

## VARIATION IN WILD POPULATIONS OF *PAPAVER DUBIUM*

### IX. LIMITED POSSIBILITIES FOR ASSORTATIVE MATING

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Received 24.viii.73

#### SUMMARY

Natural populations of *Papaver dubium* have a high frequency of homozygotes at polymorphic loci. A population was investigated with a view to ascertaining whether this homozygosity is due, in part, to assortative mating for flowering time. Successive flowers on a given plant tended to appear throughout the flowering season, the average interval between successive flowers being very much larger for plants with few than for plants with many flowers. As a result in outcrosses the correlation between mates for flowering time was very low. The same is probably true for many natural populations, since the flowering time of plants raised from seed obtained from six natural populations depended very little on when in the season the seed was collected.

#### 1. INTRODUCTION

IN the first paper in this series (Lawrence, 1965) it was suggested that, in natural populations of *Papaver dubium*, homozygotes at polymorphic loci are present at a much higher frequency than would be expected on the assumption of random mating. More recently, we have obtained further evidence supporting this suggestion. Thus we have been able to establish and maintain inbred lines with little difficulty; out of 50 lines, originating from five natural populations, 48 are still present in the ninth generation of selfing. While the presence of heterosis for the fitness character capsule number (Arthur, Rana, Gale, Humphreys and Lawrence, 1973) shows that some inbreeding depression must have occurred in the formation of these lines, the absence of an inbreeding crisis indicates that inbreeding depression is a relatively minor phenomenon in this species. Moreover, recessive morphological mutants have failed to appear on inbreeding, apart from one flower colour mutant, magenta, which appeared in some lines originating from one of our populations. In striking contrast, one round of sib-mating of the self-incompatible sister species *Papaver rhoeas* produced the usual array of individuals which were chlorophyll deficient, male sterile, female sterile or had white flowers (Ooi, personal communication).

Further supporting evidence comes from an interesting comparison within *P. dubium* and *P. rhoeas* in respect of the distribution of variation within and between families, for populations in which the two species grow together (Ooi, personal communication). Open pollinated capsules were collected from three natural populations; plants were raised on the experimental field in the following year and scored for the same seven metrical characters in both species, so that 21 comparisons could be made between the two species. Using the term "family" to denote a group of individuals having a common mother, it was found that within-family variation tended

to be larger in *P. rhoeas* than in *P. dubium*, whereas the reverse was usually true for between-family variation. As a result, the proportion of total variation attributable to differences between families was larger in *P. dubium* than in *P. rhoeas* in 19 out of 21 cases. Although it is not possible to give a unique interpretation of these results, the differences found are in the direction expected on the hypothesis that *P. dubium* inbreeds to a considerable extent, since *P. rhoeas* is known to be an obligate outbreeder, and this hypothesis provides much the simplest explanation of the data.

A relatively high degree of homozygosity at polymorphic loci in *P. dubium* could arise from (a) selfing, (b) assortative mating and possibly (c) excessive sib-mating resulting from poor seed dispersal leading to sibs growing up in close proximity. It has been shown (Humphreys and Gale, 1974) that, under experimental field conditions, about 75 per cent of seed produced derives from selfing; almost certainly this obtains also in the natural habitat, for reasons given in the reference cited. However, there remains the possibility that some of the homozygosity arises from assortative mating. In order, therefore, to complement these results, we shall describe briefly results obtained some years ago, which indicate that assortative mating is unlikely to be of major importance in this species.

## 2. SITUATIONS IN WHICH ASSORTATIVE MATING COULD OCCUR

In *P. dubium*, flowers normally open soon after dawn and the petals usually fall on the morning of the same day. Thus in a population in which most plants produced only a single flower, assortative mating for flowering time would be inevitable, since plants could mate only with those flowering on the same day. If plants produce more than one flower, the situation is more complicated. Defining flowering time (FT for short) as the time of opening of the *first* flower, we see that if successive flowers on the same plant open at widely separated intervals, then there would be little assortative mating for flowering time; for example, pollen from a second flower on an early flowering plant could be conveyed (by bees) to a first flower on a late flowering plant. In contrast, if different flowers on the same plant appeared in rapid succession, a marked degree of assortative mating would still obtain. Assortative mating for FT would, of course, lead to assortative mating for characters correlated with FT.

