI species. Results of the simulation model indicate that the transmission advantage of self-fertilization can have complex effects on *S*-allele dynamics in partial SI systems.

KEY WORDS: Allele frequency, computer simulation, frequency-dependent selection, mating system evolution, partial self-incompatibility.

Self-incompatibility (SI) in plants has long held the interest of evolutionary biologists both for its role in plant mating system evolution and for its microevolutionary properties. SI is a genetic mechanism that enables a plant to recognize and reject its own pollen (de Nettancourt 1977); when pollen and pistil express the same alleles, fertilization is prevented. The genetic loci controlling these mechanisms are referred to collectively as *S*-loci. Two basic classes of SI system are distinguished by the genetic control of the pollen mating type (de Nettancourt 1977). In gametophytic SI, pollen compatibility is determined by the haploid *S*-locus genotype of the gamete, whereas in sporophytic SI, compatibility is determined by the diploid genotype of the pollen parent. The relationship between *S*-genotype and phenotype is often complex in sporophytic SI because of dominance interactions among *S*-alleles, which may differ in the pollen and pistil. In many sporophytic SI systems, *S*-alleles form a dominance hierarchy when expressed in the pollen, and act codominantly in the stigma. This differential expression can result in nonrecipro-

cal incompatibility. That is, two genotypes that share one *S*-allele can be compatible when one plant serves as the pollen parent and incompatible when crossed in the other direction (de Nettancourt 1977).

Interest in SI from an evolutionary perspective has focused on the extraordinary allelic diversity often observed at the *S*-locus (Lawrence 2000), which is thought to be maintained by frequency-dependent selection on *S*-alleles (Wright 1939; Fisher 1958). Individuals expressing *S*-alleles that are present at high frequencies have fewer potential cross-compatible mates and therefore may experience reduced seed set (i.e., fecundity selection [Vekemans et al. 1998]), reduced siring success (pollen selection), or both. In sporophytic SI, dominance among *S*-alleles is expected to modify equilibrium frequencies such that recessive *S*-alleles are more common than dominant ones (Byers and Meagher 1992; reviewed in Schierup et al. 1997).

In many plant taxa, SI is only partially effective, such that some self-fertilization can occur (Vogler and Stephenson 2001;

Brennan et al. 2005; Mable et al. 2005; Stone et al. 2006; Mena-Ali and Stephenson 2007; reviewed in Levin 1996). “Leakiness” of SI systems has been shown to be conferred by specific *S*-alleles in some systems (Mena-Ali and Stephenson 2007) and by modifier loci in others (Good-Avila and Stephenson 2002; Mable et al. 2005). Partial SI can also result from developmental changes in the strength of SI, such that plants or flowers are strongly SI at some times but are fully or partially self-compatible (SC) at others (Stephenson et al. 2000; Goodwillie et al. 2004). It has been argued that partial expression of SI may be an adaptive strategy that promotes reproductive flexibility when pollinator or mate availability is low (Levin 1996; Stephenson et al. 2000). A theoretical model provides evidence that partial SI can be evolutionarily stable under some conditions (Vallejo-Marin and Uyenoyama 2004).

A factor that has received little consideration is the effect of leakiness in the SI mechanism on *S*-allele diversity and dynamics. The strength of negative frequency-dependent selection on *S*-alleles should be weakened because partial SI allows some (1) cross-fertilization by incompatible genotypes, and (2) self-fertilization, both of which can buffer the effects of allele frequency on male and female mating success. Weakening of frequency-dependent selection is expected to affect *S*-allele diversity (Vallejo-Marin and Uyenoyama 2004). In turn, the number and frequency distribution of *S*-alleles present might affect how selection acts on modifiers that increase or further decrease the strength of SI. For example, Vallejo-Marin and Uyenoyama (2004) found that the stability of partial SI was dependent upon the number of *S*-alleles present in a population. To my knowledge, however, the effect of modifiers of SI on *S*-allele dynamics and diversity has not yet been modeled or tested empirically.

