THE REPRODUCTIVE BIOLOGY AND OCCASIONAL SEASONAL DIMORPHISM OF *ANAGALLIS MINIMA* AND *LYTHRUM HYSSOPIFOLIA*

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ABSTRACT

Data are provided respecting the reproductive capacities of *Anagallis minima* and *Lythrum hyssopifolia.* In relation to their size, these species have high reproductive capacities and thus conform to the general character of species of intermittently available habitats. Experimental evidence indicates that the great majority of the seeds exhibit vernal germination which, in favourable conditions, is quasi-simultaneous in character. However, there is a variable proportion, usually small, of autumnal germinations resulting in a degree of seasonal dimorphism. The overwintering individuals, with their longer assimilatory activity, sometimes produce many times the average number of seeds. Germination, though favoured by light in adequate temperatures, was also found to occur in darkness. Though chiefly associated with non-calcareous soils, both species were found to germinate freely in calcareous as well as non-calcareous conditions. The proportion of dormant seeds of *Anagallis minima* was found to be no higher in the immature condition than when ripe seeds from the same individual were sown simultaneously.

1. ANAGALLIS MINIMA (L.) E. H. L. KRAUSE (CENTUNCULUS MINIMUS L.).

Of all the terrestrial flowering plants found wild in Britain *Anagallis minima* is one of the smallest, especially when, as so often obtains, the plants are crowded and in competition with *Radiola linoides,* with which it is almost invariably associated. The species of *Lemna* are appreciably smaller and, still more so, *Wolffia arrhiza,* but these are floating aquatics, and are not differentiated into stem and leaves and so are not biologically comparable. *Tillaea muscosa* is often as small, or even smaller, but it is restricted to more open sandy habitats. The reproductive capacity of *A. minima* is thus that of a species which must evade, rather than meet, competition. An estimate of the fruiting capacity has been based upon the aggregate of random collections from several widely separated habitats in Wales, Dorset, Hampshire and Sussex and representing more than one season. The number of capsules was counted on 589 plants, the results of which are shown in Fig. 1. It will be apparent from this graphic presentation that, though the average number of capsules upon a plant is 14, more than 54% of the entire population of plants produced fewer than 10 capsules; the most prevalent number is only 5. On the other hand, it will be noted that 17 (*i.e.* approximately 3%) were of exceptional size, producing an abnormally large number of fruits, ranging from 56 to 144 capsules. This latter figure is nearly thirty times the modal production, so that a few such individuals would have a significant effect upon a population's seasonal seed output.

It may be noted that tetramerous and pentamerous flowers can occur, intermingled, upon the same plant (Fig. 4) but these do not appear to be correlated with any constant difference in the seed content of the capsules they produce.

The seeds, which are trigonous with three prominent ridges (Fig. 4C), have a minutely granular surface and are dark brown or almost black when ripe. The average length is about 0·5 mm and width 0·3 mm to 0·4 mm. The average weight of a seed is 0·0337 mg.

The variation in the seed content of the capsules is presented, in Fig. 2, for 350 fruits. From this it will be seen that the number of seeds in a fruit may be as few as 4, or as many as 31, with an average approximately the same as the mode, namely 15. The average seed output is thus appreciable for a plant so small in size, namely 210 seeds.

Most of the seeds germinate in the spring, but a small proportion may germinate in the autumn and these can produce bushy plants branching towards the base thus forming lateral

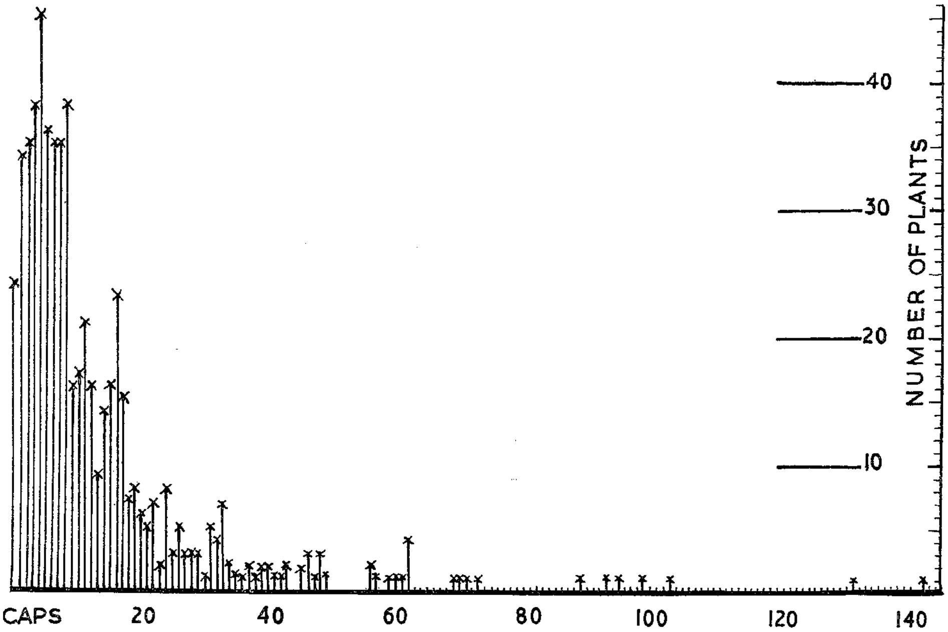

Fig. 1 Variation in number of capsules on plants of *Anagallis minima* from various localities. Ordinates, number of individual plants. Abscissae, number of capsules. Results from 589 plants; mean number of capsules per plant 14, mode 5 capsules.

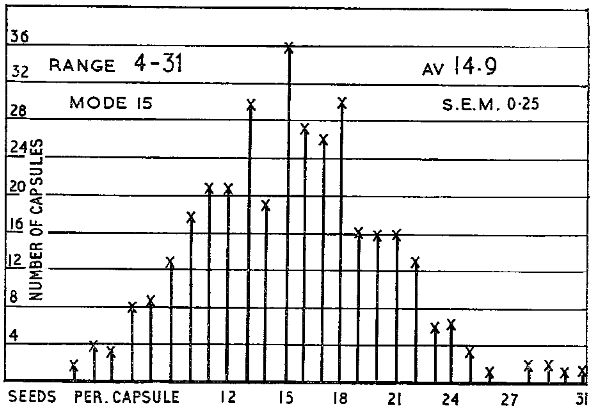

Fig. 2. Variation in seed contents of capsules of *Anagallis minima*. Ordinates, number of capsules. Abscissae, number of seeds per capsule.

