THE GROWTH OF *EUPHRASIA* IN CULTIVATION

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Abstract

Previous workers found that *Euphrasia* could be brought to maturity in cultivation whether supplied with a host-plant or not (though better growth was obtained with a host than without), and found also that a wide variety of annual and perennial herbs could act as hosts. The present paper describes chiefly cultures in clay pots, into which the Euphrasias were transplanted as seedlings. Usually growth was better when a host was provided than when it was not, but growth without a host was better than that obtained by previous workers. The development of some plants without a host was much affected by a difference of soil composition. A spurt of growth some weeks after planting with a host was taken to indicate parasitic establishment on the host, and the shorter the distance between the *Euphrasia* and its host the sooner establishment occurred. Euphrasias grown with certain *Leguminosae* were particularly vigorous and showed symptoms of a good nitrogen supply. Some severely retarded *Euphrasia* plants were probably being parasitized by their neighbours.

Euphrasias sometimes flowered very early, beginning at a very low node; this appeared to be caused by unusually high temperatures. The early-flowering species were particularly frequently affected in this way, which made it difficult to raise normal plants of these species.

Deaths of young *Euphrasia* plants took place chiefly in cold, dull weather, but were reduced by watering sparingly.

Cultures of various *Euphrasia* species with various hosts showed that certain hosts were good, and that others were bad or probably bad. There were indications of a difference between *E. pseudokerneri* and *E. anglica* in their growth on the same hosts. Different populations of the same *Euphrasia* species sometimes differed in their host-reactions. The host affected percentage establishment, mortality and vigour of the Euphrasias.

For cultivation in the open ground *Euphrasia* plants and hosts were planted in bituminized paper pots, which were embedded in the ground. Very vigorous growth was obtained in this way, using *Plantago lanceolata* as a host-plant.

The parasitic habit is probably not responsible for the taxonomic complexity of *Euphrasia*, but may be connected with its gregariousness in nature.

Previous work

The possibility of cultivating haustoria-forming Scrophulariaceae was demonstrated at the end of the last century. The behaviour in cultivation of the three semi-parasitic genera, *Rhinanthus*, *Odontites* and *Euphrasia*, was first studied by Ludwig Koch. His first paper dealt with *Rhinanthus*, and the second (1891) with *Euphrasia officinalis* L. He found that seedlings which germinated in pots grew much as wild ones do, if the pots contained old tufts of grass or grass seed sown at the same time as the *Euphrasia* seed (*i.e.* autumn). In *Rhinanthus minor*, however, Koch had found that simultaneous sowing of host and parasite gave retarded growth. He attributed this to the more rapid growth and earlier maturity of *Rhinanthus* placing a big demand on the host plants while they were still relatively young. Koch also sowed grass seed in pots with *Euphrasia* seedlings which were 3 cm tall (possibly an error for 3 mm tall). The effect of this was similar to that of simultaneous sowing with *Rhinanthus*, but worse from the point of view of the *Euphrasia* plants, which died off after 3 to 4 weeks. Euphrasias with no host-plant grew about as weakly as those with host seed sown after germination; if the seedlings were thinly and evenly distributed, they appeared starved and died off from mid-June onwards; in thick, uneven distributions some plants grew faster than the rest and were found to be attached to their neighbours by haustoria. These plants died if surrounded by few others, but if surrounded by enough others they occasionally flowered. They were prevented from fruiting by being dug up for investigation of the roots. Koch concluded that, for *Euphrasia* and *Rhinanthus*, parasitism on an autotrophic host was essential and not merely facultative.

Wettstein (1896) at first came to the same conclusion. He reported that seedlings of *E. rostkoviana* germinating in troughs in the open, in which grass seed had been sown the previous year, produced quite vigorous plants which flowered and had numerous haustoria. With no hosts the plants were dwarf, produced up to ten pairs of leaves, formed no flowers and had no haustoria. Later, however, among many seedlings grown together in pots or pricked out singly in pots after germination, he brought a few plants to the stage of flowering or fruiting (Wettstein 1897). Some of them were without haustoria, while others had haustoria on the roots of other Euphrasias. Wettstein now concluded that, though parasitism on an autotrophic host is necessary for vigorous development, individuals can flower and fruit, either alone or when behaving autoparasitically.

Heinricher's four papers on 'The Green Semiparasites', describe a lot of work on *Euphrasia*. It is first necessary, however, to describe an experiment with *Odontites odontites* (*O. verna*) (Heinricher 1898*a*). Seed was sown in a pot on 2 March 1895, and the largest plants were 2·5 to 3 cm tall by 27 April. On 29 April, it was found that seedlings of a closely-sown group had haustorial initials at the points where their roots were in contact. Two other cultures, thickly-sown, gave the following results: in one there were 36 plants on 2 August, with from 3 to 12 pairs of leaves; two plants had flower buds and branch initials. On 20 September the strongest plant was 20 cm tall, had produced 20 flowers, and its lowest capsules were ripe. In the other thickly-sown culture the plants, on 3 August, were from 2 cm tall, with four leaf-pairs, to 7–8 cm tall, with 2–3 flowers. The plants did not grow much more, and produced up to two or three fruits each. The wide individual variation of the first culture is attributed to a long period of germination, enabling some plants to get ahead by parasitizing others; the uniformity of the second is attributed to germination taking place over a short period. These results are similar to those obtained by Koch with uneven and even sowings respectively, using *Euphrasia* seed.

In addition to *Odontites*, Heinricher (1898*a*) got *Euphrasia stricta* Lehm. to flower with no host in a thickly-sown pot or garden soil. Germination began on 17 March 1896, and 70 plants were present on 15 May. Some plants that were surrounded by many others grew more strongly, and the strongest one started to flower on 8 August when 32 mm tall. Eight more were in flower on 13 September. The smallest flowering plants had stems 7–10 mm tall, their leaves were scarcely half the area of those of the largest, and their flowers were a half to a third the size. In two other pots, with 30 and 36 seedlings respectively, no plants came into flower.

Later, experiments were carried out with *E. rostkoviana* (Heinricher 1898*b*). In one pot the seedlings were abundant, and in places dense, on 17 March; flower buds appeared in May but none opened; more were formed in July, and the plants produced up to 20 leaf-pairs, but only one eventually flowered, although 80–90 had germinated. In each of five further pots, one seedling came up; these died one by one, from May to August, all without flowering.

The growth of a third species, *E. minima* Lam., in the absence of a host plant, was also investigated (Heinricher 1898*b*). In one pot 27 seedlings were present in June 1898, but they were mostly chlorotic and were attacked by aphides, and none flowered. A similar number of seedlings appeared in this pot in 1899, and six dwarf plants flowered in May. *E. minima* was also sown outdoors on a plot of gravelly, stony soil. Most plants flowered in June; three examples which were growing 2 cm apart from one another but isolated from other plants were illustrated; they were about 2 cm tall and began flowering at the third node. Another similar small isolated plant was found and its roots examined. Lateral roots had penetrated and formed many branchlets in rotting wood-fragments in the ground; root hairs were plentiful in places, but no haustoria were found.

These dwarf plants of *E. minima*, and also those of *E. stricta* mentioned earlier, resembled wild plants of *E. minima* seen in late August at Hühnerspiel, Brenner, growing on stony ground at a distance from other plants.

Heinricher concluded that *E. rostkoviana*, with one out of 90 plants flowering with no host, was the most advanced parasite, *E. stricta*, with nine out of 70 flowering with no

host, was less advanced, and *E. minima* was the least advanced. In fact, Heinricher did not grow approximately similar numbers of plants per pot of each species in the same year and with the same soil. Nor was there any duplication of pots, and his conclusions, though possibly correct, have little foundation. In any case, such a comparison would be very difficult to make because the three species probably have different optimal soil conditions. The occurrence of wild populations of *E. minima* with no apparent access to hosts, which Heinricher reports, does, however, indicate that this species is sometimes autotrophic in nature. Heinricher (1898*b*) states that, in having plenty of root hairs and in being relatively independent, *E. minima* resembles *Odontites odontites* (*O. verna*).

