SELECTION AND POPULATION STRUCTURE IN
LOLIUM

IV. CORRELATED RESPONSE TO SELECTION

J. P. COOPER

Welsh Plant Breeding Station, Aberystwyth

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1. INTRODUCTION

EARLIER papers in this series have analysed the genetic control and response to selection of a single character, date of ear emergence, in two outbreeding populations of *L. perenne* (Cooper, 1959*a* and *b*). It was concluded that most of the variation in this character was genetic and additive, that all parents were highly heterozygous, and that considerable response to selection was possible.

In the same material, records were also taken on a number of ear characters to see whether they revealed a similar genetic structure, and to detect any correlated response to selection for ear emergence. The heritability of each character has been estimated from the analysis of clonal replicates and from parent/progeny regression, and its correlated responses to selection under the different mating systems has been assessed.

2. MATERIAL AND METHODS

Operational details of the selection experiment in 1956 and 1957 have been given earlier (Cooper, 1959*b*). In each year, the original populations and selection lines were grown as seedlings, and the selected parents in each generation were put out as clonal replicates.

In 1956, records of ear characters were taken on one replicate only of the clonal material, which consisted of original population plants of Irish and Kent ryegrass, and the parents of the first two generations of selection. In 1957, records were taken on all replicates of the clonal material, on three different samples of Irish and Kent ryegrasses, and on the seedling progenies of the three generations of selection. Eighty seedlings were measured from each population and ten from each progeny.

The methods of harvesting and recording were the same for both years. Three heads were harvested, soon after anthesis, from the first flush of heading on each plant. By the time anthesis begins, all the characters measured have reached their maximum dimensions, and further delay in harvesting may result in seed shedding. The heads were air-dried in a greenhouse, and the following measurements taken on each, as illustrated in fig. 1.

- (1) *total length*, from the flag-leaf node to the tip of the inflorescence,
- (2) *ear length*, from the insertion of the lowest spikelet to the tip of the inflorescence,
- (3) *number of spikelets*,

and, measured on the sixth spikelet from the tip,

- (4) *length of empty glume*,
- (5) *length of spikelet*,
- (6) *number of florets per spikelet*.

FIG. 1.—Ear characters recorded in the present work.

3. POPULATION DIFFERENCES

A comparison of ear characters in samples of Irish and Kent ryegrasses in 1957 is given in table 1, which includes date of ear emergence for comparison. In no cases were block differences or sample/block interactions significant.

In spite of about four weeks' difference between Irish and Kent in ear emergence, no significant differences were recorded for total length, length of empty glume or length of spikelet. Kent possessed longer ears and more spikelets than Irish, but fewer florets per spikelet. Even so the total number of florets per inflorescence was greater in Kent ryegrass. No differences between samples were noted in Kent, but in Irish one sample (Ba 6650) had slightly longer ears, more spikelets and fewer florets than the others.

A further comparison is possible using clonal replicates of Irish and Kent ryegrasses in 1956 and 1957; this also provides an estimate of the repeatability of the measurements from year to year (table 2).

TABLE 1

Ear characters in Irish and Kent ryegrass populations 1957

	Irish				Kent				5 per cent. sig. diff. for	
	Ba 6650	Ba 6773	Ba 6738	Mean	Ba 6622	Ba 6740	Ba 6565	Mean	Samples	Means
Total length (cm.) . .	52.8	51.2	50.6	51.5	51.9	51.7	52.4	52.0	N.S.	N.S.
Length of ear (cm.) . .	24.1	22.9	23.0	23.3	24.4	24.9	25.1	24.8	1.06	0.61
No. of spikelets . . .	24.8	23.8	22.9	23.8	28.1	27.4	27.7	27.7	1.24	0.72
Length of spikelet (mm.) .	15.0	15.2	15.9	15.4	15.1	15.6	15.3	15.3	N.S.	N.S.
Length of empty glume (mm.)	10.3	10.2	10.0	10.2	10.7	10.2	10.5	10.4	N.S.	N.S.
No. of florets . . .	10.1	10.8	10.9	10.6	9.9	10.1	9.9	10.0	0.45	0.26
Date of ear emergence . .	30.6 April	27.8 April	28.6 April	29.0 April	22.5 May	22.7 May	20.5 May	21.9 May	1.86	1.09

The clonal material in each year gives a similar picture to that obtained from the population seedlings, Kent showing a longer ear, more spikelets and, in this case, a greater total length than Irish, while spikelet length and number of florets are again greater in Irish.

