

COMPARATIVE BIOLOGY OF EPILOBIUM HIRSUTUM
AND LYTHRUM SALICARIA

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by

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ABSTRACT

This experimental investigation deals with the comparative biology of Epilobium hirsutum L. and Lythrum salicaria L. Certain attributes of the species appear to be of high significance in determining their ecological distribution.

The seeds of both species though viable for a long time show profound differences in their temperature and soil requirements for germination.

The growth-form of Epilobium hirsutum is controlled by day length and temperature as rosettes are produced both under short-day and low temperature conditions, and tall flowering form in long-day and high temperature. Both the short-day and low temperature suppress the growth of Lythrum salicaria and tall flowering forms are produced otherwise. Q10 of growth of Lythrum salicaria is much higher than that of Epilobium hirsutum. Giberrellic acid stimulated short-day plants in both the species. Discontinuous short-day treatment (one-hour light-break) stimulated Lythrum salicaria to tall flowering form whilst Epilobium hirsutum did not respond. The performance of Lythrum salicaria is less rapidly reduced by shading than is that of Epilobium hirsutum.

Epilobium hirsutum has high nutrient requirements and

low nutrient uptake capacity under stringent conditions compared with that of Lythrum salicaria. While Lythrum salicaria responds to nutrient stringency by an adaptive increase of root/shoot ratio, Epilobium hirsutum does not. There is a greater reduction of growth of Epilobium hirsutum in the deficiency of nitrogen, phosphorus and potassium than is that of Lythrum salicaria. Potassium deficiency caused wide spread necrosis and root malformation in Epilobium hirsutum and its deficiency suppressed the formation of rhizomes and flowers. In Lythrum salicaria flower formation depends upon attainment of certain minimum weight irrespective of N.P.K. deficiency.

At high temperature Lythrum salicaria ousts Epilobium hirsutum both in rich and poor soils whilst given a chance of growth at low temperature in autumn/spring Epilobium hirsutum gains a competitive advantage in rich soil. Lythrum salicaria grows well on acid soils whereas Epilobium hirsutum fails.

Thus differences in their ecological distribution arise out of differences in their biology at several points in their life-cycles.

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I. INTRODUCTION

This study is an experimental investigation of the "Comparative Biology" of the two plant species, i.e.

Epilobium hirsutum L. and Lythrum salicaria L.

Both are pioneer species of Fen communities. The pattern of their growth and distribution, their mutual relationship when inhabiting the same area is far from simple and little or no information is available in the literature. Epilobium has a restricted range, distribution being strictly confined to base rich fens, with characteristic rhizomatous growth and dwarf rosettes in winter. It is often very aggressive in the habitats where it succeeds in becoming established. It seems to be intolerant to variations in the habitat especially as regards moisture and nutrition. Lythrum, primarily a Fen plant, has an extensive geographical distribution. It is important in the pioneer plant communities yet may also occur in other habitats. However, it shows an almost completely different habitat tolerance from Epilobium as it appears to be more calcifuge growing near poor acidic bogs, in the marshes and carrs as well as rich well aerated soils.

Although the two species studied are diverse in

habitat requirements and range of tolerance, both are often successful in occupying newly available territory. Epilobium hirsutum has the dual advantage of combining rhizomatous perennation and vegetative spread along with "rosette" form growth habit in winter while Lythrum salicaria has only root-stocks to carry it over from year to year.

It is intrinsically the biology of a species that allows its existence in one ecological situation and excludes it in another. As Clapham (1956) has pointed out, knowledge of the biology of a species furthers ecological knowledge for it throws light on the situations in which it exists and also on those in which it does not. This investigation of the comparative biology in fact consists of seeking the limits with respect to habitat and environmental conditions, imposed by the biology of the species, which if exceeded precludes their establishment.

The investigation is primarily a study of germination and growth processes as affected by the environmental conditions and leads to an understanding of the processes of adaptation to environment and the mechanisms of competition. Observations in the laboratory have been related to the behaviour of the species under natural conditions (Field experiments) in an effort to understand the general pattern of growth and distribution in the particular ecological niches

as governed by their biological prerequisites. Although the study ranges over the whole life-cycle of the species, special emphasis has been placed on the germination and early seedling growth since it is at this stage of the life-cycle that failure of establishment is greatest in terms of the number of individuals eliminated.

In the beginning the life-cycles, growth forms and breeding systems of the species are outlined. Only the known ecological distribution of the species was used to form working hypotheses from which the experimentation was derived. In the study of growth, criteria of performance are sought which are as pertinent as possible to the experiment concerned. This includes the seeking of adaptative compensating mechanisms (Whitehead, 1962) in their growth under stringent conditions, and an attempt to assess the dry weight accrued which is surplus to that required in the maintenance of the growth of the plants merely as assimilating entities. Competition and survival of the two species in different habitats has been pursued in detail. Various aspects of light in relation to plant growth have been studied. Responses to different temperatures and sensitivity to nutrients and their role in the growth and distribution has been investigated in detail. An attempt is made to relate these findings to their diverse performance and behaviour. Finally, in the light of these

studies some aspects of the ecological distribution of the species are appraised in terms of their "Comparative Biology".

II. GENERAL BIOLOGY OF THE SPECIES

The two species investigated differ considerably in their life-cycles, growth form and breeding systems. However, they have some common features. The similarities and differences are discussed below.

Life-cycle, Growth Form and Morphology

Both species have wind dispersed seeds. In Epilobium hirsutum the seed has a chalazal plume of hairs and the seeds of Lythrum salicaria are light powder or dust seeds easily carried away by wind. Seeds are all very light though, comparatively, seeds of willow herb are as much as three times heavier than those of purple loosestrife; dry weights being 0.182 mg/seed in the former and 0.062 mg/seed in the latter. Bakker (1960), Salisbury (1961), Myerscough and Whitehead I (1966), studied the rate of seed fall in still air in Tussilago farfara and some species of willow herbs respectively. These authors established that these rates of seed fall are faster than those of the air-borne fungus spore but slower than the pollen of some of the wind-pollinated plants mentioned by Gregory (1945). Bakker (1960) gave direct evidence of the achenes of T. farfara being dispersed over distances up to

4 kilometres from their parent plant. It can thus be inferred that these light propagules in Epilobium hirsutum, well adapted to wind dispersal, could be expected to be distributed over a wide area. Although the seeds of Lythrum salicaria are also dispersed by wind, unlike Epilobium they have no mechanical adaptation ~~to~~ ^{ing} facilitate their dispersal by wind. The tiny capsule is enclosed by a persistent calyx and splits open to liberate 110 to 120 seeds when fully ripe. The seeds being extremely small and light are prevented from falling to the ground by the persistent calyx, which holds them till sufficient wind arises to shake them out through the opening of the upper part of the calycine box. Such a wind is strong enough to bring about at least moderately wide dispersal of the seeds, which mainly occurs in the autumn.

According to Turrill (1948) these light powder or dust seeds are most easily carried by wind and evidence strongly favours the conclusion that such seeds are by far the most widely dispersed, so that both species are potentially very mobile.

The length of viability of the seeds is very similar in both species, and appears to be at least several years. Seeds of both species for the present work were collected in September, 1966 and after dry storage in a refrigerator for 3 years their viability in terms of percentage germination is

still the same.

In Epilobium hirsutum after germination, in the primary root system the upper lateral roots start developing faster and soon have equal importance with the primary root. As growth progresses adventitious roots of equal status arise on the hypocotyl and even later on the basal parts of the stem. These elongate rapidly and bear numerous thin laterals. The system is essentially similar to the fibrous root system of many grasses. Lily Batten (1918) studied the establishment of seedlings in Epilobium*. She found that seedlings from the seeds grown in sand had well developed root systems and were much bigger in size than those grown in clay. Not only were the root systems of clay grown plants poorly developed, but they also had fewer and shorter rootlets. Long before full seedling establishment the leaves grow enormously in size proportionately at the expense of stem elongation. Internodes are very small, 3 to 4 pairs of leaves are all crowded together on the weak stem, the seedling tends to bend to one side and the stem becomes prostrate, trailing along the soil, the short leaf petioles twisting so that the leaves appear to form two ranks on the upper side. At this stage a strong adventitious root system develops. Thick strong adventitious roots with tapering ends arise along the length of the nodes

* Plate I

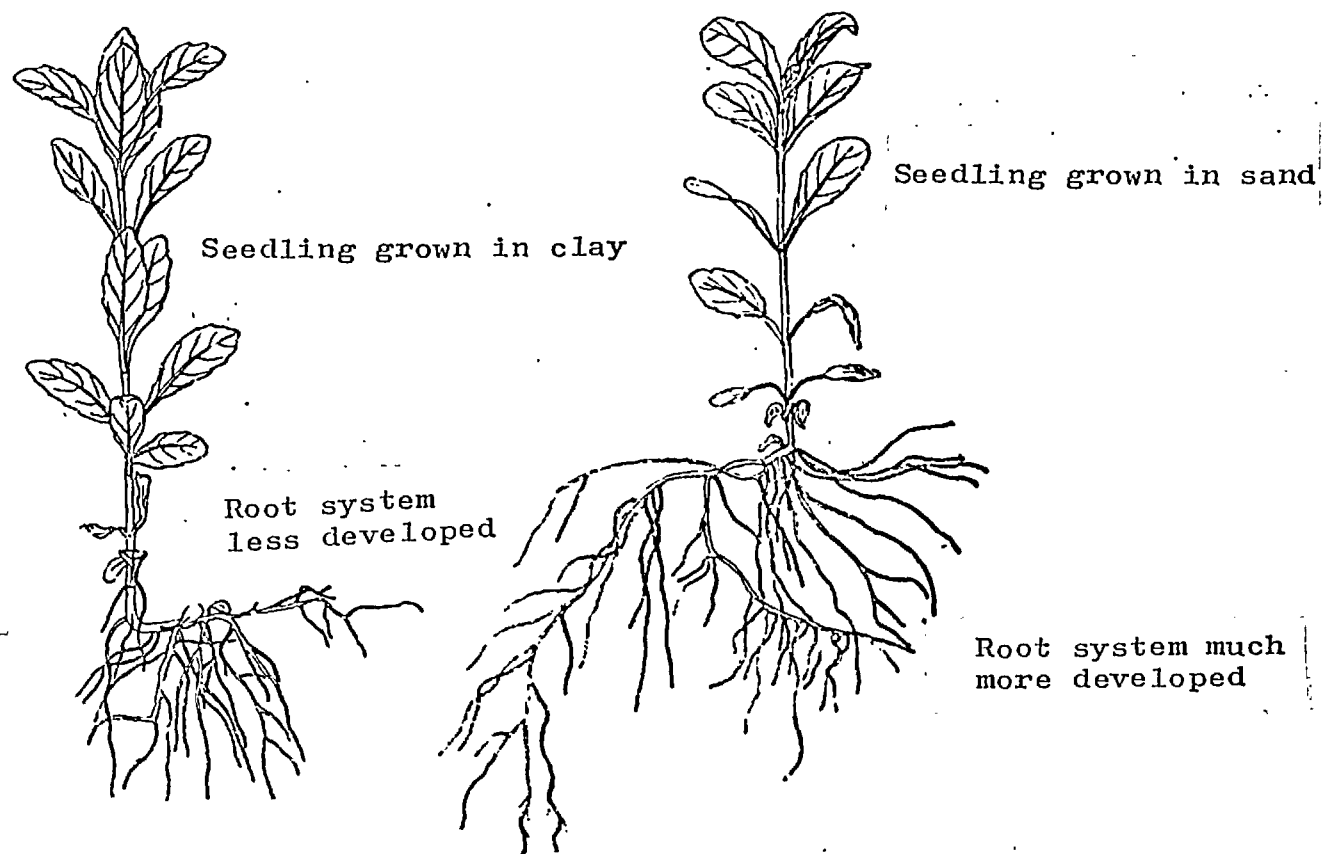


Plate 1. *EPILOBIUM HIRSUTUM*

Comparison of seedlings grown in clay and sand respectively.
($\frac{3}{4}$ natural size)

Photograph courtesy L. Batten (1918) (with permission), The
Journal of Ecology VI.

(not at the internodes) where they are in contact with the soil. These roots being contractile in nature pull the basal parts of the stem into the soil, eventually, when conditions are appropriate, the apex turns up and gives rise to an upright shoot different in character. The form of the seedling depends upon the time of the year. Autumn established seedlings develop into 'plate' like plants. Those established in early summer have elongate shoots from the start. In both cases the stem is very well developed being thick, fleshy and succulent, at the same time supporting enormously developed broad, fleshy, spatulate, sessile leaves. Gradually the stem starts to strengthen and becomes thick and woody at the base. Leaves are pubescent and oppositely arranged though the two leaves may not be at the same level; parts of the stem are also hairy. Side shoots originate after the 7th to 8th pair of leaves. Plants show little variation except some odd plants with thick, fleshy trailing stems with small decurrent leaves arranged alternately in spirals. After a long luxuriant vegetative growth for 10 to 12 weeks, flower buds start developing and at the same time the lower side shoots elongate considerably, outgrowing the main stem and also start producing flower buds. By mid-summer the whole plant is profusely flowering and may attain a height up to 150 cm.

In laboratory conditions the plant is completely in

flower 14 to 15 weeks after seed germination but in nature it continues its slow vegetative growth during late winter and cold spring until it starts flowering in late summer; four to six weeks after flowering commences some capsules are ripened and seeds being dispersed.

The main stem and the side shoots continue to elongate and flower until the autumn when the leaves and flower bracts start to die off from the base of the shoot upwards, until a few floral bracts with undehiscent capsules or depauperate flowers remain at the apex. Eventually the whole shoot dies.

While the plant is still in the prime of vegetative growth and before the initiation of side shoots and flowers takes place, stolons start developing from the axillary buds at the base of the stem and elongate. They start spreading around and the plant is firmly fastened to the soil. At the point of contact with soil they produce adventitious roots of a highly contractile nature, pulling the whole stolon down in the soil, where it continues to grow as a fleshy, colourless soft rhizome. These rhizomes are repeatedly monopodially branched and the lateral branches are also branched in turn. Thus, once established, Epilobium hirsutum is capable of exploiting continuously new volumes of soil by means of its plexus of rhizomes. The aerial shoot dies in autumn except

for the rhizome system. Some of the stolons from upper buds may spread along the soil surface and these may get strongly rooted in the soil and develop a rosette of fleshy leaves at the apex; if separated from the parent plant these develop as separate individuals and behave in the same way as the rosette form plants grown from seedling transplantation in autumn, (discussed in detail later).

In both these cases the much reduced aerial shoot dies at the end of the season except for a small poorly developed rhizome which, in the following year, produces a new, normal aerial shoot and also initiates 5 to 6 new rhizomes. Thus a rhizome initiated in one year bears an aerial shoot and new rhizomes in the following year after which it dies. A rhizome may grow several feet through the soil in the year between its initiation and the formation of the aerial shoots from it. Occasionally, small compact buds may develop in the axil of the cotyledons and first leaves. These form over-wintering rosettes like those from autumn or late summer seedling transplantations. They do not take over the root system of their parent shoot but give rise adventitiously to their own. The whole plant may thus be formed de novo. In late spring these over-wintering rosettes, whatever their origin, develop into normal plants which in due course flower and produce seeds. Thus the plant of Epilobium is equipped

with very efficient means for the replacement of the whole plant in the same year and also from year to year and thus has great potential in making territorial spread.

Lily Batten (1918) studied anatomical adaptations in rhizomes of Epilobium hirsutum to aquatic conditions. She found that a rhizome adapted to wet or Fen habitat in early spring, develops a layer of phellogen inside the endodermis and phloem fibres, capable of producing cork, concentric layers of aerenchyma and loose aerenchymatous tissue, alternating layers of suberised and non-suberised cells, depending on the environment of the plant and position of the organ concerned. In the parts of the plant growing in the air, or in drier soil, this tissue is replaced by cork mostly mechanical and protective in function. But in the rhizome and lower portion of the main axis completely submerged in water, it develops into aerenchyma storing oxygen ^{ing} to ensure healthy growth of the rhizome. Response apparently occurs most readily in that part of the rhizome which grows in the mud. Material which has not been submerged in either water or wet mud shows no development of aerenchymatous tissue, so its formation is a direct response to the external conditions of life. In the roots, however, there is no definite aerenchyma as such, but instead cortical cells are very loosely packed, and large air spaces occur in the roots of the plants grown under very moist

conditions.

The external character of the rhizome varies in appearance according to the nature of the surrounding medium. If the plant is growing either in very wet soil or submerged in water, the rhizome is succulent and the root development is very considerable, a large number of adventitious roots being developed. When, however, the soil is comparatively dry, or of sandy nature and consequently physiologically dry, the rhizome is much less fleshy and the roots are fewer. Plants of Epilobium hirsutum are therefore capable of responding to external stimulus and adapting themselves very rapidly to the medium in which they are growing. This adaptation may be completed in the life of one individual. The presence of water saturated mud causes a quicker response than the presence of water alone, while a plant changed from a dry habitat to a wet one develops aerenchyma more rapidly than it loses the power to produce the tissue when its presence has become immaterial through change of environment.

In Lythrum salicaria, on the other hand, the tap root system of the seedling is very strongly developed and persists throughout the life of the adult plant, no adventitious roots are produced. Immediately after germination the primary root grows vertically deep down into the soil, rapidly developing repeatedly branched secondary and tertiary roots.

Soon after seedling establishment roots start strengthening up, becoming hard in texture with a sclerenchymatous central core and grow as an organised, well developed, root system compared to the individualized, somewhat fleshy, soft, scarcely branched adventitious roots of Epilobium, spreading horizontally in the sub-surface of the soil. In Lythrum, towards maturity, the main root and major branches become thick and woody towards the upper end and grow many feet deep into the soil.

Unlike Epilobium there is no autumn seed germination and consequent seedling establishment. There is only late spring or early summer seed germination and seedling establishment takes place when the temperature is quite high in contrast to Epilobium. In Lythrum, the seedling grows erect with all parts proportionally developed, it has a squarish well developed stem with ^{well} ~~appropriately~~ spaced nodes and rather small linear to lanceolate leaves. This pattern of seedling growth is quite contrasting to that of Epilobium which develops as a small prostrate rosette. This condition in Epilobium may be in response to external stimuli of low temperature and short day length as seeds are capable of germination in late winter and autumn. Soon after the seedling establishment a stem grows out very rapidly to attain the normal size, with opposite and decussately arranged sessile,

lanceolate to ovate, shortly pubescent to glabrescent leaves
 ± cordate at the base. Upper leaves and floral bracts are
 alternately arranged.

Seedlings experimentally transplanted in late autumn
 do not grow beyond the 4 to 5 pairs of leaves stage and the
 shoot dies off with the onset of winter. In seedlings trans-
 planted in spring the shoot grows rapidly producing slender
 side shoots and leaves continuously decreasing in size on all
 the side shoots till the flowering spike is produced on the
 main stem as well as on well developed side shoots. Soon
 after its initiation, the floral shoot elongates considerably
 and measures up to 30 cm. or more.

The period between seed germination and flowering
 (under laboratory conditions) and seedling transplantation and
 flowering (in the field) is very short, being 8 to 10 weeks
 only compared with 14 to 15 weeks in Epilobium. In nature,
 flowering may take place in the beginning of July and con-
 tinues till September. The lowest capsules are ripe and seeds
 may be dispersed by the end of September while the whole plant
 is still green and leafy. After the upper capsules have
 ripened the whole ^{top of the} plant dies in very late autumn.

Fresh shoots arise the following spring from the
 buds on the root stump and the base of the old shoot. Usually
 3 to 4 buds arise but one takes the lead suppressing or

subordinating the others. Thus, unlike Epilobium the roots are the main organs of perennation and vegetative spread, and they can persist for several years in the same spot. A single stump is borne directly by a root, likewise a complex of persisting stem bases may be termed as pseudo-rhizome in accordance with the usage recommended by Holm (1929). Buds on these stumps developing with shoots in the spring are usually located at depths from 2 to 8 cm. and rarely in the surface layer of the soil and the species can be termed as a geophyte. The deep seated position of buds undoubtedly favours survival. In early spring these develop into small rosettes from which elongated shoots arise.

These woody root stumps have unusual anatomical features which can be considered as an adaptation to wet, marshy places and significant in perennation. Moss (1936) has shown that in such root stumps, besides the parenchymatous rays extending out from the edge of each primary xylem strand, the secondary xylem has a great deal of parenchyma and sieve tubes. Each year growth is renewed from the cambium and during the course of the growing season old tissues are isolated centrally by an internal periderm which arises in the previous year's xylem. Tissues of previous years are then successively accumulated in a compressed and shrunken state in the centre of the root. From the rings formed by successive periderms

the age of the root can be seen. These layers of interxylary periderms extend in tubular fashion throughout the entire subterranean system. The interxylary periderm formed each year over the surface of the wood is directly connected with the previous year's aerial shoot and joins the external periderm in the basal region of each of these decadent shoots. The older tissue thus separated becomes necrotic, while the newly formed vascular tissues are afforded protection by the inner and outer suberized barriers produced by phellogen arising in the parenchymatous zone of the xylem. This interxylary periderm affords the plant excellent protection against desiccation, pathogenic organisms and possibly other deliterious effects associated with the dying down of the annual shoot and consequently makes for continuance and for efficient functioning of the perennating structure, thus persistence of the plant in particular localities is made possible. Therefore, once established, a plant of Lythrum salicaria can, by means of these perennial roots and old shoot bases, persist in the same spot for years. On the other hand, Epilobium hirsutum not only continues to occupy territory but has the capability of encroaching on new territory each year. Field experiments in the marshes of Silwood Park confirm this mode of persistence and perennation. Although capable of perennating efficiently Lythrum does not possess any organs of vast vegetative spread

and multiplication compared with the production of propagules and multiplication of the plant by means of rhizomes in Epilobium.

The two species have a high potential seed output per plant. In Epilobium the average number of seeds in a capsule is 260 and a healthy and good sized plant produces more than 300 capsules in nature (although the number of capsules per plant is higher under greenhouse conditions) so a conservative estimate of production by one plant is of some 78,000 seeds. In Lythrum the average yield per capsule is 120 seeds. It was found that in 5 well developed plants the average fruit number was 900 capsules. Therefore, a good sized plant could be expected to yield about 108,000 seeds.

Breeding Systems

The breeding systems of the two species are similar in certain ways.

In Epilobium hirsutum flowers arranged in corymbose racemes are markedly protandrous and cross pollination seems to be the rule. A stigma of 4 revolute lobes exceeds the length of the longest stamens and opens long after the anthers have burst. The showy colour of the flowers attracts bees and hoverflies even in the greenhouse. However, there are reports of homogamous forms, Clapham, Tutin and Werburg (1952), with stigmas about equalling the stamens. This is confirmed by

observations in the greenhouse experiments, and when the flower opens the anthers have already burst open and the stigma is thus covered with pollen causing self pollination. However, Epilobium sets viable seeds readily in the greenhouse and furthermore it is fairly rare to find a mature capsule with any shrivelled seeds. The presence of homogamous forms, uniformity of development under comparable conditions and readiness with which it sets seeds in greenhouse conditions is suggestive of the inbreeding in E. hirsutum under controlled conditions; but, as a general rule it is the only out-breeding species in the whole genus of Epilobium because of its floral structure and markedly protandrous flowers.

In Lythrum salicaria three forms of flowers are found on different plants, Darwin (1877). In fact this is the only trimorphic British plant showing tristily. Each style type is accompanied by 2 sets of stamens of different lengths:

- (1) Short style with long and medium stamens,
- (2) Medium style with long and short stamens, and
- (3) Long style with short and medium stamens.

Three sizes of pollen grain are found, one in each of the three types of stamens. Heterostyly is a mechanism ~~to~~ helping cross pollination. Transference of pollen from high stamen to high stigmata, medium to medium and low to low amongst different flowers is considered as legitimate fertilisation.

Darwin, however, succeeded in illegitimate fertilization by putting, artificially, the pollen of long stamens on the short stigma of the same plant and vice versa. Although the seed produced is very much reduced he succeeded in showing that tristylly does not necessarily eliminate self-pollination.

A. B. Stout (1925) reported the appearance of a "semi-homomorphic form" with pistils and a set of longer stamens of equal length with a set of short stamens as well. This form appears to be highly self-fertile but the degree varies for individual plants, and some are self-sterile.

However, trimorphism, heterostyly, genetic variations in the plants under similar environmental conditions and considerable reduction in the yield ^{of seed} under laboratory conditions lead to the conclusion that the species is generally outbreeding.

Cyto-genetics and Heredity

Epilobium hirsutum appears to be a discrete diploid species with $2X = 36$, as reported by many authors like Love and Love (1942) in Central Europe, Hair (1942) in New Zealand, Raven and Moore (1964) from the material collected in Derbyshire along hedgerows, and other workers like Hakanson (1924 b), Schwemmle (1924), Turesson (1938) to name a few. However, Michaelis (1928 and 1942) has reported $2n = 54$ in Epilobium hirsutum from North Western Europe with the

possibility of the presence of polyploid populations in the extremely cold regions.

In contrast to the consistency in the chromosome numbers of Epilobium hirsutum collected from various geographical regions, the diploid chromosome number in Lythrum salicaria shows great variation depending upon the source of origin. Mulligan (1957) quoted $2X = 30$ in material collected from north temperate Asia, $2X = 60$ has been reported by La Cour (unpublished) in North America, Love and Love (1961) in Europe and Mulligan (1957) for the Canadian material of Lythrum. However, Tischler (1928 and 1929 a), Love and Love (1942 a) found $2X = 50$ in Lythrum from Central Europe. Mulligan has emphasised that, according to European and Asiatic workers, Lythrum may have two or more chromosome races. His chromosome count of $2X$ plant is 60 while others established it as 30, 50 and 60. Apparently there has never been an attempt to relate the differences in the chromosome numbers to any morphological differences that might exist in this species, such as trimorphism and tristylly. Since the different chromosome counts have been made by individual authors on materials collected from widespread sources like Canada, North America, Europe and Asia, and since there is no known way of separating these chromosome races morphologically, it is impossible to know whether one chromosome race is

confined to one particular region or they are all found in the same area, or even that the number obtained by one author is the common one. However, it is of interest to point out that the diploid counts on Lythrum by Shinke (1929 IV) as 76, 77, and by Takahashi (1931) as 85, are on Japanese material identified as L. Salicaria L. var. vulgare D.C. sub-var. genuina Kochne. This suggests that three levels of polyploidy in Lythrum may be linked up with the morphological differences.

Of all the 14 species of Epilobium in Britain, Epilobium hirsutum is the only one out-crossed to any appreciable degree. Judging from reports in Britain and on the Continent, hybrids are possible between all combinations of species with the exception of E. angustifolium and E. nerterioides, Raven and Moore (1964). Many if not all of these hybrids are at least partly fertile. Druce (1897) reported naturally occurring hybrids of Epilobium hirsutum in his Flora of Berkshire as :

X E. hirsuto-montanum, Fries, Nov.Fl.SV.iii - 185 (1842) has been found near Sunninghill.

X E. hirsuto-parviflorum, Wimm, in Verh, schbs. Ges - 125 (1848) occurs in Radley.

However, viability and propagation of these hybrids is not very satisfactory and E. hirsutum keeps itself distinct as a whole. Meiosis in interspecific hybrids has been studied

by Hair (1942), Lewis and Moore (1962) in the naturally occurring hybrids and in no case meiotic irregularities were observed.

Artificially produced hybrids TurriLL (1948) of a cross between E. hirsutum and E. parviflorum showed that a proportion or all of the offspring are dwarfed, contorted or variously malformed and many plants die before flowering. They stand distinct in the natural populations and seem to have factors that have checked growth or normal development. Reciprocal crosses gave different results suggesting the presence of extra-nuclear or cytoplasmic factors responsible for atypical growth. Most recent researches on the crosses between E. luteum and E. hirsutum show that there are some nuclear genes which play an important part in the development of the plant and that there is a complex interaction between nuclear genes, plasma genes (cytoplasmic factors) and environmental conditions, which together are responsible for normal and abnormal development.

Lewis and Moore (1962) attributed the non-viability of the hybrids in North America to the lack of genetic adaptability like their parental species to the communities in which the parents grow. Raven and Moore (1964) later suggested that in this region survival of the hybrids is rather difficult as the summers are long and dry and that the

habitats occupied by Epilobium are rather limited, normally consisting of wet meadows and stream sides where plants are members of relatively stable communities. In Britain, on the other hand, the climate is generally much moister throughout the year and most of the species of Epilobium are decidedly weedy, including E. hirsutum, frequently growing in ecologically open communities along hedgerows and in marshes in which there is a rapid turnover of individuals. Even under these conditions the proportion of hybrids still remains extremely low. This tends to suggest that although E. hirsutum is open to cross-pollination the habitual autogamy and possibly lowered cross-compatibility (Valentine, 1951; P.86) may be far more important in maintaining the species as discrete units, although lowered hybrid fitness probably operates when inter-specific crosses do occur.

In Lythrum salicaria the genetics of hybridization and the breeding system have been investigated in some detail mainly to illustrate the phenomenon of tristylly noted by many workers, as, Darwin (1877), East (1927 and 1932), Fisher (1935 and 1941), Fisher and Mather (1940 and 1942) and Barlow (1913 and 1923).

Breeding results have shown definitely that tristylly has a genetic basis. "Long" is a full recessive, since long styled plants on selfing produced only similar offspring.

"Mid" is dominant over "long" and "short" over both "mid" and "long". Sometimes "mids" though behaving as if homozygous give a small percentage of "longs" when crossed with "long". Several theories have been proposed to explain these results and it now seems most probable that they are due to a gene being represented a number of times, owing to polyploidy, in as many similar but separate chromosomes. This is clearly a "polysomic" type of inheritance and may sometimes result in ratios quite different from those obtained when only one pair of chromosomes is involved.

Generally, all three kinds of plants occur in any fair sized population. Sometimes "mids" are below 33.3%, which would be expected in balanced populations. "Mids" from some stocks yield more seeds per capsule but are less efficient as pollen parents than the "longs" and "shorts", Turrill (1948). However, contrary to this, Fisher and Mather (1940) reported that in an open pollinated population grown for 7 years at the Chelsea Physics Garden, London, determination of frequencies of three types of plants each year showed that populations approached equilibrium at which only about 22% of plants were "mid", while "long" and "short" were roughly equal in frequency because of lower fertility of both seed and pollen of the "mid" type than of the other two. "Mids" produced 16.1% fewer viable seeds. A. B. Stout (1925)

reported the appearance of a semi-homomorphic form in a cultivated population in the New York Botanical Garden. The plant set abundant seeds after self-pollination and 122 plants were raised from this seed. Of these, 60 were of the new type like the parent, 9 were long styled, 52 intermediate between the new type and long styled, and 1 was mid-styled. Such aberrant types have not been found in Britain.

The appearance of only one plant of the new type in a population together with the fact that it has not been reported previously, is suggestive of its being a mutation, heterozygous in nature with some hereditary value. The range of stamen length from mid to long suggests a relation of this form with mid-style from which the new form arose. The semi-homomorphic type of flowers is perhaps a reversion towards a simpler homomorphic type of flower which might have been the ancestral type of species.

It can be concluded that Lythrum salicaria has an extraordinary and complex genetical system for outbreeding, giving rise to mutations and polyploids which work well at least as regards short term adaptability in a variety of climates and habitats. Accordingly, Mulligan (1957) suggested that there may be a relation between ploidy and aggressiveness, life duration, habitat and so forth.

Both species are able to spread over wide areas because of their light weight, wind dispersed seeds. Although more efficient in Epilobium hirsutum as the seeds are wind borne and thus stand the chance of being carried over longer distances, exploitation of a given area is by its remarkable ability for vegetative spread by stolons and propagules. Lythrum salicaria completely lacks any efficient mechanism of ~~seed spread and there is no~~ vegetative multiplication to help invade new areas. The only chance of these seeds being spread to far distances depends on the extent to which the carriage of seeds and fruits in the soil and mud, on human footwear, in hooves of cattle and sheep, rabbits and on the feet of birds, is successful. Since seed production is very high and these disseminules are present in abundance in soil, they stand a good chance of being spread over long distances.

III. DISTRIBUTION OF THE SPECIES

1. Geographical Distribution

The distribution of the two species mainly lies within the Northern Hemisphere but Lythrum may extend in the Southern Hemisphere as well. They occur mostly in moist and wet habitats.

Lythrum salicaria is more or less cosmopolitan in distribution and is found all over the world except in extremely cold and Arctic regions. It is most prevalent in Central and Southern Europe from where it extends northwards along the southern coast of Norway and south east of Sweden (Hulten 1950) upwards, it is completely absent in the extreme north west of Finland and Denmark. It is found in abundance in central Siberia and along the warm coastal areas of the U.S.S.R. The species extends south into Honshu, Korea, China and Japan, and into the Himalayas in northern and western Asia. It also occurs in Persia, Syria, the Lebanon, Mediterranean Islands and Southern Europe in Spain, Greece and Italy. It is present in Africa, mainly in the north, and is abundant in North America. In the Southern Hemisphere it is found in abundance in south east temperate Australia but is absent in the west.

Epilobium hirsutum has Eurasiatic distribution as well as being commonly found in all the continents, but it has not been reported from Australia. Unlike Lythrum it is not very common in central and southern Europe but is dominant northwards to southern Sweden, abundant in the northern region of Denmark, Finland, North Baltica~~m~~ and northern Russia where Lythrum is completely absent. In Norway it extends up to the northernmost regions but is absent in the sub-alpine and other Arctic regions. It stretches across Europe to China, Japan and in the Himalayan regions where it is mostly confined to the western borders of West Pakistan in the Chitral and Kurran Valley, (Raven, 1962), extending eastward to Nepal. It is absent in the southern Himalayan range (in Assam, Naga Hills and Burma) and reappears again in western China and temperate Asia (in Persia, Pakistan and Afghanistan) extending in the Middle East (in Syria, the Lebanon, Egypt, the Sudan), some of the Mediterranean Islands and southern European countries. Southwards it occurs in north eastern and southern Africa. It is introduced in North America where it is well established.

2. Ecological Distribution

The geographical distribution of the two species is affected by their altitude relations. While Epilobium hirsutum is mostly confined to high altitudes, Lythrum salicaria occurs along low lying coastal areas. In the Himalayas ⁴Epilobium is

a mountain plant, rarely occurring below 1,000 m. and above 2,750 m. It is widely distributed in the open woodlands especially where it is moist, Raven (1962). In northern Europe in Norway and Sweden it extends to the height of 400 - 600 m., while *Lythrum* ranges only between 0 and 100 m.

Along the southern edge of their geographical distribution the species appear to be excluded from otherwise suitable sites by their water-relations. The distribution of both species is confined to wet marshy places, coastal areas stream banks and ditches, (Post, 1932). In North America both species are limited to bogs and margins of moist woods, and Epilobium may extend in the mountain areas. In the Middle East they are also restricted to coastal areas and marshes and in the interior may extend into the mountains where Lythrum does not go beyond the height of 3,000ft., while Epilobium extends up to 5,000ft. into extreme cold areas Post (1932).

On the northern edge of their distribution the species are probably excluded from suitable sites in other respects, as required by the temperature relations of their growth and the need for protection from the direct effects of cold weather and from the solifluction. It is more so in Lythrum than in Epilobium. Epilobium is mostly confined to northern Europe as opposed to southern and central Europe and

may extend up to the lower alpine belt but only on the south facing slopes which afford good protection from snow in winter, Hulten, (1950). Lythrum is completely absent in these regions and widely distributed in warm central and southern Europe and hot Mediterranean areas.

In the Himalayan range of its distribution Epilobium is mainly confined to the extremely cold western parts and does not extend south in the hot tropical Assam, Naga Hills, Manipur or Burma; Raven (1955). It does not extend below the main crest of the Himalayan range in the hot plains of West Pakistan or India and is absent in the mountains of southern India and Ceylon. Eastwards it extends to Nepal and reappears again in western China, but has not yet been reported between central Nepal and western China. Deep in the south, in Australia, Epilobium is completely absent, most probably because it is a plant of cold regions, whereas Lythrum is in abundance in marshes at Myponga and other moist spots in the Mount Lofty range and also in south east Australia with its long hot summers, Black (1929).

In Europe and the Balkan Peninsula especially, climatic conditions are more important than the soil in the distribution of plants. Lythrum is abundant in the Mediterranean and central European type of climate with maximum temperature and minimum rainfall in summer in the

former, with no marked minimum rainfall while maximum rainfall tends to coincide with the season of increasing temperature in the latter. It supports predominantly xeromorphic species adapted to surviving the summer drought.

Epilobium has very little distribution in central Europe and Mediterranean regions as it cannot survive the summer drought and extends northwards from the centre, essentially being a mesophytic species with a life history having its resting phase in winter with no marked minimum rainfall or minimum amount falling within the colder resting period.

The general pattern of geographical distribution shows that while Epilobium is distributed in the north temperate and extreme cold regions of Europe and the Himalayas, Lythrum is mostly absent in northern, colder regions and occurs in north temperate to tropical areas in north and western Asia and Australia.

3. Distribution in Britain

In Britain the water relations of the two species do not appear to play a great part in restricting their habitats so much as temperature in controlling their distribution.

Epilobium is common throughout most of Great Britain reaching as far north as Caithness but absent in the extreme north west, in the Hebrides, Orkney and Shetland; Clapham, Tutin and Warburg (1952). Lythrum is abundant in England,

Wales and Ireland, is less common and sometimes rare in Scotland, and absent from most of the north.

*Epilobium inhabits sites ranging in soil moisture from stream banks, pond-side mud and silted banks of dykes and marshes, Ellis (1965). It grows profusely along the banks of the Thames, Druce (1897), the drier parts of the fens, Clapham, Tutin and Warburg (1952), and is dominant in the valley but completely absent in head-water in the Breck fens, Haslam (1965). It is rarely found on dry sandy heaths Batten (1918), in chalky limestone downlands of Derbyshire, Grime and Hutchinson (1967), in dry and disturbed places along the ditches and trackways laid down across the fens on moderately deep peat, Haslam (1965). *Lythrum shares distribution with Epilobium in reed swamps at the margin of lakes and slow flowing rivers, fens and marshes, often forming large showy stands. It also occurs on stony, sheltered, unsilted shores in Esthwaite Water, Pearsall (1918), at the southern end of the lake (with a bank of morainic material) it is confined to a drier habitat and also in open as well as closed carrs, Pearsall (1918), Ellis (observation). It is found along the margins of bogs, occurring near sphagnum and various calcifuge species like Erica tetralix and Narthecium ossifragum. Yet it also grows in damp meadows on limestone, colonising flat beaches of limestone rocks and shingle, on the shores of

*Epilobium - Plate 2.

*Lythrum - Plate 3.

E. hirsutum

A

F. ulmariaI. pseudacorusI. pseudacorusE. hirsutumF. ulmaria

B

PLATE 2. Epilobium hirsutum in Wheatfen Broad.

A. Growing along the silted bank of the dyke. Succeeding Iris pseudacorus and Filipendula ulmaria.

B. Forming large monospecific stand with occasional patches of I. pseudacorus and F. ulmaria.

(Photographed on 29 August, 1969)



PLATE 3. General view. Area of Lythrum salicaria in Surlingham, Norfolk. Photographed on 28.8.61. (By courtesy of Mr. E. A. Ellis, owner of Wheatfen Broad)

Lough Conn in western Ireland, (W. D. Hamilton, 1969., Imperial College Zoology Department, Personal Communications).

In the centre of their distribution, exclusion from otherwise suitable sites by the temperature relations of growth and need for protection, almost certainly plays a part in settling their altitudinal limits. In Britain Epilobium occurs in ecologically open communities along the hedgerows and marshes, Valentine (1951) and may reach up to a height of 3,000ft., and also in Scotland; Clapham, Tutin and Warburg (1952). It is absent along the warm western coast of Ireland with its central European type of climate, Perring and Walters (1962). Lythrum, however, is a low-land species rarely occurring above the height of 500 to 1,000ft., though along the south west warmer coast of Ireland it extends up to 2,000ft., Perring and Walters, (1962). In Scotland it is confined to the coastline, and may occur well up in the mountains in Wales.

The most critical factors excluding the species from all but certain habitats in the centre of the geographical range appear to be their requirements in respect of mineral nutrients and light.

A requirement for more or less neutral to alkaline soil conditions appears to exclude Epilobium hirsutum from acid soils. Fens of the east Norfolk Broads are mostly

alkaline with a pH varying from 6.8 to 7.5 and Epilobium is the most dominant plant; Ellis (1965), but is absent to rare in carrs with pH 5.8, Turrill (1948). In headwater fens of Breckland with pH 6.0 Epilobium is absent, but it appears on dry and disturbed trackways of headwater fen and is dominant in valley fens with a pH up to 7.5, Haslam (1965). Pearsall (1918) reported complete absence of Epilobium in Esthwaite Water fens controlled by acidic waters. Yet it has been found growing in acidic boggy ditches at Silwood Park with a pH as low as 5.8 and in moist clayey Bagshot sands with a pH of 6.1.

Lythrum salicaria is found on both calcareous and non-calcareous soils, Perring and Waters, (1962). It is dominant plant of Esthwaite Water fens and marshes controlled by acidic waters, Pearsall (1918). It is more common in open carrs, at wheat-fen Broad's slightly acidic in reaction, than the drier fens; Ellis, Pers.Comm. (1967). It does not grow in thoroughly acid bogs but occurs on the margins with sphagnum and other moderately calcifuge species. Differential mineral requirements of the two species and the richness of the soil affect the distribution of the species in a given area otherwise suitable for the growth of both.

The need of a relatively high level of minerals for adequate growth appears to exclude Epilobium hirsutum from

many habitats. Its presence in a habitat is almost invariably correlated with a continuing high mineral status as on the dry silted margins of inundated drykes and hedgerows in the low-lands forming ecologically open communities. These communities probably exist under flush conditions. Lythrum salicaria, though a plant of rich fens and marshes, is more tolerant of poor soil conditions than Epilobium. In the marginal vegetation of wet succession Epilobium is particularly confined to fens with rich soils because of the high deposition of silt and minerals, while Lythrum is prevalent in headwaters and reed swamps of very low nutrient status as well as in the carrs less fertile than fens;

Peaty fens of East Anglia with rich deposits of silt are very fertile and support Epilobium as its dominant flora; Turrill (1948). Haslam (1965) noted that in the Breck fens Epilobium is dominant in valley fens and completely absent in headwater fens. The chemical composition of water in the two is similar and so is the mineral composition of ash of peat of the two types, but because of the difference in inorganic content (principally due to silting) the mineral content of the valley fen is roughly double that of headwater fens. ~~S~~He further observed that Epilobium appeared in dry places where the water-table had been abruptly lowered by over $\frac{1}{2}$ m. and have had a major soil disturbance. Thus, it seems that headwater fens are

more fertile after drying and disturbance and this coincides with the appearance of Epilobium. Epilobium is often designated as a 'nitratophilous' plant (Haslam (1965) with abundant nitrates in their shoots in spring. Jonsson (1957) concluded that although growth of Epilobium is related to the active nitrification of the soil what is more important is that establishment is more dependent on soil nitrification, and its survival may continue sometime after nitrification has ceased. However, it is perhaps more likely that it is not just lack of nitrate, the end product of nitrification, but of the concomitant soil conditions for nitrification of adequate phosphate, available nitrogen and cation supply (see Russel, 1950), that also precludes its establishment in habitats other than in those with active nitrification. Haslam (1965), however, showed that when the infertile peat of headwater fen is experimentally saturated with full nutrients Epilobium shows a high percentage of seedling germination, establishment and growth.