Heinricher also raised *Euphrasia* to the flowering and fruiting stages with host-plants, finding that the parasites were more vigorous with hosts than without, and more of them flowered. Pot cultures on indoor window-ledges suffered from unsatisfactory conditions, the best results being obtained with *E. stricta.* About 100 seeds of *E. stricta* were sown in a large pot of garden soil with seed of *Trisetum flavescens* on 27 February 1896 (Heinricher 1898*a*). *Stellaria, Capsella* and *Polygonum* came up as weeds, and most *Euphrasia* plants were closer to weeds than to *Trisetum.* Some plants evidently became established; the number of flower initials formed ranged from 1 to 16. The weakest plants were weaker than the strongest in the cultures with no host.

Better results were obtained outdoors by sowing seed in autumn on plots planted with tufts of *Carex, Luzula* and Gramineae (Heinricher 1898*a*). At a suitable time Euphrasias and hosts were dug up and haustoria were found on the host roots. Seedlings of *E. salisburgensis* were abundant on all plots on 14 April 1897 and flowering reached its peak at the end of June. Haustoria were found on:

Carex alba Scop.
Carex firma Host
Carex sempervirens Vill.
Carex brachystachys Schrank & Moll.
Luzula spadicea (All.) Lam. & DC.
Trisetum distichophyllum (Vill.) Beauv.
Sesleria caerulea Scop.

Poa alpina was also used, but it was not investigated for haustoria. It was found that the hosts tended to shade out the Euphrasias, while vigorous development occurred when the Euphrasias were not shaded but were within reach of the host roots. Under the conditions of this experiment, the host species therefore varied in suitability as hosts according to their habit, caespitose species with short leaves being best.

The following results were obtained with weeds acting as hosts:

extraordinarily vigorous growth on *Capsella bursa-pastoris;*
vigorous growth on *Trifolium pratense*;
better growth on young seedlings than on larger plants of *Dipsacus fullonum*;
giant plant on *Senecio vulgaris*, similar to result with *Capsella*;
one plant vigorous on *Sonchus oleraceus*, lower parts shaded by host rosette and etiolated, upper parts normal;
very vigorous development on *Veronica peregrina* and *V. persica.*

In some cases a *Euphrasia* plant was found to have attachments to more than one host-plant simultaneously—in one case, for example, to *Carex alba, Poa annua* and *Trifolium pratense.*

Sowings of *E. rostkoviana* and *E. minima* were made under similar conditions, and gave very similar results.

Heinricher (1910) concluded that cultivation of *Euphrasia* was easy, provided the seed was sown in summer or autumn, the density of growth of the host-plant restricted, and good illumination ensured; a wide range of species could be used as hosts.

Euphrasia rostkoviana was also grown by Neidhardt (1947). The numbers of plants per pot were not given, but numbers of seeds sown were, and germination was up to 40%. Neidhardt tried one, two, five or 100 seeds per pot with no host, one, 100 and over 100 with

Poa annua, and over 100 with *P. nemoralis* and *Agrostis tenuis*. With no host, no Euphrasias flowered; when there were 100 in a pot some grew more strongly if in a group of several close together; with one per pot, plants attained a height of 1 to 3 cm and were chlorotic; with two and five per pot they were similar but reached 5 to 6 cm. With host-plants present and many seedlings in a pot, the Euphrasias became more vigorous after 4 weeks. If the host was regularly cut back, plants reached 25 cm and began to flower at the beginning of August. If it was not cut back, the Euphrasias developed slowly, and died in June without flowering. With one seedling per pot and *Poa annua* the Euphrasias were vigorous, much-branched and up to 15 cm tall, and they began to flower at the beginning of August.

Neidhardt also got *E. rostkoviana* to grow in grass in the garden of the Hamburg-Fuhlsbuttel school, in a part of Germany where the species is not native. Germination took place in April, plants were similar to those of pot cultures and they flowered at the beginning of August. Success was not achieved in all cases, and Neidhardt states that the ground should not be too solid and should be as moist as possible, and that the hosts should be as low-growing as possible and not too dense.

Recently Wilkins (1963) has given comparisons of dry weights of *Euphrasia* grown with four hosts and no host. All the *Euphrasia* samples reacted in much the same way to the hosts, and all hosts gave superior growth to no host, the difference being marked for all except one of the Euphrasias. Successful cultivation was achieved at least once with seven other hosts. Many of the potted plants were planted out in the garden when the roots had bound the soil together sufficiently. Establishment on the host was estimated by measuring the span of the largest leaf-pair; with *Trifolium repens* the time required for establishment was about 7–10 weeks.

Methods of cultivation

The simplest method of growing *Euphrasia*, in my experience, is to dig up turf in which the plants are growing and plant it in pots.

In 1952, I collected plants of many species by this method from early May until mid-September. In the great majority of samples collected in this way some of the Euphrasias continued to grow and flower. In another instance a turf was dug up in November, and Euphrasias germinated and flowered in it the following year. In such cultures the host-plants have to be cut back to prevent them smothering the Euphrasias; this is chiefly necessary in the early stages, as the host-plants later become pot-bound.

A second method is to sow *Euphrasia* seed in pots and, at the same time or later, sow seed of host-plants in the same pots. Alternatively, germinated seedlings or rooted portions of host-plants can be added to the pots. This method was used for *E. pseudokerneri* in 1951–52.

Germination in *Euphrasia*, however, is always rather uncertain (Yeo 1961). Wastage of pot capacity and host-plant supplies can be avoided and the number of plants per pot controlled, if the *Euphrasia* seedlings are transplanted after germination. This method can be used either for pot culture or for cultivation in open ground, and it is possible to use seedlings germinated in cultivation or collected wild in March, April or May. Transplanting hosts and Euphrasias, at approximately the same time, into the pots in which they are to be grown has been my standard method of culture. For cultivation in open ground the Euphrasias and their hosts are planted in bituminized paper pots which are then planted in the soil and gradually rot.

For almost all cultures the potting soil used was John Innes compost no. 1, or slight variants of it.

Presence and absence of host-plants

The growth of several species of *Euphrasia* with and without hosts has been compared. In 1952, *E. pseudokerneri* (serial no. E42), from S. Lincolnshire, was grown from seed with several different hosts, and with no host. Diagrams of some of the plants can be seen in Fig. 1, p. 8. Flowering occurred without a host, but the diagrams show that these plants were

far weaker than some, at least, of those with hosts. Similar results were obtained with seedlings of *E. pseudokerneri* (E66) collected from Box Hill, Surrey, in April 1952.

In 1955, *E. nemorosa* (E507), collected from Cambridgeshire, was grown from seed in pots with four separate host-plants, and without a host. The weights of the plants after drying (Table 5, p. 12) show distinctly superior growth with three of the four hosts, and that the largest individual with a host was over five times the weight of the largest with no host. Two plants from this experiment are illustrated in Fig. 3, p. 21. The one grown with no host shows a very gradual increase in the size of the leaves on the main stem, and has few branches, which are confined to the upper cauline nodes and were still short at the time

TABLE 1. Length of Stem and Branches of *Euphrasia.*
(Eight Euphrasias per pan, 6–8 survived in each.)

	Mean (cm)	*Range*	*Mean (cm)*	*Range*
1957	4 *Medicago lupulina*, 8 in. pan		No host, 8 in. pan	
rostkoviana, E669, v.c.49 ..	10·4	5–13·5	10·3	1–13·5
1962	2 *Sagina procumbens*, 2 *Trifolium occidentale*, 8in. pan		No host, 5 in. pan	
occidentalis, E922, v.c.75 ..	33·0	10– 71	5·9	4– 8
nemorosa, E919, v.c.48	49·7	8– 87	15·0	9–30
confusa, E907, v.c.45	40·5	22– 84	12·7	7–17
confusa, E914, v.c.45	72·3	11–160	9·5	4–14
brevipila, E917, v.c.45	52·4	21–149	8·3	2–14
rostkoviana, E916, v.c.45 ..	42·1	24– 60	6·3	4– 9
anglica, E913, v.c.45	59·9	27– 94	14·5	6–23
1963	As 1962		No host, 8 in. pan	
confusa, E929, v.c.26	52·4	16–103	8·9	2–21
brevipila E940, v.c.98	50·0*	32– 77	16·0	10–26

* Four plants; the other four plants in the pot had a similar size range, but were pressed later.

the plant was pressed. In the plant with a host, large leaves were formed lower down the stem, but near the apex the leaves were smaller, probably in correlation with the great development of the branches.