Here stochastic computer simulation models are used to investigate the effects of selection and genetic drift on *S*-allele diversity under full versus partial sporophytic SI. Further, the partial SI model explores the specific effects on *S*-allele dynamics of self-fertilization versus cross-fertilization between incompatible mates. The models simulate the reproductive biology of two species in the genus *Leptosiphon* and allow a comparison of different breeding systems. *Leptosiphon parviflorus* has a fully effective sporophytic SI system (Goodwillie 1997); in contrast, *L. jepsonii* has a partial form of SI in which flowers are initially SI but become strongly SC by the second or third day of anthesis (Goodwillie et al. 2004). The model results are combined with an empirical comparison of *S*-phenotypes in populations of *L. parviflorus* and *L. jepsonii*. Because dominance among alleles complicates the inference of exact *S*-allele numbers from patterns of incompatibility in sporophytic SI (Brennan et al. 2002; Mable et al. 2003), the species are compared with respect to the proportion of crosses that are incompatible, a parameter that is shown in the model to be related to *S*-allele diversity. Determination of *S*-phenotypes using crossing experiments is often difficult

in partially SI species because leakiness of the mechanism obscures cross-incompatibility of plants with *S*-alleles in common (Mable et al. 2003). The breeding system of *L. jepsonii*, in which flowers are transiently SI provides a unique opportunity to assess *S*-phenotypes using crosses in a partially SI species.

Materials and Methods

COMPUTER SIMULATION MODEL

The effect of selection and genetic drift on the dynamics of *S*-alleles was compared in stochastic models for full and transient SI. Because partial SI is often hypothesized to be common in pollinator-limited conditions, the model is designed to explore evolutionary dynamics under different pollination scenarios. The conceptual models (Fig. 1) were developed into a computer simulation package using the LabVIEW (National Instruments, Austin, TX) programming language, version 7.1. Both models begin with an array of *N* individuals containing *A* *S*-alleles at equal (or as near to equal as possible) frequency, with alleles distributed randomly among individuals. *S*-alleles are modeled as a linear dominance hierarchy in pollen, in which $S_1 >$ (is dominant to) $S_2 > S_3 > \dots > S_A$, and are codominant in the stigma. This expression pattern is consistent with the results of crossing experiments for both species (Goodwillie 1997; C. Goodwillie, unpubl. data). Allele frequencies evolve for *G* generations, and population size (*N*) remains constant throughout the run. The number of alleles present, frequency of each allele, proportion of attempted crosses that are incompatible and, for the transient SI model, the proportion of seeds produced by outcrossing are reported every 10 generations.

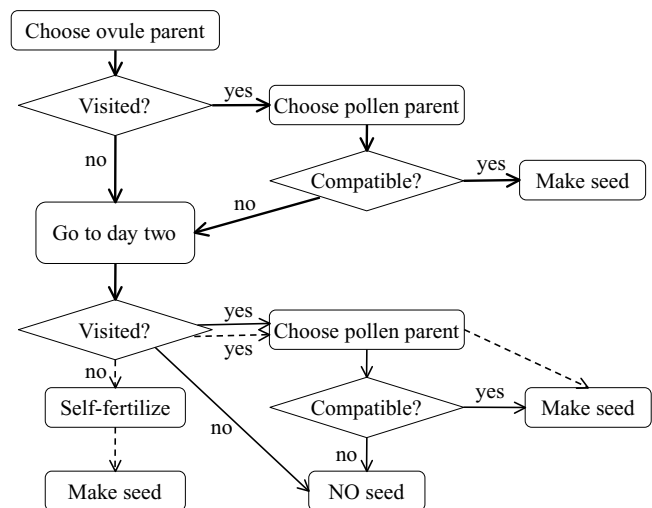


Figure 1. Schematic of simulation model. Full and transient SI models are identical on day one (heavy solid line). On day two, full SI model is indicated with solid line, transient SI model with dashed line. Algorithm is repeated each generation until *N* seeds are produced.

Because the models do not include any mutation or migration, they do not estimate true equilibrium allele number and distribution; rather the models compare the rates of loss of allelic diversity with combined selection and genetic drift, an approach that has been used previously for *S*-allele dynamics (Crosby 1966). For simplicity, the models make several simplifying assumptions, including the absence of a seed bank and equal fitness of selfed and outcrossed progeny (i.e., no inbreeding depression).

Individuals are chosen at random with replacement to serve as female parents until *N* seeds are produced. To account for the temporal changes that occur in *L. jepsonii*, the basic algorithm for both models follows the fate of a flower through two days (Fig. 1). If a seed is produced on the first day, the algorithm moves on to the next randomly chosen maternal plant. If not, the flower continues to day two. Pollinator visitation occurs if a randomly drawn number between 0 and 1 is less than *P*, a parameter that indicates the probability of visitation. Visited flowers receive pollen from a randomly chosen donor. In this simplified model, no flower receives more than two visits. The algorithm for day one is the same for the full SI and transient SI models (Fig. 1). If a flower is visited and the cross is compatible (pollen and stigma do not express a common *S*-allele), a seed is produced with alleles chosen at random from the parental genotypes. If the flower is not visited or receives incompatible pollen, no seed is produced on day one, and the flower continues on to a second day.