Thus our problem may be considered under two heads. Firstly, we consider whether populations in which a considerable proportion of plants bear just one flower are common. Even if such populations contain a number of plants with two or more flowers, the one-flowered plants would often cross *inter se*, giving rise to a degree of assortative mating. Certainly, such populations do exist (Salisbury, 1942). On the other hand, our own experience, mainly on populations in the Midlands, indicates that such "one-flowered" populations are unusual, except perhaps in cases where the soil is very poor. Thus, at least for the Midlands, we may conclude that assortative mating is unlikely to arise in the manner just described.

We therefore consider populations in which a number of flowers normally appear on a single plant. We shall describe an investigation on one such population, designed to determine intervals between the opening of successive flowers on a given plant and the extent to which the average interval between successive flowers varies from one plant to another.

## 3. MATERIALS AND METHODS

The population under study, which is known to have genetical variation for flowering time, has been described previously (Arthur, Gale and Lawrence, 1973). Two previously grassed-over plots ("north" and "south" plots) were cleared in October 1964 and about 100,000 seeds from about 100 plants growing on the University campus at a distance of about 300-400 metres from the plot were scattered on each plot. No fertiliser was given and no weeding carried out; thus we have attempted to simulate conditions which new populations of poppies encounter in nature.

A random sample of 96 plants on the north plot and of 90 plants on the south plot was taken and the time of opening of all flowers on these plants was noted.

## 4. INTERVAL BETWEEN SUCCESSIVE FLOWERS ON A GIVEN PLANT

Flowering began on 19th June. The last plant in our sample to come into flower did so on 18th July. Production of flowers continued into autumn, but throughout we shall disregard flowers opening after 8th September, since germination tests showed that the capacity to produce viable seed was lost, rather abruptly, at about this time. A few abnormal flowers which appeared at odd times have also been excluded. In our experience, almost all open pollinated flowers which appear normal set seed, provided that they do not open very late in the season, and this was also true for the present experiment.

Three plants proved to have one flower only. For every one of the remaining 183 plants, we calculated the average interval between successive flowers, defined as follows. We take the intervals, in days, between the opening of every pair of successive flowers (first-second, second-third, third-fourth, etc.) on the plant and average these intervals. This is the same as calculating

$$(\text{time of opening of last flower} - \text{time of opening of first flower}) / (\text{number of flowers} - 1).$$

The average interval varied widely with plant, ranging from 3.0 to 61.0 days. However, on plotting (figs. 1 and 2) average interval against number of flowers per plant, a major source of this variation became apparent. Plants with few flowers tend to spread them over a long period; for two-flowered plants this interval is about 37 days, rather longer than the 29 days required for all plants to come into flower. Rapid succession of flowers is found (apart from rare cases) only on plants with many flowers. It is clear from the graphs that plants with four or more flowers will, on average, be producing flowers over some two-thirds or more of the flowering season (82 days). For example, an average plant with the modal number of flowers, five, has an average interval of 14.42 days (using data from both plots). It therefore flowers over a proportion

$$(1 + 4 \times 14.42) / 82 = 0.72$$

of the flowering period. For three-flowered plants, the corresponding figure is 0.60. Clearly this is not a situation which will give rise to assortative mating.

