

## Why are there so few homomorphic multi-locus sporophytically determined self-incompatibility systems?

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**Abstract.** Homomorphic multi-locus sporophytically determined self-incompatibility systems are much rarer than multi-locus gametophytic systems. This note examines some of the possible reasons for this disparity and concludes that, while each additional locus in a gametophytic system allows increased crossing among related plants as well as a lower mutation rate to maintain a given level of variability, the same conclusion cannot be drawn for sporophytic systems.

**Key words:** Dominance – Gametophytic – Homomorphic – Self-incompatibility – Speciation – Sporophytic

### Introduction

Both gametophytic and sporophytic homomorphic self-incompatibility systems are widespread throughout the angiosperms. [Heteromorphic systems are largely sporophytic, probably reflect different evolutionary origins (Gibbs 1986), and will not be considered further in this note.] However, although two, three, and four locus gametophytic systems have been identified in several families (e.g., Lundqvist 1990, 1991), only two multi-locus sporophytic systems have been reported, those in the crucifer *Eruca sativa* (Verma et al. 1977; Lewis 1977) and the composite *Helianthus annuus* (Habura 1957; Schchori 1969), though this latter case is uncertain. It is the purpose of this note to compare some of the theoretical properties of the two

systems in order to determine whether clear possible reasons for the difference can be discerned.

### Frequency of incompatible cross-pollination

The essential nature of self-incompatibility is the prevention of selfing. However, it can also prevent the crossing of closely related plants, such as siblings or parents and offspring. For the gametophytically determined single locus systems, an  $S_1S_2$  female can be fertilised by any pollen of genotype other than  $S_1$  or  $S_2$ , whereas for the equivalent sporophytic system (i.e., a system without dominance in which the pollen bears both parental specificities),  $S_1S_2$  can only be fertilised by pollen from  $S_iS_j$  where  $i, j \neq 1, 2$ . Hence, all offspring-female parent crosses are reciprocally half-compatible and sib-sib crosses are either half or fully compatible in the gametophytic system. In contrast, consider the sporophytic cross  $S_1S_2 \times S_3S_4$ . Four offspring genotypes are possible:  $S_1S_3, S_1S_4, S_2S_3, S_2S_4$ . Those with no alleles in common are reciprocally compatible, those with one or two alleles in common are reciprocally incompatible. The sporophytic system is therefore more effective than the gametophytic in preventing close inbreeding, which should be generally advantageous, but conversely may be disadvantageous if plants are very sparsely distributed or if population size is very small.

If we have  $n$  equally frequent alleles, the proportion of pollinations expected to be incompatible for a gametophytic system is  $2/n$ . For a sporophytic system, the proportion is  $2(2n - 3)/[n(n - 1)]$ . That is, the extent of pollen ineffectiveness expected is about twice as high in the sporophytic system. For two-locus systems, the situation is more extreme. Consider the case where

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there are  $n_1$  and  $n_2$  alleles at the two loci, all alleles at a given locus being equally frequent.

For a gametophytic system,  $\binom{n_1}{2}\binom{n_2}{2} + n_1\binom{n_2}{2} + n_2\binom{n_1}{2}$  genotypes are possible, since either locus (but not both loci simultaneously) can be homozygous. For a heterozygote,  $4/(n_1n_2)$  of  $\binom{n_1}{2}\binom{n_2}{2}$  and for a homozygote  $2/(n_1n_2)$  of  $n_1\binom{n_2}{2}$  or  $n_2\binom{n_1}{2}$  possible pollinations will be incompatible, so that, altogether, the proportion of incompatible pollinations will be  $4/(n_1n_2 - 1)/[n_1n_2(n_1n_2 + n_1 + n_2 - 3)]$ .

For a sporophytic system, the proportion of incompatible pollinations is at least  $2(2n_1 - 3)/(n_1(n_1 - 1)) + 2(2n_2 - 3)/(n_2(n_2 - 1))$  since the presence of either maternal allele in the male parent ensures incompatibility in the absence of dominance. Thus, the level of cross-incompatibility will always be much higher for the sporophytic system.

The same arguments apply to three or more loci.

**Dominance**

Dominance provides a means whereby the frequency of ineffective pollination is reduced in the sporophytic system. In fact, as with the gametophytic system, but not a sporophytic system without dominance, a minimum of three alleles is necessary to avoid extinction.