Lythrum salicaria, on the other hand, is not necessarily confined to rich fens of East Anglia, Ellis (1965), but has been reported growing abundantly along infertile, unsilted, peat masked stony shores of Esthwaite Water marshes; Pearsall (1918). It may grow along the slow running waters or on dry pastures 10 to 30 cm. above the summer water level. It

is predominant in the rich fens in the zone of heavy sedimentation and silt. Reaction to phenolphthalein showed the waters of the lake stream and fen soil to be very acidic; this may be responsible for the complete absence of Epilobium in Esthwaite Water fens in spite of the rich and highly silted soils.

Once established both species seem to tolerate some shade, more so in the case of Lythrum than Epilobium.

Casual observations made at Wheatfen Broad showed Epilobium as being able to persist in moderate shade but not to flower there. It is markedly absent along the shady sides of hedgerows in the lowlands, and shows luxuriant growth on the exposed side. It is absent in the open or closed carrs. Lythrum is more tolerant of moderate shade and is more frequent in shady conditions than Epilobium. In the 'open carr' at Esthwaite Water with moderate sedimentation Alnus glutinosa and Salix cinerea are sub-dominant supporting a typical fen ground flora with Lythrum as the most abundant species while Epilobium is completely absent; Pearsall (1918). In the 'closed carr' dominated by Salix cinerea, Lythrum is quite frequent. It is certain that light intensity limits the ground flora here, however, Pearsall noted that where the trees have fallen and light intensity rises as high as 0.7 of full daylight there is dense local vegetation of Lythrum along

with Carex elata, both profusely flowering. In the old carr where light intensity averages 0.032 of full daylight all ground flora is absent and where light intensity is 0.1 of full daylight Lythrum occurs as very sparsely distributed species. In many places Lythrum grows on slopes confined to narrow wave-washed zones near the water, under the shade of moisture loving trees like Fraxinus excelsior, Alnus rotundifolia and Salix cineria. The substratum is of slightly acidic soil. It has been observed ~~that~~ in the 'Alder carr' of the East Anglian Broads dominated by Crataegus monogyna, Alnus glutinosa, Frangula alnus and Salix cinerea and Prunus spinosa, Lythrum grows abundantly under the open canopy of these trees. (Ellis, Pers. Comm. 1967).

However, lack of light, necessary to give adequate growth, together with lack of readily available nutrients, probably prevents the establishment of any of the species in well established, closely knit communities such as grassland. In such situations light at seedling level is probably low and most of the available mineral nutrients of the habitat are taken up by the plants already established in it.

Both species are affected by grazing to some extent, but their restriction to wet marshy habitats does not pose any serious threat to their elimination by intense grazing, as suggested by Ingram (1931) for Chamaenerion angustifolium.

It has been noted that rabbit grazing has done substantial damage to transplanted seedlings of Epilobium on drier sites. They seem to be very discriminatory and only Epilobium was grazed even when mixed with Lythrum seedlings. This grazing pressure at seedling stage may explain the confinement of Epilobium to wet ditches and dykes and its exclusion from otherwise suitable sites. Lythrum is also affected by grazing but damage is not as severe as in Epilobium.

In Crete Miss Pallis (1916) reported Epilobium affected by horse and cattle grazing in summer when water is very low in the Danube marshes. These animals are very selective and Lythrum in the same area has been recorded as an un-palatable species; (see, The Plant Life of Balkan Peninsula, Turri1929). In Surlingham Wheatfen and Rockland Broads, selective feeding by the coypu (*Myocastor coypus*) severely damaged the vegetation of Epilobium in 1960. Rootstocks were dug out extensively in autumn and winter, while Lythrum was avoided after some trial gnawing, Ellis (1963). He further observed the appearance of huge beds of Lythrum flourishing temporarily in freshly cleared "lows" and stinging nettles replaced Epilobium destroyed by coypus on river banks and marsh ditches. Lythrum is very palatable to pheasants and wild pigeons and tips of young shoots are readily bitten off, (Russell's observations, 1969); one experimental plot was

severely damaged.

Not only is the geographical and ecological distribution of importance, but also the habitat, the growth form and the nature of this distribution.

In Britain, Epilobium hirsutum (F. H. Whitehead, 1969, Pers. Comm.) frequently forms large monospecific stands from which nearly all other species are excluded. These stands tend to persist for many years and frequently can be seen to be expanding and encroaching on new territory. Very occasionally and only where bare mud has been produced in the depth of winter or early spring Lythrum salicaria may form large monospecific stands. These, however, tend to last for a short time only and even before the end of the first year strong colonisation by other species can occur. Examples of this behaviour by Lythrum occurred in bomb craters in fens during the last war, and on patches eaten out during the winter of East Anglian coypu infestation. Both species can occur as single individuals in a wide range of communities but the general tendency is for Epilobium to increase in the territory occupied, which is seldom the case for Lythrum. The opposite situation appears to occur on fens along the southern Dalmatian coast where Lythrum tends to form monospecific stands, though seldom of the same size or extent of the British Epilobium stands. Epilobium, on the other hand,

tends to occur as scattered individuals or small clones, never occupying the large areas as in Britain. In Central Europe north of the Panonion plain, e.g. Bohemia, Northern Slovakia, neither species tends to form monospecific stands both occurring as scattered individuals amongst the fen vegetation, although Lythrum is much more abundant than Epilobium.

4. Historical Background

The prevalence of Epilobium sensu lato pollen in late glacial deposits in north western Europe speaks of the very ancient nature of this genus, Godwin (1956). Raven (1962) concluded that the distributional area of Epilobium hirsutum must have been profoundly affected by the climatic changes that accompanied the pleistocene glacial cycles. At the height of such cycles the continuous northern Asiatic area must have been pushed southwards and into contact with its presently isolated Himalayan and west Chinese stations, just as is known to be the case in Europe for many species with a present day Arctic-montane disjunct distribution. This probably refers to Chamaenerion angustifolium, closely related to Epilobium, thought to be one of the prominent communities that existed in the late glacial era in north west Europe (Godwin, 1956) and at present shows a discontinuous distribution from Arctic Scandinavia to Kamchatka and the Aleutian

Islands (Clapham, 1953; Hulten, 1927 and 1937).

It has been suggested that the two species are excluded from the habitats in which they do not occur because of the temperature relations of their growth, their water relations, their mineral nutrient and light requirements for growth, and grazing susceptibility. These intrinsic factors of the biology of the plants operate from germination onwards and will be of greatest importance in the early stages of growth. The succeeding chapters are therefore mainly concerned with the germination and the early stages of growth, their competition and survival under various conditions of light, temperature and mineral nutrients.

IV. MATERIALS AND METHODSMATERIAL

Seeds of both the species were collected from plants growing in Wheatfen Broad (Norfolk; v. county 27). Ten plants of each species were collected in plastic bags separately by Dr. Whitehead in the 3rd week of September, 1966. The material was left exposed in the warm greenhouse for a few days for drying and complete dehiscence of some of the undehisced Epilobium hirsutum pods and full ripening of Lythrum salicaria capsules.

Seeds of Lythrum were stored in a sterilized glass bottle with the stopper wrapped in tinfoil to prevent any dampness and consequent fungal attack. Epilobium seeds were stored in polythene bags. Both types of seeds were kept in a refrigerator at a temperature of 3 to 4°C.

In all the experiments throughout the course of studies seeds were used from this stock.

Rhizomes of Epilobium were also collected from three different types of plants :

- 1) plants growing in fully exposed sunny areas, profusely flowering with abundant fruits,
- 2) tall plants growing under partial shade with a smaller

number of flowers and fewer fruits,

- 3) very tall plants from shady conditions with few flowers and practically no fruit except for some abortive pods.

METHODS

Sand Culture Techniques

In all the experiments set up to study the effect of light, plants were grown in a mixture of sand and peat in the ratio 3 : 1. Sedge peat was preferred to moss peat to avoid acid conditions. Growing plants in a sand peat mixture was considered better than water culture to study the effects of light as it could simulate to some extent the substrate conditions for germination and growth to those in nature. Sand and peat mixture was preferable to pure sand which dries up quickly through surface evaporation and may cause drought harmful for normal root growth, also because of the large size of the plants, sand alone would not make a strong substratum for anchoring the plants.

Water Culture Techniques

In other experiments involving the effects of temperature and nutrients on growth, water culture was preferred to sand culture for the following reasons:

- 1) In spite of the magnitude of the experiment and the number of plants involved, it was possible to accommodate them in a relatively smaller space and uniformity of external

conditions could be easily maintained. This was especially useful in the study of effects of temperature in the phytotrons with limited space and high relative humidity.

2) In the studies of nutrient stringency on growth, exact ratios of various nutrient elements could be maintained and could be kept pure as there was no other source of contamination.

3) In these experiments main stress was on root production and root loss through washing (as in peat and sand mixture) was eliminated.

Plants growing in different dilutions of nutrient solution were provided equal opportunity to absorb the available nutrients and the possibility of accidental growth differences were eliminated. Moreover, the main aim of these experiments was to record primary data for growth analysis and to compare the two species in respect of some standard parameters of growth, the accuracy of this comparison would depend upon the uniformity of the growing conditions. The same degree of accuracy was necessary where estimates of uptake of calcium, potassium, nitrogen and phosphorus had to be made in terms of unit weight and total plant weight under artificially controlled conditions. In addition, the nature of the effects on the growth of plants growing at different levels of deficiencies of individual elements like nitrogen,

phosphorus and potassium, can be best understood using water cultures where concentrations of various macro and micro-nutrients can be maintained at desirable levels.

Selection of Nutrient Solution

Nutrient solutions used by various workers (Loach, 1964; Sheikh, 1966; Myerscough, 1962) were tested for the growth of both the species. Neither species showed satisfactory growth in any of these solutions. Solutions used by Loach and Sheikh were very acidic (pH 4.0) while the one used by Myerscough (1962), a modification of that of Arnon and Johnson (1942), had low concentrations of potassium and nitrogen.

On the other hand, both species showed rapid and luxuriant growth in the "Long Ashton" nutrient solution (pH 5.8) producing abundant flowers and fruits. This is the most recent ~~and complete~~ of all the nutrient solutions. Hewitt (1965) commented that it is an efficient solution with an additional advantage of containing sodium and has been successfully used with a wide range of crops. This solution has been used throughout the course of studies, modifying it in various ways as required for particular experiments. Macro and micro-nutrient composition of the complete "standard nutrient solution" is given below.

Details for the weights of different salts to prepare stock solutions of each, and the volume of each to make the working standard solution.

<u>No.</u>	<u>Salt</u>	<u>Stock soln.w/v</u> <u>gm/2 litre</u>	<u>Working soln.w/v</u> <u>ml. in 1 litre</u>
1.	* KNO_3	202.00	2 ml.
2.	$\text{Ca}(\text{NO}_3)_2$	656.00	2 ml.
3.	$\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	208.00	2 ml.
4.	$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	369.00	2 ml.
5.	Sequestric acid (sodium Monedetate)	77.02	1 ml.
6.	$\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$	4.46	1 ml.
7.	$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$	0.48	1 ml.
8.	$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	0.58	1 ml.
9.	H_3BO_3	3.92	1 ml.
10	$(\text{NH}_4)_6\text{MO}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$	0.07	1 ml.
		H_2O	986 ml.

Standard concentrations of various elements in the nutrient solution.

<u>No.</u>	<u>Nutrient element</u>	<u>Concentration (p.p.m.)</u>
1.	N	140.0
2.	P	41.3
3.	K	78.0
4.	Ca	160.3
5.	Na	30.8
6.	Mg	36.4
7.	S	48.0
8.	Fe	5.6
9.	Mn	0.55

* Amount modified, in the solution used, from the original

<u>No.</u>	<u>Nutrient Element</u>	<u>Concentration (p.p.m.)</u>
10.	Cu	0.064
11.	B	0.33
12.	Zn	0.065
13.	Mo	0.048

Preparation of Solution for Use

All ingredients were mixed in appropriate proportions except $\text{Ca}(\text{NO}_3)_2$ and $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$ to make up 30 litres of solution at a time. These two salts were added later to avoid any precipitation.

The table given below gives the composition of the macro-nutrients in different dilutions of standard solution to assess the relative effect of the nutrient stringency on the growth performance of the two species.

Standard solution is referred to as "S" and various dilutions as S/10, S/50 S/500.

Summary of the Concentration of Nutrients in Different Dilutions (p.p.m.)

	Element	S	S/10	S/50	S/100	S/200	S/300	S/400	S/500
1	N	140.0	14.0	2.8	1.4	0.7	0.4666	0.35	0.28
2	P	41.3	4.13	0.826	0.413	0.2065	0.1377	0.1063	0.0826
3	K	78.0	7.8	1.56	0.78	0.39	0.26	0.195	0.156
4	Ca	160.0	16.0	3.2	1.6	0.8	0.5333	0.400	0.32
5	Na	31.0	3.10	0.62	0.31	0.155	0.1033	0.0775	0.062
6	Mg	36.0	3.6	0.72	0.36	0.18	0.12	0.09	0.072
7	S	48.0	4.8	0.96	0.48	0.24	0.16	0.12	0.096
8	Fe	5.6	0.56	0.112	0.056	0.028	0.0186	0.014	0.0112

(a) Standard nutrient solution with different levels of phosphorus deficiency.

Normal culture solution containing standard amount of phosphorus will be represented by the symbol 'P' subscripted by the letter 'S' and the rest of the deficiency levels with the number representing the amount of dilution, i.e. P/S, P/10, P/50 and O/P (no phosphorus).

To obtain various deficiency levels of phosphorus the amount of sodium-di-hydrogen orthophosphate was reduced accordingly. This resulted in the reduction of sodium as well which was compensated by the addition of corresponding quantities of sodium chloride. Manipulations in the swapping of the salts did not bring about any significant change in the pH of the solution. The pH read on the Beckman electric pH meter ranged from 5.8 to 6.5, and was supposed to be approximately uniform for the work. The adjustments in the quantities of $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$ and NaCl can be read in the table below.

<u>Salt</u>	<u>Levels of phosphorus dilutions, g/litre.</u>					
$\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	0.208	0.0208	0.00416	0.00208	0.00104	X
NaCl	X	0.0702	0.07644	0.7722	0.07761	0.078

<u>Salt</u>		Na and P concentrations in ppm.					
Na	($\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$)	31.0	3.1	0.62	0.31	0.155	X
Na	(NaCl)	---	27.9	30.38	30.69	30.845	31.00
Total	Na	31.0	31.0	31.00	31.00	31.00	31.00
	P	41.3	4.13	0.826	0.413	0.2065	X

The rest of the salts and their respective amounts were the same as used in the standard culture solution.

(b) Standard nutrient solution with different levels of potassium deficiency

<u>Salt</u>	<u>Levels of potassium dilutions, g/litre</u>					
	K/S	K/10	K/50	K/100	K/200	O/K
KNO_3	0.202	0.0202	0.00404	0.00404	0.00101	X
$\text{LiNO}_3 \cdot 3\text{H}_2\text{O}$	X	0.2214	0.24108	0.24354	0.24477	0.246

Concentrations in p.p.m.

Total	K	78.0	7.8	1.56	0.78	0.39	X
KNO_3	NO_3	124.0	12.4	2.48	1.24	0.62	X
$\text{LiNO}_3 \cdot 3\text{H}_2\text{O}$	NO_3	X	111.6	121.52	122.76	123.38	124.0
Total	NO_3	124.0	124.0	124.0	124.0	124.0	124.0

As in phosphorus, normal culture solution containing standard amount of potassium is referred to as K/S and various dilutions as K/10, K/50 O/K (no potassium). The pH values ranged from 5.8 to 6.3.

In reducing the amount of potassium in KNO_3 ,

inevitable reduction in the amount of nitrate (NO_3) was compensated by substituting with the corresponding amounts of $\text{LiNO}_3 \cdot 3\text{H}_2\text{O}$. Adjustments in the quantities of the two salts are given above.

(c) Standard nutrient solution with different levels of nitrogen deficiency

As in previous cases standard nitrogen solution and its various deficiencies will be referred to as N/S, N/10, N/50 O/N. pH values ranged from 5.8 to 6.2.

Since nitrogen in the standard solution comes from two sources (KNO_3 and $\text{Ca}(\text{NO}_3)_2$) so in producing the required deficiency levels, there is unwanted reduction in the amounts of potassium and calcium, compensated by adding corresponding quantities of CaCl_2 and KCl . The adjustments of the quantities in swapping the four salts are given in the table below.

<u>Salt</u>		<u>Levels of nitrogen dilutions. g/litre</u>					
		N/S	N/10	N/50	N/100	N/200	O/N
KNO_3		0.202	0.0202	0.00404	0.00202	0.00101	X
KCl		X	0.1341	0.14602	0.14751	0.148255	0.149
$\text{Ca}(\text{NO}_3)_2$		0.656	0.0656	0.01312	0.00656	0.00328	X
CaCl_2		X	0.3996	0.43512	0.43956	0.44178	0.444
<u>Source</u>	<u>Elem't</u>	<u>Concentration in p.p.m.</u>					
KNO_3	K	78.0	7.8	1.56	0.78	0.39	X
KCl	K	X	70.2	76.44	77.22	77.61	78.0
Total	K	78.0	78.0	78.0	78.0	78.0	78.0

Source	Element	N/S	N/10	N/50	N/100	N/200	O/N
$\text{Ca}(\text{NO}_3)_2$	Ca	160.0	16.0	3.2	1.6	0.8	X
CaCl_2	Ca	X	144.0	156.8	158.4	159.2	160.0
Total	Ca	160.0	160.0	160.0	160.0	160.0	160.0
KNO_3	N	28.0	2.8	0.56	0.28	0.14	X
$\text{Ca}(\text{NO}_3)_2$	N	112.0	11.2	2.24	1.12	0.56	X
Total	N	140.0	14.0	2.8	1.4	0.7	X

Automatic Methods for the Determination of Nitrogen, Potassium
Calcium and Phosphorus in the Plant Material

These four elements were determined with the Technicon Auto-Analyser, that has been successfully used and recommended by workers like Steckel and Flannery (1965) and Varley (1966). They showed Auto-Analyser determinations to be more accurate than any other known manual techniques for plant materials like Colorimeter (P), Flame Photometer (K and Ca) and titration techniques for nitrogen.

Determination of N, P, K and Ca was made in root, stem and leaf of all the plants grown in different dilutions of nutrient solution.

Milling the plant material

Plant materials were dried in an oven at 80°C . for 48 hours, cooled in a desiccator and then powdered in an

electric grinding mill with a 4 blade cutter and a 60 B.S. sieve. Recovery for 1 g. dried material was 98 to 99%. The resulting powder was thoroughly mixed and considered homogeneous for the analysis purposes.

Estimation of Nitrogen

Method

The method used is a modification of the procedure described by van Slyke and Hiller (1933). It consists of reacting a solution containing ammonium ions with alkaline phenol and hypochlorite. On heating the solution an intense blue colour is produced which is closely related to that of indophenol. Borsook (1935) by careful control of temperature and time increased the sensitivity of the reaction. But Russell (1944) showed that in these solutions of relatively high alkalinity, the colour was not reproduceable at or near 100°C. but was reproduceable by lowering the temperature to 37°C. but it then takes 1 to 2 hours. However, in solutions of lower concentrations of alkali, the reaction may still be carried out around 100°C. but increase in sensitivity is three times greater than when the reaction is produced by the more strongly alkaline reagents. Many investigations were made to study the factors affecting the sensitivity. However, such refinements of technique are not necessary in this method by

auto-analysis as ammonia is usually present in concentrations within the range 10 to 40 p.p.m.

Apparatus

Standard pieces of Auto-Analyser equipment are used. The colorimeter has a flow-cell of 10mm. light path and uses 625 mμ interference filters. The recorder is of the two pen type, but for the purposes of nitrogen determination only one channel is used.

Reagents

All the materials used are of recognised analytical grade and solutions are prepared with glass distilled demineralised water.

1. Sulphuric acid, nitrogen free, sp.gr. 1.84.
2. Sodium sulphate - selenium mixture:

Grind together 100g. of anhydrous sodium sulphate and 2.5g. of powdered selenium. The homogenised mixture was stored in a screw topped bottle.

3. Alkaline sodium phenate:

Weigh 250g. of phenol into a beaker and add to it 200mls. of water, warm over a gas flame until completely dissolved and then transfer to a 1,000 ml. graduated flask. 135g. of sodium hydroxide were dissolved in 500 ml. of water and cooled to room temperature. When cool, it was added slowly to the solution of phenol in the flask. The mixture was made

up to 1,000 ml. with distilled water after being shaken repeatedly. This solution is best prepared immediately before use but may be stored for a few days in a polythene bottle in a refrigerator.

4. Sodium hypochlorite:

Any commercial sodium hypochlorite solution, calcium free and containing 4 to 6% available chlorine, may be used. For convenience Jeyes 'Parazone' bleach, as purchased locally, was found to be ideal.

5. Standard nitrogen solution:

Ammonium sulphate was dried for two hours at 105°C. 4.7162 g. was accurately weighed on a Mettler balance and put in a 1,000 ml. calibrated flask. It was made up to the mark with distilled water and the flask was shaken well. This solution contains 1,000 p.p.m. of nitrogen.

6. Nitrogen working standards:

100 mls. of 1,000 p.p.m. nitrogen solution was diluted ten times in a litre flask to give a solution containing 100 p.p.m. From this solution standards were prepared ranging from 5 to 40 p.p.m. of nitrogen. To each standard, before making up to the mark in a litre flask, 2 mls. of sulphuric acid (nitrogen free) and 1 g. of anhydrous sodium sulphate were added.

Preparation of Kjeldahl Digest

Subsamples from the plant material (leaf, stem or root), previously dried at 80°C . and ground so as to pass completely through a 1 mm. screen, were further dried for two hours at 105°C .. 60 mg. of this dried and finely ground material were weighed and transferred to a 30 ml. Kjeldahl flask. 1 g. of the sodium sulphate-selenium mixture was added and then 2 ml. of nitrogen free sulphuric acid. Kjeldahl flasks were heated, gradually increasing the temperature over a two hour period until the contents of the flasks were completely clear. Heating was continued for a further 30 minutes after clearing. The flasks were allowed to cool for 5 minutes then 10ml. of demineralised water were added to each flask and gently mixed; the contents were then transferred to 100 ml. calibrated flasks. Each Kjeldahl flask was washed several times with water, each time transferring the washings to the calibrated flask. The solution was made up to the 100 ml mark in the flask and thoroughly shaken.

Operating procedure

All the component parts of the Auto-Analyser were set up accordingly and allowed to warm up for a period of 30 minutes. During this period water was continuously aspirated through the sample tube. The recorder scale range was checked with the calibration potentiometer on the colorimeter and was

then standardised with three sample cups of each standard over a range of 5 to 35 p.p.m. of nitrogen. Samples of the plant material were then analysed at the rate of 40 samples per hour. Running the equipment at the rate of 60 samples per hour was avoided to reduce the possibility of any error, as it may introduce a 2% error. Plastic sample cups were discarded after one use. Each sample solution was analysed 3 times and the mean value was taken as the true strength in p.p.m. However, it was very rare to find any discrepancy between the 3 readings.

Standard Curve

This was prepared on a special 'Technicon Auto-Analyser Plastic Chart Reader' with a chinagraph pencil from the values on the recorder chart. Values of the samples were read with this standard curve as p.p.m. concentration in 100 mls. of the aliquot. From this, the amount of nitrogen in the total weight of the organ (leaf, stem or root as the case may be) and hence in the whole plant, was calculated.

Determination of Phosphorus

Method

The method used is an adaptation of the well known standard laboratory colorimetric technique using the unreduced vanadomolybdophosphoric yellow colour. This method has advantages over various other methods using blue reduced

molybdate complexes. (For full comparison see M. L. Jackson's "Soil Chemical Analysis", Constable 1958). The many advantages are:

- (i) extreme simplicity and rapidity
- (ii) stability of yellow colour as opposed to blue colour
- (iii) freedom from interferences with a wide range of ionic species in concentrations up to 1,000 p.p.m. and adaptability to HNO_3 , HCl , H_2SO_4 and HClO_4 .

In manual colorimetric determinations it has a major disadvantage of being relatively insensitive (approximately one-tenth of the blue methods), but in the automatic determination this snag has been considerably overcome by the use of a half-time delay coil.

Glassware used during this determination was scrupulously washed and thoroughly weathered as traces of phosphoric or arsenic contamination give the same test as phosphorus and new Pyrex glassware contains up to 0.7% arsenic oxide.

Apparatus

Apparatus was set up as in nitrogen. A half-time delay coil was used in this system in order to allow sufficient time for colour development to take place, so that a reasonable sensitivity could be obtained. A flow cell with a light path of 10mm. was used and the determination was carried out

with 420 mu interference filters.

Reagents

All the materials were of "Analar" grade and glass distilled water was used in the preparation of solutions.

1. Ammonium vanadate solution:

95.5ml. of nitric acid, sp.gr. 1.42, were added to about 800ml. of water in a one litre calibrated flask to this, accurately weighed, 0.5g. of ammonium vanadate was added. The mixture was shaken at intervals until the solid had dissolved. The solution was made up to the mark when cool.

2. Ammonium molybdate solution:

15g. of ammonium molybdate was added to about 900ml. of water in a one litre calibrated flask. The flask was shaken at intervals until its contents were dissolved; the solution was made up to the mark and filtered to remove all insoluble particles.

3. Ammonium vanadate - ammonium molybdate working solution:

300ml. of the ammonium vanadate solution and 200ml of ammonium molybdate solution were mixed to make the mixture for use. A fresh mixture was always prepared before use.

4. Standard phosphorus and potassium stock solution:

Potassium dihydrogen phosphate (KH_2PO_4) was dried in the oven at 105°C . for two hours. 4.3928g. was weighed accurately and put in about 800ml. of water in a one litre

calibrated flask. When completely dissolved it was made up to the mark and shaken well. This solution contained 1,000 p.p.m. of phosphorus.

5. Standard phosphorus working solution:

100ml. of this stock solution was diluted to 1,000ml. in a one litre flask to give a solution of 100 p.p.m. strength. From this a range of standard solutions from 1 to 20 p.p.m. was prepared in 100ml. flasks.

6. Standard potassium stock and working solutions:

3.8132g. of dried KCl was dissolved and diluted to 500ml. in a calibrated flask to give a solution of 4,000 p.p.m. of potassium. 25ml. of this stock solution was diluted in a 250ml. calibrated flask to give a solution containing 400 p.p.m. of potassium.

Preparation of Ash and Ash Solution

A weighed quantity of dried, powdered plant material was placed in a tared crucible and heated in a muffle furnace for one hour; during this period the temperature was raised to 250°C. After ignition, when smoking ceased, the temperature was raised to 500°C. and heating continued for a further four hours. The white ash was cooled in a desiccator and weighed. This ash was thoroughly mixed and homogenised and 20mg. was weighed accurately in a hard glass test tube. (The quantity of the available ash depends upon the amount of plant

material. Some of my samples were as small as 10mg.. However, samples as big as 0.1g. can be used.)

The ash was digested with 6mls. of 20% V/V nitric acid for 30 minutes on a boiling water-bath. It was allowed to cool for 5 minutes and then 5mls. of water were added and thoroughly mixed. The digest was then filtered through Whatman No.1 filter paper into a 50ml. graduated flask; several washings were passed through the filter and the filtrate made up to the mark.

Operating Procedure

In addition to the double mixing coil a half-time delay coil is also used in the system. The colorimeter contains a 10mm. flow-cell and a 420 mμ filter. The sampler was set at the rate of 60 tests per hour. During the warming up period 400 p.p.m. potassium solution was continuously aspirated along the sample line. During this time the "phosphorus pen" on the recorder was set at about "100% transmission" and the recorder scale range was adjusted with the "zero adjust" potentiometer on the colorimeter.

At the end of the warm up period, the instrument was calibrated with each of the three standards, as in nitrogen. After this plant samples were analysed at the rate of 60 samples per hour. A standard calibration curve was prepared on a "Technicon Auto-Analyser plastic Chart Reader" and sample

values were determined with it.

Both phosphorus and potassium can be determined by this method. J. A. Varley (1966), on analysing 20 samples from three different crops by the methods described above, found the Technicon Auto-Analyser extremely useful and reliable for the determination of nitrogen and phosphorus in plant material. Precision is as good as with manual methods for phosphorus and better for nitrogen and potassium, but there is some discrepancy between absolute values for potassium obtained by the two methods. This may be that a manually operated flame photometer is under constant attention to keep it standardised, while manipulation and re-calibration of the flame photometer when working together with a colorimeter in an auto-analyser is not easy and there may be a drift of up to 2% of the full scale deflection after constant use for 8 hours. The determination of potassium was made together with calcium by the Steckel and Flannery technique using an autoanalyser with a double channel flame photometer.

Automatic Determination of Potassium and Calcium

Method and Chemistry

Potassium and calcium were determined by a dual channel flame photometer using lithium as the internal standard. The ions are excited by a propane-oxygen flame (2775°C). Propane and oxygen pressures are 10 p.s.i.

Preparation of Stock Solutions

1. 3% Perchloric acid solution:

30ml. of 70% reagent grade HClO_4 was diluted to 1,000ml in a one litre graduated flask.

2. Potassium stock solution:

945mg. of reagent grade, oven-dried, KCl was transferred to a 500ml. volumetric flask, dissolved and made up to volume with 3% HClO_4 . This gives a solution of 1890 p.p.m. potassium strength.

3. Calcium stock solution:

1.7764g. of excellent quality crystal Iceland spar (CaCO_3) was dissolved in 20ml. of 70% HClO_4 in a beaker. When completely dissolved it was transferred to a 500ml. flask with several washings and made up to the mark with distilled water. It contained 1420 p.p.m. of calcium.

4. Working standard solutions of potassium and calcium:

Potassium and calcium stock solutions were diluted with 3% HClO_4 to give the following range of working standard solutions. In addition, 18, 12, 6 and 3 p.p.m. of potassium was obtained by diluting 24 p.p.m. potassium; and 3, 6, 9 and 12 p.p.m. of calcium by diluting 18 p.p.m. of calcium standard solution to cover the concentrations of potassium in some aliquots.

Concentrations of potassium and calcium standard solutions for analysis of plant tissue samples using the autoanalyser.

No.	Volume of stock solution taken ml.	Concentrations obtained by diluting stock to 100ml. final vol.	
		Potassium (1890 ppm) stock	Calcium (1420 ppm) stock
1	1.25	24.0 ppm	18.0 ppm
2	1.6	30.0 "	22.5 "
3	2.0	37.8 "	28.5 "
4	2.5	47.7 "	35.7 "
5	3.2	60.0 "	45.0 "
6	4.0	75.6 "	56.7 "
7	5.0	95.1 "	71.4 "
8	6.3	120.0 "	89.7 "
9	8.0	151.2 "	113.1 "
10	12.0	226.8 "	-
11	16.0	302.4 "	-
12	22.0	415.8 "	-

Reagents

Internal standard for calcium and potassium:

Only one internal standard was used for both i.e.

LiNO_3 solution. 0.9359g. of lithium nitrate trihydrate

($\text{LiNO}_3 + \text{H}_2\text{O}$), (or 0.525g. of anhydrous LiNO_3) was dissolved in 0.05 M Boric acid solution (0.3% H_3BO_3) in a beaker. Contents were transferred into a one litre flask and made up to the mark with the same 0.05 M H_3BO_3 solution.

Plant Tissue Ashing Procedure

100mg. of twice dried powdered plant material was accurately weighed and transferred to a 30ml. Pyrex Kjeldahl flask. To this 1ml. of concentrated HNO_3 and 1 ml. of 70% HClO_4 was added.

The sample was wet ashed on a micro-Kjeldahl digestion rack (wire gauzes removed) with low heat from micro-burner tubes at first to avoid strong foaming and bouncing, and then at full heat for approximately 15 minutes to clear the contents. Of the 16 samples digested 2 were caramelized. The flask was removed, air cooled for a minute and 1 ml. of HNO_3 poured down the side of the flask neck and oxidation was then continued for a further 5 minutes. (A duplicate sample was prepared to find out the difference between the normal and the one which caramelized.) When the oxidation was complete the flasks were removed from the digestion rack and allowed to cool for 2 to 3 minutes, 10ml. of water was added and the contents thoroughly shaken to eliminate KClO_4 crystallization. The solution was transferred to a 50ml. volumetric flask with several washings and made up to the

mark and mixed for further analysis.

Autoanalyser Operating Procedure

The automatic sampler was set at 35 samples per hour. In the manifold for two element determination for the concentration ranges shown in the p.p.m. table, a set of sample-diluent-air tubes feeds to a mixing coil. This feature allowed for changes in the ratio of sample and diluent, thus providing for changes in the concentration range of each element being determined. (Phosphorus can also be determined from this aliquot but it required additional apparatus - an electronic range expander attached to a separate recorder - missing from the autoanalyser in this laboratory). During the warming up period the two pens of the recorder were marked as potassium and calcium, corresponding to the two channels of the dual channel flame photometer, and were set at about 95% transmission with the calibration potentiometer on the flame photometer. Calibration curves for potassium and calcium were linear.

Chlorophyll Determination

All the chlorophylls (a+ b) were extracted in 80% acetone and their amount was determined by spectrophotometry. A comparative study of the chlorophylls under various light treatments was carried out.

Final Procedure for Extraction

1. All the glassware used was cleaned with chromic acid and washed six times with distilled water after preliminary washing with tap water and sterilized at 100°C.
2. A random leaf sample representative of the whole plant and spreading over three plants was taken. Its fresh weight was determined and leaf area measured before starting its disintegration. A duplicate sample was also taken to find the equivalent dry weight for the known fresh weight.
3. Medium sized leaf samples were first of all roughly crushed in a 3in. diameter mortar, then a teaspoonful of fine sterilized sand, with a pinch of MgCO_3 , was added to make the crushing homogenous (carborundum powder can be used instead). The crushed sample was ground thoroughly with a small amount of extractant acetone for three minutes. 2 to 4ml. of anhydrous acetone were added and thoroughly mixed. The extract was filtered through a sintered glass filter (G.4) of 3cm. diameter and the filtrate collected in a calibrated test tube. A water pump was used for filtration. The whole process was repeated with two to three washings of the mortar with 2ml. of 80% acetone to clear the traces. The final extract was made up to 10ml. with 80% acetone in the calibrated tube and closed with parafilm and stored in a refrigerator when not used immediately.

4. Concentrated extract was diluted ten times so that it would have a suitable dilution for use in the Beckman spectrophotometer.

5. The spectrophotometer was put on the "visible" light source and the slit control lever on "Narrow". Spectrophotometer cells were filled with 80% acetone and the reference was set to 100% transmission. The sample voil was then replaced by a solid black block and transmission was set to "zero". The voil filled with leaf extract sample was substituted for the black block and the readings on the scale were taken on various wavelengths for a test sample. Maximum absorption was found to be at $m\mu$ 663 for chlorophyll 'a' and a second peak at $m\mu$ 645 was maxima for chlorophyll 'b'.

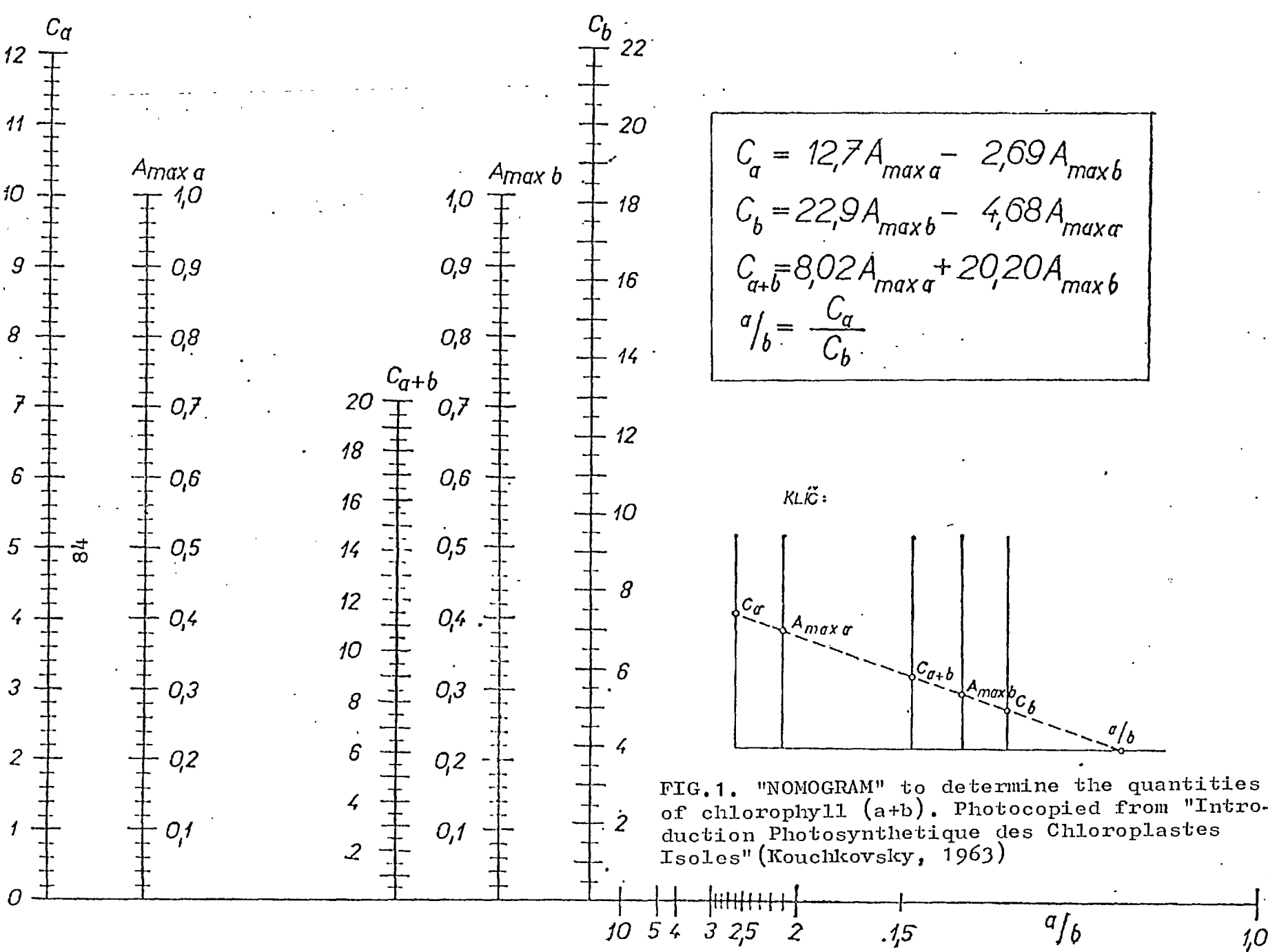
6. Readings taken for chlorophyll a + b for different plant samples were recorded in the tables and the amount of chlorophyll was determined with the help of a 'Nomogram', attached here as follows: (Fig. 1).

Amax a reading at $m\mu$ 663 (chlorophyll 'a')

Amax b reading at $m\mu$ 645 (chlorophyll 'b')

Ca concentration of chlorophyll 'a' in $\mu\text{g/ml}$ of the extract

Cb Concentration of chlorophyll 'b' in $\mu\text{g/ml}$ of the extract



Obr. 9. 8 Spojnicový nomogram pro určení obsahu chlorofylů a, b, jejich součtu (a + b) a poměru a : b z výsledků spektrofotometrického měření extraktů v 80% acetonu při dvou vlnových délkách. Nomogram je založen na

$a + b$.. Total concentration of $a + b$ in $\mu\text{g/ml}$ of the extract.

a/b is the ratio of chlorophyll 'a' to 'b'.

Calculations

1.
$$\frac{\mu\text{g/ml 'a + b' x volume of extract}}{\text{sq.cm.}} = \mu\text{g/cm}^2 \text{ of leaf area}$$
2.
$$\frac{\mu\text{g/ml 'a + b' x volume of extract}}{\text{Fresh weight (mg)}} = \mu\text{g/mg F.W.}$$

$$= \text{mg/g F.W.}$$

From 2. the amount of chlorophyll per gram dry weight can be calculated.

Manometric Techniques

In one experiment the effect of light (i) short photo-period with continuous light, and (ii) with light-break, on the respiration rate of the two plants was studied using Warburg constant volume manometers. Since the whole equipment (Warburg drum type) was purchased new in 1967, all the flasks and corresponding manometers were calibrated first of all before starting the actual work. (Full details of the calibration of the respirometers are described on page 46 in "Manometric Techniques" by Umbreit, Burris and Stauffer (1964).

Synopsis of Procedure to Measure Oxygen

Uptake in Respiration.

1. A random sample of leaf was collected in water and leaf

discs were cut with a cork borer no."3" to have discs of appropriate size. The discs were dried carefully between filter papers and accurately weighed. Duplicate samples were also weighed to determine dry weight.

2. All the glassware - flasks and manometers - were scrupulously washed in chromic acid and sterilized at 100°C.

3. 0.2ml. of 15% KOH was put in the central well of the flask.

4. The vent of the side arm was sealed by turning and adjusting the greased stopper.

5. Leaf discs were placed in the central chamber floating on water.

6. A roll of 2 sq.cm. filter paper was inserted in the central well to increase the carbon dioxide absorbing surface.

7. The flask was moderately greased and attached to the side arm of the manometer with springs.

8. It was placed in the constant temperature tank at 25°C.

9. A thermobarometer, simply a duplication of flask and manometer, with 2ml. of water was also put alongside the other manometers to register changes in atmospheric pressure which were later added or subtracted from the experimental pressure changes in the closed system of the manometer.

10. Flasks were then set to shake at the speed of 120 shakings per minute; ideal for oxygen uptake.

11. After ten minutes the flask was ground in the cone of the manometer by rotating, and the stoppers in the flasks and all connections were made air-tight. The flasks were allowed to equilibrate for ten minutes and then the level of fluid was adjusted in the manometer for the final set up.

Measuring Carbon Dioxide Given Off

During Respiration

The same procedure was followed as for oxygen uptake but steps 3 and 6 were omitted. All the manometers measuring carbon dioxide liberation were placed by the side of those measuring oxygen uptake. Carbon dioxide liberated during respiration is left free inside the closed system and causes pressure changes which can be directly read on the manometers. It is essential that both determinations, oxygen absorption and carbon dioxide liberation, should be made at the same time and under similar conditions. Tissue in both flasks is respiring in exactly the same way, but in one carbon dioxide was absorbed (with alkali) on its release while in the other (without alkali) it was not, so it can be measured.

Although in the second flask tissue is respiring in the presence of carbon dioxide, it generally has little effect on the rate of respiration.

Calculations

Formula for oxygen.

$$XO_2 = hO_2 \times KO_2$$

XO_2 = μ l O_2 taken up per unit of time.

hO_2 = the change in the manometer fluid level after adding or subtracting the change due to atmospheric pressure.

$$KO_2 = \text{flask constant for oxygen} = \frac{Vg \frac{273}{T} + Vf \alpha}{Po}$$

Vg = volume of gas phase in flask and manometer up to level of manometric fluid.

Vf = volume of fluid in vessel

Po = standard pressure which is 10,000 mm. for Kreb's fluid used in manometric studies.

