INTER-POPULATION VARIATION IN PERENNIAL RYEGRASS

2. POPULATION VARIANCE COEFFICIENTS

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1. INTRODUCTION

A NUMBER of authors have described results of genetic analysis of inter-population variation in *Lolium perenne* using diallel analyses of parental (intra-population) and F_1 (inter-population) family *means* of various seed, seedling and adult measurements (Fejer, 1958; Breese, 1960; Beddows, Breese and Lewis, 1963; Hayward and Breese, 1963, 1966; Thomas, 1965, 1967). So far, however, no attention has been focussed on effecting similar analyses on *variance statistics* from within diallel cross families—even though they may be analysed in the same manner as averages—an approach which has been usefully employed in diallel analysis of *inbred* lines where variances were regarded as stability measures for certain characters, see *e.g.* Jinks and Mather (1955), Paxman (1956) and Broadhurst and Jinks, 1966. It is somewhat uncertain whether the *coefficients of variation* from an inter-population diallel in the outbreeding species *Lolium perenne* when subjected to the analyses below might likewise be regarded as stability measures; this point is however, considered in some detail in the discussion.

The 6×6 diallel cross system from which these coefficients of variation were calculated has previously been described by Thomas *loc. cit.*, when analysis of population *means* was presented for the same seed and seedling characters considered here. Before continuing, it is deemed profitable to reiterate these conclusions and those of the authors, *loc. cit.*, concerned with this species. Briefly, they found that for the majority of the characters they analysed, the main genetic control over heritable variation of averages was attributable to general combining ability or additivity. However, in many cases (references underlined) reciprocal effects which were predominantly ascribable to average, or constant maternal effects were observed for a large proportion of the characters concerned. In some instances reciprocal effects were more important than genetic, particularly when early growth measurements were considered.

2. MATERIALS AND METHODS

The method of diallel cross construction, a description of the six populations utilised (the former notation of 1-6 will be adhered to again), the design and layout of the sowing and a description of the measurements taken has previously been given (Thomas, *loc. cit.*). Not all the characters previously analysed as averages are re-analysed here as coefficients of variation—

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a reduction to three characters representative of the kind and range of developmental measurements under consideration having been undertaken for ease of presentation. These characters are seed weight, third leaf area and tiller number at the sixth leaf stage. The coefficient of variation was chosen as a convenient variance statistic rather than the variance since it is less dependent on the average value—which was previously shown to differ from cross to cross.

Analysis of the diallel families was based on the calculated coefficients of variation from eight plants in each family within each of the four replicates. The four estimates for any one cross for seed weight do not, of course, constitute really valid replications since the expression of the character is determined prior to sowing. However, the procedure was not considered a serious objection for this character since Thomas (1965) indicated that similar results were obtained in analysis of population means, at least, whether estimates of random variation were calculated on the basis used here or by a more legitimate process.

3. RESULTS

The coefficients of variation for all combinations of crosses, for the three characters considered are shown in diallel table form in table 1; these are

TABLE 1

Diallel table of values for coefficients of variation. These are average values, × 1000, for coefficients from the four replicates. In each cross position, the top value is that for seed weight, the middle for third leaf area and the bottom for tiller number at the sixth leaf stage

	1	2	3	4	5	6
1	319	319	293	297	332	341
	264	328	228	183	292	239
	270	305	273	255	222	237
2	300	291	333	348	400	350
	334	276	436	284	317	367
	251	215	276	238	193	228
3	267	241	334	263	249	332
	167	301	305	256	159	275
	239	153	275	230	280	264
4	169	240	226	251	310	267
	207	246	314	292	310	290
	204	282	201	309	282	329
5	308	336	169	336	217	341
	218	334	252	239	226	277
	244	225	278	244	223	326
6	377	334	337	236	239	295
	225	378	332	358	212	246
	244	367	337	373	301	280

average values for coefficients from the four replicates. The genetic situation is investigated by means of the " Hayman " (1954) analysis of variance of diallel crosses. Here each main effect a, b, (sub-divided into b_1 b_2 and b_3), c and d, is tested against its particular interaction with replicates. It is clear that there is, in no case, evidence for either constant (c) or residual (d)

reciprocal differences attributable for instance, to maternal effects. All the heritable variation appears to be zygotic in origin since the a item indicating an average, or constant effect of each parent (usually referred to either as additivity or general combining ability) is significant in all three cases and the b item denoting residual zygotic effects (dominance/epistasis or specific combining ability) is also significant for seed weight and third leaf area. For these latter two characters we can examine the three sub-divided items of b-b_1, b_2, and b_3, to pinpoint the nature of this residual variation. In the two instances both b_2 and b_3 are significant indicating that, for some populations at least, " parental " and " F_1 " mean values are different, although since b_1 is non-significant there is no difference between the overall parental and progeny means. The significance of b_2 is usually taken to indicate asymmetrical gene distribution and b_3, " left over " non additive genetic variation

Thus the genetic situation is characterised by an absence of reciprocal effects and that average or constant zygotic effects are present for all three characters coupled with residual zygotic effects in the instance of seed weight and tiller number.

