Watsonia, **8**, 263–276 (1971).

Studies on British Poppies 4. Some aspects of variability in the British species of *Papaver* and their relation to breeding mechanisms and ecology

S. ROGERS

Department of Biology, Queen Elizabeth College, London

ABSTRACT

The patterns of intra-specific variation in the British species of *Papaver* have been studied using mainly characters of the ripe capsules. The results, considered in relation to the breeding mechanisms of the species, show that in the outbreeding *P. rhoeas* variation is primarily between individuals and the variation within populations is generally such that any variation between them is not significant. In the self-compatible species, *P. dubium* and *P. lecoqii*, on the other hand, the variation between populations is generally highly significant. Some populations nevertheless show more internal variation than others and this appears to parallel a variation in the degree of inbreeding.

INTRODUCTION

The five species used in this study fall into two sections of the genus as classified by Fedde (1909), the section Orthorhoeades including *P. rhoeas*, *P. dubium* and *P. lecoqii* whilst *P. argemone* and *P. hybridum* are included in the Argemonorhoeades.

In many respects the species are all similar, being annual plants inhabiting open communities such as annual crops, waste ground and recently disturbed roadside verges. Yet, in the south of Britain at least, only *P. rhoeas* is universally abundant; *P. dubium* is only locally abundant, whilst the other three species are very localised in their distribution.

The existence of large populations of *P. rhoeas* focusses attention upon its variability, especially in obvious characters such as flower colour, foliage colour and form, and capsule shape. This has resulted in the description of numerous varieties. Thus Fedde's list (1909) comprises twenty varieties and six subvarieties, based on foliage form, petal colour, the nature of the indumentum, the form of the stigmatic disc and the habit of growth. There is little information regarding variability in the other species. Fedde lists nine varieties of *P. dubium* based mainly on foliage characters but also including *P. dubium* var. *lecoqii* (Lamotte) Fedde, a taxon now reinstated as a species. In his description Fedde points out the essential difference in capsule form between his var. *lecoqii* and *P. dubium*. Thus, of the latter he wrote: 'capsula . . . ad basim paulatim attenuata', whilst of *P. lecoqii* he said: 'ad basim plus minusve subito rotundato-attenuata'. Fedde's seven varieties of *P. argemone* include two distinguished by small size and non-incised foliage. Plants of this type are not uncommon in corn crops and it may be that this growth habit results more from habitat conditions than from genetic differences; the other varieties are based on the development of the capsule setae, the indumentum, and the entire or laciniate nature of the petals. This latter variant also occurs in other members of the genus e.g. the Shirley section of *P. rhoeas*, and *P. somniferum*. There are only one or two records for each of the five varieties of *P. hybridum* described by Fedde and none of these is from British material. The taxonomic literature thus supports field observation in suggesting that *P. rhoeas* is far more variable than the other species.

In attempting to assess this variability and correlate it with the reproductive biology of the species, attention was confined to the capsules as providing characters which could readily be measured and recorded. Data relevant to reproductive biology are being considered in another paper in this series but their significance in relation to the variability patterns found will be discussed here.

METHODS

The shape of the capsule was expressed in terms of

(1) the length/breadth ratio.

(2) an angle expressing the contraction of the capsule base, referred to hereafter as the base angle. Length and breadth were measured directly using callipers. The base angle was obtained indirectly from a silhouette projected at a standard

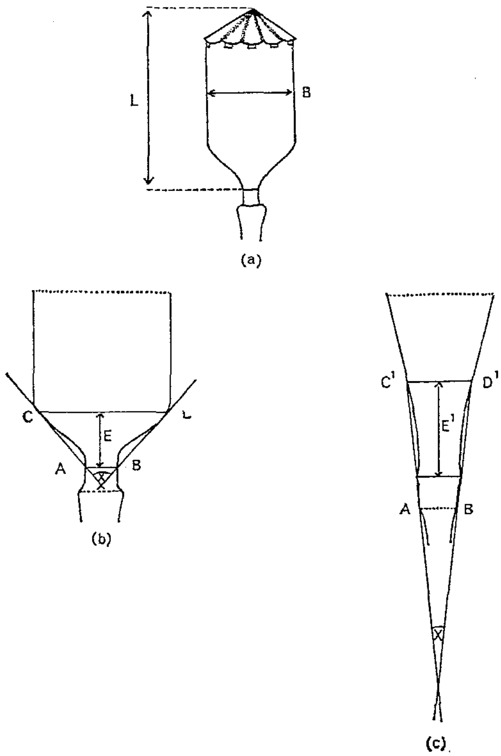

FIGURE 1. Capsule Measurements
(a) Length/breadth ratio – all species. L = length from top of flower scar to apex of disc; B = capsule diameter (calliper measurement). (b) and (c) Base angles; (b) in short-capsuled species and (c) in long-capsuled species. A–B diameter of top of flower scar. C–D diameter 5 mm (E) above A–B. C′ D′ diameter 10 mm (E′) above A–B. x = base angle. All measurements at 3 diameters magnification.

magnification of 3 diameters on to graph paper. The lower measurement taken in all species was that of the diameter of the top of the flower scar (A–B in Fig. 1). For the short-capsuled species the second measurement (C–D) was taken 0·5 cm (E) above this, but in the long-capsuled species it was found necessary to employ the diameter 10 mm above the top of the flower scar to ensure that the maximum width of the capsule was recorded. The angle was obtained by calculation from the formula

$$x = 2\tan^{-1}\frac{(CD - AB)}{E}$$

RESULTS

(1) CAPSULE VARIATION WITHIN THE SPECIES

The data are summarised in Table 1 and statistical analyses were carried out using the F-test so that within sample-variation and between-sample variation could be compared (Tables 3a & 3b).