shoots that may root from their lower nodes (Fig. 3A & 4B). The largest plant of this type observed was 10 cm in height. It had a spread of 15 cm with roots arising from 10 of the basal nodes. The capsules numbered 443 and a random sample, of 25 of these, exhibited a range in seed content from 11 to 24 with an average of 16·4. The abnormally large number of fruits is not, therefore, associated with any diminution in their average content. In Fig. 3 are shown drawings portraying one of these bushy autumnal plants and, for comparison, an average specimen of the vernal individuals from the same sowing. It is these autumnal plants that mostly provide the exceptionally fruitful individuals represented on the right-hand side

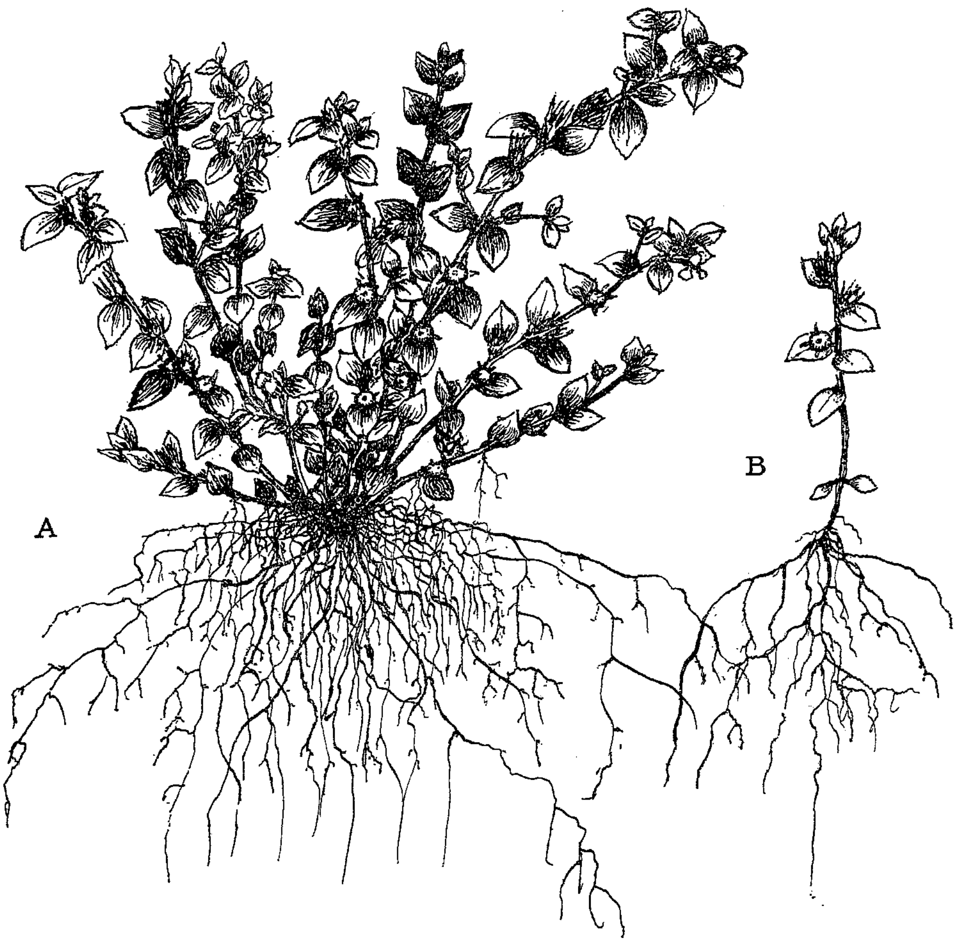

Fig. 3. Plants of *Anagallis minima* from the same sowing, the larger from a seed germinating in the autumn, the smaller from a vernal germination. Both seedlings drawn 22 June. Estimated seed outputs based on number of fruits and flowers *c.* 830 and 110.

of the graph in Fig. 1. It should, however, be added that similar, though less extreme, exuberance may be exhibited by plants derived from the vernal germination when these occur in isolation and subject to but little competition.

It is then evident that this species exhibits a measure of seasonal dimorphism. Neither the vernal nor the autumnal individuals come into flower till the short nights and long days of summer so that the vegetative life of the latter is appreciably greater than that of the vernal individuals, and the assimilatory capital correspondingly greater. (Specimens placed in Herb. Kew (**K**).)

The proportion of these autumnal germinating seeds appears to vary greatly. Thus from one sample of 600 seeds, harvested in 1964 and sown as soon as they were shed, only 4 germinated in September (*i.e.* 0·67%) and 45% of the remainder in April of the following year. In September 1965 a small sample of only 150 seeds yielded 5 seedlings in October (*i.e.* 3·3%), whilst 326 seeds which ripened and were sown in late October of the same year produced 8 autumnal seedlings (2·4%). Other samples yielded 0·3% and 0·7%. But yet another large sample of 1200 seeds provided no autumnal germinations whatever.

It was found that these autumnal seedlings could survive the winter conditions, probably because they have not flowered or fruited. It is known that various annuals are able to survive as perennials if flowering oı fruiting be systematically prevented.

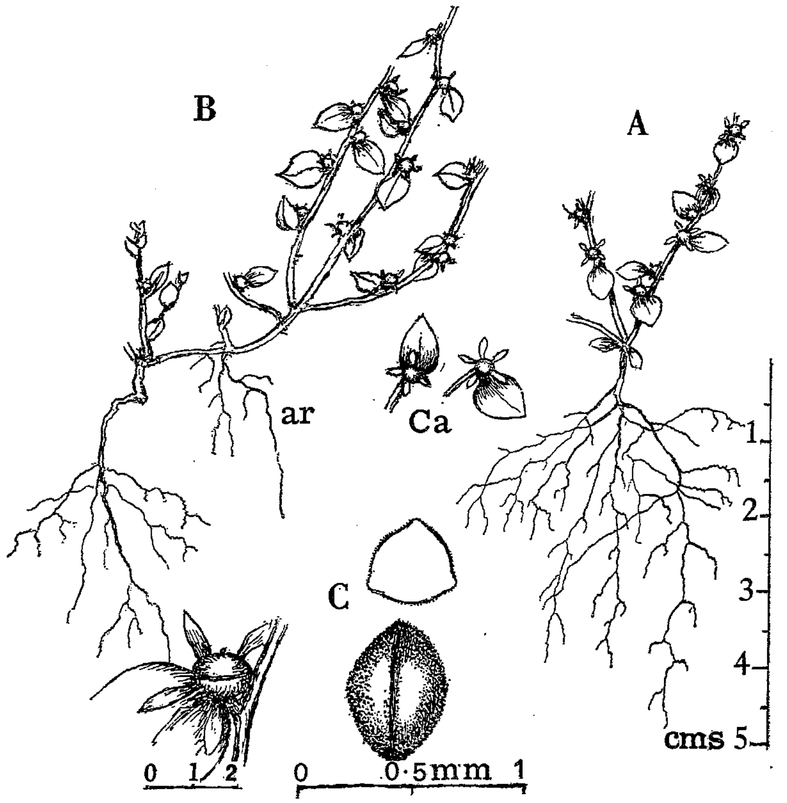

Fig. 4. A. Mature plant of *A. minima* showing depth and extent of root-system. B. Prostrate branch of large plant showing nodal rooting (ar.). Ca. A tetramerous and a pentamerous calyx from the same plant. C. A dehiscent capsule and a seed shown in side-view and in section.