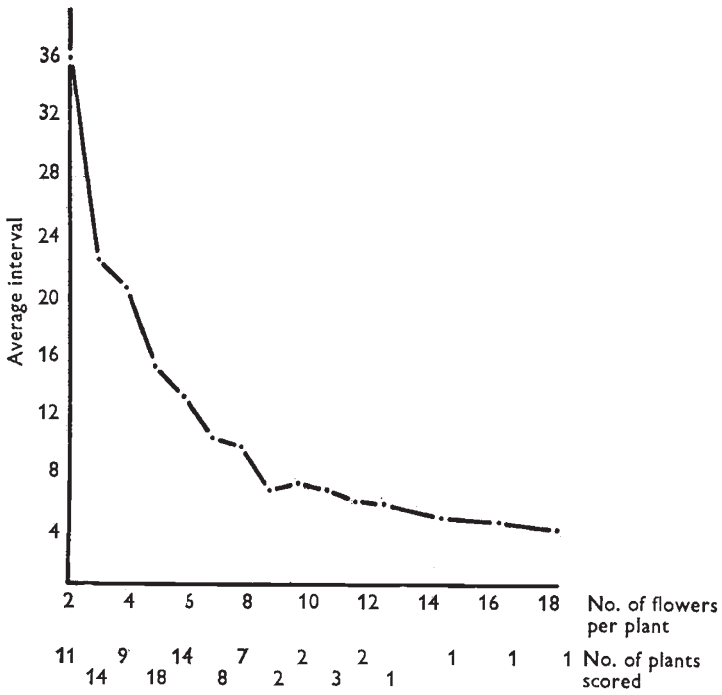


FIG. 1.—Decline of average interval (days) with number of flowers. North plot.

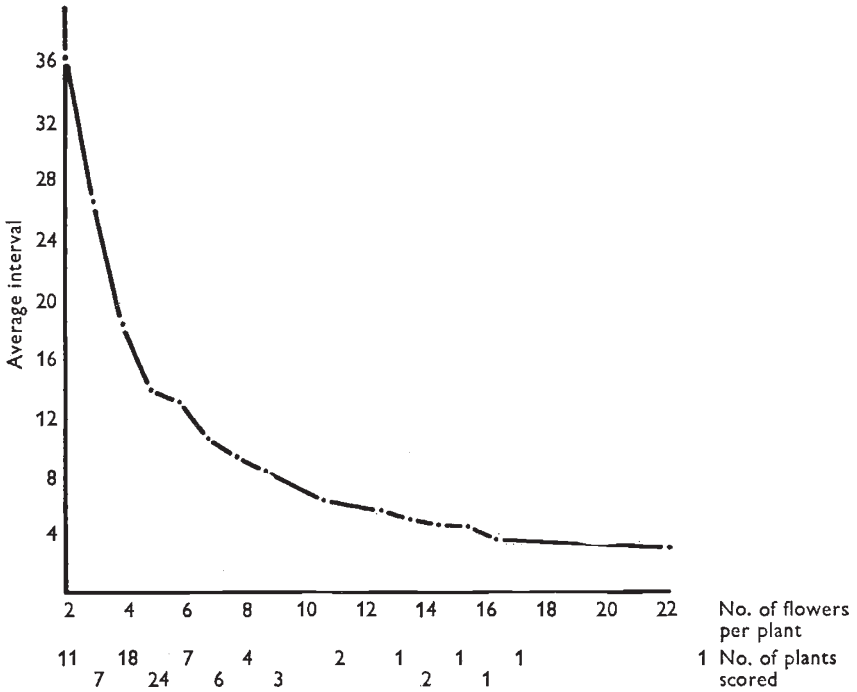


FIG. 2.—Decline of average interval (days) with number of flowers. South plot.

## 5. NUMBER OF MATES AVAILABLE TO A GIVEN PLANT

We may represent our results in a slightly different way by first asking: with how many plants on the same plot *could* a given plant cross? That is, how many plants have a flower open on one or other of the days on which the given plant has a flower open? Since the distributions of number of flowers per plant and also of average interval are similar in the two plots, we have carried out this (rather laborious) analysis for the south plot only.

Since there were 90 plants in the sample on the south plot, a given plant could outcross with up to 89 of the others. Out of the latter, some will be "available mates" for the given plant, in that any one of them could have crossed with the given plant at some stage in the season. Some of these available mates will have the same FT as the given plant; if these were to form a substantial proportion of the available mates, a considerable degree of assortative mating would occur.

