

VARIATION IN WILD POPULATIONS OF *PAPAVER DUBIUM* XI. FURTHER STUDIES ON DIRECTION OF DOMINANCE.

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SUMMARY

Previous studies of potence for a small number of metrical traits in *Papaver dubium* suggested that juvenile characters exhibited potence in the direction of rapid development, implying a past history of natural selection for rapid development in the populations studied. In order to check this conclusion, 32 inbred lines were used in an augmented biparental crossing design and 17 characters, of which 12 reflect rate of development, were scored on the progenies. Results confirmed earlier ideas with respect to juvenile characters and flowering time; selection appears to have been for rapid development, but with the optimum not at the extreme of the range. Capsule number and flower diameter also showed substantial potence in the positive direction, but in three other adult characters, potence showed no consistent directional tendencies, suggesting that any selection on these has been of the stabilising type.

1. INTRODUCTION

WITH continued directional selection for a metrical trait, we expect dominance to evolve in the direction of the favoured phenotype, whereas with stabilising selection dominance would be ambidirectional or absent. Hence with stabilising selection little or no potence would be found (Mather, 1960). Thus it should be possible to determine the past history of natural selection for a trait from a study of potence.

In earlier attempts to measure potence in *Papaver dubium* (summarised in Arthur, Rana, Gale, Humphreys and Lawrence, 1973), the plants crossed were not highly inbred. As a result, the magnitude of potence was underestimated (Kearsey, 1970). However, the data gave clear evidence of directional dominance for increased capsule number (CN), as would be expected for such an important component of fitness. For juvenile characters, measured at about 11 weeks after sowing, and for flowering time (FT) results were less clear-cut, dominance apparently being very incomplete but nevertheless with a definite directional trend implying past selection for rapid development for the characters leaf number (LN), diameter (D) and flowering time; data on height (H) and elevation (E), though inconclusive in themselves, were consistent with the notion of selection for rapid development at the juvenile stage. Stigmatic ray number (SR) gave no real indication of dominance, implying stabilising selection for that character.

In the present experiment we have attempted to improve our procedure in a number of ways. Parent plants were from inbred lines (not available at the time of the previous study), with a history of eight successive selfings.

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Secondly, the number of characters scored has been considerably increased, providing a more extensive basis for generalisations about potency, particularly at the juvenile stage. To the juvenile characters previously measured we have added, at five weeks after sowing, length of largest leaf (L5), width of largest leaf (W5), number of leaflets in the largest leaf (LE5) and width of basal dissection of the apical leaflet of the largest leaf (WB5). Elevation was measured at five rather than 11 weeks, the phenotypic range being much greater at the earlier stage; it will now be denoted E5. Leaf number, height and diameter were measured at seven as well as 11 weeks—these will be distinguished as LN7, LN11 and so on. At flowering time, we have the additional characters flower diameter (FD), height (HF) and bud number (BF).

An augmented biparental crossing scheme (Kearsey, 1970) was used as being technically the simplest for our purpose. In this scheme, parent plants are paired up at random and the members of every pair selfed and crossed reciprocally. In an effort to improve precision, the number of offspring per mating was raised to 15.

2. MATERIALS AND METHODS

Thirty-two inbred lines were used, eight lines being ultimately derived from each of the following natural populations: Wellesbourne, Welford, Blakedown and University campus. As we are interested here in potency within populations, plants were crossed to plants from the same population, *i.e.* for every population, the eight inbred lines were paired at random and the members of a pair crossed reciprocally and selfed. Thus there were 16 augmented biparental sets of crosses (four per population), each set comprising reciprocal F_1 's and the two parents selfed, making 64 families in all. Fifteen progeny plants were raised per family.