α = solubility in reaction liquid of gas involved.
(For values of α see "Manometric Techniques" by Umbreit)

Calculation of carbon dioxide given off during respiration

In the carbon dioxide flask two processes are going on simultaneously:

1. Oxygen is being absorbed
2. Carbon dioxide is being produced.

(a) Manometric change occurring from O_2 absorption

$$hO_2 = XO_2 / KO_2 \quad \text{since } XO_2 = hO_2 \times KO_2$$

(b) Manometric change occurring from CO_2 production

$$h\text{CO}_2 = X\text{CO}_2/\text{KCO}_2$$

The final observed reading h in the CO_2 flask
(without KOH) would be the resultant of the two, i.e.

$$h = h\text{O}_2 + h\text{CO}_2 = X\text{O}_2/\text{KO}_2 + X\text{CO}_2/\text{KCO}_2$$

hence:

$$X\text{CO}_2 = \left(h - \frac{X\text{O}_2}{\text{KO}_2}\right)\text{KCO}_2$$

$$\text{Respiratory Quotient} = \text{R.Q.} = \frac{\text{CO}_2 \text{ produced}}{\text{O}_2 \text{ consumed}}$$

Growth Analysis

Growth analysis is of great importance in the study of comparative performance of plants (in terms of various vital processes and their visible morphological attributes) under different environmental conditions. The ultimate form of the plant is the result of interaction between its genotype and phenotype. While genotype is fixed phenotype is affected considerably by the synthetic environmental complex. Phenotype is not only modified but may also become adapted to the changed environments. Considerable analysis of these adaptations into their major components is inevitable in relation to the study of comparative biology of two plants.

However, it has been considered that detailed manipulation of observations and too fine an analysis would merely confuse the understanding of actual processes involved. What is important is that the physical attributes of the plants, as effected by the environments, must be clearly distinguished in the study of the comparative performance of the two plants. Although the progress curves of total plant dry weight and leaf area show in simplest terms the performance of plants, in addition ~~there~~ can also be derived from the primary data a

number of relations which may be more significant. These measures of growth can be considered, as already discussed by Evans and Hughes (1961) with some addition by Myerscough and Whitehead II (1967), as falling into two main groups. One group consists essentially of estimates of the morphogenetic condition of the plant at the time of harvest. The other group gives estimates and illustrations of the course of growth processes during the experiment. Most of these have been used to analyse the performance of the plants and some new parameters have been devised to illustrate further details of the growth.

The following is a summary of the growth measures:

Estimates of morphogenetic condition

(a) Relating to the whole plant

- (i) The leaf area ratio i.e. the area of the leaves/
total dry weight of the plant.
- (ii) Root/shoot ratio i.e. the dry weight of root/the
dry weight of the shoot.

(b) Relating to parts of the plant

- (i) Specific leaf area i.e. the leaf area/the dry weight
of the leaves.
- (ii) Leaf/shoot ratio i.e. the dry weight of the leaves/
the dry weight of the shoot
- (iii) Root/leaf area ratio i.e. the dry weight of the

root/the area of the leaves.

- (iv) Root/leaf ratio i.e. the dry weight of the root/
the dry weight of the leaves.

Estimates of the course of growth processes

- (i) Mean relative growth rate, in terms of the total dry weight of the plants.
- (ii) Mean relative rate of increase of leaf area.
- (iii) Mean unit leaf rate (synonymous with net assimilation rate of Gregory (1926)). The choice of the term "mean unit leaf rate" is in accordance with the arguments of Coombe (1960) and Evans and Hughes (1961).
- (iv) The dry weight accumulated during growth "surplus" to that required for the maintenance of the assimilating entity found by Whitehead and Myerscough (1962).

The mean relative growth rate $\bar{R}$ over a time interval is (derived from R - the relative growth rate at any instant) as follows:

$$\bar{R} = \left(\log_e W_2 - \log_e W_1 \right) (t_2 - t_1)^{-1}$$

For full details of derivation see Whitehead and Myerscough (1962).

Similarly, mean relative rate of leaf area increase

($\bar{R}L$) over a time interval is similarly derived as:

$$\bar{R}L = (\log_e L_2 - \log_e L_1) (\tau_2 - \tau_1)$$

These estimates have usually been considered separately by many workers and only rarely used together indirectly in considering growth processes. Whitehead and Myerscough (1962) found that the ratio of mean relative growth rate to mean relative rate of leaf area increase ($\bar{R}/\bar{R}L$) has considerable biological importance and can also be used in the accurate determination of the mean unit leaf rate, i.e. net assimilation rate ($\bar{E}$).

The expression for deriving the value of the index α becomes:

$$\alpha = \frac{\log W_2 - \log W_1}{\log L_2 - \log L_1} = \frac{\log_e W_2 - \log_e W_1}{\log_e L_2 - \log_e L_1} = \frac{\bar{R}}{\bar{R}L}$$

In the author's own words the interpretation of experiments involving the comparison of the performance of plants under different conditions is made easier and more revealing when α values are used instead of the more usual parameters of growth analysis i.e. $\bar{R}$ and $\bar{R}L$. Either of these two parameters, taken separately, can only indicate a change of one of the important processes resulting in ultimate plant form. Comparison, by eye, of the graphs of these two parameters can only indicate probabilities of relationship but no

exact measure of their interdependence at each stage of growth.

The surplus dry weight is calculated with the help of α values for various harvest intervals as shown by the equation (Whitehead and Myerscough, 1962).

$$S = (\alpha - 1)W$$

where S = "surplus" and W = total dry weight.

α , here, instead of being calculated for specific harvest intervals is calculated from an initial harvest to a series of successive harvests i.e. between H_1 and H_2 , H_1 and H_3 , ... H_1 and H_n , and, particularly in comparison with total dry weight, is of great value in assessing the performance of plants under a range of conditions. Even if identical dry weights may be attained in a given period under two sets of conditions through the operation of some compensating mechanism, the more efficient and economic plants show higher values of α .

Estimation of net assimilation rate

It is customary to assume a simple relationship between W and L regardless of how they are increasing with time. The most commonly assumed relationship is a linear one when:

$$\bar{E}(t_2 - t_1) = (\log_e L_2 - \log_e L_1) \frac{W_2 - W_1}{L_2 - L_1} \dots \dots \dots I$$

$\bar{E}(t_2 - t_1) \dots$ (on the recommendation of Evans and Hughes, 1962)

If the dry weight is related to the square of the leaf area (Briggs, unpublished; see Coombe 1960), it has been shown that:

$$\bar{E}(t_2 - t_1) = \frac{2(W_2 - W_1)}{(L_2 + L_1)} \quad \dots \dots \dots (II)$$

Evans and Hughes (1962) also pointed out that this equation is also valid when the leaf area is increasing linearly with time,* Williams (1946) has determined the values of $\bar{E}$ by a ~~geographical~~ graphical method and showed these values to be intermediate between those of the linear and square assumptions of the W to L relationship. However, Coombe (1960) showed that the differences in the estimates of $\bar{E}$ between these two assumptions are small and can be ignored when L_2/L_1 is smaller than 2. He points out that where L_2/L_1 is large it is important to use whichever is the better of the two assumptions in calculating $\bar{E}$.* Whitehead (1962) showed that where L_2/L_1 is large α values ($\bar{R}/\bar{RL}$) become of prime importance and $\bar{E}$ between any two harvests (irrespective of the individual relationship of W and L with time) is represented by the equation:

$$\bar{E} = \frac{W_2 - W_1}{L_2^\alpha - L_1^\alpha} (L_2^{\alpha-1} - L_1^{\alpha-1}) \frac{\alpha}{\alpha-1} \quad \dots \dots (III)$$

* for young stages of certain plants.

* read as Whitehead and Myerscough (1962)

(for full details see Whitehead and Myerscough, 1962).

Sinha (1965, Ph.D. Thesis) showed that in experimental investigations dealing with comparative assessment of different taxa of plants, any formula is as good as the other and the taxon with higher values of $\bar{E}$ maintains it with all the formulae. He calculated $\bar{E}$ for plants grown under three light conditions (i.e. 100%, 70% and 40%) using equation I and II and found that values calculated by (I) are consistently higher and more logical than with (II) and makes the comparison of $\bar{E}$ much easier. Estimations based on Whitehead's formula are more close to that of (I) than (II) and for the purpose of comparison all three formulae gave the same conclusion. However, Whitehead and Myerscough (1966) showed that values of $\bar{E}$ calculated by equation (I) are less than those by (III) and the differences are all less than $\pm 10\%$ of the values by (I) and $9/10$ of the differences are less than $\pm 5\%$.

In view of this, calculations of $\bar{E}$ using equation I have been considered sufficient to compare the relative performance of two plants under various conditions of growth. It is both rapid and accurate considering the amount of work involved.

It is the usual practice to express $\bar{R}$, $\bar{RL}$ and $\bar{E}$ in units of weight and leaf/area/week.

In addition to the above mentioned growth parameters two new parameters have been devised to elucidate some growth processes which could not otherwise be easily appreciated by using the usual known growth parameters. Their significance will be discussed later in the appropriate experiments.

1. Proportionate dry weights of the plant parts

This is simply calculated as percentage weight of each organ (root, stem and leaf) to the total dry weight at any stage of the growth and can be referred to as percentage proportionate weight.

$$= \frac{\text{Wt.of (root, stem or leaf)} \times 100}{\text{Total dry weight of plant}}$$

This device has been found very useful to find out the distribution of assimilates in the plant parts at various stages of growth and under various environmental conditions.

2. Percentage increase in dry weight over the initial dry weight

This can be calculated as follows for any stage of growth:

$$\frac{(\text{Total dry weight} - \text{Initial dry weight}) \times 100}{\text{Initial dry weight}}$$

The assessment of comparative growth on dry weight basis is difficult where the plants start from unequal seed

and seedling weights which affect the subsequent growth and dry weight. By calculating the percentage dry weight, this initial advantage is eliminated and comparison becomes more realistic.

Statistical Analysis

The primary data are presented simply as mean dry weight and mean leaf area per plant. In the germination studies and accessory data such as leaf number, rhizome number and weight, shoot height, etc. only the standard error of mean was determined. Students t-test was employed where only two items were involved. The recommendations of Cochran (1938) have been applied in performing analysis of variance, i.e. the data was first examined for skewness by comparing the treatment means with range encountered with a treatment. If the range increased with the means the data was transformed. It was found convenient to perform analysis of variance on the $\log_e$ transformed values of primary data as these values were also used in various estimates of growth processes. Transformed data is given separately from the actual means in the result tables and where a least significant difference is quoted it refers only to the transformed data and not to the actual means.

P = 0.05 level of significance is generally

considered satisfactory.

Species x treatment interactions were studied and significant differences, given below the table, have been calculated from between the treatment error variance.

- * indicates F values significant at the $P = 0.05$ level
- ** values significant at the $P = 0.01$ level, and
- *** values significant at the $P = 0.001$ level.

V. GERMINATION

The establishment of a seed-plant in a habitat is usually precluded if its seeds cannot germinate there. Furthermore, it will be excluded from a habitat if germination does take place, but is at a time when, or in a position where, the seedling will be eliminated due to pressure from rapidly growing other seedlings or because of its own biology and mode of growth. The successful timing of germination may be in relation to season, or to chance modification of the habitat when seedling establishment can take place. The time the seed is shed, the mobility of the seed due to the presence of some efficient dispersal mechanism, the longevity of seed and the presence of dormancy mechanisms influence the time and position at which germination occurs. In this chapter experimental investigations of some of the conditions influencing germination are described, and assessment of the results of this and other work is attempted in terms of the "Biology of the species".

Method

In the experiments described below, illumination was provided except when germination in "dark" was being investigated. All germination studies were carried out in

constant controlled temperature rooms at 70% relative humidity at the College Field Station at Silwood Park. In all experiments illumination was given by five 80 watt. 5ft. long fluorescent tubes. These were evenly spaced over a width of two feet and held at 18in. above the bench supporting the petri-dishes in which seeds were set to germinate. Within the area, beneath the lights used for germinating the seeds, there was illumination of 465 ± 20 foot candles at bench level.

The seeds in all experiments were sown on the surface of the germination substratum. Germination was scored in terms of the number of seeds with emerged radicles and also of seedlings with expanded cotyledons. However, it was observed that not a single seed whose radicle emerged failed to give rise to seedlings with expanded cotyledons. So germination in all experiments is recorded here only as the number of seedlings with expanded cotyledons. Constant readings for five successive days of the number of germinating seeds were regarded as the limit of germination, shown in the graphs as percentage of the number of seeds sown. In the case of seeds germinated in the dark, germination was scored in the term of seedlings whose hypocotyls were exposed from the seeds.

In every experiment a set number of seeds were sown on each petri-dish and a single petri-dish held seeds of one

species only. In addition, any shrivelled or empty looking seed was discarded so that, as far as possible, only fully developed seeds were sown.

Experiment No.1

(October, 1966)

The effect of temperature on the germination of
Lythrum salicaria and *Epilobium hirsutum* in light and dark.

Method

This experiment compared the germination rates of the two species under set conditions of illumination and darkness at five different temperatures, 10°C., 15°C., 20°C., 25°C. and 30°C. Illumination used was standard 465 $\pm$ 20 foot candles. In 15°C., 20°C. and 25°C. "C. T. Rooms" temperature was very accurately controlled with an average variation from the mean as -0.3 and +0.6. In 10°C. room minimum temperature recorded under the lights during the experiment was 8.6°C. and the maximum 11.4°C. Of the averages taken between the maximum and minimum for a particular period 9.2°C. was the lowest and 10.5°C. the highest recorded. In this temperature room there were only three fluorescent tubes and illumination was 322 $\pm$ 15 F.C. However, Whitehead and Myerscough (1966) did not notice any appreciable difference in percentage germination when illumination was reduced to one half in some species of *Epilobium*. For germination at 30°C. a small

wooden compartment was used in a 27.5°C . unilluminated controlled temperature room. It was fixed with three fluorescent tubes each 2ft.5in.long, a small ventilator and automatic time control switch. Since the compartment was small illumination was within the same range as for other temperatures. During the course of germination daily records of temperature maxima and minima were made using a thermohydrograph under the lights within the area used for germination. 28.7°C . was the lowest and 31.8°C . the highest temperature recorded during the experiment. Of the daily averages taken between the maximum and minimum temperatures 29.7°C . was the lowest and 30.7°C . the highest recorded. Whitehead and Myerscough I (1960) with the help of thermocouples found that in petri-dishes under illuminated conditions, general atmospheric temperature inside the petri-dishes was about 2°C . higher than outside them. According to them, this "glasshouse" effect was not taken into account by Ottenwälder (1914): and it is probable that the temperature difference between his highest and lowest illumination (ranging from 500 to $\frac{1}{400}$ hefner candles) is likely to have been in the range of 2°C ., rather than his stated minimum variation of 0.5°C .

The seeds were set to germinate on filter paper supported underneath by a thick pad of filter sheet which can absorb and retain moisture for longer periods.

Filter paper and pad were saturated with roughly 50ml. of distilled water. Any moisture loss from the dishes during the course of germination was made good with distilled water kept at the same temperature. At each temperature five replicates with 100 seeds per replicate were provided for each species for germination both in light as well as dark. 100 petri-dishes were thoroughly washed, sterilized and fixed with filter paper and pads and no water was added. Seeds of Epilobium, 100 per petri-dish, were put in 50 petri-dishes and the rest of the 50 contained Lythrum seeds, 100 per petri-dish. Five replicates of each species at each temperature were put under the light conditions on 24 October, 1966, starting from 30°C. at 10 a.m. to other temperatures at seven minute intervals, during which water was added to the dishes in each temperature room. Seeds were then arranged in rows of 10 x 10 to facilitate counting. Germination was investigated at each temperature in turn maintaining the same sequence exactly 24 hours after they were put in the treatment. Petri-dishes were marked for their respective replicate number and read in the same sequence in which they were put. In all these different temperatures light was controlled for 16 hours a day.

Petri-dishes sown for "dark" germination were kept in biscuit tins and put in the respective C. T. Rooms at 8 a.m.

on 25 October, when the lights are off under routine conditions. Readings of seed germination were taken at the same time on each day with the help of a magnifying lens under diffused torch light so that light stimulation of germination was reduced to a negligible level. Each dish was taken out of the box for a few seconds to note the germination. The tins were wrapped up in black polythene sheets, so that all illumination was excluded, and were placed beside the illuminated petri-dishes.

Results

Results have been presented graphically. Figs. 2 and 3 show the time course of germination of the two species in light and dark. There is no germination in Lythrum at 10°C. and very little at 15°C. in light. In both Lythrum and Epilobium there is no germination at 10°C. and 15°C. in dark. From the graphs it can be seen that in both species, at the three higher temperatures (20°C., 25°C. and 30°C.) there is an initial surge of germination. In all cases this initial surge continues for approximately ten days and maximum germination in each respective temperature is reached during this period. In Epilobium at 15°C., although final percentage germination is higher than at 25°C. and 30°C., there is no initial surge, it starts late and is slow but regular. It is still slower and irregular at 10°C. In Lythrum, at higher

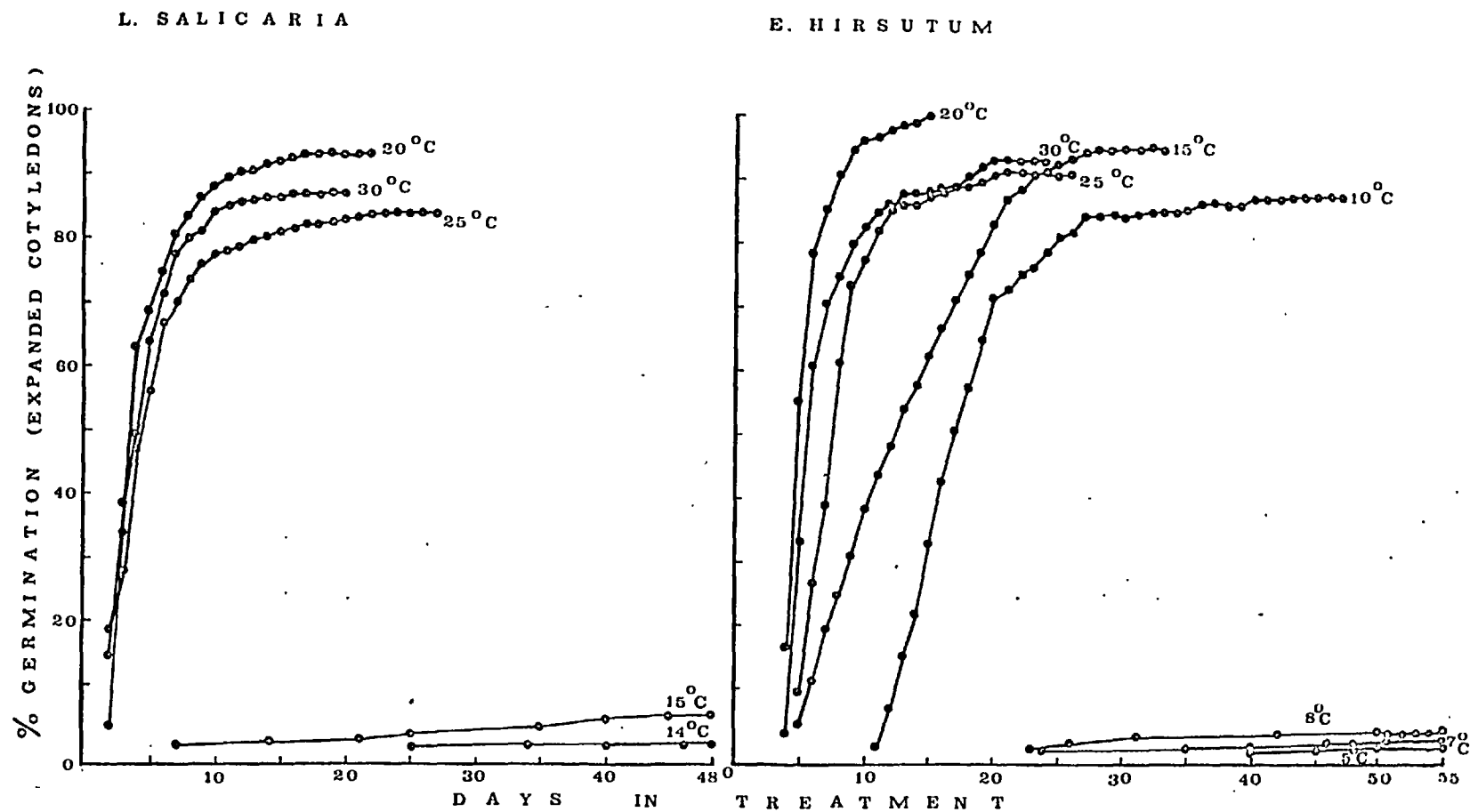
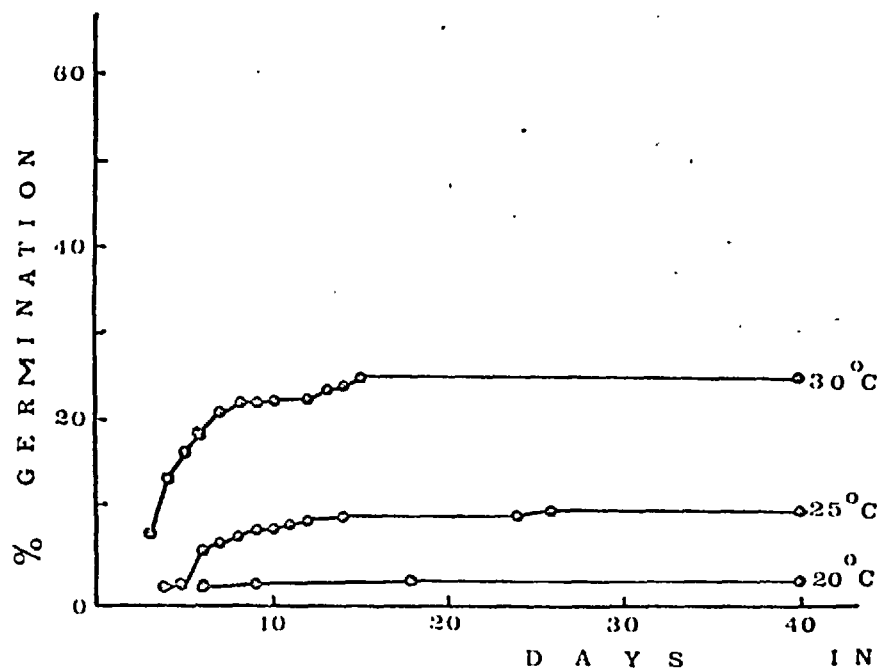


FIG. 2. Effect of differing temperature levels on germination (light).

I. SALICARIA



E. HIRSUTUM

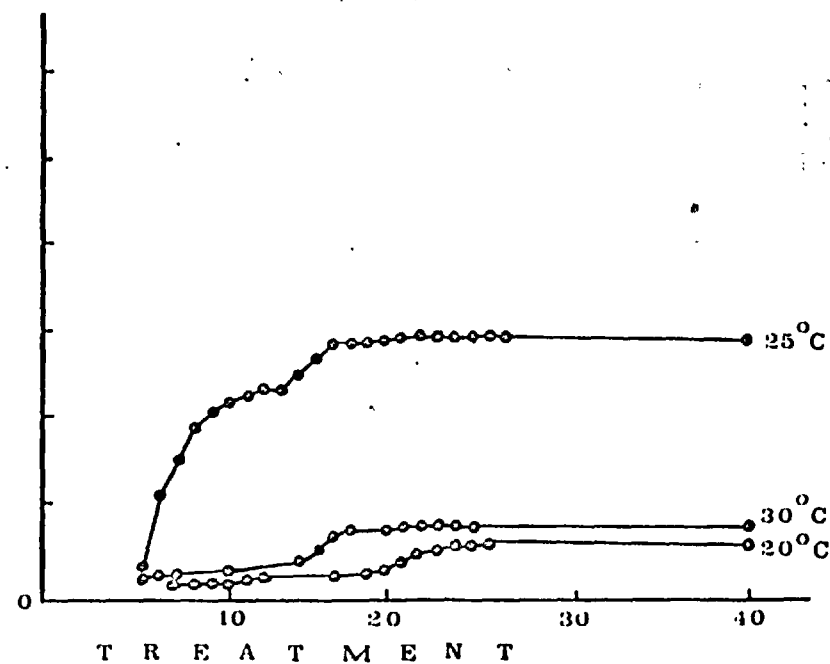


FIG. 3. Effect of differing temperature levels on germination (dark).

temperatures the radicle emerges only 24 hours after starting treatment, the cotyledons start emerging and expanding two to three days later.

The delay in germination can be appreciated from the estimation of "half time" values for the initial surge in germination (Myerscough and Whitehead 1966). These values are calculated from the time course of germination. The time at which half the number of seedlings had germinated are plotted against their respective temperatures (Fig. 4a). It makes patent the delayed progress of the initial surge of germination in both species at decreasing temperature levels. Fig. 4(b) shows that maximum germination in both species is at 20°C. and with the rise in temperature there is a slight decline. In Epilobium there is a gradual fall from the maximal with decrease in temperature to 10°C. In Lythrum there is a reduction of germination to a negligible minimum as the temperature drops from 20°C.

Fig. 4(b) shows percentage germination and rate in both species in "dark" as well. In Lythrum with a rise in temperature there is a rise in percentage germination, but in Epilobium maximum germination is attained in 25°C. above and below which there is a sudden decline. The slow progress of dark germination at various temperatures can be appreciated

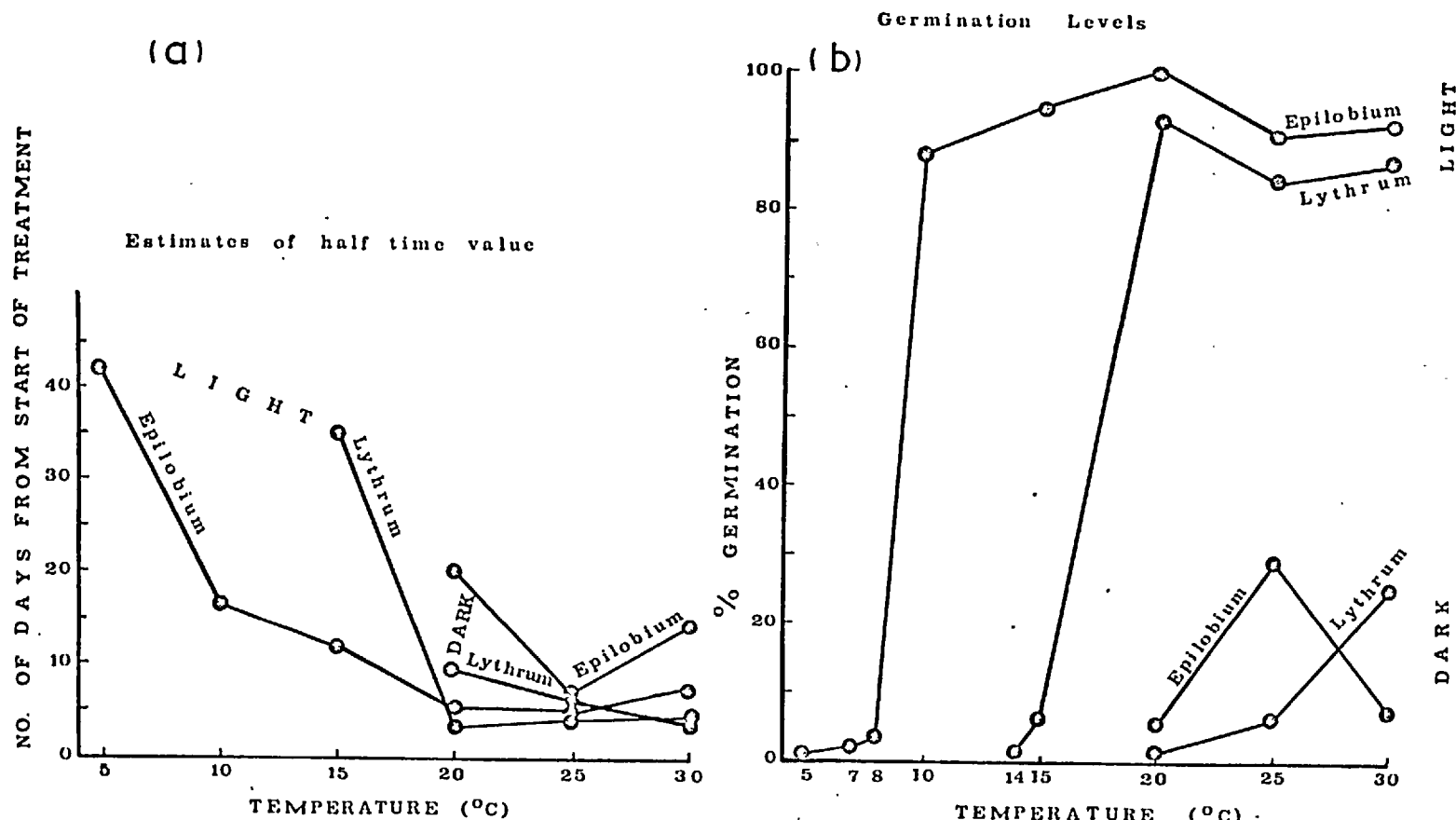


FIG. 4. Effect of differing temperature levels:
 (a) On the time taken to reach half the percentage emergence in light and dark. (Half time values)
 (b) Maximum germination level in light and dark.

by their "half time" values as in Fig. 4(a).

When the petri-dishes were finally removed from their particular temperatures, those whose seeds had not shown any significant germination were placed in 20°C. until their germination reached the maximum level. (It was not the same as in the normal experiment because some of the seeds were grown over by fungus, especially Lythrum). However, it was interesting to note that Lythrum seeds kept under light at 10°C. and 15°C. were quicker to germinate than those in the dark. This raises the possibility that the seeds in "light" were already activated but held in check by the low temperature and also that activation of the seeds by light takes an appreciable time. Seeds removed from "dark" and from other temperatures also reached their maxima in due course of time.

Before discussing the results of this experiment another closely related experiment based on the results of this experiment will be described.

Experiment No. II

Critical temperature for germination in Lythrum salicaria and Epilobium hirsutum.

The results of the previous experiment show that in Epilobium there is gradual reduction in germination when temperature falls from 20°C. but a sudden loss of germinability

in Lythrum. This difference in response may be very significant in nature. For this reason it is important to determine the critical lowest limit of germination in both species.

Method

Epilobium seeds were set to germinate at four low temperatures, 0°C., 3°C., 5°C. and 7°C. Later their germination was also studied in 8°C. in a phytotron while another experiment was in progress. Lythrum seeds were treated only at 12°C. and 14°C. for their critical temperature.

Petri-dishes containing 100 seeds per replicate and 5 replicates per treatment were prepared in the same way as for the previous experiment. Replicates were also set for dark germination in both species at 0°C. and 5°C. to study the response to germination after exposure to low temperature in light and dark. All the required temperatures were not readily available, and cooled incubators were employed depending upon their availability, so all the studies were not carried out at the same time but extended over a period of seven months.

An ordinary 60 watt bulb was installed inside the incubator and temperature was adjusted accordingly. Because of lack of temperature and light control, illumination was continuous 24 hours a day. Humidity was also uncontrolled. Temperature control was not very accurate and had to be

adjusted frequently. Average variation of the mean was $+0.8^{\circ}$ and -1.2°C . Mostly it was adjusted below the required mean so that it could fluctuate between the mean and the lower limit of variation (-1.2°C .), thus making some allowance for the "glasshouse" effect.

Results

There was no germination in dark at any temperature in either species.

In light there was no germination of Lythrum at 12°C . after 60 days in treatment. There was no germination of Epilobium at 0°C . and 3°C . But, in one replicate of Epilobium at 3°C . there was radicle emergence in 5 seeds which may have been caused by chance exposure to high temperature. All other results are also presented in Fig. 2. in the respective species to facilitate the comparison and overall temperature effect in relation to the previous experiment.

In Lythrum there was 1.2% germination in 14°C . Epilobium showed 1.0% germination at 5°C . The seedlings of both species at these temperatures did not look very healthy and shrivelled after some time. There was 2.0% germination at 7°C . and 3.4% at 8°C . in the case of Epilobium. In all these temperatures germination was greatly delayed.

Some Lythrum seeds in all temperatures both in light and dark were severely attacked by fungus under moist

conditions.

A respectable percentage of healthy surviving seeds showed germination with their cotyledons fully expanded when exposed to light at 20°C. Seeds in light were the first to germinate. In Epilobium a lesser number of seeds were overgrown by fungus (possibly because of their hard seed coat) and responded quickly to show full healthy germination at 20°C. in light. Response was better than in Lythrum, in that those kept in dark were quick to germinate. This may be because of their bigger size and resistance of the seedcoat to fungal attack.

Anyway, it is clear that seeds in either species do not lose their viability when kept under unfavourable conditions of low temperature and darkness and respond promptly when exposed to favourable conditions.

Discussion

From the results of these two experiments it is clear that a range of temperature has differential effect on the seed germinability of the two species. A cursory glance at the graphs shows that with Lythrum salicaria germination is an all or none phenomenon. Response is prompt to the stimulus of favourable temperature and is lost abruptly if it falls below the minimum favourable, i.e. 20°C. (favourable = more than 50% germination). Epilobium hirsutum also responds quickly

to favourable high temperatures like Lythrum but there is no loss of perception at slightly lower temperatures, i.e. 10°C. and 15°C. and the response is rather delayed, slow and diffused but stimulating at the same time so that percentage germination is higher in 15°C. than 25 and 30°C., and at 10°C. it reaches almost the same level. The critical lower limit of germination in Lythrum is 14°C. (1.2%) and 5°C. in Epilobium with 1.0% germination.

In dark both species fail to germinate below 20°C. In Lythrum there is an increase in percentage germination with the rise in temperature and a maximum is attained at 30°C. (available temperature). In Epilobium there is a sudden drop after the maximum is attained in 25°C. It can be concluded that both species are partially dependent on light for germination above 20°C. (more so in Epilobium than in Lythrum) and fully dependent below 20°C.

These results are in general agreement with others' work. Kinzel (1908); Lehmann (1911, 1912, 1915); Ottenwalder (1914); Gassner (1915); Neithammer (1927, 1927 a); Myerscough and Whitehead (1966), showed that light stimulated the germination of seeds in various species of Epilobium. Fassbender (1925) studied germination in Epilobium hirsutum and Lythrum salicaria in light and dark.

Lehmann (1911, 1912 and 1915) and Ottenwalder (1914)

reported some germination in dark for E. roseum, E. hirsutum, E. montanum, E. parviflorum and E. adnatum. Myerscough (1962) failed to get any germination in dark for E. roseum and E. montanum. He argued that they had looked, from time to time, at the seeds germinating in dark, implicit in the presentation of their results where they gave time course of germination, implying that brief exposure to light might have activated the seeds. Materials collected from different sources may give different results, as in Chamaenerion angustifolium from Canadian source (Kinzel, 1908 and Kitchen, 1959). Present results in Epilobium hirsutum agree with those of Lehmann and Ottenwalder and it can be positively asserted that Epilobium does show appreciable dark germination at a particular temperature ($25^{\circ}\text{C}.$) and temperatures above and below it have a depressing effect (20 and $30^{\circ}\text{C}.$) although at all three temperatures seeds had been exposed to controlled diffused light for brief intervals to find increments in the germination. Gassner (1915) reported appreciable dark germination in E. hirsutum and E. roseum. Hesse (1924) found 23% germination in dark in E. hirsutum and 6.5% in E. montanum at a temperature of 16 to $20^{\circ}\text{C}.$ Data of Stiles (1950) and Koller (1955) compiled by Mayer and Mayber (1963), (see 'The Germination of Seeds' by Mayer and Mayber, page 196) also shows that in dark in E. hirsutum germination is significantly

promoted at high and alternating temperatures, while low temperature does not help to promote germination. Fassbender (1925) showed similar results in E. hirsutum and L. salicaria. He reported, in both of these species, in a daily regime of alternating temperature from 20°C. to 30°C. in dark a much higher germination percentage than at these constant temperatures.

Isikawa (1955) working on Japanese material discovered photoperiodic response in the light-stimulated seeds of Epilobium, in that germination is effected not only by short illumination, but also by alternations between dark and light, i.e. by photoperiod, and that this response is of short photoperiodic nature. Thus in light-requiring seeds, which germinate under illumination of from 2 to 21 hours, germination is promoted by interruption of the light period by darkness.

Some chemicals are known to stimulate dark germination in Epilobium. Hesse (1924) showed KNO_3 to promote dark germination in E. hirsutum and E. montanum along with a number of seeds of other species as Veronica, Hypericum and Eragrostis. E. hirsutum showed only 23% germination in dark in water at 16 to 20°C., but treatment with KNO_3 increased it to 40% while the increase in E. montanum was from 5.5% to 89%. Furthermore, stimulation is dependent on the

concentration of KNO_3 and higher concentrations caused decline in E. montanum. Fassbender (1925), however, could not find any acid promotion of dark germination to any appreciable degree under constant temperatures in E. hirsutum or L. salicaria.

The main conclusion is that with Epilobium germination in the dark only takes place at approximately 25°C . to any great extent, above and below this temperature some sporadic germination takes place.

If, however, we look at the germination in light, we find that there are high rates of germination at all temperatures from 10 to 30°C . This would indicate that there is a light requirement for germination at all temperatures except at approximately 25°C . In Lythrum, as the temperature rises less is light a prerequisite for germination in dark. Markedly lower critical germination temperature and significantly higher percentage germination at 10 and 15°C ., where Lythrum completely fails, may give Epilobium an advantage in nature and make it more versatile under particular environmental conditions.

This successful tolerance of a wide temperature range in Epilobium hirsutum and high temperature requirements of Lythrum salicaria may have far reaching ecological significance in the distribution and establishment of the two

species under different environmental conditions. These possibilities will be discussed later.

Experiment No. III

(April, 1967)

Germinability of *Epilobium hirsutum* and
Lythrum salicaria in soil and sand.

An experiment was conducted to find the effect of soil on germination and the comparative germinability of the two species in different media. (This experiment was also necessary to find a suitable medium to raise seedlings of both species on mass scale for use in field and laboratory experiments).

Dark brown clayey peat from the bank of a stream in Silwood Park was collected from near a mixed clump of *Chamaenerion angustifolium*, *Rubus fruticosus* and *Urtica dioica*. pH measured in the laboratory (Beckman Electric pH meter) was 5.8. Soil was dried at 30°C., homogenised and roughly sieved. Ten clay pots were filled with the soil and another ten with sterilized sand. Both types of pots were saturated with water and clay saucers, filled with water, were put under the pots to maintain a constant water supply.

100 seeds per pot of either species were sown in half the number of pots of either species, so there were five replicates of each species in sand as well as soil and were

kept in a 20°C. constant control temperature room. After three weeks, when germination was more or less complete, they were moved to a glasshouse where temperature fluctuated between 22 and 25°C. Seeds were dispersed uniformly on the surface of sand or soil. All the pots were covered with thin transparent polythene bags of appropriate size, held in position around the rim of the pots by rubber bands. This was to keep the atmosphere over the soil/sand surface more humid as Myerscough and Whitehead (1966) reported the effect of "cloche" conditions on germination, in that if the soil surface is left uncovered there is delay in germination and also fewer seeds germinate. During the course of the experiment soil and sand surfaces were not allowed to dry out and periodic watering was carried out, with a medicinal syringe, so that the seeds and soil surface were not disturbed.

Results

These are presented graphically in Fig. 5. Results of germination on filter paper are also plotted for comparison.

Both species show delayed germination in soil. In Epilobium sand germination does not very much fall short of that on the filter paper but soil germination is $\frac{1}{3}$ of that of sand. In Lythrum germination on sand starts late and a lesser number of seeds germinate compared to those on filter paper. But, germination in soil is much better than in Epilobium and

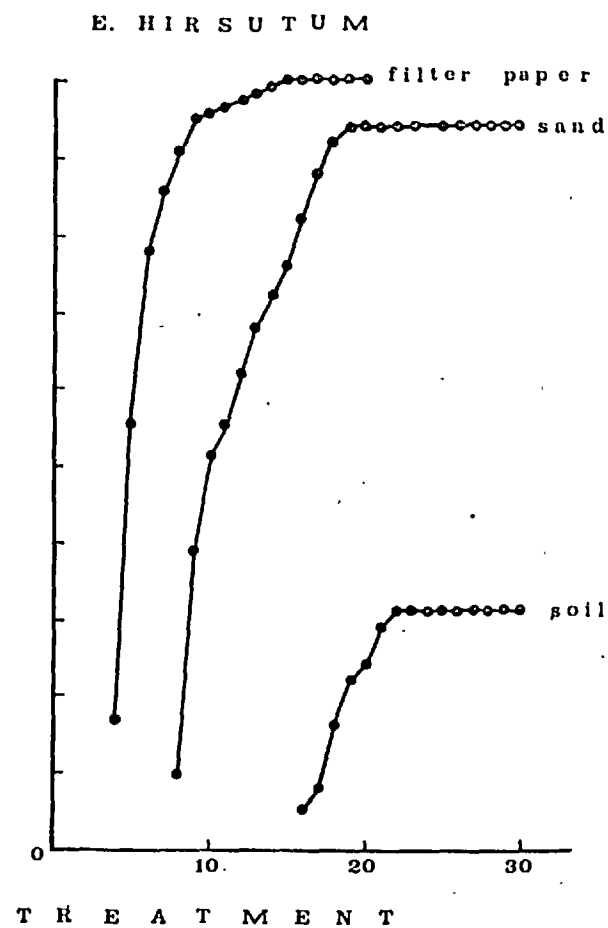
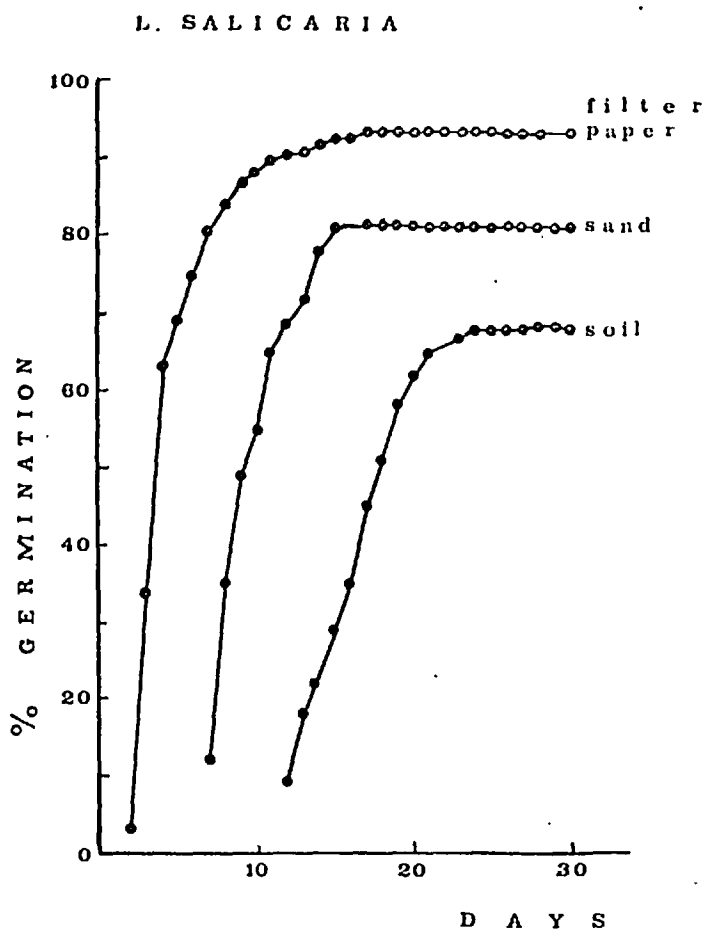


FIG. 5. Effect of different media on the germinability in light at 20°C.

is $\frac{4}{5}$ of the sand germination.