Owing to the very exceptional size of the plant referred to above, with 443 fruits, it was not incorporated in the graph (Fig. 1); but that such plants can develop with an output of, perhaps, over 7,000 seeds, emphasizes the importance that such autumnal plants may have for the survival of the species. 3 % of these overwintering seedlings could provide from one third to even as many seeds, as the 97 % vernal individuals.

A very striking feature to which F. Townsend (1883 p. 280) drew attention and which my own experience emphatically confirms, is that *Anagallis minima* 'is much more abundant in some seasons than in others', a feature which might well be influenced markedly by the prevalence or paucity of autumnal survivors.

If there be an inhibitor, or inhibitors, in the seeds of *A. minima*, which varies in amount in the different seeds in a normal manner, it may be suggested that these autumnal-germinating seeds may in fact represent those which contain little or none, whilst the others gradually lose their inhibition and germinate when the augmenting temperature of spring permits. Sowings of seeds saved from plants that had germinated in the autumn did not give rise to populations with any apparent increase in the proportion of autumn germinations, from which one may infer that, if there be any segregating genetic component it is not normally significant.

With stored seeds I have obtained as low a proportion as 10 % spring seedlings, but with freshly harvested ripe seeds sown in September the following spring germinations were obtained (Table 1).

The average spring germination, from these and other sowings, was 48·5 % with a maximum of 87 %. The great majority of the germinations occurred within four days after

TABLE 1. Spring germination of *Anagallis minima* seeds sown in September.

Date of sowing	*Number of seeds sown*	*April germination*
15 Sept. 1964	600	37% in 4 days (41·5% in 10 days)
1 Sept. 1964	321	48% in 12 days
19 Sept. 1965	711	37% in 25 days
19 Sept. 1965	610	63% in 12 days

the first seedlings appeared, so that, apart from the small percentage autumnal germination, there is also a marked quasi-simultaneous tendency (Fig. 6). Soon after the radicle emerges, a ring of prop-root-hairs develops around the collet, a behaviour shared by other species of this type of habitat. The roots penetrate the substrate rapidly (Fig. 5A) and the rooting depth of the adult plants, which is normally about 5 cm, is soon attained. The cotyledons are elliptical (Fig. 5B) and the first few leaves are opposite or sub-opposite (Fig. 5C) becoming more obviously alternate as the plants mature. Thus in the leaf insertion of the seedling and in the nodal rooting of the larger mature plants the resemblance to *Anagallis arvensis* is striking.

Kinzel (1927) found that immature seeds of *Anagallis minima* germinated more rapidly than the mature seeds and he concluded that the ripe seeds not only were slower but a much smaller proportion germinated in the spring although later germinations increased the percentage.

Development of the very large plants, to which reference has been made, permitted the collection of an adequate number (from 320 to 350 in each sowing) of (a) yellow-green,

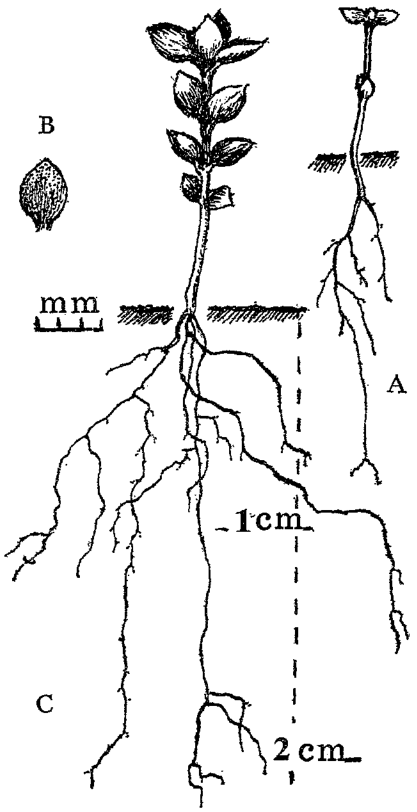

Fig. 5. *Anagallis minima*. A. Seedling. B. Cotyledon. C. Young plant showing sub-opposite leaves.