Values for the number of available mates, both those with the same and those with different FT, varied a great deal from one plant to another. However, on averaging available mates over all given plants with the same number of flowers, a simple picture emerged, illustrated in fig. 3.

The tendency for number of available mates having the same FT as the given plant to increase with number of flowers per plant, although small and only just statistically significant, is probably genuine. Plants which will ultimately have a small number of flowers tend also to flower late (Arthur *et al.*, 1973); such plants with a late FT comprise only a small part of the population, so that few plants with the same FT are present.

The sharp rise in number of available mates, with a different FT to that of the given plant, as the number of flowers per plant rises, illustrates how critical is the distribution of number of flowers per plant in the population as a whole. In our case, averaging over all 90 plants in our sample, we find that the average number of available mates with the same FT was 6.27 (6.96 per cent) and of those with a different FT 23.36 (26.17 per cent), so that a plant, when outcrossing, usually crossed with a plant having a different FT. There remains the possibility that among the latter, there were a disproportionate number of plants with FT similar to that of the given plant. That this was not the case is easily demonstrated. We obtain a crude estimate of the marital correlation for outcrosses by picking, for every plant, a mate chosen at random from all its available mates and calculate the correlation between FT of plant and of chosen mate. The resulting estimate proved to be 0.12.

One qualification must, however, be made. The number of seeds produced by earlier flowers on a given plant is larger than that produced by later flowers. Thus it is not strictly correct to treat all flowers equally, as we have in fact done. Thus were it the case that later flowers contributed very little to the next generation, it would indeed be best to omit them from our calculations. Generally, some system of weighting flowers by seed output should be employed, but since we have seed counts for alternate flowers only, we have not attempted any weighting, as this would involve estimating seed output for many of the capsules by interpolation or extrapolation of dubious validity. For example, for plants with four capsules we would have a regression curve based on two points only for estimating

seed output for capsules two and four; we have no reliable method for finding the shape of this curve, which is almost certainly not linear.

On the other hand, the importance of this difficulty should not be exaggerated. Thus (Arthur *et al.*, 1973) for plants having the modal capsule

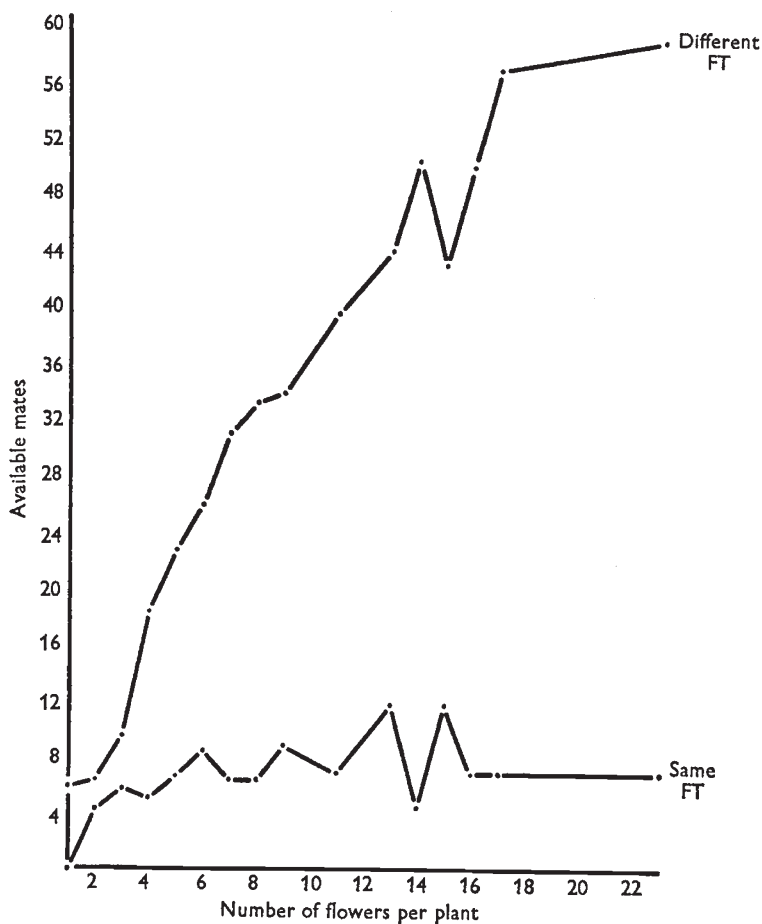


FIG. 3.—Number of available mates out of a possible maximum of 89.

