A STUDY OF VARIATION *EUPHRASIA* BY MEANS OF OUTDOOR CULTIVATION

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ABSTRACT

Samples of *Euphrasia* from populations at six localities on chalk or limestone in the Midlands and south-east of England were cultivated in the garden in order to compare them without interference from environmental effects. The variation between populations in the wild and in cultivation is described. It was concluded that five samples were more or less normal *E. nemorosa*, differing only slightly from one another; also that one of them was mixed with, and apparently hybridising with, *E. stricta* (not previously known in Britain, and possibly an alien introduction). One population appeared to represent a slightly divergent ecotype of *E. nemorosa* and another an extreme ecotype of the same species. A hybrid between the latter and *E. pseudokerneri* appeared among the plants cultivated. Four more samples were grown a year later and it was concluded that these comprised three normal forms of *E. nemorosa* and a form of *E. confusa*.

Two forms of *E. anglica* showed fairly marked differences although growing only three-quarters of a mile apart. The differences may have been caused by hybridisation at one of the localities.

The cultures provided instructive information on interspecific and intraspecific variation in a taxonomic group in which the most closely related species are very similar to one another and in which variation within species is considerable.

INTRODUCTION

Owing to the fact that the species of *Euphrasia* are annual and semi-parasitic plants they show great variations in vigour. These may be seen within populations, but overall differences of vigour occur between populations as well. Ignorance of the effects of this variation on morphology suggested that the sampling of wild populations for morphological study would be unreliable. A large-scale garden trial cultivation was therefore undertaken to investigate variation in *E. nemorosa*. A small trial of *E. anglica* was carried out at the same time, and further populations of *E. nemorosa* were later compared by the same method.

The species of *Euphrasia* are variable, ill-defined, and subject to hybridisation, though each has several characters by which it normally differs from its nearest relatives (Yeo, 1955). In spite of the difficulty of recognizing even species on the basis of small and relatively inconstant characters, *E. nemorosa* was subdivided by Pugsley (1930) into five varieties, and Warburg (1952) stated that three of them were distinct ecologically and might prove to be worthy of treatment as subspecies. It was thought that the cultures might help in the understanding of some of these varieties, especially of var. *calcarea* Pugsl., since most of the samples of this species were collected from chalk or limestone.

COMPARISON OF SEVEN EUPHRASIA SAMPLES GROWN IN THE GARDEN

Description of experiment

The ' whalehide pot ' method of cultivation was used in this experiment, which was carried out at Leicester in 1953. Each bituminized paper pot was planted in March with one seedling of *Euphrasia* and one of *Plantago lanceolata* ; the pots were then embedded in the garden; *Euphrasia* and host plants that died during the few days occupied by this process were replaced at once. The aim of the experiment was to compare the offspring

*Most of the work here described was done during the tenure of a Research Scholarship at the then University College of Leicester.

of wild populations from six localities when grown in the same environment. Six samples were grown in a set of randomised blocks, an arrangement which permits an analysis of variance to be made on the statistical data. There were six blocks, each consisting of six rows of fourteen *Euphrasia* plants each. Each sample of *Euphrasia* was represented by one row in each block. The individual plants were assigned to the blocks at random, and the order of the rows in each block was also chosen at random. A seventh sample, of which few seedlings were available, was grown in a row of ten plants near the main experiment.

On four occasions from mid-May to mid-June a record was made of the survival of the Euphrasias, signs of establishment on the host, and signs of disorder in the plants.

Leaves and flowers were taken from the plants and mounted on cellulose tape on glass. From each plant two leaves were taken, one subtending the last-but-one normally-developed branch or pair of branches (called ' leaf 2 '), and one from the fourth node above the uppermost branch or pair of branches (called ' bract 4 '). One flower from each plant was mounted; the aim in collecting these was to obtain mature full-sized flowers which had not begun to wrinkle or shrink. Most of the flowers chosen were therefore ones which had not been shed but which could be pulled off easily. The mounting was begun on 29 July 1953. Between 27 August and 7 September all the plants were pressed, except for some which were pressed early because they were wilting.

The height of the pressed plants was measured, and various measurements were made on the mounted leaves and flowers. For this purpose, the lantern-plate cover-glasses on which they were mounted were put into a projector and measurements were made on their enlarged images. In addition, photographs were taken of individual plants in the garden, and photographic contact-prints were made of the mounted leaves and flowers.