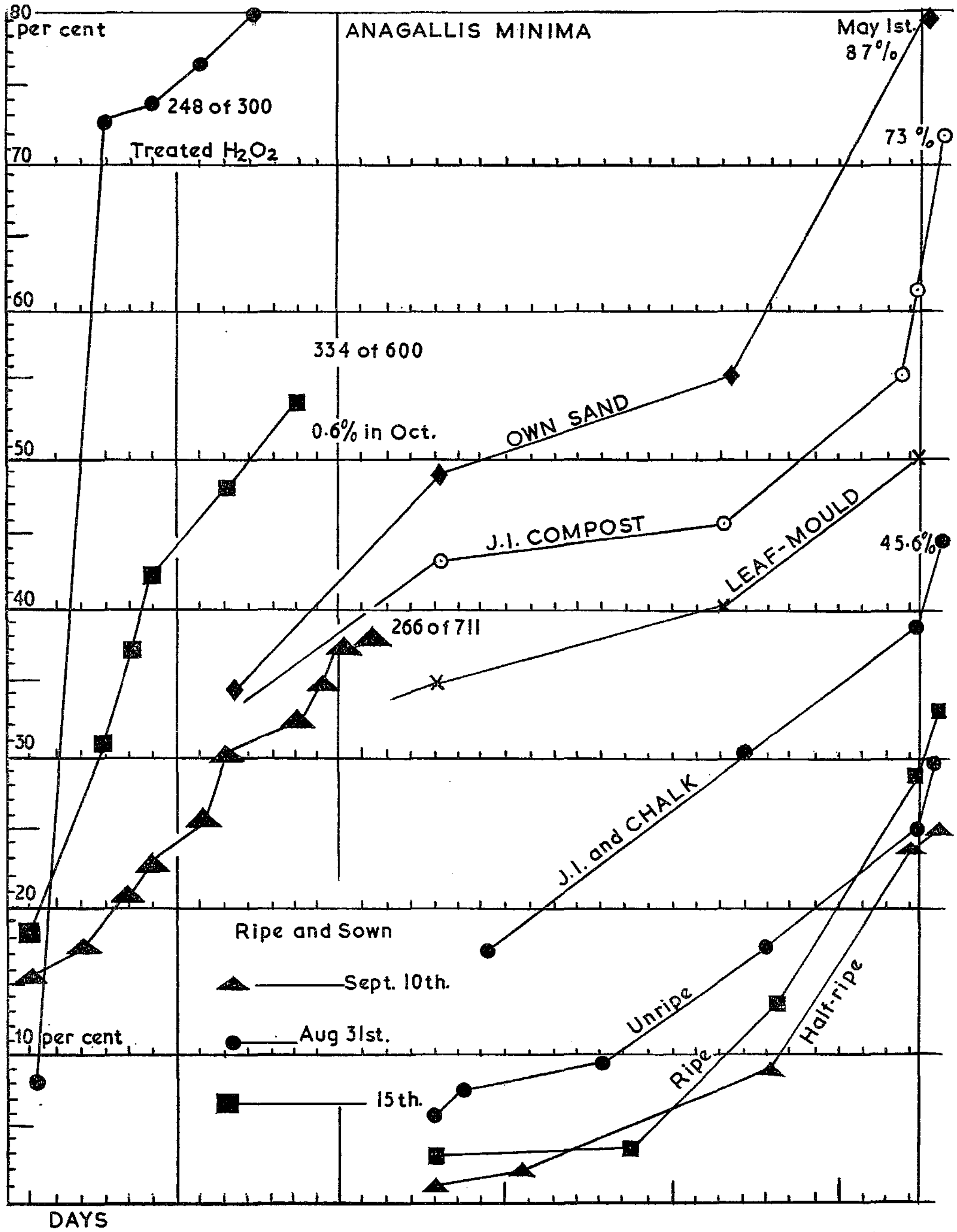

Fig. 6. Germination of *Anagallis minima* sown on various dates and various soils, also of seeds in three stages of maturity.

immature seeds; (b) half-ripe, brown seeds: and (c) purplish-black, fully mature seeds: all from a single individual plant. These were sown, immediately after harvesting them, on 10 October under identical conditions. None of the seeds germinated till March. On 23 March the immature seeds had yielded 6·2%, the half-ripe seeds 1·4% and the ripe seeds 3·2%—a difference far less pronounced than that in Kinzel's experiments but showing the same pattern. However, this was not maintained (see Fig. 6) and by 29 April the percentage germinations were: immature seeds 30·0%, half-ripe seeds 26·3%, ripe seeds 34·4%. It is quite evident that seeds harvested in different seasons may differ greatly in the percentage germinations which they yield. Thus the maximum obtained from seeds harvested in the inclement summer of 1962 was 10·9%. Those harvested in 1964 yielded from 36·8% to 45·1% whilst some of the seeds ripened in 1965 yielded over 80%. Moreover, seeds from different plants which ripened at different times would appear to vary, not merely as to whether any germinate in the autumn and, if so, what proportion, but also as to the percentage that germinate in the spring. If the proportion of naturally dormant seeds is higher in those fruits which are formed first than in those formed later, the discrepancy in our results might be expected especially if, as seems not improbable, Kinzel's seeds were obtained from several individuals.

A series of sowings on various types of soil with seeds ripening in the late autumn yielded very few autumnal seedlings and curiously enough only on the soil exhibiting the lowest percentage germination. The germinations, otherwise, all occurred in April and the totals attained were as follows: on sandy soil (obtained from an *A. minima* locality) 87·0%: on leaf-mould 50·7%: on 'John Innes' compost 73·5%: on 'John Innes' compost plus chalk, 45·6%: on acid peat plus sand, 26·6% (Fig. 6). Since *Anagallis minima* is usually regarded as somewhat calcifuge in its occurrence, the appreciable germination on the soil to which chalk was added is noteworthy, and of especial interest in the light of Professor Good's (1948) observation that this species is not uncommon in Dorset, 'in the grassy rides of certain woods on the chalk'.

The flowers of *Anagallis minima* are self-compatible and frequently pollinated in bud so that cool, wet summers with a paucity of sunshine are unlikely to preclude the production of a normal crop of seeds. It is, however, a species which exhibits very striking fluctuations of population to which attention has already been drawn. One factor that could produce an appreciable increase in the population would be any marked augmentation of autumnal germinations leading to a larger proportion of plants with high seed yields. Nevertheless the available evidence indicates that whilst this might lead to a doubling or even trebling of the population in the following year it could scarcely account for the spectacular increase of numbers sometimes observed. At adequate temperatures, germination of the seeds can occur in darkness though it takes place more readily in light. But experiments have shown that although, occasionally, over 80% of the seeds shed in the autumn may germinate the following spring, the proportion may be as low as 10% and the average of the vernal germination is normally under half of the seeds sown in the autumn. (cf. Fig. 6). That the residual seeds are not infertile, but merely dormant, was shown by Kinzel, who found they germinated subsequently, and this is confirmed by the high percentage that can be induced to germinate in the first season by appropriate treatment. Thus I have obtained 81% germination in a period of four days after treatment of the seeds with hydrogen peroxide (Fig. 6). The germination of 98% which Kinzel obtained with immature seeds would appear to suggest that the seed coat may be involved in this natural dormancy and the response to hydrogen peroxide is not inconsistent with such an interpretation. It is not unlikely that the sudden increase in population numbers may be an outcome of the germination of an accumulation of dormant seeds, especially as this increase would appear to be normally associated with a population decline in the following season.

Anagallis minima is one of a group of species of intermittently wet habitats that have exhibited a marked diminution of frequency during the past hundred years. Counties in which this species formerly occurred but where it is now probably extinct are: Cambridgeshire, Bedfordshire, Buckinghamshire, Hertfordshire, S. Lancashire, Worcestershire and possibly Essex and also Middlesex. In addition there are 11 vice-counties in England and Wales, 10 in Scotland and 8 in Ireland for which there are no recent records. Indeed the species may have gone from about one-third of its former stations (cf. Map. p. 204. Perring & Walters 1962). Most of these areas of real or suspected loss in Great Britain are towards the drier eastern side of the country and may probably be associated with the secular fall in the water table. The causes of this declining frequency must not, however, be confused with those responsible for the fluctuations in abundance that are recurrent phenomena. Nevertheless, with such an inconspicuous plant the temporary decline might readily be mistaken for a permanent trend, except where observation has extended over a period of years.