(a) *PAPAVER RHOEAS.* Capsule shape in *P. rhoeas* shows a wide range of variation both in length/breadth ratio and base angle. The results expressed graphically in Fig. 2a and Fig. 5e are based on 'three capsule means' for every plant sampled during the investigation. Statistical analysis of the within and between-plant variation was performed using five-capsule-per-plant samples from thirty randomly selected plants in a single population. The analysis was repeated for four populations from widely separated localities in southern England. In each case, the analysis showed the between-plant variation to be highly significant (P < 0·001 or 0·01 in one case) in spite of the considerable phenotypic variation within individuals (Table 3a).

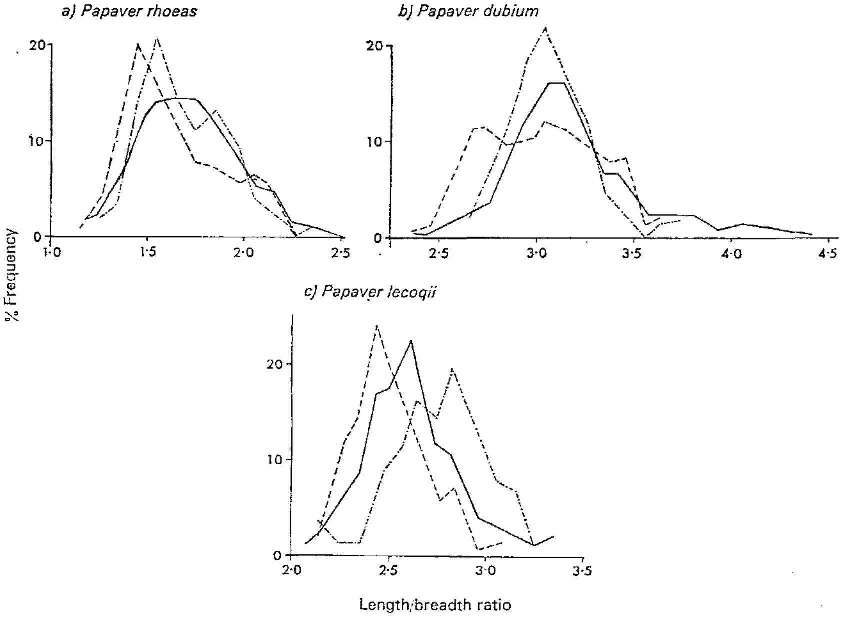

FIGURE 2. Frequency distribution of capsule length/breadth ratios for three species of *Papaver*. Continuous line: all data; broken lines: sample populations. Ordinates are % frequencies.

TABLE 1. SUMMARY OF CAPSULE ANALYSIS RESULTS

		SPECIES			INDIVIDUALS	
		Minimum	Maximum	Range	Normal range of variability	Maximum range
L/B Ratios	*P. rhoeas*	1·1	2·9	1·8	0·2–0·5	0·7
	P. hybridum	1·2	2·0	0·8	0·2–0·3	0·63
	P. dubium	2·3	4·5	2·2	0·35–0·9	1·47
	P. lecoqii	2·0	3·1	1·1	0·35–0·65	0·74
	P. argemone	2·6	4·5	1·9	0·4–1·0	1·5
Base Angles	*P. rhoeas*	10	105	95	10–30	47
	P. hybridum	49	95	46	12–30	44
	P. dubium	4	42	38	7–22	36
	P. lecoqii	19	52	33	8–16	24
	P. argemone	4	37·6	33·6	11–23	31

To anticipate the criticism that variation within the individual is not fairly represented in a five capsule sample, the same analysis was carried out using ten and fifteen capsule samples from twenty plants of known and different origin grown in a botanic garden. Between-plant variation reached the same level of significance and the five capsule sample was accordingly taken as representing adequately the variation within the individual. Smaller individual samples are in any case preferable since relatively few plants in wild populations produce as many as ten fully matured capsules.