Differences between years occurred in all ear length characters (total length, ear length and number of spikelets) which were higher in 1957 than in 1956. The spikelet measurements, however, were fairly constant in the two years.

Most of the ear characters showed good repeatability from year to year though usually not as high as for date of ear emergence. The order of repeatabilities derived from clonal replication between years agrees fairly well with that of the heritabilities derived from replication within a single year (table 3), suggesting that the characters show the same relative stability to environmental fluctuations between and within years.

4. HERITABILITY OF EAR CHARACTERS

Methods for the separation of genetic from environmental variation, and for its analysis into additive and non-additive components have been discussed earlier (Cooper, 1959a). In the present work, the

TABLE 2
Ear characters in clonal replicates of Irish and Kent ryegrass
1956 and 1957

39 plants of Irish, 32 plants of Kent

	1956 Mean	1957 Mean	Difference 1956-57	Correlation 1956-57
Total length (cm.)				
Irish	41.0	44.2	+3.2*	0.81**
Kent	43.2	47.0	+3.8***	0.52**
(Difference)	+2.2*	+2.8*		
Length of ear (cm.)				
Irish	17.7	19.9	+2.2**	0.76**
Kent	19.7	23.5	+3.8***	0.58**
(Difference)	+2.0***	+3.6***		
No. of spikelets				
Irish	19.1	21.9	+2.8 N.S.	0.61**
Kent	22.1	26.5	+4.4***	0.49**
(Difference)	+3.0***	+4.6***		
Length of empty glume (mm.)				
Irish	10.6	10.6	0.0 N.S.	0.94***
Kent	9.9	10.3	+0.4 N.S.	0.80**
(Difference)	-0.7 N.S.	-0.3 N.S.		
Length of spikelet (mm.)				
Irish	15.7	16.3	+0.6 N.S.	0.71***
Kent	14.3	15.1	+0.9 N.S.	0.61**
(Difference)	-1.4**	-1.2*		
No. of florets				
Irish	10.2	11.1	+0.9*	0.70**
Kent	9.5	10.0	+0.5 N.S.	0.69**
(Difference)	-0.7 N.S.	-1.1*		
Date of ear emergence				
Irish	10.9 May	5.1 May	-5.8***	0.93***
Kent	26.2 May	23.2 May	-3.0 N.S.	0.96**
(Difference)	+15.3***	+18.1***		

* $P = 0.05-0.01$

** $P = 0.01-0.001$

*** $P < 0.001$

genetic and environmental variations have been estimated from the analysis of variance of replicated clones, while the additive (*i.e.* fixable) genetic variation has been assessed from the regression of progeny means on mid-parent values. Individual records were taken on three heads from each plant, and a measure of within-plant variation or "developmental error" is available for all material.

TABLE 3

Analysis of variance components from clonal replicates, 1957

	Mean	V_G	V_B	V_{GB}	V_E	V_T	V_G/V_T	$\sqrt{V_G \times 100}$ Mean
Total length (cm.)								
Irish	45.1	21.05	0.77	6.00	5.93	33.75	0.62	10.2
Kent	46.5	58.81	0.60	8.58	4.01	72.00	0.81	16.5
Length of ear (cm.)								
Irish	21.0	7.90	0.06	1.40	1.57	10.93	0.72	13.4
Kent	22.6	15.87	0.09	0.77	2.83	19.56	0.80	17.7
No. of spikelets								
Irish	22.3	11.87	0.08	—0.10	5.10	16.95	0.70	15.4
Kent	25.2	10.07	0.09	1.22	4.14	15.52	0.64	12.2
Length of empty glume (mm.)								
Irish	10.1	3.42	0.06	0.02	0.93	4.39	0.77	18.2
Kent	9.8	3.63	0.01	0.38	0.65	4.67	0.77	19.5
No. of florets								
Irish	11.2	0.92	0.03	0.84	1.54	3.33	0.27	8.6
Kent	10.3	2.18	0.11	0.91	1.35	4.55	0.47	14.3
Length of spikelet (mm.)								
Irish	16.9	3.11	0.18	1.67	1.97	6.93	0.44	10.4
Kent	15.0	4.97	0.21	1.03	1.60	7.81	0.63	14.9