On day two, the full and transient SI models diverge (Fig. 1). With full SI, the algorithm for day two is simply a repeat of day one. If a flower is not visited or does not receive compatible pollen, no seed is produced. Thus, with full SI, cross-incompatibility can limit seed set (i.e., fecundity selection or incomplete reproductive compensation [Vallejo-Marin and Uyenoyama 2004]). In contrast, with transient SI any flower that is visited on the second day produces a seed by cross-fertilization. This occurs because flowers are now SC and therefore universally compatible with any pollen donor. Transient SI flowers that are not visited on day two produce a seed by self-fertilization. Thus, with transient SI, frequency-dependent selection can act only through success as a pollen donor; seed set is assured on day two by universal compatibility or by selfing. The transient SI model is constructed such that no selfing occurs when all flowers are visited (when $P = 1$). Although this is probably somewhat unrealistic, comparison of results for $P = 1$ versus $P < 1$ under transient SI provides a useful means of assessing the specific effects of selfing in *S*-allele dynamics of a partially SI species.

S-allelic diversity was compared with full and transient SI under unlimited and limited pollinator visitation ($P = 1$ and $P = 0.5$, respectively). Simulations began with 50 alleles and were run for 3000 generations with population sizes of 500, 1500, 2500, and 3500. Each set of parameter values was replicated on 25 runs. The number of alleles present was recorded at quasi-equilibrium,

defined here as the first period of at least 400 generations in which allele number remained constant.

Data from a subset of these simulations (full SI, $P = 0.5$ and transient SI, $P = 0.5$ models, $N = 500$) were used to explore in more detail the dynamics and consequences of *S*-allele diversity. On each run, the proportion of incompatible crosses on day one and expected heterozygosity ($H_E = 1 - \sum_{i=1}^n p_i^2$, where p is the frequency of each allele) were recorded for generations at which the number of alleles present equaled 5, 10, 15, 20, 25, 30, and 35. When a given allele number persisted for multiple generation intervals, a datapoint for one generation was chosen at random from each run. Values were averaged across the 25 replicate runs. The proportion of seeds that were outcrossed was also recorded as a function of allele number in the transient SI model.

The effect of dominance on allele frequencies was compared among full and transient SI models under unlimited and limited pollinator visitation. To simplify the analysis, additional simulations were run with parameters that permitted constant allele numbers throughout the run: $N = 5000$ and initial allele number of 10. The frequency of each allele in the dominance hierarchy was recorded after 300 generations, at which point alleles appeared to have reached quasi-equilibrium distributions.

EMPIRICAL EXPERIMENTS

Study species

Leptosiphon, a genus of spring annuals of western North America, includes fully SI, partially SI and highly selfing species (Goodwillie 1999). *Leptosiphon parviflorus* and *L. jepsonii* are similar in morphology and ecology and co-occur in northern California. Both are cross-pollinated primarily by long-tongued flies (Weber and Goodwillie 2007). Populations of *L. parviflorus* in northern CA are fully SI throughout the floral life span, whereas flowers of most *L. jepsonii* plants are SI when they first open but become SC in 24–48 h, allowing delayed selfing (Goodwillie et al. 2004). Outcrossing rates for *L. jepsonii* indicate mixed self- and cross-fertilization (Goodwillie and Ness 2005). In most populations of *L. jepsonii* sampled, plants that are immediately SC upon flower opening also occur at low frequencies (Goodwillie and Ness 2005). The transient form of SI in *L. jepsonii* appears to be a derived form of the sporophytic SI system seen in *L. parviflorus* and other species in the genus. The fully SI species that shares the most recent common ancestor with *L. jepsonii* is *L. androsaceus* (Goodwillie 1999; Bell and Patterson 2000); however, because *L. androsaceus* populations comparable in size to those of *L. jepsonii* were not available, the closely related *L. parviflorus* was used instead.