So, of the two species Epilobium is more sensitive to unfavourable substratum than Lythrum. This reduction in germination in soil in Epilobium may be due to the acidic nature and lower nutrient status.

When the pots were moved into the greenhouse seedlings of Juncus effusus started developing very fast in pots with soil. Growth in Epilobium was very slow and the seedlings started turning red after forming two pairs of leaves. Soon Juncus seedlings filled the whole pot and completely suppressed the growth of Epilobium seedlings, so that not a single seedling developed into a young plant. Lythrum seedlings developed into young plants in all the pots in a few weeks. Growth of Juncus was not very thick and most of the Lythrum plants were taller than the Juncus plants. Both Lythrum and Epilobium seedlings in sand were fed on standard nutrient solution and grew into normal plants, though very unequal because of their confinement in a small area.

One replicate in each treatment, in each species, was removed for the study of the root system after germination was completed and Epilobium seedling had started to turn red. In soil, Lythrum roots were long, well developed and penetrated very deep into the soil, while Epilobium roots were not only small and poorly developed but were growing over the

soil surface rather than deep into the soil. In sand, the root system of both species was very well developed.

Lily Batten (1918) also established that Epilobium seedlings grown in clay have less developed root systems compared to those grown in sand with more fully developed root systems.

The nature of the soil is known to effect the germination of many seeds. Some seeds respond to the calcium contents of the soil in their germination behaviour (Mayber and Mayer, 1963), Faheem (personal communication, 1969) found Silwood soil, near the lake, deficient in calcium in his studies on Filipendula ulmaria. The prevalence of Epilobium in highly alkaline (pH 7.3 at places), rich, Wheatfen Broads of Norfolk and exclusion from relatively acidic marshes, suggests that its germinability is effected by calcium content, pH values and nutrient status of the soil. Haslam's experiments (1965) also show that the nature and fertility of the soil effects the germination of Epilobium. In Breck Fens she found higher percentage germination in the Valley Fen, with rich alkaline soil, than in the Headwater Fen, with relatively poor and slightly acidic soil. Seedlings in the Valley Fen peat survived and established themselves as young plants, but most of the Headwater seedlings turned red-brown and died soon after their germination; (in fact they did not develop more than one pair of fully developed true leaves). In further

experiments addition of calcium and nitrogen promoted the rate and frequency of germination.

Lythrum seems to be indifferent to the calcium content of the soil and its presence in all types of marshes and fens shows its tolerance to a wide range of soils, both as regards their nutrient status and pH relations.

Experiment No. IV

The germinability of seeds of *Epilobium hirsutum* and *Lythrum salicaria* after a period of cold, dry storage.

Seeds of both species used throughout the course of the studies were collected in September, 1966 and stored in a refrigerator at 3 to 4°C. They always showed abundant germination when seedlings were raised for various experiments. On 23 September, 1969, three years after they were collected, the effect of dry storage was studied on the various aspects of their germinability.

Replicates were prepared in the same way as in previous experiments and set to germinate at 20°C.

Results

The results are shown in Fig. 6. In both species germination is slightly delayed but the initial surge in germination is still there. In Epilobium, after three years of storage, seeds almost reached the same level of germination as when they were first collected. In Lythrum there

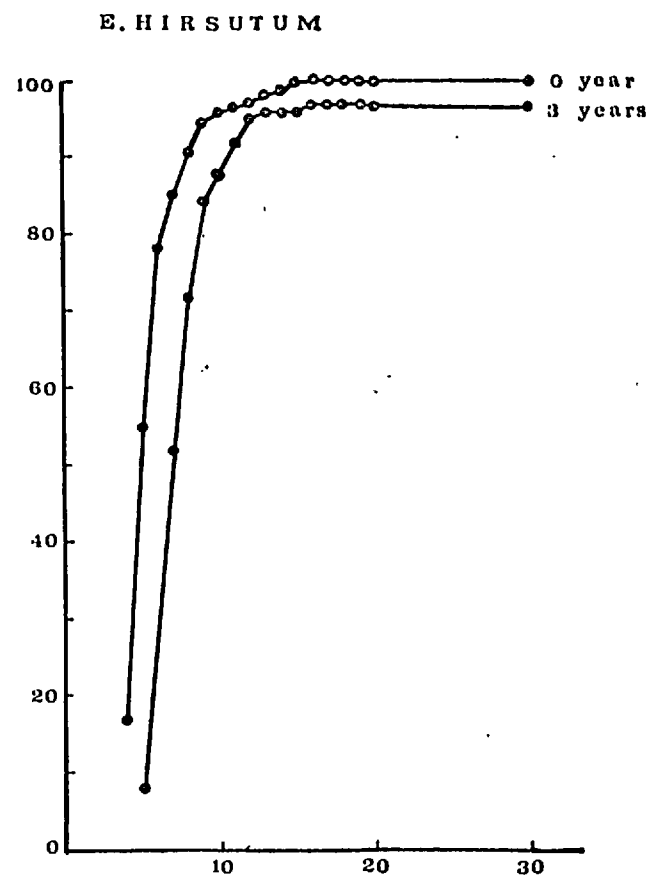
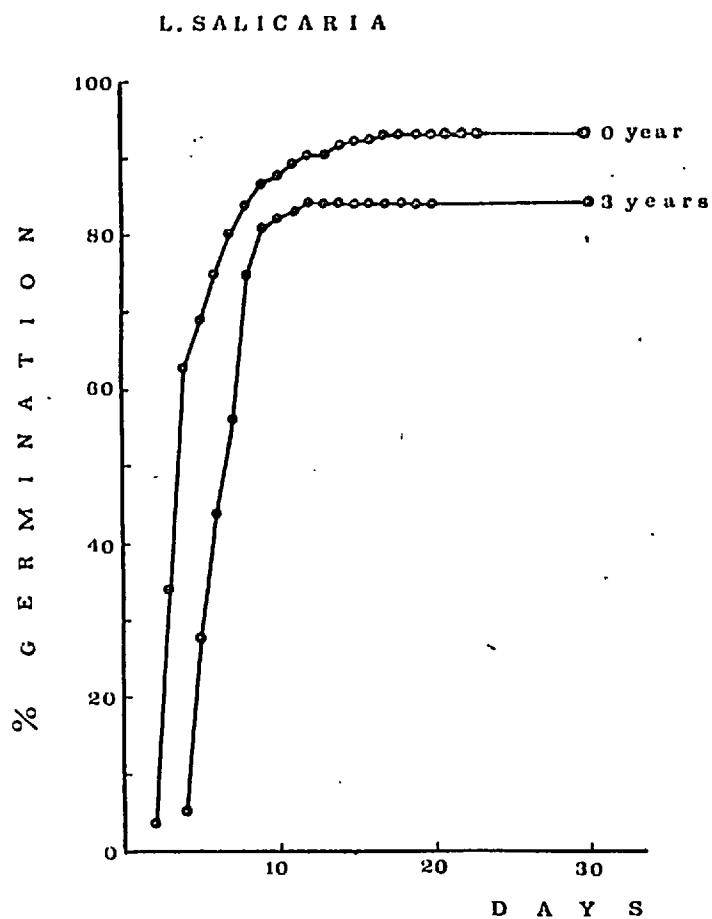


FIG. 6. Effect of cold dry storage on germinability in light at 20°C.

was some reduction in the rate and percentage of germination. It is possible that, because of the light weight and thin seed coat, some seeds might have undergone desiccation and shrivelling after such long storage. But the drop is not such as to warrant any doubts on the germinability of seeds after storage. Epilobium seeds are relatively heavier, with hard seed coats, and thus resistant to any shrivelling and desiccation.

It can safely be concluded that in both species, seeds did not show any appreciable decrease in performance after three years of storage and that viability may be in terms of years.

Adaptive Mechanisms in Germination

Results of the experiments show that germination in both species is differentially effected by the external environmental factors any of which can determine whether a given seed will germinate in a certain place or not. These laboratory observations, when related to the behaviour of the seeds in their natural habitats, indicate the presence of some adaptive mechanisms regulating their germination. These adaptations bestow definite advantages and may have special value in the survival of the species.

An attempt is made here to correlate the laboratory

findings with the habitat factors in an effort to find any such adaptations.

Probably the most crucial factor in determining successful germination in soil is a suitable combination of temperature and moisture. Also important is the occurrence of germination at a time which will favour the subsequent growth and survival of the seedlings, depending upon their biological requirements and inbuilt growth habits.

High temperature requirements in Lythrum salicaria is an adaptation to summer germination. In the absence of any growth in winter (no over-wintering rosettes), immediate germination after seeds have been shed from the plants would lead to the killing of the seedlings in the following cold winter. But in Epilobium hirsutum late germination is followed by establishment of winter "plates", commonly found in nature, and low temperature requirements for germination is an adaptation to this form of growth. The postponement of germination gives Lythrum a better chance for survival in the summer.

Restriction of Epilobium to wet places shows that seeds are adapted to germinate in an excess of moisture and the presence of hairs (hygroscopic in nature) increase their chances of being dispersed to wet places. Waterlogging does not effect germination of seeds in Epilobium species

(Myerscough and Whitehead 1966).

L. Batten (1918) found that Epilobium shows better germination and seedling establishment when completely submerged in moving, muddy water, but seedlings soon die off under water stringent conditions. Even in stagnant water they can germinate, but the seedlings are weakly. This enhanced rate of effective germination may be due to their contact with moist soil over their whole surface, allowing them to take up water faster than the surface sown seeds. It is probable that continuous soaking increases the permeability of the testa and the occurrence of Epilobium in fens, drying pools and puddles, suggests that this requirement is an adaptation to this specific habitat. Besides being adapted to wet germination, burial of the seeds in mud for a certain period of time and then exposure to air promotes germination, (Mayer and Mayber, 1963). Epilobium seedlings appeared very quickly on soil disturbances in Breck Fens (Haslam, 1965). Mall (1954) suggested that such seeds have an additional requirement of low temperature for a period of time for their germination.

High percentage germination in Epilobium at lower temperatures, within limits (10 and 15°C.), shows that a lower temperature in the presence of light has a stimulating effect on germination. Data of Stiles (1950) and Keller (1955), on

Epilobium compiled by Mayer and Mayber (1963), also suggests the presence of an interaction of light and temperature, in that seeds are sensitive to light at low temperatures but not at others. They found significant promotion in germination by the combination of low temperatures and light but the combination of high or alternating temperatures and light did not promote germination. In these experiments the highest percentage germination at 20 and 15°C. and at 10°C., almost as much as in 25 and 30°C., indicates the presence of this interaction of light and low temperature. Mayer and Mayber (1963) asserted that the ecological significance, if any, of these complex interactions cannot be easily understood. Its presence in Epilobium and absence in Lythrum can be attributed as an adaptation to their pattern of growth and distribution.

Dependence on light and high temperatures prevent the germination of Lythrum for most parts of the year, in Britain, except for a short while in early summer. Promotion of effective germination in Epilobium, as a result of the stimulatory effect of the interaction of low temperature and light, enables it to germinate for most of the year (except in some snowy mid-winter months) in the English climate. This adaptive mechanism in germination is the necessary accompaniment to its existence as dwarf "plates" during the winter, and this growth form determines how well a seedling will

subsequently be able to establish itself. So the regulatory effects of the adaptive mechanisms in germination are directly related to the biology of the species and its growth habit.

In Lythrum maturity is reached in three months in nature. The rate of growth is much higher than in Epilobium and there are no winter rosettes. Absence of any adaptive interaction can be attributed to the lack of necessity, as shown by the biology of the species. On the contrary a different type of adaptation can be seen here. It is dominantly distributed in the southern and central European countries where there is a period of drought in hot summer months and climates are at two extremes (Turrill, 1929); here Epilobium is less abundant. Survival of Lythrum is determined by the time of its seed germination. This occurs in early spring when temperatures rise suddenly accompanied by maximum rainfall which ensures seedling growth and establishment. So high temperature requirements prevent Lythrum from exposing its seedlings to unfavourable low temperatures of the winter.

Promotion of germination and continued steady growth at low temperatures may partly explain the prevalence of Epilobium in colder and mountainous regions of the world. In the light of these arguments it is easy to understand the dominance of Epilobium hirsutum in the British type of

climate and that of Lythrum salicaria in the continental type of climate.

Germination in Relation to the
Biology of the Species

Summarising the conclusions of the work described in this chapter, it is apparent that Lythrum salicaria is tolerant of soils of poor nutrient status and acidic nature while Epilobium hirsutum prefers rich and alkaline soils. In Epilobium germination and subsequent seedling establishment takes place in mud. In both species there is an absolute light requirement for germination at low temperatures. Combination of low temperature and light promotes germination in Epilobium. Critical lower temperature limit for Epilobium is 5°C. and 14°C. for Lythrum. In the dark germination increases with a rise in temperature in Lythrum, but there is no such relationship in Epilobium. Seeds of both species remain viable for many years.

From the time of its seed dispersal, with the temperature requirements for its germination, seedling establishment in Epilobium can take place for most parts of the year except in some severe winter months. Since both short-day rosettes and normal long-day forms exist in nature, so both autumn and spring germinations are equally successful, but

the latter seems a preferable possibility. Seeds which get buried deep in the soil can remain dormant for many years and the chance disturbance of the soil would allow the germination and establishment of the seedlings. Similarly, long term viability of the seed does not minimise the chances of survival if it fails to find suitable environments for germination. Because of strongly developed dormancy mechanisms under unfavourable conditions and the retention of viability for many years, the species would seem to possess a great potential of dispersal in the form of dormant seeds. Thus, it would seem to possess a high capacity for exploiting chance modification of the habitats by the establishment of a large number of seedlings for a greater part of the year in the British climate.

Germination and establishment of Lythrum is restricted to late spring or early summer in Britain. The absence of short-day forms precludes its establishment in autumn. Seeds buried deep after dispersal would tend to germinate in darkness with the increase in temperature during the summer. Like Epilobium, it also has a large potential for exploiting chance disturbance of the habitat, but only for a short time (late spring or early summer).

There is greater tolerance to wider climatic and habitat conditions in Lythrum salicaria compared to the

confinement of Epilobium hirsutum to narrow ecological niches. However, in both species long term viability of seeds and spread of germination over a period of time has great survival value.

VI. THE EFFECT OF LIGHT ON GROWTH

The species under investigation, as seen from their distribution and overall performance in natural habitats, behave differently in respect of their general response to edaphic factors, seasonal variations and available visible radiation. Occurrence of Lythrum salicaria in open and closed carrs, reported by Pearsall (1918), and the absence of Epilobium hirsutum from the shady conditions indicate differential tolerance of the two species to light, which may be an important factor controlling their localized ecological distribution in the same habitat.

In Chapter III lack of sufficient illumination for adequate growth was put forward as a probable reason which might prevent seedling establishment in many, otherwise, suitable situations.

In Chapter II seasonal variations in the form of the shoot of Epilobium, depending upon the time of its seedling establishment, was mentioned. The possibility that this is controlled by day length was investigated together with the effect of day length on the shoot form of the seedlings of Lythrum, although any day length effect in this case is likely to have little meaning in terms of the biology of the species

in Britain as the time of its seed germination and seedling establishment is limited to early summer because of the dependence on high temperature (Chapter V). Its short day form, however, becomes of great importance in countries with warm winters such as the south Adriatic coast.

Light is known to influence the whole course of development of plants, exerting a profound effect upon the characteristic form and structure. This action is brought about by changes in the quality, direction, intensity and duration of the light. Both the quality and direction of light may have some localised influence on plant growth but in this particular case have little ecological significance in nature.

Changes in light intensity bring about changes in plant growth; this response varies from species to species so that the adaptative tolerances to light intensity may be important in the distribution of species in nature. The duration of light, i.e. day length, exerts profound effects on the rate of development, flowering, fruiting and on morphology and anatomy and therefore may greatly affect plant distribution.

In this present study of the "Comparative Biology" of these two species, light intensity and light duration appear to be variables of great ecological importance. The

effects of these two aspects of light have been investigated in detail to find out their bearing on the growth and distribution of these species.

Experiment No. V

The effect of light intensity on the growth and morphology of *Lythrum salicaria* and *Epilobium hirsutum*.

In an attempt to study these species in terms of growth and morphogenesis, investigations were made of their performance under varying degrees of artificial shading. It is possible to establish exact quantitative relationships under rigorously controlled conditions. Light intensity has a marked regulatory effect on growth in so far as it controls stem elongation, branching, leaf expansion and leaf shape, as shown by Burkholder as early as 1936. Light relations of terrestrial plant communities have been reviewed by Anderson (1964). Blackman and Rutter (1946 to 1950) emphasized the ecological importance of the logarithmic relationship between net assimilation rate and light intensity, and adaptations in vegetative growth by alterations in the light level. Shade tolerance and avoidance has been studied in many flowering plants by Grime (1966). Blackman and Rutter (1946 to 1950), in a series of papers emphasized the role of light intensity

and its interaction with mineral nutrient supply as a factor controlling the growth and distribution of Scilla nonscripta.

Whitehead (1956), by co-ordinating field and laboratory studies, first of all, showed that the growth form and some leaf characters are related to the light intensity. Differences in the growth form between plants of Cerastium atrovirens from different habitats are so striking that some taxonomists, (G. C. Druce, 1920) have ranked them as subspecies. Whitehead, by growing the seeds of different forms from different sources, under uniform conditions, found that irrespective of parent form the gross morphology and growth form of all plants approximated to a single type. He further asserted that variation in physiogomy arises from phenotypic flexibility rather than from genetic difference; that this variation has survival value in nature and at least in some extreme habitats, growth form and habitat conditions are correlated (Whitehead, 1962).

In later studies (Whitehead; The New Phytologist, 61, 59) he showed that plants possess a "compensating mechanism" whereby advantageous modifications of the phenotype are produced in response to environmental change.

Evans and Hughes (1961) emphasised that ecology and morphogenesis of some woodland plants (Impatiens parviflora) can best be understood by combining the results of laboratory

and field studies. They found that several aspects of light regime prove to have important influences on growth. The unit leaf rate is practically proportional to mean total daily radiation up to $100\text{cal./cm}^2/\text{day}$ and almost independent above $300\text{cal./cm}^2/\text{day}$, in which region it is, however, effected by day length. Specific leaf area has a marked ontogenetic drift and is much affected by mean total daily radiation. Leaf weight ratio is practically independent of mean daily total radiation but is slightly affected by day length.

The present work, however, is more concerned with a comparison of performance in relation to light intensity, rather than detailed investigation of general response of plants to light. In this context, studies of Myerscough and Whitehead (I 1966 and II 1967) are of great importance in the demonstration of the comparative experimental studies as a key to the understanding of the ecology, establishment and distribution of the closely related species of flowering plants. In the course of investigations involving comparative growth of several species over a range of environmental conditions, they found that all species do not react exactly alike, some species are more plastic than others and show efficient functioning of compensating adaptative changes, like increase in leaf area in response to decrease in light

intensity (Chamaenerion angustifolium). Adaptive compensating mechanisms and the ratio of relative growth rate increase to the relative increase in leaf area (α value as called by the authors) are of special interest in the comparative study of the morphogenetic condition of the plants to assess the degree of response to the various levels of light and the determination of the dry weight accrued, which is surplus to that required in the maintenance of growth of the plants merely as assimilating entities and which is, therefore, available for the formation of organs of reproduction and vegetative spread.

Methods and Experimental Details

Growth of the seedlings of Epilobium and Lythrum was investigated in the glasshouse at three levels of daylight. Two levels of less than full daylight were obtained in tents of various thicknesses of terylene netting, two layers of terylene for medium shade and four layers for deep shade; the terylene was supported by wooden frames each covering an area 8ft.x 4ft.x 5ft. The area of full daylight was selected in such a way as to avoid any shade effect from the terylene tents or any other experimental equipment in the greenhouse. The natural illumination was supplemented by artificial lights (400 watt Philips bulbs were used) to

increase the duration of day length to 16 hours and to increase the general level of illumination, as the weather for most of the period over which the experiment was run remained cloudy and natural illumination was very low.

The relative levels of daylight were obtained by adjusting the height of the bulbs as required. The intensity of light in each tent was measured in the first week of the start of the experiment by an "EEL" Lightmaster Photometer". Readings were taken on clear sunny days and uniformly cloudy days. It was found that daylight levels in the three sites were fairly constant every day within the limits, except in exceptionally bright sunshine. But these bright intervals were of very short duration. Light readings in the afternoon of a normal day are as given in Table I.

TABLE I. Relative Levels of Light Intensity

Full light (No terylene)	Two layers of terylene	Four layers of terylene
2020 $\pm$ 45 F.C.	1400 $\pm$ 31 F.C.	780 $\pm$ 18 F.C.

The intensity of light inside each tent, as calculated in terms of percentage of light in the open tent, was found to be 70% and 40% and for the purpose of subsequent

description the three levels will be referred to as full or 100% daylight, 70% daylight and 40% daylight.

However, keeping in mind the limitations of the greenhouse conditions and the variations, there is no intention of attempting to interpret results of this experiment as directly related to similar levels of relative daylight in natural situations, for, in nature, the instantaneous values of relative daylight in shady conditions are constantly changing. Nor is there any attempt to relate the results to any integrated value of relative day length in natural situations, as the rate of the photosynthetic process is not only related to an integrated level in a varying light regime, but is also very much related to the magnitude and frequency of flashes of high illumination. Rather, the intention is to compare the general performance, and find out adaptations, if any, in the growth of the two species in conditions of shade, and thence to assess the relative likelihood of seedling establishment and subsequent growth in natural shade conditions, in terms of the general biology of the species.

The seedlings used in the experiment were raised in sand culture in wooden trays. Seeds were set to germinate on 17 February, 1967. Seedlings were transplanted into the pots in the first week of March when the cotyledons were fully expanded and the first pairs of leaves were being initiated.

The surface of the bench, in each treatment, was covered with black polythene and a $1\frac{1}{2}$ in. thick layer of sand was spread on it, thoroughly saturated with water to maintain adequate moisture in the pots. Seedlings were selected for uniformity of size. 600 pots were prepared so that there were 100 pots of each species for each treatment. Small pots of 3in. size were used first and as the plants grew bigger after a few harvests they were transferred into 5in. pots as there was more space available, and later, towards fruit formation, into 7in. pots. After three weeks of growth in the pots, the plants were fed on standard Long Ashton nutrient solution on alternate days. Later, during the course of the experiment when the shade plants grew very tall in the two lower light intensities, they were transferred into new 7ft. high tents with the same light intensities.

Temperature was uncontrolled although the greenhouse was heated. At the start of the experiment it fluctuated between 18 and 22°C. and later between 25 and 28°C. towards the end of the experiment. The atmosphere inside the tents was more humid than in the full light treatment.

The experiment was laid out as a simple randomized block with the two species indiscriminately mixed in each treatment. The plants were spaced so as to avoid mutual shading. During the course of the experiment their positions

within each treatment were changed, at random, several times.

Fifteen plants, selected at random per species per treatment were harvested in each of the first five harvests, and in the last two harvests only five plants in each because of the labour involved.* Plants were harvested in the same order as they were put in the treatment. Roots were washed carefully so that the root loss was minimum. At each harvest the developmental stage and the general morphological condition of the plants were noted.

Roots were washed with distilled water. Sessile leaves were separated from the main stem and branches of each replicate. Leaf area was determined by means of an "EEL" leaf area meter. Root, stem and leaves of each replicate were enclosed in appropriate sized brown envelopes, properly labelled for the organ, replicate number, species and harvest number, etc, and put into a ventilated oven to dry out at 80°C for 48 hours. These packages of dried material were cooled and stored in desiccators and weighed on a Stanton balance. The primary data were recorded in the form of dry weights of roots, stems and leaves together with leaf area. Various estimates of growth and growth analyses were calculated from this primary data.

After about four weeks of growth there was a mild attack of aphids on plants of both species. External

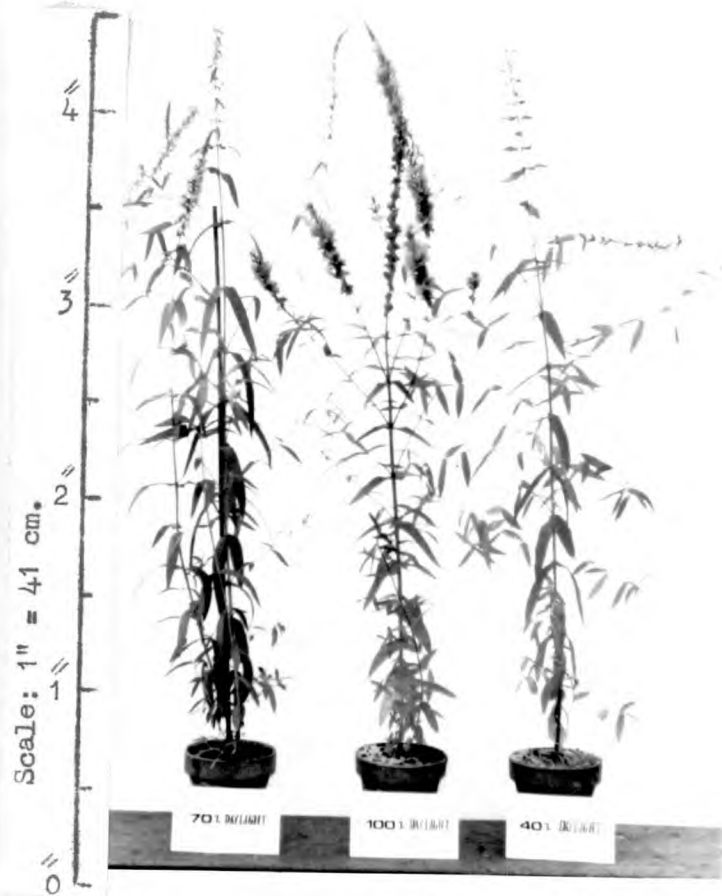
* so, in addition to the initial harvest at the time of transplantation a series of 7 successive harvests were made at fortnightly intervals for growth analysis, and an 8th harvest was taken 5 weeks later to count the number of fruits etc.

application of Melathonian powder was very effective in getting rid of them. "Shell Vapona strips" were hung, henceforth, on each tent to eradicate the aphids completely.

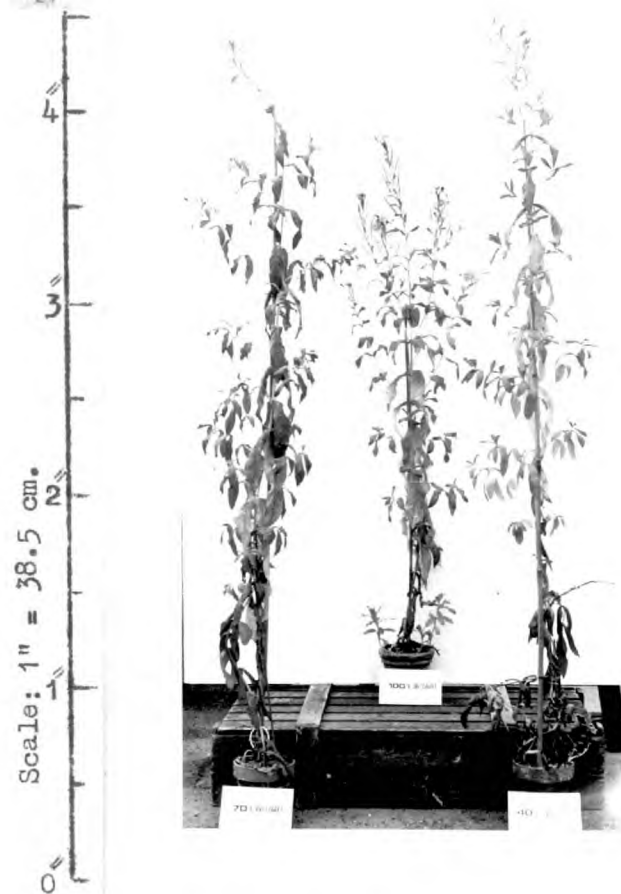
Samples for chlorophyll extraction were collected during the interval between harvest 5 and 6 when the plants were fully mature and flowering. A random sample, representative of the leaves of 5 different plants, was then taken for each species and each light intensity. Each sample contained from $\frac{1}{2}$ to $\frac{1}{4}$ of the leaf from the alternating pairs of leaves. Five replicate samples were collected in water and washed twice in distilled water and dried in filter paper before use. Their leaf areas and fresh weights were determined. Duplicate samples were also collected to find out equivalent dry weights.

Observations

The appearance of plants prior to their final harvest are shown in Plate 4. On the whole, the development of the plants of both species was greatly slowed down at 40% daylight level but still it was comparable to those at other daylight levels, and in all cases the stem bore organs other than leaves, i.e. flowers and fruits. In the beginning vegetative growth was vigorous in all the light intensities, but after the 4th harvest the first two pairs of leaves in



Lythrum salicaria



Epilobium hirsutum

PLATE 4 Plants grown under a range of daylight levels, i.e. 40%, 70% and 100% daylights.
(Photographed after 105 days in the treatments at the time of Harvest VII).

Epilobium began to die off, usually being broken off at their base by the developing rhizome buds.

In Epilobium at harvest 3 the first rhizome initials were visible and they started growing rapidly after that. Initials were many and strong in full daylight and their number and size greatly reduced in 40% daylight. A strong system of adventitious, sharply tapering, contractile roots associated with rhizome development was obvious at harvest 3. It was most strongly developed in full daylight and least in the 40% daylight plants. Rhizomes produced from the stem above the soil level were greenish and slightly woody, bore rudimentary leaves on the nodes, pulled by strongly contractile roots towards their apex into the sand and peat mixture where they grew underground to the length of several centimetres. Rudimentary leaves on the portion of the rhizome exposed to air grew into small green leaves. On the other hand, rhizomes arising from the lower stem surface which remained buried in the soil from the very beginning, were soft and hyaline with rudimentary scale leaves and sparsely developed root system. Both types of rhizomes were repeatedly branched.

In Table 2 are recorded the number of rhizomes in Epilobium at various harvests.

TABLE 2.

Harvest	Levels of Daylight		
	100%	70%	40%
	Mean no. of rhizomes developed		
3	3.6 ($\pm$ 0.40)	1.8 ($\pm$ 0.20)	X
4	5.22($\pm$ 0.39)	3.87($\pm$ 0.38)	2.0 ($\pm$ 0.30)
5	7.8 ($\pm$ 0.39)	6.4 ($\pm$ 0.40)	2.8 ($\pm$ 0.25)
6	8.66($\pm$ 0.40)	7.3 ($\pm$ 0.35)	4.1 ($\pm$ 0.38)
7	10.5 ($\pm$ 0.93)	9.6 ($\pm$ 0.62)	4.8 ($\pm$ 0.39)

It can be seen that between full daylight and 70% daylight levels there is no marked difference in the production of rhizomes but a consistent trend is apparent. In 40% daylight level rhizome production is significantly less than at either 100% or 70% levels. Bakker (1952), Myerscough and Whitehead I (1967) also noted the general tendency of rhizome development to be retarded in shade.

The leaves differed between the 100%, 70% and 40% daylight plants in both species and showed greatest modification in response to light intensity, stems became more and more elongated, slender and less woody with the decrease in light intensity. Roots were poorly developed in the shade conditions.

In Epilobium individual leaves at the same developmental stage became progressively larger with the decrease in light intensity, but the total leaf area was always higher in the full daylight. This is due to development of numerous side shoots with plenty of leaves compared to fewer side shoots and sparsely placed leaves in the shade. This tendency of a smaller number of leafy lateral branches at lower light intensities with larger leaves on the main axis was also reported by Hughes (1959,b).

In Lythrum not only was there a progressive increase in the leaf size but the leaf area in 70% light intensity was higher than the full daylight over the main growth period; towards the end of the experiment it increased in full light as a result of the production of numerous side shoots and leaves. In Epilobium towards the last harvest the lower, older leaves on the stem started to yellow and fall off with a consequent reduction in total leaf area at the 7th harvest. With the decrease in light intensity leaves became increasingly pale green in colour in both species, though it was less marked in Lythrum.

Differences in the leaf texture of plants growing in various intensities of light were very marked. In full light they were thick with abundant tomentum, much thinner, with gradually less tomentum, in increasingly shady conditions.

Gourley and Nightingale (1921), Shidey (1932), Bakker (1952) and Myerscough and Whitehead I (1967) also noted larger leaf areas in leaves of comparable developmental stage with fewer stomata per unit of leaf in shade conditions. Palisade is many layered in plants of full light compared to those growing in progressively lower shades (Whitehead, 1954) where palisade is one or two layered and transversely elongated parenchyma is well developed. The comparative measurements of the epidermal cells demonstrated that the length of cells is greater in shade than in sun plants.

Again, passing down to 40% daylight, leaves of a comparable plastochron tended to have a greater leaf area, but when the stems had taken on their elongated form, the position at which the leaves were held on the stem was somewhat different at varying levels of daylight. In full daylight the higher the leaf was up the stem the greater was the angle it was held above the horizontal. In 70% and 40% daylight all the leaves were held less horizontally and more or less declined while the older leaves on the main stem were slightly rolled in along their margins and lay parallel with the stem.

Stems of both species were regularly taller in shade than in full sunlight. The differences in the 70% and 40% daylight plants were not marked but were very marked between

full light and shade plants at the time of the last harvest, as shown in the table below.

TABLE 3.

Plant	Levels of Daylight		
	Height of stem in cms. at 7th harvest		
	100%	70%	40%
<u>Lythrum</u>	115.8 ($\pm$ 3.9)	150.1 ($\pm$ 4.08)	154.2 ($\pm$ 2.2)
<u>Epilobium</u>	123.0 ($\pm$ 5.48)	159.1 ($\pm$ 3.11)	162.8 ($\pm$ 3.2)

In Epilobium, with the decrease in light intensity, there was no reduction in the number of axillary branches but their size was greatly reduced and many upper side shoots did not show much elongation after their initial development. In contrast, 70% plants of Lythrum were more numerously branched compared to those in full light intensity, and their side shoots were larger and better developed. This can be seen from Plate 4.

Flowering started a fortnight earlier in Lythrum than in Epilobium where the first floral buds were still developing. In each species there was both delay and reduction in the number of flowers with the decrease in light intensity, as shown in Table 4.

TABLE 4. (a)

Mean no. flowers at various levels of daylight

<u>Lythrum salicaria</u>			
Harvest	100%	70%	40%
3	15.6($\pm$ 1.72)	X	X
4	120.2($\pm$ 6.00)	50.4($\pm$ 5.7)	10.2($\pm$ 1.65)
5	302.8($\pm$ 11.2)	128.8($\pm$ 10.88)	40.8($\pm$ 5.28)
6	608.6($\pm$ 29.36)	380.6($\pm$ 21.1)	200.8($\pm$ 11.79)
7	975.8($\pm$ 39.76)	580.6($\pm$ 27.5)	440.4($\pm$ 17.8)

(b) Epilobium hirsutum

4	10.2($\pm$ 1.42)	X	X
5	54.0($\pm$ 3.7)	8.4($\pm$ 1.15)	X
6	127.6($\pm$ 8.79)	24.2($\pm$ 4.58)	15.8($\pm$ 1.6)
7	450.5($\pm$ 19.53)	168.1($\pm$ 12.88)	65.0($\pm$ 5.38)

After harvest 7 no further harvest was made for growth analysis but plants in each treatment were left to develop fruits and seeds. By the time of harvest 5 some flowers had already developed into fruits in full daylight Epilobium. Harvest 8 was taken four weeks later when fruits in both species were fully formed. There was delay and reduction in the number of fruits with the delay in light

intensity, as shown in Table 5.

TABLE 5. (a)

Mean no. of capsules per plant at
different daylight levels.

Lythrum salicaria

Harvest	100%	70%	40%
7	352.7($\pm$ 12.82)	X	X
8	520.4($\pm$ 37.95)	150.6($\pm$ 13.37)	92.0($\pm$ 5.38)

(b) Epilobium hirsutum

5	6.2($\pm$ 1.05)	X	X
6	34.8($\pm$ 2.28)	X	X
7	187.3($\pm$ 10.97)	24.4($\pm$ 1.78)	X
8	585.6($\pm$ 23.97)	145.2($\pm$ 9.71)	120.8($\pm$ 5.91)

Dry weights of fruits and seeds were also determined. Four replicate samples each of 50 fruits were taken. Results are shown in Table 6.

TABLE 6.

(a) Mean dry weight per 50 fruits (mg.)				
Daylight levels.				
Plant	100%	70%	40%	L.S.D. (P=.05)
<u>Lythrum</u>	381.2	297.6	278.2	14.268
<u>Epilobium</u>	1708.5	1625.8	1031.5	18.377
(b) Mean seed dry weight per 50 fruits (mg.)				
<u>Lythrum</u>	210.66	148.82	132.24	27.798
<u>Epilobium</u>	1075.00	946.25	685.18	36.949
(c) Mean dry weight per 100 seeds (mg.)				
<u>Lythrum</u>	5.46	5.31	5.26	0.3126
<u>Epilobium</u>	16.27	15.98	14.76	1.6432

It can be seen that with the decrease in light intensity there is a great reduction in the collective dry weight of 50 fruits and their seeds (Table 6(a) and (b)), but the mean dry weight per 100 seeds remains similar at all light intensities. In low light intensities, because there is less available "surplus" dry weight for reproductive organs, plants show an adaptation by reducing the number of capsules per plant and number of seeds per capsule corresponding to the light intensity, but maintain similar seed

weight at all light intensities. In both species at lower light levels the capsules took a long time to ripen the seeds. Seeds of both species from all light intensities were fully viable. It is concluded that under lower light intensities both species retain full viability of seeds at the expense of their number.

The general pattern of growth behaviour in both species was essentially similar, with a comparable rate of development of the main stem down to the 40% level, a larger area in the leaves of the same plastochron and a decreased reproductive output with decreasing daylight. But in Lythrum, within limits at lower daylight intensities, there were more and longer side shoots compared to the depressing effect on elongation of side shoots in Epilobium.

Rhizomes collected from three different types of Epilobium plants (see Chapter IV "Material") were grown in sand and peat mixture in wooden trays at 20°C. Squashes of the root tips were prepared using the acetocarmine technique to study the chromosome number. No difference in the chromosome number was observed. Later these rhizomes, when they had developed young shoots, were transferred to the full daylight intensity tent, on 25 March, 1967. These plants grew at a faster rate than the seed grown plants and after completing their vegetative growth in 8 weeks all three types of

plants started producing flowers at the same time. There was no marked visible difference in their size and flower number. Flowers from all three types developed fruits and seeds. Seeds from the three types of fruits were viable and germinated without any delay and in approximately the same numbers.

These observations are completely in agreement with the experiment described, that the reproductive growth is severely affected by the reduction in light intensity and when these plants are provided with full illumination the flower and fruit formation is completely restored.

It can be concluded that changes in the daylight can affect the phenotype and its degree of expression but the genotype remains unaffected.

Results

The results of the chlorophyll estimation and growth in terms of different growth analysis estimates were as compiled below.

1. Chlorophyll content of leaves

The results of the determinations based on unit fresh weight, dry weight and leaf area are summarised in Table 7.

TABLE 7.

(a)	Total amount of chlorophyll <u>mg/g Fresh Weight</u>			
Species	Light intensity			L.S.D. (P at .05 * and .01)**
	100%	70%	40%	
<u>Lythrum</u>	2.122	1.886	1.799	(0.1849*)
<u>Epilobium</u>	2.107	1.673	1.598	(0.2522**)

(b)	Total amount of chlorophyll <u>mg/g Dry Weight</u>			
<u>Lythrum</u>	9.650	10.008	11.663	(1.455*)
<u>Epilobium</u>	8.391	9.463	10.836	(1.985**)

(c)	Total amount of chlorophyll <u>ug/cm²</u>			
<u>Lythrum</u>	46.20	36.12	29.01	(2.7575*)
<u>Epilobium</u>	35.31	28.45	23.73	(3.8134**)

In general, chlorophyll contents of Lythrum are higher than Epilobium and very significantly so when determination is based on unit leaf area. With a decrease in light intensity, relatively speaking, there is less reduction in

Lythrum than Epilobium. In determinations on dry weight basis there is a regular increase with shading in both species. This is because leaves in shade become thinner and lighter with a high specific leaf area.

Evans and Hughes (1961) found that in Impatiens parviflora the chlorophyll content of leaves, per unit area of leaf surface, was roughly the same for all levels of shading although the content on a dry weight or fresh weight basis showed a systematic increase with shading. It is, however, said that shade leaves of the more plastic species have a higher chlorophyll content compared with corresponding sun leaves or sun species (see Plant Ecology: Weaver and Clements, P.P.382). This may account for the differences between the present results and that of Evans and Hughes (1961) as Impatiens parviflora is a shade loving woodland annual. Henrici (1926 to 1927) reported that chlorophyll contents of a plant vary with the environmental conditions and increasing age of the plant.

2. Increase in dry weight

Fig. 7 shows the increase of dry weight with time for the two species at the three daylight levels. Dry weight production is affected in both by a decrease in the light intensity. Of the two species dry weight production in

Epilobium is relatively more affected at 70% than in Lythrum. Dry weight in the 70% Lythrum plants is very close to the 100% plants and differences are insignificant at harvest 4 and 5. In Epilobium the 70% and 40% plants tend to have similar dry weights, especially in the earlier harvest, while the 100% plants have significantly higher dry weights at all the harvests after initial adjustment. (See Appendix),

3. Increase of leaf area

The general pattern of increase in leaf area with time is shown in Fig. 8. It is very similar in the three daylight intensities. In Epilobium it follows the pattern of dry weight and there is a decrease in leaf area with decreasing daylight, except at the last harvest where the 70% plants have a higher leaf area because of the senescence of leaves in the 100% plants due to their early maturation. However, differences at both daylight levels are insignificant at this stage. The 70% plants of Lythrum maintained higher leaf areas from 4th harvest onwards except the last from the 100% plants, but differences were insignificant.* Again, the 100% and 70% daylight plants in Lythrum are very close together and 70% and 40% daylight Epilobium plants tend to be similar in their leaf area.