Further results are presented in Table 1.* The beneficial effects of providing a host are evident in all samples except the first. Even here, some benefit can be inferred, if it is assumed that the *Euphrasia*, had it not been parasitically established, would have been adversely affected by the competition of the *Medicago*. In fact some of the plants of E669 with *Medicago* showed visible indications of rather superior growth, compared with that with no host, which are not shown by the measurements. In view of the postulated competitive effect of the host the comparison in 1962 between plants with a host in 8 in. pans and plants with no host in 5 in. pans is probably not unfair. In fact, growth of host-less plants in 5 in. pans was much the same as in 8 in. pans.

An apparent indication of establishment on the host is that the apex of the plant becomes a fresher green, probably because of a more rapid expansion of the youngest leaves, which soon become conspicuously larger than their predecessors. After this, new leaves are formed at a greater rate, and usually the branches begin to grow. There is a great contrast between such plants and those with an apparently unsuitable host, which may remain almost static and are likely to die.

* Euphrasias often produce some flexuous capillary branches at the base; in all cases where branches have been measured these have been ignored.

In general, pot-grown Euphrasias which appear to be established on the host resemble well-developed wild Euphrasias; those that do not appear to be established, or are not provided with a host-plant, are inferior and resemble the starved-looking Euphrasias that can also be found in nature. The time from germination to establishment is usually 4 to 10 weeks, but may be as much as 17.

Proximity to host-plants

In 1955, *E. nemorosa* (E507), from Cambridgeshire, was grown in pots at varying distances from the host-plant. A correlation appeared between the time required for apparent establishment on the host and the distance between host and parasite.

Euphrasias planted 2·5 cm from the host appeared to be established about a week earlier than those 4·5 cm from it, and about a fortnight earlier than those 6·5 cm distant. Another effect of distance was that, of the Euphrasias planted 6·5 cm from the host, a considerably lower percentage became established than was the case with those planted closer to the host.

Leguminous hosts

Comparisons of various host-species are given later, but the effect of some Leguminosae was distinctive and will now be described separately. The effect showed itself in the great vigour of the *Euphrasia* plants and in their dark green, often glossy, leaves. It was first seen in Euphrasias grown in their own turf in 1952. With *E. anglica* (E67 and E76), from Surrey, the legume concerned was *Medicago lupulina*, with *E. occidentalis* (E73), from S. Hampshire, it was *Trifolium repens*, and with *E. pseudokerneri* (E75), from Cambridgeshire, it was *Anthyllis vulneraria*. Each of these Euphrasias was also growing in other turves (either in the same pot or in separate ones) containing few or no Leguminosae, and here they were much less vigorous and were paler green. *M. lupulina*, with a slight admixture of *Anthyllis vulneraria*, had the same good effect on many plants of *E. nemorosa* (E74), growing in a turf collected near Cambridge.

Table 10, p. 17, shows that four Leguminosae were used as hosts more than once in pot culture, and that three of them usually gave medium or good growth. With these three the *Euphrasia* plants almost always had particularly dark green foliage.

In their luxuriant growth and dark green leaves, Euphrasias growing with suitable Leguminous species showed symptoms of a good supply of nitrogen, which they must have been getting either through their haustoria or through the soil after its release by the legumes. The former hypothesis seems more probable, in view of the differences existing between individual Euphrasias in separate turves in the same pot.

The legume which Table 10 shows was a poor host was *Trifolium dubium*. Its unsuitability was not caused by an absence of bacterial root-nodules, however, for these were seen to be present when the seedlings were planted out with the Euphrasias.

Mutual parasitism

Koch (1891) and Wettstein (1897) reported that *Euphrasia* plants can parasitize one another, and their work has been summarized in another paper (Yeo 1961), where their observations on haustorial connections between individual *Euphrasia* plants were confirmed. The cultural effect of this—the markedly superior development of a few plants in a pot containing many seedlings—has also been observed by the present writer. A further cultural effect, probably due to the same cause, is that occasionally some, but not all, of the Euphrasias in a pot provided with a host fail to show signs of establishment, or fail to grow much after establishment. For example, a plant of *E. anglica* (E180), from S. Somerset, and a plant of a form of *E. micrantha* (E231), from E. Donegal, each growing in a small pot with *Sagina apetala*, remained very small, while the other three Euphrasias in each pot grew quite vigorously. Further, a plant of *E. nemorosa* (E897), from W. Sussex, apparently established on 8 June 1961, had only 16 cm of stem and branches when pressed on 9 September, while by this date its nearest neighbour (growing about 3 cm away and established only a week earlier) had produced 290 cm.

Time of flowering

The various species of *Euphrasia* are characterized by their time of flowering. Examples of late-flowering species are *E. pseudokerneri* and, in at least part of its range, *E. nemorosa*. These usually start flowering in late July or early August, at about the 10th to 16th node. Most species, on the other hand, begin to flower about mid-June at the sixth to tenth node; these are mountain meadow types (*E. brevipila* and *E. rostkoviana*) and pasture species (*E. confusa*, *E. anglica*, etc.). The high mountain species, *E. frigida*, *E. rivularis* and *E. cambrica*, usually begin flowering in June or July at the second to sixth node.

It will be seen from Fig. 1, however, that certain plants of *E. pseudokerneri* (E42) cultivated in 1952, some with no host and some with *Pelargonium* × *hortorum*, began flowering at the third to fifth node. The first flower buds were seen on 28 March, and the first flowers opened shortly before 21 April. The plants completed a very brief life cycle and died in a natural way and not from disease. This precocious flowering was evidently due to the very high temperatures prevailing in March in the greenhouse, which often exceeded 25° C. This suggests that temperature is one of the main factors controlling flowering in *Euphrasia*, and that given sufficiently high temperatures *E. pseudokerneri* can be made to flower at about as low a node as the high mountain species. On 21 March, these plants that flowered and died early had three or four leaves with visible teeth, whereas the plants numbered three and seven in Fig. 1, had only nought to two. It seems, therefore, that, being at a sufficiently early stage of development in March, these two plants were unable to respond to high temperatures by premature flowering and death. In fact, although one of them was without a host plant, both were ultimately able to develop more fully than those that appeared more vigorous in March.

Other plants of *E. pseudokerneri* (E42), grown as part of the same experiment but with *Plantago lanceolata* for host, flowered rather less precociously—early in May, at the fifth to seventh node—and they survived until July or August. Two plants of the same population of *E. pseudokerneri*, cultivated in 1952 in their own turf, flowered from the sixth to eighth node, then produced branches at higher nodes, and then flowered again. This was evidently the result of temperature fluctuations, and it shows that the conversion of a shoot from the vegetative to the flowering state is reversible.

Precocious flowering of very young plants after hot weather has occurred repeatedly in my greenhouse cultures. It is generally difficult to get naturally early-flowering forms to become established before coming into flower and, once flowering has begun to drain the reserves of tiny plants, there is little chance of subsequent establishment inducing vigorous growth. Thus in 1961 20 plants of a form of *E. brevipila* (E870), from Sweden, were grown with various host-plants. Sixteen Euphrasias had flower buds visible by mid-May. All but three of these produced one or two flowers and were then pressed, as they did not appear to be capable of producing any more; they were all about 1 cm tall. One of the three exceptions was a little larger and produced five flowers. The other two appeared to become established on the host, and were moderately vigorous.

Precocious flowering of *Euphrasia* sometimes takes place in nature, presumably as the result of an early hot spell. *E. pseudokerneri* and *E. nemorosa* were found flowering in Bedfordshire on 15 June 1952 and in Cambridgeshire on 12 June 1957, high temperatures having been recorded in Cambridge in mid-May 1952 and at the end of May in both 1952 and 1957. All these early-flowering Euphrasias appeared to be established on host-plants, and had begun flowering at the fifth to seventh node.

Effects of soil

No investigation was made of the influence of soil on growth, but the following observations suggest that small differences in soil constitution may be important for seedling Euphrasias.

Seedlings of *Euphrasia anglica* (E240) were collected in Leicestershire on 28 February 1953. They were intended to be a reserve for cultivation experiments but were not needed

for this purpose. Three or 4 days after collection, about 120 seedlings were removed from their turf and planted in two pots (numbered 1 and 2) in approximately equal numbers. On 22 May pot 1 had 42 seedlings and pot 2 had 39. In pot 1 the two smallest plants were pale green throughout, while the rest were medium green, but paler at the top; all the plants in pot 2, however, were distinctly chlorotic, the upper leaves being quite yellowish, and all the leaves appeared slightly fleshy. On 12 June, two plants in pot 1 had their first flowers open, three more were ready to bloom shortly, and others had flower buds. In pot 2 all the plants were chlorotic and no flower buds were visible.

