SELECTION AND POPULATION STRUCTURE IN *LOLIUM*

II. GENETIC CONTROL OF DATE OF EAR EMERGENCE

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Received 14.xi.58

1. INTRODUCTION

A COMPARATIVE study of the heading behaviour of three contrasting ryegrass strains, Wimmera, Irish and Kent (Cooper, 1959) showed that in addition to the broad differences between the strains, appreciable genetic variation occurred between plants within each strain. These differences in heading behaviour could be traced to genetic differences in both "winter requirement" for short-day or cold before floral induction, and also the need for long photoperiods for floral initiation. Previous studies in the outbreeding species of *Lolium* (Cooper, 1954) had shown that both these responses were under polygenic control, and that most parents were heterozygous for genes controlling flowering responses.

In selecting for any character, two parameters are important; firstly, the amount of genetic variation in the population, and secondly, the precision with which it is transmitted, *i.e.* the heritability. These together give a measure of the possible rate of change under selection, since the expected genetic gain is the product of the heritability and the selection differential.

The present paper attempts to estimate the genetic variation in date of ear emergence within two perennial ryegrass populations, Irish and Kent, to calculate its heritability and hence to predict the potential advance under selection. The genetic control of the "winter requirement" for floral induction has also been studied and will be reported later.

The genetic variation has been assessed in two ways; firstly, from the analysis of replicated clones, both within and between years, providing an estimate of the environmental and the *total* genetic variation; and secondly, by the regression of progeny means on mid-parent values, thus distinguishing the *additive* portion of the genetic variance, *i.e.* that part which is fixable by selection. In Mather's notation (Mather, 1949), this total genetic variance of the population can be denoted by $\frac{1}{2}D + \frac{1}{4}H$, where D is the additive portion due to differences between alleles at the same locus, and H is that due to dominance.

2. ANALYSIS OF REPLICATED CLONES

For a character such as ear emergence, where the initial size of the plantlet is not critical, a separation of environmental and *total* genetic variation is readily obtained by the use of clonal replicates. A number of clones of Irish and Kent ryegrass were therefore planted out in replicated blocks in the field in the autumn of 1954, 1955 and 1956, and the date of ear emergence was recorded for each plant the following spring. The exact dates of planting are given in table 1.

TABLE 1
Sowing and planting dates of seedlings and clones

Year recorded	Seedlings		Clones planted
	Sown	Planted	
1954	28 Aug. 53	29 Sept. 53	...
1955	23 Aug. 54	12 Oct. 54	18 Oct. 54 *
1956	13 Aug. 55	13 Oct. 55	13 Oct. 55
1957	13 Aug. 56	25 Oct. 56	16 Nov. 56

* In pots outdoors.

(a) *Within years*

The components of variation due to genotype, block and error (including block-genotype interaction) were assessed within each year as shown in table 2. In 1955, only two replicates of each genotype were available and these were randomised within one block, so block differences cannot be calculated for that year. The 1956 and 1957 material also included clones derived from single crosses and selfings within the original populations. The results for these clones are given separately.

Over the three years, the error variance of a single spaced plant varied from 1.25 to 4.58 days, and this is of the same order as found earlier for homozygous lines of *Lolium temulentum* (Cooper, 1954). There were no regular differences between Irish and Kent, or between the original population plants and the progeny derived from them by pair-crossing or selfing. The variation due to blocks was very low, and by far the greatest portion of the variation within the strains was genetic. The proportion of the total variation attributable to genetic differences between clones, giving a measure of heritability in the broad sense is above 0.85 in all cases. The genetic variance of the groups from pair-crosses and selfings is higher than that of the original populations, since these groups included plants deliberately selected for extremely early and extremely late ear emergence.

