VARIATION IN WILD POPULATIONS OF *PAPAVER DUBIUM*

XII. DIRECTION OF DOMINANCE DURING DEVELOPMENT

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SUMMARY

Five juvenile characters which increased or decreased regularly during development showed dominance in the direction of rapid development throughout the vegetative stage. For these characters, a difference between the mean of the F_1 's and the mean of corresponding inbreds appeared very early in the life cycle and was maintained thereafter, sometimes being augmented by more rapid growth of F_1 's than of inbreds. Two other characters, while agreeing in general with this pattern of growth, deviated from it at one stage of their development.

1. INTRODUCTION

EARLIER results on potence for juvenile characters in *Papaver dubium* have been interpreted as indicating dominance and hence natural selection in the direction of rapid development (Arthur, Rana, Gale, Humphreys and Lawrence, 1973; Gale, Solomon, Thomas and Zuberi, 1976). However, in these earlier studies, specific characters were measured only once or twice during the life cycle. It is possible, therefore, that the direction of potence for a given character at the times at which measurements were made is not typical of the performance for that character throughout the vegetative stage. By making repeated estimates of potence throughout the juvenile stage we can determine when the directional potence first appears and whether it persists up to time of flowering. Should such persistence be found, we can establish whether F_1 's regularly grow faster than the corresponding inbreds or, alternatively, whether on average F_1 's grow at the same rate as inbreds once the initial difference in performance between F_1 's and inbreds has appeared.

2. MATERIALS AND METHODS

Two inbred lines from each of five natural populations (Wellesbourne, Luddington, Welford, Blakedown, University) were selfed and crossed reciprocally, thus giving one augmented biparental set of crosses per population, each set comprising reciprocal F_1 's and the two parents selfed, making 20 families in all. Five progeny plants were raised per family.

The following characters were measured: elevation (E), length (L), width (W) and number of leaflets (LE) of the outermost leaf; leaf number (LN), height (H) and diameter (D) of the plant. Measurements were made at half-weekly intervals and were started as early as possible, at $1\frac{1}{2}$ weeks after sowing for all characters except for E and LE. It is very difficult to score E before 3 weeks after sowing and scoring of LE must await the appearance of the first dissected (rather than the earlier spade-shaped)

leaves. Scoring of E and LE began at 3 and $2\frac{1}{2}$ weeks after sowing respectively.

Plants were (in accordance with our usual practice) initially raised in the glasshouse, moved to cold frames immediately after the $4\frac{1}{2}$ -week measurements and planted in the experimental field immediately after the 7-week measurements.

Measurements of L, W, H and D were continued up to the time when the first plant flowered (14 weeks after sowing). By 11 weeks, LE and LN were becoming too large for accurate scoring and measurements had to be discontinued. E cannot be scored accurately in the field, so measurements for that character ceased after week 7.

3. ANALYSIS OF RESULTS

Let $F_1(t_1)$, $F_1(t_2)$ represent the performance of an F_1 plant at time t_1 , t_2 respectively and let $P(t_1)$, $P(t_2)$ be the corresponding performances of an inbred plant. If, on average, F_1 's grow at the same rate as inbreds over the time interval $(t_2 - t_1)$, that is

$$\frac{E\{F_1(t_2)\}}{E\{F_1(t_1)\}} = \frac{E\{P(t_2)\}}{E\{P(t_1)\}}$$

we have

$$\begin{aligned} \log E\{F_1(t_2)\} - \log E\{F_1(t_1)\} &= \log E\{P(t_2)\} - \log E\{P(t_1)\} \\ \text{i.e. } \log E\{F_1(t_2)\} - \log E\{P(t_2)\} &= \log E\{F_1(t_1)\} - \log E\{P(t_1)\} \end{aligned}$$

Hence if we regress the logarithms of the estimated means, namely $\log \bar{F}_1$ and $\log \bar{P}$ against time we shall, given equal growth rates, obtain two parallel lines. This will happen irrespective of whether or not growth is exponential, although only if growth is exponential will the regression lines be straight.