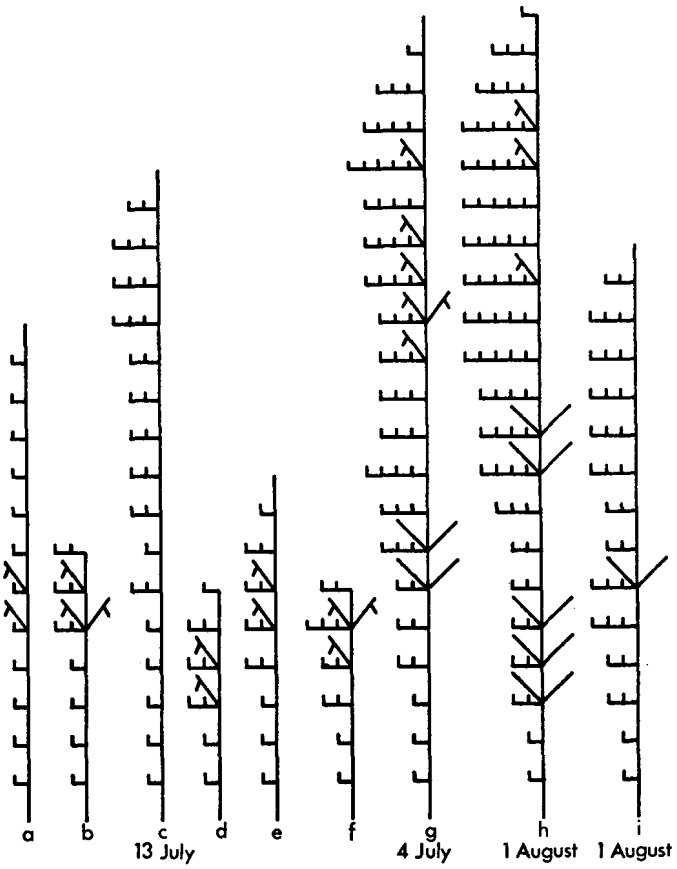

Fig. 1. Diagrams of *Euphrasia pseudokerneri* plants. (*a*)-(*c*) without a host; (*d*)-(*g*) with *Pelargonium* × *hortorum*; (*h*) with *Carex caryophyllea*; (*i*) with *Bromus erectus*. Horizontal bars = nodes; cross-pieces on them show leaf-tooth number. Sloping bars = branches. Forks = flowers. Un-dated diagrams represent plants that had completed their development.

The poorer condition of the plants in pot 2, was probably due to differences of soil. The soil in pot 2 appeared lighter in colour and had less peat at the surface than that in pot 1; also, unlike the soil in pot 1, it had mosses and green algae developing on it by 22 May.

Euphrasia plants sometimes show chlorosis before establishment and, using John Innes compost, this is especially prevalent in *E. micrantha*, *E. anglica* and *E. rostkoviana*.

Watering

During the spring and early summer, Euphrasias in pots in an unheated greenhouse are liable to die if there is a spell of cold, heavily overcast or damp weather. The entire plant wilts, and dies in a day or two; this can occur in unestablished or in vigorously growing

plants that have been established for a week or so. The best watering policy seems to be to keep the Euphrasias rather dry during April and the first part of May, as they endure this well, and then to water more freely to encourage growth. After watering, the plants and the soil surface should be encouraged to dry off quickly; and no water at all should be given in cold dull weather.

TABLE 2. Length measurements of *Euphrasia pseudokerneri* grown in 1952.

	Pot No.	*Host*	*Length in cm of stem plus branches of each plant*
E42	1	None	5·0, 2·5, 1·5
	2	*Festuca ovina*	20, 16, 9, 6, 3, 0·5
	3	*Koeleria cristata*	1
	4	*Festuca ovina* and *Koeleria cristata*	46, 32, 11, 9, 5
	5	*Pelargonium* × *hortorum*	92, 2, 2, 1
	6	*Plantago lanceolata*	17, 13, 10, 4, 1
	7	*Prunella vulgaris*	1, 1, 1, 1, 1
	8	*Plantago lanceolata* and *Prunella vulgaris*	32, 28, 0·5
	9	*Thymus drucei*	0·5, 0·5, 0·5
	10	*Festuca ovina* and *Thymus drucei*	1
E70	1	Original turf	199, 60, 37, 25, 17, 7
	2	*Carex caryophyllea*	64
	3	*Bromus erectus*	18, 6
	4	*Sieglingia decumbens*	63, 30
	5	*Hieracium pilosella*	67

GROWTH OF E. PSEUDOKERNERI, E. ANGLICA AND E. NEMOROSA WITH VARIOUS HOST-PLANTS

The growth of *E. pseudokerneri* with various hosts was compared in 1952 by cultivation in pots. A group of pots 5½ in. in diameter was prepared in November 1951; the soil consisted of loam covered by a layer of sand. (It was hoped that it would be possible to trace haustorial connections easily in the sand layer, but there was little branching of roots in it as it turned out.) Seeds or plants of the host species were sown or planted in each pot, together with seed of the *Euphrasia* (E42), from S. Lincolnshire. Germination of the *Euphrasia* occurred in January, February and March. On 29 April 1952, seedlings of *E. pseudokerneri* (E70) were collected from the same locality and some of them were planted, at the same time as their host-plants, in pots 3½ in. in diameter. The rest of these seedlings were left in their turf, and this was also potted up; other species in the turf were *Carex caryophyllea*, *Thymus drucei* and three or four species of grass.

The development of the plants was regularly recorded, the dates of appearance of the leaves, branch initials and flower buds being noted, in addition to the leaf tooth number; notes were made later to show which branches developed and which flower buds opened. Some of these observations are reproduced in Fig. 1.

The E42 and E70 plants were eventually pressed and the total length of stem and branches measured (Table 2).

The plants were pressed on various dates but, with a few exceptions, all appeared to have completed or nearly completed their growth.

It is clear that some plants were good hosts; there is one inconsistent result in that the *Euphrasia* plant with *Festuca* and *Thymus* did not develop, although those in the two other pots containing *Festuca* developed quite well.

The dwarf plant with *Koeleria*, when dug up on 5 June, was found to have its roots surrounded by those of the grass, and a dwarf plant with *Thymus*, dug up dead on 10 May,

was found to have a few detached haustoria, suggesting that parasitic union had been effected but had not proved beneficial, presumably because the host failed to provide what the *Euphrasia* required. The occurrence of some feeble plants in pots with apparently good hosts has been discussed in general on p. 6. It is known, however, that in some of the E42 plants growth was prevented by precocious flowering.

TABLE 3. Number of *Euphrasia* plants of different degrees of vigour with various host species

E. pseudokerneri (*E226*), *Surrey*

Host	*Grade*					
	1	2	3	4	5	6
	Poor		*Moderate*		*Good*	
Anthyllis vulneraria					1	4
Medicago lupulina				1	3	2
Hieracium pilosella			1	1	2	1
Thymus drucei	1	1		1	1	
Dactylis glomerata		1			1	
Agrostis gigantea		1	1	2		
Festuca ovina				1		
Luzula campestris				1		
Achillea millefolium				1		
Sieglingia decumbens		2	1	1		
Carex flacca	1		3			
Brachypodium pinnatum ..		3	1			
Koeleria cristata..	1	2	1			
Bromus erectus		3				
Plantago lanceolata	1	1				
Carex demissa	1	1				
Carex caryophyllea	2	2				
Carex pilulifera	2					

E. anglica (*E157*), *Surrey*

Host	*Grade*					
	1	2	3	4	5	6
	Poor		*Moderate*		*Good*	
Luzula campestris					1	
Agrostis gigantea				2	1	
Anthyllis vulneraria					1	
Brachypodium pinnatum ..				1		
Medicago lupulina			1			
Carex caryophyllea			3			
Carex pilulifera			1			
Achillea millefolium			1			
Helianthemum chamaecistus ..	1	2				
Hieracium pilosella		1				
Bromus erectus		1				
Carex flacca	2	1				
Carex demissa	2					
Thymus drucei	1					

The *Euphrasia* plants grown from seed took 72–95 days from germination to establishment. Those grown from wild-collected seedlings became established 40–60 days after potting-up with the host-plants.

