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Genetic analysis of production characters in *Lolium*

1. Triple test cross analysis of spaced plant performance

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Summary. The genetical control of heading date and dry matter production in an 'F2' population of *Lolium perenne* are presented from analyses of triple-test-crosses and basic generations. The data is derived from spaced plant trials at sites in the United Kingdom (UK) and Italy in different years. Despite the wide initial cross between UK bred material and an Italian accession, there was no significant evidence for epistasis, while additive and dominance variation were generally present with partial to complete dominance for all traits. Linear regression onto the environmental means accounted for all the G×E variation for dry matter production in the establishment and aftermath cuts, but not for heading date or the hay cut. The b values measuring responsiveness to the environment were clearly heritable and showed partial dominance. Predictions of the likely performance of recombinant inbred lines and second cycle hybrids were sufficiently promising to support further investigation of these approaches to breeding in this crop.

Key words: *Lolium* – F1 hybrids – Recombinant inbred lines – Triple test crosses – Genotype by environment interaction

Introduction

The synthetic variety has been the system of variety construction adopted for the majority of grasses, of which *Loliums* are the predominant species in temperate agriculture. Traditional breeding methods have involved phenotypic selection at the spaced plant level, polycross progeny, testing under simulated sward conditions, followed by the identification of superior clones for the establishment of a synthetic variety. In spite of the considerable effort that has gone into breeding along these lines, only a limited improvement in annual dry matter production has been achieved. In comparison with many other crops which have attained an increase of about 1% per annum in harvestable yield, ryegrass improvements, as measured by cutting trials, are only of the order of 0.2% for diploid cultivars (Hayward, unpublished). Greater success has been achieved in other objectives such as seasonal production and herbage quality.

Several reasons have been put forward to account for this limited improvement in annual yield, such as: spaced plant versus sward relationships (Lazenby and Rogers 1964), the low heritability of production characters and the intensity of selection (van Bogaert 1977; Hayward 1983). To overcome some of these problems alternative selection systems have been proposed such as the use of physiological selection criteria (Wilson 1976) or selection under competitive conditions (van Dijk and Winkelhorst 1978; Hayward and Vivero 1985).

To date such selection procedures have led to limited success at an experimental stage only. They are based on the premise that extensive genetic variation is present in the source material for all characters of interest and that those characters are directly correlated with sward performance. These novel approaches are still, however, based upon exploitation of the selected individuals through a synthetic variety.

The synthetic system of variety construction utilizes additive (and to a lesser extent dominance) and epistatic variation (Breese 1972) and is an ideal method for cross-pollinated species such as *Lolium*. It has several advantages in terms of population improvement as a means of recombining variation prior to further

cycles of selection (Wright 1974; Gallais 1977). This characteristic can, however, create problems in that it provides an avenue for the release of variation during generations of seed multiplication, with the further opportunity for selection and change in varietal performance to take place. Some recent studies in *Lolium perenne* have shown, for example, that even where selection has been intensively applied and a positive response achieved, there is still sufficient residual variation present for rapid loss of the desired trait to occur (Hayward and Abdullah 1985).

A further problem of the synthetic is that it is dependent on the identification of a number of superior individuals which will combine well together. It has been suggested that too few a number may lead to inbreeding depression, while too many will lower the overall performance (van Bogaert 1984).

In order to overcome these difficulties in ryegrass breeding and to more fully exploit the considerable variation which is known to exist within the species (Breese and Tyler 1986), it has been proposed that alternative systems of variety construction be adopted, namely F1 hybrids or recombinant inbred lines (Hayward 1985).

Techniques for the production of F1 hybrids in ryegrass have been hampered by a lack of effective pollination control mechanisms, although several attempts have been made using male sterility (Kobabe 1983) and the semihybrid system (Foster 1971). Earlier studies of the genetic organization of some natural populations of *Lolium perenne* showed an absence of the appropriate forms of gene action desirable for the production of F1 hybrids (Hayward and Breese 1968; Breese and Hayward 1972). More recently however, hybridization of geographically isolated and genetically very distinct populations has shown that considerable heterosis may be encountered (Hayward and McAdam 1983; Humphreys 1984; Wilkins 1985). The present series of investigations are aimed at gaining an understanding of the genetic basis of such heterosis and determining if it is a type which may only be utilized in hybrids or, as seems more likely from studies of this phenomenon, that it may eventually be captured in superior inbred lines (Jinks 1981).