We may note in passing that it would not be appropriate, for the *present* set of data, to transform the individual observations to logarithms and regress the means of the logarithms $\log \bar{F}_1$, $\log \bar{P}$. For if (as happened in practice) C the coefficient of variation is small we have, to a good approximation

$$E(\log x) = \log E(x) - \frac{1}{2}C^2$$

Thus a difference between lines in mean logarithm will represent a difference between lines in the logarithm of the mean only if F_1 's and inbreds have the same coefficient of variation for a given character; in general, we have found this not to hold for our characters. Thus we must regress $\log \bar{F}_1$, $\log \bar{P}$ with the disadvantage that within-family variation cannot be used to supply an estimate of error.

In that our results indicate that the standard error of the overall mean for a given character increased linearly with the mean itself as plants developed, log means should have about the same variances at the different stages of the experiment, so that an unweighted regression analysis will be appropriate.

One further problem is the damage (which seems inevitable) during planting; in the present case, plants recovered rather slowly from this damage, presumably due to cold weather. Some characters therefore showed a marked decline after transplanting and did not fully recover

for some weeks. We decided, therefore, to exclude the $7\frac{1}{2}$ - $9\frac{1}{2}$ week results, inclusive, for L, W and D and have, for each of these, carried out separate analyses for the periods before planting and after 10 weeks; for LN, where recovery was quicker, we have similarly excluded the $7\frac{1}{2}$ - $8\frac{1}{2}$ week results. For height, we have carried out separate analyses for the first increasing phase, the decreasing phase and second increasing phase (see fig. 4 below).

4. RESULTS

To illustrate the analysis, we give in table 1 results and analysis of variance for L over the period $1\frac{1}{2}$ -7 weeks (inclusive). In this table, "lines"

TABLE 1
Results and analysis of variance for leaf length

Time (weeks)	$\text{Log}_e \bar{P}$	$\text{Log}_e \bar{F}_1$			
$1\frac{1}{2}$	1.5217	1.6174			
2	2.2680	2.3046			
$2\frac{1}{2}$	2.6561	2.6783			
3	2.9339	2.9560			
$3\frac{1}{2}$	3.3308	3.3824			
4	3.6174	3.6307			
$4\frac{1}{2}$	3.9072	3.9489			
5	4.0332	4.0566			
$5\frac{1}{2}$	4.2262	4.2405			
6	4.4280	4.4771			
$6\frac{1}{2}$	4.6369	4.6819			
7	4.7350	4.7746			

Item	S.S.	d.f.	M.S.	V.R.	P
Lines	0.008618	1	0.008618	47.1	<0.1%
Linear	21.111905	1	21.111905	115365.6	<0.1%
Quadratic	0.872653	1	0.872653	4768.6	<0.1%
Remainder	0.133017	9	0.014780	80.8	<0.1%
Lines $\times$ Linear	0.000177	1	0.000177	<1	N.S.
Lines $\times$ Quadratic	0.000972	1	0.000972	5.3	5-2½%
Lines $\times$ Remainder	0.001644	9	0.000183	—	—

refers to the average difference over time between $\log \bar{F}_1$ and $\log \bar{P}$. The lines $\times$ remainder mean square was used as error throughout. A similar analysis was used for other characters. Linear, quadratic and residual mean squares always came out significant but in spite of the significant residuals we have not attempted to fit higher order regressions. For the data in table 1, (linear + quadratic) accounts for over 99 per cent of the between-times variation, the corresponding figure for the other analyses exceeding 94 per cent apart from one special case of 89 per cent (for height at $6\frac{1}{2}$ - $8\frac{1}{2}$ weeks) to be discussed below. It became clear on inspection of the graphs of log mean against time (see *e.g.* figs. 1 and 2) that the residual variation represents irregularities in growth due presumably to irregular variation in the environment and has very little biological significance in the present context.