In 1953, *E. pseudokerneri* (E226), this time collected in Surrey, was again grown with various hosts and compared with *E. anglica* (E157), also from Surrey. Four *Euphrasia* seedlings were planted in each pot, the pots being $3\frac{3}{4}$–4 in. in diameter. For each species of *Euphrasia* there were two pots with each of 21 host species. There were two host-plants per pot, except in the case of *Achillea millefolium* where there was only one per pot. The hosts were of known origin and were in the form of young seedlings or portions of newly-divided plants. The pots were plunged in an ash-bed in a sheltered but sunny position at Leicester.

The Euphrasias and hosts were planted out from 28 to 31 March. By 20 April, many Euphrasias were dead and many damaged, apparently because of frost. Replacements were made, but not all the pots could be brought up to their full numbers.

Most of the Euphrasias were pressed on 20 September, but a few were pressed on 1 and 3 September. They were graded into six sizes; a 'type-plant' of *E. pseudokerneri* was chosen for each size, and the other plants of this species were then classified into the six grades by comparing them with the 'type-plants'. Silhouettes of two of the latter are shown in Fig. 2, p. 12. The plants of *E. anglica* were comparatively sparsely branched and these were graded according to their length of stem and branches, as indicated in Table 3, where the performance of both *Euphrasia* species is shown. The number of host species is less than 21 because, with some hosts, all the Euphrasias died. Owing to the small numbers of Euphrasias with each host species, it is inadvisable to conclude, from the results of this experiment, that any host is a poor one (though some are clearly good). Thus, the previous year *E. pseudokerneri* had grown well on *Plantago lanceolata* and on *Carex caryophyllea*, and on some occasions *E. anglica* has grown well on *Medicago lupulina*. It is shown in the experiment with *E. nemorosa* described next that some hosts, though they produce good growth in established plants, are also liable to give a high proportion of failures to become established. This factor could be responsible for the variations of behaviour with the hosts just mentioned. It cannot be claimed with confidence that *E. pseudokerneri* and *E. anglica* differ in their host reactions, but the table shows that, on the whole, *E. pseudokerneri* grew better with dicotyledonous plants than with monocotyledons, whereas this superiority of dicotyledons was not evident in the case of *E. anglica*.

In 1955, many plants of *E. nemorosa* (E507), from Cambridgeshire, were grown in $5\frac{1}{2}$-in. diameter pots with four host species, and with no host (=*NH*). The four host species were:

Hieracium pilosella (=*H*),
Plantago lanceolata (=*P*),
Bromus erectus (=*Bs*),
Medicago lupulina (=*M*).

There were 1–6 Euphrasias per pot, and either one or three host-plants in the *H*, *P*, *Bs* and *M* pots. The Euphrasias and hosts were potted up as young seedlings. The Euphrasias were placed near the edges of the pots, and hosts were placed in the middle, except when only one *Euphrasia* and one host were present. During growth, the host-plants were cut back where they tended to shade Euphrasias.

The potting up was done on 8 and 9 April. Some replacements were already necessary on 10 April, and further deaths were observed throughout the period of cultivation. Observations were made on all plants about once a week from 8 May to 4 July. On 13 August a note was made of the survival or death of the plants, and the following day all were pressed.

The appearance of two of the Euphrasias can be seen in Fig. 3, p. 21. The overall mean weight of the plants with each host species is given in the fourth line of Table 4. *H* and *P* gave high mean weights, *M* a fairly high mean, and *Bs* a slightly smaller mean than

Fig. 2. Plants of *Euphrasia pseudokerneri*, × ½. Left, grown with *Hieracium pilosella* (size-grade 5). Right, grown with *Anthyllis vulneraria* (size grade 6).

TABLE 4. Mean weights (in g) of Euphrasias after pressing.
(The number of plants in each class is given in brackets.)

Number of plants per pot						
Euphrasias	*Hosts*	*H*	*P*	*Bs*	*M*	*NH*
1 or 2	1	·33 (8)	·48 (4)	·07 (3)	·23 (4)	·15 (12)
3 or 4	1 or 3	·41 (10)	·49 (8)	·08 (4)	·28 (14)	·14 (10)
5 or 6	1 or 3	·32 (5)	·17 (5)	·13 (6)	·25 (11)	·08 (6)
1 to 6	1 or 3	·36 (23)	·39 (17)	·10 (13)	·26 (29)	·13 (28)

TABLE 5. Variation of *Euphrasia* according to host species

	H	*P*	*Bs*	*M*	*NH*
Percentage established	73%	64%	64%	76%	—
Average wt. of plants (g)	·36	·39	·10	·26	·13
Standard deviation	·374	·363	·115	·151	·068
Wt. of largest individual (g) ..	1·6	1·3	·3	·7	·3
Mortality, 8 May–4 July	20%	16%	41%	3%	16%
Mortality, 8 May–13 August ..	23%	40%	55%	12%	16%

NH. The result with no host has been discussed on pp. 5 and 6. Many of the Euphrasias with *Bromus erectus* appeared to become established in the period 8 May to 21 June. Presumably they received little benefit from this host, and suffered competition from it.

Establishments occurred mainly during the first 4 weeks of the 8-week observation period. It was found that there was little variation in the time of establishment on the different hosts, but the total percentage of *Euphrasia* plants that became established varied according to host (Table 5).

Table 5 also shows that the mortality of the Euphrasias was low with the hosts *M* and *H*, and high with *P* and *Bs*; *M* and *H* also showed better establishment. This bears out an impression obtained during my work on *Euphrasia* that plants which are not established on the host are more liable to die than those which are. The very low mortality with no host (none between 4 July and 13 August) supports the theory that, if Euphrasias are in the same pot as a fully autotrophic plant from which they receive no benefits by parasitism, they will be at a severe disadvantage compared with Euphrasias in a pot by themselves.

For experimental work it is desirable to have a high percentage of plants becoming established, a high average weight, little variation in weight, and low mortality. Euphrasias with *Bs* and *NH* show little variation in weight, but both are unsatisfactory in their low average weight, as is *Bs* in its high mortality. *P* has the highest average weight, but its establishment percentage is relatively low and its mortality high. *H* and *M* present the best combinations of characters. Since plants weighing 0·2 g and upwards are quite well developed, *M*'s lower average weight than *H*'s is not a serious disadvantage, and it is more than counterbalanced by a smaller variation in weight and by lower mortality. The experiment, therefore, shows that *M* is the most useful host plant of those tested.

Further host comparisons involving Medicago lupulina

I have generally used *Medicago lupulina* as the host on which to raise my Euphrasias. However, this has been less successful with species from the West, the North and the mountain areas of Britain than with the south-eastern species. In the case of *E. scottica* this could have been due to its being an inhabitant of wet places, and one year some plants of a sample of *E. scottica* (E782), from W. Ross, were grown in a pot embedded in wet peat, but this special treatment produced little or no improvement in their growth compared with the rest of the sample.

In 1960, when several northern and western species became available, samples were grown in a particularly cool and shady situation with *M. lupulina*, but again with poor results. At the same time some of these species, together with the southern *E. anglica* and the widespread *E. confusa*, were grown with various hosts in an unshaded greenhouse. For these, *Poa pratensis* and (as in the shady position) *M. lupulina* were very poor hosts, but quite good results were obtained with *Sagina procumbens* for *E. anglica* (E849), *E. brevipila* (E806), *E. confusa* (E803, E834), from Yorkshire, and *E. rostkoviana* (E855), while *Trifolium occidentale* D. E. Coombe gave good results with *E. brevipila* (E860) and *E. rostkoviana* (E857), both from Kirkcudbrightshire. In addition, some samples were planted with *M. lupulina* in the greenhouse, and gave slightly worse results than in the shade; these were *E. borealis* var. *zetlandica* Pugsl. (E851), *E. curta* (E853) and *E. rotundifolia* (E845).

These results suggested that temperature and humidity were not the main causes of difficulty in growing these plants, and that unsuitability of host-plant was probably the main cause.