The ability to produce recombinant inbred lines in ryegrass as an alternative system of variety synthesis requires the breakdown of the genetically controlled incompatibility system and the establishment of self fertility. It has long been known that inbred lines in ryegrass can be obtained by enforced selfing (Jenkin 1931; Utz and Oettler 1977) or by the possible transfer of self-fertility genes from the closely related self-compatible members of the genus (Nitzsche 1983). The production of such inbred lines offers the opportunity for overcoming some of the difficulties pertaining to the synthetic variety. The present series of experiments are aimed at assessing the optimum strategy for variety synthesis in ryegrass, as well as assessing some of the other difficulties of selection such as performance under spaced plant versus sward conditions, adaptation across seasons and sites and indirect selection criteria.

Materials and methods

Material

The material described in this paper derives from three different sources of *Lolium perenne,* the synthetic variety S24 and wild collections from the Po Valley in Northern Italy and from the Monmouthshire Moors in Wales. The S24 and Po Valley material are relatively short-lived, early flowering, hay types while the third is a longer-lived pasture type (Hayward and Breese 1968).

Three plants were chosen at random from both the S24 and Po Valley material and three sets of inter-population crosses set up reciprocally to produce derived populations D/E, F/G, H/I (Cornish 1979). A seventh population (P) was produced from the Monmouthshire Moors material.

Population F was chosen for detailed biometrical analysis, and the two parents P1 (Po Valley) and P2 (S24) together with one of their F1's (F 4) were used to produce a set of standard "basic generations" – ie. parents, F1, F2 and backcrosses – and also to provide the testers (pollen parents) for a "triple-test-cross" (TTC) mating design (Kearsey and Jinks 1968). The seed parents of the TTC were obtained not from selfing the F1 (F 4) but by intercrossing with another plant from the same population. They thus constituted a pseudo F2. Although neither parents were inbred, it was assumed that given their different origins and phenotype, there would be much more genetic variation between them than within them.

Some 35 'F2' were each split into 4 cloned replicates, one each for crossing to the three testers and the fourth to check on selfing rates. Selfs and crosses were produced independently in 1981, 1982 and 1983. In 1981 and 1982 the seed parents involved in crosses were all hand emasculated at Birmingham. It was not possible to obtain sufficient seed of all the necessary "basic generations" in 1981 or 1982, so only TTC seed was used. Moreover, only those families for which there were 100 or more seeds were grown. Since tests of selfing rate among the seed parents proved very low ($< 0.5\%$), subsequent seed was produced in pollen proof isolation chambers without emasculation at the Welsh Plant Breeding Station (WPBS). This facilitated the production of larger quantities of seed both from crosses and from selfs, so that TTC and "basic generation" seed was available for the 1984 trials.

Seven separate trials are reported, three of which derived from seed produced in 1981 and 1982 and do not include the "basic generations" while the other four contain all material. Four control varieties (S24, Premo, Mantilla and Cropper) were also raised in every trial. Six of these trials were located in the UK – Birmingham 1982, 1983 & 1984 (B82; B83; B84); Aberystwyth 1982 & 1984 (A82; A84); Edinburgh 1984 (E84) – while the seventh was in Perugia, Italy in 1984 (P84).

In all trials every family was represented by five plants with complete individual randomisation in a single block from the date of sowing. Seed for all trials was sown in early spring in glasshouses, and transplanted to the field at 60 cm spacings in early summer in each year.