The *Euphrasia* seed for this experiment was extracted from many different plants of large or fairly large gatherings of herbarium specimens. The samples will be referred to by their serial numbers. The six samples used in the main part of this experiment were :

E151A Juniper Top, Box Hill, Surrey, v.c. 17; flinty, rabbit-grazed turf on chalk;
E166 Watlington Hill, Oxon., v.c. 23; chalky field;
E167A near Medmenham, Bucks., v.c. 24; chalky field (with E167B, see below);
E210 Waltham Quarry, Waltham on the Wolds, Leics., v.c. 55; grassland on oolite;
E211 near Croxton Kerrial, on Leics.-Lincs. border, v.c. 53/55; grassy track on oolite, about 6 miles from E210;
E215 Bedford Purlieus, Northants., v.c. 32; woodland ride on oolite, about 19 miles from E211 and about 17 miles from E210.

The additional group of 10 plants grown nearby, numbered E167B, was from the same locality as E167A and was growing mixed with it; all samples, with the probable exception of E167A, were considered to be *Euphrasia nemorosa*. At Box Hill the population of E151A was in contact with and apparently hybridising with *E. pseudokerneri*. Plants thought to be hybrids were excluded from the gathering.

Effect of replacement of dead seedlings

Many seedlings of *Euphrasia*, and some of the host, were replaced from 22 to 26 April, about four weeks after the initial potting-up and early replacement of the Euphrasias and hosts. Survival during May and June was slightly less good where replacements had been made, but the percentage of survivors probably established on the host was approximately the same whether replacements had taken place or not.

Variation between populations in survival and establishment

Table 1 shows that there was considerable variation in survival up to 31 May between the different samples. This variation was greater than that between the blocks, each of which contained all the samples. The table shows a similar result for establishment on the

host. These figures show that the populations differed from one another in characters affecting their establishment on the host provided and their survival in the garden at Leicester.

TABLE 1. Survival and establishment of *Euphrasia* in 1953 in the garden

	% of Euphrasias alive on 22-26 April that survived until 31 May	*% of surviving Euphrasias probably established on host on 31 May*
Sample		
E151A	50	44
E166	73	83
E167A	81	84
E210	93	85
E211	92	94
E215	82	67
Block		
1	83	74
2	85	75
3	87	75
4	77	81
5	75	80
6	74	81

Deaths of plants later in the season, after they had become established on the host, were mostly due to fraying of the stem base, which in turn was probably the result of attacks of damping-off fungi upon the young seedlings. Many plants which did not die wilted readily in dry weather from this cause. However, the sample E151A, which suffered the heaviest mortality before establishment, showed no ill effects from stem-fraying, apparently because of its dwarf habit.

Variation between populations in habit

Variation in habit is illustrated by photographs of some of the living plants, and by height measurements. Some of the leaf characters will also be considered here.

The plants grew with great luxuriance, and as a result all samples were much more bushy than their wild parents had been. Sample E151A (Plate 10a) was dwarf, with short internodes, few branches, and flowering from a relatively low node. The leaves were very thick and readily developed anthocyanin; their green colour was pale and they were not shiny. The areas between the veins were flat on the upper surface of the leaves and very slightly concave beneath; the veins appeared on the upper surface as narrow grooves. In all these characters E151A was different from all the other samples, except E167A, which resembled it in its development of anthocyanin.

Sample E166 (Plate 10b) was characterised in habit by its small leaves which left the branches more exposed than in other samples.

The remaining samples were all very similar in habit, but E167A (Plate 10c) was distinguishable by its leaf-shape, which will be described later, and by the considerable development of anthocyanin in its leaves.

The other three samples, E210, E211 and E215, could not be distinguished from one another in the garden by habit and foliage. It can be seen from Plate 10d, that the leaf surface was similar to that of E166 and E167A.

The measurements of plant height, together with numerical data obtained for ten other characters (Table 2), have been subjected to an analysis of variance. This work was kindly carried out by Dr. D. A. Wilkins at the Scottish Plant Breeding Station. It was found that, in all eleven characters, differences existed among the populations significant at the 0·1% level of probability.

For the character of plant height (character 1), Tables 2 and 3 show that E151A was significantly shorter than all other samples, and that sample E167A was significantly shorter than the two tallest samples. Table 2 shows that E151A was in fact only about half the height of E210 and E211.

Variation between populations in leaves

The leaves of the populations are illustrated in Fig. 1 a-f. Differences between samples E166, E210, E211 and E215 are not very noticeable in the silhouettes, but E151A and E167A are conspicuously distinct. E151A (Fig. 1a) has disproportionately few teeth for the size of its leaves and the teeth are necessarily relatively large (Table 2, character 5). The same applies to E167A (Fig. 1c) in lesser degree, but this sample has the longest teeth of all. The leaves of E167A are also more elongated and have the teeth directed more towards the apex than in other samples. Table 3 shows which of the measured or counted differences are statistically significant. It is noteworthy that there are no significant foliar or habit differences between E210, E211 and E215, which were the samples that could not be distinguished by these characters when they were being grown. A comparison of the figures for the length and breadth of the leaves (Table 2) indicates a variation between the samples in leaf shape.