As stated above, the magnitude of potency will be underestimated unless parent plants are highly inbred. Hence it is important to determine, at least approximately, how much residual heterozygosity was present in our inbred lines. For *P. dubium* this is straightforward, since natural selection during the course of inbreeding is not substantial. This being so, the probability that the total length heterozygous in a given line exceeds X morgans is (Fisher, 1965, p. 114)

$$e^{-X/a} e^{-m} \left\{ (e^m - 1) + \frac{X}{1!a} (e^m - 1 - m) + \frac{X^2}{2!a^2} \left(e^m - 1 - m - \frac{m^2}{2!} \right) + \dots \right\}$$

where m = expected number of heterozygous tracts per line and a = expected length of such a tract. Now *P. dubium* has 21 pairs of chromosomes ($v = 21$) and a total map length (L) of about 17 morgans (Humphreys, personal communication). Moreover, the number of successive selfings (n) was 8. Thus we have (Bennett, 1953, 1954; Fisher, 1954).

$$m = L\left(\frac{1}{2}\right)^n (2n + v/L) = 1.1445$$

$$a = L\left(\frac{1}{2}\right)^n / m = 0.05802 \text{ morgans,}$$

from which it appears that the probability of total length heterozygous in a given line exceeding 0.5 morgans is only 0.0023. Thus the probability that none of our 32 lines has a total length heterozygous exceeding 0.5 morgans is

$$(1 - 0.0023)^{32} = 0.93.$$

The above argument assumes that the wild plants from which the lines were derived were completely heterozygous. In fact, the wild plants were already fairly homozygous, particularly since selfing is common in this species (Humphreys and Gale, 1974). Thus there will be very little residual heterozygosity in our lines and thus no serious tendency to underestimate potency.

3. RESULTS

The results are summarised in table 1, where we give, for each character, the overall mean of selfed progenies and corresponding overall mean of F_1 progenies.

TABLE 1
Summary of results from progenies of augmented biparental matings

Character	Mean of selfs	Mean of F_1 's	Number of sets with potency		χ_1^2	Number of sets showing heterosis	
			+ve	-ve		for rapid development	for slow development
E5	23.87	19.47	2	14	9.00**	9	1
L5	57.71	62.15	15	1	12.25***	9	1
W5	12.85	14.08	16	0	16.00***	9	0
LE5	4.22	4.66	15	1	12.25***	9	0
WB5	2.68	3.10	14	2	9.00**	8	1
LN7	19.85	20.38	12	4	4.00*	4	0
LN11	25.41	26.51	14	2	9.00**	6	1
H7	70.35	66.32	4	12	4.00*	6	1
H11	44.10	45.57	12	4	4.00*	5	0
D7	227.11	238.62	14	2	9.00**	8	1
D11	286.27	313.50	16	0	16.00***	8	0
FT	27.03	25.87	4	12	4.00*	3	0
FD	73.79	75.88	14	2	9.00**	—	—
HF	480.77	488.71	11	5	2.25	—	—
BF	23.71	25.72	10	6	1.00	—	—
SR	21.56	21.81	10	5	1.67	—	—
CN	102.33	117.58	16	0	16.00***	—	—

Twelve sets showed heterosis for greater capsule number and 7 sets heterosis for greater flower diameter.

We have tested the significance of potency in two ways. The first is the analysis of variance, in which we calculate, for each character, the following mean squares:

Average potency (1 d.f.)

Potency \times populations (3 d.f.)

Potency \times sets within populations (12 d.f.)

Within families (896 d.f. in cases where no plants were missing)

A few plants died before all characters could be measured (27 by the end of the season). Hence analyses were carried out on family means, the within family mean square being divided by the harmonic mean of the number of plants scored for the given character in each of the 64 families.

Apart from SR and CN, all characters gave a significant potency \times sets within populations mean square. The potency \times sets within populations

mean square, being significant, was the appropriate mean square for testing the potence \times populations item for all characters except SR and CN and was used also in the latter cases to preserve comparability.

Potence \times populations was significant only for LE5 and SR. Thus for all characters except two, potence was much the same in magnitude and direction in the different populations, suggesting that optimum phenotypes were much the same in the different populations.

Average potence can, of course, be tested using as error the potence \times populations mean square; when the latter was non-significant, it was pooled with the potence \times sets within populations mean square to give a combined error mean square for 15 d.f. However, an alternative approach is available; we count the number of sets in which estimated potence is positive and the number of sets in which it is negative and test for departure from 1:1 by the usual χ^2 test. Results are given in table 1 (for SR, one set gave no potence). We should note that the two approaches are not strictly equivalent, in that the analysis of variance will detect potence *on average* whereas the sign test detects the presence of potence which is consistent in direction *in general*. In practice, the two approaches gave consistent results except for LE5 and H11; in both cases a significant χ^2 was obtained but average potence was not significant. For LE5, with 15 cases of positive potence, the discrepancy is very marked, but is not a problem. The source of the discrepancy is the very low sensitivity of the analysis of variance for detecting mean potence for this character, since the potence \times populations mean square with only 3 d.f. had to be used as error. Thus for LE5, the sign test is decidedly the most appropriate. We discuss H11 in the next section.