This can be further appreciated from Fig. 9 obtained by correlating the gain of leaf area to gain in

* See Appendix

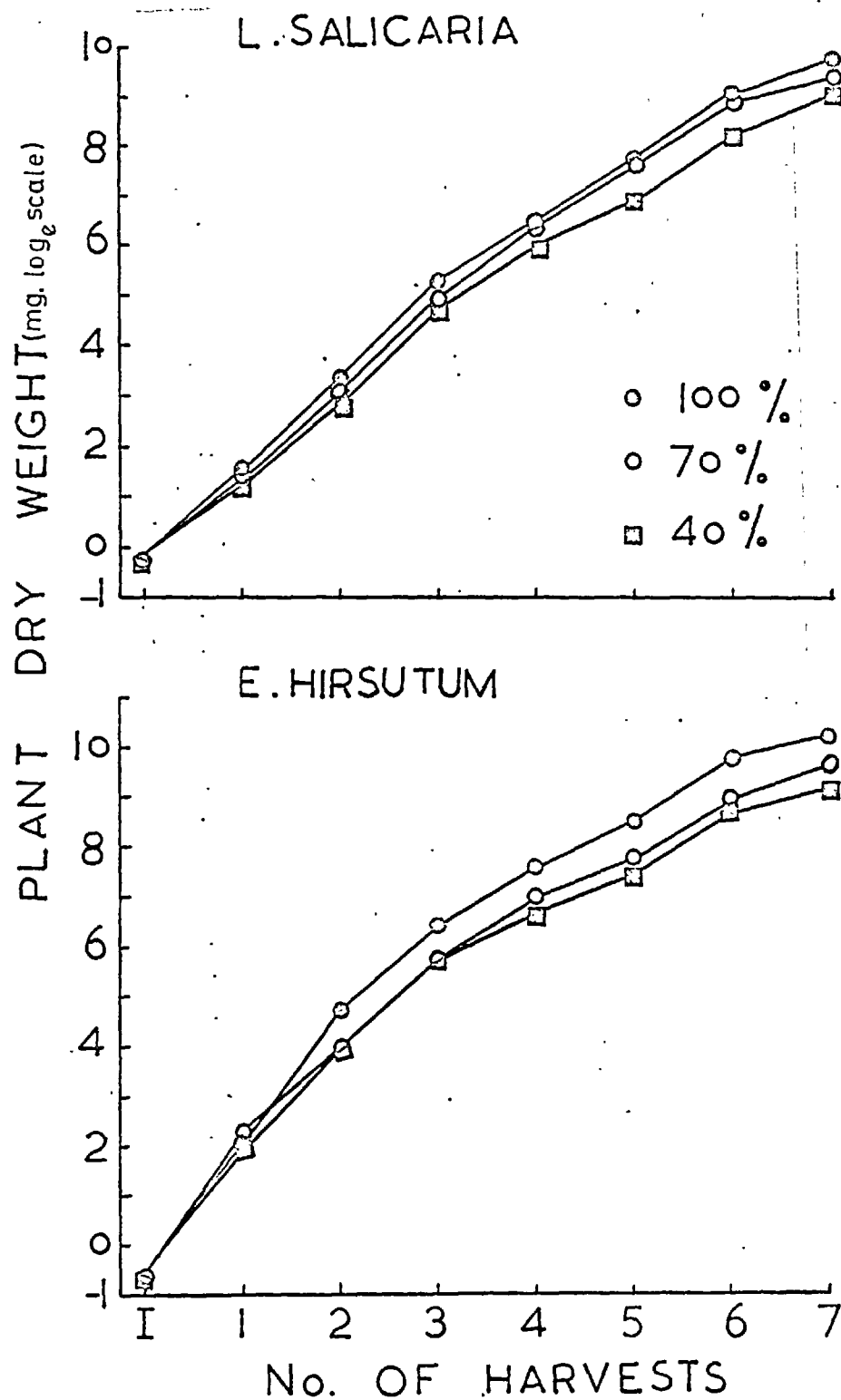


FIG. 7. Effect of different daylight levels on increase of plant dry weight with time.

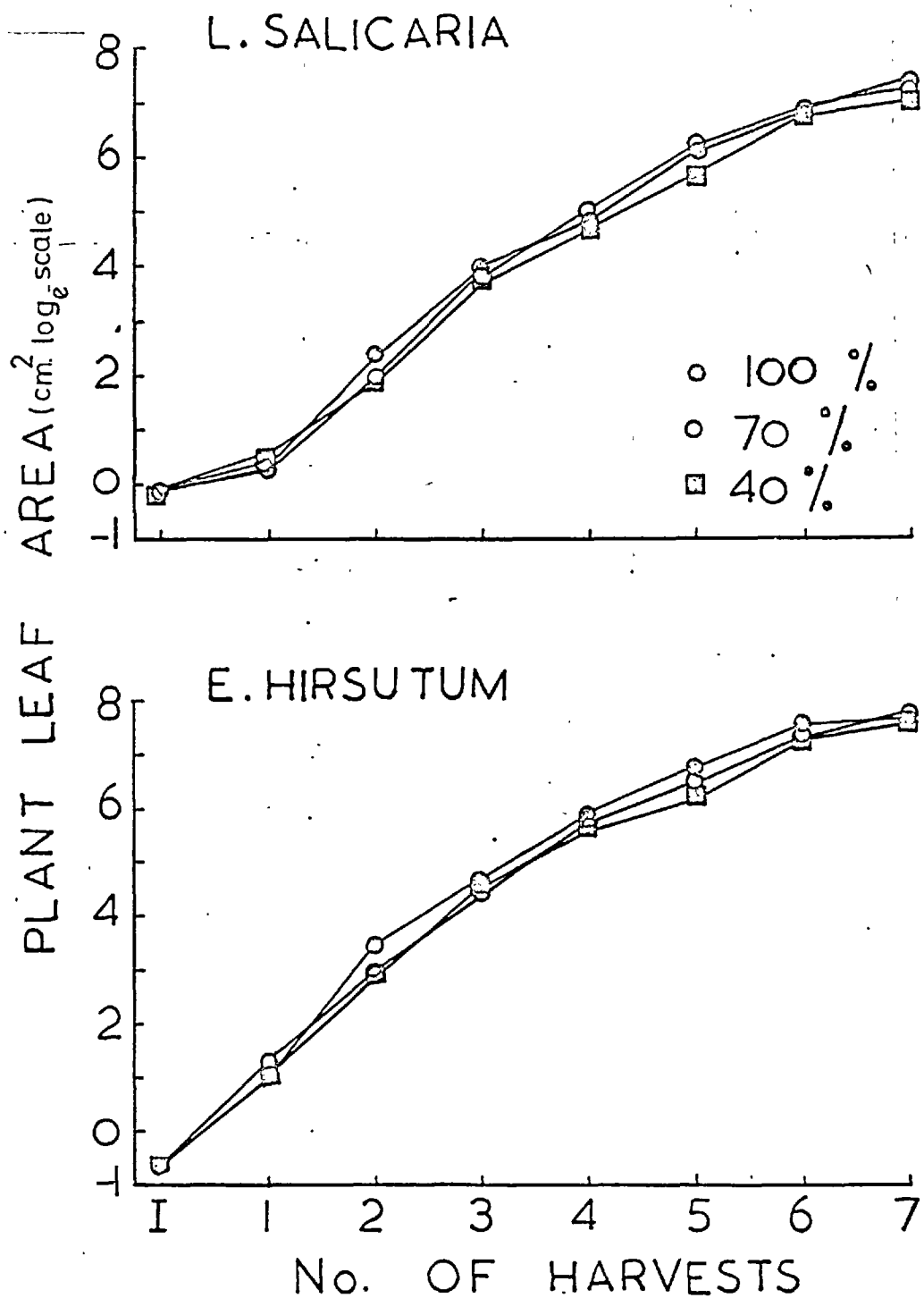


FIG. 8. Effect of different daylight levels on increase of plant leaf area with time: (I = initial harvest)

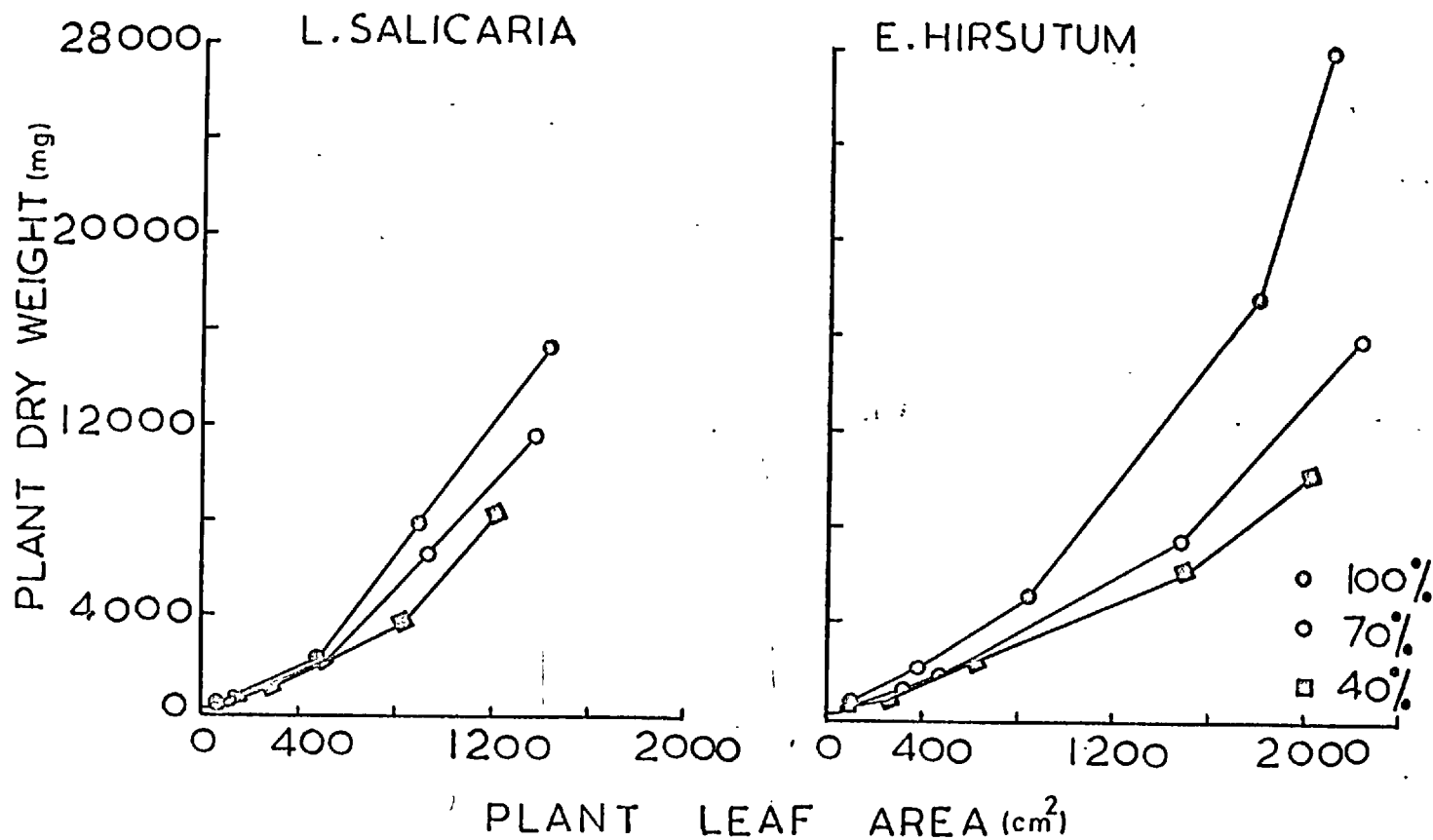


FIG. 9. Effect of different daylength levels on relation between plant leaf area and dry weight for harvests three to seven inclusive.

plant dry weight. While the general pattern is similar, the degree of relationship is markedly different. Similar leaf areas are obtained in Lythrum with very small differences in the dry weights in the 70% and 100% plants, but in Epilobium the difference is such that the dry weight in the 100% plants is almost twice that of the 70% for similar leaf areas. It can be noted that in Lythrum there is something of a compensating mechanism in response to decreased light intensity, while Epilobium has a very poor one. However, in none of these species is it as efficiently developed as in Chamaenerion angustifolium and Tussilago farfara (Myerscough and Whitehead II 1967).

4. Mean unit leaf rate

The correlation between the leaf area and dry weight is suggestive of higher mean unit leaf rates in the full daylight plants than in the shade plants. ~~This can be seen in Fig. 10 (calculated from the initial to each subsequent harvest), and Fig. 11 (calculated between the harvest intervals).~~

~~In Fig. 10 the pattern is the same in the two species but a relative decrease of unit leaf rate with a decrease in light intensity is more significant in Epilobium than in Lythrum and in the last two harvests values are higher~~

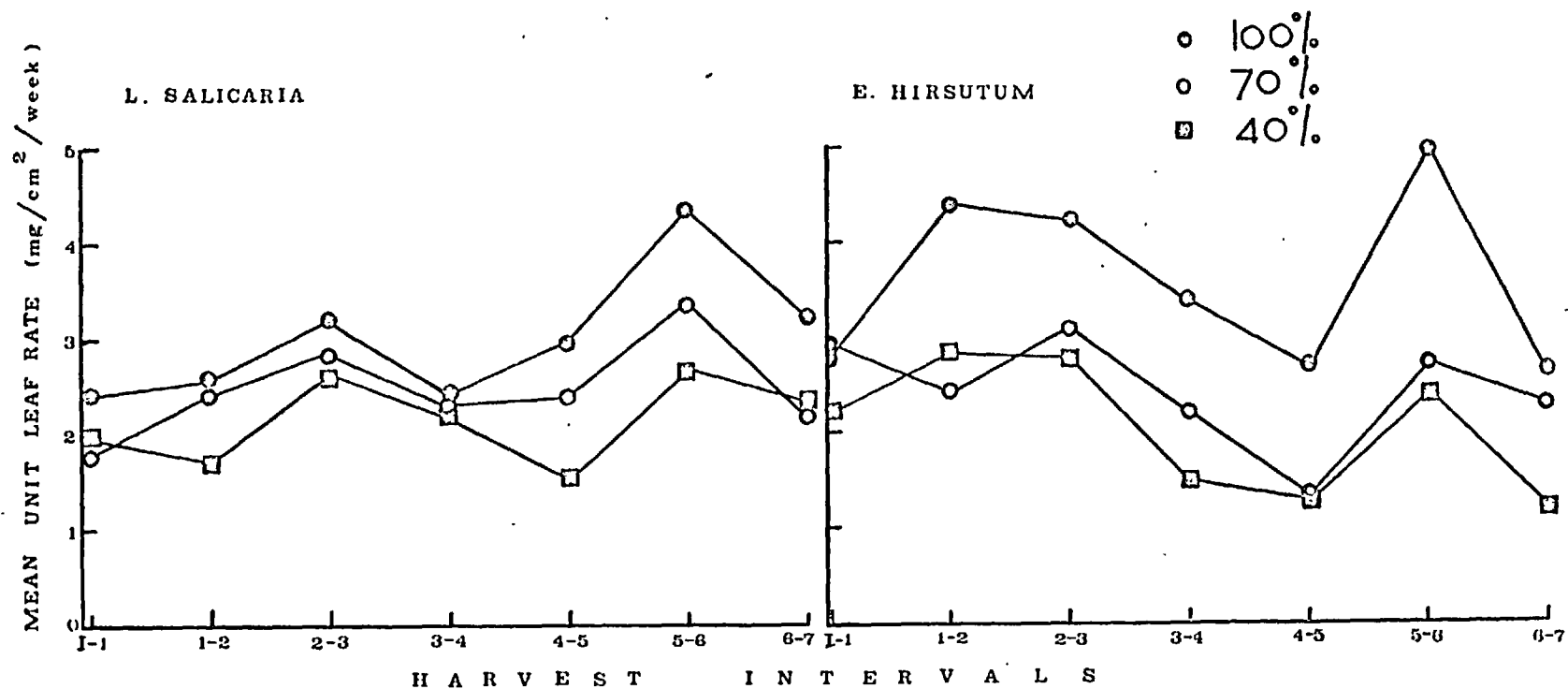


FIG. 11. Effect of different daylight levels on mean unit leaf rate.
(Calculated between the successive harvest intervals.
I = initial harvest)

~~in the shade plants of Lythrum than their counterparts in Epilobium.~~ Similar results can be seen from Fig. 11 with the difference that in the last interval, fall in the unit rate at high and low light intensity is more marked in Epilobium than in Lythrum. These differences in the performance can be attributed to the different growth rates, growth habit and attainment of maturity in the plant. By the time of the last harvest interval, mature leaves of the 100% daylight Epilobium plants were yellow and undergoing senescence so a sudden drop in the unit leaf rate is to be expected. In Lythrum not only is the senescence of older leaves later, but numerous leaves and branches are formed during the flowering period so that higher unit leaf rates are maintained. These higher unit leaf rates in Lythrum at 70% and 40% daylight contribute to the relatively greater efficiency of this species in shady conditions.

5. Ratio between the mean relative growth rate to the mean relative leaf area increase (α value)

As seen in Fig. 12, the basic pattern of the morphogenetic condition in the two species at various light intensities is similar but for the last interval. It can be noted that low light plants are relatively more leafy than the full daylight plants. The very high α value in 100% Epilobium plants in the last harvest interval is because of

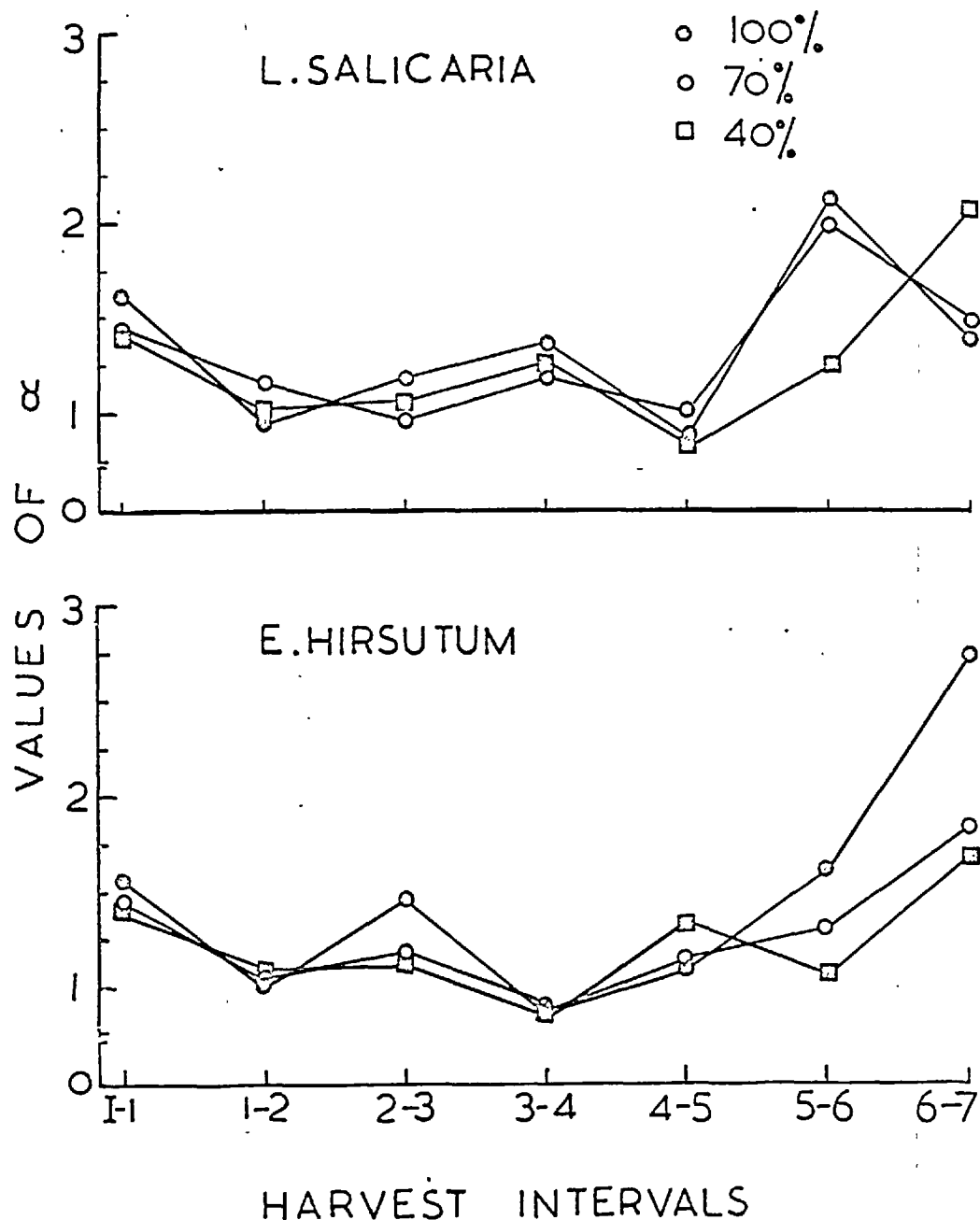


FIG. 12. Effect of different daylight levels on the ratio, mean relative growth rate to mean relative rate of leaf area increase (α). (Calculated between successive harvest intervals) (I = initial harvest)

decreased leafiness with age (partly by senescence), also reported by Myerscough and Whitehead II (1967). Lythrum is known to remain green in nature even after flower formation and ripening of the fruits and, for relatively little increase in the dry weight, relative increase in leaf area is very high, so there is a fall in α value at the last harvest interval. Moreover, plants produced numerous leaves and small branches after flower formation. The odd behaviour of the 40% Lythrum plants is because of the delayed growth progress and the peak of α values reached in the 100% and 70% in the previous interval is reached here only after a further delay of two weeks.

Comparing the morphogenetic differentiation of the two species, it can be seen from Fig. 12 that the 100% and 70% plants in Lythrum follow the same course of development, especially in the later harvest, while the 70% and 40% Epilobium are closer together and the 100% plants are very distinct. This closer association between the 100% and 70% Lythrum plants, and the 70% and 40% Epilobium plants can also be seen in the unit leaf rates in Figs. 10 and 11. It is suggested that Lythrum is tolerant of partial shade and its morphogenetic differentiation is not much affected, but a decrease in light intensity has a depressing effect on the growth rate and differentiation in Epilobium.

6. Leaf area ratio and specific leaf area

These can be seen in Figs 13 and 14 respectively. It can be seen from the leaf area ratios that with time all the plants become less leafy but that those at lower light intensities remain comparatively more leafy than those at higher light intensities. This effect of light intensity on L.A.R.'s has also been shown by Evans and Hughes (1961) and Myerscough and Whitehead (1966). Of the two species, the fall in values with time is more marked in Epilobium at 100% than in Lythrum.

Specific leaf area (Fig. 14) follows the same pattern in the two species. Higher values of specific leaf area at lower light intensities show the spread of a relatively smaller leaf weight over a greater area resulting in thinner leaves, more so in Epilobium than in Lythrum.

7. Leaf-shoot and root-shoot ratios

These are shown in Figs. 15 and 16 respectively. It can be seen that Lythrum has more shoot than leaf in the intermediate harvests than Epilobium and this is reversed in the later harvests. This would account for the higher unit leaf rates in Lythrum in the later harvest especially at the 70% and 40% daylight levels (Fig. 10 and 11).

Relatively speaking, root formation is more affected by a decrease in light intensity than shoot formation,

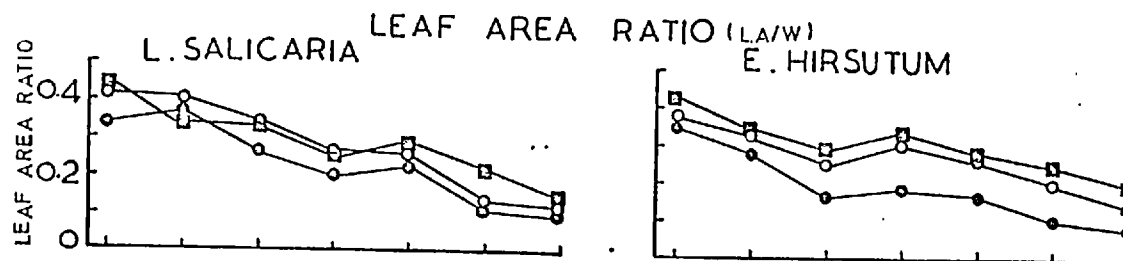


Fig. 13.

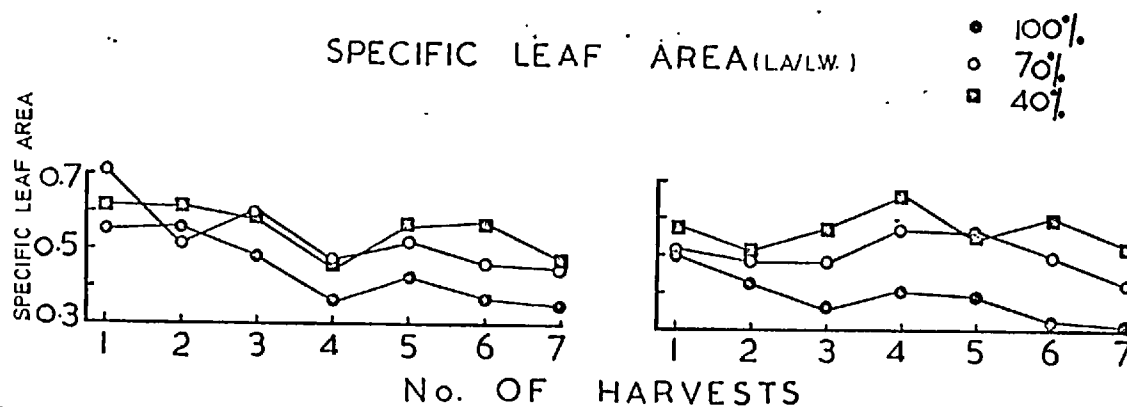


Fig. 14.

Effect of different daylight levels on growth

FIG. 13. Leaf area ratio

Fig. 14. Specific leaf area

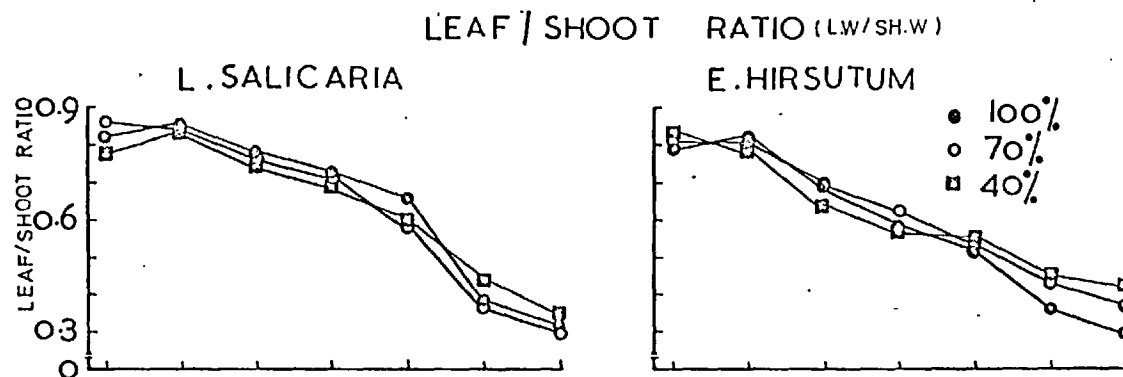


Fig. 15.

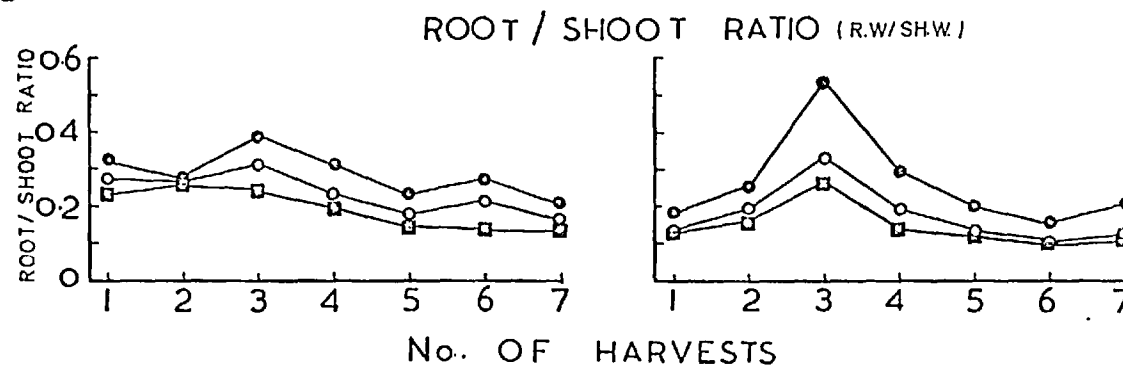


Fig. 16.

Effect of different daylight levels on growth.

FIG. 15. Leaf/Shoot ratio

FIG. 16. Root/Shoot ratio

and there is a systematic decrease in root shoot ratio, i.e. relatively more shoot is produced at the expense of root. In the first three harvests developmental drift leads to a gradual rise in the ratio, which is more marked in Epilobium than in Lythrum. In later harvests the values show a steady decline (Fig. 16).

8. Root/leaf and root/leaf area ratios

These are shown in Figs 17 and 18 respectively. These values follow the same pattern as the root shoot ratios in each species. Very high values in the 100% Epilobium plants in the last harvest are due to the decreasing leafy condition because of senescence and the fall of the lower leaves. It can be seen that root production is very small in Epilobium compared to Lythrum in the first two harvests. Root development in Epilobium was more affected by decrease in light intensity than in Lythrum.

9. Percentage dry weight proportions of root stem and leaf.

Differences in patterns of the various ratios in the two species can be attributed to different ontogenetic differentiation at various stages of growth. This can be realized by calculating dry weight percentages of the plant components at each harvest. These are shown graphically in Fig. 19. Root, stem and leaf follow the same course of

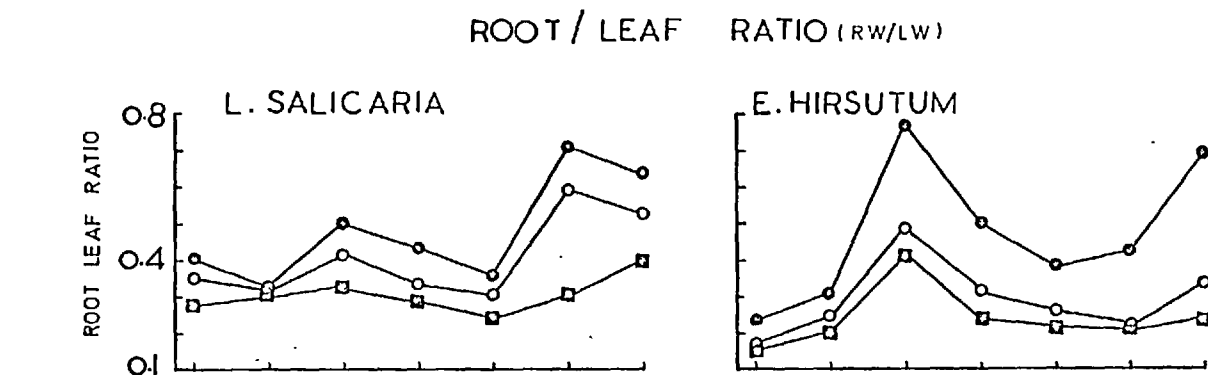


Fig. 17.

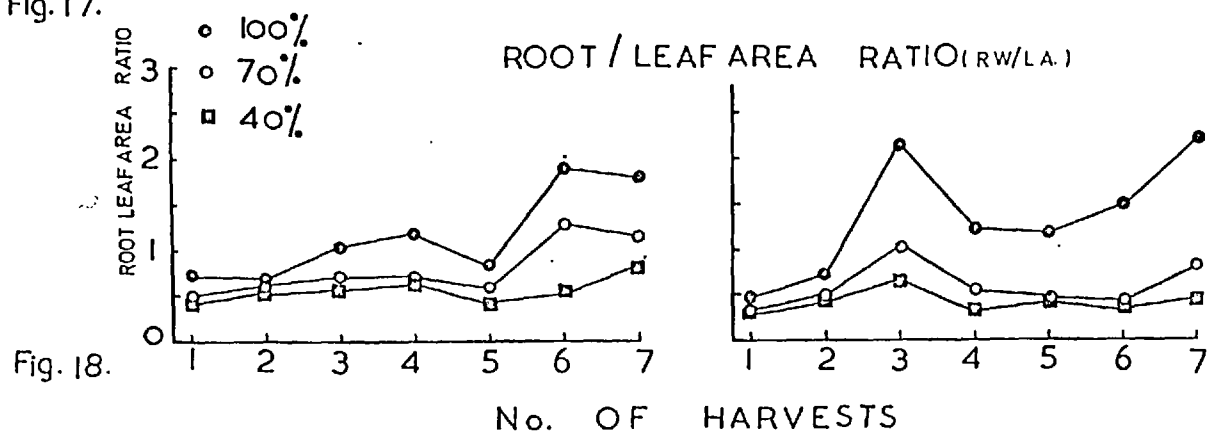


Fig. 18.

Effect of different daylight levels on growth.

FIG. 17. Root/Leaf ratio

FIG. 18. Root/Leaf area ratio

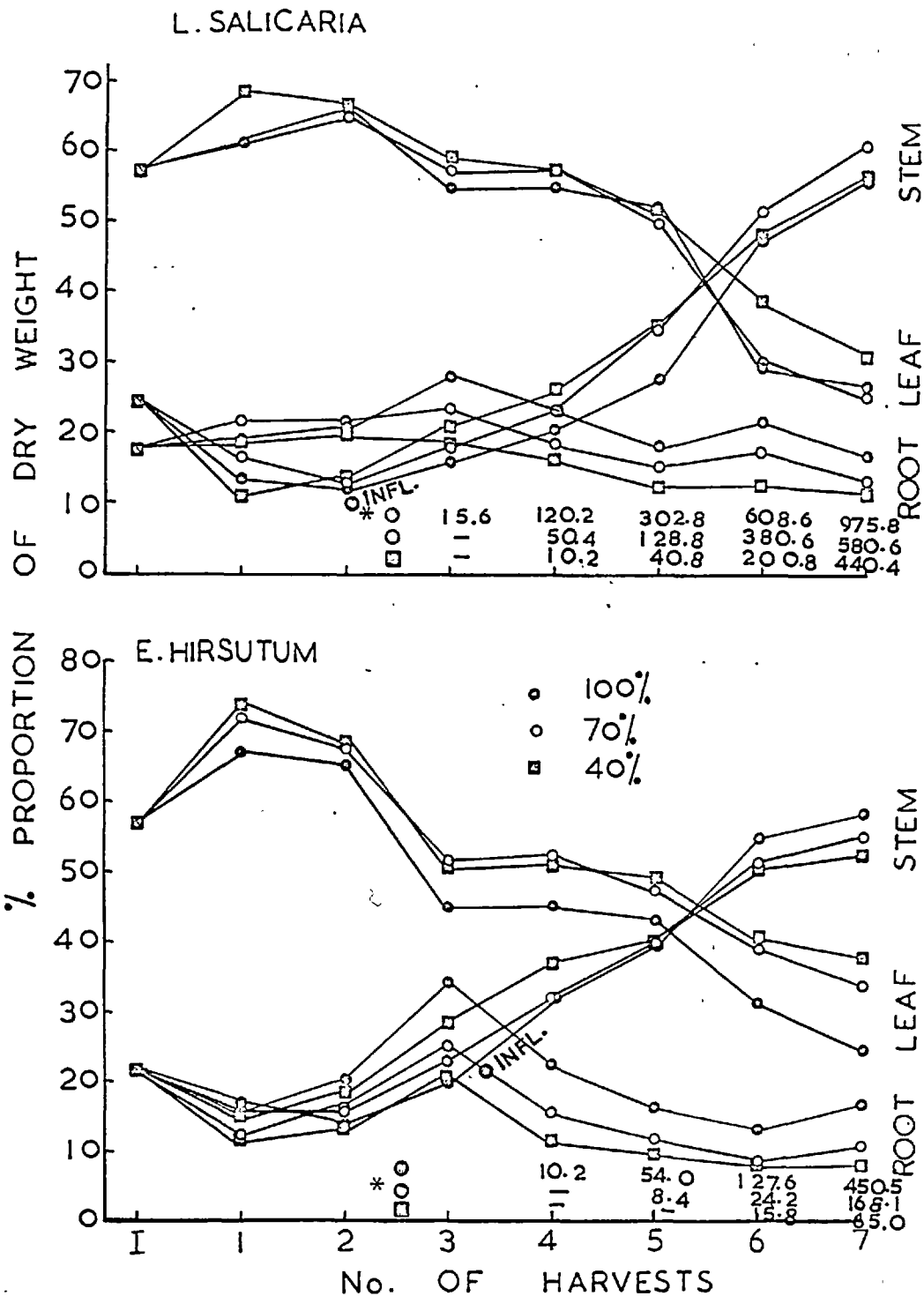


FIG. 19.

Effect of different daylight levels on percentage proportionate distribution of total dry weight to leaves, stems and roots at successive harvests. (I = initial harvest)

*number of flowers at respective harvests.

differentiation in both species in all light intensities, but they show profound differences in the degree of their expression at some crucial phases of development.

There is decreased root proportion in Epilobium in the earlier stages of establishment and then a sharp rise during the vegetative growth followed by a steady decline after the initiation of inflorescence. In contrast, in Lythrum root proportion during establishment is very high, almost double that of Epilobium in the low light intensities and, relatively, root proportion is higher throughout the course of growth. Epilobium root is more effected by a decrease in light intensity. High root proportion in Lythrum, especially in the earlier stages, is at the cost of the stem which has very low proportion during the period of vegetative growth compared to Epilobium. During the reproductive phase of growth the stem increases in proportion at the expense of both leaf and root. It is earlier and more significant in Epilobium than in Lythrum. Decrease in light intensity has opposite effects on stem and root except for the last two harvests in Epilobium.

Leaves in both species constitute the highest proportion from establishment to the prime of vegetative growth. With the initiation of inflorescence, there is a steady decline followed by a sharp fall in the last stages. The

decrease in leafiness is earlier and sharper in Epilobium especially in the 100% plants, which are very distinct from the 70% and 40% plants. Lythrum retains its leafiness for a longer period even during the reproductive phase of growth at the lower light intensities; this is achieved at the expense of the stem. Epilobium plants become stemy very early in growth while Lythrum plants remain leafy for a long time.

It is clear that the two plants show different ontogenetic differentiation during establishment. While in Lythrum the root has a high proportion at the expense of the stem and is relatively unaffected by light intensity, in Epilobium it is the opposite, the root has the lowest proportion, especially in shade, and the stem is well developed.

This difference is very important in the early establishment of seedlings of the two species, in shade, in nature. With the onset of flowering the plants become woody, more at the expense of leaf than of root.

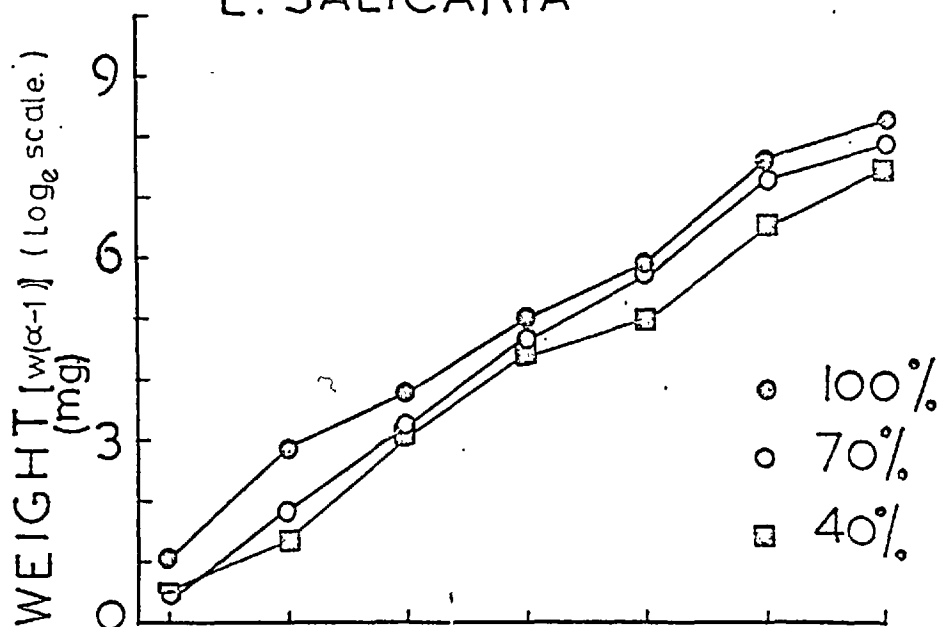
The life form or pattern of ontogenetic differentiation is very distinct in the two species in the early stages of growth, but is similar within each species under different light intensities. It is suggested that these phenotype expressions of the plants are genetically controlled and independent of the environment, but the environment may effect the degree of expression of these phenotypic attributes.

This variability in the degree of expression would determine the success of the same phenotype under different daylight levels in nature.

10. Surplus dry weight

Continued reduction in leafiness with age was correlated with the formation of fruits and organs of vegetative spread in Epilobium. Their production in different levels of daylight depends upon the amount of "surplus" dry weight, represented as $W(\alpha - 1)$, (see Whitehead and Myerscough, 1962). These values of "surplus" dry weight are presented graphically in Fig. 20. In both species it decreases with the fall in light intensity, but the gap between the 100% and 70% daylight levels in Lythrum is not as marked as in Epilobium. There is a correlation between this surplus dry weight and the number of fruits produced in both the species (Fig. 21). In Epilobium there is also a general correlation between surplus dry weight and the number of rhizomes produced (Fig. 22).

