Polyploidy and Gender Dimorphism

Miller and Venable (*1*) claimed that polyploidy is a "trigger of unrecognized importance" for the evolution of gender dimorphism, an idea originally proposed by Jennings (*2*) and Baker (*3*). In our opinion, their phylogenetic analysis of North American *Lycium* (Solanaceae) does not support the claimed associations between polyploidy, self-fertility, and gender dimorphism. There is no support (bootstrap <50%) for the sister group to the gynodioecious clade, and collapsing the nodes supported by <50% bootstrap results in an unresolved polytomy at the base of *Lycium* + *Grabowskia*. Thus, the inferred ancestral state for the gynodioecious clade may not even be self-incompatibility. The limited taxonomic sampling, which encompassed 13 of some 100 species of *Lycium*, and limited geographic sampling, which included no Asian, African, or Australian species of *Lycium*, further reduces confidence in the published topology. And only a single concurrent origin of dimorphism and polyploidy was hypothesized, which makes it difficult to assess the temporal order and statistical significance of the character changes.

As evidence for self-compatibility, Miller and Venable cited a greater proportion of selfed pollen tubes at the base of the style in dimorphic species relative to cosexuals [figure 4 of (*1*)], but they did not give the total number of pollen tubes reaching the base. Because the hermaphrodites of the dimorphic species specialize as males and set very few seeds, however, the total number of pollen tubes reaching the base of the style is likely to differ substantially between the cosexual and dimorphic species. Consequently, the log ratio of outcross to self pollen tubes reaching the base of the style is also likely to differ, and self-compatibility will easily get confounded with gender specialization in the hermaphrodites of the dimorphic species.

Self-incompatibility and dioecy are known to occur in genera (*4*) not mentioned in table 1 of (*1*). Moreover, in half of the genera presented in that table, the ancestor may be polyploid rather than diploid. Miller and Venable mentioned 37 related pairs of taxa where polyploidy disrupted self-incompatibility, yet they do not discuss the frequency of gender dimorphism in these taxa.

The authors claim that the combined appearance of polyploidy and consequent loss of self-incompatibility play an important role in the evolution of gender dimorphism. To demonstrate the importance of the pathway with both loss of self-incompatibility and polyploidy in the evolution of gender dimorphism, however, it is not sufficient to demonstrate that the pathway exists, as Miller and Venable have done in table 1 of (*1*). Instead, one must also demonstrate that gender dimorphism arises more frequently via this pathway than via other pathways. Self-incompatibility systems have been lost repeatedly, often in the absence of polyploidy (*5*). Indeed, theoretical modeling and empirical evidence both suggest that inbreeding depression is stronger in diploid than in polyploid species (*6*, *7*). Hence, male sterile mutants would be even more likely to invade in diploid than in polyploid species that have lost self-incompatibility.

Figure 1 schematically illustrates this issue. If gender dimorphism is equally or more frequently associated with self-compatible diploid taxa than with self-compatible polyploid taxa (each being derived from self-incompatible diploid ancestors), as depicted in Fig. 1A, the result suggests that the loss of self-incompatibility but not polyploidy is important in the evolution of gender dimorphism. If, by contrast, gender dimorphism is equally or more frequently associated with polyploid self-incompatible taxa than with polyploid self-compatible taxa (both derived from diploid self-incompatible ancestors), as depicted in Fig. 1B, the result suggests that polyploidy but not loss of self-incompatibility is important in the evolution of gender dimorphism.

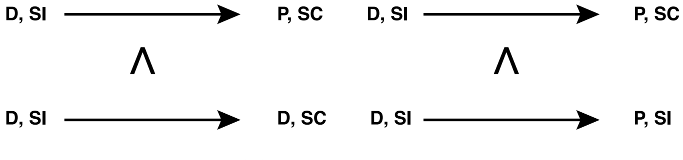

Fig. 1. Hypothetical pathways for the evolution of gender dimorphism from cosexual ancestors. D, diploid; P, polyploid; SI, self-incompatible; SC, self-compatible. All species are derived from diploid, self-incompatible ancestors. (**A**) Situation in which gender dimorphism is more often associated with diploid self-compatible species than with polyploid self-compatible species. (**B**) Situation in which gender dimorphism is more often associated with polyploid self-incompatible species than with polyploid self-compatible species.

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Response: Although Jennings (*1*) and Baker (*2*) did remark on the potential connections among polyploidy, loss of incompatibility, and gender dimorphism, our study (*3*) was, to our knowledge, the first to document this scenario in nature and to provide comparative evidence suggesting its significance for the evolution of gender dimorphism in plants.