TABLE 2. Averages of measurements made on *Euphrasia* plants

(Measurements in cm for character 1, in mm for characters 2-11; greatest and least averages for each character are in bold type)

	Population					
	E151A	E166	E167A	E210	E211	E215
Habit character						
1. Height of plant after pressing	**12·7**	22·7	18·9	**25·4**	25·0	22·6
Foliar characters						
2. Length of ' bract 4 ' (see p. 225)	**9·41**	10·2	**13·2**	12·2	11·9	10·7
3. Breadth of ' bract 4 '	11·2	**10·4**	11·9	**13·0**	12·0	11·7
4. Greatest no. of teeth on a side of ' bract 4 '	**0·53**	0·91	0·73	**1·10**	0·97	1·02
5. Length of distal side of a tooth on the widest part of ' bract 4 '	1·90	**1·56**	**2·09**	1·97	1·74	1·91
Floral characters						
6. Length of upper lip of corolla plus tube	7·31	**6·56**	7·79	7·56	7·60	**7·93**
7. Length of lower lip of corolla plus tube	8·19	**7·60**	9·04	8·74	8·67	**9·17**
8. Length of mid-lobe of lower lip of corolla	**2·90**	**2·13**	2·76	2·70	2·67	2·71
9. Depth of emargination of mid-lobe of lower lip of corolla	**0·59**	0·60	0·81	0·79	0·90	**0·99**
10. Breadth of base of mid-lobe of lower lip of corolla	1·3	**1·2**	1·5	**1·7**	1·6	1·6
11. Greatest breadth of mid-lobe of lower lip of corolla	2·27	**1·97**	2·37	2·71	2·73	**3·07**

TABLE 3. Characters in which pairs of *Euphrasia* samples showed a statistically significant difference ($P = 0{\cdot}1\%$)

(Characters numbered as in Table 2)

Pairs of samples	*Characters in which pairs of samples differed significantly*		
	Habit	*Foliar*	*Floral*
E151A and E166	1	4, 5	6, 7, 8, 11
E151A and E167A	1	2, 4	6, 7, 9
E151A and E210	1	2, 3, 4	7, 9, 10, 11
E151A and E211	1	2, 4	8, 9, 10, 11
E151A and E215	1	4	6, 7, 9, 10, 11
E166 and E167A		2, 4, 5	6, 7, 8, 9, 10, 11
E166 and E210		3, 4, 5	6, 7, 8, 9, 10, 11
E166 and E211			6, 7, 8, 9, 10, 11
E166 and E215		5	6, 7, 8, 9, 10, 11
E167A and E210	1	4	10, 11
E167A and E211	1	4, 5	11
E167A and E215		2, 4	9, 11
E210 and E211			9
E210 and E215			9, 11
E211 and E215			7, 11

Leaves of two untypical plants, plant 1 of E151A (counting from left to right) and plant 2 of E167A, have been included in Fig. 1. These will be discussed later.

The number of teeth on a side of ' bract 4 ' attained for each population the following maxima :—

E151A	4 teeth	(attained by about $\frac{3}{4}$ of plants)
E166	7 teeth	(attained by about $\frac{1}{2}$ of plants)
E167A	6 teeth	(attained by about $\frac{1}{8}$ of plants)
E210	9 teeth	(attained by about $\frac{1}{5}$ of plants)
E211	8 teeth	(attained by about $\frac{1}{6}$ of plants)
E215	8 teeth	(attained by about $\frac{1}{3}$ of plants)

When the two untypical plants were omitted, each population produced its maximum tooth-number in each of the six blocks of the field trial. It seems, therefore, that there was a characteristic maximum tooth-number for each population, which was not attained by all individuals. It is interesting to note that E210 had a greater maximum tooth-number than E211 and E215, which it closely resembled (p. 226).

Variation between populations in flowers

This variation is also shown by Tables 2 and 3, and some flowers are illustrated in Fig. 2 a-f, p. 230. It is clear that samples E151A and E166 were the most distinctive in flower shape : E151A by its fan-shaped lower lip with the lobes shallowly emarginate and weakly dilated in relation to their length, and E166 by its small size and narrowly emarginate lobes, the lobules on either side of the emargination tending to turn in. E210, E211 and E215, with no significant habit or foliar differences, were also found to differ in their flowers. The tables show that E210 has a less deeply emarginate mid-lobe than the other two, E215 has a longer lower lip and tube than E211, and E215 has a wider (more dilated) mid-lobe than either E210 or E211.