Table 1. Skeleton anovars for TTC's over n trials

Item	df	Expected mean squares
Epistasis		
CF	1	$\sigma^2 + 30\ \sigma^2_{EP.E} + 30n\ \sigma^2_{EP} + 390n\ k^2_{EP}$
Environ (E)	n−1	$\sigma^2 + 30\ \sigma^2_{EP.E} + 390\ \sigma^2_{E(EP)}$
Genotype (EP)	12	$\sigma^2 + 30\ \sigma^2_{EP.E} + 30n\ \sigma^2_{EP}$
EP×E	12(n−1)	$\sigma^2 + 30\ \sigma^2_{EP.E}$
Error[a]	156n	σ^2
Additive		
Environ (E)	n−1	$\sigma^2_W + 10\ \sigma^2_{AE} + 240\ \sigma^2_{E(A)}$
Genotype (A)	23	$\sigma^2_W + 10\ \sigma^2_{AE} + 10n\ \sigma^2_A$
A×E	23(n−1)	$\sigma^2_W + 10\ \sigma^2_{AE}$
Error[a]	192n	σ^2_W
Dominance		
CF	1	$\sigma^2_W + 10\ \sigma^2_{DE} + 10n\ \sigma^2_D + 120n\ k^2_D$
Environ (E)	n−1	$\sigma^2_W + 10\ \sigma^2_{DE} + 240\sigma^2_{E(D)}$
Genotype (D)	23	$\sigma^2_W + 10\ \sigma^2_{DE} + 10n\ \sigma^2_D$
D×E	23(n−1)	$\sigma^2_W + 10\ \sigma^2_{DE}$
Error[a]	192n	σ^2_W

$\sigma^2_A = \frac{1}{8}$ D: $\sigma^2_D = \frac{1}{8}$ H: $\sigma^2_W = \frac{1}{8}$ D + $\frac{1}{8}$ H + E

[a] Actual number may be less due to loss of plants

The following production characters were scored on all individuals:

HD Heading date in days – March 1st = day 1
ECDW Establishment cut dry weight in gm. (Total of 2 cuts in some trials).
HCDW Dry weight of the hay cut 21 days post ear-emergence.
ACDW Dry weight at the aftermath cut(s).

After the last plant was scored for HCDW, all plants were cut back so that the subsequent ACDW scores represent regrowth over a fixed period of time. Although attempts were made to record ECDW and ACDW at comparable times over all trials, this was seldom possible.

Analytical methods

Triple-test-cross. Attempts to produce every family (3×35) in all seven TTC's, were not successful. The analyses presented are confined to those families represented in all seven trials, namely those derived from 24 'F2's crossed to P1 and P2 and a subset of 13 crossed to the F1; a total of 61 families. Although originally all families contained five plants a few were subsequently lost. The means (and within family variances) of all families in every trial were calculated and all subsequent analyses on these families are based on these means.

The analyses of variance follow the procedure described by Kearsey and Jinks (1968) and their form are indicated in Table 1, together with the genetical expectations of the items. Because a pseudo 'F2' was used, estimates of D and H will be over – and under – estimated, respectively, due to segregation at loci for which the parents do not differ (Kearsey and Jinks 1968).

Table 2. Mean performance of TTC and control families in each trial for the four production traits. (See text for definition and units of traits)

Trait	Year scored	Site			
		B'ham	Aber	Edin	Per
(a) TTC					
HD	1983	68.3	66.0	–	–
	1984	61.2	58.9[a]	–	–
	1985	74.7	71.3	68.7	49.5
ECDW	1982	119.8	91.7	–	–
	1983	56.2	–	–	–
	1984	48.2	27.9	55.9	168.2
HCDW	1983	122.8	92.2	–	–
	1984	73.5	40.3[a]	–	–
	1985	40.4	70.2	–	140.1
ACDW	1983	15.5	14.7	–	–
	1984	–	–	–	–
	1985	17.2	36.8	–	–
(b) Controls					
HD	1983	83.2	78.1	–	–
	1984	69.1	65.0[a]	–	–
	1985	83.7	80.9	77.9	56.9
ECDW	1982	197.8	140.3	–	–
	1983	72.5	–	–	–
	1984	85.5	55.1	126.6	245.1
HCDW	1983	187.5	143.0	–	–
	1984	93.6	39.2[a]	–	–
	1985	76.6	108.1	–	154.0
ACDW	1983	30.1	21.6	–	–
	1984	–	–	–	–
	1985	29.0	62.2	–	–

[a] Score for A82 in second harvest year

Basic generations. The eight basic generations appeared in all four 1984 experiments. Data were tested for differences between generations and environments by standard two-way anovar. Models involving m, [d], [h], [i], [j], [l], [dm] and [hm] (Cavalli 1952; Mather and Jinks 1982) were fitted to the means of each trial by weighted least squares. For those traits for which there was no G×E interaction, models were also fitted to the overall means of the trials. The simplest model to account for the observed variation was accepted.