By bulking the individual data for each of the four populations used to obtain

TABLE 2. CAPSULE MEASUREMENTS OF SEED PARENTS AND PROGENY

		SEED PARENT		FAMILY		
		L/B Ratio	Base Angle	L/B Ratio	Base Angle	Inbreeding/ Outbreeding Ratio
P. rhoeas	1	1·49–1·74	71–82	1·15–2·25	33–98	0
	2	1·65–1·78	60–69	1·25–2·45	18–83	0
	3	2·18–2·33	10–33	1·55–2·95	18–83	0
	4	1·2–1·48	66–95	1·15–2·55	20–103	0
P. dubium	1	3·0–3·62	8–19	2·55–3·75	5–40	0·56/1
	2	2·7–3·2	12–28	2·55–3·65	4–27·5	2·5/1
P. lecoqii	—	2·25–2·7	24–41	2·15–3·05	21·5–47·5	1·18/1

$$\text{Inbreeding/outbreeding ratio} = \frac{S}{(T-S)}$$

where S = mean number of potentially viable seeds following unaided self pollination

T = mean number of potentially viable seeds following open pollination

TABLE 3 (a) VARIATION WITHIN POPULATIONS

	Variance Estimates	L/B	BA	L/B	BA	L/B	BA	L/B	BA	L/B	BA
		1		2		3		4		5	
P. rhoeas	between individuals	1·21	1557	0·0833	489·2	0·067	519·3	0·203	914·2		
	within individuals	0·23	129	0·032	99·09	0·006	69·6	0·005	396·9		
	F =	5·1*	12·06*	2·59*	4·94*	11·16*	7·46*	36·9*	2·3*		
P. dubium	between individuals	0·1609	62	0·1998	49·7	0·1186	37·09	0·116	96·27	0·3110	59·04
	within individuals	0·0297	17·7	0·1613	36·40	0·045	25·02	0·035	8·07	0·054	23·94
	F =	5·41*	3·6*	1·23	0·13	2·6†	1·48	3·31†	11·9†	5·78†	2·64†
P. lecoqii	between individuals	0·0700	39·4	0·0412	17·96	0·086	99·27				
	within individuals	0·0265	45·0	0·024	20·02	0·0224	15·66				
	F =	2·6*	0·87	1·71	0·89	3·83	6·33*				
P. argemone	between individuals	0·137	44·4								
	within individuals	0·109	610								
	F =	1·256	0·073								
P. hybridum	between individuals	0·049	171								
	within individuals	0·016	99·4								
	F =	3·06	1·72								

* significant P = 0·1% † significant P = 1%

(b) VARIATION BETWEEN POPULATIONS

	Variance Estimates	L/B ratio	Base Angle
P. rhoeas (4 populations)	Between populations	0·0146	1576
	Within populations	0·0423	247
	F =	0·3379	6·38†
P. dubium (5 populations)	Between populations	0·4546	54·5
	Within populations	0·0496	13·2
	F =	9·16*	4·12*
P. lecoqii (3 populations)	Between populations	0·2584	38·5
	Within populations	0·0155	10·8
	F =	16·67*	3·56°

* significant P = 0·1% † significant P = 1% ° significant P = 5%

the five capsule samples analyses, it was possible to use the F-test to compare within- and between-population variation. In respect of length/breadth ratio the within-population variation was such that a significant between-population variation was not obtained.

(b) *PAPAVER DUBIUM.* As in *P. rhoeas* there is much phenotypic variation within the individual in the expression of the capsule characters, but unlike that species, large populations of *P. dubium* do not generally embrace the entire range of variation of the species. However, the length/breadth ratio results shown graphically in Fig. 2b indicate that different populations vary in this respect, some showing a relatively high degree of uniformity and giving high frequencies over a relatively narrow range of variation, while others seem much more variable and hence yield low frequencies over a wider range of variation.

Analysis of the data shows that the within-individual variation and between-individual variation do not differ significantly in a population of the former type, whereas in one of the latter type the between-individual variation is significantly greater than the phenotypic plasticity (Table 3a). The implication of this would seem to be that populations of the latter type are genetically more heterozygous than those of the former type and such variations in population structure may be related to intraspecific variation in the breeding mechanism.

In spite of the differing amounts of variability within populations, there is nevertheless a significant between-population variation in both characters (Table 3b).

(c) *PAPAVER LECOQII.* This species has the smallest range of variation of the long-capsuled species, both in length/breadth ratios and base angles. The range of variation in both characters overlaps that of *P. dubium*; but the modal frequencies of the two species are quite widely separated and when both characters are considered there is no difficulty in assigning capsule samples to the correct species (Fig. 3).

	Modal frequencies	
	P. dubium	*P. lecoqii*
Length/breadth ratio	3·0 – 3·2	2·6 – 2·7
Base angle	25 – 30	35 – 40

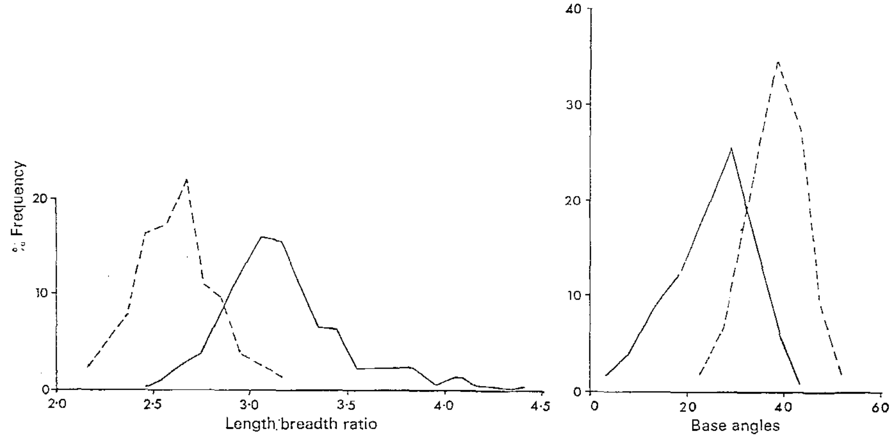

FIGURE 3. *Papaver dubium* and *P. lecoqii*: Comparison of capsule characters. Continuous line: *P. dubium*; broken line: *P. lecoqii*. Ordinates are % frequencies.