TABLE 2
Date of ear emergence: Partition of variation from replicated clones 1955-57

	Irish							Kent						
	Mean	V _g	V _b	V _e	V _t	V _g /V _t	Number of Clones	Mean	V _g	V _b	V _e	V _t	V _g /V _t	Number of Clones
1955 Original population	11.4 May	72.87	...	2.75	75.62	0.964	24	27.6 May	37.98	...	1.25	39.23	0.968	16
1956 Original population	10.9 May	27.91	0.35	2.86	31.22	0.894	24	25.6 May	66.00	0.60	3.02	69.62	0.948	15
Crosses . . .	12.7 May	58.06	0.25	2.23	60.54	0.959	16	25.9 May	160.08	0.47	2.86	163.41	0.979	14
Selfings . . .	12.9 May	62.89	0.13	3.88	66.90	0.940	15	1.7 June	149.42	0.16	3.36	152.94	0.977	8
1957 Original population	1.9 May	28.09	0.12	4.25	32.46	0.865	38	24.9 May	89.60	-0.04	2.93	92.49	0.969	34
Crosses . . .	6.9 May	111.93	0.86	4.58	117.37	0.945	8	23.6 May	203.18	0.08	3.12	206.38	0.984	15
Selfings . . .	4.5 May	95.56	0.25	3.31	99.12	0.954	9	2.6 June	204.75	0.03	3.09	207.27	0.988	5

Analysis of variance, Irish 1956

	dF	SS	MS	Expectation
Genotypes . . .	23	3276.2	142.4	V _e +5V _g
Blocks . . .	4	45.3	11.3	V _e +24V _b
Error . . .	92	263.5	2.86	V _e
Total . . .	119	3585.0	...	

(b) *Between years*

The above estimates of genetic variation were calculated for each year independently, but it is important to know the "repeatability" of this character from year to year. It has been shown earlier (Cooper,

TABLE 3
Date of ear emergence: Correlation between years for clonal plants

	Mean			Correlation			No. of clones
	1955	1956	1957	55/56	55/57	56/57	
Irish Outbred . . .	11.0 M	10.0 M	4.5 M	+0.938	+0.862	+0.940	24
Selfed . . .	18.8 M	13.0 M	7.5 M	+0.935	+0.956	+0.819	14
Kent Outbred . . .	27.8 M	25.8 M	23.5 M	+0.861	+0.912	+0.944	16
Selfed . . .	1.9 J	31.1 M	29.5 M	+0.934	+0.917	+0.923	10

1959) that Irish perennial ryegrass shows considerable variation between years and that most of this variation can be attributed to spring temperatures during inflorescence development. In the present work, a number of clones of Irish and Kent ryegrass were recorded in

TABLE 4
Date of ear emergence: Genotype-year interaction 1956-57

	V_g	V_y	V_{gy}	V_e	V_t	V_g/V_t	No. of clones
Irish	52.7	17.0	2.5	3.6	75.8	0.695	24
Kent	119.4	4.5	5.3	3.0	132.2	0.903	27
Combined . . .	154.8	9.5	4.9	3.3	172.5	0.897	51

Analysis of variance: Irish

	dF	SS	MS	Expectation
Genotypes	23	12,505	543.7	$V_e + 5V_{gy} + 10V_g$
Years	1	2,059	2059.0	$V_e + 5V_{gy} + 120V_y$
Genotype/Year . . .	23	375	16.3	$V_e + 5V_{gy}$
Genotypes within years .	47	14,939	317.9	V_e
Error	192	687	3.6	
Total	239	15,626		

all three years, 1955 to 1957. The mean dates of ear emergence and the correlations between years are shown in table 3, while fig. 1 illustrates the correlation between one early year (1957) and one late year (1956).

The correlations between years were high and did not differ significantly between the Irish and Kent clones, nor between the out-crossed and inbred material, although date of ear emergence shows marked inbreeding depression and the selfed plants were invariably later than the corresponding outcrosses.

FIG. 1.—Correlation between years: clonal replicates of Irish and Kent ryegrass. 1956 and 1957.

A more detailed analysis of the extent of genotype/year interaction is presented in table 4, for one late year (1956) and one early year (1957). In both Irish and Kent, significant interaction occurs, but it is small compared to differences between genotypes. The difference between the two years is large in Irish, but smaller in Kent.

In conclusion, it can be said that most of the variation within

populations is genetic, and that different genotypes maintain the same relative order of expression from year to year.