Plants grown in 1961, largely from the same samples as were used in 1960, gave the results shown in Tables 6 and 7; these show, in most cases, a marked superiority of *Sagina*, *Trifolium*, or a mixture of the two, over *Medicago*. Two stocks of *M. lupulina* are referred to in Table 6, the new one being superior to the old for *E. confusa* × *E. occidentalis* and for *E. nemorosa*. The old stock of this host had been maintained and reproduced annually from seed since 1952, and the new one was obtained in 1961 by collecting seedlings from the herbaceous bed for Leguminosae in the University Botanic Garden, Cambridge. The new

TABLE 6. Total length (in cm) of stem and branches of Euphrasias grown with various host-plants, 1961. (No. before colon = no. of surviving Euphrasias; no. after colon = mean length; no. in brackets = length of largest plant. Every pot contained ten Euphrasias and four host-plants.)

	E. brevipila		*E. confusa* × *occidentalis*	*E. anglica*	*E. nemorosa*	*E. micrantha*
	E806	*E870*	*E900*	*E849*	*E897*	*E891*
Vice-county	*65*	(*Sweden*)	99	*6*	*13*	*1*
Medicago lupulina (old stock) 3 pots	3:8·7 (12)	5:1·6 (4)	5:6 (8)	4:13·3 (21)	4:49·3 (79)	2:10·5 (12)
M. lupulina (new stock) 3 pots	2:14 (15)	5:1·6 (4)	5:29 (75)	2:14 (16)	4:92·8 (138)	4:7·3 (22)
Sagina procumbens 3 pots	4:53·3 (85)	5:4·8 (14)	3:54·3 (88)	3:24·7 (43)	5:120 (249)	0:—
Trifolium occidentale 3 pots	4:19·8 (34)	5:2·8 (10)	5:13·4 (32)	5:27·3 (41)	5:52·8 (134)	3:36·3 (74)

stock was more vigorous, had larger leaflets and was less affected by heavy attacks of red spider mite.

It can be seen from Table 6 that *E. micrantha* failed to survive with *Sagina* as host, but in 1961 E837 grew very well on *Sagina procumbens* seedlings which germinated in its original seed pot. *E. micrantha* is particularly liable to show signs of ill-health before establishment, and this no doubt contributed to the poor results shown in these tables.

It thus seems to be the case that there are many species of *Euphrasia* (particularly the northern ones) for which *M. lupulina* is not a favourable host-plant. For some *Euphrasia* species, however, even if *Medicago* is usually unsuitable, there are certain populations which will grow well on it. For example, quite good plants of *E. brevipila* and *E. rostkoviana* have sometimes been grown on *Medicago*, and very vigorous plants of *E. brevipila* from Poland have also been grown on it.

TABLE 7. Total length (in cm) of stem and branches of Euphrasias. (Explanation as for Table 6.)

	E. borealis var. *zetlandica* *E851*	*E. rotundifolia* *E845*	*E. scottica* *E864*	*E. curta* *E853*	*E. rostkoviana* *E855*
Vice-county	*112*	*108*	*73*	*73*	*73*
1960 Shady frame with *Medicago lupulina*	0:—	3:1·7 (2)	0:—	5:6 (10)	4:7·3 (8)
1961 Greenhouse with *Sagina procumbens* mixed with *Trifolium occidentale*	7:7·6 (24)	3:5 (8)	2:31 (38)	6:14 (20)	1:90 (90)

CULTIVATION OF THREE EUPHRASIA SPECIES WITH FOUR HOST SPECIES

In this experiment *Euphrasia borealis* (E329), from NW Yorkshire, was grown indoors and outdoors, and *E. nemorosa* (E417), from Staffordshire, and *E. occidentalis* (E351), from W. Cornwall, were grown indoors only.

Medicago lupulina (=*M*), *Plantago lanceolata* (=*P*) and *Trifolium dubium* (=*T*) were used as host-plants for the Euphrasias indoors. Each *Euphrasia* species and each host species was represented by one pan, and each pan contained four seedlings of the host-plant near the centre, and eight seedlings of *Euphrasia* towards the edge; in addition, there was a second pan of *E. occidentalis* with *Medicago*, provided with six host seedlings. A total of six Euphrasias died and were replaced in the first 3 weeks.

E. borealis was grown outdoors with the same three hosts and with *Briza media* (=*Ba*), by the method described on p. 4. Each pot was planted with one *Euphrasia* and one host seedling on 11 May 1954. Replacements of dead Euphrasias were made from time to time until 30 May. On 2 June the pots were embedded in the soil of the experimental ground; there was a row of ten pots with each host, and the rows were placed 2 ft apart. On 11 July observations were made on the state of the plants outdoors, and on 3 September, all but four very small ones were pressed.

Stem and branch lengths of the indoor and outdoor Euphrasias, after pressing, are given in Table 8, which shows the average size of the plants and, for the indoor cultures, the aggregate growth in each pot. (*E. borealis* and *E. occidentalis* are naturally more sparingly branched than *E. nemorosa*.) The growing period of *E. borealis* indoors with *M* was 21 days shorter than with *P*, but five or six of the eight plants with *M* had more or less finished growing when the plants were pressed on 23 July. *E. occidentalis* grew very much better with *M* in pot 2 than in pot 1. Pot 2, however, had been set up much earlier, and the Euphrasias had become established on the host 8 weeks earlier than those in pot 1. The death of all the indoor plants of *E. borealis* with T is probably accounted for by the unsatisfactoriness of this host.

TABLE 8. Total length (in cm) of stem and branches of Euphrasias.
(No. before colon = no. of surviving Euphrasias; no. after colon = mean length.)

					Total length for each pot		
	Ba	*M*	*P*	*T*	*M*	*P*	*T*
occidentalis (pot 1)	—	7:11	4:7·5	2:3·5	74	30	7
occidentalis (pot 2)	—	5:28	—	—	140	—	—
nemorosa	—	7:65	5:178*	7:12	453	890	84
borealis (indoors)	—	8:15	5:28	0:—	119	139	—
borealis (outdoors)	0:—	4:10	5:42	3:2	—	—	—

* Length estimated from the measurements of selected branches.

This indoor cultivation can be summed up by saying that *M* and *P* were good hosts for *E. nemorosa* and *E. borealis*, *M* was fairly good for *E. occidentalis*, and *T* was very poor for all the Euphrasias. It will be noted that more Euphrasias of all species survived with *M* than with *P*. The difference between *M* and *P* in the results for vigour and survival of *E. nemorosa* is thus the same as that obtained with a different population of *E. nemorosa* in 1955.

Though P was a better host for *E. borealis* outdoors than in, *M* showed the reverse behaviour. Possibly, in open soil, the roots of *M* branch at too deep a level to benefit the Euphrasias. Four out of five outdoor plants of *E. borealis* with *P* were very vigorous with large

or very large leaves. A sixth plant was also vigorous, but, owing to some accident, only a fragment of it was alive at the time of pressing, so that it could not be measured.

The observations that were made on 11 July on the plants of *E. borealis* in this trial are given in Table 9; here, as in Table 8, *P* appears as the best host for *E. borealis* outdoors, *M* is again second best, and *T* and *Ba* are both very poor.

TABLE 9. Observations on *E. borealis* outdoors, 11 July, 1954.

	Host			
	Trifolium dubium	*Plantago lanceolata*	*Briza media*	*Medicago lupulina*
Number alive	8	10	5	9
Number apparently host-established	0	8 or 9	0	3 possibly
Number flowering	3	8	3	5

GARDEN CULTIVATION

In 1953, at Leicester, a considerable number of plants of *E. nemorosa* and *E. stricta* was grown with *Plantago lanceolata* raised from seed (Yeo 1962). The bituminized paper pots (see p. 4) were plunged in the experimental plot on 31 March to 2 April. Between 22 and 26 April many dead plantains and Euphrasias were replaced. For this purpose the pots were lifted out of the ground. Of the 448 plants present after replacements had been made, 337 were alive on 19 July. Pronounced signs of establishment on the host in a few plants, and slight symptoms in many others, were seen on 12 May, 7 to 8 weeks after potting up. By 19 July only two plants out of 337 were not established. Nearly all the plants that were healthy became extraordinarily large-leaved and vigorous. Generally they were much more luxuriant than the most vigorous plants to be found in nature. Most of them were similar in size to a plant of *E. nemorosa* grown in the same way in 1956 which weighed 21 g after drying, and their upper cauline leaves were commonly 16–19 mm long and 16–18 mm wide. They may be contrasted with another plant of *E. nemorosa*, grown in a greenhouse, which was about as large as the normal maximum for wild plants of this species of *Euphrasia*, and which weighed only 1·6 g (with a stem-plus-branch length of 214 cm).