Quantification of cross-incompatibility

Four populations each of *L. jepsonii* and *L. parviflorus* in Napa or Sonoma County were chosen to include one small (<3000

individuals), one large (>100,000) and two intermediate-sized populations of each species. Plants with mature fruits were collected haphazardly at sites spanning the spatial extent of the population. Care was taken to sample plants that were separated by at least 3 m. Several plants of each maternal seed family were raised in a growth room at East Carolina University for use in diallel crosses. Crossing experiments required flowers that were SI for at least one day so that compatible and incompatible crosses could be distinguished. Plants were confirmed to be SI (in *L. parviflorus*) or transiently SI (in *L. jepsonii*) by hand self-pollinating day-one flowers. Stigmas were collected 3 h after pollination, and pollen tubes were viewed with epifluorescence microscopy using an aniline blue staining method, as described previously (Goodwillie et al. 2004). Day-one flowers that produced a mean < 5 self-pollen tubes were considered to be SI.

From each population, 12 unrelated plants (i.e., from different maternal families) that were confirmed to be SI or transiently SI were used for full diallel crossing experiments. Diallel size was limited by the number of flowers available on *L. jepsonii* plants. All crosses were replicated on at least two flowers. On each cross-pollinated stigma, pollen tubes were viewed as described above to assess compatibility. A cross was scored as incompatible for mean pollen tube numbers <5 and scored as compatible for means > 25. When results of the two replicates differed substantially, crosses were carried out on two additional flowers. The hypothesis that the transiently SI species will have higher rates of cross-incompatibility, reflecting lower *S*-allele diversity, was evaluated using a one-tailed *t*-test, with homogeneity of variance not assumed.

Results

COMPUTER SIMULATIONS

The number of *S*-alleles present at quasi-equilibrium increased with *N* for all models, reflecting the expected relationship between population size and the rate of allele extinction through genetic drift (Table 1). The number of generations to reach quasi-equilibrium ranged among models from 1100 to 2500. For a given population size, more *S*-alleles were present with full SI than with transient SI. Limiting pollinator visitation ($P = 0.5$ as compared to $P = 1$) increased the number of *S*-alleles maintained with full SI but decreased the number of *S*-alleles with transient SI (Table 1). With both full and transient SI, the proportion of day-one crosses that were incompatible was negatively related to allele number (Fig. 2A). For a given number of *S*-alleles, cross-incompatibility was generally higher with transient SI than with full SI. This appears to be caused by differences in allele distributions under the two models; expected heterozygosity as a function of allele number was lower for transient than for full SI (Fig. 2B). With transient SI and pollinator limitation, the proportion of seeds that were out-

Table 1. Effects of population size, probability of pollinator visitation ($P < 1$ indicates pollinator limitation), and full vs. transient SI on the number of *S*-alleles at quasi-equilibrium, defined as the first period of at least 400 generations in which allele number remained constant.

	Population size			
	500	1500	2500	3500
Full SI, $P=1$	11.04 (1.34)	18.4 (1.76)	22.84 (1.86)	26.72 (2.52)
Full SI, $P=0.5$	12.84 (0.9)	22.28 (1.86)	30.4 (1.47)	34.68 (2.64)
Transient SI, $P=1$	7.56 (1.45)	13.68 (1.7)	18.84 (2.25)	22.08 (2.93)
Transient SI, $P=0.5$	3.6 (0.76)	6.48 (1.29)	8.88 (1.56)	10.4 (2.02)

All runs began with 50 alleles. Means (and standard deviations) of 25 replicate runs are presented.

crossed increased with the number of alleles (Fig. 2C). Dominant alleles occurred at lowest frequencies with full SI (for both $P = 1$ and $P = 0.5$) and at highest frequencies in the transient SI model with pollinator limitation and selfing (Fig. 3). With transient SI and complete outcrossing, no relationship between dominance and frequency was evident.

EMPIRICAL EXPERIMENTS

Across all populations, 99% of crosses were definitively classified as incompatible or compatible using the set criterion for pollen tube numbers. The great majority of compatible crosses had mean pollen tube numbers > 50. In less than 2% of all crosses, the two replicate pollinations gave inconsistent results, and additional replicates were required to determine compatibility. The mean proportion of crosses that were incompatible was significantly lower in *L. parviflorus* (0.026), the fully SI species, than in *L. jepsonii* (0.215), the partially SI species ($t = -5.19$, $df = 3$, $P = 0.014$). Of the total crosses that were incompatible in at least one direction, the proportion that was compatible in the other (i.e., nonreciprocally incompatible) was 0.33 in *L. parviflorus* and 0.44 in *L. jepsonii*. For neither species was there evidence for a relationship between population size and the proportion of incompatible crosses (*L. parviflorus*: small 0.046, intermediate 0.0 and 0.039, large 0.019; *L. jepsonii*: small 0.21, intermediate 0.177 and 0.189, large 0.282).