4. DISCUSSION

The form of genetic control over the coefficient of variation for these three characters is, for our present purposes, adequately described in the concluding remarks of the previous section. However, our main concern here lies with deciding whether this control over the limits of deviation from the average values of the crosses represents a control over stability or reflects some other aspect of the genetic system. As implied in the introduction no such difficulties would arise if the parental populations were homozygous inbred lines, but here we are dealing with outbreeding parental races. The crucial point is not, however, the nature of the breeding system, but whether our populations are homozygous with respect to the loci by which they differ for these three characters. If the former supposition is assumed to operate, we can safely consider that the form of control over stability has been established. If, however, the parental populations are presumed to be still heterozygous with respect to some of these loci, the genetic effects referred to above may only reflect differing degrees of parental heterozygosity in which case our discussion need go no further. Although our present experiment does not enable us to decide between these interpretations, nevertheless, we might more easily favour the former hypotheses since none of the authors concerned with this species and referred to in the introduction were able to demonstrate the existence of heterozygosity between populations for *mean* values of a number of characters and thus with respect to one another the parental groups could be regarded as homozygous for those characters considered. Although we need not necessarily extrapolate from this that our populations are relatively homozygous with respect to genes controlling the fluctuation around mean values, it would be more reasonable to accept this hypothesis than one diametrically opposed remembering that our populations here are widely separated climatic races. Indeed, further graphical analyses by the Wr/Vr methods of Jinks and Hayman, 1953, and Dickinson and Jinks, 1956, of the three characters considered here, although not included above, exhibit none of the configurations associated with heterozygosity. If we consequently are more prepared to favour parental homozygosity, we must obviously

accept that these coefficients represent estimates of stability and we can in this light examine our results in more detail.

The interpretation of the findings in terms of stability measures is relatively uncomplicated. There is clear evidence of genetic control for the three characters since in every instance at least one of the zygotic items entered in table 2, is significant and furthermore there is no evidence for any non-nuclear parental influences since the c and d items are always insignificant. This genetic control would appear to be entirely attributable to additive gene differences between parental populations (significance of a) for tiller number at the sixth leaf whereas in addition, dominance (b) is present for the remaining two characters. However, since in no case is the b_1 item significant

TABLE 2

Hayman (1954a) analysis of variance of diallel tables, for coefficients of variation

Item	D.F.	Seed weight M.S.	Third leaf arrea M.S.	Tiller number (at sixth leaf stage) M.S.
a	5	172*	353**	172**
b_1	1	48	22	1
b_2	5	129*	175*	68
b_3	9	151**	147*	103
b	15	131***	148**	84
c	5	119	139	88
d	10	68	49	65
B	3	73	114	15
Ba	15	42	51	26
Bb_1	3	58	40	2
Bb_2	15	41	48	38
Bb_3	27	37	64	55
Bb	45	38	57	46
Bc	15	64	61	61
Bd	30	51	81	54

it follows that there exists no overall differences between the " homozygous " parental lines and their " heterozygous " " F_1 ", although for seed weight and third leaf area the significance of both b_2 and b_3 does suggest some heterogeneity in this pattern. Thus, broadly speaking this finding is in agreement with those of Mather and Jinks, 1955; Paxman, 1956 and Broadhurst and Jinks, 1966, who also find no evidence of greater parental instability than appears in the " F_1 " in their inbred populations.

In studies of homeostasis a question often raised is whether there exists a general control over stability throughout the organism. This would, for instance, be reflected here in a correspondence of the genetic control over all three characters—a thesis which does not strike us as obviously tenable since although two of the characters have quite a similar control, this control differs in type for the third. Furthermore, in an analysis of co-variance for third leaf area and tiller number, removing the effect of seed weight made no real difference to either the conclusions reached above or indeed the actual variance ratios of table 2, (see Thomas, 1965). Lastly it may be added that the correlation between corresponding values for tiller number and leaf area from table 1 was negligible (r, 34, d.f. = 0·014). Mather, 1953, has pointed

out that " we should expect the levels of stability achieved in respect of different characters to vary with the selective properties of the characters " and thus accepting this dictum these findings of ours would not seem particularly surprising. It does nevertheless strike us as rather unusual that we have clearly demonstrated the absence of any extra nuclear population differences in stability whereas, as has been emphasised previously, reciprocal effects (usually maternal in origin) were often responsible for a proportion of the heritable variation of means in this species. Indeed, Beddows *et al.*, 1963, and Thomas, 1965, find that the mean values for seed weight is entirely under maternal control and Thomas *loc. cit.*, further demonstrates that third leaf area and tiller number is under both zygotic and maternal influence. It is furthermore valid to note that Thomas *loc. cit.*, suggested that his results represented reasonably good evidence that these maternal effects might be attributable to fixation of plasmagene effects such as those described by Breese *et al.*, 1966, who could find no other reasonable explanation for their obtained responses to artificial selection within a genotype—*i.e.* between clones. Thus, it might be suggested that maternal extra-nuclear effects allow change (as defined by Broadhurst and Jinks, 1966) in mean values although genotypic influences are also present and that when stability is at stake, a more rigid and entirely zygotic influence must be allowed. Although this line of conjecture might be profitable, it is somewhat hazardous to continue since further suppositions would imply a greater reliance on a real connection between the coefficients of variation and stability than our present experiment allows.

The concluding remarks will be confined to a belated justification of the use of the coefficient of variation rather than the variance in the above study. The main condition for the use of the former statistic is that it is more likely to be independent of the mean. This situation is satisfied since the results presented above are in marked contrast to those for means—Thomas *loc. cit.*, and secondly it might be remarked that analysis of variances gave almost identical results to analyses of means.

5. SUMMARY

1. Analyses of coefficients of variation from a diallel between six climatic races of *Lolium perenne* for three seed and seedling measures indicated that all were under genetic control; no non-nuclear influences were detected.

2. It was argued that these coefficients might very well represent a measure of stability of the three characters and the results were discussed in this light.

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