The host-plants were also very vigorous and were several times cut back severely to stop them from covering the Euphrasias and to check their growth somewhat. The last time the severe cutting-back was done, some Euphrasias were getting bushy, and the plantains overshadowed by them did not recover their vigour. Subsequently, these Euphrasias appeared to suffer somewhat. It appears that, when the plantain is liable to be overshadowed, some of its leaves that project out beyond the shadow of the *Euphrasia* should be left untrimmed.

Many of the Euphrasias that died did so in July, after establishment on the host and after a period of wilting. It was thought that the wilting was caused by the fraying of the base of the stem, which resulted from the twisting of the stem as the head of the plant blew about in the wind. The movement of the plants in the wind doubtless brought on the wilting symptoms, but the stems may previously have been weakened by attacks of damping-off fungus at the seedling stage, as weaknesses at the bases of the stems were found in *E. nemorosa* cultivated in the greenhouse in 1955. The weak zone in these plants was discoloured and thinner than normal, and it sometimes broke when a plant was pulled up for pressing. In the absence of wind, the weakness had no effect on the vigour of the plants, some of the largest having the weakest stems. Damping-off had been particularly troublesome among the young seedlings of this population.

TABLE 10. Host-plants and *Euphrasia* species grown with them.
(Country of origin of *Euphrasia* indicated if not Great Britain or Ireland.)

Clay-pot cultivation	*No. of samples in which the indicated degree of vigour was attained*		
	Poor	*Medium*	*Good*
Ranunculus repens			
E. anglica		1	
Coronopus squamatus			
E. stricta Lehm...		1 (Channel Is.)	
E. brevipila			1 (Poland)
Helianthemum chamaecistus			
E. anglica	1		
Sagina apetala			
E. nemorosa		1	
E. confusa		1	
E. rostkoviana		1	
E. anglica		1	
Sagina procumbens			
E. micrantha		1	1
E. occidentalis			1
E. nemorosa			1
E. stricta Lehm...		1 (Channel Is.)	
E. confusa	1	1	2
E. brevipila		1 (Sweden)	1
E. rostkoviana			1
E. anglica			1
Pelargonium × *hortorum* Bailey			
E. pseudokerneri			1
Medicago lupulina			
E. micrantha		1	3 (1 North America)
E. scottica		1	
E. scottica × *E. confusa*	1	1	
E. curta var. *rupestris* Pugsl.		1	
E. occidentalis	1	2	15 (2 France)
E. nemorosa		6 (1 France)	12 (1 France)
E. stricta Lehm...	1 (Germany)	1 (Poland)	5 (2 France, 2 Germany, 1 Channel Is.)
E. pseudokerneri			6
E. confusa	3	2	6
E. borealis		1	
E. brevipila	6 (2 Sweden)	6 (1 Poland)	4 (1 Sweden)
E. rostkoviana	1	2 (1 Italy)	2 (1 Poland)
E. montana	1		
E. hirtella		1 (France)	

TABLE 10—*cont.*

Clay-pot cultivation	*No. of samples in which the indicated degree of vigour was attained*		
	Poor	*Medium*	*Good*
Medicago lupulina—cont.			
E. anglica	1	6	5
E. anglica × *E. nemorosa*			1
E. vigursii		1	
E. salisburgensis		1 (France)	1 (Austria)
E. salisburgensis var. *hibernica* Pugsl.			1
Trifolium repens			
E. stricta Lehm.		1 (Poland)	
Trifolium occidentale Coombe			
E. micrantha			1
E. nemorosa		1	
E. confusa			1
E. borealis		1	
E. brevipila		1 (Sweden)	1
E. rostkoviana			1
E. anglica			1
Trifolium dubium			
E. occidentalis	1		
E. nemorosa	1		
E. borealis	1		
Anthyllis vulneraria			
E. foulaensis			1
E. curta. var. *rupestris* Pugsl.		1	
E. occidentalis		1	
E. pseudokerneri			1
E. anglica			1
E. confusa			1
Epilobium parviflorum			
E. rostkoviana		1	
Calluna vulgaris			
E. micrantha	1	1	
Calluna vulgaris and *Erica cinerea* mixed			
E. micrantha			1
Thymus drucei			
E. occidentalis		1	
E. pseudokerneri	1		1
E. anglica	1		
E. salisburgensis			1 (Austria)
Prunella vulgaris			
E. pseudokerneri	1		
Plantago lanceolata			
E. occidentalis	1	1	1
E. nemorosa			2
E. pseudokerneri	1		1
E. borealis			1
E. anglica	1		
Plantago coronopus			
E. occidentalis	1		

TABLE 10—*cont.*

Clay-pot cultivation	*No. of samples in which the indicated degree of vigour was attained*		
	Poor	*Medium*	*Good*
Achillea millefolium			
E. pseudokerneri		2	
E. anglica		1	
Leontodon autumnalis			
E. foulaensis	1		
E. occidentalis	2		
E. anglica	8		
E. vigursii	1		
Hieracium pilosella			
E. nemorosa			1
E. pseudokerneri			2
Luzula campestris			
E. micrantha	1		
E. occidentalis	1		
E. pseudokerneri		1	
E. rostkoviana	2	2	1
E. anglica			1
E. rivularis		1	
Carex demissa			
E. pseudokerneri	1		
E. anglica	1		
Carex flacca			
E. pseudokerneri		1	
E. anglica	1		
Carex pilulifera			
E. micrantha	1		
Carex caryophyllea			
E. pseudokerneri			1
E. confusa	6	1	
E. anglica		1	
Sieglingia decumbens			
E. occidentalis		1	
E. nemorosa		1	
E. pseudokerneri		1	1
Festuca ovina			
E. pseudokerneri		1	1
Poa pratensis			
E. confusa	2		
E. rostkoviana	1		
Poa trivialis			
E. micrantha		1	
E. pseudokerneri		1	
Dactylis glomerata			
E. pseudokerneri			1
Bromus erectus ..			
E. occidentalis		1	
E. nemorosa		1	
E. pseudokerneri	1	1	
E. anglica		1	
Brachypodium pinnatum			
E. pseudokerneri		1	
E. anglica		1	

TABLE 10—*cont.*

	No. of samples in which the indicated degree of vigour was attained		
Clay-pot cultivation	*Poor*	*Medium*	*Good*
Koeleria cristata			
E. micrantha	2		
E. confusa × *E. micrantha*	4		
E. curta var. *rupestris* Pugsl. ..	1		
E. nemorosa	2		
E. pseudokerneri	1	1	
E. confusa	1		
Agrostis tenuis			
E. occidentalis		1	
E. nemorosa		1	
Agrostis gigantea			
E. pseudokerneri		1	
E. anglica			1
Cultivation in open ground	*Poor*	*Good*	*Very Good*
Medicago lupulina			
E. borealis	1		
Trifolium dubium			
E. borealis	1		
Plantago lanceolata			
E. occidentalis		1 (France)	
E. nemorosa			9
E. pseudokerneri		1	
E. confusa			2
E. stricta Lehm.			1
E. borealis		1	
Luzula campestris			
E. anglica			2
Briza media			
E. borealis	1		
Koeleria cristata			
E. micrantha form	1		
E. vigursii		1	

Other Euphrasias were also tried with other hosts in 1953. Two Euphrasias were planted in each bituminized pot, and the hosts were pieces of divided plants with some roots present; one piece per pot was used.

The most successful populations were two of *E. anglica* (E168 and E219), from Leicestershire, each represented by ten pots with *Luzula campestris*. On 31 May (about 8 to 9 weeks after potting up) many of these Euphrasias showed signs of establishment on the host, and on 21 June nearly all were established. The plants grew vigorously, having fairly large leaves and numerous branches. They did not attain anything like the size of the largest plants of *E. nemorosa* grown outdoors with *Plantago lanceolata*, however, probably because of their lower node of flowering.

On *Koeleria cristata*, a form of *E. micrantha* (E231), from E. Donegal, made little progress. On 26 June, two plants out of 16 showed signs of being established on the host,

though five others (apparently not established) were flowering. On 31 August, three out of the 12 survivors may have been established, but none was vigorous. In *E. vigursii* (E197), from S. Devon, the first signs of establishment on the same host were seen (in one plant) on 18 May, but it was not until 30 July that nearly all were established. They were, therefore, about 5 weeks behind *E. anglica* in becoming established. They eventually became about as vigorous as the plants of their parent wild population, and they varied quite considerably in vigour.