3. PARENT-PROGENY REGRESSION

While the analysis of replicated clones allows of the separation of environmental and *total* genetic variation, in order to distinguish between *additive* and *non-additive* genetic variation a breeding test is necessary. In the present work, records from both pair-crosses and selfings have been used. The exact sowing and planting dates are given in table 1.

TABLE 5

Degree of assortative mating: Correlation between parents of pair-crosses

	Irish		Kent	
	<i>r</i>	No. of families	<i>r</i>	No. of families
1955	+0.749	9	+0.873	9
1956	+0.924	16	+0.934	14
1957	+0.553	16	+0.653	7

The crosses were made according to the mutual pollination method of Jenkin (1931*a*), using positive assortative mating for date of ear emergence. The degree of assortative mating, as measured by the correlation between parents, is given in table 5. It is high in 1955 and 1956 but lower in 1957. Such mutual pollination without emasculation means that some self-pollination can occur, but the degree of self-fertility is very low in most plants. Table 6 gives estimates for the Irish and Kent ryegrass used in the present work, together with combined data from Jenkin (1931*b*) on ryegrass from various sources. Furthermore, the positive assortative mating and consequent high correlation between parents will decrease the effect of an occasional selfing on either the means or variances of the progenies. In a comparison in 1955 (see table 8), the variance of selfed progenies was of the same order as that of corresponding pair-crosses.

The heritability of date of ear emergence has been assessed from these crosses by parent-progeny regression and correlation. While the regression coefficient measures the linear relation between parents and progeny, the correlation coefficient indicates the amount of scatter around this line. The maximum value for the regression of progeny on an individual parent ranges from $\frac{1}{2}$ under random mating to 1 under complete genetic assortative mating (*i.e.* selfing). Incomplete assortative mating will fall between these limits. In the present

calculations, however, the difficulty of allowing for the degree of assortative mating has been overcome by using the regression of the progeny mean on the mid-parent value, which has a maximum value of 1, irrespective of the breeding system. Estimates are given in

TABLE 6
Self-fertility in Lolium perenne

Seeds per 100 spikelets	Percentage of plants		
	Irish	Kent	Data from Jenkin (1931 <i>b</i>)
0-5 . . .	37.6	25.0	50.0
6-10 . . .	8.1	15.0	19.0
11-15 . . .	12.1	10.0	6.0
16-20 . . .	4.4	0.0	6.0
21-50 . . .	24.5	35.0	14.0
51-100 . . .	12.0	10.0	3.0
More than 100 .	1.3	5.0	2.0
	(66 plants)	(22 plants)	...

table 7 for pair-crosses of Irish and Kent in 1955, 1956 and 1957, and for selfings in 1955 only, while fig. 2 illustrates the behaviour of pair-crosses and selfings in 1955, and fig. 3 that of pair-crosses only in 1956.

TABLE 7
Heritability of date of ear emergence 1955-57

	Irish			Kent			Combined		
	b	r	No.	b	r	No.	b	r	No.
1955 Crosses * .	0.72 ± 0.062	$+0.98$	9	0.94 ± 0.082	$+0.98$	9	0.87 ± 0.049	$+0.98$	18
Selfings * .	0.64 ± 0.045	$+0.98$	8	0.96 ± 0.013	$+0.95$	7	0.82 ± 0.059	$+0.97$	15
1956 Crosses .	0.79 ± 0.063	$+0.96$	15	0.83 ± 0.060	$+0.96$	14	0.87 ± 0.033	$+0.98$	30
1957 Crosses .	0.87 ± 0.186	$+0.78$	16	0.97 ± 0.157	$+0.94$	7	1.04 ± 0.058	$+0.97$	23

All progeny means based on 50 seedlings.

* Parents in pots in gardens, progeny in field.

Except for 1955, the regression coefficients for Irish and Kent are similar and close to 1.0, but there is a tendency for the progeny from both extremely early and extremely late parents to approach closer to the population mean.

In 1955, the parent clones were grown in pots in the experimental garden, while the progenies were put out as spaced plants in the field. The high spring temperatures in the garden resulted in earlier heading in the parent clones, the acceleration being greater in the earlier

FIG. 2.—Heritability of date of ear emergence in Irish and Kent ryegrass. 1955.