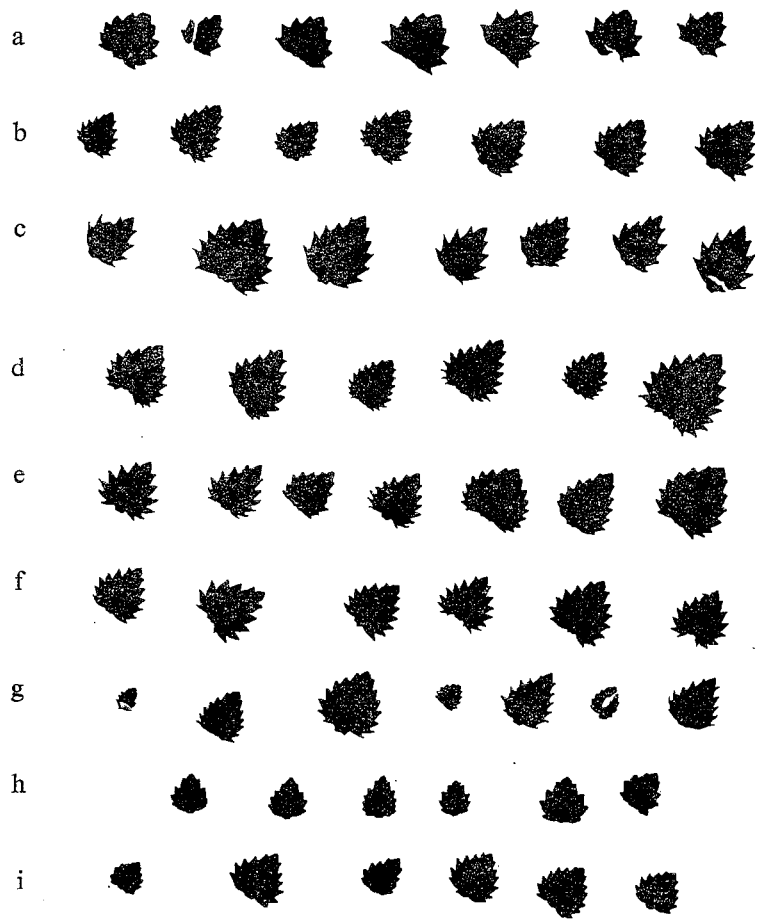

Fig. 1. Leaf silhouettes of *Euphrasia*, × ⅔. a–g, ' bract 4 '; h and i, ' bract 6.' a, E151A; b, E166; c, E167A; d, E210; e, E211; f, E215; g, E167B; h, E168; i, E219.

Variation within populations

Dr. Wilkins calculated the standard deviations of each of the six populations for one foliar and one floral character. These are given in Table 4; they show that E210 and E211 were the most variable populations. The wild populations at the localities of E210 and E211 were numerically larger than the other four populations, and they were certainly sampled over a larger area than the others, except possibly E167A, which also formed an extensive population although it was not extremely abundant.

Population E151A was very uniform. However, it included one untypical plant that stood out sharply from the rest. Compared with the other plants of this population, it will be seen from Fig. 1a that this plant had 5 teeth on a side of ' bract 4 ' instead of 3 or 4. In addition the corolla lobes were broader, the leaf surface not so flat, the habit more branched, and the flowers more abundant.

This untypical plant was evidently a hybrid between E151A and *E. pseudokerneri* which grew at the same locality, and it seems likely that it was an F1 hybrid, in view of the effort made to exclude hybrids from the original collection of E151A.