Specimen analysis of variance

Irish	Total length, 1957 (five replicates)			
	dF	SS	MS	
Genotypes	37	12566.3	339.63	$V_E + 3V_{GB} + 15V_G$
Blocks	4	446.1	111.52	$V_E + 3V_{GB} + 114V_B$
Genotype/block interaction .	148	3543.0	23.93	$V_E + 3V_{GB}$
Between plants	189	16555.4	87.59	V_E
Within plants	380	2254.9	5.93	
	569			

$$V_T = V_G + V_B + V_{GB} + V_E$$

(i) *Analysis of clonal replicates*

The total variation for each character has been separated into genetic variation (V_G), block variation (V_B), block/genotype interaction (V_{GB}) and within-plant variation (V_E) (table 3). This separation then estimates the heritability in the broad sense as

$$\frac{V_G}{V_G + V_B + V_{GB} + V_E}$$

These measurements were made in 1956 and 1957 on the same clonal genotypes of Irish and Kent ryegrass. Both years and both populations gave a similar picture, but only the 1957 results are presented here. For the ear length group of measurements and length of empty glume, most of the variation is genetic, but for spikelet length and number of florets, the within-plant variation is of the same order as the genetic variation and the heritability is consequently lower. For all characters, block effects or genotype/block interactions are usually less than the within-plant variation.

TABLE 4
Heritabilities from parent/progeny regressions
Irish and Kent ryegrasses, 1957

	Irish				Kent			
	Parent mean	Progeny mean	<i>r</i>	<i>b</i>	Parent mean	Progeny mean	<i>r</i>	<i>b</i>
Total length (cm.) .	45.3	49.6	0.75***	1.06** ±0.20	48.1	51.9	0.96***	0.95*** ±0.17
Ear length (cm.) .	21.1	21.9	0.56**	0.82* ±0.26	24.0	25.0	0.83***	0.81*** ±0.16
No. of spikelets .	22.3	22.3	0.83***	0.74*** ±0.15	26.3	27.4	0.54*	0.51* ±0.23
Length of empty glume (mm.)	11.1	10.2	0.84***	0.83*** ±0.12	10.3	9.6	0.61*	0.47* ±0.18
Length of spikelet (mm.)	16.9	14.2	0.13 N.S.	0.14 N.S. ±0.28	15.0	13.0	0.62*	0.36* ±0.13
No. of florets . . .	11.4	10.1	-0.10 N.S.	-0.09 N.S. ±0.21	1.02	0.94	0.51*	0.20* ±0.09
Date of ear emergence	3.7 May	29.5 April	0.88***	0.89*** ±0.11	24.7 May	22.2 May	0.98***	0.93*** ±0.08
	<i>n</i> = 23				<i>n</i> = 14			

The genetic coefficient of variation

$$\left(\frac{\sqrt{V_G} \times 100}{\text{Mean}} \right)$$

which gives a rough measure of the relative improvement to be expected under selection, shows values of 8 to 20 per cent., being greatest for length of empty glume, and least for spikelet length and number of florets.

It must be remembered, however, that these estimates derived from replicated clones refer to the total genetic variation visible in the initial population. The *additive* genetic variation, *i.e.* that which is fixable by selection, can only be estimated from breeding tests.

(ii) *Parent-progeny regression*

In the present work, the *additive* genetic variation has been estimated from the regression of the progeny mean on the mid-parent value for 23 pair-crosses of Irish and 14 of Kent ryegrass, records of parents and progeny from the same year, 1957, being used. The parents were mated at random for ear characters, so no corrections for non-random mating are necessary (Reeve, 1953).