Results

Analysis of mean performance: environmental differences

There were large and significant differences in performance over the various sites and years for both TTC families and controls (Table 2). The plants at Aberystwyth consistently headed earlier than those in Birmingham by two to three days while those in Edinburgh and particularly Perugia were earlier still. With the exception of HCDW in 1985 and it's subsequent ACDW, the dry matter yields in both establishment

Table 3. TTC anovars for epistasis

Item	HD		ECDW		HCDW		ACDW	
	df	MS	df	MS	df	MS	df	MS
CF	1	62.6	1	444.0	1	1,035.0	1	549.1*
Envir (E)	7	30.3	6	1,050.2	6	3,899.4**	3	188.8
Geno (EP)	12	28.2	12	1,482.7	12	657.5	12	67.0
EP×E	84	23.3	72	2,175.2*	72	772.7	36	83.3
Error	1,205	24.9	1,076	1,592.6	1,045	1,144.3	532	95.9

* <5%; ** <1%

Table 4. TTC anovars for additive and non-additive variation

Item	HD		ECDW		HCDW		ACDW	
	df	MS	df	MS	df	MS	df	MS
Additive								
Envir (E)	7	15,363.0***	6	574,197.7**	6	352,589.5***	3	26,549.0**
Geno (A)	23	174.3**	23	8,057.6***	23	4,803.6***	23	183.5
A×E	161	35.2**	138	2,684.7***	138	1,330.7***	69	167.8**
Dominance								
CF	1	17,252.5**	1	221.1	1	191,027.6**	1	17,526.1***
Envir (E)	7	182.5**	6	10,394.0***	6	9,222.5***	3	808.3***
Geno (D)	23	88.9**	23	3,391.7*	23	2,328.1**	23	203.4
D×E	161	27.7**	138	1,877.7	138	1,194.8	69	171.1**
Error	1,475	23.8	1,328	1,722.9	1,278	999.3	658	95.6

* <5%; ** <1%; *** <0.1%

and hay cuts were higher in Birmingham than Aberystwyth, while for the one year that we have data for all four sites, Perugia had the highest yield followed by Edinburgh. There was remarkable consistency between ECDW and HCDW for all trials apart from the exception above. Differences between sites within years were greater than those between years within sites for HD and ECDW, though this was largely due to the inclusion of the extreme site, Perugia. These effects did not appear for HCDW and ACDW.

Analysis of mean performance: genetical differences

The analyses of variance combined over all sites and years (environments) (Table 3) showed little evidence for the presence of epistasis, apart from 'G×E' for ECDW and 'environments' for HCDW and the CF (i type epistasis) for ACDW. No other item in the four analyses attained significance while variance ratios were often less than unity. Of the analyses carried out on each separate environment, the only significant epistatic items were one CF for HD in Edinburgh in 1984 and CF's for HCDW and ACDW in Birmingham in 1983. Since only three items out of 52 were significant, we can conclude that epistasis was not a major factor for any of the traits.

The analyses of additive and non-additive effects combined over trials are shown in Table 4. There are highly significant 'genotype' and 'genotype by environment' items for additive effects for all traits apart from ACDW. The non-additive effects, which, in the absence of epistasis we can take to be dominance, are also significant for all traits (see 'genotypes' item) apart from ACDW. They also depend on the environment in each case, while HD and ACDW display G×E interaction. The significant CF for dominance in the analyses of HD and HCDW data reflects the fact that the progeny of P1 (Po Valley) headed about three days earlier and had a lower yield than those of S24.