Irish crosses	$Y = 0.72X + 7.76$
„ selfings	$Y = 0.64X + 14.65$
Kent crosses	$Y = 0.94X + 5.17$
„ selfings	$Y = 0.96X + 10.39$

material. The regression of progeny on mid-parent value was therefore rather lower (0.72 and 0.64) in this year for the early-flowering Irish but remained high for Kent ryegrass. This effect is well shown if the results for 1955 (fig. 2) are compared with the corresponding date for 1956 (fig. 3) when all parents and progeny were grown in the field.

These high regression coefficients indicate that most of the genetic variation is additive. Their absolute values will not have been affected by the positive assortative mating for ear emergence, but their accuracy of estimation will have been increased.

The correlations between mid-parent and progeny means are above 0.9, except for Irish crosses in 1957, with no apparent difference between Irish and Kent or between crosses and selfings. The parent and progeny means, however, show an inbreeding depression on selfing of about 5.6 days in each strain.

FIG. 3.—Heritability of date of ear emergence in Irish and Kent ryegrass. 1956.

$$\text{Irish crosses} \quad Y = 0.79X + 3.03$$

$$\text{Kent crosses} \quad Y = 0.83X + 2.76$$

In conclusion, these data from pair-crosses and selfings indicate that date of ear emergence is highly heritable in both populations, but is affected by inbreeding depression. Most of the genetic variance is additive, and considerable response to selection should be possible.

4. VARIATION WITHIN PROGENIES FROM PAIR-CROSSING AND SELFING

In spite of the high heritability of date of ear emergence as calculated from parent-progeny regression, the results show that most parents

from the original populations are rather heterozygous for genes controlling this character. This is illustrated in table 8 which gives the means and variances of the original populations, of the parents used for crossing, and the means, mean variance, and the variance of means of their progenies for the three years, 1955 to 1957. The table

TABLE 8

Date of ear emergence : Variation within progenies from pair-crosses and selfings

	Irish			Kent		
	1955	1956	1957	1955	1956	1957
<i>Original populations</i>						
Mean of means . . .	17.4 M	7.3 M	28.9 A	1.7 J	24.4 M	22.3 M
Mean var.	29.8	12.9	22.5	24.5	26.5	44.6
No. of lots	2	13	6	1	6	6
<i>Pair-crosses</i>						
Parents—						
Mean	12.0 M*	12.4 M	2.0 M	27.6 M*	26.6 M	24.8 M
Var.	67.3	54.7	23.6	47.2	150.4	54.4
Progenies—						
Mean of means . .	16.5 M	12.8 M	27.5 A	31.0 M	24.8 M	22.0 M
Mean var.	21.1	12.3	17.7	10.8	23.0	17.2
Var. of means . .	37.0	36.9	29.4	43.6	109.7	57.9
No. of families . .	9	16	16	9	14	7
<i>Selfings</i>						
Parents—						
Mean	11.2 M*	...	...	28.6 M*	...	...
Var.	127.5	...	...	74.2	...	...
Progenies—						
Mean of means . .	21.6 M	...	...	6.9 J	...	...
Mean var.	21.6	...	...	31.1	...	...
Var. of means . .	49.0	...	...	76.0	...	...
No. of families . .	8	...	...	7	...	...
<i>Error variance of single plant (E_1)</i>	2.75	2.86	4.25	1.25	3.02	2.93
<i>Error variance of mean of 50 (E_2)</i>	0.055	0.057	0.085	0.025	0.060	0.059

* Parents in pots in gardens.

Progeny means and variances based on 50 plants.

also includes estimates, derived from replicated clones, of the error variance of single spaced plants, (E_1) and of the means of 50 (E_2).

The means of the populations varied from year to year but their variances were of the same order, ranging from 12.9 to 44.6. In all cases, the variance of the parental group was larger than that of the original population, the result of using some very early and very late plants as parents.