FIG. 2.—Heritability of total length in Irish and Kent perennial ryegrass.
(Irish = O, Kent = Δ).

Table 4 gives details of the parent and progeny means, the correlations between them, and the regression of the progeny mean on the mid-parent value, while figs. 2 and 3 illustrate the behaviour of one highly heritable character (total length), and one with low heritability (number of florets).

As discussed earlier (Cooper, 1959*a*), the regression of progeny on mid-parent estimates the quantitative advance likely to be obtained under selection, while the correlation coefficient measures the deviation from linearity of the progeny values. The correlation coefficient also makes it possible to estimate heritability when parents and progeny

may differ in scale, for instance, when they are recorded in different years or in different environments.

The regression and correlation coefficients agree well for each character, and as found earlier (Cooper, 1959*a*), the date of ear emergence shows a very high heritability in both populations.

In Irish ryegrass, the ear length group of measurements, and length of the empty glume are highly heritable, while spikelet length and number of florets show little, if any, heritable variation. The order

FIG. 3.—Heritability of number of florets in Irish and Kent perennial ryegrass. (Irish = O, Kent = Δ).

of these results agrees with those obtained from the analysis of clonal replicates.

In Kent, the situation is slightly different. Total length and ear length again show high heritabilities, but the estimates for number of spikelets and length of empty glume are somewhat lower, though still about 50 per cent. In this strain, length of spikelet and number of florets also show some heritable variation. The amount of genetic variation for a particular character can evidently differ from one population to another.

The high parent-progeny regression for most of these ear characters indicates that rapid immediate response to selection should be possible.

In addition, considerable genetic variation occurs within each progeny (table 8), and it is clear that most parents are highly heterozygous. As with ear emergence, this storage of genetic variation should allow of extensive long-term changes under selection.

5. CORRELATION BETWEEN CHARACTERS

Although the high additive heritability of most ear characters suggests that selection for each of them individually should prove effective, selection for two or more at the same time will be hindered if a negative correlation exists between the different criteria of selection.

TABLE 5

Phenotypic correlations between characters in seedlings of the initial populations

Kent (n=78)							
	Total length	Length of ear	No. of spikelets	Length of empty glume	Length of spikelet	No. of florets	Date of ear emergence
Total length . . .		0.07	0.46***	0.40***	0.29**	0.09	0.18
Length of ear . . .	0.05		0.58***	0.34**	0.28**	0.05	-0.37***
No. of spikelets . . .	0.24*	0.03		0.15	0.05	0.03	-0.11
Length of empty glume .	0.12	0.12	-0.26*		0.14	0.27*	0.00
Length of spikelet . . .	0.08	0.20	-0.26*	0.42***		0.59***	-0.03
No. of florets . . .	0.03	0.04	-0.26*	0.24*	0.72***		-0.09
Date of ear emergence .	0.04	-0.01	-0.10	0.01	-0.30**	-0.20	

Irish (n=78)

* $P = 0.05-0.01$

** $P = 0.01-0.001$

*** $P < 0.001$

Conversely, if these are positively correlated, the advance under selection should be accelerated.

The correlations of the ear measurements with each other and with date of ear emergence can thus be used to predict the expected correlated response to selection, and this prediction can then be checked against the responses actually obtained in the selection experiment.

(i) *Phenotypic correlations in the initial populations*

Phenotypic correlations between all the characters were calculated for the two initial populations of Irish and Kent ryegrass. The results (table 5) show a positive correlation between number of spikelets and total length in both strains, but between number of spikelets and ear

length in Kent only. There was, surprisingly, no correlation between total length and ear length in either strain. Negative correlations were obtained between number of spikelets and spikelet size (length of empty glume, length of spikelet, number of florets) in Irish but not in Kent. Length of spikelet and number of florets were highly correlated in both strains, while length of empty glume and length of spikelet were correlated in Irish but not in Kent.

There were few correlations with date of ear emergence, only length of ear in Irish and length of spikelet in Kent showing a slight negative correlation with ear emergence.

