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Quantitatively determined self-incompatibility

1. Theoretical considerations

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Summary. It has been reported that incomplete self-incompatibility could be determined in *Borago officinalis* by many genes. Simple ten-gene models for such enforced cross-fertilization have been developed and their properties examined by computer simulation. Mutation rates necessary to maintain a given level of variability in small populations are high, as already determined theoretically for oligogenic self-incompatibility systems. However, the extent of ineffective pollination is very much greater in the ten-gene system. This finding may be verifiable in borage if it is indeed self-incompatible.

Key words: Self-incompatibility – Simulation – Polygenes – *Borago officinalis*

Introduction

In 1971, Crowe reported that borage (*Borago officinalis* L.) had an outbreeding system which consisted of incompletely effective self-incompatibility determined by many genes. This was the first report of polygenically determined self-incompatibility, though up to four independent major genes have been claimed to be responsible for gametophytically determined self-incompatibility (Lundqvist et al. 1973; Østerbye 1975). It has proved very difficult to gain a complete understanding of these systems (Østerbye 1986).

While the population dynamics of both gametophytic and sporophytic systems have been extensively examined, there has been little work on the theory of a polygenic system, even though it has long been postulated that this might be the ancestral origin of all self-incompatibility systems (Bateman 1952; Østerbye 1975).

Accordingly, we are re-evaluating this type of system, both theoretically and also in borage (to be reported in a subsequent paper). Other complex systems are currently being re-examined by others (Warren et al. 1988).

We consider here some of the problems inherent in forming a satisfactory model and some of the outcomes of a particular model.

Model systems

The self-incompatibility systems determined by a few major genes have been extensively evaluated both theoretically and by simulation. While it is possible to develop a truncation model for polygenic self-incompatibility, i.e. a model whereby self-incompatibility is a threshold phenomenon, this obscures what will happen to the individual genes contributing to the phenotype. Accordingly, we have chosen to model a specific multigenic system, in the hope that general lessons may be drawn from its behaviour.

Table 1. Numbers of genes fixed in 20,000 generations in a population of size 100, with stringency $c = 0.1$ and mutation rate $\mu = 4.10^{-6}$. (Means of four replicates of each trial ± standard error)

Breakdown rate	No. of genes fixed	Proportion of incompatible pollinations
0.1	4.5 ± 0.4	0.35 ± 0.01
0.2	4.5 ± 0.5	0.31 ± 0.01
0.3	5.5 ± 0.5	0.31 ± 0.01
0.4	5.2 ± 0.5	0.27 ± 0.01
0.5	6.2 ± 0.5	0.24 ± 0.01

Table 2. Mutation rate necessary to maintain segregation of the diallelic genes

Population size	Stringency c	Breakdown rate	Proportion of incompatible pollination	Mutation rate ($\times 10^{-4}$)	No. trials
100	0.1	0.1	0.288±0.010	2.96±0.64	4
		0.2	0.259±0.010	3.08±0.64	4
		0.3	0.235±0.010	3.35±0.64	4
		0.4	0.216±0.010	3.37±0.64	4
		0.5	0.159±0.007	5.02±0.45	4
	0.25	0.1	0.661±0.009	0.00±0.26	5
		0.2	0.600±0.009	0.29±0.26	5
		0.3	0.538±0.009	0.26±0.26	5
		0.4	0.468±0.009	0.81±0.26	5
		0.5	0.400±0.007	1.83±0.18	5
250	0.1	0.1	0.278±0.005	0.010±0.118	4
		0.2	0.251±0.005	0.024±0.118	4
		0.3	0.214±0.005	0.084±0.118	4
		0.4	0.162±0.005	0.252±0.118	4
		0.5	0.163±0.004	0.157±0.083	4
	0.25	0.1	0.663±0.005	0±0	4
		0.2	0.593±0.005	0±0	4
		0.3	0.519±0.005	0±0	4
		0.4	0.457±0.005	0±0	4
		0.5	0.380±0.004	0±0	4

Table 3. Mutation rate necessary to maintain segregation of the diallelic genes with a sporophytic system