Phenotypic variability within the individual in the length/breadth ratio of the capsule is much less than in *P. dubium*, and in some populations the between-individual variation is significant whereas in others it is not (Table 3a). The variation between populations is highly significant (Table 3b) and while a proportion of the individuals from one population will invariably fall within the variation range of another, yet each is distinct, at least in respect of this particular character. The same is not true, however, of the capsule base shape, where an inherently small range of variation in the species coupled with much phenotypic plasticity tend to preclude the observation of any significant difference between individuals or populations.

(d) COMPARISON OF *PAPAVER RHOEAS, P. DUBIUM* AND *P. LECOQII*

The differences between these three species are most readily appreciated by comparing the numerical and graphical results obtained from families of known

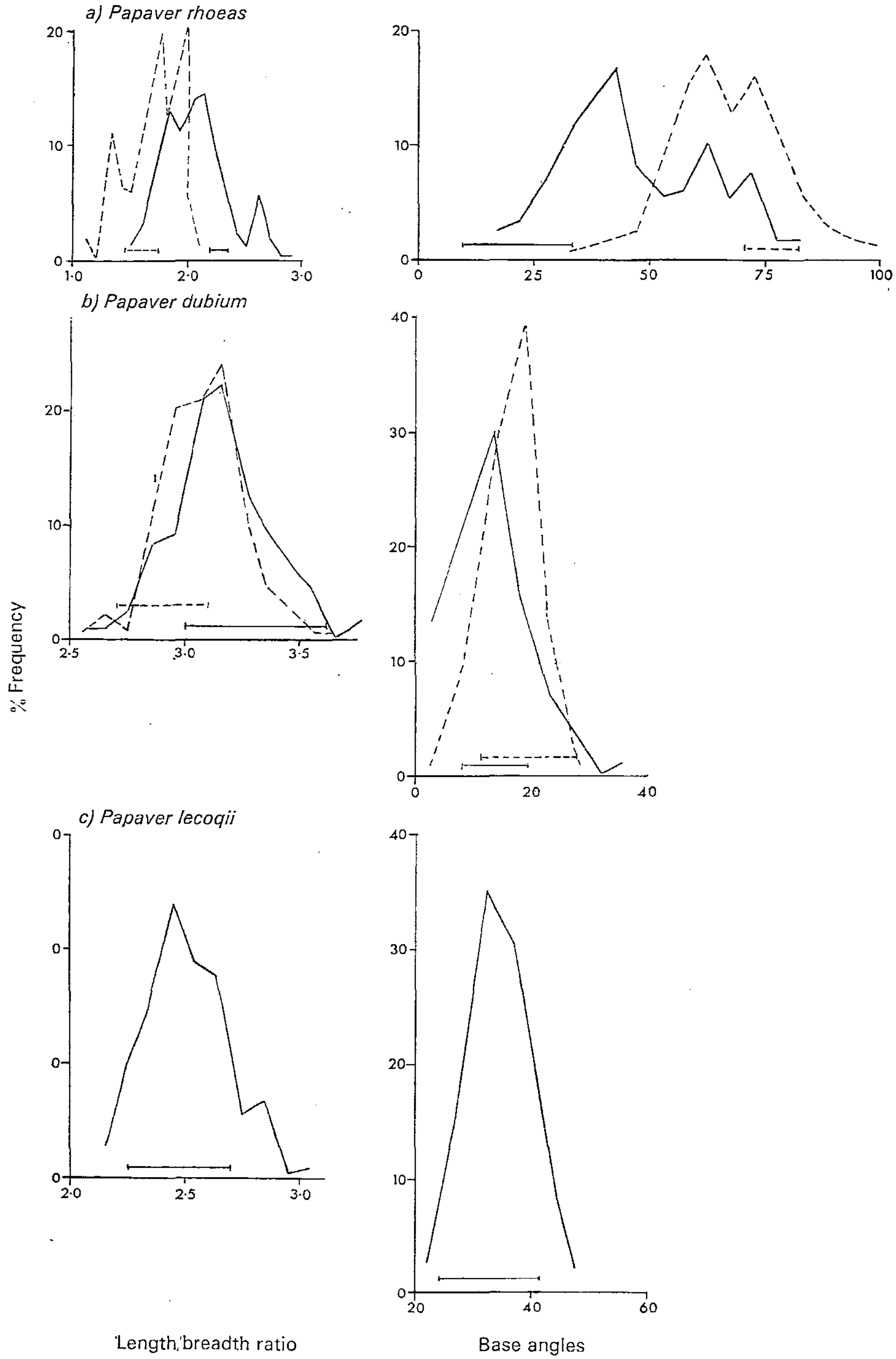

Figure 4. Comparison of the variability in capsules of families of plants from known seed parents.