(ii) *Phenotypic and genetic correlations from clonal replicates*

The above measurements on population seedlings, however, only provide estimates of phenotypic correlations, while in predicting the correlated response to selection it is genetic correlations which are important. Both phenotypic and genetic correlations were therefore calculated for the clonal plants of Irish and Kent ryegrasses used as parents in the pair-crosses.

The genetic correlations were obtained from the following formula (Hazel, 1943):

$$r_g = \sqrt{\frac{b.A_p B_o \times b.A_o B_p}{b.A_o A_p \times b.B_o B_p}} = \sqrt{\frac{\text{cov}.A_p B_o \times \text{cov}.A_o B_p}{\text{cov}.A_o A_p \times \text{cov}.B_o B_p}}$$

where $b.A_p B_o$ represents the regression of character B in the progeny on character A in the parent, and so on. In the present work, mating was at random for ear characters, so no correction for non-random mating was necessary (Reeve, 1953). Where the two regression coefficients, or covariances, of the numerator are of opposite sign, an imaginary figure is obtained, indicating that the genetic correlation is not significantly different from zero. Similarly, where one of the regression coefficients or covariances in the denominator is zero or negative, indicating the absence of genetic variation, there can be no genetic correlation.

The phenotypic correlations derived from the clonal replicates were not always the same as those obtained from the population seedlings. Total length and ear length were highly correlated in both strains, as were length of spikelet and number of florets, but number of spikelets and ear length were correlated in Irish only. Rather surprisingly, length of spikelet and number of florets were positively correlated with ear length in Kent. There were again few significant correlations with date of ear emergence, except for total length in Irish, and spikelet length and number of florets in Kent.

The corresponding phenotypic and genetic correlations were usually of the same order and in the same direction (table 6). This is not unexpected as all the material was grown in the same field in the

same year and both block effects and block/genotype interactions were small (table 3). The most noticeable difference lies in the relation between spikelet length and number of florets in Irish. There was a high phenotypic correlation between these two characters, but since no additive genetic variation could be detected for floret number, there could be no genetic correlation. In Kent ryegrass, on the other hand,

TABLE 6

Phenotypic and genetic correlations between ear characters in clones of Irish and Kent perennial ryegrasses, 1957

Kent (n=14)							
	Length	Length of ear	No. of spikelets	Length of empty glume	Length of spikelet	No. of florets	Date of ear emergence
Total length . . .		0.78** (0.69)	0.36 (0.53)	0.09 (0.25)	0.46 (0.59)	0.26 (0.37)	0.09 (±0)
Ear length . . .	0.65*** (0.75)		0.36 (0.24)	0.47 (0.65)	0.70** (0.49)	0.56* (0.25)	-0.09 (±0)
No. of spikelets . . .	0.51* (0.57)	0.63** (0.58)		0.05 (±0)	-0.02 (-0.55)	-0.19 (-0.89)	0.35 (0.66)
Length of empty glume	0.22 (0.16)	0.50* (0.35)	0.05 (±0)		0.44 (0.59)	0.38 (0.22)	-0.12 (±0)
Length of spikelet . . .	0.18 (±0)	0.27 (±0)	-0.23 (-0.626)	0.32 (±0)		0.82*** (0.93)	-0.57* (-0.59)
No. of florets . . .	0.14 (±0)	0.24 (±0)	0.12 (±0)	0.02 (±0)	0.65*** (±0)		-0.50* (-0.33)
Date of ear emergence	0.44* (0.45)	-0.13 (±0)	0.19 (0.44)	-0.17 (-0.03)	-0.21 (-0.53)	0.07 (±0)	

Irish (n=23)

(Phenotypic correlations without brackets, genetic correlations inside brackets.)

* $P = 0.05-0.01$

** $P = 0.01-0.001$

*** $P < 0.001$

both the genetic and phenotypic correlations between these two characters were high.

