ARE THERE MORE THAN TWO SELF-INCOMPATIBILITY LOCI IN THE GRASSES?

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Received 18.viii.83

The genetic control of self-incompatibility has been investigated in a number of members of the Gramineae (table 1). The majority of these studies have revealed that the incompatibility system is controlled by two multi-allelic loci with gametophytic determination of pollen behaviour.

TABLE 1
Incompatibility systems identified in grass species

Species	Two locus system	Other system
<i>Secale cereale</i>	Lundqvist (1954, 1956)	
<i>Festuca pratensis</i>	Lundqvist (1955, 1961a)	
<i>Phalaris coerulescens</i>	Hayman (1956)	
<i>Hordeum bulbosum</i>	Lundqvist (1962)	
<i>Dactylis aschersoniana</i>	Lundqvist (1965)	
<i>Briza media</i>	Murray (1964)	
<i>B. spicata</i>		Murray (1979)
<i>Lolium perenne</i>	Cornish, Hayward & Lawrence (1979)	Hayward & Wright (1971) Spoor (1976) McCraw & Spoor (1983b)
<i>L. multiflorum</i>	Fearon, Hayward & Lawrence (1983)	Hay (1978) McCraw & Spoor (1983a)
<i>L. rigidum</i>		McCraw & Spoor (1983a)

Apart from the case (Murray, 1979) all exceptions have been found in *Lolium* species. However, despite claims to the contrary, careful examination of all these reports reveals that the data are not satisfactorily explained by considering three or even four loci though gametophytic determination of pollen behaviour has always been shown.

In a two locus system sixteen different types of progeny arise when the parents of a cross are heterozygous for different alleles at each locus, e.g., $S_{1.2}Z_{1.2} \times S_{3.4}Z_{3.4}$. With the exception of the families considered by Hayward and Wright (1971), all *Lolium* progenies described which gave results inconsistent with a two locus system had at least 17 different incompatibility types. Indeed, no progeny cited ever had two members with the same incompatibility genotypes as detected by the results of *in vitro* pollination tests (Lundqvist, 1961b).

A three locus system where the parents of the cross are heterozygous for different alleles at each locus, e.g., $S'_{1.2}S_{1.2}Z_{1.2} \times S'_{3.4}S_{3.4}Z_{3.4}$, leads to 64 different types of progeny. However, in a progeny of say, 28, the probability that all 28 will be of different genotypes is 9.1168×10^{-4} (Feller, 1957, vol. 1, p. 30).

The probabilities of obtaining all members of the progeny of different incompatibility status for the *Lolium* species in which a three locus system has been claimed are shown in table 2. Further, since all sets of observations are independent, the data may be grouped by species (table 3).

The same analysis can be applied to the data considering a four locus system which leads to a maximum of 256 different types of progeny and the probabilities are shown in tables 2 and 3.

TABLE 2

Likelihood of obtaining all members of a progeny of different incompatibility status under (a) a three locus system, (b) a four locus system

Author	Species	Family size	Probability (a)	(b)
Spoor (1976)	<i>L. perenne</i>	28	0.00091	0.2160
Hay (1978)	<i>L. multiflorum</i>	26	0.00266	0.2688
McCraw & Spoor (1983a)	<i>L. rigidum</i>	25	0.00436	0.2979
	<i>L. rigidum</i>	25	0.00436	0.2979
	<i>L. rigidum</i>	27	0.00158	0.2415
	<i>L. multiflorum</i>	27	0.00158	0.2415
	<i>L. multiflorum</i>	17	0.09676	0.5810
McCraw & Spoor (1983b)	<i>L. perenne</i>	23	0.01089	0.3611

The data from Hayward & Wright (1971) are not considered as no claim that a three locus model satisfied these results was made.

TABLE 3

Pooling the results for each Lolium species in table 2

		Total probability (a)	(b)
<i>L. perenne</i>	0.00091×0.01089	$= 9.90 \times 10^{-6}$	0.0780
<i>L. multiflorum</i>	$0.00266 \times 0.00158 \times 0.09676$	$= 4.07 \times 10^{-7}$	0.0377
<i>L. rigidum</i>	$0.00436 \times 0.00436 \times 0.00158$	$= 3.00 \times 10^{-8}$	0.0214

Thus, as only one of the reported families has a probability of more than 5 per cent of occurring under a three locus system, such a system does not provide a satisfactory explanation for the results. A four locus model seems acceptable for *L. perenne*. However, alternative explanations for these results being at variance with those of Cornish *et al.*, (1979) for *L. perenne* and Fearon *et al.*, (1983) for *L. multiflorum* would appear to lie in the way in which Spoor (1976), Hay (1978) and McCraw and Spoor (1983a and b) have interpreted the results of *in vitro* pollination tests. For example, McCraw and Spoor (1983b) described some "self-compatible" plants as follows: "More than half (11 out of 23) of the plants were self-compatible when pollinated *in vitro*. When these plants were allowed to self-pollinate *in vivo*, two seeds were produced by plant 5 while the other ten plants did not set any seed". If *in vitro* pollination tests scored by these workers gave misleading results about the true self-incompatibility status of these plants then the interpretation of all their *in vitro* tests must be regarded as problematic.

In addition McCraw and Spoor (1983*a*) present tables showing compatible pollinations in which, in some cases, plants which are reciprocally self-incompatible are classified as being different when they differ in only 2 or 3 of more than 90 pollination tests and in others, *e.g.*, fig. 4 (*loc. cit.*) where data in the diallel tables seem too meagre for any realistic conclusions to be drawn with respect to the similarity of the plants.

Thus a critical analysis of the conflicting results leads to acceptance of the accuracy of the results of Cornish *et al.*, (1979) for *L. perenne* and Fearon *et al.*, (1983) for *L. multiflorum* which indicate a two locus, multi-allelic gametophytic system of incompatibility in these species, especially as the results of their pollination tests are well substantiated by extensive data on seed set (Cornish *et al.*, 1980; Fearon *et al.*, 1983).

Acknowledgements. I would like to thank Dr O. Mayo for his help and encouragement in the preparation of this manuscript.

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