Discussion

The results of stochastic simulation models provide evidence to support the hypothesis that weakening of SI can affect the dynamics and diversity of *S*-alleles. Regardless of the extent of pollinator limitation, allelic diversity was lower at quasi-equilibrium with

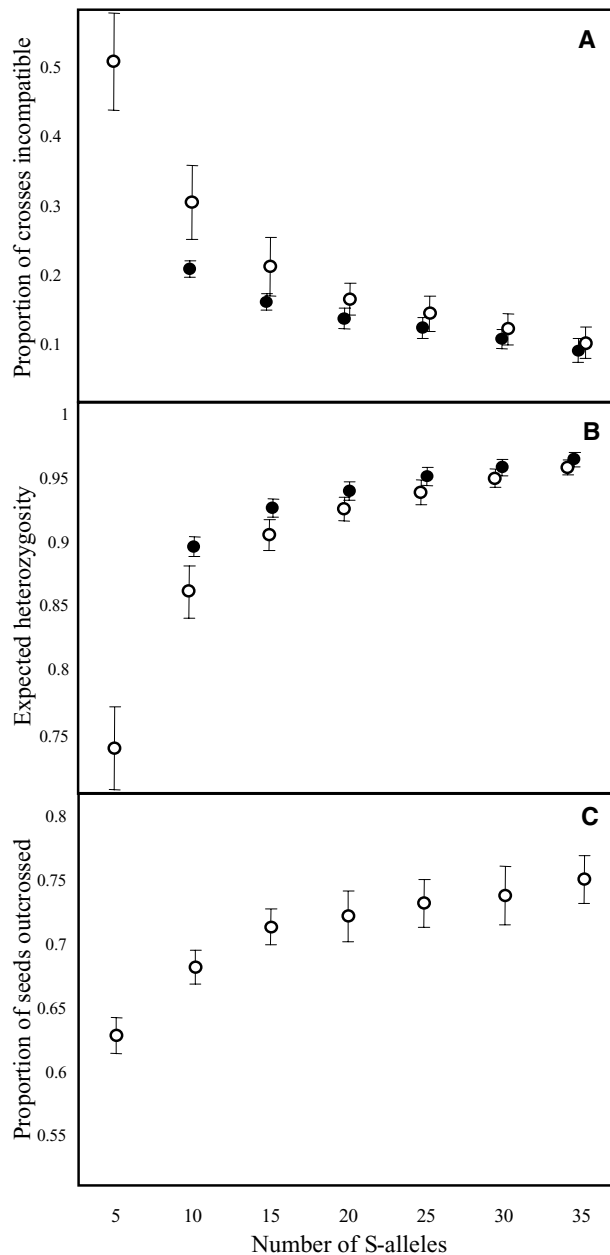


Figure 2. Results of simulation models as a function of number of alleles present. (A) Proportion of crosses attempted on day one that are incompatible; (B) Expected heterozygosity; (C) Proportion of seeds produced by cross-fertilization. Datapoints are means from 25 runs for $N = 500$ with initial allele number of 50; error bars indicate one standard deviation. Solid circles show results from the full SI model, $P = 0.5$; open circles show results from the transient SI model, $P = 0.5$. P = probability of pollinator visitation. Data for allele number of five are missing for full SI model because all runs retained more than five alleles.

transient SI than in the fully SI model for a given population size. Although the model was designed to simulate the specific transient form of SI in *L. jepsonii*, the fundamental result of reduced S -allele diversity is likely to extend to other more common forms

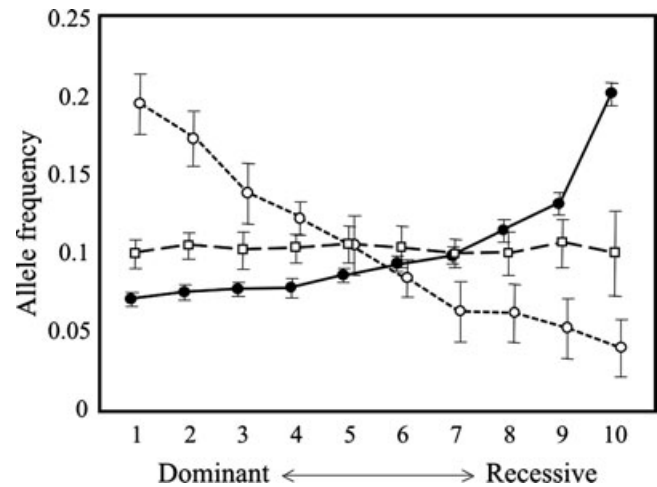


Figure 3. Frequency of S -alleles as a function of position in the dominance hierarchy under full SI, $P = 0.5$ (solid line), transient SI, $P = 1$ (long dashes), and transient SI, $P = 0.5$ (short dashes). P = the probability of pollinator visitation. Values plotted are mean frequencies after 300 generations of 12 replicate runs with $N = 5000$; error bars indicate one standard deviation. All runs began with 10 S -alleles, and no alleles were lost during the course of the runs.