The close association with *Radiola linoides* is important in this context since although this species is also small it is, owing to its pale green colour towards maturity, quite readily recognized and exhibits similar fluctuations of abundance apparently contemporaneous with those of *Anagallis minima*. In one Hampshire locality, in 1959, *Radiola linoides* was very common and two years later abundant when it was accompanied by occasional individuals of *Anagallis minima*. Subsequently the frequency of *Radiola* diminished and during 1964 and 1966 it was only sparsely present. Diligent search in both these years failed to discover any individuals of *A. minima*, which suggests a decline that is real and not merely apparent. If the population surges be due, as suggested, to germination of dormant seeds, the following year (providing climatic conditions were favourable) might be expected to exhibit a large population derived from the seeds of the numerous individuals so that whilst the initial augmentation could be abrupt the decline might be gradual. The augmented population of *A. minima* in 1959 and its abrupt disappearance is consistent with the hypothesis that the increase was due to flushing of dormant seeds whilst renewal of the supply of these was prevented by unfavourable climatic conditions.

2. LYTHRUM HYSSOPIFOLIA L.

In southern England *Lythrum hyssopifolia* is commonly a summer annual, occurring usually as a casual introduced with foreign seed but, very locally, appears to have persisted in a wild condition over many years. Although, as a casual, it has been found in a diversity of habitats its more permanent stations have been in open vegetation subject to winter inundation. In common with other 'mud-species' it is liable to disruptions in the habitat but has probably been an established wild plant in a few south-eastern counties. Now, however, except as a casual, it is possibly confined to Cambridgeshire (Perring & Walters 1962, Perring, Sell & Walters 1964). *L. hyssopifolia* is thus another of the diminishing damp-habitat species, but the fact that it bears a folk-name, 'Grass Poly', would suggest that it was not uncommon before SE. England became so greatly suburbanized, when suitable habitats were widespread.

Reproduction.

Any valid estimates of fruiting capacity require to be based upon a random sample of adequate size, a stipulation that may present an obstacle when studying a rare species. Examination of only 16 individuals of average size for the species suggested a mean capsule production of 73 capsules per plant (Salisbury 1942). Since this species had become naturalized in a damp hollow in my garden in Sussex all the plants were allowed to grow untended and the entire populations of two seasons, numbering 105 plants, were examined for fruit production as a basis for estimation. For convenience of presentation, owing to the wide range of plant size, the capsule numbers have been grouped into classes of which the upper limits differ by increments of 20 capsules. The results are presented in Fig. 7 from which it is manifest that the variation curve is markedly asymmetrical. The average number of fruits borne upon a plant, based upon the whole array, is 197 capsules. If, however, we exclude the 10 exceptionally large plants with over 500 fruits this mean is approximately halved. The greater portion of the plants, about 60%, yielded between 40 and 100 capsules which would suggest that the mean, derived from the small random sample from a wild habitat, may not have been far from the norm. It is to be noted that in 1967, which was an unfavourable year for *L. hyssopifolia*, with no very large individuals, the entire population of 62 plants yielded an average of only 63 capsules.

The high average of the larger sample is attributable to the occurrence of a few very robust plants bearing between 1,700 and 3,000 capsules. Such an admixture of a small proportion of outstandingly large plants in a population of prevailingly small individuals I recall observing as a feature of this species, many years ago, in the ditches of Brittany. Such

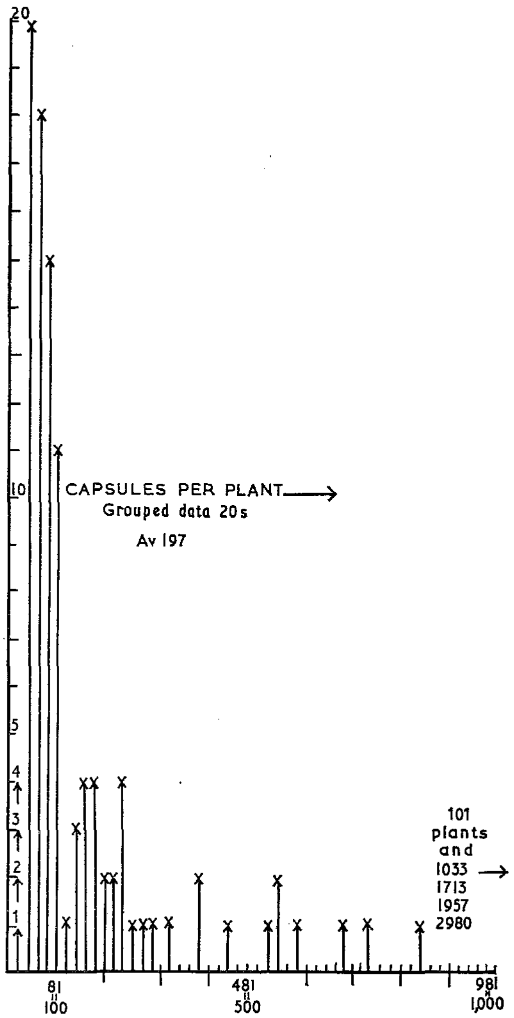

Fig. 7. Variation in the number of capsules produced upon plants of *Lythrum hyssopifolia*. Ordinates represent the number of individuals. Abscissae represent the numbers of capsules upon a plant grouped in increments of twenty capsules. Four plants bearing over 1,000 capsules are omitted from the histogram.

appears to be a characteristic in particular seasons and is a feature that becomes significant in relation to the germination behaviour to be dealt with later in this paper. One aspect of the morphology of these exceptionally large plants calls for comment. Most Floras emphasize the solitary character of the flowers of *Lythrum hyssopifolia*, a condition that is undoubtedly the prevalent one, even of the most robust specimens. However, Hegi (1927 p. 754) mentions the rare occurrence of a pair of flowers. The nodes of the major axes of the largest plants, as shown in Fig. 9, may on rare occasions bear capsules that are not only paired but even clustered, the latter condition being of especial interest since it is that which obtains in the congener *Lythrum salicaria*.

The fruits of *L. hyssopifolia* are approximately cylindrical in form, from 4 mm to 10 mm in length, containing four rows of seeds that impose a slightly nodular appearance on the ripe capsules (Fig. 8). The fruits split open at the apex, but the valves do not separate widely. The 100 capsules examined were found to contain from 13 to 37 seeds, with an average of 25·1 (standard error of mean 0·5). From Fig. 7 it will be seen that this average corresponds with the modal region of the variation curve.