Population size	Stringency c	Breakdown rate	Proportion of incompatible pollination	Mutation rate ($\times 10^{-3}$)	No. trials
100	0.1	0.1	0.562±0.011	0.132±0.042	4
		0.2	0.507±0.015	0.212±0.060	4
		0.3	0.442±0.015	0.245±0.060	4
		0.4	0.385±0.015	0.334±0.060	4
		0.5	0.322±0.015	0.426±0.060	4
	0.25	0.1	0.703±0.201	0.036±0.004	4
		0.2	0.572±0.160	0.102±0.024	4
		0.3	0.460±0.003	0.197±0.143	4
		0.4	0.356±0.006	0.296±0.188	4
		0.5	0.277±0.004	0.348±0.122	4
250	0.1	0.1	0.534±0.005	0.000±0.011	4
		0.2	0.474±0.007	0.008±0.015	4
		0.3	0.435±0.007	0.006±0.015	4
		0.4	0.366±0.007	0.019±0.015	4
		0.5	0.309±0.007	0.048±0.015	4
	0.25	0.1	0.840±0.003	0.000±0.013	4
		0.2	0.743±0.004	0.000±0.019	4
		0.3	0.637±0.004	0.016±0.019	4
		0.4	0.571±0.004	0.041±0.019	4
		0.5	0.483±0.004	0.068±0.019	4

We have considered ten independent loci, limited to two alleles per locus, with complete additivity and with the probability of successful fertilization proportional to the genetical distance between the pollen and style, each organ contributing equally. That is, there are 21 possible stylar genotypes which may be assigned values $g_s = 0, 1, 2, \dots, 20$ and 11 possible pollen genotypes which may be assigned values $g_p = 0, 2, 4, \dots, 20$, i.e. pollen and style are made equal in contribution. Incompatibility then occurs if $(g_s - g_p)/20 < c$, where c can be chosen to represent

Table 4. Proportion of incompatible pollination in a population of 500 plants with gametophytic self-incompatibility. (The expectation is independent of population size)

No. of self-incompatibility loci	No. of alleles per locus	Proportion of incompatible pollinations	
		Observed	Expected
1	30	0.080	0.033
2	15	0.035	0.015
3	10	0.021	0.006

different degrees of stringency; that is, the least stringent condition is c = 0, where any pollination is effective, the most stringent being somewhat less than c = 0.5, at which point only one generation of the effective pollination would be possible. We have also allowed for varying proportions of system breakdown, whether on crossing or selfing. This appeared likely in the case of borage, given that complete self-sterility seems to be rare (Crowe 1971; Mayo, unpublished data). Tables 1 and 2 show the results of some of the trials.

A sporophytic system has also been considered. Here, g_s and g_p are determined equally, in the manner described for g_s in the gametophytic system. In this case, selfing is only possible when the system breaks down, whereas in the gametophytic system, selfing is possible without breakdown. Table 3 shows some of the results of these simulations.

Discussion

Table 4 shows results obtained for the well-established gametophytic systems by methods presented earlier (Mayo 1966, 1971). The theoretical expectations for the proportion of incompatible pollination are those of Lundqvist (1956). These values are extremely low compared with those reported above. Even if there were only three alleles at a single locus, only two-thirds of random pollinations would be expected to be ineffective, so that the very high values reported for the sporophytic multifactorial system seem abnormally high and those of the gametophytic multifactorial system also seem excessively high. However, in the work we are carrying out on borage, we found in one trial that seed set, which has a maximum of four seeds per flower, had a mean of 1.53 ± 0.18 in 68 outcrossed offspring of selfed individuals. This suggests that the results, although a priori improbable, are not inconsistent with the observations one can make. On the other hand, the simulation estimates of rates of mutation necessary to maintain a substantial amount of variation are not much different from those reported for the single locus gametophytic system (Mayo 1966). If population sizes are large, these rates will be irrelevant, as pointed out by Fisher (1958). More work is needed on the problem of population size.

Charlesworth (1988) has suggested that gametophytic systems are likely to be more unstable than sporophytic systems, on account of their inherently greater susceptibility to the spread and fixation of genes allowing self-fertilization. We have not modelled this contingency, but it should be noted that in our systems both the maintenance mutation rate and the equilibrial level of ineffective pollination are higher in the sporophytic system; hence, the gametophytic system appears more likely to persist. Which system is more likely to arise remains a matter for speculation. Dominance modification is the key process to consider and we have only examined a completely additive model.

We have also omitted linkage from our model. Mulcahy and Mulcahy (1983) have argued that there may be many loci involved in pollen-style interactions and the apparent gametophytic self-incompatibility is an artefact of the types of analyses which have been conducted. However, their widely criticised hypothesis was based on a supergene or gene cluster. While some properties of a very large number of alleles at one locus resemble those of a very large number of distinct loci (Penrose 1969), this is not generally the case, so that this postulated system is not relevant here. In any event, some of the predictions of this hypothesis, e.g. that mapping should not be possible if there is more than one self-incompatibility gene, are simply wrong (Leach and Hayman 1987). However, it is possible that one or more of the gametophytic self-incompatibility loci is a supergene, and it is also possible that some of the identified major genes may be linked, though there is no conclusive evidence for this speculation.

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