The largest genetic correlations with ear emergence in Irish ryegrass were positive for total length and number of spikelets and negative for spikelet length, while in Kent there were a positive correlation for number of spikelets, and negative for spikelet length and number of florets. One would therefore expect these characters to show a correlated response to selection for ear emergence. There were few high genetic correlations between the other measurements suggesting that most of the ear characters could be selected independently.

6. CORRELATED RESPONSE TO SELECTION

Correlated response to selection was assessed on the third generation material in 1957 by taking the early and late selection lines derived from the same initial group of parents, and determining the significance of the difference between them for each ear measurement. Ten seedlings were measured in each line. It will be recalled that early and late selection lines had been established from a number of initial groups of four, two and one plant, and that by the third generation considerable response in ear emergence had occurred within each group (Cooper, 1959*b*).

TABLE 7
Correlated responses to selection for date of ear emergence

	Irish							Kent						
	Negative response			No response	Positive response			Negative response			No response	Positive response		
	***	**	*		*	**	***	***	**	*		*	**	***
Total length	...	...	...	8	1	...	...	...	...	...	5	...	...	2
Ear length	...	...	1	6	...	2	...	1	...	...	5	...	1	...
No. of spikelets	...	...	...	7	2	...	...	...	1	...	2	...	2	2
Length of empty glume	2	2	...	4	1	...	...	1	...	1	5	...	...	...
Length of spikelet	1	2	1	5	...	...	...	2	1	1	3	...	...	...
No. of florets	...	...	2	7	...	...	...	1	...	1	5	...	...	...

(Figures refer to number of pairs of lines showing each type of response.)

* $P = 0.05-0.01$
 ** $P = 0.01-0.001$
 *** $P < 0.001$

A summary of the results is given in table 7 for Irish and Kent separately. There were no regular differences between the lines derived from four-way crosses, pair-crosses or selfings followed by sib-mating, and these have been bulked in the table. Most pairs of lines showed a correlated response in one or more characters but the different ear characters seemed to change quite independently of each other. In both strains, selection for lateness tends to produce an increase in the ear length characters (total length, ear length, number of spikelets) and a decrease in spikelet size (length of empty glume, spikelet length, number of florets) but the direction of response is not invariable. In Irish, for instance, one group has given a negative response for ear length and another a positive response for length of empty glume.

The changes in ear characters which occur as a result of selection for ear emergence bear no regular relation to the genetic correlations calculated from the initial material, and may well be a result of chance

TABLE 8
Effect of mating systems on ear characters

	Total length (cm.)		Length of ear (cm.)		No. of spikelets		Length of empty glume (mm.)		Length of spikelet (mm.)		No. of florets		No. of families
	Means of		Means of		Means of		Means of		Means of		Means of		
	means	variances	means	variances	means	variances	means	variances	means	variances	means	variances	
(a) Irish													
Original populations . . .	51.6	35.4	23.4	11.4	23.9	10.3	10.2	3.3	15.4	4.8	10.6	2.03	3
1st generation													
Pair crosses . . .	48.0	20.1	21.6	10.2	22.0	7.2	11.2	3.4	14.8	1.5	10.6	1.57	4
Selfings . . .	35.8	*	17.6	*	19.7	*	10.9	*	16.2	*	11.8	*	4
3rd generation													
Four-way crosses . . .	48.1	28.6	21.9	10.8	22.8	5.5	9.9	2.9	14.2	3.3	10.1	2.29	4
Sib-crosses . . .	38.5	24.7	16.3	10.2	19.5	8.4	9.5	1.5	13.4	2.6	10.3	1.44	7
Selfing/sib-crosses . . .	38.7	22.5	19.6	7.3	22.2	8.7	10.5	2.3	13.4	1.6	10.3	1.23	6
Selfed lines . . .	34.8	10.4	17.4	4.1	21.0	2.5	10.0	1.4	13.4	0.9	9.9	0.99	3
Developmental error													
Outbred . . .	2.0			0.52		1.70		0.31		0.66		0.51	
2nd generation selfings	1.4			1.36		2.04		0.31		0.50		0.51	
(b) Kent													
Original populations . . .	52.1	33.2	24.9	11.9	27.8	13.3	10.4	3.2	15.3	5.3	10.0	2.27	3
1st generation													
Pair crosses . . .	53.2	20.2	27.1	9.9	28.9	6.3	9.7	2.1	12.7	1.7	9.3	1.01	4
Selfings . . .	40.5	*	20.5	*	23.0	*	10.0	*	14.5	*	8.9	*	4
3rd generation													
Four-way crosses . . .	51.3	31.0	24.1	9.8	26.1	10.7	10.0	1.1	12.8	1.2	8.9	1.11	4
Sib-crosses . . .	51.2	41.4	23.1	9.1	26.4	15.0	9.8	1.9	12.7	2.2	9.3	0.99	5
Selfing/sib-crosses . . .	50.6	10.7	24.9	3.5	25.1	3.9	9.2	1.1	13.4	1.7	9.2	2.07	3
Selfed lines . . .	44.1	22.1	22.1	10.2	19.9	7.3	9.9	2.0	12.0	2.8	9.3	1.79	3
Developmental error													
Outbred . . .	1.3			0.94		1.38		0.22		0.53		0.45	
2nd generation selfings	0.6			1.05		1.82		0.45		0.79		0.53	