4. INFERRED TYPE OF NATURAL SELECTION

If the fittest genotype lies at or near the extreme of the genotype range, we expect complete dominance at all or most loci, dominance always being in the same direction. Thus potence would be in the same direction in all sets (apart from the odd case due to sampling error) and would usually be accompanied by heterosis, *i.e.* the F_1 mean would exceed that of the fitter self-progeny in the same set. Capsule number, in which potence was always positive (*i.e.* towards more capsules) and heterosis was found in 12 sets, comes closest to the situation just described, so that we infer that selection for this character is strongly directional towards more capsules, thus confirming conclusions reached previously.

For the juvenile characters and flowering time, potence was consistent in direction for most sets, although complete consistency was found only for W5 and D11. However, for all such characters, the number of sets with positive potence: the number of sets with negative potence always departed significantly from 1:1. Now, if we take a group of *P. dubium* plants and observe how the mean for various characters changes with time, we find that during the course of development elevation steadily falls, whereas length, width and number of leaflets of the largest leaf and also leaf number and diameter steadily rise. Width of basal dissection follows a rather irregular course, but is definitely increasing around the time when measurements were made in the present experiment. Height follows a complicated but highly repeatable pattern, falling in the middle juvenile stage but rising in the late juvenile stage; in the present experiment, average height was still falling at

seven weeks but rising at 11 weeks. Thus all the juvenile characters and flowering time show the same pattern, potence being in the direction of more rapid development, implying selection for rapid development, at least up to the time of flowering. We may note in passing that in the case of height, where selection for rapid development will lead to negative potence at one stage but positive potence later, we may expect the odd set in which at 11 weeks potence is not merely in the "wrong" direction but fairly large in magnitude, representing a laggardly set. For H11, one set did show large negative potence; as a result average potence was not significant in the analysis of variance, in spite of the fact that a significant majority of sets showed potence.

In that selection has been for rapid development, a set will be said to show heterosis for a juvenile character or for flowering time if, on average, the F_1 shows more rapid development than the most rapidly developing of the two corresponding selfs. It will be seen from table 1 that, for these characters, the number of sets showing heterosis for a given character did not exceed nine and that for some characters one set showed heterosis in the "wrong" direction, *i.e.* the F_1 was slower developing than the slower self. Perhaps these cases of heterosis in the wrong direction should not be taken too seriously, since none was significant, whereas out of the 84 cases of heterosis in the right direction, 20 were significant. However, these results do suggest that dominance is less complete than in the case of CN. The data on potence confirms this; while there were (see table 1) 166 cases of potence in the right direction (91 significant) there were 26 cases in the wrong direction. Six of the latter turned out to be significant. While two of these involve H11 and may thus represent laggardly sets, two of the remaining four were highly significant ($P < 0.1$ per cent) and therefore unlikely to be due to chance, in spite of the fact that we have carried out so many tests. Thus we may conclude with confidence that for juvenile characters and flowering time, dominance is directional but not complete. Hence while rapidly developing plants are at a selective advantage, the optimum is not at the extreme of the range. As was suggested earlier (Arthur *et al.*, 1973) plants with genotypes conferring very rapid juvenile development might show a tendency to premature rapid development of the seedling, during a temporary period of mild weather in winter or early spring and thus be under a selective disadvantage in some years.

Finally, we consider characters measured at flowering time. Of these, only flower diameter showed significant directional potence, indicating larger flowers as selectively advantageous. Height and bud number both gave some indication of ambidirectional dominance; neither showed significant average potence but for height two sets gave significant positive and three sets significant negative potence and for buds six sets gave significant positive and four sets significant negative potence. Stigmatic ray number showed no significant average potence and indeed potence reached significance in one set only. It seems then that any selection operating on height at flowering time, bud number or stigmatic ray number is stabilising in type.

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