Estimates of components (Table 5) show that the G×E items were as large or larger than the genotype effects for all traits. The dominance ratios allowing for this interaction were moderate. They were generally less than unity, though ACDW attained a value of 1.45. Broad heritabilities were all less than 30%.

When analyses were carried out on each separate trial, we found that additive and dominance effects were significant for 5 and 3 sets for HD, 4 and 1 for

ECDW, 5 and 2 for HCDW, and 3 and 2 for ACDW. The average values of the genetic parameters proved to be:

	$\sqrt{H/D}$	h_b^2	h_n^2
HD	0.67	0.39	0.32
ECDW	0.44	0.34	0.29
HCDW	0.51	0.32	0.26
ACDW	0.93	0.31	0.21

Clearly, the removal of the effects of G×E had increased the estimates of heritability.

Genotype environment interaction

The extensive genotype environment interaction was further examined by analysing the responsiveness of families to the different environments. The mean for each character in every environment was calculated by averaging over all crosses to P1 and P2. These values (Table 2 a) were taken as the environmental means. The linear regression of family mean onto environmental mean (bi) and the 'Remainder' MS from the regression anovar (MSi) – where i = 1 to 61 – were calculated for all 61 families (24 each from L1 and L2, and 13 from L3). These bi values were then used as data for the standard TTC anovar, the results of such an analysis being shown in Table 6. This effectively amounts to a repartition of the 'environment' and 'families × environments' SS of Tables 3 and 4.

Again there was little evidence of epistasis with the notable exception of ECDW: no other items approach significance. In regard to the main additive and dominance effects, it would appear that the G×E had been satisfactorily removed by the linear regression for ECDW and ACDW as the 'Remainder' MS's were not significant; indeed they were marginally smaller than the variance within families. Both of these traits had highly significant additive and non-additive variation for the b values, although for the reasons mentioned above this may be partly attributed to epistasis for ECDW. In the case of the remaining traits, HD and HCDW, the 'Remainder' MS's had values similar to the G×E MS's in Table 4, and the linear regression approach failed to explain the interaction. Nonetheless, there was residual additive variation for the b's for HD.

There was a difference between the average b's of families derived from P1 and P2 (L1, L2): for ECDW and HCDW bL1 > bL2, while for ACDW it was reversed. Thus for ECDW and HCDW, P2 (S24) appeared to be providing genes for high mean performance and low responsiveness.

Table 5. Estimates of genetical components from the TTC analyses over all environments (see Table 1 for explanation of σ^2)

Item	HD	ECDW	HCDW	ACDW
$\sigma^2_{E(A)}$	63.87	2,381.30	1,463.58	109.92
σ^2_A	1.74	76.76	49.61	0.39
σ^2_{AE}	1.14	96.18	33.14	7.22
$\sigma^2_{E(D)}$	0.65	35.48	33.45	2.66
σ^2_D	0.77	21.63	16.19	0.81
σ^2_{DE}	0.39	15.48	19.55	7.55
σ^2_W	23.8	1,722.9	999.3	95.6
D	13.9	614.0	396.9	3.1
H	6.2	173.0	129.5	6.5
E	21.3	1,624.5	933.5	94.4
$\sqrt{H/D}$	0.67	0.53	0.57	1.45
h_b^2	0.29	0.18	0.20	0.03
h_n^2	0.23	0.16	0.17	0.02

Correlations

Between sites. The consistency of performance of families across environments has been examined by means of the product moment correlation. For this purpose, we have used the 24 L1 + L2 values in every environment and hence we are looking at additive genetic correlations across environments. They are shown in Table 7 together with the corresponding correlations onto the mean values over all environments. With 22 df, these correlations must be greater than 0.4 to achieve significance.