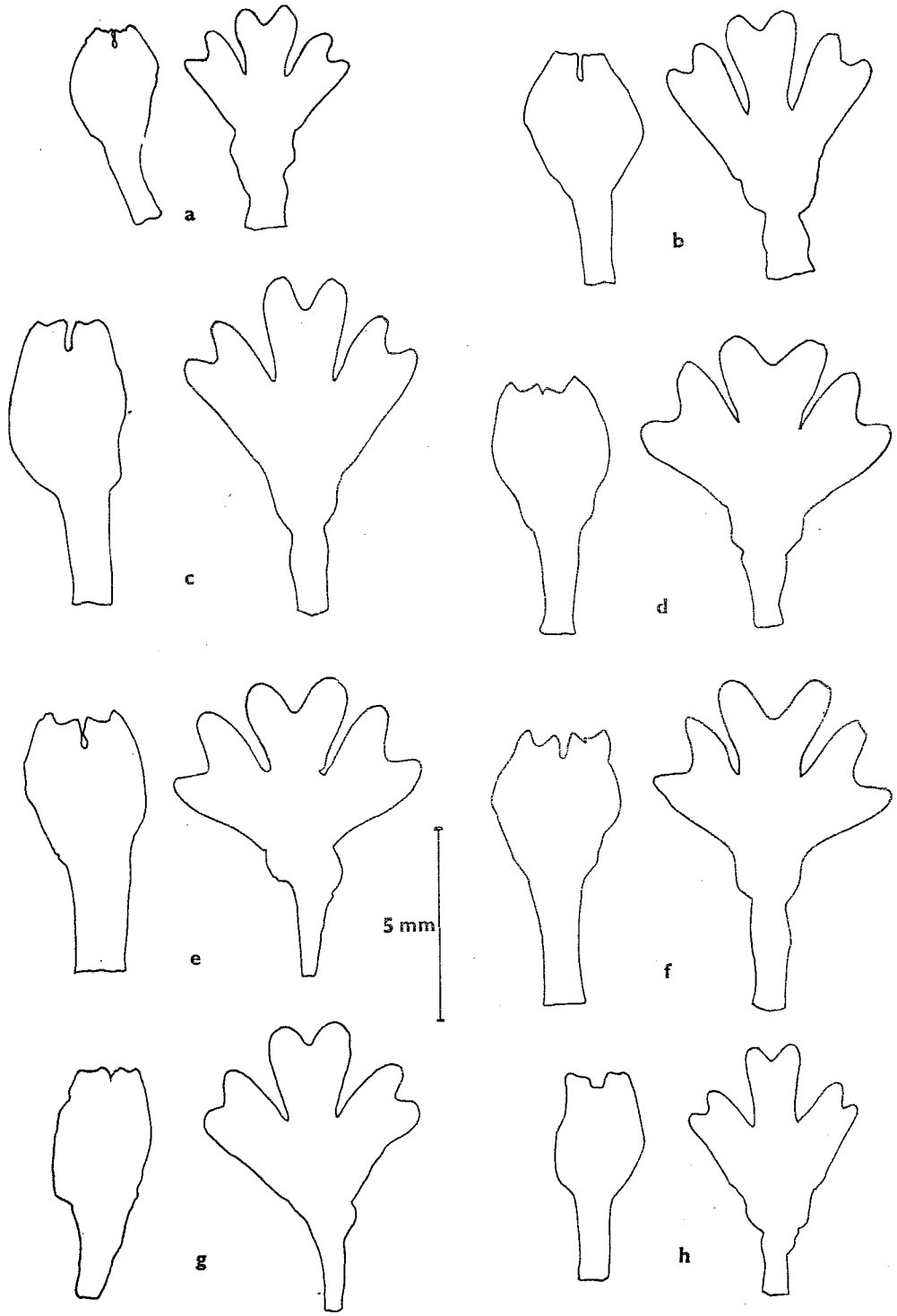

Fig. 2. Corollas of *Euphrasia*, upper and lower lips separated. a, E166; b, E151A; c, E167A; d, E210; e, E211; f, E215; g, E219; h, E168.

TABLE 4. Standard deviations for *Euphrasia* populations
(Unit of measurement = 1 mm)

Population	*Standard deviation for length of 'bract 4'*	*Standard deviation for greatest width of mid-lobe of lower corolla-lip*
E151A	0·97	·217
E166	1·83	·181
E167A	1·62	·374
E210	2·34	·390
E211	1·96	·501
E215	1·62	·326

The other plant with an untypical leaf shape belonged to population E167A. The leaf of this plant was, however, similar in shape to those of the populations E166, E210, E211 and E215; it was the only 'bract 4' produced by E167A with more than six teeth on one side. Leaves of this shape also occurred in plants 1, 2, 3, 4 and possibly 6 of E167B (Fig. 1g), counting from left to right). The leaves of the only other two survivors out of the original ten plants of E167B were like those of E167A , though the leaf of plant 5 is perhaps intermediate, as were some of the leaves of E167A. The occurrence of intermediate leaf-shapes suggests that the two forms were hybridising.

Comparison of wild and cultivated plants

The wild plants of E151A were extremely dwarf and compact, but freely branched. The leaves were few-toothed, and fleshy-looking but shiny. The plants were seeding freely when collected on 24 July 1952, which is an early date for *E. nemorosa* to be in such an advanced condition. E166 was taller and had longer internodes than E151A, but was dwarfer and had smaller leaves and flowers than the other populations. E167A had a distinctive leaf-shape, but was otherwise rather similar in habit to the remaining three populations. The latter were all collected on the same day, and appeared to differ slightly from one another, E211 having stout, dense flowering spikes, and E215 particularly long internodes, compared with E210.

Population E151A, which was the most distinct in the field, was also the most distinct in cultivation. Its few leaf-teeth, dwarf habit, and early flowering were shown to be hereditary, although the internodes were not quite as short in cultivation as in nature. The leaves became even more fleshy in cultivation, and developed a flat, non-shiny surface.

In cultivation, population E166 was little different from E210, E211 and E215, except in its small leaves and flowers; it looked about as distinct as it did in the wild. E167A in the main retained its characteristic leaf-shape in cultivation. The slight differences which E210, E211 and E215 showed in the wild disappeared in cultivation, where they could not easily be distinguished by eye. E215 was in fact the shortest of these three in cultivation, in spite of having had the longest internodes in the wild. On the other hand small differences between these samples were detected statistically.