As Brunet and Liston suggest, support for the sister group to the gynodioecious clade in the published *Lycium* phylogeny is weak; however, a broader phylogenetic analysis, including 25 species from five continents (*4*), gave similar results. The gynodioecious clade is strongly supported, and its sister group does not change in the most parsimonious trees. More to the point, any putative sister group is very likely self-incompatible and diploid, because all cosexual *Lycium* tested to date are self-incompatible diploids. Self-incompatibility is both ancestral and widespread in *Lycium*; alleles at the *S*-locus show transgeneric evolution and are more closely related to *S*-alleles in other Solanaceous genera than to other *S*-alleles in *Lycium* [reference 23 in (*3*)]. The transition in *Lycium* from diploid self-incompatible cosexuality to polyploid self-compatible gender dimorphism happened too fast to leave a phylogenetic record of the order of the transitions, but our hypothesized order seems the most plausible (*5*).

We did not confound self-compatibility in the hermaphrodites of the dimorphic species with gender specialization, as Brunet and Liston suggest. The dimorphic hermaphrodites, whether selfed or outcrossed, have numbers of pollen tubes similar to the numbers for outcrossed, but not selfed, cosexual species (*4*). The self-incompatibility reaction was seen in selfed cosexuals, but not in selfed dimorphic hermaphrodites (*4*).

That self-incompatibility and dimorphism occur together in some plant taxa shows that dimorphism evolves through a variety of scenarios—hardly a surprising finding (*6*). Table 1 in (*3*) includes only examples where both polyploidy and gender dimorphism are apparently derived. Our survey [p. 2337 and figure 1 in (*3*)] was done to test the first step in the proposed scenario. The frequency of dimorphism among these self-compatible polyploids is roughly one-third. These data probably do not provide a reasonable test for the frequency of dimorphism among recently self-compatible polyploids (among other things, cases of experimental induction of polyploidy were included). Yet they suggest that our scenario may be common, in view of the frequency of polyploid events in self-incompatible groups in nature. Many polyploid, self-compatible species may remain self-compatible cosexuals [p. 2337 of (*3*)]; we suggest that gender dimorphism is but one outcome following such an event.

Our scenario does not require that inbreeding depression be stronger in polyploids than diploids. It need only be strong enough to permit, in combination with any resource compensation, the invasion of females. Nonetheless, we would argue that the paucity of currently available data makes the widespread acceptance of the view that inbreeding depression is weaker in polyploids premature. This result depends upon the model of mutation assumed (*7*), and the available empirical evidence is at best mixed (*8, 9*).

We view the final argument of Brunet and Liston—that establishing the importance of the scenario described in (*3*) requires demonstrating that this scenario arises more frequently than others—as unjustified, because we never asserted that our scenario was the most important for the evolution of gender dimorphism. Still, their suggestion that statistics on frequencies of different evolutionary events could be used to support the proposed scenario is reasonable. Formulating the correct comparisons to document the proposed mechanism is subtle, however, and we are not convinced that the comparisons Brunet and Liston suggest are the crucial ones. Rather, we contend that there is comparative support for polyploidy as a trigger for the evolution of gender dimorphism, as long as (i) polyploidy results in the breakdown of self-incompatibility, and (ii) self-compatibility triggers gender dimorphism in polyploids, as is widely accepted for diploids. An appropriate comparison for (i) would be to ask whether the frequency of loss of self-incompatibility following polyploid speciation from self-incompatible diploid hermaphroditic ancestors is greater than the frequency of loss of self-incompatibility following non-polyploid speciation. An appropriate test for (ii) would be to ask whether the frequency of gender dimorphism is higher in self-compatible than in self-incompatible polyploids.

With regard to (i), in the survey reported in (*3*), self-incompatibility was lost in 70% of the polyploid species associated with self-incompatible diploid hermaphrodites. We do not have a frequency for the loss of self-incompatibility following non-polyploid speciation, but the natural history of self-incompatibility suggests it is probably lower than 70% [see, e.g., (*10*)]. As for (ii), roughly, one-third of these same 70% self-compatible polyploids are dimorphic, whereas gender dimorphism is absent among the self-incompatible polyploids in this survey. Comparative data on the relative frequencies of these events and other transitions to gender dimorphism will be a welcome addition to our understanding of the importance of different scenarios.

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References and Notes

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5. Polyploid self-compatibility is often derived from diploid self-incompatibility even when gender dimorphism does not subsequently evolve [references in (*3*)]. Also, experimental work shows unequivocally that polyploidization of self-incompatible taxa usually breaks down incompatibility, so there is strong mechanistic support for the order of the first two events. This suggests that gender dimorphism is the last event in the sequence.
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