The individual seeds are oval, somewhat trigonous, but with one face sometimes flattened or evenly concave (see Fig. 8), about 0·6 mm in diameter and with an average weight, based upon a number of large samples, of from 0·117 mg. to 0·133 mg. The seeds may ripen as early as September, but most ripen in October and November.

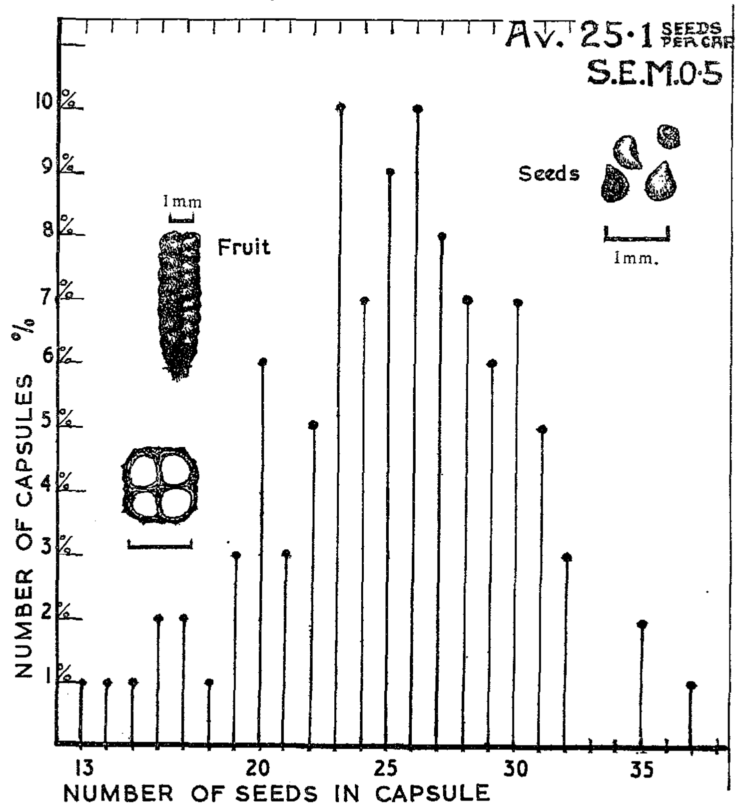

Fig. 8. Variation in the number of seeds in 100 fruits of *Lythrum hyssopifolia*. Ordinates represent the numbers of capsules. Abscissae represent the numbers of seeds. Inset are drawings showing the fruit in side view and in transverse section, also seeds viewed from the sides and end.

As shown in Fig. 9, the capsules are borne almost adpressed to the fruiting axes and, as a consequence, the seeds are not readily jerked out through the terminal aperture by gusts of wind, the less so since the plants normally grow in sheltered depressions. In fact, the seeds may be retained within the capsules until the entire plant has withered and becomes disintegrated during the late winter and early spring. From the foregoing data it would appear that in a favourable season an average output is about 5,000 seeds whereas, even in a less favourable one, an output of nearly 2,000 is suggested by the meagre sample previously reported.

Such high outputs in relation to the size of the plants conform with the very generally large potential that characterizes species of intermittently available habitats. It should be noted moreover that the productivity of the largest plants examined would range between 43,000 and 75,000 seeds! Such very prolific individuals do not, however, occur every season and, if we omit them from our estimation, the average output is about 3,200 seeds.

Germination

Since constant temperatures do not occur in natural conditions and may produce results that are grossly misleading, all germination experiments were carried out subject to the natural daily fluctuations of temperature. Similarly, since markedly different germination behaviour may be exhibited by stored seeds when compared with those freshly shed (Salisbury 1965), and seeds of different strains of a species sometimes exhibit significantly different temporal responses (Salisbury 1962), light can only be shed upon the biology of the species under natural conditions if we sow seed that is derived from a single individual only and which has been freshly shed. In gardening practice stored seeds are the rule rather than the exception and commonly the seeds are of mixed parentage, so that experiments with such in constant temperatures can be of great practical importance (Thompson 1967) but may have little or no relevance to the natural occurrence of the species concerned.

Early maturing seeds germinated readily in the autumn when sown under conditions providing daily maxima of about 16° C. But, towards the northern limits of the species' range an absence of adequate warmth may normally preclude germination of all seeds except those that ripen precociously, until the subsequent vernal rise of temperature. Sixty years ago, I recall the plentitude of *Lythrum hyssopifolia* which, in April, occupied the floor of the shallower ditches in Brittany; some of these plants, from their size, were doubtless autumnal in origin. Here in Sussex, the small proportion of seedlings appearing in the autumn is liable to be killed in winter by the more severe frosts but, when such overwintering seedlings have survived, it was noted that they could develop into the very large plants to which reference has already been made. It is to be anticipated that the prevalence of such would diminish towards the northern limit of the species range.

One thousand three hundred and fifty seeds from freshly dehisced capsules of a large plant, were collected and sown in November 1964 in an unheated glasshouse attaining daily maximum temperatures of about 19° C. Within one week from the first germination, nearly 900 seedlings had developed and within 10 days a total of over 70% germination was attained (Fig. 9). In the autumn of 1965 further seed samples were collected. Of these, 500 were sown on damp soil in full daylight and two batches from the same plant, of 243 seeds and 215 seeds respectively, were sown under precisely similar conditions except that they were maintained in dim light. As the curves in Fig. 10 show, the germinations under dim light were somewhat slower but the final percentages attained were not dissimilar to that in the unshaded condition. The total germination was low (42% to 45%) compared with the yield in other years, but was completed in 11 days. Furthermore, in full daylight, three-quarters of the total number of seedlings had developed within three days of the inception of germination.

Two-hundred and fifty seeds were collected and sown on 3 September 1967. 14 days later the first seedling appeared and by 1 October only 12 seeds had germinated (4·8%) which is probably indicative of the small proportion of autumnal seedlings which normally develop, but the facts mentioned show that with suitable temperatures autumnal germination can occur freely

Good germination was obtained with seeds which had been harvested in October and placed in a seed-envelope which was kept in an unheated outhouse for two months. We can therefore infer that maintenance of the moist conditions that normally obtain in the wild state is not an essential condition for the retention of viability. Since, as already stated, many of the seeds do not escape from the capsules till the spring, such retained seeds were collected from plants on 8 February and sown at once. Germination did not begin till nearly a month later, namely 6 March, but within the subsequent 9 days over 70% of the seeds had germinated. So, not only is it apparent that the belated shedding of the seeds does not impair their viability but that the quasi-simultaneous germination behaviour of the majority of the seeds is likewise unaffected.

