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Stability of self-incompatibility systems

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Summary. Multi-locus self-incompatibility systems offer few obvious adaptive advantages to the species possessing them. However, the gametophytic system's independent gene action allows the separate genes in a two gene system to behave as if they were individually not involved in a systematic disruption of panmixia. Under such circumstances, fixation of one of the two genes is readily obtained if an allele possesses a selective advantage. The resulting single gene system (the classic *Nicotiana* system) is then resistant to disruption, except by genes which allow selfing, which rapidly reach fixation.

Key words: Gametophytic self-incompatibility – Selfing – Linkage disequilibrium

Introduction

It is well known (see Mayo 1966 for discussion) that since the probability of extinction of a gametophytically determined self-incompatibility system is non-zero, long term stability of such systems is problematic. However, they are one of the most widespread outbreeding mechanisms in the Angiosperms, so that the quasi-stability which they exhibit is certainly substantial (Anderson and Stebbins 1984). Thus, discussion of this quasi-stability is of some interest.

Gametophytic self-incompatibility systems are characterized by large numbers of alleles, and it has long been established that a high mutation rate is necessary to maintain the numbers seen in relatively small populations. This has proven very difficult to explain, since mutations to novel specificities have not been observed, but an explanation may come about if the self- incompatibility mechanism itself is understood, a prospect now in sight (Anderson et al. 1986). Maintenance of variability is less dependent on a high mutation rate in tetraploid or multi-locus systems (Mayo 1971), and may be one of the reasons for the persistence of such systems (Mayo 1978).

Two other ways in which stability may be investigated are through the population dynamics of more than one gene locus, either genes linked to a self-incompatibility locus, or the dynamics of the multi-locus systems themselves; and through the process of attainment of self-fertility through the fixation of genes which override the effects of the incompatibility system.

Materials and methods

The behaviour of pairs of gene loci

The main problem of investigating the population dynamics of self-incompatibility systems is that data are few; in particular little is known of their linkage relationships. However, this is changing (Leach and Hayman 1987). Thus, the results of simulation, while interesting, require much more experimental validation.

What has been demonstrated for a locus linked to a single gene self-incompatibility locus is that the linkage disequilibrium is very different from that between any two autosomal genes not associated with a breeding system (Leach et al. 1986). Thus, linkage disequilibrium can either steadily decline to zero, oscillate as decline proceeds, or otherwise depart from a steady decline. Furthermore, linkage equilibrium may be established before genotypic frequencies reach their panmictic expectations.

If one also considers selective differences at the locus linked to the self-incompatibility gene, similar phenomena occur: for example, linkage equilibrium may be established while selection is still bringing about a decline in the frequency of a deleterious gene. Overall, although a gametophytic self-incompatibility system will delay the loss of a deleterious gene or the fixation of an advantageous gene, it will not allow the sheltering of lethals.

When one considers the population genetics of multi-locus systems, the data are even more scanty. Table 1 shows some of the very limited information on frequencies of numbers of alleles. By the method of Bateman (1947) (see also Fisher 1947),

Table 1. Numbers of genes at the two self-incompatibility loci in a population of *Lolium perenne* (Fearon and Lawrence, personal communication)

No. of occurrences		1	2	3	4–5	6	7–9	10–12	No. plants sampled
No. of alleles	*S*	12	1	2	0	1	0	1	38
	Z	12	2	0	1	0	2	0	39

Table 2. Allelic frequency distribution in the two-locus system, with 20 alleles at each locus. (Simulation over at least 500 generations)

Frequency class	0–0.025	0.025–0.05	0.05–0.075	0.075–0.1	0.1–0.125	0.125–0.15	0.15–0.175
$n=100$	0.375	0.225	0.125	0.150	0.075	0.025	0.025
$n=500$	0.425	0.088	0.187	0.125	0.112	0.05	0.012

estimates of the numbers of alleles in the population are 34.1 for the *S* and 35.3 for the *Z* locus. The allelic frequencies at the two loci are homogeneous ($P=0.39$ by Fisher's "exact" test). They also show the same type of distribution, i.e. very long-tailed, that is seen for the single locus system (see Mayo 1966) and for simulated populations of the two-locus system (Table 2). (20 alleles have been simulated at each locus as a likely lower limit for the real number, population size in Fearon and Lawrence's case being unknown.) Fearon and Lawrence's data (personal communication to CRL) do not, however, allow assessment of departures from Hardy-Weinberg equilibrium at either locus, nor allow assessment of gametic association between the *S* and *Z* loci. In simulated populations of sizes between 100 and 500, whether with small or large numbers of alleles, we find that gene frequencies change very slowly from generation to generation, that there is Hardy-Weinberg equilibrium at each locus, and that there is no correlation between the numbers of homozygotes at the two loci, either in the same generation or in alternating generations. Thus, in these small populations, there is little evidence of the genotypic association expected in infinite populations (Weber et al. 1982), apart from the absence of dual homozygotes. This may relate to the fact that the true, long-tailed allele frequency distribution has not been modelled in the deterministic analyses of Weber et al. (1982) and Charlesworth (1979).