Suppose that we have a dominant series of three alleles,  $S_1, S_2, S_3$ , such that pollen phenotypes are as follows:

Male parent	$S_1S_2$	$S_1S_3$	$S_2S_3$
Pollen phenotype	$S_1$	$S_1$	$S_2$

Then all homozygous genotypes except  $S_1S_1$  are possible and the crosses and their outcomes are as shown in Table 1, on the assumption that the alleles act independently in the style. Dominance in the style, whether following the same ordering as that in the pollen or different, would yield a different system with different properties; we have considered this particular system because it has already been identified and some of its properties examined (Imrie et al. 1972). Other possible systems have been considered by Lewis (1979).

Imrie et al. (1972) calculated that equilibrium frequencies for the three alleles were, approximately, 0.198, 0.258 and 0.544. To obtain an analytical solution, one needs to solve the recurrence equations

$$Ty'_1 = \frac{1}{2}y_1y_3 + \frac{1}{4}y_1y_4 + y_2y_3 + \frac{1}{2}y_2y_4$$

$$Ty'_2 = \frac{1}{4}y_1y_4 + y_1y_5 + \frac{1}{2}y_2y_4 + \frac{1}{2}y_2y_5$$

$$Ty'_3 = \frac{1}{2}y_1y_3 + \frac{1}{4}y_1y_4$$

$$Ty'_4 = \frac{1}{4}y_1y_4 + y_1y_5 + y_2y_3 + \frac{1}{2}y_2y_4 + 2y_3y_5 + y_4y_5$$

$$Ty'_5 = \frac{1}{2}y_2y_4 + \frac{1}{2}y_2y_5 + y_4y_5$$

where

$$T = y_1y_3 + y_1y_4 + 2y_1y_5 + 2y_2y_3 + 2y_2y_4 + y_2y_5 + 2y_3y_5 + 2y_4y_5.$$

Recessivity is advantageous, in the sense that it allows the system to persist with a lower overall level of variability; the fact that the frequency of an allele increases with its degree of recessivity is not necessarily of any benefit to the plant bearing it. As Fisher (1941) was the first to show, the dynamics of a breeding system are not always determined by the fitness of the individual genotypes. What one can note is that evolution of recessivity would be relatively likely within a sporophytic system, since it would arise through diminution of function, always likely to be recessive in itself on the theory of Kacser and Burns (1981); the difficulty, as always with such systems, would be the generation of distinct specificities. (Mutations that alter a gametophytic to a sporophytic system or vice versa present a lesser difficulty, since there will be alterations in the promoter to yield a different tissue specificity.) We can also note that new alleles recessive to all previous alleles will be at an advantage to all other alleles and therefore will be less likely to be lost through drift than alleles having a level of recessivity already represented in the population.

If a two-locus system were to arise through duplication, what would its properties be? There is some evidence relevant to gametophytic systems. Fearon et al. (1984) showed in tetraploid perennial ryegrass that if at each of the two loci the pollen possessed an allele of the same specificity as one of those present in

**Table 1.** Compatible and incompatible crosses and their outcomes

		$S_{12}$ $y_1$	$S_{13}$ $y_2$	$S_{22}$ $y_3$	$S_{23}$ $y_4$	$S_{33}$ $y_5$
$S_{12}$	$y_1$	—	—	—	—	$1/2 S_{13}$ $1/2 S_{23}$
$S_{13}$	$y_2$	—	—	$1/2 S_{12}$ $1/2 S_{23}$	$1/4 S_{12}$ $1/4 S_{13}$ $1/4 S_{23}$ $1/4 S_{33}$	—
$S_{22}$	$y_3$	$1/2 S_{12}$ $1/2 S_{22}$	$1/2 S_{12}$ $1/2 S_{23}$	—	—	$S_{23}$
$S_{23}$	$y_4$	$1/4 S_{12}$ $1/4 S_{13}$ $1/4 S_{22}$ $1/4 S_{23}$	$1/4 S_{12}$ $1/4 S_{13}$ $1/4 S_{23}$ $1/4 S_{33}$	—	—	$1/2 S_{23}$ $1/2 S_{33}$
$S_{33}$	$y_5$	$1/2 S_{13}$ $1/2 S_{23}$	$1/2 S_{13}$ $1/2 S_{33}$	$S_{23}$	$1/2 S_{23}$ $1/2 S_{33}$	—

the style, the pollination would be ineffective, i.e., there was no dominance or epistacy, this work confirming the single-locus result of Lundqvist (1957). In contrast, Lewis (1947) showed in artificial tetraploids of *Oenothera organensis* that one cannot assume that lack of a pollen-parent genotypic effect on the haploid pollen means that there will be independent (co-dominant) allelic action in diploid pollen. Hence, one cannot assume with any certainty (though one can hypothesize) that epistacy would not occur in a duplicated single-locus sporophytic system. If this were the case, however, consider a possible outcome:  $S_{12}$  duplicated to  $S_{12}S'_{12}$  and pollinated by  $S_{34}$ . Ignoring the complications of unequal crossing-over (inviable gametes, etc.), the progeny would be