A still later collection of seeds was obtained from capsules of dead plants, on 15 March 1967. As the number of seeds obtainable from a single plant was, at this stage, small, an aggregate from several plants was utilized and of these 500 seeds were sown in the dark and 850 in the light. No attempt was made to examine those in darkness until those exposed to light had begun to germinate, so that any germination in darkness could not be attributable to the brief exposures to illumination that examination would have necessitated. The results are shown in Fig. 11 from which it is apparent that germination began on the same

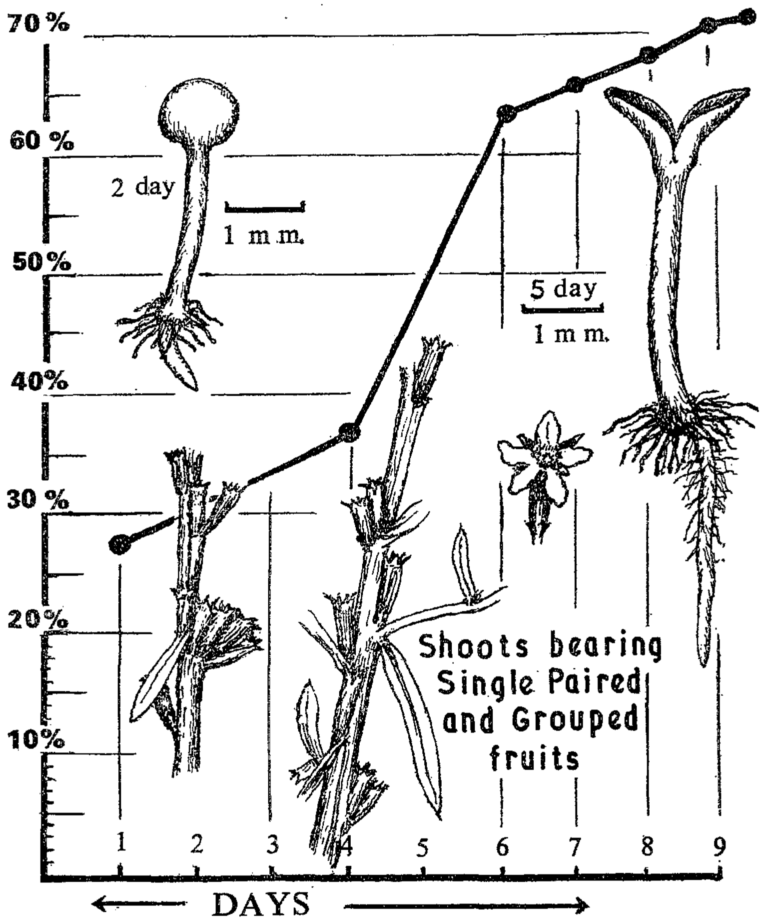

Fig. 9. Germination of 1,350 seeds from a single plant, ripe and sown November 1964. Ordinates represent percentage germination and abscissae days from first germination. Inset are shown two stages of the seedling with skirt of root-hairs upon the collet. A single flower is shown and also the paired and clustered fruits borne upon a very robust plant.

day in darkness as in light, namely 26th March, 11 days after being sown. The process, it will be noted, was far more prolonged than with the earlier harvestings but in bright light the total attained after 46 days was 93·5% and of these 75% had germinated within the first fortnight. In darkness the total attained was only 27·8% spread over a period of four weeks. As, however, no further germinations occurred in the dark during the following four weeks, the culture was transferred to full daylight whereupon, after five days, germinations were resumed and extended over a period of 15 days, though only adding 20 seedlings to the total (i.e. plus 4%). The curves in Fig. 11 indicate the fluctuations of maximum and minimum temperatures during the germination period which suggest that the magnitude of the temperature changes played little significant part in determining the course of germinations in the light, but it is noteworthy that the marked germination flushes in the dark followed abrupt rises in the maximum daytime temperatures. It is important to emphasize that, whereas in the comparatively sunless summer of 1965 the various harvestings of seed had a viability of less than 45%, the seeds of plants growing under precisely similar conditions in 1964, except climatic ones, yielded an average germination of over 70% (Fig. 9), also that the major part of the germinations occurred during the first six days. In the figures the percentages are those of the total number of seeds sown but, if the percentages are calculated on the basis of the total of apparently viable seeds, it becomes manifest that the prevailingly quasi-

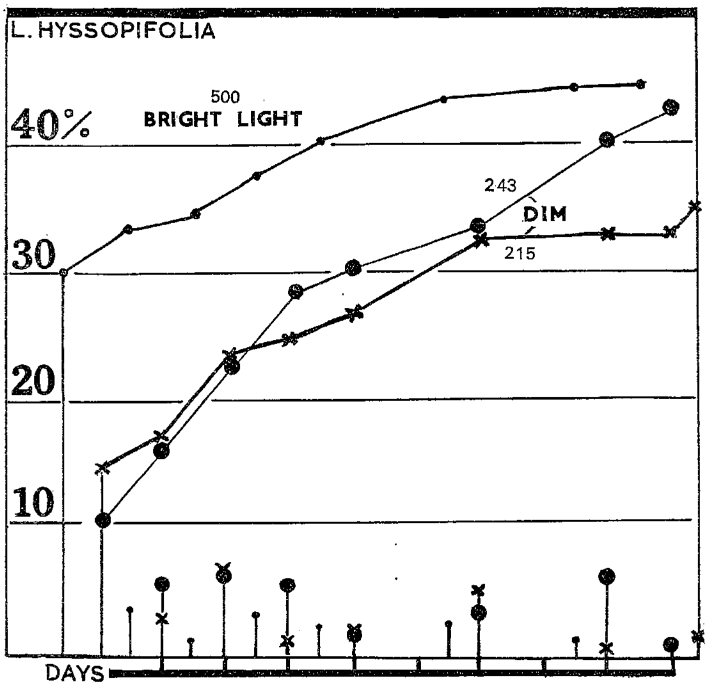

Fig. 10. Germination of *Lythrum hyssopifolia* seeds in bright light and in dim light. Seed ripe and sown 15 November 1965. Ordinates represent percentage germination and abscissae days after first germination.

simultaneous nature of the germination is very pronounced, since the percentage germinating within the first six days is, on the basis of this calculation, between 88 % and 98 %.

Although *L. hyssopifolia* is more especially associated with peaty and sandy conditions the seeds were found to germinate and the seedlings to grow as readily when supplied with hard tap-water as with soft rain-water. 150 seeds sown in September, on mud kept moist with tap-water, attained 43·5 % in 15 days whilst the same number of seeds on mud moistened with rain-water attained 44·6% in the same period. Both yielded further germinations in the following March, amounting in each to approximately 6%. It is evident therefore that *L. hyssopifolia* cannot be classed as a calcifuge species. The average daily maxima during this experiment averaged 25° C and doubtless accounts for the high autumnal germination.