L. SALICARIA



E. HIRSUTUM

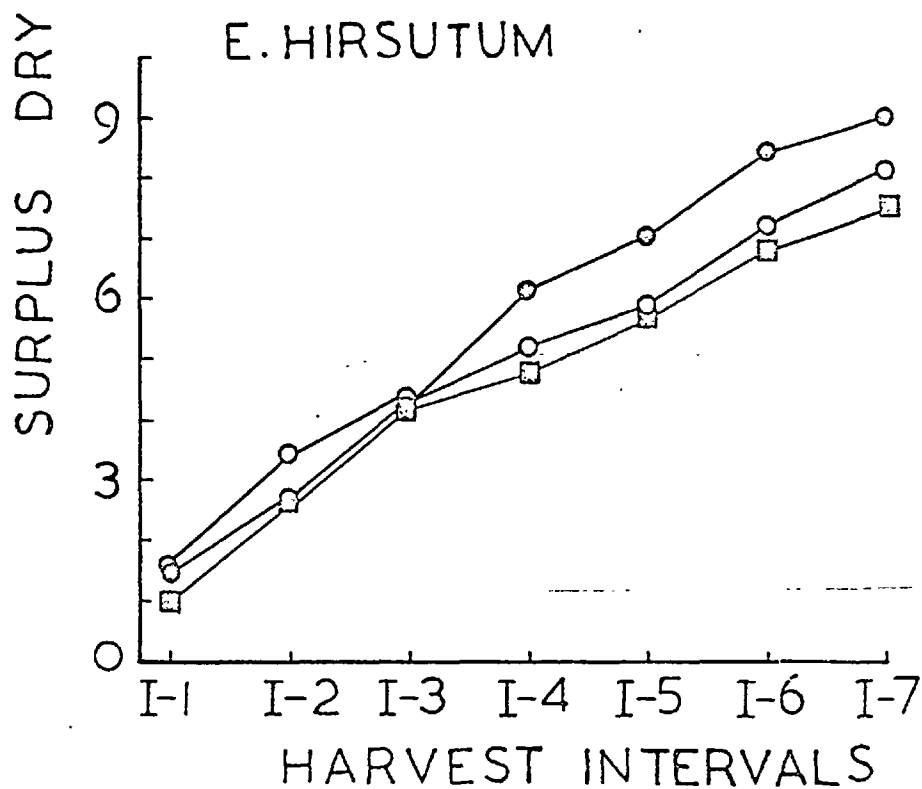


FIG. 20. Effect of different daylight levels on "surplus dry weight. (I = initial harvest)

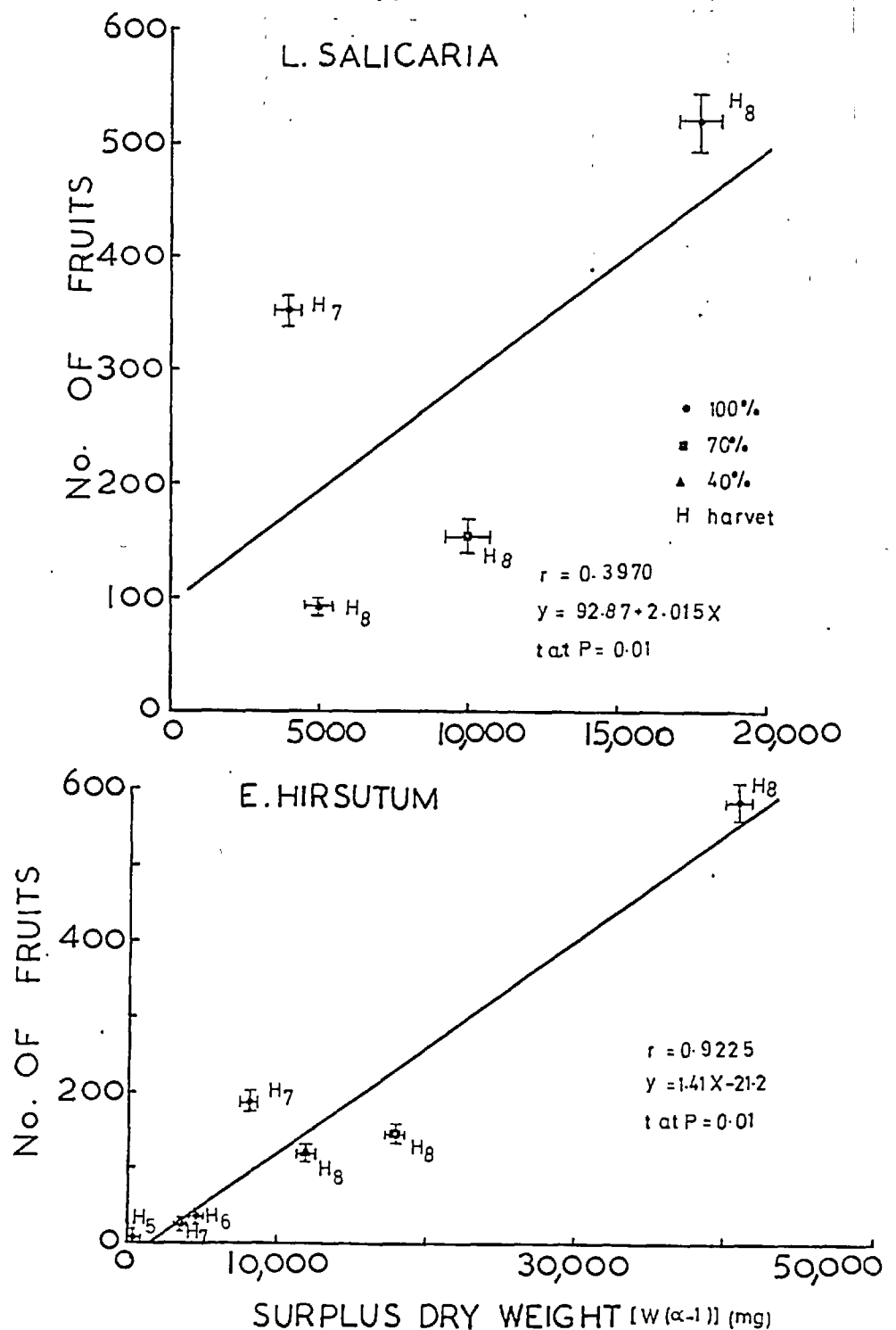


FIG. 21. Effect of different daylight levels on growth
Regression of surplus dry weight on fruit
number (capsules) per plant.

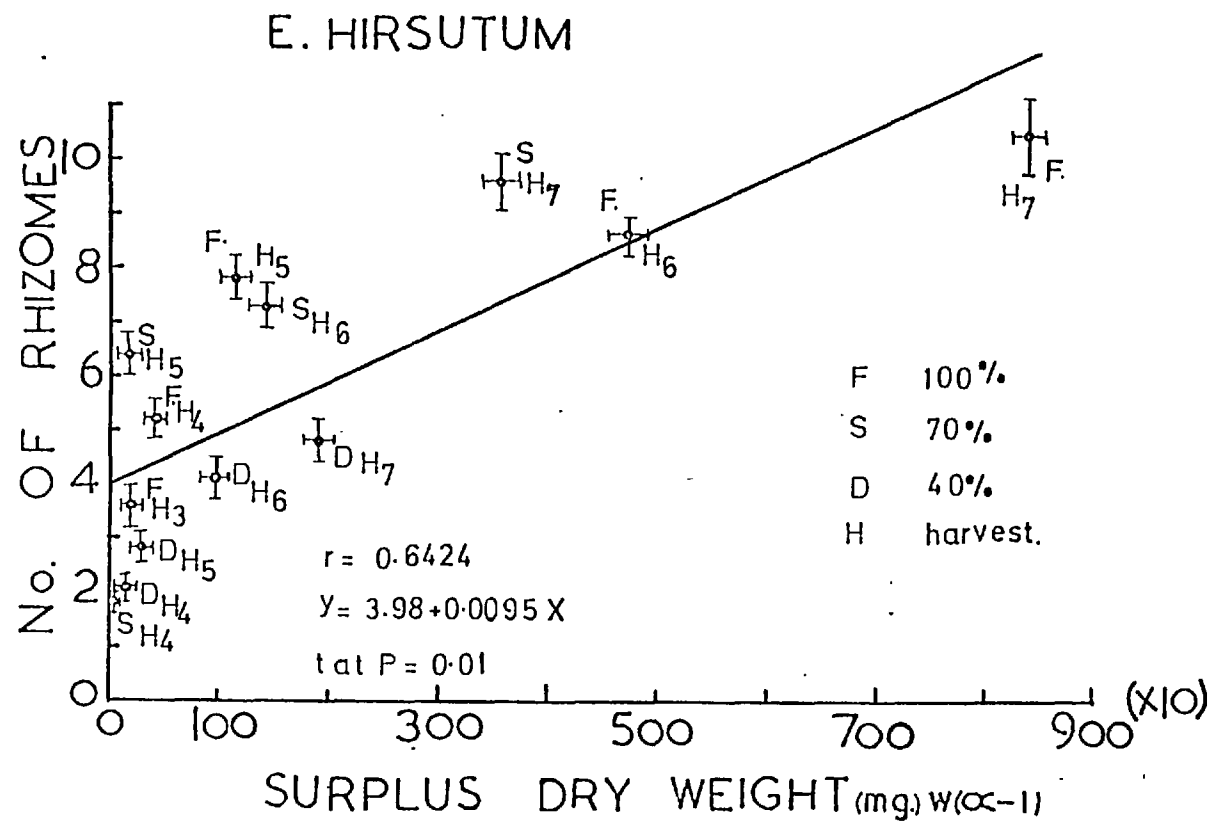


FIG. 22. Effect of daylight levels on growth
 Regression of surplus dry weight on rhizome number.

General Discussion and Conclusions

The data presented show that the two species are affected by a decrease in daylight levels. Dry matter production is more affected than the leaf area. Of the two species Epilobium is more affected by a decrease in light intensity than Lythrum. As seen from various estimates of growth processes the 100% and 70% Lythrum plants are very close to each other, and the 70% and 40% Epilobium^{plants}/are always close to each other and distinct from the 100% plants.

Different daylight levels affect the morphogenetic differentiation in the two plants in such a way that in Epilobium the proportion of root is very small at low light levels compared with Lythrum, and the plants are excessively leafy. Lythrum seedlings, in moderate shade, are relatively stable with a high proportion of root at the expense of the stem for a greater part of their vegetative growth (Fig. 19). Initiation of inflorescence and flower formation is three weeks earlier in Lythrum. The duration of the life cycle is longer in Epilobium than in Lythrum; this, coupled with a slower growth rate, affects the ageing of the plants and, towards the last harvests, yellowing and senescence of the leaves was very conspicuous. In Lythrum, on the contrary, not only is the growth rate faster but the plant produces

countless new leaves and floral bracts during flowering. This retention of leafiness for a longer period can also be seen from Fig. 19.

It can be argued that the photosynthetic efficiency of a plant depends upon the functional life of the leaves determining the unit leaf rates. Relatively less reduction of chlorophyll contents in shade, coupled with faster growth rate and completion of its life cycle in a short time, would enable Lythrum to survive as an efficient photosynthetic entity in moderate shade. Epilobium, on the other hand, takes a long time to complete its life cycle, decreased leafiness with age, as a result of yellowing and senescence, increases the proportion and working time of the respiratory tissue to the photosynthetic tissue and, in the absence of any marked compensatory mechanism, the plant becomes a comparatively less efficient photosynthetic entity and can no longer establish and grow even in moderate shade.

These advantageous tendencies in Lythrum are further helped by the presence of a "compensating mechanism" which makes growth and survival in shade more effective. The performance, assessed in terms of estimates of "surplus" dry weight relative to total dry weight, also shows that Epilobium, under lower light intensities, undergoes relatively more reduction. This contrast also holds good in the relative

"reduction" in the number of side shoots produced and their elongation, and also the number of flowers.

It is evident, that under the conditions in which this experiment was performed, that the performance of seedlings was more severely curtailed by shade in Epilobium than in Lythrum.

In short, the relative difference in frequency in which they occur in shady situations in nature, graded as it is with Epilobium the least frequently and Lythrum the most frequently occurring species, is to be explained in the morphogenetic differentiation, growth rate and the presence of a compensating mechanism.

So it is asserted, once again, that it is the biology of a species which sets barriers to its ecological distribution and excludes its establishment in the habitats otherwise suitable for its growth.

Experiment No. VIThe effect of day length on the germination
and growth form of *Epilobium hirsutum* and *Lythrum salicaria*Experimental procedure

Two chambers, each 6ft. x 6ft. x 8ft., lined with thick black polythene, were erected on the central bench of the greenhouse in November, 1966. In each illumination was provided by four 400 watt Philips bulbs. In one, duration of light was adjusted for 9 hours (8 a.m. to 5 p.m.) and in the other for 16 hours (7 a.m. to 11 p.m.) on a 24 hour cycle. These day lengths were selected as they are roughly related to the optimum short day and long day conditions in Britain, so the results could be directly correlated to the establishment and growth of the two species in nature. Although the greenhouse was heated the temperature in the two chambers was uncontrolled. However, the bulbs, besides providing illumination, also generated enough heat, but in the short day chamber after 9 hours of illumination the temperature was lower than in the long day chamber. These differences in temperature were considered to have no significant effect on the results for the purpose for which the experiment was performed. On the contrary, it simulated natural conditions as short days are associated with lower temperatures. Day time

temperature fluctuated between 23 and 26°C. depending upon the outside weather; at night and in the early hours of the morning it varied from 18 to 20°C.

Seeds of both species were set to germinate separately in each chamber on 10 November, 1966. Full germination was earlier by two days in the long day chamber in both species. However, by 30 November seedlings in both chambers had their cotyledons fully expanded and the initiation of the first pair of leaves was visible. At this stage seedlings of both species were selected for uniformity of size and transplanted, separately, into pots. 80 pots per species, per treatment, were prepared. Other experimental details were similar to those in Experiment V. Five other harvests (excluding the initial harvest at the time of transplantation) were made per species per treatment at regular intervals of 15 days. Ten replicates of each species were taken.

Observations

At each harvest the morphology of the plants in each treatment was studied. The appearance of the plants just before the last harvest are shown in Plate 5.

Epilobium developed characteristic over-wintering prostrate forms in the short day (9 hours), whilst their elongate flowering form characteristic was produced in the 16 hour day length. In Lythrum, flattened button shaped plants



Lythrum salicaria (a)



Epilobium hirsutum (b)

PLATE 5 Growth forms in a day length of 9 hours light and in a day length of 16 hours light. (Photographed after 73 days in the treatments, i.e. just before Harvest V).

were produced in the short day conditions and normal tall summer plants in the long photoperiod. Long day forms were similar to the full daylight plants of Experiment V.

At the second harvest Epilobium plants in the 9 hour treatment were extremely leafy, the leaves all crowded together on a very reduced weak stem. The stems were almost parallel to the soil surface and the sub-sessile leaves had their petioles twisted in such a way as to expose their rounded to spatulate blades to the light. Later on the leaves became oval to oblong, extremely soft, fleshy and devoid of hairs and lush green. After the third harvest the stem became thicker but remained soft and succulent. Internode lengths were extremely small and nodes slightly alternately arranged in a closed spiral. The stem in a typical, full grown, prostrate form at the time of the last harvest was $7.2 (^+ 0.8)$ cm. long with 14 to 15 nodes bearing pairs of leaves. Two to three axillary buds were produced in most of the plants towards the fourth harvest, each of which, in time, developed into a short daughter plant with its own root system but still attached to the parent plant.

In some of the short day forms, in Epilobium, the stem started elongating towards the fifth harvest, bearing very small alternately arranged leaves. These stems were very thick with strong initials of adventitious roots all

around the stem at the internodes but not at the nodes. Some of the axillary branch shoots were also elongated with initials of adventitious roots. Those adventitious roots arising on the lower side of the stem when in contact with the moist soil surface became strongly contractile, pulling the whole shoot very close to the soil surface.

The plants of Lythrum in the 9 hour short day treatment were extremely small in the first three harvests and not many morphological changes were visible. The stem was extremely reduced and 5 to 6 pairs of leaves seemed to arise directly from the tuberous root, which grew thicker and more woody with time. There were a few fibrous roots arising from its surface. Towards the last harvest the stem started elongating, irregularly, in many plants and the average length was $1.5 \left(\pm 0.6 \right)$ cm. with 7 to 9 pairs of small oblong leaves arranged distichously. The stem was prostrate, lying flat on the soil surface. Two or three other minute shoots with small scaly leaves were also present on the tuberous roots but did not elongate. The leaves were also very much affected by the short day treatment and were much smaller than those of the long day plants. A fully developed leaf was not more than 1 cm. in length. Mature leaves were thick, glabrous and dark green, arising oppositely on a very reduced stem whose growing point was protected by a pair of reddish-

green scaly leaves.

A casual comparison of growth in the two species, in short day conditions, gave the impression that in Epilobium there was a reduction of stem elongation but no effect on the leaves. In Lythrum, on the contrary, there was extreme reduction of stem and leaves and the whole growth process seemed to be suppressed. Primary data were collected as in Experiment V.

Analysis of Growth

Results of various growth processes are discussed as follows.

1.. Dry matter production

The increase in dry weight with time is shown in Fig. 23. In both species dry weight production was severely affected by differences in the photoperiod. More striking was the different response of Epilobium and Lythrum to the short day treatment. The difference was such that the mean dry plant weight, in the short photoperiod, at the final harvest ranged from 126.0 ($\pm$ 11.8)mg., approximately $1/58$ of its long day form, in Lythrum to 1999.0 ($\pm$ 65.3)mg., approximately $1/10$ of its long day form, in Epilobium.

Of the two species, Epilobium is known to grow during the short days of autumn in Britain and over-wintering "plates" occur in nature. Lythrum, however, never grows in

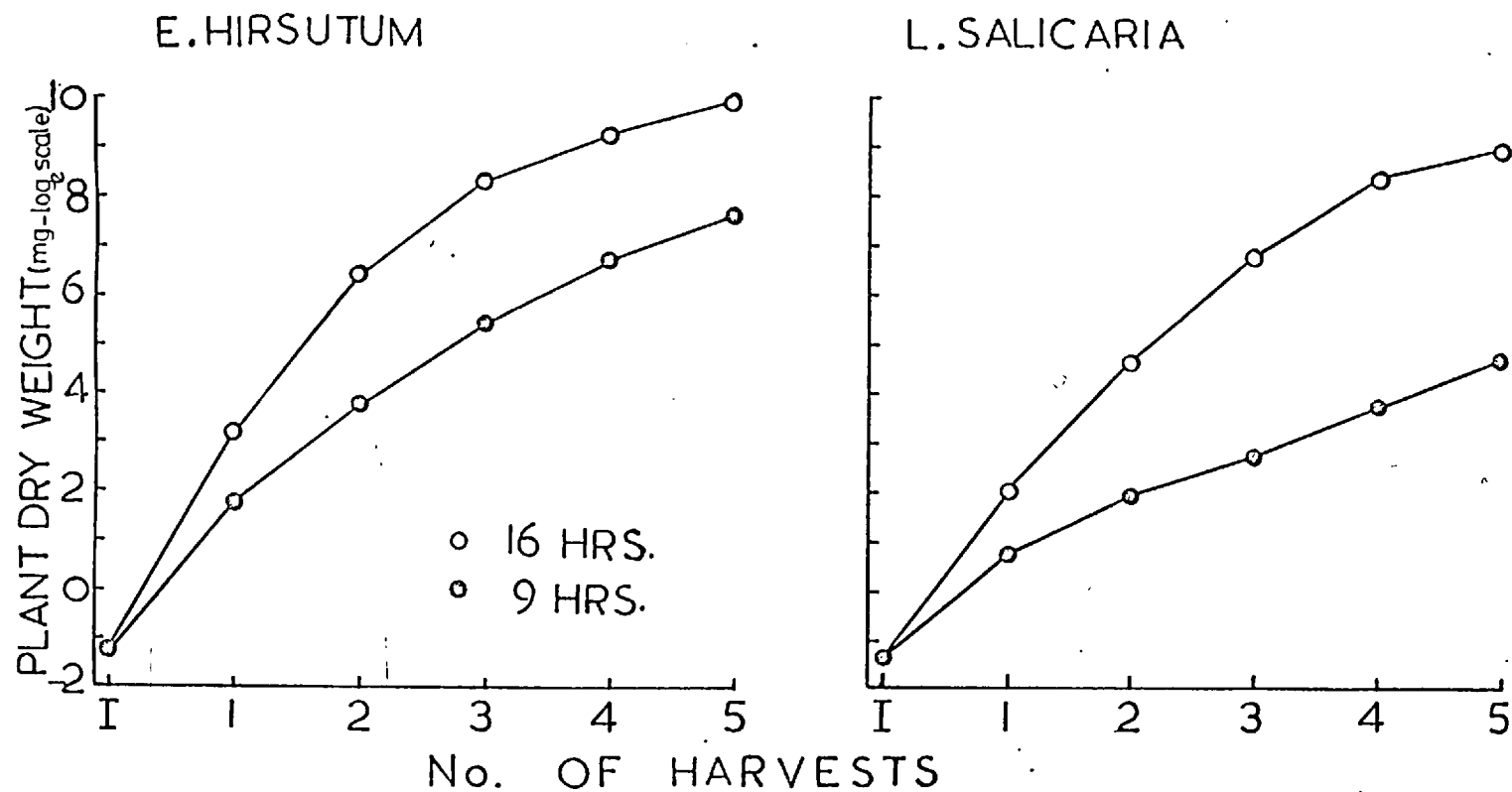


FIG. 23. Effect of daylength levels on increase of plant dry weight with time.

short day conditions in nature, in Britain, so it can be expected to show by far the least growth in terms of dry matter production in experimental conditions. Differences in the total dry weight in the long day plants of the two species can, in general, be attributed to the effect of seed size, as Epilobium seed is three times as heavy as that of Lythrum. As shown in later experiments (Experiment XII) when seedlings, of equal size, of the two species were transplanted in standard culture solution the plants showed similar weights at the end of the experiment. However, the difference in the total dry weight in the two species under short day conditions cannot be attributed to the difference in seed size. The possibility of the suppressive effect of temperature can also be excluded, as during the course of the experiment it fluctuated between 20 and 26°C. and it was never below 18°C. On the other hand the great reduction in the dry weight of Lythrum in the 9 hour treatment is suggestive of suppression of its growth under short day conditions.

However, difference in the response of the two species suggests that in short photoperiods, Epilobium can make appreciable growth and Lythrum none.

2. Increase of leaf area

Fig. 24 shows that the pattern of increase of leaf area with time, in each species, follows a similar course to

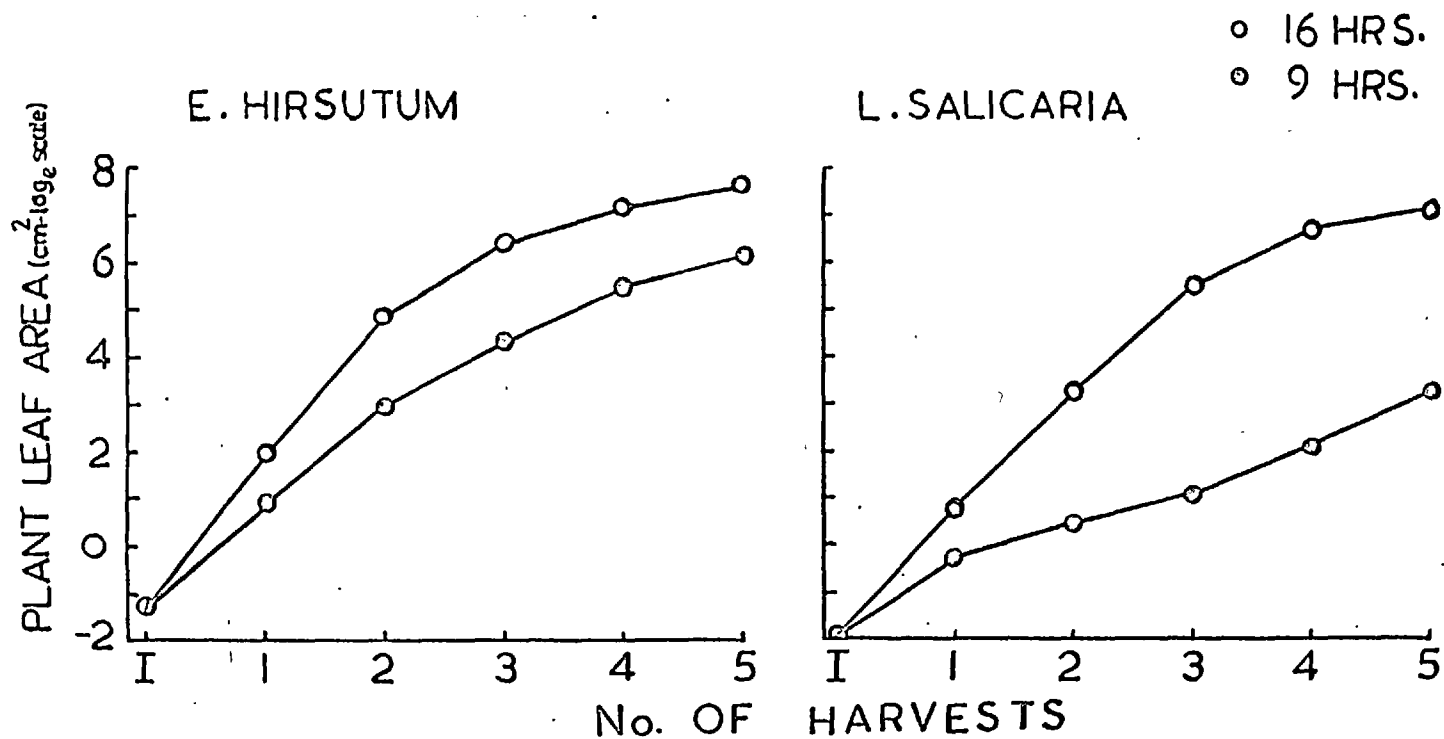


FIG. 24. Effect of daylength levels on increase of plant leaf area with time.

the dry weight increment curve in each photoperiod. In Lythrum, however, reduction in leaf area is greater, proportionately, than the dry weight in the short photoperiod.

3. Ratio of mean relative growth rate to
mean relative rate of leaf area increase

Fig. 25 shows that in Epilobium the pattern of α values with time in the two day length treatments is similar, but there is a difference in the degree of expression. Lower values in the 9 hour treatment are due to the proportionately greater increase in leaf area to the dry weight increase when compared with plants from the 16 hour treatment. The contrasting pattern of α values in Lythrum in the two day length treatments is suggestive of different morphogenetic differentiation. In plants from the 16 hour treatment, during the early phase of growth, there was a tendency to proportionately greater leaf area increase compared to the dry weight increase, so there was a steady decline in α values up to harvest three, in the later phase of growth the proportion of increased growth rate to leaf area increase was reversed and there was a rise in α values. In the 9 hour treatment the higher α values, in the earlier period of growth, were due to relatively little leaf area increase and, in the later phase of growth, there was a greater relative leaf area increase so that α values showed a downward trend.

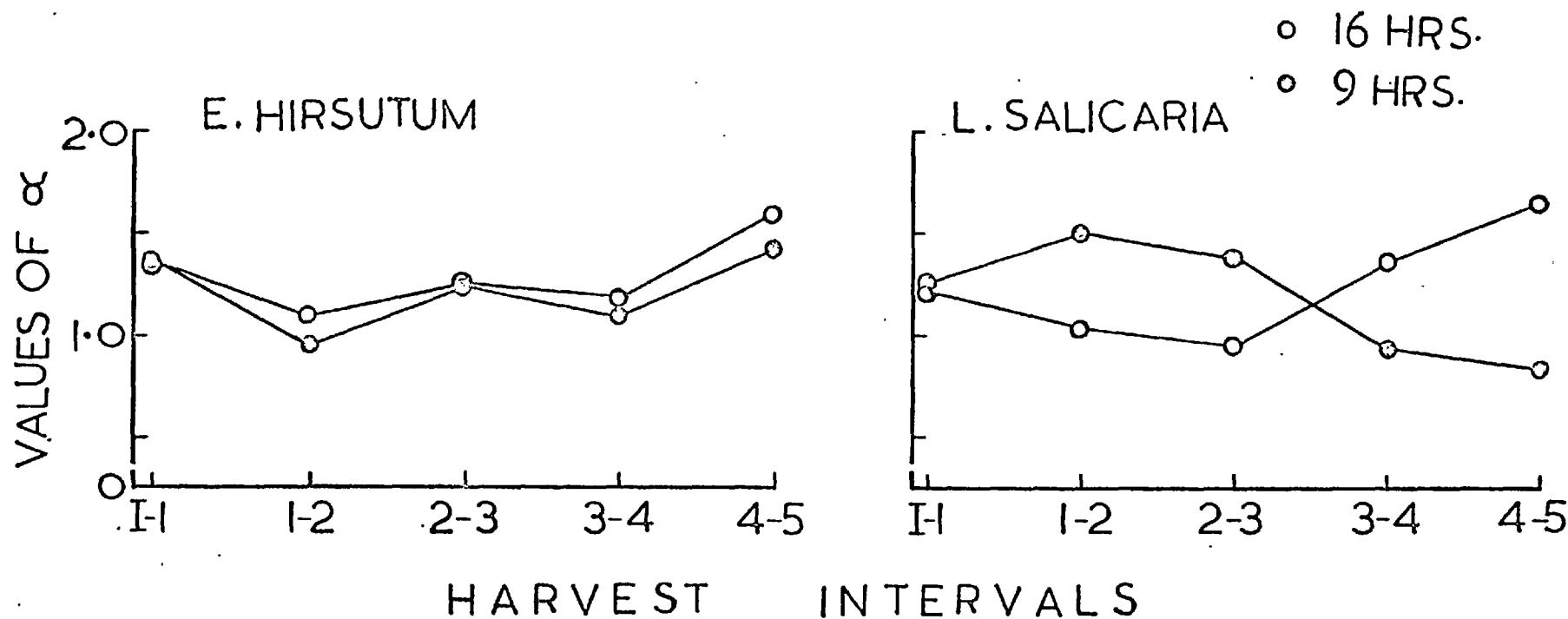


FIG. 25. Effect of daylength levels on the ratio, mean relative growth rate to mean relative rate of leaf area increase (α) for successive harvest intervals. (I = initial harvest)

It is clear from the α index that in the 9 hour treatment growth did not proceed as an integrated whole and there was lack of co-ordination between the leaf area and dry weight increase of the plant. Due to this, the plant could not grow as an efficient functional photosynthetic entity. This lack of co-ordination between leaf area increase and dry weight increase can be due to a suppression of growth of the leaves, which may have a physiological basis as well, as is indicated by the Giberrellic acid experiment described later. Comparatively better growth in Epilobium in the 9-hour treatment is due to this plant not suffering from this lack of co-ordination so that by increasing the proportion of photosynthetic tissue in the form of leaves rather than storing its photosynthate in the roots, and thus increasing the proportion of respiratory tissue, is to its advantage.

4. Mean unit leaf rate

The different patterns of morphogenetic differentiation in the 9 hour treatment of the two species can be seen in their mean unit leaf rates as well, this is shown in ~~Fig. 26 (calculated from initial to a series of subsequent~~ ~~harvests) and~~ Fig. 27 (calculated between the harvest intervals). From both these figures it can be seen that in the 9 hour treatment Epilobium follows the same pattern as in the 16 hour treatment, but the difference between the two is of

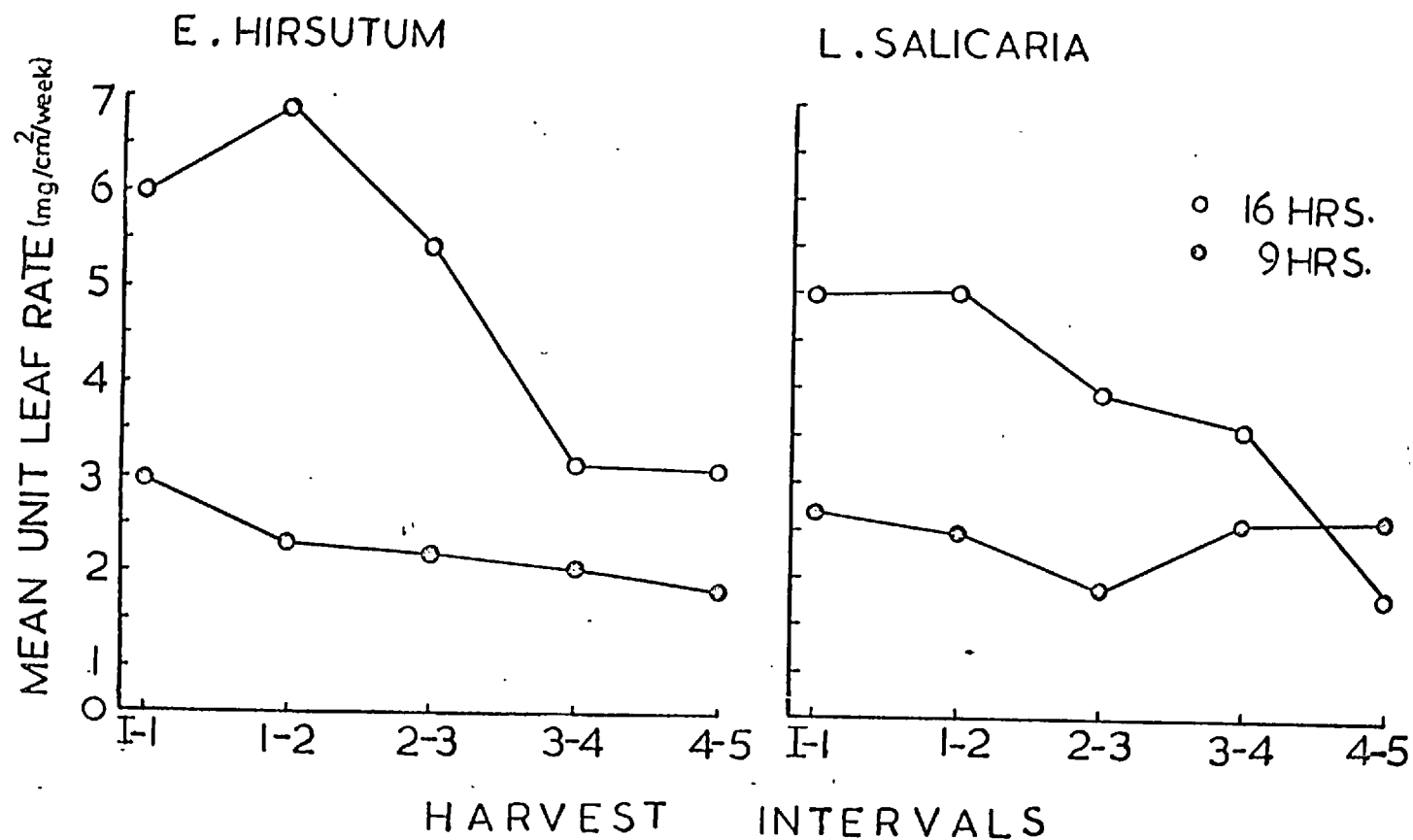


FIG. 27. Effect of daylength levels on mean unit leaf rate.
 (Calculated between the successive harvest intervals)
 (I = initial harvest)

high magnitude.

In the 9 hour treatment Lythrum plants there is very little increase in mean unit leaf rate with time (~~Fig. 24~~). In Fig. 27 the Lythrum plants in the 16 hour treatment show a steady decline in the values with each harvest interval. Values of the 9 hour treatment plants remain more or less similar for all the intervals except (2 to 3) where there was a sudden increase in the leaf area.

5. Leaf area ratio

Fig. 28 shows that in Epilobium both long day and short day plants follow the same pattern of gradual decrease in the leaf area ratio with time, but excessive leafiness in the 9 hour treatment plants can be appreciated by their very high leaf area ratio values. In Lythrum, again there is contrast in the pattern of the results from the two treatments. Because of the suppression of leaf expansion in the earlier harvest, there is a decline in the values and a rise towards the last two harvest (4 and 5) due to a sudden leaf expansion.

6. Root/shoot ratio

As can be seen in Fig. 29, the pattern is similar for the two treatments of Epilobium and the values are the same at the last harvest. It is clear that under short day illumination the dwarfed shoot system of Epilobium was

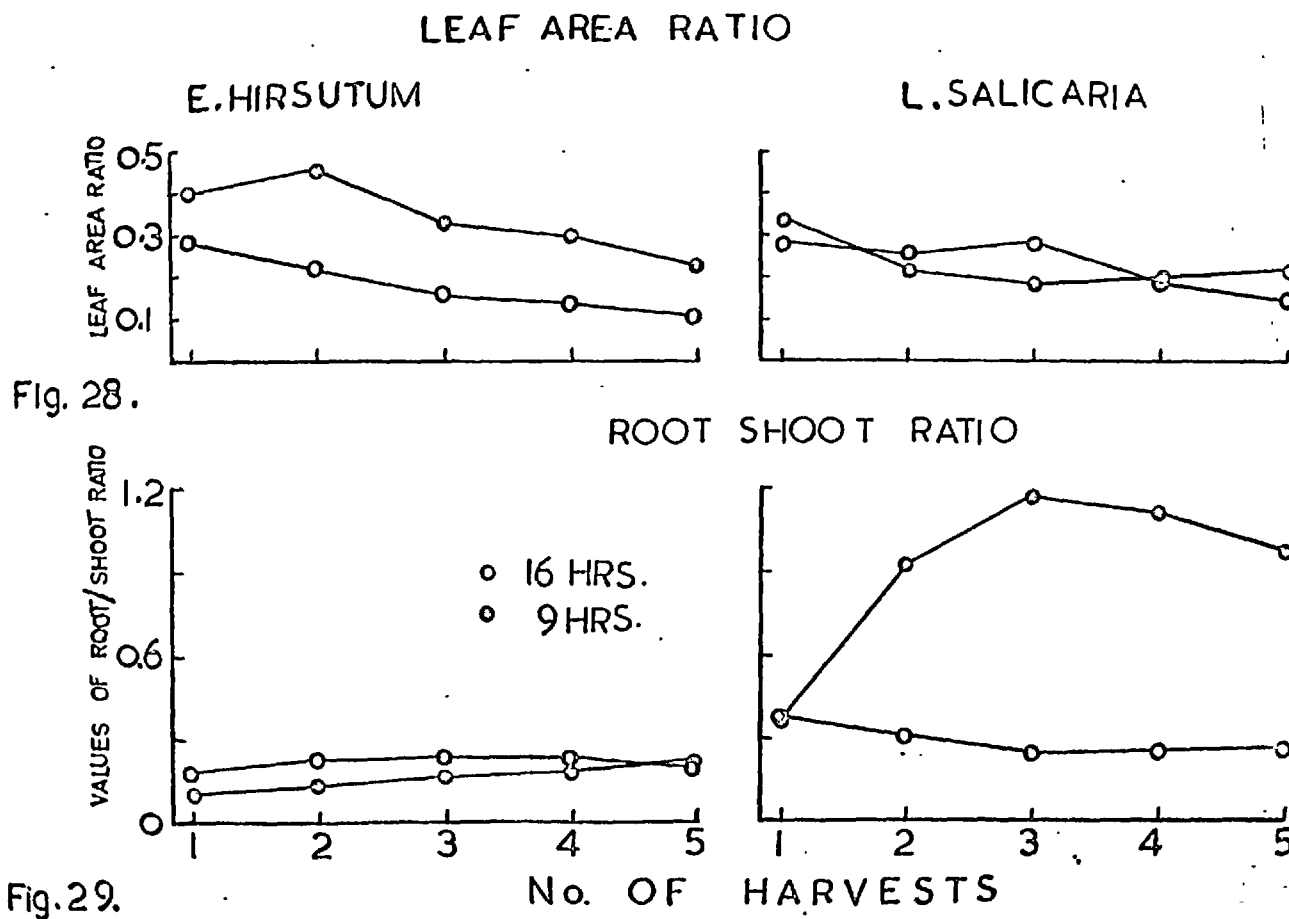


Fig. 28.

Fig. 29.

Effect of daylength levels on growth.

FIG. 28. Leaf area ratio.

FIG. 29. Root/Shoot ratio.

furnished with a correspondingly meagre root system. The attainment of similar values of root/shoot ratio towards the end of the experiment showed that the growth of both shoot and root, although greatly retarded, was approximately to the same extent at least in the last harvest. Thus the growth of the root system appears to be directly related to the shoot growth. This tendency was also shown by Weaver and Himmel (1929) in many long day plants, such as Red clover, Radish, Iris and Oats.

In the long day Lythrum plants there is a gradual decrease in values with time, but in the short day plants there is a sharp rise followed by a slight decline in the last harvests, and the pattern of values is reverse to that of long day plants.

The different patterns of root/shoot ratios in the 9 hour treatment plants of the two species indicate that in Epilobium the degree of the expression of shoot and root is equally curtailed by short day conditions but in Lythrum there is greater diversion of assimilates from shoot increase to increased root production.

7. Percentage proportion of leaf, stem and root.

The differences in the behaviour of the short day plants of the two species, as seen in the various estimates of growth processes, can be better understood by the study of

the percentage proportions of their root, stem and leaves. This is shown in Fig. 30. In Epilobium the pattern of growth of the three components is essentially similar, but the large difference in magnitude of leaf and stem proportions in the two treatments is so great that this similarity tends to be obscured. The root proportion in the two treatments follows exactly the same pattern and the value is the same at the last harvest. The main difference between the long day and short day forms is that in the long day, with the passage of time, there is an increase in the proportion of stem weight at the expense of the proportion of leaf, but this does not happen in the short day form and leaf proportion remains the larger component of the plant. It can be seen that, although the proportion of root to shoot in the last harvest is similar in the two treatments, the proportions within the shoot differs in that the long day plants are more stemy and the short day plants more leafy.

On the other hand, in the short day Lythrum plants the pattern of the proportions of root, stem and leaves is the reverse to that of its long day form. In the long day Lythrum plants the pattern of the three components is similar to the long day Epilobium plants, but in the short day plants there is a gradual increase, with time, in the root proportion at the expense of the proportions of both leaves and

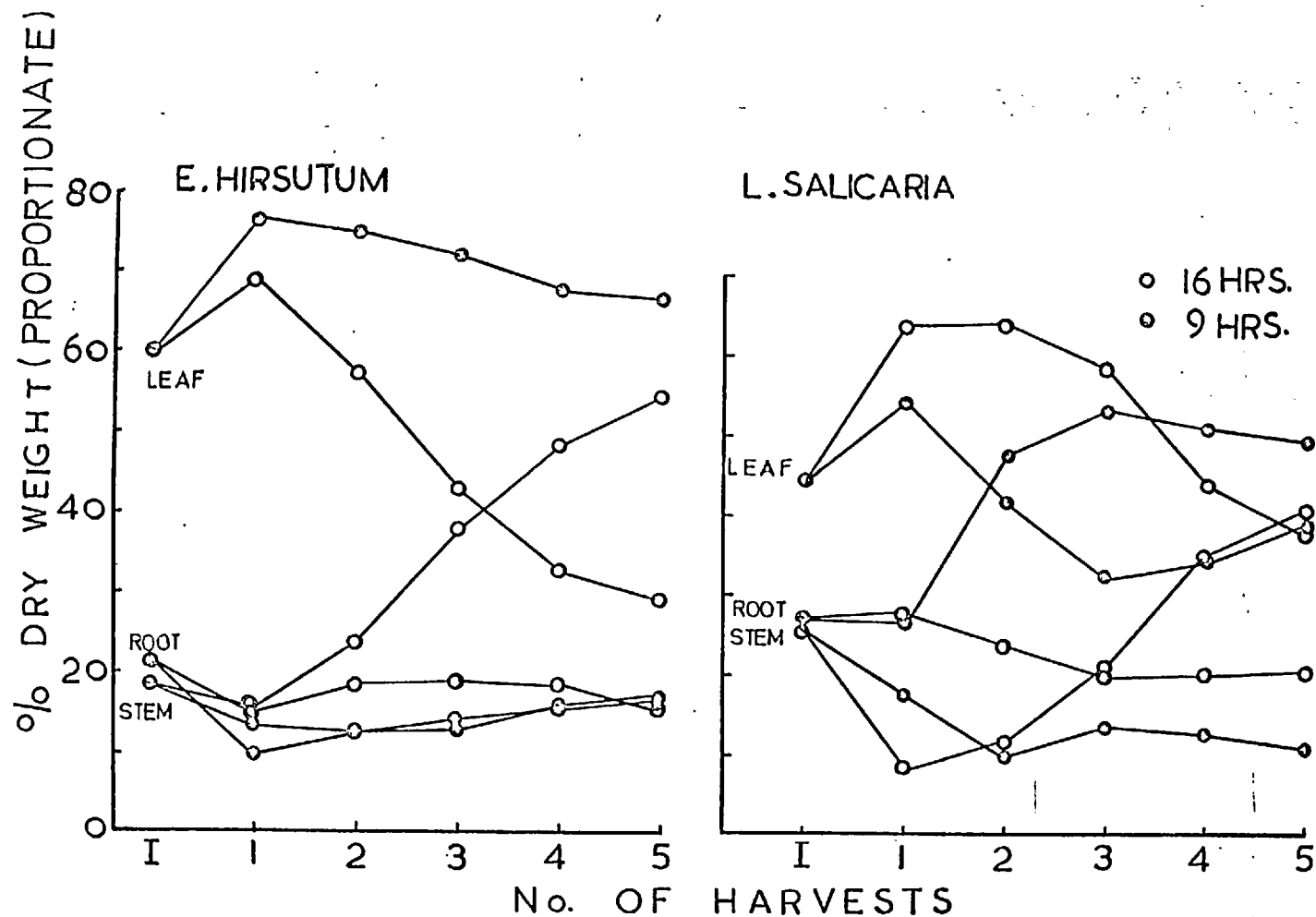


FIG. 30. Effect of daylength levels on percentage proportionate distribution of total dry weight to leaves, stems and roots at successive harvests.

and stem. Extreme suppression of leaf and stem development in the 9 hour treatment can be seen from the sharp decline in their proportions in the first three harvests, but in the later harvests there is the same rise in the leaf proportions.