CULTIVATION OF FURTHER SAMPLES IN 1954

In 1954 an attempt was made to repeat the 1953 experiment on a smaller scale, using another five *Euphrasia* populations. The plants were grown at Cambridge by the method used at Leicester, but conditions were apparently less favourable, and very few plants survived. However, a fairly good idea of the characters of four of the populations was obtained. These were believed to be *E. nemorosa* and were as follows :

E417 between Warslow and Elkstones, Staffs., v.c. 39; long grass and stony patches by roadside on acid moorland but accompanied by some more or less calcicolous plants;
E421 Friday Street, Surrey, v.c. 17; sandy field;
E429 West Harling Heath, W. Norfolk, v.c. 28; calcareous sandy soil;
E430 Devil's Dyke, Cambs., v.c. 29; on part of chalk dyke levelled in 1943.

In general appearance the cultivated plants of three populations (E417, E421 and E430), although distinguishable by eye, were much like E210, E211 and E215 grown in 1953. E417 showed the closest resemblance to the 1953 samples just mentioned, being very vigorous and rather large-leaved. E430 and E421 were rather smaller plants with somethat narrower leaves, E421 differing from E430 in that its branches diverged for a greater proportion of their length and became vertical only at the tips. The fourth population, E429, had smaller leaves and thinner stems than the others, and it was not so tall as E417. Most of the E429 plants were quite luxuriant, however, for they produced a great profusion of branches; these were usually widely spreading and somewhat flexuous.

The flowers were largest in E417 and smallest in E430, and the flowers of E429 differed from those of the other samples in being lilac instead of white. The flower-shape was different in each sample.

Wild populations of the 1954 culture

The differences between the 1954 samples in cultivation were mostly similar to differences seen in the wild plants from the same localities. The distinctive features of the cultivated E429 were all evident in the wild except for the low spreading habit.

Comparison of samples of E. anglica grown in the garden

Two samples of *E. anglica* were grown in the garden at Leicester in 1953. There were ten 'whalehide' pots for each sample, and each pot was planted with two *Euphrasia* seedlings and a plant of *Luzula campestris*. The pots of each sample were arranged in a row, the two rows being side by side. The seed of the two samples (E168 and E219) was collected from two localities three-quarters of a mile apart in Charnwood Forest, Leicestershire.

The two populations differed in habit in cultivation, E168 having shorter internodes than E219. The average height after pressing of the 13 surviving plants of E168 was 7·2 cm (range : 3·3–9·3 cm), and that of the 16 survivors of E219 was 11·1 cm (range: 4·4–16·5 cm).

'Bract 6,' defined in the same way as 'bract 4' (p. 225), was mounted for each plant (Fig. 1h, i). In E168 the bracts did not attain so large a size as in E219, and they also had fewer teeth, the greatest number of teeth on a side of 'bract 6' averaging 5·0 in E168 (range: 4–6) and 6·2 in E219 (range: 5–7).

The flowers of E168 were smaller, but more uniform in size, than those of E219, and they also differed from them in shape (Fig. 2g, h, p. 230). Some measurements were made on the flowers. The depth of emargination of the mid-lobe of the lower lip averaged 0·39 mm in E168 and 0·67 mm in E219. In E168 the width of the mid-lobe averaged 1·29 mm at the base and 1·63 mm at the widest point, while in E219 it averaged 1·49 mm at the base and 2·23 mm at the widest point.

Taxonomy

The three most distinct forms of supposed *E. nemorosa* that were cultivated were E151A, E167A and E429. In order to look for further populations of the type of E151A I spent two days in 1954 at Box Hill and Mickleham Downs. The area from which E151A had been collected was revisited and the same form collected again. Several other gatherings of *E. nemorosa* from both grassy fields and dry chalky slopes were made, but none was at all like E151A. They appeared to be fairly normal forms of *E. nemorosa*, although

those from the poorest habitats were the most dwarf. The form represented by E151A appears to deserve taxonomic recognition on morphological grounds, but it does not seem to be worth while to accord it such recognition when only one colony is known. In view of its similarity to *E. nemorosa* in leaf-outline and flower-size, it seems best to regard it as an extreme ecotype of that species.

Regarding the plants from Medmenham (E167A and B), I consider that two species were present, *E. stricta* Lehm., represented by nearly all the cultivated plants of E167A, and *E. nemorosa*, represented by one cultivated plant of E167A and four or five of E167B. Other samples of *E. stricta*, obtained from foreign sources, that I cultivated, had long, very acute leaf-teeth, similar to those of E167A, and they were usually rather few in number. The upper cauline or lower floral leaves were usually rather narrow, and some had a rather rounded base, but others were truncate. Usually *E. stricta* has rather large lilac flowers, and few short erect branches. These two characters were lacking in E167A. However, they are not always present in *E. stricta*, and Professor W. Rothmaler, to whom I sent plants of the same type as E167A, collected in 1954 from the same locality, considered that they were *E. stricta* forma *parviflora* Sag.