In table 2, we summarise our results in terms of average values over time of $\log \bar{P}$ and $\log \bar{F}_1$ and also give estimates $\hat{b}_1$ and $\hat{b}_2$ of linear and

TABLE 2
Means and regression coefficients

Character	Time (weeks)	t	c	Mean		b_1		b_1	
				P	F_1	P	F_1	P	F_1
L	1½-7	4.25	2.9792	3.5245	3.5624	***	0.5418	-0.0747	-0.0699
L	10-14	12.00	1.6667	4.8785	4.9338	***	0.1483	0.0181	0.0126
W	1½-7	4.25	2.9792	2.3084	2.3463	***	0.4966	-0.0861	-0.0853
W	10-14	12.00	1.6667	3.7756	3.8219	***	0.2087	0.0388	0.0353
D	1½-7	4.25	2.9792	3.9029	3.9417	***	0.6202	-0.0919	-0.0884
D	10-14	12.00	1.6667	5.5042	5.5661	***	0.1541	0.0141	0.0133
E	3-7	5.00	1.6667	2.6886	2.5169	**	-0.7346	-0.1373	-0.1989
LE	2½-11	7.25	5.3125	2.0824	2.1267	***	0.3909	-0.0182	-0.0208
LN	1½-7	4.25	2.9792	2.0650	2.0896	***	0.4581	-0.0726	-0.0686
LN	9-11	10.00	0.5000	3.3147	3.3154		0.1589	0.0555	0.0455
H	1½-6½	4.00	2.5000	3.2927	3.3180	*	0.4151	-0.0552	-0.0490
H	6½-8½	7.50	0.5000	3.6469	3.5921		-0.5621	0.0982	0.1349
H	8½-14	11.25	2.9792	3.7108	3.6737	*	0.2242	0.0517	0.0564

Significant levels refer to the difference between values for inbreds and F_1 's.

quadratic regression coefficients; to preserve comparability for characters measured at different times, these regression coefficients are defined in terms of the equation

$$y = \bar{y} + b_1 (t - \bar{t}) + b_2 \{ (t - \bar{t})^2 - c \}$$

where y is the fitted value of the log mean at time t and c is a constant which is easily found from tables of orthogonal polynomials and is entered for each case in table 2. We also give significance levels for differences between inbreds and F_1 's for average values and regression coefficients. Statistical significance does not, of course, necessarily imply biological importance, which must be determined from the effect of differences in regression coefficients on the magnitude of differences between regression lines at various times. In the present case, however, differences which are significant turn out to be important.

Results for L, W and D are rather similar. In each case, $\log \bar{F}_1$ exceeds $\log \bar{P}$ from the start and this difference remains near-constant in magnitude for the first half of the vegetative stage. Towards the end of the vegetative stage, however, F_1 's show more rapid growth than inbreds, leading to a more marked difference in favour of F_1 's (see fig. 1). In the case of E (which, unlike the other characters steadily falls during development) a

FIG. 1. Change of logarithm of mean leaf length with time.

difference indicating more rapid development of F_1 's first appears on the second occasion of measurement. Some 2 weeks later, a marked difference of growth rate between F_1 's and inbreds (table 2) becomes noticeable, leading to a large difference between lines by 7 weeks after sowing (see fig. 2). For LE $\log \bar{F}_1$ exceeded $\log \bar{P}$ from the third occasion of measurement onwards, after which the difference persisted up to the last occasion of measurement (11 weeks) with no significant differences in growth rate (table 2). The slight initial delay in establishing F_1 superiority may have

FIG. 2. Change of logarithm of mean elevation with time.

little significance. At the earliest stages, some plants were still producing only spade-shaped leaves; these plants were scored as having one leaflet. Perhaps the slightly anomalous results were due to this.

Thus for L, W, D, E and LE potence for all, or nearly all, the vegetative stage scored was in the direction of rapid development, appearing very early in the life cycle and thereafter being maintained and sometimes augmented.