of partial SI. Accelerated loss of S -alleles with partial SI results from three potential factors in this model. First, although cross-incompatibility can limit seed set in the full SI model, compatibility assures seed set on the second day of flowering with transient SI; thus, the fecundity component of frequency-dependent selection is removed. Second, cross-compatibility on day two reduces the strength of selection on S -alleles that acts through male out-cross success. Third, self-fertilization can further reduce S -allele diversity, for reasons explored below. Although the model does not arrive at true evolutionary equilibria, it predicts that partially SI populations will have lower numbers of S -alleles at equilibrium than fully SI populations given equivalent rates of S -allele introduction through migration or mutation.

The model results are qualitatively consistent with the pattern that emerged from diallel crosses in a partially and fully SI species. *Leptosiphon jepsonii* has higher rates of cross-incompatibility relative to its fully SI congener, which suggests lower S -allele diversity in the partially SI species. However, it is premature to conclude that differences in rates of cross-incompatibility in the two species indicate differences in equilibrium S -allele numbers or can be attributed solely to the strength of SI. For example, reduced diversity in *L. jepsonii* could be explained in part by smaller founding population sizes, smaller effective population sizes, or lower rates of migration, all of which might be expected in a partially selfing species. Differences in the species' ranges also could be a contributing factor; *L. parviflorus* is more widely distributed than *L. jepsonii*, which is restricted to the CA North Coast Ranges. Moreover, the association between cross-incompatibility and

S-allele number could be affected by the evenness of the distribution of *S*-allele frequencies as suggested by the results of this model (see Fig. 2A,B). Therefore, higher rates of cross-incompatibility in *L. jepsonii* might be caused in part by a more uneven frequency of *S*-alleles, and not solely to lower allele numbers. In contrast to the model results, neither species showed a relationship between population size and rates of cross-compatibility. Differences among populations in migration rates might obscure such a relationship. Alternatively, population sizes have been observed to fluctuate rapidly in these species, and populations may not be at equilibrium.

The simulation model suggests novel insights into the effects of selfing on *S*-allele dynamics in partially SI populations. When pollinators are limited ($P < 1$) and some self-fertilization occurs, *S*-allele dynamics are affected not only by the reduced strength of frequency-dependent selection but also by its interaction with the automatic transmission advantage of selfing (Fisher 1941). The transmission advantage arises because the seed parent passes along two copies of each gene through selfed seeds, but only one copy through outcrossed seeds. In this model of transient SI, the transmission advantage can create positive frequency-dependent selection that counters the typical negative feedback on *S*-alleles. Individuals expressing an *S*-allele that occurs at a high frequency are likely to experience cross-incompatibility on day one, and cross-incompatibility that prevents outcrossing on day one allows an opportunity for selfing on day two. In turn, selfing gives a transmission advantage to the common *S*-allele, leading to even higher frequencies, more cross-incompatibility, higher rates of selfing and higher transmission rates are experienced by that allele. This positive feedback loop is promoted by the transient nature of the SI in the model, in which selfing occurs only when outcrossing fails. The result may be extendible, however, to other forms of partial SI in which selfing provides reproductive compensation for cross-incompatible matings. Further modeling is required to explore the implications of biological factors that distinguish this from other forms of partial SI.

The transmission advantage of selfing also has a dramatic effect on the relationship between *S*-allele dominance and frequency in these models (Fig. 3). In the full SI model, dominant alleles are held at lower frequencies than recessive ones because dominant alleles are more often expressed and therefore more likely to experience cross-incompatibility. This is congruent with general support for the “recessive effect” in models and empirical studies of sporophytic SI (reviewed in Schierup et al. 1997; Billiard et al. 2007, but see Schierup et al. 2000). However, in the transient SI model, individuals with dominant alleles are more likely to self on day two because their higher rates of cross-incompatibility reduce the probability of outcrossing on day one. Therefore, dominant alleles more often enjoy the transmission advantage of selfing and, as a result, increase to higher frequencies than recessive alleles.