It may be noted that the seedling has cotyledons which in outline are almost circular at first (Fig. 9), although, from basal development, they become elongated later. The collet bears a conspicuous 'skirt' of root hairs, as in other mud-species such as *Limosella aquatica* (Salisbury 1967a) and *Elatine hexandra* (Salisbury 1967b).

Dry seeds shed upon the water will float but, when wet, they sink so that local dispersal is perhaps largely by rain wash. More distant dispersal is probably in mud carried upon the feet of water-birds.

Lythrum hyssopifolia is a species of central and southern Europe which occurs towards its northern limits only as a casual. As a summer annual it can evade the cold season in the seed state but its elimination as a permanent constituent of the flora further north may be because the large and prolific autumnal individuals are rarely if ever produced, so that the population fails to receive this periodic and substantial reinforcement.

Discussion

The two species we have here considered both exhibit larger individuals that develop from autumnal seedlings and smaller individuals that germinated in the spring. We thus witness a measure of seasonal dimorphism which invites comparison with that exhibited by

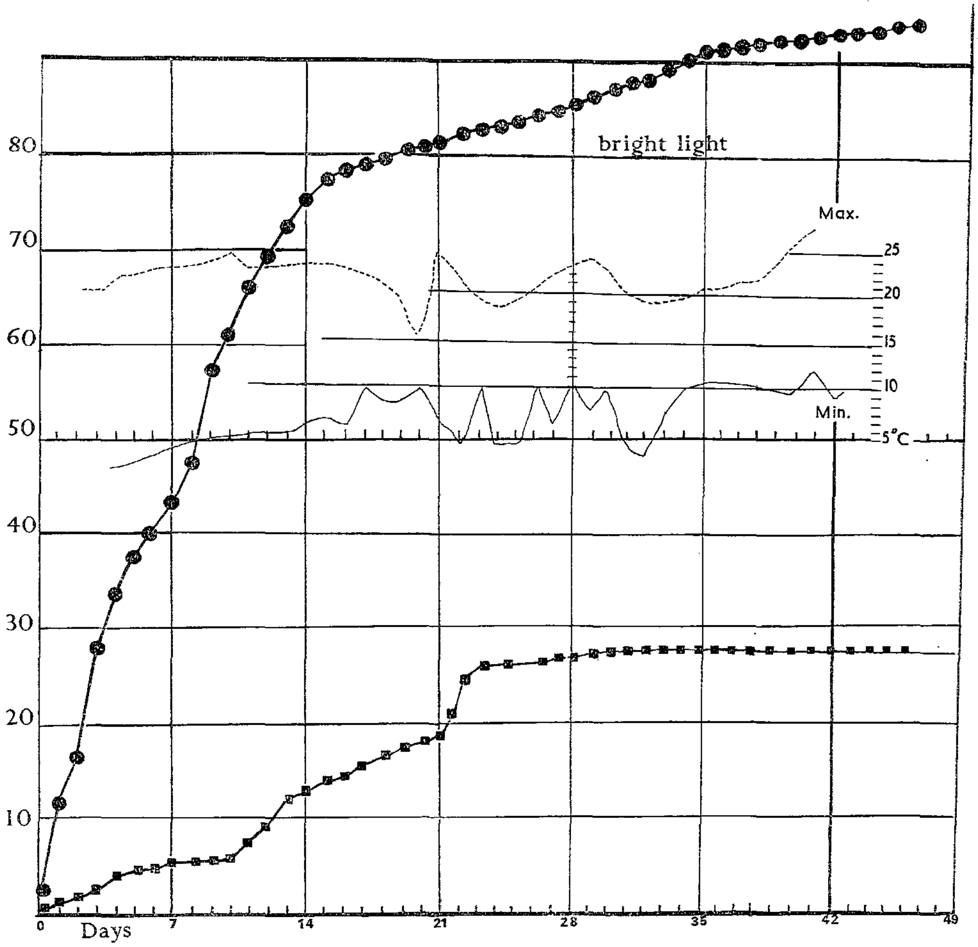

Fig. 11. Germination of late-ripening seeds retained in the capsules of *L. hyssopifolia*. Sown 15 March 1967. Ordinates represent total percentage germinations. Abscissae represent days after first germination. Upper graph percentages of 850 seeds sown in bright light. Lower graph percentages of 500 seeds in darkness. Final germinations 787 (92·6%) in light during 46 days and 139 (27·9%) in the dark during 34 days.

species of *Gentianella* and *Euphrasia*. In these genera the individuals derived from autumnal seedlings flower in the late spring and are commonly single-flowered and unbranched, or feebly so, and very few-flowered. Those derived from spring seedlings which flower in the autumn are, in contrast, usually freely branched and many-flowered as was pointed out by Wettstein (1896). Warburg (1962) expressed the view that *Gentianella baltica* and *Gentianella campestris* may well be the annual and biennial states of the same species.

This reversal of the prevailing habit compared with the species *Anagallis minima* and *Lythrum hyssopifolia* is associated with the fact that the Euphrasias and Gentians referred to flower in relation to the long-nights and short-days, so that whereas the autumnal seedlings of *Euphrasia* which flower in late spring or early summer, are short-lived and consequently small, the vernal seedlings do not come into flower till the days shorten in the autumn and hence have a much larger assimilatory capital which enables the freely-branched and bushy habit to be attained. The photoperiodic stimulus for flower production of the two species here considered is the short night and long day but the response is essentially comparable. In *Anagallis minima* the distinction between the two states would appear to be to some extent intrinsic since, however favourable the environmental conditions, the percentage of seeds that would germinate in the autumn always proved to be small. *Lythrum hyssopifolia*, however, appears to be largely, perhaps entirely, extrinsically determined and in some degree accidental. We have seen that ripe seeds of *L. hyssopifolia* removed from the capsules in September and subjected to high daytime temperatures will germinate freely, but in natural conditions the seeds are in fact commonly retained in the capsules and shedding is so delayed that in our latitudes, for most of the seeds, the conditions requisite for germination do not obtain till the rise of temperature in the spring, and in consequence the proportion of large, autumnal, plants is small or absent and such as may occur are at risk from severe frost. It is, perhaps, such plants of *Lythrum hyssopifolia* with a more prolonged period of vegetative activity to which Jepson (1923) refers as attaining 'even 60 cm' in California. We may also note that *Anagallis minima* reaches up to 12·5 cm in the same region.

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