NOTES AND COMMENTS

THE GENETIC ORGANISATION OF POPULATIONS OF THE INBREEDING SPECIES *LOLIUM TEMULENTUM*

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1. Introduction

Natural populations of autogamous species are generally expected to be composed of a few completely homozygous lines, closely adapted to the environment in which they are found. The number of such lines will depend upon the heterogeneity of the environment, but is expected to be relatively small, with each line forming a sizeable fraction of the population (Stebbins, 1950). Occasional outcrossing between such lines will produce plants of varying degrees of heterozygosity in which subsequent fertilisation will be predominantly autogamous. Continuation of this process over generations will confer some capacity for the selection of newly adapted lines more suitable for the prevailing environment (Darlington and Mather, 1949).

Recent theoretical and experimental work has indicated that such inbreeding populations are organised with greater complexity to the extent that variation at the population level may be as great as in self-incompatible species (Kannenberg and Allard, 1967; Allard, Jain and Workman, 1968). The present experiment examines the variation in a series of populations of the supposedly inbreeding, annual species, *Lolium temulentum.*

2. Material and methods

Lolium temulentum has a widespread distribution over mid and southern Europe, North Africa and temperate Asia. The origin of the five populations examined is shown in table 1.

Table 1

Populations of Lolium temulentun

Population	Origin
1	Botanical garden, Rouen, France
2	Wild ecotype, Coimbra, Portugal
3	Botanical garden, Stuttgart, E. Germany
4	Wild ecotype, Bremen, Germany
5	Wild ecotype, Bisotoon, Iran

This annual species is naturally cleistogamous and, even though occasional entire anthers can be found exserted from florets, it is claimed that self-fertilisation will be procured from the remaining anthers (Beddows, 1931).

The material in the present experiment consisted of the second selfed generation progeny of twenty individuals from each of the populations. In obtaining this S_2 generation self-fertilisation of the parental and S_1 plants was ensured by enclosing the floral spikes in a glassine bag prior to anthesis. To provide the S_2 generation, five plants within each of the twenty progeny families of the S_1 generation were selfed, each genotype family could thus be identified by direct descent from parental plants of the original populations. Ten seeds of each of the available genotype families were sown in December 1969 in a randomised block layout in a heated glasshouse receiving supplementary lighting (18 h.). Data were recorded on germination and on a series of leaf and tiller characters at 25 and 36 days after sowing. When less than five plants had germinated within a family, that family was omitted from the analysis. This also necessitated a reduction in the number of parental plants assessed.

The analysis consisted of an orthodox hierarchical analysis of variance. The genotype families could be arranged in increasing levels of complexity to reveal differences between populations, between progeny families within populations, between genotypes within progeny families, and finally between individuals within each genotype family. The three major levels reveal differences between populations, heterogeneity of individuals within populations, and homo- or heterozygosity of these. The final item was used for testing the third level in the hierarchy.

3. Results and discussion

The analysis of variance of four characters, days to germination, rate of leaf and tiller production, and length of fifth leaf on the main tiller, are presented in table 2.

Table 2

Analysis of variance of the S_2 generation for four characters. (*Mean squares presented*)

	d.f.	Rate of germination	Rate of leaf production	Rate of tiller production	Length of fifth leaf
Between populations	4	197***	1·44***	4·10*	749***
Between progeny families within populations	88	20***	0·22***	1·46***	74***
Between genotypes within progeny families	233	7***	0·12***	0·41***	12***
Within genotypes	1532	2	0·02	0·07	5

* P = 0·05. *** P = 0·001.

For all characters the population item is significant, revealing the existence of differences between these five collections of *Lolium temulentum*. Ecological differentiation may well be expected in view of the great geographical separation of the sites of origin (*see* table 1).

The second and third levels of the analysis are also significant throughout, indicating that the populations are groups of heterogenous individuals some or all of which may be heterozygous for the loci controlling these quantitative characters (table 2).

A further indication of the extent of heterozygosity within each population may be obtained from a more detailed analysis of the variation exhibited by

each progeny family within a population. The significance of the between-genotype item within each such family indicates whether the parental plant in the original population from which it was derived, is segregating. Application of this analysis to the data for the two characters, length of fifth leaf and rate of tiller production, indicate that for each, the populations are a mixture of homozygotes and heterozygotes. The number of plants segregating within each population for either or both characters is shown in table 3.

These preliminary investigations reveal that populations of the supposedly self-fertilising *Lolium temulentum* contain a wealth of variability both of the " homozygotic and heterozygotic potential states " (Darlington and Mather, 1949). This variability belies the uniform appearance of such populations (coefficients of variation ranged in the parental populations from 6 per cent.

TABLE 3

Number of plants segregating in each population for leaf length and tiller production

Population	Segregating tiller	Segregating leaf	Leaf and tiller	Non-segregating
1	0	1	2	4
2	7	3	4	3
3	4	3	5	6
4	9	1	6	2
5	6	1	4	2

to 25 per cent. for the character number of days between sowing and ear emergence, compared with 48 per cent. in the outbreeding species *Lolium multiflorum* (Jackson, unpublished) and provides the capacity for adaptive changes to meet altered conditions of the environment. This situation is comparable to that described in barley by Allard and his co-workers (for review and further references see Allard *et al.*, 1968), but contrasts somewhat with the *Festuca microstachys* complex (Kannenberg and Allard, 1967) where populations are composed of a large number of distinct homozygotes, each genotype being represented by one or two individuals within the population. In populations of this latter species it would appear that variability is maintained to satisfy current requirements for survival without the capacity for adaptive change other than by chance outcrossing. It has been proposed that the population phenotype arises as a result of the integration and interaction of individuals, and not as a result of interactions at the chromosome or gene level (Kannenberg and Allard, *loc. cit.*). In the populations of *Lolium temulentum* examined here, however, the high frequency of heterozygotes (approximately 80 per cent. of the plants are segregating with respect to just one of the two characters examined) would suggest that interaction at the genic level is important, or, alternatively, a high degree of outcrossing occurs in this supposedly self-pollinating species. It may well be that this is a further example of the case described by Schutz and Usanis (1969), where a higher relative fitness of heterozygotes under a frequency-dependent competitive situation would maintain an excess of such heterozygotes in the population even where the degree of outcrossing is at a minimum. It does, however, emphasise the need for a closer examination of the breeding behaviour and genetic organisation of natural populations.

4. Summary

1. An examination of five populations of the inbreeding species *Lolium temulentum* by the assessment of the second selfed generation has revealed that there are population differences for the characters rate of germination, rate of leaf and tiller production, and length of fifth leaf.

2. Further analyses show that they are heterogenous collections of individuals which may be homozygous or heterozygous at the loci controlling these characters.

5. References

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