It is interesting to note that in the short day Epilobium plants, leaf is proportionately the largest component of the plant, while in the short day Lythrum plants root is the largest component.

As emphasised in Experiment V, these morphological patterns are genetically controlled and not changed in nature by the external environments which affect only the degree of expression. This is true in the case of Epilobium since the basic pattern remains the same but with a very marked difference in the degree of expression. Even in the 9 hour treatment, towards the last harvests, the plants showed a small, but definite, tendency for an increase in stem proportion at the expense of leaves similar to that of the 16-hour plants. On the other hand, in Lythrum in short day conditions the pattern is completely changed because of the suppression of growth of the plants.

Discussion

The data presented show that there was a significant effect of difference in the duration of daylight on the dry matter production and the general tendency was a reduction in

the dry matter production in the short day conditions. There was a striking contrast in the dry weight gain under short day conditions. In Epilobium the reduction in the dry weight seemed to be proportional to the reduction in the duration of the light period and dwarf rosettes were produced, but in Lythrum there was no proportionate reduction in growth but a suppression of growth and the whole development of the plant seemed to be blocked. Furthermore, the effect of the short day condition on leaf and stem was different in the two species. While in Epilobium only stem elongation was affected, in Lythrum both leaf growth and stem elongation were equally affected. The result was that Epilobium could grow into small rosettes while Lythrum could not grow at all. These differences seem to be innate and characteristic features of the two species, at least under the circumstances which simulate conditions of their natural growing season.

These contrasting growth patterns of the two species, in short day conditions, can be understood in terms of the presence of a compensatory mechanism in the morphogenetic differentiation of Epilobium, where 70 to 80% of the assimilates were being employed in increasing leaf area in lieu of the retardation of stem growth. However, in Lythrum, because of the absence of this compensatory leaf area increase, assimilates were diverted to the root. This re-direction of

the assimilates under short day conditions was such that in Epilobium the proportion of the photosynthetic tissue was much higher than the non-photosynthetic tissue which was favourable for the survival of the plant. In Lythrum this proportion was reversed and led to the suppression of growth from the very beginning, resulting in the elimination of the plant. Various estimates of the growth have shown the different morphogenetic differentiation of the two species under short day conditions.

It is concluded that the growth form of the shoot of Epilobium hirsutum is dependent on day length, and the plant is capable of growth as a viable photosynthetic entity in short day conditions. Myerscough and Whitehead II (1967) also reported short day rosettes in other species of Epilobium, such as E. montanum and E. adenocaulon. On the other hand, in Lythrum salicaria short day conditions have a suppressive effect on growth, and the plant can grow only under long day conditions.

Ecological Importance

The ability of Epilobium to grow under short day conditions gives it an important advantage over Lythrum as it can grow during the winter, in Britain, if the seedlings become established in autumn. This ability may be interpreted

as an ecological adaptation of its growth under natural conditions.

Since rosettes are capable of growing to a fairly big size, in favourable conditions plants may be able to make appreciably more growth in winter. During this long period of vegetative growth daughter rosettes may also develop from the axillary buds of the lower leaves, with their own root system, and if separated accidentally from the parental plants will develop into separate plants. This tendency of vegetative multiplication and relatively high growth rate in short day conditions may underlie the aggressiveness of the species in the habitats where it succeeds to establish itself, as claimed in the introduction.

Experiment VII

Effect of different photoperiods on growth and the determination of the critical photoperiod.

At the end of harvest five, in the last experiment, six short day plants of each species were tested for their response to six other photoperiods (selected at one hour intervals, as 10, 11, 12, 13, 14 and 15 hours) to find out the critical photoperiod for flowering in each species. Pots

were clearly marked, exposed to the particular photoperiod and then returned to the dark. The whole operation was carried out manually as there were not adequate facilities to raise six automatic light controlled chambers. The treatment was started on 2 March, 1967 and completed on 21 April, 1970.

Observations

The final appearances of the plants are shown in Plate 6 (a and b).

Response was very quick in the 14 and 15 hour photoperiod in Lythrum in the first week of treatment, stem elongation being very marked. By the end of the second week plants of both day lengths started flowering. During this period response was negligible in the 10 and 11 hour photoperiod plants and very small in those in the 12 and 13 hour photoperiods. The 12 hour treatment plant did not make any great progress in the third week, but there was an abrupt elongation in the shoot of the 13 hour treatment plant followed by flowering in a few days. There was no flowering at all in the 12 hour plant, even after a further four weeks of treatment.

In the 13 to 15 hour photoperiod Lythrum plants two important changes were noted before flowering. First, there was a tremendous stem elongation and all the suppressed shoots also showed elongation. There was no elongation in the



Lythrum salicaria (a)

Scale: 1" = 30 cm.



Epilobium hirsutum (b)

PLATE 6 Growth form of plants in a range of photoperiods. (Photographed after 7 weeks in the treatments. These plants were previously treated in a 9-hour photoperiod for 10 weeks).

lower internodes of the already existing stem but it became thicker and woody. Secondly, the leaves showed great expansion and changed from small, lanceolate - oblong shape to elliptical - ovate leaves with cordate bases. In plants of the 12 hour treatment leaves were completely transformed, but stem did not show enough elongation to develop into a floral shoot. On the basis of these observations, 13 hours seems to be the critical photoperiod, but the development of a fairly large inflorescence suggests that the actual critical photoperiod to initiate flowering may be between 12 and 13 hours and most probably 12.5 hours.

Unlike Lythrum, Epilobium showed an equal response in all the day lengths in the first and second week of treatment. However, in the third week the 15 hour photoperiod plant showed complete transformation, its stem elongated rapidly and started flowering in the fourth week. A week later the 14 hour photoperiod plant also started flowering but, comparatively, it was a much smaller plant than the 15 hour treatment plant, fewer flowers being produced. While in Lythrum plants in these photoperiods were similar and flowered at the same time, Epilobium plants in other photoperiods showed great elongation in stem but did not flower in the seven weeks of treatment. So, the critical photoperiod for Epilobium is 14 hours.

In Epilobium, in general, the response to different photoperiods was very different from that of Lythrum. Although the transformation of a vegetative shoot into a floral shoot was slower and delayed there was still a definite response at all levels of day length. As seen in Plate 6, there was an elongation of the internodes in the 10 hour photoperiod plant, but the leaves remained large as in the 9 hour treatment. In the 11 hour treatment the plant was longer than that in the 10 hour treatment but had, essentially, a similar structure. In the 12 hour treatment, along with stem elongation there was a change in the leaf structure and, in addition to the large leaves of the short day form, most of the leaves of the new shoot were small and oval to elliptical in shape. This trend reached its climax in the 13 hour treatment plant which was extremely stemy with spirally arranged oval leaves along the length of the shoot. Even the 14 and 15 hour treatment plants showed these small, oval leaves in the middle portion of their stems, but the rest of the leaves were like those of a normal plant.

It appeared that transformation in Epilobium was a gradual and phased process and the plant could develop only up to a particular phase in each photoperiod, beyond which its development stopped. This was evident from the behaviour of the 13 and 14 hour photoperiod plants, and the retention

of small oval leaves on the stem of the 14 hour photoperiod plant show that it passed through this phase earlier, in a very short time, but the 13 hour photoperiod plant could not develop beyond this phase.

Discussion

Response to a range of photoperiods is markedly different in the two species. Response was abrupt and quick in Lythrum and there was a sudden transformation from a non-flowering into a flowering plant. In Epilobium the response was diffused and there was a phased transformation of a non-flowering plant into a flowering one.

This differential response can be attributed to their growth behaviour under short day conditions and can be better understood on the basis of the proportional development of their different parts.

In Epilobium, under short day conditions, leaves constitute 70% of the plant. During morphogenetic transformation, with the increase in photoperiod the stem increased at the expense of the leaves and the assimilates used in the leaf production were employed in the stem formation. The degree of this transformation, from leafy to stemy conditions, is dependent on the available photoperiod. This transformation was at its climax in the 13 hour photoperiod plant,

but then there was not enough photosynthate to produce extra leaves and flowers. At this stage the plant had a thick, juicy stem with spirally arranged tiny oval leaves, while leafy stolons at the base provided necessary photosynthetic material. In the 14 hour photoperiod the plant was able to produce the critical minimum photosynthate necessary for flowering etc. It is clear that a plant had to re-adjust the whole of its internal balance to change from a leafy rosette into a normal stemy plant. This re-adjustment takes a longer period of time and long photoperiods to be completed.

In Lythrum there was suppression of growth under short day conditions and it continued up to the 12 hour photoperiod, but as soon as the inhibitory influence of unfavourable photoperiods was removed and the most favourable or critical photoperiod was reached, the dwarf plant suddenly shot up into a fully fledged normal flowering plant. Like seed germination behaviour, the perception of a favourable photoperiod was an all or none phenomenon and there was nothing inbetween. In other words, in Lythrum when the minimum requirements were fulfilled the plant was triggered off to develop into a normal plant.

Response was essentially different in the two species, in Epilobium it was a phased and gradual morphogenetic transformation, but in Lythrum it was a sudden surge of

growth as a result of removal of inhibitory forces.

Ecological importance

This slow perception of photo-stimulus in Epilobium can be interpreted as an adaptation to its occurrence in nature. The over-wintering rosettes are enabled to continue their growth in response to the increasing day lengths with the arrival of summer, and gradually develop into a flowering shoot when the required day length is reached. So, slow response is an adaptation in Epilobium leading to its establishment and survival in nature. In Lythrum there is no winter growth in Britain as germination can take place only in the summer when the critical photoperiod necessary for flowering is naturally provided.

Both plants are, therefore, very well adjusted to their growth in nature. The ability to grow under short day conditions in Epilobium seems to be complementary to its germinability at low temperatures, which coincides with short photoperiods in nature, and in these terms the difference in the response of the two species to a range of photoperiods was determined by the differences in their biology.

It is, therefore, concluded that slow response in Epilobium may be of adaptative significance during the long course of growth from germination to flowering and in passing from minimum to maximum photoperiodic conditions in nature.

Experiment VIII

The effect of Gibberellic acid on the shoot elongation of short day plants.

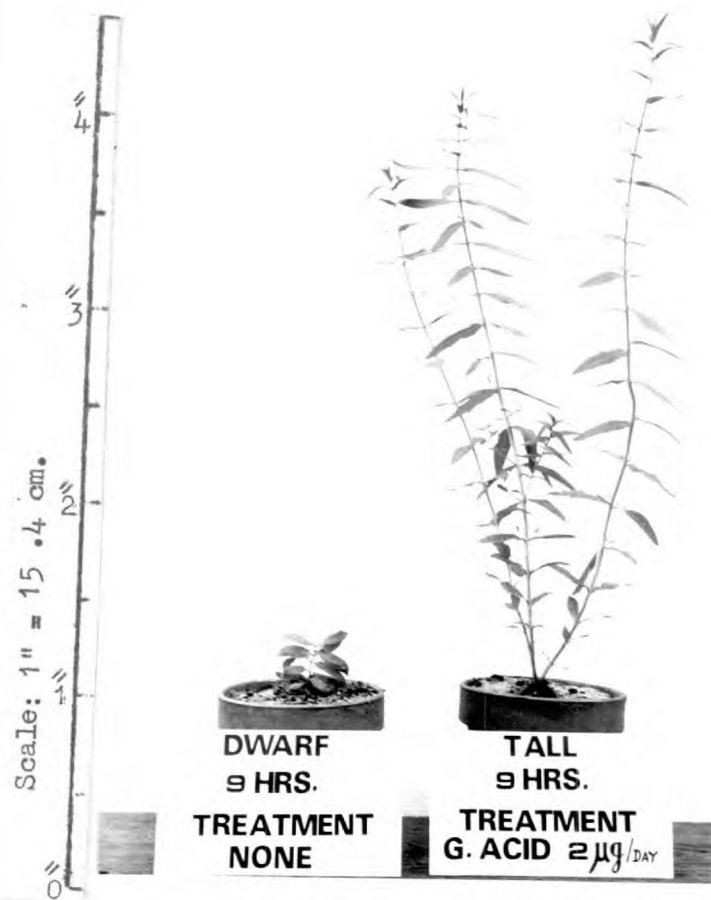
At the end of Experiment VII two short day plants of each species were treated with Gibberellic acid.* 0.1 ml. of 20 p.p.m. Gibberellic acid solution was applied to the shoot apex, by a micro-pipette, regularly after every 24 hours for 30 days, and the treated plants were kept along with untreated plants under 9-hour daily illumination. In an additional short day Lythrum plant, equal treatment was given to the suppressed shoots as well, along with the leading shoot.

Observations

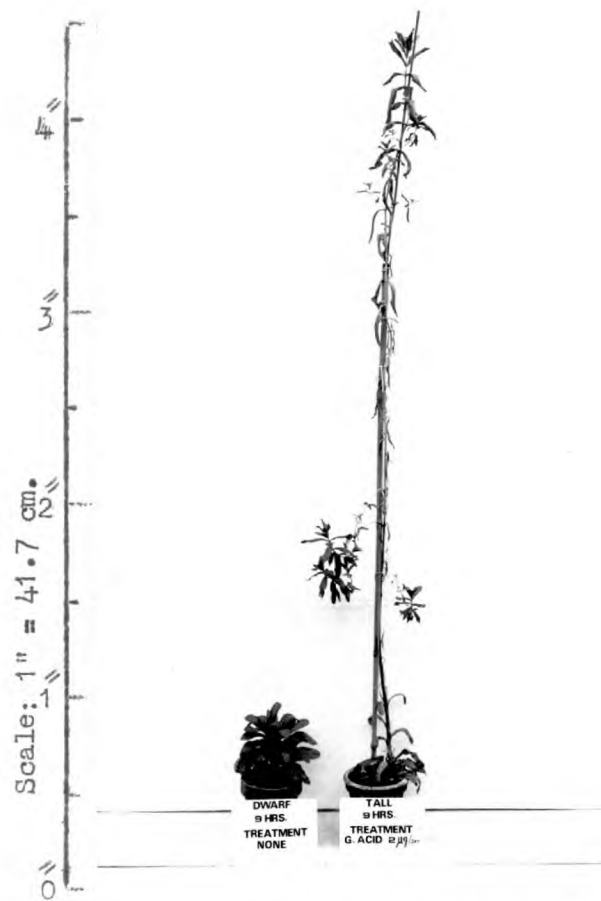
The final appearance of the plants at the end of the treatment is shown in Plate 7 (a and b). Epilobium was quick to respond, and stimulation of growth was very marked by the end of the first week. Lythrum started responding slowly after the first week of treatment. In Lythrum all the treated plants responded similarly whether treatment was applied to the leading shoot or to all the shoots. Side shoots were also produced in the axil of the leaves.

Measurements of the height of the plants at the end of the treatment are as given in Table 8.

* Treatment started on 4th March and finished on 3rd April.



Lythrum salicaria (a)



Epilobium hirsutum (b)

PLATE 7 Effect of Gibberellic acid treatment on shoot elongation of short-day plants.
(Photographed after 30 days of treatment. These plants were previously treated in a 9-hour photoperiod for 10 weeks.)

TABLE 8. Mean Height of Gibberellic Acid
Treated Plants (in cm.)

<u>Lythrum salicaria</u>	..	..	..	54.0 cm.
<u>Epilobium hirsutum</u>	..	..	..	175.0 cm.

Both plants showed complete morphological changes. In Lythrum already formed internodes started elongating and the shoot continued growth at the apex. Leaves also showed expansion and changed shape from oblong to ovate with cordate bases, but there was no flowering. In Epilobium, the stem showed tremendous elongation but the leaves did not change much; they were extremely soft and oblongly elongated with their margins rolled inwards. After the second week of treatment most of the leaves in the middle of the stem started decaying.

Discussion

From the results it is clear that application of Gibberellic acid removed the inhibition in the apical meristem imposed by the short photoperiod, and full growth of stem and leaves started. Sachs et al (1959) established that growth caused by Gibberellic acid is due to stimulation of cell division in a region immediately below the stem apex. Haber and Luippold (1960) found that cell elongation was also stimulated.

Growth stimulation by Gibberellic acid has been shown by many workers: Phinney et al (1957) on dwarf corn; McCombe and Carr (1958) on dwarf peas; Wittever and Bukovac (1957.a) on bean plants; and many others.

Although application of Gibberellic acid changed the vegetative growth from that typical of short day conditions to a form resembling that of long day conditions flowering did not occur.

Experiment IX

The effect of a light break on growth in short photoperiodic conditions. (May, 1967)

The suppression of growth in Lythrum and the ability of Epilobium to grow under short day conditions together with the difference in their response to a series of photoperiods led to the hypothesis that the photoperiodic control of growth in these two plants is not simple.

In Epilobium, stem elongation and flower production were two distinct and separate phenomena, while in Lythrum they were so interwoven and interdependent that it is impossible to think of them as separable.

Another question arising from the previous experiments was whether stem elongation and flowering depended upon

the availability of a critical quantity of light energy or a critical photoperiod or both.

Several workers (Melchers, 1956; Snyder, 1940; Bunsow, 1953; Carr, 1952; Wareing, 1954; Bunning, 1960; and Hamner, 1960) have shown that a light perturbation in the middle of the long dark period of a short day treatment produced the same photoperiodic response as a long day.*

Methods

Two specially made chambers (each 6ft.x 3ft.x 5ft.) were placed adjacent to each other on the floor of the greenhouse. Each was fitted with an exhaust fan and 12 adjustable fluorescent tubes, each 5ft. long. Each chamber was completely covered with thick black polythene and maximum precautions were taken to exclude the natural daylight. The illumination level was 900 F.C. Since this experiment was performed in the summer, the temperature was higher than in Experiment VI and varied from 27 to 32°C. on very hot days, but usually daytime temperatures varied between 22 and 25°C.

One chamber was set at 9-hours continuous illumination, from 9.00 a.m. to 6.00 p.m., and the other at 8-hours continuous illumination, from 9.00 a.m. to 5.00 p.m., and 1-hour, of the same intensity, at midnight, from 12.00 p.m. to 1.00 a.m. By this arrangement two purposes were achieved.

* (see - Environmental control of plant growth, by Evans, 1963)

1. In both chambers the plants were exposed to a short photoperiod of 9-hours, continuous in one and discontinuous in the other ($8 + 1 = 9$ -hours). So the energy received by the plants in each chamber was similar though received differently.

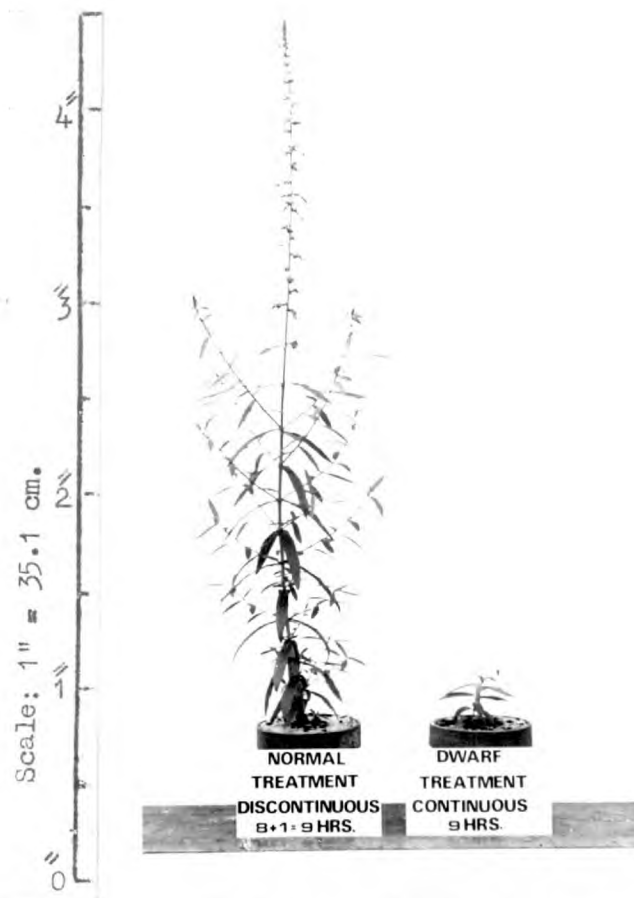
2. In the chamber with discontinuous illumination, the continuity of the 15-hour dark period was broken by the interpolation of one hour of illumination.

Seeds were germinated at 25°C . and seedlings of uniform size were transplanted in an advanced stage of growth, when they were forming a second pair of leaves. 125 pots per species per treatment were prepared. The rest of the experimental procedure was the same as in Experiment V. Six harvests were made regularly at intervals of two weeks, in addition to the initial harvest at the time of transplantation. 15 replicates were taken for each species for each treatment. A seventh harvest was made in Lythrum, five weeks later, as most of the lower leaves in Epilobium, in both treatments, were decayed at this stage, so the plants were not considered suitable for this harvest.

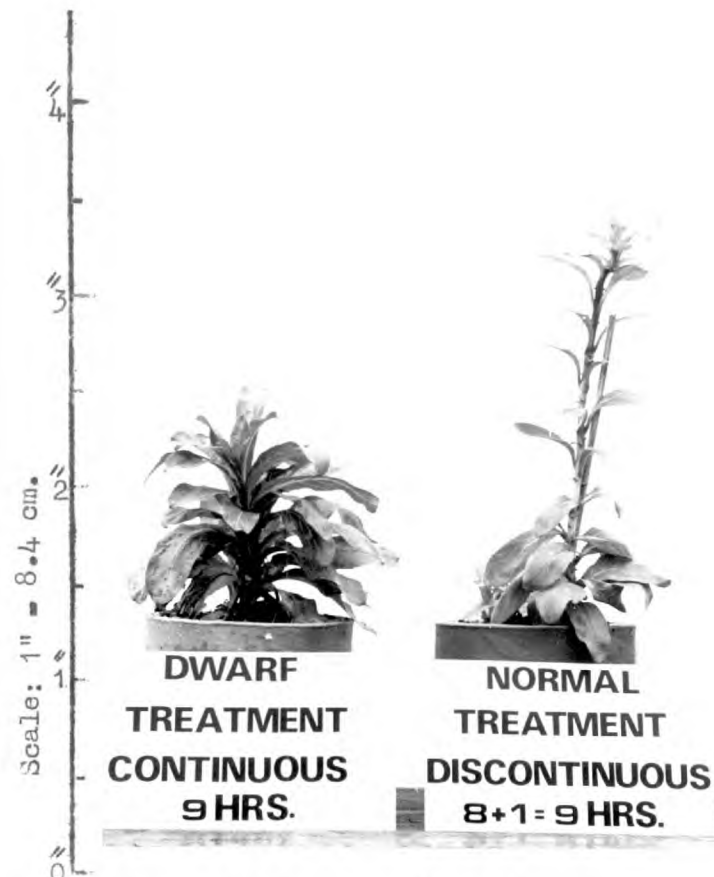
Observations

The appearance of the plants at the time of the sixth harvest is shown in Plate 8 (a and b).

Both Epilobium and Lythrum in the 9-hour continuous



Lythrum salicaria (a)



Epilobium hirsutum (b)

PLATE 8 Effect of light-break on growth form in short photoperiodic conditions.
(Photographed after 90 days in the treatments, i.e. at the time of
Harvest VI).

photoperiod showed growth similar to that described for these plants in Experiment VI, but with the difference that suppression of growth in Lythrum was not so great since the seedlings transplanted in this experiment were in a more advanced state of growth.

In the 8 + 1-hour treatment Epilobium plants did not show much difference from the 9-hour treatment plants, but the stem showed a tendency to elongate towards the last two harvests and the leaves became smaller in size and arranged spirally on the stem. However, the increase in stem length was not very remarkable and plants in the two treatments were very similar.

On the other hand, Lythrum, in the discontinuous photoperiod, showed a complete transformation from a dwarf to a typical long day plant. At the time of harvest three, in this treatment, the stem started elongating and there was initiation of axillary shoots. By the end of harvest four the plants were growing like normal long day plants, with side shoots considerably elongated and inflorescences being formed. In the last two regular harvests the plants showed tremendous elongation and the inflorescences measured more than 25 cm. in length.

The final size of the plants in the various treatments and the number of nodes bearing fully expanded leaves at

the time of the last harvest are given below in Tables 9 and 10.

TABLE 9. Size of Plants at the Sixth Harvest

Length of stem in cm.

<u>Plant</u>	<u>Treatment</u>	
	8 + 1-hour	9-hour
<u>Lythrum</u>	128.8($\pm$ 10.6)	10.2($\pm$ 2.8)
<u>Epilobium</u>	18.4($\pm$ 2.2)	12.8($\pm$ 1.6)

TABLE 10. Number of Nodes Bearing Expanded Leaves

on the Main Stem at the Sixth Harvest

<u>Plant</u>	<u>Treatment</u>	
	8 + 1-hour	9-hour
<u>Lythrum</u>	72 - 82	14 - 18
<u>Epilobium</u>	24 - 30	26 - 28

Although the 8 + 1-hour photoperiod plants developed into normal long day plants they were not as well developed as the 16-hour photoperiod plants, as shown in Plate 9.



PLATE 9.

LYTHRUM SALICARIA

Growth form in a day length of continuous 16 hours light (right, long photoperiod)

Growth form in a day length of continuous 9 hours light (central, short photoperiod)

Growth form in a day length of discontinuous 9 hours (8+1) light (left, short photoperiod)

(Photographed at the time of harvest VI, i.e. after 90 days of treatment.)

The main stem and side shoots were weaker and thinner in the 8+1-hour treatment compared to the strong and woody stem and branches of the 16-hour treatment. However, the leaves were greener than in the 16-hour treatment. Although the inflorescence on the main stem in the two types of plants was more or less similar in length, in the 16-hour treatment whorls of the flowers in the spike were densely arranged with four flowers in each whorl while in the 8+1-hour treatment whorls were sparsely arranged with two to three flowers in each.

Upper side shoots also produced small inflorescences after a long time. On the whole, plants in the 8+1-hour treatment looked less developed than those in the 16-hour treatment.

Another important point was that all the flowers were abortive and not a single one developed into fruit even after very long treatment, and by the time of the seventh harvest (at an exceptionally longer interval of 5 weeks) all the flowers had fallen away from the plant.

Primary data was recorded as before.

Results

The results, in terms of different growth analysis estimates, were as follows.

1. Increase in dry weight

Fig. 31 shows the increase in dry weight with time. The general pattern is similar in the two species.

In Epilobium dry weight is higher in the 9-hour treated plants for the first four harvests but later the 8 + 1-hour treatment plants take over. On the other hand, dry weight in Lythrum in the 9-hour treatment is very much reduced compared to the 8 + 1-hour treatment in all the harvests. It is eight times less in harvest four and approximately four times less in the rest of the harvests.

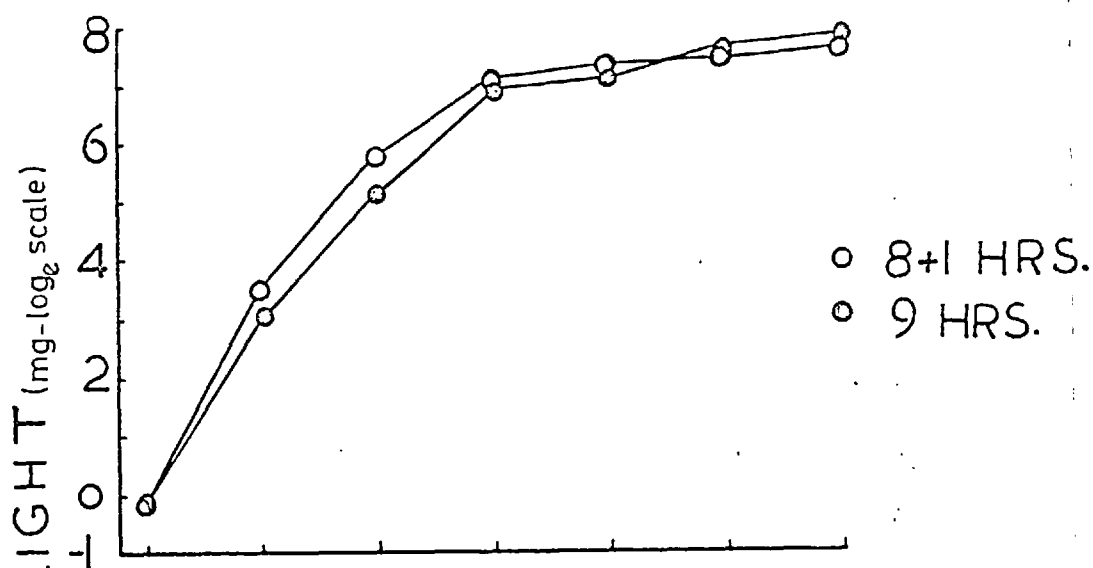
2. Increase in leaf area

This is shown in Fig. 32. In Epilobium it follows the same pattern as dry weight. Lythrum plants in the 8 + 1 hour treatment show a tremendous increase in leaf area after the first harvest. At intermediate harvests leaf area is eight to ten times higher than in the 9-hour treatment and in the later harvests the ratio is 4 : 1. (See Appendix)

3. Ratio of mean relative increase in growth rate to mean relative leaf area increase (α values)

These values, calculated for the periods between the successive harvest intervals, are shown in Fig. 33. In Epilobium, in both treatments, there is relatively greater leaf area increase than dry weight increase, and there is a gradual fall in α values which reaches its climax in the 9-hour treatment at the fourth interval. In the last two harvests, relative dry weight increase is much higher than the rate of leaf area increase and the α values rise very sharply.

E. HIRSUTUM



L. SALICARIA

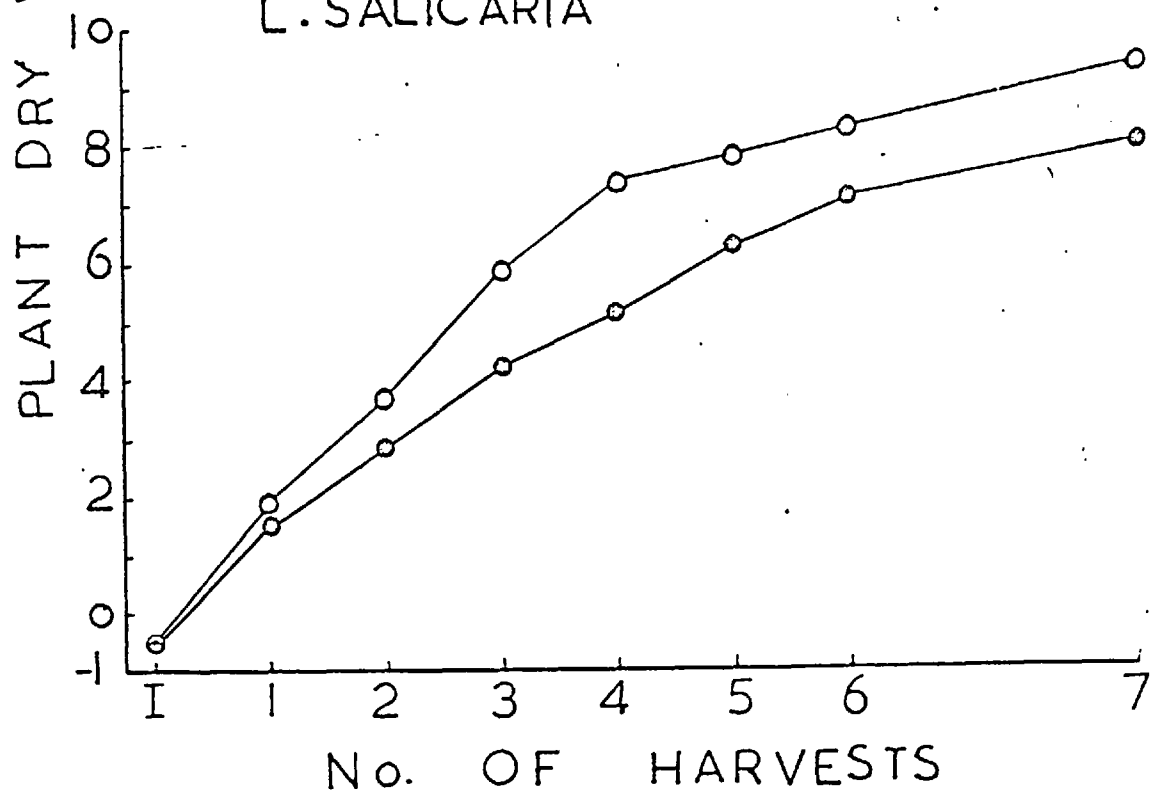
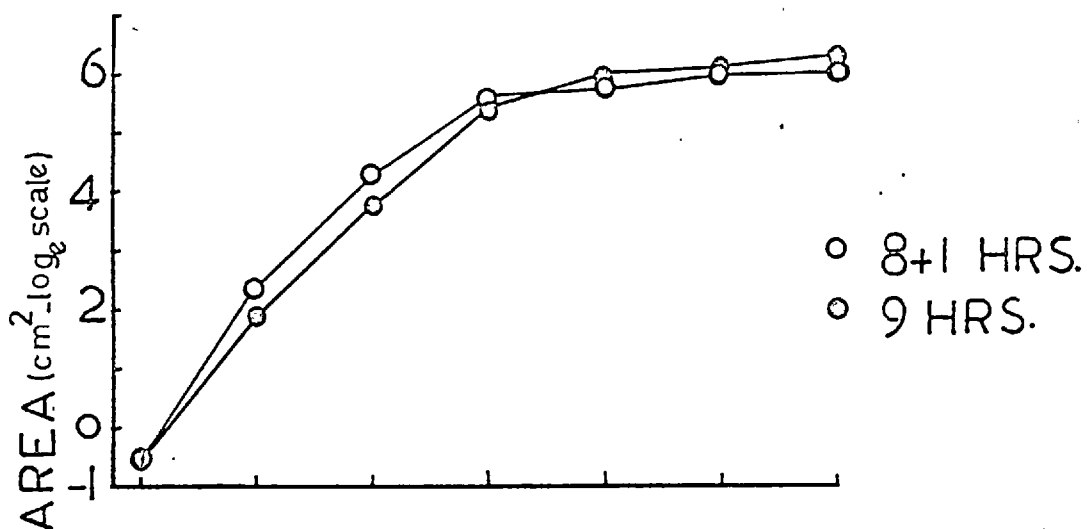


FIG. 31. Effect of light-break on growth in short photoperiodic conditions. Increase of plant dry weight with time.

E. HIRSUTUM



L. SALICARIA

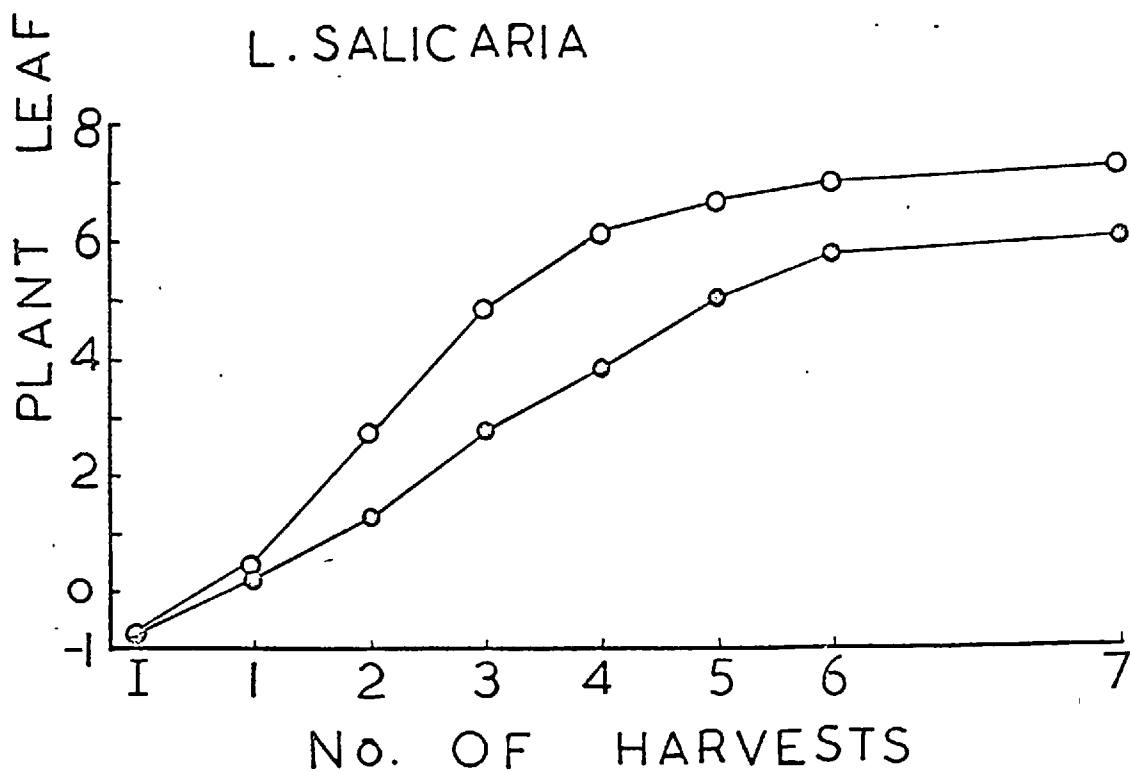


FIG. 32. Effect of light-break on growth in short photoperiodic conditions. Increase of plant leaf area with time.

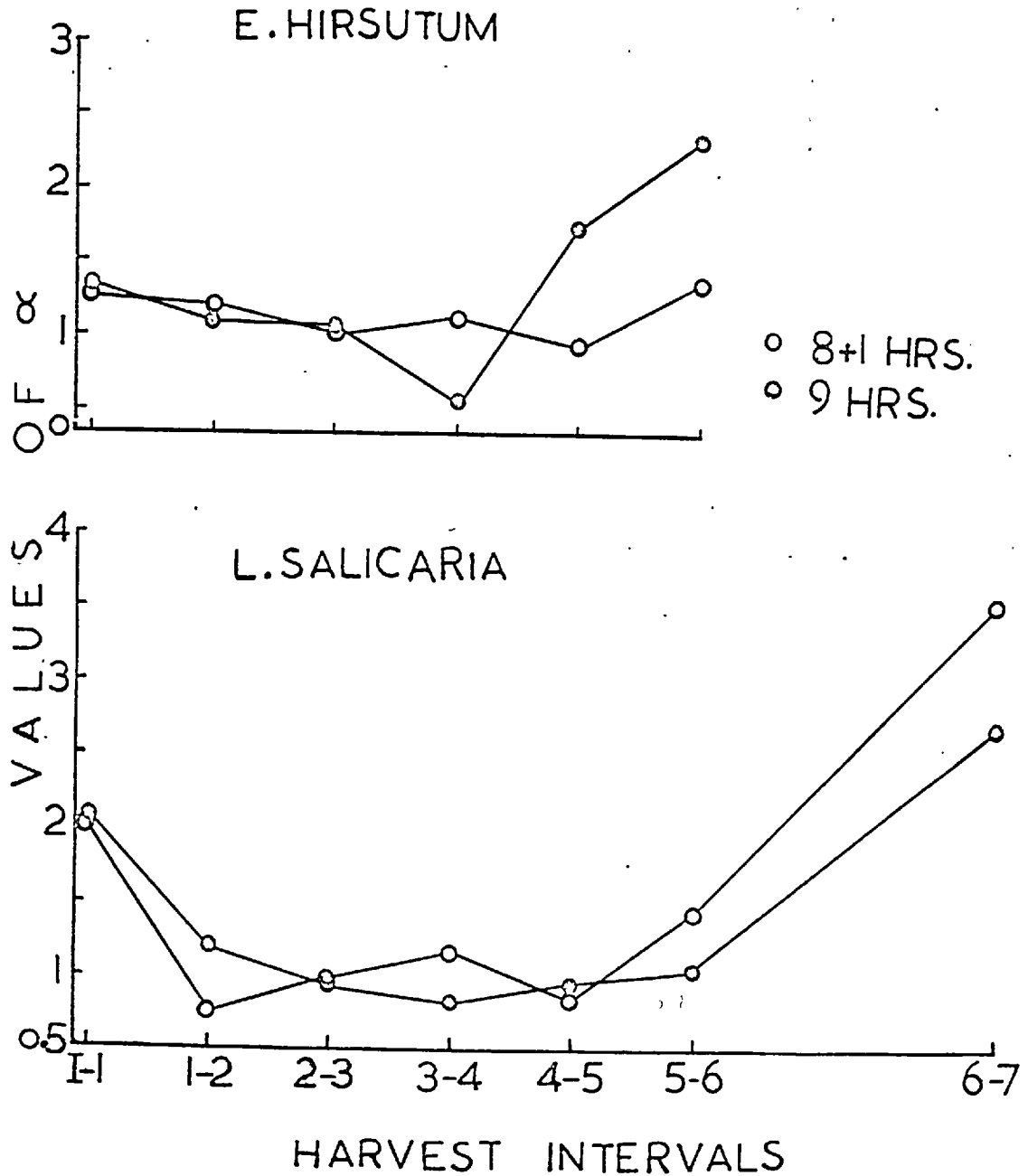


FIG. 33. Effect of light-break on growth in short photoperiodic conditions. Ratio of mean relative growth rate to mean relative rate of leaf area increase (α). Calculated between successive harvest intervals. (I = initial harvest)

It is clear that the 9-hour treatment plants pass through an excessively leafy stage in their morphogenetic adjustment, but in the 8+1-hour treatment the increase in leaf area is more or less proportionate to the increase in dry weight, except in the last interval, and the α values rise sharply. On the whole, the pattern of morphogenetic differentiation is similar in the two treatments.

The pattern of the morphogenetic differentiation is dissimilar in Lythrum in the two treatments. There is an abrupt fall in the α value in the second interval in the 8+1-hour treatment followed by a steady rise, and another decline at the fifth interval followed by a great rise of the values in the last two intervals. In the 9-hour treatment there is a steady decline in the values in the first four intervals followed by a steady rise in the later intervals.

It is clear that the morphogenetic differentiation in the 8+1-hour treatment has a first phase of excessive leaf area increase proportionate to the dry weight increase, followed by a phase of integrated growth with relatively greater dry weight increase. The second decline in the values is in preparation for flowering when the stem elongates considerably, producing countless bracts and small leaves. Different morphogenetic changes taking place in the two treatments can be well appreciated by this ratio. While the

8 + 1-hour treatment plants undergo adjustments and readjustments in their relative leaf area and dry weight increase to develop into long day tall flowering plants, those in the 9-hour treatment do not show any such adjustment during the period of growth.

4. Mean unit leaf rate

In Lythrum the morphogenetic adjustments between leaf area and dry weight in the 8 + 1-hour treatment at various stages of growth can also be seen in the mean unit leaf rates in Fig. 34 (calculated for the intervals between successive harvests). The pattern is irregular in the 9-hour treatment as there is no co-ordination between leaf area increase and dry weight increase. In the 8 + 1-hour treatment the value is very high in the first interval, followed by a regular, gradual decline in the values which start rising again in the last two harvests.