It is important to note that two factors not included in the model can counteract the genetic transmission advantage of selfing, both of which are therefore expected to temper the positive feedback effects of selfing on *S*-allele distribution and diversity described above. First, selfing may diminish a plant’s success as an outcross pollen parent, a phenomenon termed pollen discounting (Holsinger et al. 1984). Second, inbreeding depression is expected to counter the genetic transmission advantage of selfing. Greenhouse experiments have found mild-to-moderate levels of inbreeding depression in populations of *L. jepsonii* (Goodwillie and Knight 2006), which suggests that the magnitude of the effects of selfing on *S*-allele dynamics in real populations is likely to be somewhat less than those predicted by the model. Additionally, because the models do not include migration they cannot address the relationship between dominance and the likelihood of *S*-allele establishment, an effect that has been shown in other models (Schierup et al. 1997) and that might also be influenced by partial SI.

The results of this model highlight the effect of pollination biology in the dynamics of *S*-alleles and selfing. When pollinator visitation is high and selfing is preempted by deposition of cross-pollen, the effect of transience in the SI mechanism is solely to allow fertilization by mates that share *S*-phenotypes. The rate of loss of *S*-alleles in the transient SI model is accelerated by pollinator limitation because, under these conditions, self-fertilization occurs (Table 1). In contrast, pollinator limitation maintains higher *S*-allele diversity in the full SI model because it increases the chance that cross-incompatibility will limit seed set, strengthening fecundity selection on *S*-alleles. This result is complementary to previous models showing that selection on modifiers of SI is affected by the degree of pollen limitation (Vallejo-Marin and Uyenoyama 2004; Porcher and Lande 2005); together these theoretical results emphasize the role of pollination ecology in the trajectory of SI evolution.

The implications of these results for the evolution of partial SI systems demand consideration. *S*-allele diversity has been shown theoretically to influence selection on modifiers of SI (Vallejo-Marin and Uyenoyama 2004; Porcher and Lande 2005). The results of the current model suggest that the strength of SI can, in turn, influence the dynamics of *S*-alleles. Further theoretical exploration will benefit from a consideration of how these two factors may coevolve. The simulation model presented here also suggests complex, although subtle, interacting effects of *S*-allele diversity and the rate of self-fertilization in populations. The transient SI model shows a slight reduction in the rate of outcrossing when *S*-allele numbers are low and rates of cross-incompatibility are high; the rate of selfing of individuals or populations may then depend not only on modifiers of SI expression but also to some extent on the number and frequency of *S*-alleles in a population.

ACKNOWLEDGMENTS

I thank R. Danell for contributing ideas and developing the simulation software. M. Uyenoyama and M. Vallejo-Marin offered useful discussion at the outset of the project. B. Burne, N. Merli, and S. Warren provided skilled assistance with diallel crosses and pollen tube counts. The article was substantially improved by the insightful comments of two anonymous reviewers and the Associate Editor. This work was supported by NSF grant DEB-0212903 to CG.