In pair-crosses under random mating, both the genetic variance of the progeny means and the mean genetic variance of the progeny would be expected to be about half that of the parental group, since, in Mather's notation (Mather, 1949) :

$$\text{Variance of parental group} = \frac{1}{2}D + \frac{1}{4}H + E_1$$

$$\text{Mean variance of progenies} = \frac{1}{4}D + \frac{3}{16}H + E_1$$

$$\text{Variance of progeny means} = \frac{1}{4}D + \frac{1}{16}H + E_2$$

Under assortative mating, however, as shown by Breese (1956), while the mean variance of the progenies remains comparatively unaffected, the variance of progeny means is considerably increased, approaching in the extreme case that expected under selfing ($\frac{1}{2}D + \frac{1}{16}H + E_1$). In the present results under such assortative mating, the variance of progeny means is always well above that expected on the basis of random mating, when compared to the parental group.

In the selfings, which were available in 1955 only, the parental group also showed a higher variance than the original population. In this case, the expected progeny variances are as follows :

$$\text{Mean variance of progenies} = \frac{1}{4}D + \frac{1}{8}H + E_1$$

$$\text{Variance of progeny means} = \frac{1}{2}D + \frac{1}{16}H + E_2$$

In accordance with this expectation, the variance of progeny means is rather larger for the selfings than for the pair-crosses, even with assortative mating, while, for Irish at least, the mean variances are of the same order.

Even so, the mean variance from crossing two plants of similar phenotype, or from selfing one, is well above the error variance of a single clone, indicating considerable heterozygosity of the parents. The mean variances of the Irish and Kent progenies are of the same order, suggesting a similar degree of heterozygosity, or storage of variation, within plants from the two populations.

The comparatively small variance of the original populations, not much greater than that within a single pair-cross, suggests that selection for uniformity of heading within the seed crop is quite stringent. A single date of harvesting severely limits the range of parents which can be represented in the next generation. Plants which flower too early will lose seed by shedding, while plants which are too late may not ripen seed before harvest (Cooper, 1959). Such selection against extremely early and extremely late plants as female parents will be reinforced by the inevitable positive assortative mating for flowering date within the seed crop, so that extremely early and extremely late parents will also tend to be excluded as pollen parents.

In view of the complexities of this genetical situation which involve (i) non-random mating in the original population, (ii) heterozygosity of all parents, (iii) selection of parents to increase the variance of the parental group, and (iv) positive assortative mating for flowering

time, no attempt has been made to derive strict estimates of the components of variation, D , H and E from the present data. However, as shown in table 2, E is small and does not vary greatly between years, between strains, or between outcrossed and inbred material; while the high parent-progeny regressions indicate that most of the genetic variance is additive. Considerable response to selection should therefore be possible.

5. DISCUSSION

The estimation of genetic variation and heritability involves the analysis of the total variation into those portions due to genotype, to the environment, and to genotype/environment interaction. The genetic component can be further analysed into those parts resulting from additive gene action, from dominance, and from other gene interactions.

A preliminary separation of environmental from *total* genetic variation can be obtained from replicated clones, from homozygous lines or from the F_1 s between them. In herbage species, replicated clones have been used by Burton and Devane (1953) and by Fejer (1958), while homozygous lines have been used by Burton (1952) and by Davern, Peak and Morley (1957). The variation within clones or within homozygous lines is taken as a measure of environmental variation, and the heritability in the broad sense is calculated as :

$$\frac{V_T - V_E}{V_T}$$

or, in Mather's notation :

$$\frac{\frac{1}{2}D + \frac{1}{4}H}{\frac{1}{2}D + \frac{1}{4}H + E}$$

assuming that the sample is random, and is derived from a randomly-breeding population. A low heritability may therefore simply mean little genetic variation.

The estimation of the *total* genetic variation, however, only gives a maximum figure for the genetic variance and for the heritability. In predicting the potential response to selection, it is the *additive* (*i.e.* easily fixable) part of the genetic variance which is important, and this can only be assessed by a breeding test. Where homozygous parental lines are available, and both selfing and crossing are practicable, a number of estimates of genetic parameters are possible (Mather, 1949), and a recent refinement of these techniques is the analysis of diallel crosses, which allows of the separation of non-additive genetic variance into dominance and non-allelic gene interaction (Jinks, 1954, 1956; Dickinson and Jinks, 1956).

In the outbreeding perennial herbage grasses, however, homozygous material is not usually available and selfing is often difficult or impossible. A more usual procedure has therefore been to use the regression or correlation between parent and progeny, the progeny being obtained either by pair-crossing, selfing or open-pollination.