For LN, results were not so clear-cut. A difference in favour of the F_1 's appeared on the first occasion of measurement, but over the period 1½-7 weeks F_1 's showed a significantly lower growth rate than inbreds, leading to a slow convergence of the fitted lines, although both for the actual data (fig. 3) and for the fitted lines the F_1 was still slightly superior at 7 weeks. During the period 9-11 weeks, no significant differences between lines were detected. Now in the dominance study of Gale *et al.* (1976) significant *overall* potence for greater leaf number was detected at this late stage, but for the four sets common to both experiments no significant potence for leaf number was detected; hence the two sets of results are not in fact discrepant. Moreover, in view of the significantly slower growth rate of F_1 's at an earlier stage, the absence of detectable potence at this late stage is unlikely to be due to the smallish size of the experiment or to chance close similarity between parental inbred lines in the same set for genes controlling leaf number at the late stage. The fade-out of potence at this stage must therefore be accepted as genuine for the sets used in the present experiment. The previous results show that some other sets still show potence at this stage. We conclude that the proportion of loci controlling leaf number which show dominance is smaller at the late than at the early vegetative stage, with the implication that for this character natural selection

changes during development from mainly directional to more stabilising in type.

Finally, we consider H (fig. 4). We have plotted values and carried out separate analyses for $1\frac{1}{2}$ - $6\frac{1}{2}$ weeks inclusive, $6\frac{1}{2}$ - $8\frac{1}{2}$ weeks inclusive and $8\frac{1}{2}$ -14 weeks inclusive in order to ascertain behaviour of the plants during the three fairly distinct phases of development for this character. With potency in the direction of more rapid development, we should expect F_1 's to be taller than inbreds in the first ascending phase of growth, shorter than inbreds in the descending phase and taller than inbreds in the second ascending phase. Most, but not all, of our results are in accordance with this expectation. F_1 's were taller than inbreds throughout the first ascending

FIG. 3. Change of logarithm of mean leaf number with time.

FIG. 4. Change of logarithm of mean height with time.

phase; the significantly smaller value of b_1 for F_1 's than for inbreds during this phase presumably indicating the more rapid approach of F_1 's to the descending phase. During the latter (for which the regression has as expected a noticeable significant cubic component) the F_1 's are shorter than the inbreds, the difference being not quite significant ($P = 7.6$ per cent). During the second ascending phase, the F_1 's rose at a significantly more rapid rate than inbreds (table 2). The one unexpected result was that the F_1 's reached a lower minimum than the inbreds; several weeks then elapsed before the more rapid growth of the F_1 's raised their height above that of the inbreds. This finding of negative average potency for height at a latish stage of growth does not accord with previous experience and clearly requires further investigation.

Thus all characters studied showed potency in the direction of more rapid development during the first half of the vegetative stage, indicating a past history of natural selection for rapid development. This also holds for the late vegetative stage in the case of L, W, D and LE; for H, the situation is complicated by the low minimum attained by the F_1 's but otherwise accords with selection for rapid development. For LN, selection at this late stage has shifted from directional to a more stabilising type.

One interesting feature is the very early appearance of potency for our characters. This cannot be attributed to differences in the weight of seed from which our plants were raised, since the F_1 seed was slightly lighter than the inbred, although not significantly so. A further possibility is that the F_1 seed germinate before the inbred; using the 16 augmented biparental sets from the previous (Gale *et al.*, 1976) experiment we have found significant potency for short "splitting time", that is the time between treatment of the seed (to encourage germination) and the time at which the testa splits. However, it turned out that only a small proportion of the variation between families for our characters could be attributed to differences between families in splitting time. This being so, it seems unlikely that the difference between F_1 and inbreds for splitting time could be a major antecedent cause of the early potency shown by the other characters. The potency for early splitting is presumably yet another manifestation of selection for rapid development.

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5. REFERENCES

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