* Only 4 plants from each family measured, so no variance available.

association of genes in the parents used in each generation. They may also in part result from the linkage and reassortment of genes controlling ear characters with genes for date of ear emergence (Mather and Harrison, 1949).

7. EFFECT OF MATING SYSTEM

In addition to any correlated response to selection, the means and variances of the ear characters may change as a result of the different intensities of inbreeding practised. The effect of the mating system on each ear character has therefore been assessed by averaging the means and variances of all lines under the same mating system in the same generation, *i.e.* with the same theoretical coefficient of inbreeding (table 8). These can then be compared with three different measures of outbred material, (i) the original populations, (ii) the first-generation progenies from pair-crosses, and (iii) the progenies produced by outcrossing in the third generation. The influence of inbreeding on the within-plant variation has also been assessed from clonal material of the original populations and of the selfed lines in the second generation. Since the material was randomised, and block differences were small, the significance of the difference between any two means can be roughly assessed by a "*t*" test; significant differences at 5 per cent. are of the order of 2.3 cm. for total length, 1.2 cm. for ear length and 1.2 for number of spikelets. The spikelet measurements show few significant differences.

Pronounced inbreeding depression is shown by the ear length characters (total length, ear length, number of spikelets), but not to any appreciable extent by the spikelet measurements (figs. 4 and 5). The four-way crosses, which were based on four unrelated parents and continued by selecting four plants in each generation, seem to maintain their vigour quite satisfactorily when compared to the three outbred standards. Sib-crossing, however, usually results in a decrease in vigour, as assessed by ear length characters, while continued selfing has an even greater effect.

A decrease in genetic variance might be expected within the selection lines as a result of the inbreeding accompanying the selection programme. For most characters, such a decrease does occur in the first generation pair-crosses, but the subsequent decrease is less than expected, except for the selfed lines in Irish ryegrass, which after three generations show greatly reduced variances for most characters although still above the level attributable to developmental error (figs. 4 and 5).

There appears to be no regular change in the "developmental error" of these ear characters accompanying inbreeding, although for length of ear and number of spikelets in both strains, and for the spikelet measurements in Kent, the second generation selfed lines show somewhat higher within-plant variances.

Both the maintenance of genetic variation under continued inbreeding, and the lack of change in the within-plant variation are

FIG. 4.—Effect of mating system on total length in Irish and Kent perennial ryegrass.

FIG. 5.—Effect of mating system on length of empty glume in Irish and Kent perennial ryegrass.

features which have been found earlier for date of ear emergence also (Cooper, 1959*b*); they may well be a result of natural selection for balanced heterozygotes during the course of the experiment.