The use of such methods in the herbage grasses has been reviewed by Burton (1952) and by Fejer (1958). For pair-crosses, heritability in the narrow sense is estimated as the regression of the progeny mean on the mid-parent value, while for open pollination (assuming random mating) it is given by twice the regression of the progeny mean on the female parent.

In the assessment of heritabilities from pair-crosses, random mating has often been thought necessary, but Reeve (1953) points out that unless the situation is complicated by dominance and non-allelic interaction, the maximum heritability values can be obtained by (a) selecting parents to increase their variance above that of the original population, and (b) using positive assortative mating to increase the variance of the mid-parent value. Both these methods are combined in the usual type of selection experiment, and in most plant or animal breeding programmes.

In the present work, the methods employed have been determined by the outbreeding and largely self-incompatible nature of the crop, and it is interesting that the results obtained, although derived from simple regression analysis, agree well with those obtained by more refined methods in self-fertilising species. In *Nicotiana rustica*, for instance, Mather and Vines (1952) found that most of the genetic variance for flowering time was additive, that there was no interaction between years, and that the error variance of a single plant was about 6 to 10 days. This material was further studied by Jinks (1954, 1956) using a diallel analysis of the parents and F_1 s which he later extended to the F_2 and backcross generations. From the parent and F_1 analysis he concluded that time of flowering showed incomplete though significant dominance, but a complete absence of non-allelic interaction, while the F_2 and backcross analyses showed only slight non-allelic interaction. Great seasonal differences occurred in the size of the genetic components of variation. In further analyses of the genetic/environment interaction, Allard (1956) suggested that for time of flowering the additive genetic effects were comparatively stable, but that dominance effects varied in different environments.

Similar conclusions are drawn by Davern, Peak and Morley (1957) from their analysis of flowering time in the self-fertilising *Trifolium subterraneum*. The repeatability of parental lines between years was high (86 per cent.), and no large block effects were noted. The regressions of the F_1 means on mid-parent values and of F_3 means on F_2 parents were not significantly different from unity, indicating that most of the genetic variation was additive.

The same general pattern is revealed in most studies on the genetic control of flowering time. Most of the genetic variation seems to be additive, with little dominance or non-allelic interaction. Selection in the past has presumably been for an intermediate phenotype, which would not be expected to lead to fixation of alleles, or to the development of directional dominance. Considerable response to

future selection should therefore be possible, and such has proved to be the case in the present ryegrass strains, Irish and Kent. The results of four years' selection for early and late ear emergence will be reported in the next paper, and the actual response to selection compared to that expected from the present estimates of additive genetic variance and heritability.

6. SUMMARY

1. This paper attempts to estimate the genetic variation for date of ear emergence within Irish and Kent ryegrass, to calculate its heritability, and hence predict the potential advance under selection.

2. The genetic variation has been assessed in two ways: (i) from the analysis of replicated clones, and (ii) from the regression of progeny means on mid-parent values.

3. Most of the variation within each population in any one year is genetic, block effects being small, and the repeatability between years is also high, although variation in absolute values occurs between early and late years.

4. Estimates derived from parent-progeny regression show that most of the genetic variation is additive, although marked inbreeding depression occurs on selfing, and that considerable response to selection would be expected for this character.

5. In spite of the high heritability of date of ear emergence, most parents from Irish and Kent ryegrass are highly heterozygous for genes controlling ear emergence, and the variance of progenies from selfing or pair-crossing is of the same order as that of the original population.

6. Methods for the estimation of genetic variation and heritability in herbage plants are discussed, and it is concluded that in other species also flowering time seems to show mainly additive genetic variance, with little or no dominance.

Acknowledgments.—It is a pleasure to acknowledge the facilities provided and interest shown by Professor E. T. Jones, former Director, and Professor P. T. Thomas, present Director of the Welsh Plant Breeding Station. I am grateful to Dr M. Borrill and to Dr E. L. Breese of the Grass Breeding Section for helpful discussion, and my thanks are due to Miss Irene D. Rees for valuable assistance with the manuscript.

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