After the publication of Wettstein's (1896) monograph, *E. stricta* was widely reported from Britain. In Pugsley's (1930) revision, however, *E. stricta* was not accepted as occurring in Britain; plants previously identified as *E. stricta* were referred by him to *E. nemorosa*, *E. confusa* and *E. pseudokerneri*. I find these identifications acceptable, but I have encountered a few populations of *E. nemorosa* in which there were resemblances to *E. stricta*, and it may be that *E. stricta* was formerly in Britain, or has been introduced from time to time, but has in most places been unable to maintain itself as a distinct entity. Probably *E. stricta* was introduced at Medmenham, possibly at the same time as another alien that was growing with it, namely *Prunella laciniata*. A description of *E. stricta* follows.

EUPHRASIA STRICTA, Wolf ex J. F. Lehmann, Primae linae Florae Herbipolensis, 43 (1809), *emend.* Host, Flora Austriaca, **2**, 185 (1831).

Stem erect, usually with 0–4 pairs of erect branches, cauline and few to many of the lower floral internodes 1½–3 times as long as the leaves, upper floral shorter than the leaves; flowering commencing at the 7th to 12th node. Leaves glabrous or nearly so, usually strongly pigmented with anthocyanin; cauline ovate or narrowly ovate, obtuse or acute, up to *c.* 14 mm long, with up to 5 pairs of obtuse, acute or aristate teeth; floral leaves relatively broader, ovate or rhombic, acute, more or less rounded or cuneate at base, with 4–6 acute or aristate teeth, teeth of upper cauline and floral leaves directed towards the apex of the leaves. Calyx 4·5–6 mm long, with long slender aristate teeth. Corolla white or lilac with the usual markings, (5·5–) 8–11 mm long, measured from base of tube to apex of upper lip. Capsule rounded, truncate or retuse at apex, 4–6 mm long, almost always distinctly shorter than the calyx-teeth.

E. stricta is widespread in Europe as a plant of dry grassland. It is best distinguished from *E. nemorosa* and *E. pseudokerneri*, its nearest allies in Britain, by its habit and foliage.

The National Grid Reference of the locality at Medmenham, Bucks., v. c. 24, is 41/8186. The plant was collected from a chalky pasture and a rough field by a wood on 12 August 1952 (Yeo, no. E167A, E169A) and 19 August 1953 (Yeo, no. E401A, E402A).

The small leaves, short internodes, ascending main stem, and abundant, spreading and often flexuous, branches of E429 are characters of *E. confusa*. Wild plants from the Breckland locality of E429 differed from the cultivated E429 in being more erect and *nemorosa*-like in habit. Excursions to the Breckland, made since 1954, have shown that plants which are identical with *E. confusa* from the West of England occur there; in addition, there are many populations which, although similar to *E. confusa*, show some resemblance to *E. nemorosa*. Most of these populations are probably best referred to *E. confusa*, a species which was first identified as occurring in the Breckland by Pugsley in 1939 (specimen in **CGE**).

The experiments described here have emphasized the differences between these three distinctive forms. The hereditary character of the distinctive habit of E151A has been confirmed and a number of lesser differences which together have a considerable effect on the appearance of the cultivated plants have been brought out; the distinctive leaf-shape of E167A was easier to appreciate in the luxuriant cultivated plants; the small leaf-size of E429 was still evident in the luxuriant plants, while habit differences from *E. nemorosa* were increased.

The remaining samples of *E. nemorosa* were all slightly different from each other in cultivation but the differences were not always the same as the ones they showed in the wild; the experiment thus revealed examples of phenotypic and genotypic variation between populations of generally similar plants. This general similarity was evident among samples collected over a fairly wide geographical area. The most distinct population among these was the small-leaved, small-flowered E166 from Watlington Hill. Its characters are probably a response to the dryness of the habitat, and the form can thus be regarded as an ecotype of *E. nemorosa*, though a much less extreme one than E151A.

The differences shown by the two populations of *E. anglica* that were grown are quite considerable in view of their separation in the wild by only three-quarters of a mile. However, *E. nemorosa* was growing with E219, but not with E168.

Conclusions

Cultivation showed that all samples compared differed genetically. This indicates some degree of reproductive isolation, which in most cases must be due to the spatial separation of colonies. Where the differences are slight they can tentatively be attributed to chance; where they are rather larger and have been classed as ecotypic they can be attributed to response through selection to special habitat conditions. The differences, of a similar magnitude to the ecotypic ones, between the two populations of the diploid species *E. anglica* which were compared may well be due to introgressive hybridisation, for the tetraploid *E. nemorosa* was growing with E219, but not with E168. There is evidence (Yeo 1956) that introgression takes place from tetraploid species into diploid species of *Euphrasia*, and it is, therefore, possible that this had occurred at the locality of E219.