The same method of cultivation was used at Cambridge in 1954. In one experiment, populations of *E. nemorosa* and *E. confusa* were grown; mortality was very heavy, but the survivors grew very vigorously on *Plantago lanceolata* grown from seed.

In 1956, the method was again used to see whether better survival could be obtained at Cambridge. *E. nemorosa* (E608), from Cambridgeshire, was grown in four rows of ten pots each. The 40 pots were each planted with one *Euphrasia* and one *Plantago lanceolata* seedling on 4 April. The rows of pots were then planted in the garden, each on a different date. However, the mortality of the Euphrasias awaiting planting in the garden was nearly as severe as that of those already planted out, so that late planting-out gave little advantage. In fact, there were again very few survivors, but most of them grew extremely vigorously.

List of host-plants

The host-plants employed in all my experiments are listed in Table 10, together with a rough indication of how well various *Euphrasia* samples grew on them. This indication is based on the most vigorous *Euphrasia* plant raised in each case.

Fig. 3. Plants of *Euphrasia nemorosa* after pressing on 14 August 1955, × ½. Left, one of two plants grown in a pot with no host; weight 0·2 g. Right, one of three plants grown in a pot with one plant of *Medicago lupulina*; weight 0·7 g.

Particularly poor hosts seem to be *Leontodon autumnalis* and *Koeleria cristata*; Gramineae in general seem to be mediocre hosts, while some of the best hosts are to be found among the Leguminosae. Indications that *Medicago lupulina* may be a better host for some species of *Euphrasia* than for others have already been mentioned; *Luzula campestris* may be a similar case, for it appears to be better on the whole for the species of the diploid Series Hirtellae (*E. anglica*, *E. rostkoviana* and *E. rivularis*) than for the tetraploid species of two other Series.

TABLE 11. Growth of Euphrasias without host-plants.

Species	*Date when pressed*	*Pot diam.*	*No. of Euphrasias*	*Height in mm*	*No. not flowering*	*No. fruiting*
		inches				
micrantha, E185A, S. Somerset ..	2/9/53	5½	fairly numerous	20–40	few	rather few
occidentalis, E192, E. Cornwall ..	2/9/53	5½	fairly numerous	6–15	few	many
2 pots	2/9/53	5½	very numerous	2–15	many	many
occidentalis, E351, W. Cornwall	9/7/54	3	5	45–80	0	5
2 pots	9/7/54	3	18	15–55	4	10
nemorosa, E196, S. Devon	2/9/53	5½	extremely numerous	10–50	many	moderate no.
nemorosa, E421, Surrey	9/7/54	3	4	10–40	3	0
2 pots	9/7/54	3	9	8–20	5	3
nemorosa, E417, Staffordshire ..	27/8/54	3	15	17–35	11	0
confusa, E172, S. Somerset	2/9/53	5½	fairly numerous	7–35	few	moderate no.
confusa, E208, Derbyshire	2/9/53	5½	numerous	6–36	few	many
brevipila, E325, W. Sutherland ..	9/7/54	3	6	7–30	1	5
brevipila var. *reayensis* Pugsl., E308, W. Sutherland	24/7/54	3	6	37–70	1	1
rostkoviana, E239, S. Kerry	26/8/53	5½	15	12–65	2	13
anglica, E180, S. Somerset	2/9/53	5½	fairly numerous	10–40	several	many

BEHAVIOUR OF EUPHRASIA WHEN GROWN WITHOUT A HOST

A silhouette of a *Euphrasia* plant fruiting in the absence of a host-plant can be seen in Fig. 3. Table 11 shows how the surplus seedlings of *Euphrasia* grew in their seed-pots without hosts in 1953 and 1954. The seedlings were too crowded to be fairly compared with plants grown in the presence of a host. However, the table shows that fruiting took place in nearly all samples. The capsules contained perfectly normal-looking seeds. The conditions of growth of three samples, E351 (*E. occidentalis*), E417 and E421 (both *E. nemorosa*), were closely similar, but the first grew much better than the other two, being evidently less affected by the lack of a host. *E. nemorosa* and *E. confusa* were the only species which produced branches and these are normally the most branched species.

DISCUSSION

Euphrasias in cultivation are decidedly more subject to disease than autotrophic plants from similar habitats. This applies both before and after establishment, but it varies greatly from one population to another and also from species to species. Careful treatment can minimize losses to some extent and, though some losses must be expected, there is no serious obstacle to the cultivation of the majority of *Euphrasia* species for experimental purposes, even when this requires the pricking-out of young seedlings.

A wide range of possible host species for *Euphrasia* in cultivation was reported by Heinricher and this has been amply confirmed by my cultures. This lack of host-specificity has also been demonstrated in the field by Wettstein (1897) and Crosby-Browne (1950). These facts make it appear unlikely that the existence of numerous critical species in *Euphrasia* is related to host-specificity. It may be noted that *Euphrasia micrantha* can grow on a number of hosts and not only on *Calluna vulgaris* and *Erica cinerea*, though it is rarely found in nature except in close proximity to one or both of these species.

Certain species appear to be unsuitable as hosts for all species of *Euphrasia* tried, while others vary in suitability according to the species of *Euphrasia*.

There are a number of possible factors involved in the unsuitability of host-plants, though it has not been possible to investigate these in most of the cultures described.

Euphrasias may be prevented from parasitizing plants growing with them by the inability of the haustoria to penetrate their roots, owing to their physical structure or to physiological obstacles. There might also be physiological obstacles to the formation of the haustoria themselves, or to the absorption of nutriment once the haustoria had penetrated. These obstacles to absorption could be complete or only partial. Extraction of nourishment must also be affected by the quantities of food materials available in the host. Most of these factors could be influenced by the age, stage of growth and vigour of the potential host. If penetrability of roots varies inversely with their age, some parts of the root system of an individual plant will be more impervious than others; one can imagine the susceptible zone of a root system growing rapidly away from a *Euphrasia* plant, so that the parasitic attack becomes increasingly unsuccessful. On the other hand, a host-plant which continually produces new roots from the crown will continue to be susceptible to attack by a *Euphrasia* growing near it.

The possibility also exists of intraspecific variation in susceptibility on the part of hosts and in parasitic capacity on the part of the Euphrasias; such variation might affect whole populations or only individuals.

There seems to be little connection between the suitability of a host and its systematic position. It would seem that the good growth of *Euphrasia* on most Leguminosae is connected with the nitrogen-fixing activities of the root-nodules of these plants, notwithstanding the clearly established unsuitability of nodulated *Trifolium dubium*.

Euphrasias grown in cultivation normally retain their important taxonomic characters, and it is therefore clear that modifications caused by hosts are not the cause of the systematic complexity of the group. In fact, the hosts appear to cause only variation in vigour. Late establishment may have a marked effect on the habit of a *Euphrasia*, but this can occur with any host on which establishment is possible.

The marked effect of a soil difference on the growth of *Euphrasia* without a host probably explains the generally greater success (compared with that of earlier workers) that I have had in growing *Euphrasia* in this way. It may also explain some of the variation in the results of Heinricher and Wettstein which led to a public dispute between them (Heinricher 1898*c*, Wettstein 1898).

The parasitism of *Euphrasia* may contribute to its marked gregariousness in nature. One sometimes finds dense isolated colonies, apparently consisting of hundreds of plants packed into a few square feet, with very few outliers. Weight of numbers may help them to compete with other vegetation, and where the density falls below a critical value the Euphrasias may, under some conditions, be entirely eliminated. The decline of an artificial colony in my garden following a disturbance which buried deeply many of the seeds, suggested that seedling density was important; this may act through autoparasitism allowing a sufficient number of seedlings to survive a difficult period early in their lives in a sufficiently vigorous condition.

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Postscript.—In 1963 a plant of *Stellaria media* coming up in a pot of *E. nemorosa* seedlings led to very quick establishment and remarkably vigorous growth. This host, and other quick-growing weeds (see p. 3), may be useful in the cultivation of the more precociously flowering Euphrasias. As, however, the host in this instance quickly declined in vigour, they should perhaps be combined with other, slower-growing species.

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