Results

Attainment of self-fertility

Fisher (1941) was probably the first to point out that a gene which allowed self-fertilization in a self-incompatible plant would rapidly reach fixation, unless it was at a severe disadvantage through diminished viability in its carriers. Such genes occur in heteromorphic self-incompatibility systems, and their rate of increase has long been the subject of controversy (see Bodmer 1984; Piper et al. 1985). There is good evidence that in species showing both facultative self-pollination through cleistogamy and facultative cross-pollination through chasmogamy, plants arising from the latter have much higher viability (Mitchell-Olds and Waller 1985).

Hence, species in which there is almost complete inbreeding or almost complete outbreeding are expected to be much more frequent than species with intermediate frequencies of the two types of fertilization, and this is usually the case (Lande and Schemske 1985; Schemske and Lande 1985; Waller 1986). There are examples of such breeding systems, however, especially in forest trees. For example, Brown et al. (1975) found 76% outcrossing in *Eucalyptus obliqua,* and Cheliak et al. (1985) found 88% outcrossing in *Pinus banksiana.* In this latter case, there was a significant decline in the outcrossing rate over a four year period of observation. In neither species was the outbreeding mechanism fully elucidated, so that the high frequency of self-pollination cannot be attributed to the breakdown of a well defined self-incompatibility system. One of us (CRL) has, however, identified apparent genetical breakdown in the two locus gametophytic self-incompatibility system of rye (*Secale cereale*). Lundquist (1958) reported incompatibility breakdown caused by mutants with lost pollen specificity. This was little influenced by genes other than the *S* and *Z* incompatibility genes (Lundquist 1960, 1968). In the new work cited here, self-fertility appears to arise as a consequence either of a simple mutation at the *S* locus or at a closely linked locus. (Disturbed segregation ratios for an isozyme locus known to be linked to the *S* locus observed at a linked locus in some cases of selfing.)

It is of considerable interest to determine what factors influence the spread of genes which allow selfing or possibly incompatible pollination but not selfing, especially as there is evidence that mixed pollination can allow self-fertilization when pure self-pollination is ineffective (Visser and Marcucci 1984).

Accordingly, we have simulated populations of annual plants having the single locus gametophytic self-incompatibility system (Mayo 1966). We have incorporated the possibility of pollination of a given plant by up to four other plants as well as itself, and have made the probability of pollination by a given plant decline linearly with distance from the other plant. We have also made fertilization dependent to a modest extent on the proportion of compatible pollen; this makes little difference to the results.

We have then examined the approach to loss or fixation of an unlinked gene where a newly occurring mutant allows incompatible pollination either including selfing (Table 3) or excluding selfing (Table 4). This latter case corresponds either to a long established incompatibility system in which selfing is invariably lethal through homozygous recessives or to a system in which selfing is qualitatively different from incompatible crossing in a way not related to self-incompatibility. This is not realistic, given that selfing is usually possible when the incompatibility barrier can be breached, but represents the limiting case of inbreeding depression.

In Tables 3 and 4, we find that such genes are likely to be lost rapidly unless selfing is possible, i.e., selfing (as Fisher and others have noted) is a greater reproductive advantage than almost anything else. We also note that such genes are more likely to be fixed if the

Table 3. Fate of a new mutant which allows incompatible pollination. Selfing is possible

Population size	Initial no. of s.i. genes	Fixation			Loss		
		No. trials	Time	No. s.i. genes remaining	No. trials	Time	No. s.i. genes remaining
100	3	11	92.64± 5.27	2.64±0.15	6	3.33±6.17	3.0±0.0
	4	6	101.33±10.18	2.67±0.42	7	4.43±1.25	4.0±0.0
	6	2	82.00±11.00	3.5 ±1.5	10	10.30±4.27	5.9±0.1
500	3	4	156.50±11.75	3.0 ±0.0	8	5.50±1.39	3.0±0.0
	4	4	202.00±12.86	3.75±0.25	11	3.45±0.76	4.0±0.0
	6	5	236.40± 7.88	4.20±0.58	7	10.00±5.05	6.0±0.0

Table 4. Fate of a new mutant which allows incompatible pollination. Selfing is lethal

Population size	Initial no. of s.i. genes	Fixation			Loss		
		No. trials	Time	No. s.i. genes remaining	No. trials	Time	No. s.i. genes remaining
100	3	4	121.25± 6.49	2.75±0.25	19	6.00±1.58	3.0±0.0
	4	2	218.0 ± 0.00	3.0 ±0.0	10	4.30±1.09	3.0±0.0
	6	1	149.0	4.0	11	4.19±1.58	6.0±0.0
500	3	6	270.0 ± 52.93	2.83±0.17	6	4.83±1.66	3.0±0.0
	4	3	546.67±233.68	3.67±0.33	12	4.91±1.96	4.0±0.0
	6	1	369.0	4.0	11	20.19±8.45	6.0±0.0

proportion of incompatible pollinations to be expected under random mating is very large. That is, the more alleles there are in such a system, the more protection it has against breakdown of the system. This is to be expected a priori, but nonetheless may be part of the explanation of the very large numbers of alleles usually found in such systems. Finally, a result consistently obtained but not shown in the tables, is that genes which allow self-pollination can exist for a hundred or more generations once their frequency rises above a few percent, and in such cases they are almost invariably fixed.

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