LITERATURE CITED

- Bell, C. D., and R. W. Patterson. 2000. Molecular phylogeny and biogeography of *Linanthus* (Polemoniaceae). *Am. J. Bot.* 87:1857–1870.
- Billiard, S., V. Castric, and X. Vekemans. 2007. A general model to explore complex dominance patterns in plant sporophytic self-incompatibility systems. *Genetics* 175:1351–1369.
- Brennan, A., S. A. Harris, D. A. Tabah, and S. J. Hiscock. 2002. The population genetics of sporophytic self-incompatibility in *Senecio squalidus* L. (Asteraceae) I: S allele diversity in a natural population. *Heredity* 89:430–438.
- Brennan, A. C., S. A. Harris, and S. J. Hiscock. 2005. Modes and rates of selfing and associated inbreeding depression in the self-incompatible plant *Senecio squalidus* (Asteraceae): a successful colonizing species in the British Isles. *New Phytol.* 168:475–486.
- Byers, D. L., and T. R. Meagher. 1992. Mate availability in small populations of plant-species with homomorphic sporophytic self-incompatibility. *Heredity* 68:353–359.
- Crosby, J. L. 1966. Self-incompatibility alleles in the population of *Oenothera organensis*. *Evolution* 20:567–579.
- de Nettancourt, D. 1977. Incompatibility in angiosperms. Springer-Verlag, Berlin.
- Fisher, R. A. 1941. Average excess and average effect of a gene substitution. *Ann. Eugen.* 11:53–63.
- . 1958. *The genetical theory of natural selection*. Dover, New York.
- Good-Avila, S. V., and A. G. Stephenson. 2002. The inheritance of modifiers conferring self-fertility in the partially self-incompatible perennial, *Campanula rapunculoides* L. (Campanulaceae). *Evolution* 56:263–272.
- Goodwillie, C. 1997. The genetic control of self-incompatibility in *Linanthus parviflorus* (Polemoniaceae). *Heredity* 79:424–432.
- . 1999. Multiple origins of self-compatibility in *Linanthus* section *Leptosiphon* (Polemoniaceae): phylogenetic evidence from internal-transcribed-spacer sequence data. *Evolution* 53:1387–1395.
- Goodwillie, C., and M. C. Knight. 2006. Inbreeding depression and mixed mating in *Leptosiphon jepsonii*: a comparison of three populations. *Ann. Bot.* 98:351–360.
- Goodwillie, C., and J. Ness. 2005. Correlated evolution in floral morphology and the timing of self-compatibility in *Leptosiphon jepsonii* (Polemoniaceae). *Int. J. Plant Sci.* 166:741–751.
- Goodwillie, C., K. Partis, and J. West. 2004. Transient self-incompatibility confers delayed selfing in *Leptosiphon jepsonii* (Polemoniaceae). *Int. J. Plant Sci.* 165:387–394.
- Holsinger, K. E., Feldman, M. W., and F. B. Christiansen. 1984. The evolution of self-fertilization in plants: a population genetic model. *Am. Nat.* 124:446–453.
- Lawrence, M. J. 2000. Population genetics of the homomorphic self-incompatibility polymorphisms in flowering plants. *Ann. Bot.* 85(Suppl. A):221–226.
- Levin, D. A. 1996. The evolutionary significance of pseudo-self-fertility. *Am. Nat.* 148:321–332.
- Mable, B. K., M. H. Schierup, and D. Charlesworth. 2003. Estimating the number, frequency, and dominance of S-alleles in a natural population of *Arabidopsis lyrata* (Brassicaceae) with sporophytic control of self-incompatibility. *Heredity* 90:422–431.
- Mable, B. K., A. V. Robertson, S. Dart, C. Di Berardo, and L. Witham. 2005. Breakdown of self-incompatibility in the perennial *Arabidopsis lyrata* (Brassicaceae) and its genetic consequences. *Evolution* 59:1437–1448.
- Mena-Ali, J. I., and A. G. Stephenson. 2007. Segregation analyses of partial self-incompatibility in self and cross progeny of *Solanum carolinense* reveal a leaky S-allele. *Genetics* 177:501–510.
- Porcher, E., and R. Lande. 2005. Loss of gametophytic self-incompatibility with evolution of inbreeding depression. *Evolution* 59:46–60.
- Schierup, M. H., X. Vekemans, and F. B. Christiansen. 1997. Evolutionary dynamics of sporophytic self-incompatibility alleles in plants. *Genetics* 147:835–846.
- Schierup, M. H., X. Vekemans, and D. Charlesworth. 2000. The effect of subdivision on variation at multi-allelic loci under balancing selection. *Genet. Res.* 76:51–62.
- Stephenson, A. G., S. V. Good, and D. W. Vogler. 2000. Interrelationships among inbreeding depression, plasticity in the self-incompatibility system, and the breeding system of *Campanula rapunculoides* L. (Campanulaceae). *Ann. Bot.* 85:211–219.
- Stone, J. L., M. A. Sasuclark, and C. P. Blomberg. 2006. Variation in the self-incompatibility response within and among populations of the tropical shrub *Witheringia solanacea* (Solanaceae). *Am. J. Bot.* 93:592–598.
- Vallejo-Marin, M., and M. K. Uyenoyama. 2004. On the evolutionary costs of self-incompatibility: incomplete reproductive compensation due to pollen limitation. *Evolution* 58:1924–1935.
- Vekemans, X., M. H. Schierup, and F. B. Christiansen. 1998. Mate availability and fecundity selection in multi-allelic self-incompatibility systems in plants. *Evolution* 52:19–29.
- Vogler, D. W., and A. G. Stephenson. 2001. The potential for mixed mating in a self-incompatible plant. *Int. J. Plant Sci.* 162:801–805.
- Weber, J. J., and C. Goodwillie. 2007. Timing of self-compatibility, flower longevity, and potential for male outcross success in *Leptosiphon jepsonii* (Polemoniaceae). *Am. J. Bot.* 94:1338–1343.
- Wright, S. 1939. The distribution of self-sterility alleles in populations. *Genetics* 24:538–552.

Associate Editor: J. Kohn