Of the 76 correlations between sites, all but 7 are positive: of the remainder, half are significantly different from zero. It is of interest to ask if the differences between the 28 correlations in Table 7 are real or due to chance sampling. Since a non-zero correlation is expected, these correlations must first be transformed to z (where $z = 0.5[\log_e(1+r) - \log_e(1-r)]$) which has a theoretical variance $\sigma_z^2 = 1/(n-3)$ (where n = the number of items correlated: 24 in this case) (Fisher 1944). Thus we can combine the correlation coefficients using z to estimate the mean r, and calculate the observed variance of s_z^2. If the variation in r is due solely to chance, then $\varepsilon s_z^2 = \sigma_z^2$, and we can test this as a χ^2 ($\chi^2 = s_z^2(k-1)/\sigma_z^2$ where k is the number of correlation coefficients). HD had a mean r = 0.36 over the 28 pairs of environments and a chi-square index of dispersion test shows the 28 r's to be significantly heterogeneous ($P = 0.047$). Inspection of the correlations clearly shows those involving Perugia to be much smaller than the rest. Removing these leaves 21 correlations between UK sites which are homogeneous ($P = 0.90$) with a

Table 6. TTC anovars of b values measuring linear responsiveness over environments

Item	HD		ECDW		HCDW		ACDW	
	df	MS	df	MS	df	MS	df	MS
Additive	23	59.7**	23	6,093.7**	23	1,567.5	23	301.7**
Dominance CF	1	4.8	1	36,287.0**	1	4,579.3	1	1,843.0*
Dominance	23	30.4	23	5,414.8**	23	1,789.6	23	360.5**
Remainder	288	32.4**	240	1,629.3	240	1,340.9**	96	94.8
Within fams	1,475	23.8	1,328	1,722.9	1,278	999.3	658	95.6
Epistasis CF	1	0.1	1	107.7	1	81.1	1	105.1
Epistasis	12	17.9	12	4,760.2**	12	704.3	12	115.6
Remainder	234	30.6	195	1,856.1	195	1,399.1	78	98.6
Within fams	1,205	24.9	1,076	1,592.6	1,045	1,144.3	532	95.9

* $<5\%$; ** $<1\%$

Table 7. Additive genetic correlations between trials 1–8 (correlations >0.4 are significant at 5%); (i), (ii) refer to 1st and 2nd harvest year for A82

	Trials							
	B82 1	B83 2	B84 3	A82 (i) 4	A84 5	E84 6	P84 7	A82 (ii) 8
HD								
2	0.50							
3	0.29	0.29						
4	0.55	0.63	0.59					
5	0.63	0.44	0.27	0.55				
6	0.49	0.18	0.49	0.48	0.35			
7	0.26	0.30	0.04	0.19	0.13	−0.10		
8	0.48	0.32	0.27	0.60	0.50	0.23	−0.20	
Pooled	0.81	0.70	0.61	0.87	0.71	0.58	0.39	0.54
ECDW								
2	0.29							
3	0.60	0.53						
4	0.42	0.49	0.34					
5	0.51	0.31	0.37	0.59				
6	0.14	−0.20	0.15	0.15	0.03			
7	0.31	0.18	0.55	0.23	0.16	0.29		
Pooled	0.77	0.46	0.81	0.58	0.52	0.36	0.77	
HCDW								
2	0.71							
3	0.08	0.29						
4	0.53	0.40	0.31					
5	0.15	0.11	0.28	0.36				
6	–	–	–	–	–			
7	0.42	0.43	0.13	0.28	−0.17	–		
8	0.20	0.07	−0.08	0.41	0.31	–	0.24	
Pooled	0.81	0.73	0.42	0.81	0.47	–	0.54	0.43
ACDW								
2	–							
3	0.22	–						
4	−0.23	–	0.05					
5	−0.30	–	0.06	0.53				
Pooled	0.26	–	0.57	0.53	0.74	–	–	–

mean r = 0.48. There is no evidence that the inter-site correlations differ. The other three traits all have homogeneous correlations:

Trait	r	Probability of homogeneity
ECDW	0.32	0.40
HCDW	0.27	0.37
ACDW	0.06	0.88

In the cases of HD and HCDW we have scored exactly the same plants in two successive years (A82), while the remaining data involve the progeny of repeat crosses raised in different sites. Their correlations at 0.60 and 0.41 respectively were only slightly higher than average.