The two families of *P. rhoeas* correspond to families 1 (broken line) and 3 (continuous line) in Table 2. In *P. dubium*, family 1 in Table 2 is represented by the unbroken line and family 2 by the broken line. The horizontal lines represent the range of character variation in the seed parent. Ordinates are % frequencies.

seed origin. Each family of twenty plants was raised in outdoor plots from a sample of the seed from a single open-pollinated capsule.

In Fig. 4 the data from samples of 15 capsules/plant from 2 families of *P. rhoeas*, 2 of *P. dubium* and 1 of *P. lecoqii* are compared with the 3 capsule means of their respective seed parents. Table 2 gives the summarised capsule data for each family, together with that for two other families of *P. rhoeas* and the inbreeding/outbreeding ratio for each family.

In *P. rhoeas* the salient features are the wide range of phenotypic variation in the progeny relative to that within the known parent and the efficiency of the barrier to self-fertilization. These features, together with the significant between-plant variation establish beyond doubt the genetic heterozygosity of the species.

In both the long-capsuled species, by contrast, the capsule variability of the progeny does not greatly exceed that of the known parent, and this pointer towards a measure of genetic homozygosity in these species would seem to be reinforced by the results of breeding experiments, which show a proportion of the seed set to be self-fertilized. The difference between the degree of inbreeding in the two families of *P. dubium* has been discussed previously, and while the striking uniformity of family 2 correlates with its high inbreeding/outbreeding ratio, too much significance should not be attached to a single result.

(e) *PAPAVER ARGEMONE* AND *PAPAVER HYBRIDUM*

Phenotypic variation within the individuals of *P. argemone* in the one large population examined was such that variation between them was not significant. Individuals from this population were subsequently shown to be strongly inbreeding so that the results, as far as they go, are consistent. No other wild population of sufficient size was obtained to permit of the variation between populations being analysed.

Individual plants of *P. hybridum* also show considerable variation in capsule shape. However, conflicting results were obtained from the only wild population analysed. In length/breadth ratio the variation between individuals was significant in spite of individual phenotypic variability but in base angle the variation between individuals was not significant. It is obvious that more information is required for this species before attempting to relate its variation-pattern to its intensive inbreeding.

(2) GENERAL CONSIDERATIONS

It is apparent from this study that the long narrow type of capsule, characteristic of *P. dubium*, *P. lecoqii* and *P. argemone*, is more variable in length/breadth ratio than the short, broad type of *P. rhoeas* and *P. hybridum*. Conversely, the more abruptly contracted capsule base of the short-capsuled species is more variable than the tapering form of the long-capsuled species. Since the base angle is inherently less variable in the *P. dubium* type of capsule, and variation within the individual may represent an appreciable part of the total species variation, results for this character do not show the same clearly defined differences as are obtained with the larger angles and bigger total variation of the *P. rhoeas* type of capsule base. In all species, the expression of the individual genotype is subject to appreciable phenotypic modification and the significance of inter- and intra-specific variation can, therefore, only be considered in relation to that within the individual.

Expressed graphically both the length/breadth ratio and base angle data correspond closely to normal curves in all the species, suggesting that capsule form, in common with other variations of a quantitative nature, is polygenically determined.

In the short-capsuled species observation suggests a correlation between the length/breadth ratio and the base angle, a high ratio being associated with a low angle and conversely. This association of the characters is less apparent in the long-capsuled species.

(3) SOME OTHER ASPECTS OF VARIABILITY IN *PAPAVER RHOEAS*

(a) PEDICEL HAIRS

The two forms of multicellular pedicel hair occurring in the genus *Papaver* are illustrated in Fig. 5. In the spreading form each hair has a cushion-like swollen base and stands out stiffly at approximately a right-angle to the stem. In the adpressed or strigose form the hair is bent through a right-angle just above its point of origin so that it lies parallel to the stem, often pressed closely to it. An intermediate form 'semi-adpressed' also occurs in which the hair base is adpressed but the tip stands outwards instead of lying close to the pedicel. This form has been observed in *P. nudicaule* by Fabergé (1943) and in *P. rhoeas* by Turrill (1946). The adpressed forms in *P. rhoeas* have been variously designated taxonomically as *P. strigosum* (Boenn.) Schur, *P.* × *strigosum* (Boenn.) Schur and *P. rhoeas* f. *strigosum* Boenn. Field scoring shows that the frequency of the 'adpressed' character is always low but that it varies from one population and district to another. The highest incidence observed was 8 %, compared with a mean of 2·95%, and this was encountered in one of the most southerly populations examined. Over the relatively small south-north distances involved in this survey, however, it was not possible to ascertain whether the incidence of adpressed hairs declines in frequency northwards as suggested by Turrill (*loc. cit.*).

Families raised from 'adpressed' plants pollinated naturally in the field show an approximate ratio of 3 spreading: 1 adpressed. This would point to 'adpressed' being a simple recessive as suggested by previous authors (Rasmuson 1920), and also indicates that in populations where it does occur a considerable number of spreading hair plants are heterozygous for the gene since all the seed is, of necessity, cross-fertilized. Some further information relevant to the inheritance of the character was obtained from hybrids between *P. rhoeas* and *P. dubium*. The latter species invariably has adpressed hairs. *P. rhoeas* (adpressed) × *P. dubium*, and the reciprocal cross yielded progeny all with adpressed hairs. *P. rhoeas* (spreading) × *P. dubium* yielded equal numbers of spreading and adpressed. This is in partial agreement with the results obtained by Rasmuson (1920) and interpreted by him as indicating the dominance of spreading hairs in *P. rhoeas*.