8. DISCUSSION

The present records on the individual ear characters reveal a similar genetic structure to that shown by date of ear emergence (Cooper, 1959*b*). For most characters, considerable additive genetic variation exists in both populations, all parents are highly heterozygous, and rapid response to selection should therefore be possible, except perhaps for floret number or spikelet length in Irish ryegrass. These findings may have some practical implication in selecting for high seed yield, although Davies (1954) reports that in S23 perennial ryegrass, intrinsic seed fertility, measured as percentage seed set, is more important than number of florets per inflorescence in determining final seed yield. It is intended to measure both male and female fertility in these selection lines in later generations.

These records also provide information as to the optimum number of foundation plants on which to base a strain of ryegrass. As discussed earlier (Cooper, 1959*b*) the argument has been that too few plants might give rise to inbreeding depression during subsequent multiplication, while too many, besides being difficult for the breeder to handle, might release too much variation. The present results show that for ear characters, as for date of ear emergence, one individual carries a great deal of potential genetic variation, which can be rapidly released by segregation and recombination. Furthermore, in the four-way crosses, there has been little, if any, loss of vigour during three generations of multiplication, and little decrease in genetic variation compared to the original population. This suggests that four unrelated plants should be quite adequate as the basis of a strain of perennial ryegrass.

The correlation between the ear characters and their correlated response to selection give further information on the genetic structure of these ryegrass populations, and from the plant breeding point of view indicate possible limitations to selection for two or more characters simultaneously.

In spite of the developmental relationship of some of the characters, for instance, that between spikelet number and length of ear (Hänsel, 1951), few high genetic correlations have been obtained. There is evidently appreciable independent genetic control of these characters and it should be possible to select for them independently.

This conclusion is borne out by the pattern of correlated response to selection for date of ear emergence. As table 7 shows, although changes in ear characters have occurred in some of the selection lines, these changes are not inevitable, and are not always in the same direction for a particular character. There is, however, a tendency in both Irish and Kent for the ear length measurements to increase

and the spikelet measurements to decrease with selection for lateness of heading.

There are two possible mechanisms for correlated response to selection: (i) pleiotropic action of single genes or combinations of genes, or (ii) linkage of genes controlling different characters. In the present case, there is no high genetic correlation between date of ear emergence and any of the other ear characters, nor is there an invariable correlated response in one particular direction. Both these points seem to rule out large pleiotropic effects of single genes or gene combinations.

A more probable mechanism for these changes is the linkage of genes controlling ear characters with those controlling date of heading in the same balanced combinations. Selection for early and late date of heading will thus result in the reassortment of these genes controlling ear characters. This reassortment of linked genes as a result of selection for one particular character was first suggested by Mather and Harrison (1949) to explain the irregular pattern of correlated response to selection for high and low chaeta number in *Drosophila*.

Changes may also occur as a result of the chance association of genes in the parents selected. Clayton, Knight, Morris and Robertson (1957), for instance, working on *Drosophila melanogaster*, conclude that if the genetic correlation between two characters is low, the main source of correlated response is genetic sampling, especially in small populations. In the present work on *Lolium* the genetic correlations are low, and the chance association of genes is likely to be intensified by the small number of parents selected in each generation.

9. SUMMARY

1. A number of ear characters have been recorded in initial populations of Irish and Kent ryegrass, and in three generations of families selected for early and late ear emergence. The heritability of each character has been calculated from the analysis of clonal replicates and from parent-progeny regression, and the phenotypic and genetic correlations between the characters and their correlated response to selection have also been estimated.

2. Total length, ear length, spikelet number and length of empty glume are highly heritable in both strains, with considerable additive genetic variation. Floret number and length of spikelet show little genetic variation in Irish but more in Kent.

3. Pronounced inbreeding depression is shown by the ear length group of measurements, but not by the spikelet measurements. The four-way mating system, based on four unrelated plants, was sufficient to maintain vigour for all characters during the three generations of selection.

4. The corresponding phenotypic and genetic correlations were usually of the same order and in the same direction. There were few significant correlations between date of ear emergence and the other

ear measurements and it should be possible to select independently for most of these characters.

5. Although changes in ear characters occurred in some of the selection lines, they were not inevitable, and not always in the same direction. It is suggested that these changes result either from the chance association of genes in the parents selected in each generation or from linkage, rather than from large pleiotropic effects.

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