The additive genetic correlations between the performance at each site and the overall performance over all sites were generally high for all traits, particularly among the UK sites (Table 7).

Between mean performance and responsiveness. The correlations between the average values of L1 + L2 over all environments and their b values are shown for each trait in Table 8. These proved to be surprisingly large, positive and significant: 0.81 for ECDW, somewhat less for HCDW (0.54) and ACDW (0.52). Though still positive, that for HD (0.23) is not significant. These indicate positive correlations between mean performance and responsiveness.

Between traits. After averaging L1 + L2 over environments, the correlations between traits for means and b's are as shown in Table 8. None of the correlations between the b's achieve significance, though that between HCDW and ECDW (0.38) approaches it. Among the correlations on the means, those involving HCDW with ECDW were large, positive and highly significant.

Basic generations

The simplest genetic models to fit the means of the basic generations in the 1984 trials are given in Table 9. As there was no interaction between generations and sites for HCDW and ACDW, models are also given for the data pooled over sites.

There was no evidence of epistasis for any trait, although it was not possible to find an appropriate model for HD for Perugia. This was mainly due to both F1 and F2 means showing heterosis, but in opposite directions. Since Po Valley was P1, negative [d] indicates that Po Valley flowered earlier and yielded less than S24. Dominance was for early flowering and high yield and there was heterosis for yield in most cases. In two cases (HD-A84 and ECDW-84) there was evidence for a maternal effect associated with an F1 mother.

Discussion

This initial series of experiments has provided information on the relative importance of the differing forms of gene action and environmental effects responsible for the variation which may be generated from a cross of two distinct lines of *Lolium perenne*. Unlike earlier studies to determine the genetic control of variation in *Lolium* (Fejer 1958; Cooper 1959; Cooper and Edwards 1961; Hayward 1967; Thomas 1967; Hayward

Table 8. Additive genetic correlations

i) Correlations between means and b's:

HD	ECDW	HCDW	ACDW
0.23	0.81	0.54	0.52

ii) Correlations between traits:

a) Means

	HD	ECDW	HCDW
ECDW	−0.10		
HCDW	0.12	0.60	
ACDW	0.16	0.17	0.61

b) b's

	HD	ECDW	HCDW
ECDW	−0.03		
HCDW	0.08	0.38	
ACDW	0.12	−0.29	−0.14

Table 9. Estimates of first degree parameters fitted to basic generations and tests of models

	m	[d]	[h]	[hm]	χ^2	P (%)
HD						
B84	73.77	−4.81	–	–	4.37	63
A84	70.17	−2.85	−5.23	3.49	6.90	14
E84	66.87	–	–	–	8.91	26
P84	no model will fit					
ECDW						
B84	26.82	–	55.70	–	5.44	49
A84	20.77	–	19.77	–	3.80	70
E84	58.74	−28.30	40.14	−36.35	6.93	14
P84	167.35	–	–	–	10.88	14
HCDW						
B84	45.36	−30.30	–	–	5.50	48
A84	61.27	−33.09	27.40	–	10.54	6
P84	152.77	–	–	–	2.30	94
Pooled	90.31	−21.49	–	–	6.20	40
ACDW						
B84	20.85	–	–	–	5.28	51
A84	30.06	−17.47	21.55	–	7.78	17
Pooled	19.64	−17.05	18.74	–	8.80	7

and Breese 1968; Hayward and Lawrence 1970), this analysis was used to gain an understanding of what new combinations of genes may be derived from this cross, and utilized either as recombinant inbred lines or second generation F1 hybrids. Furthermore, the analysis provides information on the performance of these lines over a range of environmental conditions, the efficiency of selection and the interrelationship of characters.

The analyses of the TTC and basic generations all support a basically simple model of the genetical control of the four traits. For both sets of characters – the timing of inflorescence emergence and productivity at the various growth stages – differences between the parental lines were due to genes showing mainly additive and dominance effects with no evidence of epistasis.

Dominance was for early heading and high dry-matter production, though despite heterosis for dry matter production in many trials, dominance ratios were generally less than unity. In this cross, therefore, it seems likely that heterosis was due to dispersed dominant genes, though the use of a 'pseudo F2' in the TTC would result in dominance being underestimated.