Fig. 5e shows that there is no significant difference in capsule characters between spreading- and adpressed-hair plants, and this may be taken as further evidence in favour of the view that the adpressed variant is a simple allelic one which does not merit taxonomic rank.

(b) PETAL BLOTCH

Taxonomic descriptions of *P. rhoeas* usually imply that a black blotch at the base of each petal is a frequent occurrence. Data collected from forty populations in twelve vice-counties of England show that only approximately one-fifth of the plants have blotched petals. Two hundred and fifty-four plants from 27 populations were scored for both presence and size of blotch and in only just over 2% was the blotch found to be large and conspicuous. Both Newton (1929) and Philp (1933b) associate the development of the blotch with a dominant gene B, the recessive of which produces a white blotch, yellow anthers, white or tinged filaments, white stigmatic rays and a light-coloured seed testa. This recessive has been seen only once in all the wild populations examined though it is characteristic of the cultivated Shirley poppy. The other phenotypic characters which Philp and Newton ascribe to B, namely dark purple filaments and anthers, purple rays and dark rays and dark seed coats, are all present in the plants lacking the petal blotch.

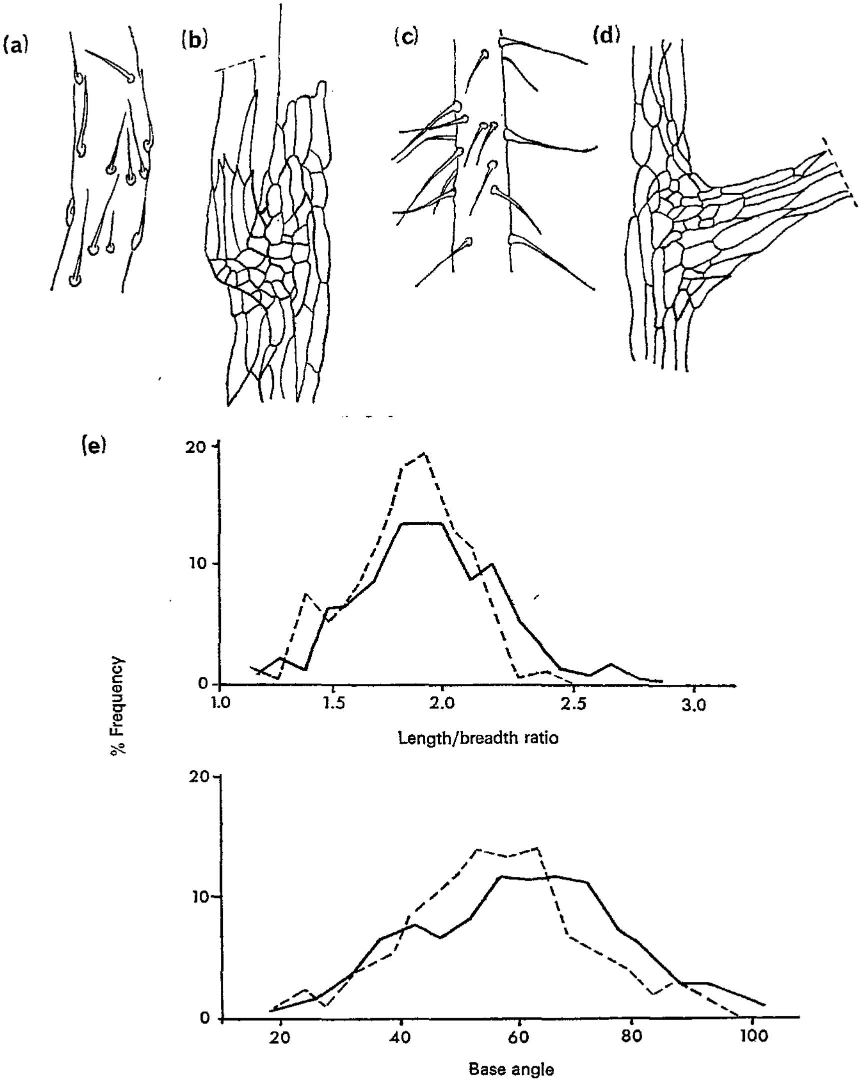

FIGURE 5. *Papaver rhoeas*: Variation in pedicel hairs.
(a) Adpressed pedicel hairs (× 7) and (b) detail of hair base (× 115); (c) spreading pedicel hairs (× 7) and (d) detail of hair base (× 115); (e) capsule characters in spreading (continuous line) and adpressed (broken line) hair plants. Ordinates are % frequencies.