Another population of *E. anglica*, growing some miles away from E168 and also unmixed with any other species, was cultivated in the greenhouse with additional plants of E168 and, although found to differ from it in flower-shape, leaf-shape and habit, the differences were never greater, and were mostly smaller, than those between E168 and E219.

The differences between sample E167A and the samples of *E. nemorosa* compared with it are considered to indicate that E167A is *E. stricta*, while the differences between E429 and samples referred to *E. nemorosa* are considered to indicate that E429 is *E. confusa*.

There were indications that hybridisation was taking place between *E. nemorosa* and *E. stricta*, two rather similar species with the same chromosome number which would be expected to hybridize freely, judging by the behaviour of other *Euphrasia* species.

The observations on variation within *E. nemorosa* can do no more than provide a useful initial contribution to the material required for the evaluation of the varieties of this species.

Cultivation was considered necessary in order to eliminate the effects of phenotypic variation in vigour before making morphological comparisons. However, the results of comparing the very well-grown plants of rather uniform vigour suggest that at least leaf-shape and flower-shape can be reasonably satisfactorily compared in wild material on the basis of selections of the more vigorous individuals.

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THE BRITISH FORMS OF *TUBERARIA GUTTATA* (L.) FOURREAU

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ABSTRACT

An account is given of the variation in British *Tuberaria guttata*, and of its previous taxonomic treatment : the taxonomic value of various characters is examined. Most of the Welsh and Irish plants including the type population of *Helianthemum breweri* Planch. differ from *T. guttata* as it occurs in the Channel Isles and northern France in their shorter stature, the more common presence of bracts and other characters. All the characters said to distinguish *breweri* intergrade continuously with those of typical *guttata* in both herbarium and cultivated material, and are only loosely correlated. The more compact Welsh and Irish plants appear to be comparable with plants in similar exposed coastal habitats in north-west France. It is concluded that *T. guttata* shows ecotypic differentiation in relation to exposure on the Atlantic coast of Europe, and that the populations combining short diffuse habit and numerous bracts may be of polytopic origin. It is suggested that they should not be given formal taxonomic recognition.

1. INTRODUCTION

Like a number of other widespread Mediterranean species, *Tuberaria guttata* extends northwards up the west coast of Europe to a northern limit in the British Isles. Up to the north coast of France its distribution is more or less continuous, and the Channel Islands lie on the northern fringe of this essentially continuous area. But north of the English Channel its range is disjunct, and it occurs only in widely separated colonies on the coasts of north Wales and western Ireland. Plants from the best known of these colonies, on Holyhead Mountain in Anglesey, were described by Planchon in 1844 as a new species, *Helianthemum breweri*, and, as a variety or subspecies, *breweri* has become firmly established in the British literature. Authors have differed considerably in the value they have attached to the various characters said to separate it from typical *T. guttata*, and in the British populations that they have referred to *breweri* and to *guttata*. Most seem to have assumed that it was deserving of taxonomic recognition, and that all British plants could be assigned satisfactorily either to *breweri* or to *guttata*. The purpose of this paper is to show that none of the delimitations of *breweri* proposed hitherto is completely satisfactory, and that the variation pattern in *T. guttata* in Britain and neighbouring parts of the Continent is more complicated, and taxonomically intractable, than has usually been assumed.

2. THE HISTORY OF HELIANTHEMUM BREWERI PLANCH.

The Holyhead colony of *Tuberaria guttata* was discovered by Samuel Brewer in 1726 (see Hyde 1930). Dillenius wrote to Brewer on 31 May 1727 ' I desire him (i.e. the Rev. Mr. Green) to look after the plant you sent from Holyhead . . . . It is a *Cistus* and seems to be new.' Brewer received further specimens of the plant from Mr. Green on 5 August 1727. Dillenius had evidently intended to describe the plant himself, but, in the event, it was first mentioned in print over half a century later by Hudson (1778), as '*Cistus guttatus* . . . . Habitat *in pratis arenosis, in monte* Llech ddû *prope* Holyhead *in insula* Mona.' Curtis (1775–98) figured under the same name a bracteate and spotted-petalled plant, but did not say whether it was wild or cultivated, and gave the Isle of Man as a locality, evidently mistranslating ' Insula Mona.' In this he was followed by Sowerby & Smith (1790–1814, t. 544), who figure a rather stiffly formal little plant with numerous bracts and say that ' Having no hopes of obtaining wild specimens in a state fit for drawing, we have been

PLATE 10

a

b

c

d

Euphrasia plants growing in the garden; the plants were luxuriant and each photograph shows only a portion of a plant. a, E151A; b, E166; c, E167A; d, E211.