In contrast to the studies mentioned earlier where dominance was generally absent, its occurrence in the present material may be accounted for by the origin of the parents. Considerable genetic diversity has been shown to exist between ecotypes of *Lolium perenne* of North Italian provenance and natural populations and cultivars from Northern Europe (Hayward 1985; Humphreys 1984). Clearly attendant with this differentiation has been the accumulation of dominant genes as a result of the differing directional selective forces which have operated upon the populations. This is especially true in the bred cultivar S24 in which selection for productivity has been shown by Breese (1960) to have led to directional dominance for high yield.

Broad heritabilities on an individual plant basis were low – ranging from 0.03 for ACDW to 0.29 for HD – when estimated from the overall analysis. The average values within any one trial were higher, particularly for ACDW (0.31), reflecting the considerable variability both within and between trials.

The variability in responsiveness over trials appears to be largely predictable for ECDW and ACDW, being almost entirely genetically determined and involving varying linear responses to the environmental means. These linear responses are under the control of genes which show predominantly additive and dominance variation, though there is some evidence for significant epistasis for ECDW. The other two traits (HD and HCDW, i.e. characters measured at a fixed physiological stage), show little reduction of their G×E following the application of linear models to the environmental means, though there are significant additive and dominance components associated with their responses. This pattern of control is in contrast to that established by Hill and Samuel (1971) for a diallel cross in *Lolium perenne* where, for comparable yield determinations, the response was under the control of additive genes only. The occurrence of dominance in the present experiment may again reflect the genetic diversity of the parental lots.

The large and positive correlations between the mean values and linear responsiveness in the TTC (L1 + L2), particularly for DW (Table 8i), suggests that both characters are under the control of the same sets of genes or the genes are closely linked. It may be difficult to manipulate them independently though it does imply that further improvements in productivity could be achieved by selection for either of these characteristics. The positive correlation between both the ECDW and HCDW means and b values and their negative or non-significant correlations with ACDW parameters would indicate that it may be possible to select genotypes which are stable or responsive for at least two of the production traits, though it may prove difficult for all three.

Correlations between mean performance of L1 + L2 over sites and years are generally low (Table 7), though as was shown earlier these correlations are homogeneous for each trait. These low correlations also hold true for the same plants scored at the same site in two successive years A82(i), (ii). The average values of these correlations given earlier are as expected given the low heritabilities. The maximum value of an inter-trial correlation for (L1 + L2) is given by:

$$\sigma_A^2/(\sigma_A^2 + 1/k\,\sigma_w^2)$$

Table 10. Predictions of the proportion of recombinant inbred lines and second cycle hybrids likely to exceed the mean of the 4 controls

		Inbreds %	F1's %
HD	B84	0.23	0.17
	A84	0.23	0.002
	E84	0.13	0.014
ECDW	B84	4.60	12.92
	A84	0.003	0.003
	E84	0.079	0.085
	P84	6.68	2.94
HCDW	B84	6.30	3.92
	A84	1.88	2.33
ACDW	B84	10.57	5.48
	A84	0.45	2.74

Using the values shown in Table 5 and for k = 10 (2 families of size 5), the following maximum correlations are obtained:

HD = 0.42; ECDW = 0.31; HCDW = 0.33; ACDW = 0.04

These clearly match those observed (0.42, 0.32, 0.27, 0.06) very closely. In fact, to increase the correlation for HD to 0.9 would require k = 123, or families of size 62 rather than of size 5 as used here.

The predictions of the proportions of recombinant inbred lines and F1's likely to outperform the controls (Table 10) are variable, though suggesting reasonable frequencies (> 1%) in many cases for DW. The F1's do not appear to have any advantage in this respect over the inbreds, but this may be due to our underestimation of the dominance. Both approaches to variety synthesis would seem a very practical possibility for all three production traits, but would depend upon having the necessary control of the reproductive systems (Hayward 1985). These predictions also assume that spaced plant performance is a reliable guide to sward performance.

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