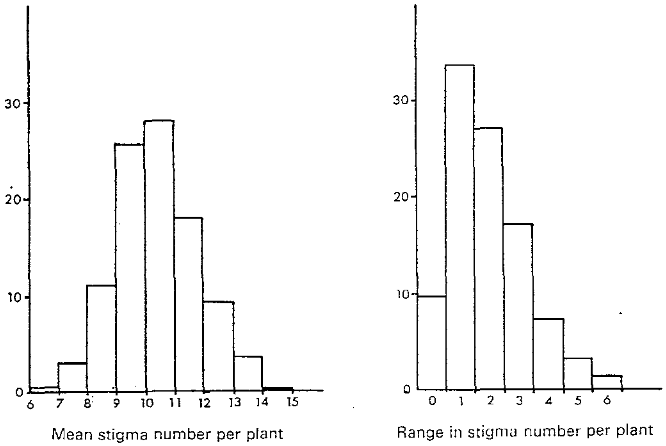

FIGURE 6. *Papaver rhoeas*: Variation in stigma ray number (data from all plants sampled). Ordinates are % frequencies.

(c) THE NUMBER OF STIGMATIC RAYS

The expression of this character varies within as well as between individuals. Using a sample of three capsules per plant the mean stigma number varied from 6 to 14 with the highest frequencies between 9 and 11. Less than 10% of the plants had the same number of rays on the three capsules examined, a variation of 1 or 2 being the most frequent. The maximum within-plant variation observed was 6 and on this basis the between-plant variation is significant ($P < 0{\cdot}001$) (Fig. 6). It would seem, therefore, that stigmatic ray, and hence placenta number has a genetic basis, though this is subject to considerable phenotypic modification. The expected association between ray number and capsule size is by no means invariable; small capsules may have numerous rays and large ones relatively few. It is not known to what extent stigma, and hence placenta, number might affect the reproductive potential of a capsule. A larger number of placentae would suggest a greater seed-bearing surface within the ovary and possibly, therefore, more seeds, but this would need to be considered in relation to capsule size.

DISCUSSION

(1) VARIATION PATTERNS AND BREEDING MECHANISM

The species of *Papaver* in Britain are seen to exhibit two fundamentally different patterns of variation. One, exemplified by *P. rhoeas*, presents obvious visual differences between individuals within a population, whilst comparison of large populations shows no statistically significant difference between them, at least in respect of the characters investigated. In the second pattern, exemplified by *P. dubium* and *P. lecoqii*, visual individuality is less apparent, and in the characters studied inter-individual variation reaches significance within some populations, but not within others. Populations, however, do differ significantly from one another. The overall picture thus resembles that described by Baker (1953) in *Armeria maritima*, where the subsp. *maritima* showed variation between individuals while in the subsp. *californica* populations were much more uniform internally but differed significantly from one another. This was found to be correlated with breeding mechanism, subsp. *maritima* being self-incompatible while subsp. *californica* is self-compatible.

There seems to be a fairly close parallel between the situation in these two species and that described by Imam & Allard (1965) in the wild oat, *Avena fatua*. Like the poppies, *A. fatua* is an annual species and an opportunist colonizer of bare ground and annual arable crops. It has frequently been reiterated that success in such situations requires a high degree of adaptation, hence gene combinations conferring this are maintained by self-compatibility, rigorous inbreeding and low recombination (Grant 1958, Baker 1959). While the premium for the opportunist colonizer is on adaptations such as rapid germination and establishment, a short vegetative phase and a high reproductive capacity, the flexibility that is demanded of it is the ability to mature successfully regardless of seasonal and climatic fluctuations, macro- and micro-edaphic variation and interspecific competition. Some degree of heterozygosity would thus also appear to be an advantage.

In *Avena fatua* this is achieved by a flexibility of the genetic system in which inbreeding maintains a fairly high level of homozygosity but a low level of outcrossing permits of recombination and diversity of genotypes. The resemblance between *P. dubium* and *A. fatua* goes further, in that the degree of inbreeding in *P. dubium* varies from one population to another as does the mean amount of outcrossing in the *Avena* populations studied by Imam & Allard (1965).

It seems likely from the variation studies that the pattern of breeding behaviour in *P. lecoqii* is similar.

P. rhoeas on the other hand is rigorously outbreeding and there is no evidence of any breakdown in its incompatibility mechanism. There is a high degree of genetic heterozygosity which is obvious in characters such as petal colour, petal blotch and stigmatic ray number. Such a species would seem to be less well equipped than a self-compatible one to maintain those combinations of genes conferring adaptive advantage. *A priori*, therefore, one might expect it to be less successful as a colonizing species, but in reality it is the only one of the five native species which, in the absence of the selective weedkiller, becomes a major weed.

Rigorous outbreeding implies chromosomal heterozygosity but this need not imply an absolute genic heterozygosity. Selection pressure against a less well adapted recessive homozygote would tend to reduce the frequency of the recessive allele in populations (MacArthur & Connell 1966) and would also favour a low mutation rate from the dominant habitat-adapted allele. Most phenotypes would consequently approximate to the optimum for such a character while maintaining a much higher level of heterozygosity in those characters subjected to less rigorous selection.

Compared with *Avena fatua*, the reproductive capacity of *P. rhoeas* is enormous and the proportion of the seed output which produces the next generation of plants is correspondingly small. There is thus an enormous surplus of genotypes and the small proportion of obviously ill-adapted phenotypes that occurs in natural populations is unlikely to have any significant effect on ultimate population size.