number of five, average seed counts for the first, third and fifth capsules proved to be

644, 342, 236

respectively. Clearly, the later flowers do make a substantial contribution to total seed output. Further details leading to the same conclusion are given in the reference cited.

Moreover, we have exaggerated the possibility of assortative mating by counting all plants equally. In practice, a quite disproportionate amount of total seed production will come from plants with many flowers, particularly since these produce a disproportionately large amount of seed per flower (Arthur *et al.*, 1973). As we have shown, it is just these plants which are most likely when outcrossing to mate with plants with a different FT.

## 6. THE SITUATION IN OTHER POPULATIONS

We now consider whether our conclusions can be generalised to other populations. Here we shall use an indirect approach. Let us suppose that, in contrast to our experimental population, we have a population in which most plants produce successive flowers over a short period of time. Suppose that we visit such a population at regular intervals during the period when the seed is ripening and collect seeds from ripe capsules. At earlier visits, we should mainly be collecting seed from plants whose first flower appeared early, since seed from plants with a later FT would not yet be ripe. On the other hand, on our last visit, we should obtain seed mainly from plants with a late FT, since seed from plants with an early FT would already have been shed and would not be available for collection.

TABLE 1  
*Contribution of time of collection of seed to total variation for flowering time*

Population	Number of plants raised	Estimated components of variation		
		$\hat{\sigma}_v^2$	$\hat{\sigma}_c^2$	$\hat{\sigma}_w^2$
Wellesbourne	1449	3.9	43.4	38.4
Luddington	927	0.3	15.6	29.0
Welford	269	3.0	33.5	40.2
Blakedown (roadside)	427	2.1	32.6	31.5
Blakedown (field)	1109	1.5	32.2	32.6
University	698	0.0	16.6	29.5

$\hat{\sigma}_v^2$  = Between visits component.

$\hat{\sigma}_c^2$  = Within visits, between capsules component.

$\hat{\sigma}_w^2$  = Within capsules component.

Six natural populations, all showing heritable variation for FT, were visited at fortnightly intervals in 1965, the first visit being made when the seed began to ripen and the last when seed production appeared to be at an end. The number of visits to the various populations were as follows:

Wellesbourne 5, Luddington 6, Welford 5, Blakedown (roadside) 5, Blakedown (field) 4, University campus 4.

Plants were raised from this seed in 1966 and scored for FT. For five populations, no significant differences between plants derived from seed obtained on different visits were detected. For the Wellesbourne population, a significant difference was found, but it was noticeable that this arose because plants derived from the first visit flowered earlier than those from other visits. For the latter, no significant differences between visits were found. The experiment was on a large scale, so that all but the most trivial differences were readily detectable. Probably the anomalous result at Wellesbourne was due to our having collected, on the first visit, capsules deriving mainly from first flowers on plants with an early FT.

The situation is perhaps most clearly illustrated by the values of estimated components of variance, given in table 1. It will be seen that the between-visits component contributes very little to total variation in any of our populations.

These results could be reconciled with the hypothesis that assortative mating is of importance in our species if we assume that seed from plants



with an early FT ripened very much more slowly than seed from plants in the same population with a late FT. Our experience with field experiments indicates that this does not happen. Moreover, although one can imagine climatic conditions which might bring about such a difference in ripening time, it will be recalled that the weather in 1965 was almost uniformly inclement, with no hot dry period which could speed up ripening.

*Acknowledgments.*—We are indebted to Dr J. H. Croft, Dr M. J. Kearsey and Mr M. G. Freeman for assistance in collecting seed from natural populations. This work was supported by the Agricultural Research Council.

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