$$S_1S'_1/S_3 \quad S_1S'_1/S_4 \quad S_1S'_2/S_3 \quad S_1S'_2/S_4 \quad S_2S'_1/S_3 \quad S_2S'_1/S_4 \\ (1 - \Theta)/8 \quad (1 - \Theta)/8 \quad \Theta/8 \quad \Theta/8 \quad \Theta/8 \quad \Theta/8$$

$$S_2S'_2/S_3 \quad S_2S'_2/S_4 \\ (1 - \Theta)/8 \quad (1 - \Theta)/8$$

compared with

$$S_{13} \quad S_{14} \quad S_{23} \quad S_{24} \\ 1/4 \quad 1/4 \quad 1/4 \quad 1/4$$

$\Theta$  may be expected to be low in general, but if there is any recombination, then the recombinant types will reject three types of haploid pollen, rather than two as normal, and the pollen carrying two alleles will be at no reproductive advantage if there is paternal dominance/epistasis, and at a disadvantage if there is independent action in the gametophyte. Thus, there will be weak selection against multiple loci that arise by duplication.

In the hypothetical multilocus systems simulated by Mayo and Leach (1989), the sporophytic system always manifested a higher level of incompatible pollination than the comparable gametophytic system, as might be expected from the argument above. However, those systems were quantitative in nature, with undifferentiated alleles at all loci. This perhaps strengthens the general argument that multilocus sporophytic systems have no advantage over their single-locus equivalents.

### Maintenance of variability

Any self-incompatibility system should maintain heterozygosity at unrelated loci at a level higher than is the case where complete or partial inbreeding is involved. However, it is not the case that a high level of outbreeding is always associated with a high level of heterozygosity or variability, even when population sizes are large. We have shown (Leach and Mayo 1991) for borago, *Borago officinalis*, which was mainly out-

crossed in our studies, that the level of heterozygosity is extremely low, well below 0.01 in all of about 15 populations studied from sources in Australia, France and the United Kingdom. Les et al. (1991) studied a sporophytically self-incompatible species, *Aster furcatus*, and found an equally low level of heterozygosity, which they attributed to the species's extreme rarity. The ability of the species to propagate itself clonally may be as important, however.

What is not known, but is appropriate for further study, is whether sporophytic systems maintain variability better at unrelated loci than do gametophytic systems. This seems unlikely a priori, given that the higher levels of incompatible pollination encountered with a sporophytic system will lead to a lower effective population size.

We have simulated hypothetical multi-locus gametophytic and sporophytic systems and have found that the mutation rates necessary to maintain segregation at a given number of diallelic loci were always higher in a sporophytic than in a gametophytic system (Mayo and Leach 1989). Imrie et al. (1972) simulated a single-locus sporophytic system and concluded that a high mutation rate was needed to maintain a large number of alleles in populations smaller than about 1000, as is the case for gametophytic systems (Wright 1964; Mayo 1966). However, multi-locus sporophytic systems have not been studied, so no predicted mutation rates are available, as they are for gametophytic systems (Mayo 1978).

### Speciation

Many models of speciation have been developed that depend on an initial event that renders some members of a population infertile in crosses with most members of that population. What these models virtually always reveal is the very low probability of satisfactory reproductive isolation if mean fitness of the isolated subpopulation is close to that of the original population (see for example, Gregorius 1992; Spirito 1992). This is largely because there must be very low initial fitness of the individuals heterozygous for the gene or genes determining the inability to cross with most members of the original population. Most hypothetical events that could lead to multilocus systems (translocation, duplication, etc.) occurring in a system based on a single sporophytic locus with dominance produce new genotypes at a substantial disadvantage to most potential genotypes of the pre-existing system. Thus, speciation following on an event that creates an isolated subpopulation does not appear a likely explanation for the rarity of multilocus systems.

Many workers (e.g., Lewis 1979) have espoused "the view that the multi-gene [gametophytic] systems are primitive, and the one-gene system is an advanced

derivative". If this were the case, and the dominance that must characterise sporophytic systems is an evolved dominance, as discussed above, then this would also enhance the rarity of multi-locus sporophytic systems, given the increased number of mutational events that would be required to contribute to the development of such a system coupled with its lack of selective advantage.

## Conclusion

Multilocus sporophytic self-incompatibility systems have some inherent disadvantages, relative to the single-locus system, that make them unlikely to arise frequently in the course of evolution. However, such systems should be searched for, since sampling could have contributed to the observed disparity, given the relatively higher frequency of gametophytic systems of all kinds among the homomorphic systems.

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