(2) ECOLOGY

The genetic heterozygosity of *P. rhoeas* would appear to enable it to exploit a much wider range of habitats than any of the other species. *P. lecoqii*, *P. arge-*

mone and *P. hybridum* are confined to calcareous soils, and *P. dubium* (while showing no pH restriction on light-textured soils) does not colonize heavy soils. Both *P. hybridum* and *P. lecoqii* seem to be reaching the northern limit of their distribution in the British Isles, scarcely extending beyond the southern half of the country (Perring & Walters 1962, Perring & Sell 1968). Both have only a short period of inherent seed dormancy and the seedlings are consequently vulnerable to both winter mortality and destruction by autumn or early spring cultivations. The other three species generally have a longer period of inherent dormancy (Harper 1960), resulting in spring germination. This may allow their further extension northwards into central and north-west Scotland and also into Scandinavia (Mowat & Walters 1964). Little is known regarding seed longevity as a factor in survival other than a reported viability of five years for *P. rhoeas* (Brenchley & Warrington 1933).

(3) THE POPPIES AS WEEDS

The poppies show many of the characters of the ideal weed summarised by Baker (1965). It seems unlikely that the ecological adaptability of *P. rhoeas* is endowed by a general purpose genotype of the type he postulates as being possessed by many successful weeds, since it has none of the necessary genetic attributes – a history of hybridization, polyploidy, complex heterozygosity, agamospermy or self-compatibility. The long-capsuled species, while apparently having the more favourable genetic systems for the opportunist coloniser, do not seem to have acquired the ideal combination of genes to turn them into aggressive weeds under British conditions.

It would seem that there is no one ideal genetic system for the aggressive weed; some achieve success by means of rigorous inbreeding, some by a flexible mixture of in- and outbreeding and at least a few by rigorous outbreeding coupled with a high reproductive capacity.

A marked phenotypic plasticity is also a feature of the the poppies. It is apparent in the variation found within individual plants (as in the capsule samples) but also, more significantly, in the plastic response of a diversity of different genotypes to density (Harper 1961). Such plasticity permits individual response to the immediate situation. Presumably it is genetically controlled and as such would be expected to have a strong selective advantage in unstable environments.

ACKNOWLEDGMENTS

The work described in these papers formed part of a thesis accepted for the degree of Ph.D. in the University of London. The help of Dr M. A. P. Madge of Royal Holloway College is gratefully acknowledged.

REFERENCES

BAKER, H. G. (1953). Race formation and reproductive method in flowering plants. *Symp. Soc. exp. Biol.*, 7: 114–145.

BAKER, H. G. (1959). Reproductive methods as factors in speciation in flowering plants. *Cold Spring Harbor Symposium*, **24**: 117–190.

BAKER, H. G. (1965). Characteristics and modes of origin of weeds, in BAKER, H. G. & STEBBINS, G. L., ed. *The genetics of colonizing species*. New York and London.

BRENCHLEY, W. & WARRINGTON, K. (1933). The weed seed population of arable soil. II. Influence of crop, soil, and methods of cultivation upon the relative abundance of viable seeds. *J. Ecol.*, **21**: 103–127.

FABERGÉ, A. C. (1943). Genetics of the Scapiflora section of *Papaver*. II. The garden Iceland poppy. *J. Genet.*, **44**: 366–385.

FEDDE, F. (1909). Papaveraceae, in ENGLER, A., ed. *Das Pflanzenreich*, vol. 40, pp. 366–385.

GRANT, V. (1958). The regulation of recombination in plants. *Cold Spring Harbor Symposium*, **23**: 337–360.

HARPER, J. L. (1960). Factors controlling plant numbers, in HARPER, J. L., ed. *The Biology of Weeds*. Oxford.

HARPER, J. L. (1961). Approaches to the study of plant competition. *Symp. Soc. exp. Biol.*, **15**: 1–39.

IMAM, A. G. & ALLARD, R. W. (1965). Population studies in predominately self-pollinated species. IV. *Genetics*, **51**: 49–62.

MACARTHUR, R. & CONNELL, J. (1966). *The biology of populations*. London.

MOWAT, A. B. & WALTERS, S. M. (1964). *Papaver*, in TUTIN, T. G., *et alia*, ed. *Flora Europaea*, vol. 1. Cambridge.

NEWTON, W. C. F. (1929). The inheritance of flower colour in *Papaver rhoeas* and related forms. *J. Genet.*, **21**: 389–404.

PERRING, F. H. & SELL, P. D., ed. (1968). *Critical supplement to the Atlas of the British Flora*. London.

PERRING, F. H. & WALTERS, S. M., ed. (1962). *Atlas of the British Flora*. London.

PHILP, J. (1933a). The genetics of *Papaver commutatum* and its hybrids with *P. rhoeas*. *J. Genet.*, **28**: 169–174.

PHILP, J. (1933b). The genetics of *Papaver rhoeas* and related forms. *J. Genet.*, **28**: 175–203.

RASMUSON, H. (1920). Über einige genetische Versuche mit *Papaver rhoeas* und *Papaver laevigatum*. *Hereditas*, **1**: 107–115.

TURRILL, W. B. (1946). *British Plant Life*. London.

WINGE, Ö. (1932). Experiments with *Papaver rhoeas f. strigosum* Boenn. *Trudy Lab. Genet.*, **9**: 115–120.