In Epilobium the two treatments follow the same pattern in all essentials and there is an abrupt to slow fall in the values with time. Irregularity in the 9-hour treatment at the third and fifth interval is because of its excessive leafiness and morphogenetic adjustment during growth. Values became similar in the last interval.

~~In Fig. 35 are shown the mean unit leaf rates (calculated from the initial to each successive harvest).~~

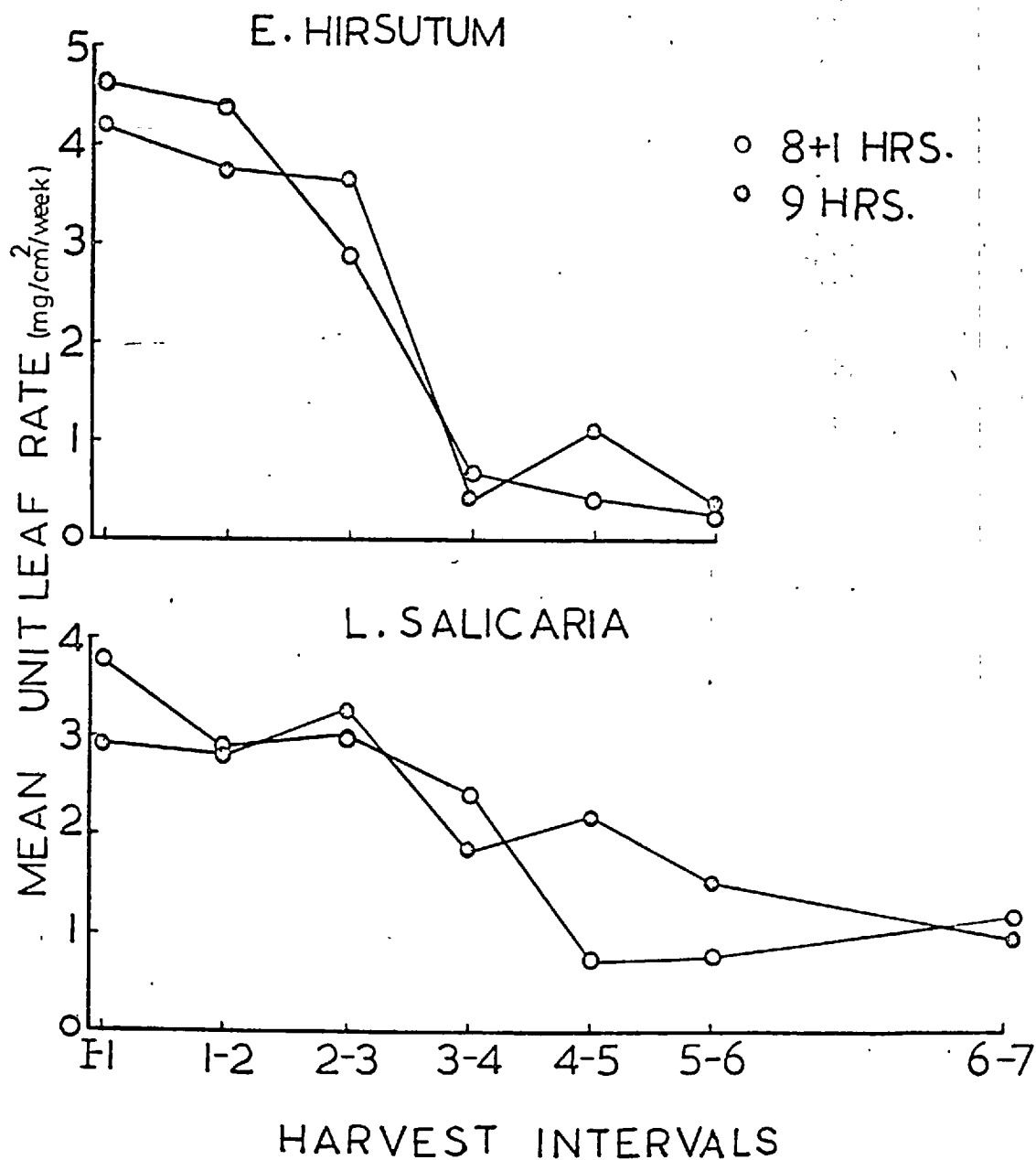


FIG. 34. Effect of light-break on growth in short photoperiodic conditions. Mean unit leaf rate calculated for between harvest intervals. (I = initial harvest)

While the values become similar in the two treatments of Epilobium, the 8 + 1-hour treatment of Lythrum shows consistently higher values than the 9-hour treatment and the difference is very marked in the last interval. Lower unit rates in the first three intervals in the 8 + 1-hour treatment can be attributed to the morphogenetic changes the plant has to undergo to break the barriers inhibiting its growth to develop into a long day flowering plant. Lack of any sharp rise in the unit rate in the intermediate harvests may be due to the fact that growth was directed to accomplishing various functions, such as branching, flower formation, etc., and under the limited amount of available light energy the morphogenetic change was such that the plant could not become an efficient photosynthetic entity, except at the time of the last harvest when there was no plant growth as such.

5. Leaf area ratio

In Lythrum, in the second and third harvests, a great increase in leaf area in the 8 + 1-hour treatment in response to morphogenetic adjustment can be seen from the leaf area ratio in Fig. 36. In the later harvests the two treatments follow a similar pattern and their values also become similar. The pattern in the two treatments of Epilobium is similar over a period of time.

6. Root/shoot ratio

While the pattern and the values of this ratio are similar in the two treatments of Epilobium (Fig. 37), they are diametrically opposed in the two treatments of Lythrum except for the last interval when their trend becomes parallel.

7. Percentage proportions of leaf, stem and root

This is shown in Fig. 38. The pattern of root, stem and leaves is similar in the two treatments of Epilobium, except for the difference in the proportion of stem and leaves in harvests four and five. In general, a higher proportion of leaf is at the expense of stem. In Lythrum the pattern of growth of these components is very much affected by the two treatments, especially the stem and root which follow a separate course of differentiation. The 8 + 1-hour treatment has a tendency to increase the leaf area in the first three harvests, followed by a steady decline. The pattern is similar in the 9-hour treatment. There is a gradual increase in the proportion of stem at the expense of leaf while the root remains relatively unaffected. In the long interval between the sixth and seventh harvests there is a tremendous rise in the proportion of root at the expense of stem and leaf. Looking at the trend, it is the stem which is more affected rather than the leaf. In the 9-hour

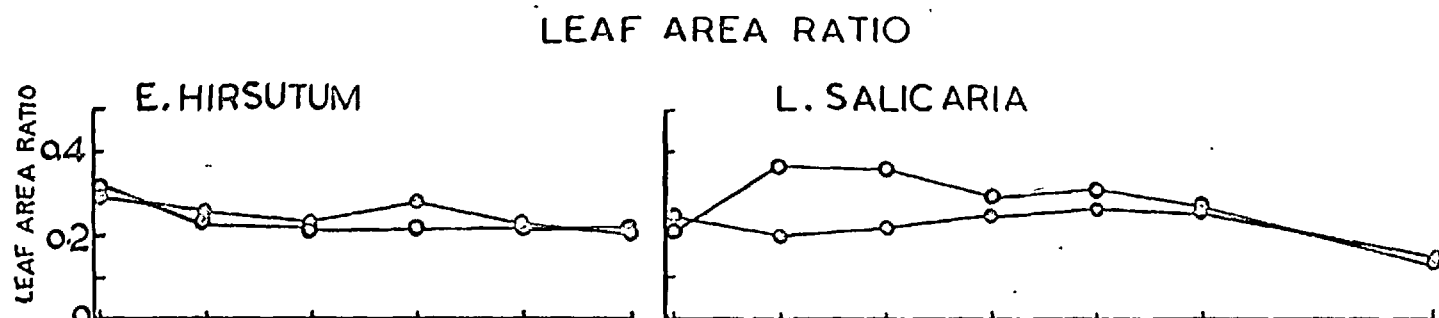


Fig. 36.

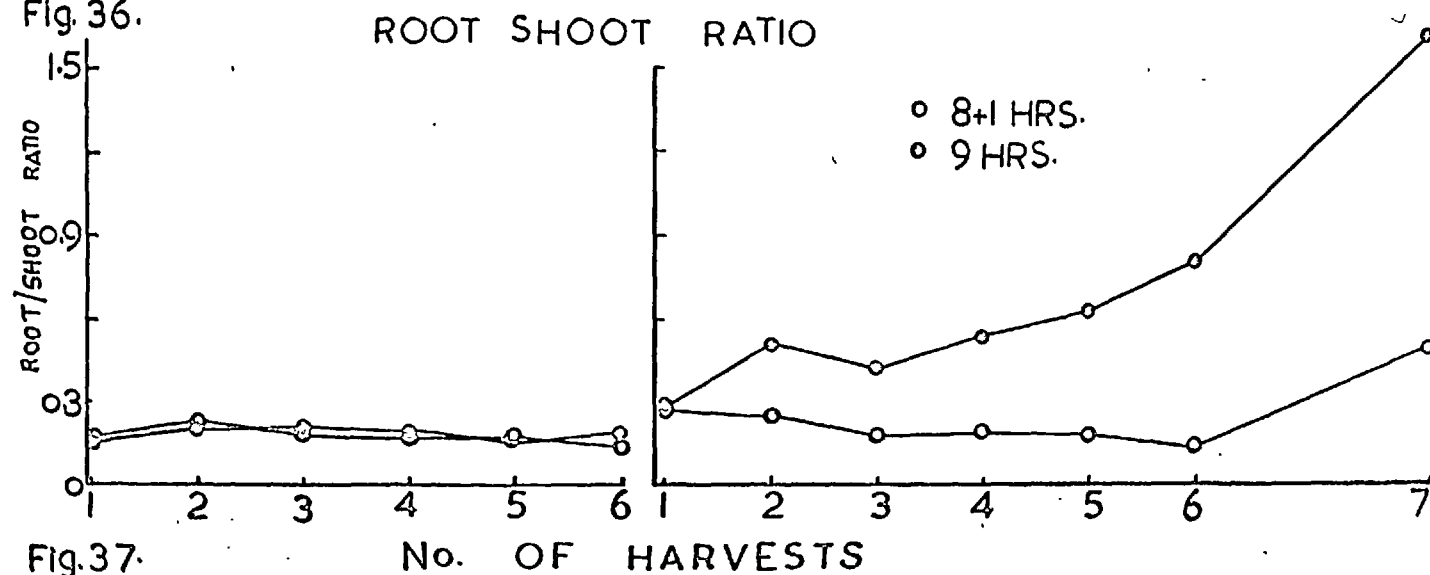


Fig. 37.

Effect of light-break on growth in short photoperiodic conditions.

FIG. 36. Leaf area ratio.

FIG. 37. Root/Shoot ratio.

E. HIRSUTUM

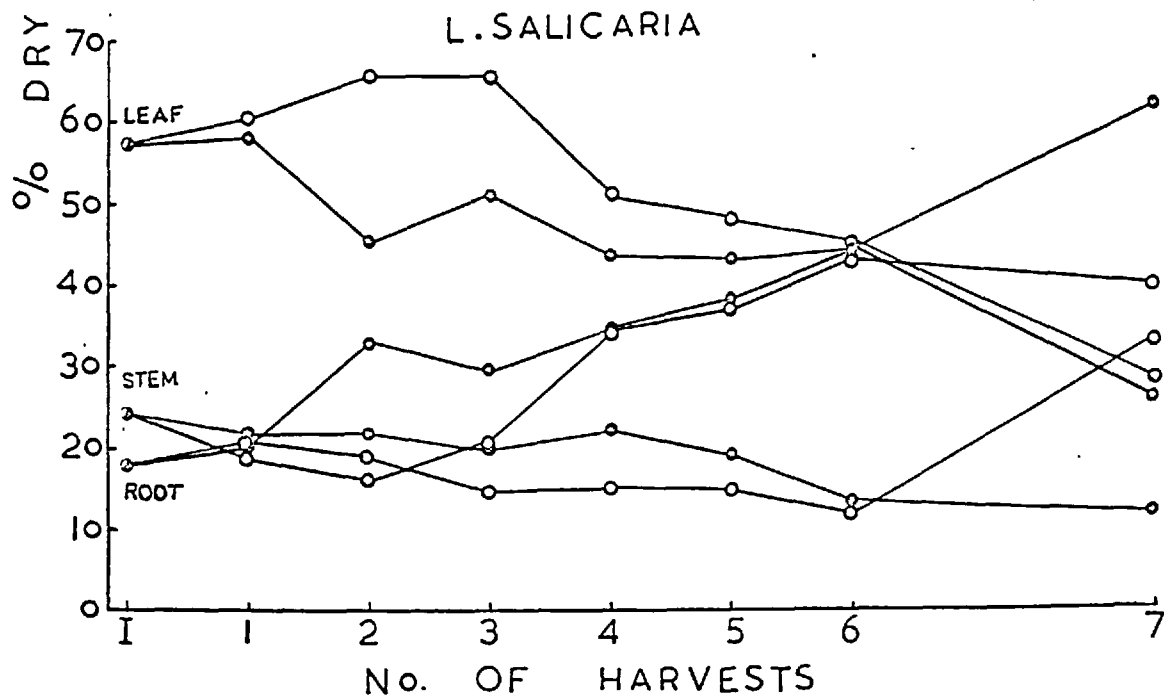
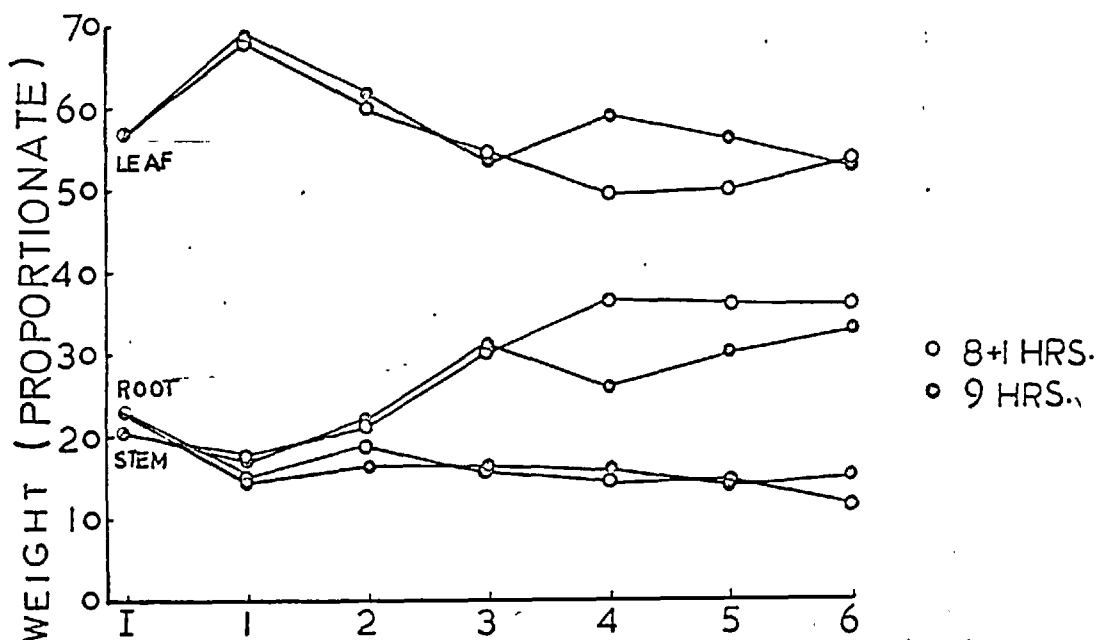


FIG. 38. Effect of light-break on growth in short photoperiodic conditions. Percentage proportional distribution of total dry weight to leaves, stems and roots at successive harvests.

treatment there is a steady increase in the proportion of root, mostly at the expense of the leaf, while there is a gradual decrease in the proportion of stem.

Before discussing the results of the growth analysis, the results of chlorophyll extractions and respiration will be described.

Chlorophyll contents

The chlorophyll content of both species in each treatment were determined after the sixth harvest using the technique and procedure described in Experiment V. Results are given in Table 11.

TABLE 11.

(a) Estimation based on fresh weight of the leaves, as mg/g. F.W.

<u>Plant</u>	<u>Treatment</u>		<u>L.S.D.</u>
	8+1-hours	9-hours	
<u>Lythrum</u>	3.217	3.059	(0.10188 * 0.14284 **)
<u>Epilobium</u>	1.829	1.536	

(b) Estimation based on dry weight of leaves as mg/g. D.W.

<u>Lythrum</u>	16.407	15.759	(1.6001 * 2.2433 **)
<u>Epilobium</u>	15.759	11.362	

(c) Estimation based on leaf area as $\mu\text{g}/\text{cm}^2$

<u>Lythrum</u>	47.36	38.34	(2.2903 *)
<u>Epilobium</u>	37.62	39.05	(3.2906 ***)

L.S.D. = Least Significant Difference

* = P at 0.05

*** = P at 0.01

It is clear that the chlorophyll content of Lythrum is higher than that of Epilobium and that the chlorophyll content is higher in the 8+1-hour treatment than in the 9-hour treatment except in Epilobium, when estimated on leaf area basis, but the difference is not significant. Similarly on this basis the 9-hour treatment Epilobium has a slightly higher chlorophyll content than the corresponding Lythrum.

Determination of respiration rates

Like chlorophyll content, respiration rates were determined after the sixth harvest. Uniform samples of leaf discs representative of different leaves of the plants were taken. Details have been described in Chapter IV.

Results calculated on the fresh weight basis of the leaves are summarised in the following table.

TABLE 12.

(a) <u>O₂ absorbed μl/g. F.W./hr.</u>			
<u>Plant</u>	<u>Treatment</u>		<u>L.S.D.</u>
	8=1-hour	9-hour	
<u>Lythrum</u>	324.511	264.201	(45.885 * 56.456 **)
<u>Epilobium</u>	229.401	215.017	
(b) <u>CO₂ liberated μl/g. F.W./hr.</u>			
<u>Lythrum</u>	246.67	231.55	48.025 *
<u>Epilobium</u>	211.61	199.67	
(c) <u>Respiratory Quotient</u> $\frac{CO_2}{O_2}$			
<u>Lythrum</u>	0.760	0.876	
<u>Epilobium</u>	0.936	0.920	
L.S.D. * P at 0.05			
** P at 0.02			

While the respiratory rates are similar in the two treatments of Epilobium, Lythrum plants in the 8+1-hour treatment show a marked difference from the 9-hour treatment and this can be directly related to the morphogenetic changes the 8+1-hour plants undergo. These morphological changes were brought about by physiological changes in metabolism

affecting the rate of oxygen absorption. It is suggested that the morphogenetic break-through in the 8+1-hour treatment plants required extra energy.

General Discussion

The data presented show that the growth relations in the two species were differently affected by a light break in a long dark period. It has been shown that Epilobium was not affected by the light break in terms of an increase in dry weight or leaf area. In the 8+1-hour treatment there was not any significant change in the morphogenetic pattern of differentiation, chlorophyll content and the rate of respiration, so it should be considered a short day plant.

Lythrum, on the other hand, was not only significantly affected by the difference in the treatment, but the 8+1-hour treatment plant showed a complete transformation (from a dwarf plant with suppressed growth, as in the 9-hour continuous treatment) to a typical long day flowering plant. There was a tremendous increase in leaf area and dry weight in the 8 +1-hour treatment and the whole pattern of morphogenetic differentiation was changed. As shown in Fig. 38, during this morphogenetic transformation the assimilates were distributed in such a way that a higher proportion was diverted to the leaves in the beginning, at the expense of stem and root, and the stem suffered more than the root. When this

first stage of the morphogenetic change was completed, stem proportion started increasing at the expense of the leaf. This sequence was quite logical as leaves must be developed first to provide food material for the elongation of stem and branching etc. later on.

The only anomaly was the sudden rise in the proportion of root at the expense of stem during the long interval of five weeks, from harvest six to seven. This occurred at a time when flower formation was complete and fruit formation was to start, but there was no fruit formation and all the flowers fell away during this time. This might have been the result of ~~diversification~~ diversion of the assimilates from the stem to the root, so no surplus material was available for the fruit and seed formation. On the other hand, it can also be considered that the light break in the dark period succeeds in removing the growth inhibitory effect of the short photoperiod to a great extent, but it falls short of complete success as the fruit and seed formation is not achieved. The tremendous increase in the root proportion suggests a tendency of reversal to the 9-hour growth pattern. The question arises, why does it happen with Lythrum and not with Epilobium? Presumably two different systems of morphogenetic control are operating.

While these physiological and genetic considerations

will be discussed later, it is interesting to note that the patterns of the development of leaf, stem and root are genetically controlled and adapted to the growth habit of the plant. Though environment may affect the degree of expression of these components, the basic pattern remains unchanged. As shown in the photoperiod experiment (No. VI), Fig. 30, although there is a contrast in the leaf and stem proportions of the 9-hour and the 16-hour treatment plants, the root/shoot ratio remains similar at the end. Since these two forms of growth occur in nature, so there is an internal adjustment within the components to cope with the changed environment, but the general trend of the pattern remains unaltered. However, in Lythrum in the 9-hour treatment, the basic pattern is completely changed and the root/shoot ratio is altered. It shows that if a plant is not adapted to grow under short photoperiods, there will be a conflict between the genetically controlled phenotypic expressions of the plant and the short photoperiod conditions, and this will result in the suppression of growth in the absence of any adaptative mechanism.

A light break brings about the morphogenetic transformation and restoration of proportions of root, stem and leaf to their natural expression as in the long day plants. In this respect the light break can be considered as simulation of the extension of the short day, in a broader sense,

although technically the plant receives the same amount of light energy as in the 9-hour treatment.

That interruption of the dark period by a short light interval is, in a way, simulation of the extension of the day length, has been shown by Jacobs, Davis and Bullwinkel (1959) (see Photoperiodism by Withrow, P.P.393). They succeeded in inducing flowering in Coleus blumei growing in short day conditions by extending the day length, and found that treatment given by extending the normal day gave equivalent results for flowering to those by interrupting the night. Highkin and Hanson (1954), working on tomato plants, found that although a two hour interruption of night increased the growth in the plant, it was significantly less in terms of height and weight than that obtained by the extension of the day by two hours. In contrast, a light interval during the night had no significant effect on sunflowers and only a small effect on peas. Similarly, Hamner (1960) reported flowering in long day plants, like Hyoscyamos niger and Silene asmeria, was promoted when a long dark period was interrupted by a short period of illumination.

Physiological basis of the restoration of
growth and flowering by a light break

Vegetative growth and flowering in plants is controlled by the same chemical substance, phytochrome.

Hendricks and Borthwick (1963) postulated that it regulates the growth by the action of "P₇₃₀" in the formation of "Florigens" for flowering and "Gibberellins" for stem elongation etc.

The synthesis and destruction of these components is markedly influenced by photoperiodic cycles and temperature and the environmental conditions under which synthesis of photochrome pigments occur differ from plant to plant (Myer and Anderson, 1960). Looking from this view point, adaptation of Epilobium in nature to grow in cold weather for most parts of its life-cycle with exposure to longer dark periods than light periods, in contrast to Lythrum, adapted to summer growth with long light periods and short dark periods, would mean that the nature of the physiological reactions must be different in the two species and this may underlie the difference in their growth responses under short day conditions (Experiment VI). With the decrease in the photoperiod there may be a reduction in the amount of these substances in Epilobium (as there is proportionate reduction in the growth), but in Lythrum there may be complete suppression or destruction of these substances because of the lack of growth in short day conditions.

That Gibberellic acid caused excessive growth in Epilobium may be a reflection of the accumulative effect of

the, already present, natural gibberellins and added G. acid. As Lythrum could hardly reach half the height of a normal plant it can be safely assumed that here all the natural gibberellins were either suppressed or rendered non-functional and artificially provided G. acid was not enough to enable the plant to grow to normal size.

Hamner (1963), Myer and Anerson (1960) emphasized that photoperiodic responses are localized in the leaves. In this connection, the effect of the short photoperiod on the leaf growth in Epilobium and Lythrum is very important, (see Experiment VI). Leaves, being the locus of photoperiodic induction, and this is taken to mean that phytochrome pigments are produced in the leaves from where they are transported elsewhere to cause stem elongation and flowering, then in short day Epilobium plants, physiologically speaking, gibberellin synthesis is not blocked but their transportation to the stem is affected. Gradual response, demonstrated in the stem elongation to a series of photoperiods, show that utilization of these natural gibberellins is regulated by the duration of the photoperiod. Activation and synthesis of florigen depends upon a particular photoperiod to cause flowering. So, stem elongation and flower formation are two separate phenomena in Epilobium as they are controlled by two separate compounds whose synthesis and action are not

co-ordinated.

Lythrum, on the other hand, is very different physiologically. Because of the suppression of leaf growth in short day conditions, gibberellin synthesis also seems to be blocked but, unlike Epilobium, there is no response to any photoperiod which is less than the critical photoperiod, but there is a sudden response and transformation from a dwarf, suppressed plant to a flowering tall plant when the critical photoperiod is reached. It seems that both gibberellins and florigens are synthesised simultaneously and act at the same time provided a certain critical photoperiod is made available.

This difference in the time of synthesis and the mode of action may be responsible for the different responses in Epilobium and Lythrum to short photoperiods and a series of photoperiods, and can help to explain why stem elongation and flower formation are two distinct and separate phenomena in Epilobium but not in Lythrum.

Reversal of growth in the 8+1-hour treatment in Lythrum suggests that the physiological block~~ade~~, on the synthesis of gibberellins and florigens, is removed and the plant resumes a normal course of growth.

Broader implications of the light break and its Ecological importance

In an attempt to rationalise the importance of the

light break in nature, the life cycles and natural adaptations of these plants are reviewed briefly.

The occurrence of overwintering rosettes in Epilobium shows that it passes through seasonal changes in the length of photoperiod during its annual growth cycle. This situation has important implications both for the development of the plant in nature and in its geographical distribution. Since the plant grows for most of the year as a leafy rosette before it can flower in summer, it is evident that in its growth, for most of its life-cycle, it is not only adapted to short photoperiods but also to long dark periods.

Lythrum does not undergo any seasonal changes in the length of photoperiod in its annual growth cycle. The plant starts and completes its whole life-cycle during the long photoperiods. The important point here is that while Epilobium is adapted in nature to long dark periods, Lythrum is adapted to very short dark periods. This line of argument raises the possibility that suppression of growth in short day Lythrum plants may not be because of the short photoperiods but because of the very long dark period to which it is not adapted in nature.

Results of this experiment support this hypothesis and when the continuity of the long dark period is broken by

a period of short illumination, the dark-imposed suppressive effect on growth is removed and the plant resumes its normal course of growth. These morphogenetic changes are brought about by physiological changes, and a higher rate of oxygen absorption and a higher chlorophyll content suggest that the course of physiological reactions is also reversed.

Since Epilobium is naturally adapted to grow under short photoperiods, so lack of any response to the light break can be understood to have no effect on the growth.

In connection with this line of argument the relationship between endogenous rhythms in plants and photoperiodism, as advocated by Hamner (1958), is very relevant, (see Environmental Control of Plant Growth, ed. by Evans). The ability of Epilobium to grow in all seasons suggests that the endogenous rhythm of this plant is not controlled by any length of daily photoperiod, but in Lythrum there is photoperiodic control of the endogenous rhythm and it is governed by long photoperiods. Growing Lythrum in short day conditions completely upsets this innate rhythm, which results in the suppression of growth. Hamner also suggested that in many cases just one stimulus of light is enough to evoke the oscillation. It is, therefore, suggested that a short light break in the continuity of the long dark period might have restored the innate endogenous rhythm in the 8+1-hour

treatment in Lythrum and the plant resumed a normal course of growth.

Interaction between total amount of radiation
and photoperiod

Resumption of normal growth in the 8+1-hour treatment in Lythrum shows that, at least under these experimental conditions, there is no correlation between the amount of energy and growth, as the same amount of energy given in a different way (i.e. for the continuous 9-hour treatment) does not cause any appreciable growth and flowering in the plant. It can be inferred that, within limits, the plant is independent of light energy for growth and flowering but dependent on the periodic induction (mode of action) of the light energy. On the other hand, in Epilobium there is a direct relationship between the growth accomplished and the total amount of radiation received (Experiment VII).

While in Epilobium there is a gradual increase in growth with the increase in day length in a 24-hour cycle, in Lythrum there is no growth response at all if the proportionate length of dark period is greater than the light period, (in Experiment VII there was no appreciable difference in the 9, 10, 11, and 12-hour plants, and they were within the same range of dwarfism) but once this proportion of light and dark periods is reversed there is an abrupt and tremendous growth

response. It seems that it is the reduction in the length of the dark period which exerts a controlling influence on the growth and flowering of Lythrum. This is in accordance with its adaptations to natural growing conditions, as in none of the phases of its growth cycle is it confronted with a dark period longer than the light period. This reduction in the dark period of illumination in the middle of the long, dark period, so that a long photoperiod of 8-hours is followed by a short dark period of 7-hours and a situation similar to natural growing conditions is created.

So, the two plants have a diametrically opposed response to the daily period of light and total amount of radiation. While Epilobium is dependent on both the long photoperiods and total amount of radiation, growth and flowering in Lythrum is regulated by the duration of the dark period in a daily cycle of 24-hours, if the minimum required radiation is provided. This peculiar photoperiodic behaviour in Lythrum may be linked with the genetic versatility and polyploid vigour, enabling it to grow at a faster rate in the favourable period of the growing season and to complete its life cycle in a relatively short time compared with Epilobium. These inbuilt mechanisms of Lythrum may explain its occurrence in an English type of climate which is unfavourable for its growth for most of the year.

On the basis of the argument advanced above, an interpretation that a light break in a dark period is in a way, an extension of the short photoperiod does not hold good in the case of Lythrum, as it is not so much the extension of the photoperiod but the proportion of light and dark periods that controls growth and flowering in this plant.

Light in relation to the biology of the species

The successful germination of seeds of both species in short and long day conditions, and ~~respectable~~^{the} growth in each species at various levels of shade, show that the light sensitivity of the seeds in germination is not a direct mechanism, allowing germination to occur only under conditions in which adequate growth for the subsequent establishment and survival of the seedlings can take place.

Light, however, seems to have special significance in regulating the germination in these two species. With their extremely small seeds it is important from the survival view point, as they contain very little food, that they germinate under conditions where photosynthesis can occur very soon after germination.

An attempt is made here to relate the findings of these experiments with the growth, establishment and distribution of these plants in nature.

As shown in Experiment V, Epilobium is committed to an extremely leafy growth in its early seedling establishment stage, especially in shade conditions. This leafiness is at the expense of the roots which is contrary, at this crucial stage of growth, to the needs of the plant for more root to fix itself as a viable unit. On the other hand Lythrum, at this stage shows a proportionate and co-ordinated growth of root, stem and leaf even in moderate shade (70% daylight level).

At this stage, investment in terms of root production is more important than leaf expansion to withstand the pressure from other plants growing in the same habitat. This would mean that even when Epilobium seeds germinate at all levels of shade, the greatest proportion of their number will be eliminated, but in Lythrum they stand as fair a chance in moderate shade (70% daylight level) as in full light to establish themselves. This propensity of Lythrum to be able to establish itself in relatively shady conditions is further helped by a relatively faster growth rate. The pattern of differentiation is such that more of the products of assimilation are utilized in the production of leaves, as seen in the leaf area ratios, and this would mean higher net assimilation rates at low light intensities.

This experimental evidence agrees with the observations of Ellis (1964) in the Wheat Fen Broad and Pearsall

(1918) in Esthwaite Water, that Lythrum grows in both open and closed carrs and its abundance is related to light intensity. On the other hand, Epilobium has always been known to exist as open ecological communities in fens and along hedgerows.

The luxuriant growth of Epilobium under short-day conditions gives it an advantage over Lythrum in being able to grow and propagate all the year round. This advantage may underlie the aggressiveness of this species in the areas it succeeds in occupying. The quantity of light, discussed so far, has been of great importance in determining the localized distribution of the two species in the same habitat, but the different photoperiodic responses in the two species seem to affect their geographical distribution.

The requirement of long photoperiods for successful flowering and reproductive growth would naturally exclude Epilobium from the tropics and subtropics where days are not longer than 12 to 13 hours and it would be unable to accomplish its sexual reproduction. The tendency of Epilobium to spread northwards (northern-most Europe up to Sweden; North Africa and North America) from temperate Asia indicates the photoperiodic control of its distribution, as the days are longer by at least three hours in the northern hemisphere.

The trend in the geographical distribution of

Lythrum is in direct contrast to that of Epilobium as it ranges from northern to temperate regions (where it is dominant in plant communities) and may go as far as the subtropics of Australia. Even in the British Isles Epilobium is common throughout the northern regions, while Lythrum is less frequent in Scotland and absent from most of the north.

So it is the biology of the species which sets barriers to its ecological and geographical distribution.

VII. EFFECTS OF MINERAL NUTRIENT CONDITIONS
ON GROWTH

While discussing the ecological distribution of the species in Chapter III, it was suggested that some aspects of edaphic factors affect the establishment and growth of the species in the same habitats. It was pointed out that the relative levels of available nutrients were usually most critical in excluding the establishment, particularly that of Epilobium, in otherwise suitable sites. On the other hand, Lythrum appeared to be somewhat less sensitive to the nutrient status of the soil for its establishment and growth. Sometimes it has been found growing in bogs and marshes, where it has become generally known that the underlying peats and ground waters are extremely low in mineral nutrients. These and other observations raise the obvious question as to what are the nutrient relations of these plants and how does Lythrum obtain sufficient nutrients to become established and grow fully to maturity in soils of low nutrient status.

In this chapter various aspects of the nutrition of the two species have been investigated in detail. The effects of the nutrient stringency on growth have been studied.

Uptake of major nutrients under conditions of stringency is described. Growth of the plants in nitrogen, potassium and phosphorus deficiencies was investigated to find out the relative importance of the major nutrients. In all these studies the performance of the two species was gauged in general terms of development and of dry weight gain, their assimilation rates and the presence or absence of any adaptive mechanisms in their growth under conditions of stringency.

Experiment X

Effect of different dilutions of a standard nutrient solution on growth.

To understand the nutrient relations of the two species, it was considered important to grow them in a series of dilutions of the standard nutrient solution to find out the critical level of nutrition below which their growth is insignificant. In this way it was hoped to gain some information about the range of the mineral nutrients which each species can tolerate under natural conditions.

Experimental details

Forty day old seedlings of both species raised in sand culture were sorted out for uniformity of size. The

seedlings were much bigger than those used in the Light experiments since the initiation of a third pair of leaves was in progress. Seedlings of each species were grown separately in a series of six different dilutions of Long Ashton standard culture solution, designated as S, S/10, S/50, S/100, S/200, S/300. (For details of formulae and strength of nutrients in each dilution see Chapter IV, Materials and Methods).

Four wooden tanks, each of 50 litre capacity (two for each species) were used for 'S' plants. Four other tanks of the same capacity were used for the S/10 and S/50 plants, and six glass tanks each of 15 litre capacity were used for the three remaining dilutions of the nutrient solution. The wooden tanks were lined internally by a double layer of thick black polythene and the glass tanks were painted black on the outside. Tops for the tanks were made from perspex sheets of medium thickness, painted black, and holes were drilled, one inch apart, in regular rows. The tanks were arranged in two rows in the greenhouse and properly labelled for each species and dilutions of the solution.

Different dilutions of the nutrient solution were prepared in bulk and the respective tanks filled with them. An interlinked system of glass and polyvinyl tubings (with micro-holes in the polyvinyl tubings) was passed through the

series of tanks for aeration of the culture solutions. The whole system was connected at one end to an air-pump by rubber tubing. The solutions were regularly aerated for six hours every day and the solution in each tank was renewed after three weeks. In the later stages of growth the tanks of 'S' plants were topped up after every week, as with the increase in plant size there was excessive utilization of the nutrient solution. Natural daylight was supplemented by artificial illumination from four banks of fluorescent tubes (5 tubes in each) hanging in a row four feet above the tanks. Plants were illuminated for 16 hours per day.

Transplantation of the seedlings starting from the 'S' solution was carried out in six days and completed on 2 June, 1968. 250 seedlings, per species, per dilution were transplanted except in the 'S' solution. Only 150 seedlings of each species were transplanted 2in. apart in this solution. Seedlings which did not start responding (damaged in transplantation) after a few days of transplantation were removed from the tanks. In addition to the initial harvest five other harvests were taken at 15 day intervals. In the 'S' solution, 25 plants and in the other solutions 40 plants at each harvest were picked out at random for growth analysis. In the last two harvests only 10 plants per harvest from the standard solution were used because of the labour involved. The higher numbers of replicates were very important for the accuracy of the mean values

especially at the lower dilutions of the nutrient solution. In the standard solution in the last two harvests many plants had to be removed from the tank to reduce the competition to the minimum possible level because of the limited space and large plant size. This inevitably resulted in the reduction of the sample size. After five harvests the remaining plants in all dilutions were left to see in which lowest dilution flowering occurs in both species.

Temperature was uncontrolled throughout the experiment and varied from 25 to 30°C.

Primary data for different harvests were collected as in the previous experiments.

Observations

The differences in the plants of the 'S' and S/10 treatments were very large. While plants in the 'S' solution were huge and profusely branched, the plants in the S/10 dilution were greatly reduced in size and did not branch. In the rest of the dilutions the size and degree of development of the plants showed large successive reductions with the increased dilution. In both species, plants grown in S/100 to S/300 were very minute, more so in Epilobium than in Lythrum. In all the dilutions in Lythrum there was a large reduction in the shoot with the increase in dilution, but marked improvement in the root system. In Epilobium, on the

other hand, both shoot and root were equally affected by the successive dilutions of the solution. This can be seen from Plate 10 (a, b and c). Within each species the area of leaves of the same plastochron was greatly reduced at each successive dilution level. In Epilobium there was a large development of a red colouration in every dilution from S/10 to S/300 and especially in the last three dilutions. But in Lythrum in the S/10 dilution the plants did not show any marked red colouration, and in the other dilutions its intensity increased with the increase in dilution. The extent of the development of the plants at the final harvest was as follows.

Epilobium hirsutum

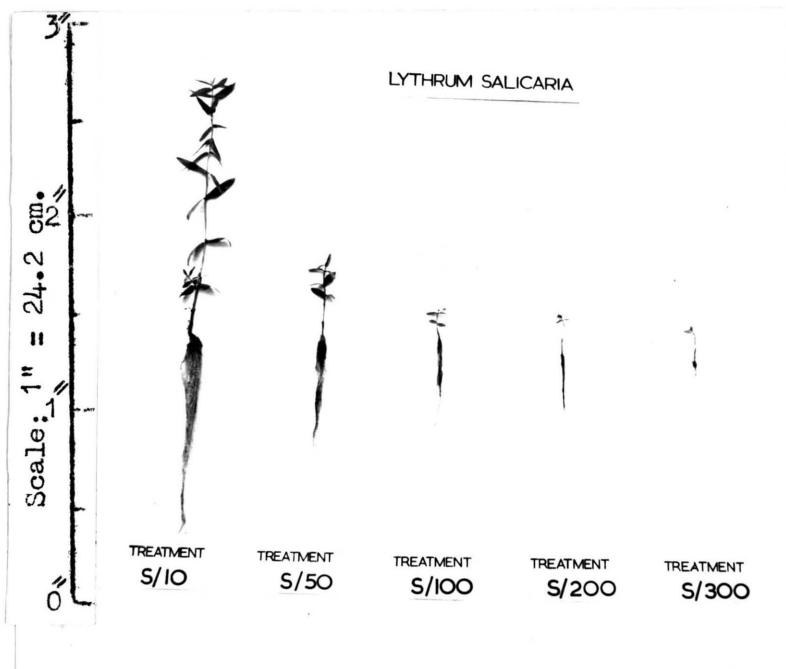
In the standard solution, plants were 155 cm. in length (110 cm.S + 45 cm.R) with 24 to 26 pairs of nodes on the main stem with expanded leaves (including floral bracts) and eleven repeatedly branched "rhizomes". There were up to 23 fully developed side shoots and the plant started to flower on the 59 day after transplantation. By the time of the last harvest the plants had an average of 326 flowers most of which had started to develop into fruits. At the S/10 dilution the plants were 48 cm. long (26 cm.S + 22 cm.R) and the main stem had developed some 13 to 14 pairs of leaves of which the lower two pairs in most of the plants were dried and



PLATE 10.(a) Plants grown in a standard nutrient solution.

(Photographed 75 days after the start of the treatment, i.e. at the time of harvest V.)

(b)



(c)

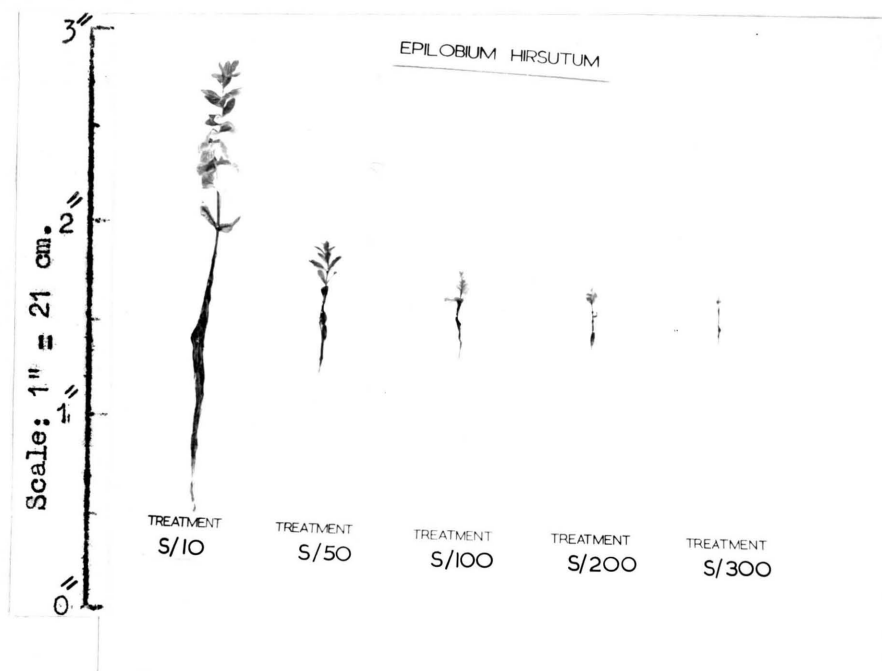


PLATE 10.(b and c) Plants grown in various dilutions of a standard nutrient solution. (Photographed 75 days from the start of the treatment, i.e. at the time of harvest V.)

crumpled. All the plants were unbranched, except some odd ones with a pair of suppressed axillary shoots (0.75 cm. long) in the axils of the upper leaves. Towards the last harvests the lower eight pairs of leaves were reddish. There was no rhizome formation and the plants did not flower or produce flower buds even four weeks after the last harvest. There was a great reduction in size at the S/50 and S/100 dilutions and the shoot length was 7 cm. and 5 cm. respectively and six to eight pairs of very small leaves had developed. At the S/200 dilution the plants were extremely reduced and minute and at the S/300 dilution with four to five pairs of minute leaves. In the last four dilutions all the leaves and the major part of the stem had developed intense red colouration by the time of last harvest.

Lythrum salicaria

The plants grown in the standard solution had a length of some 186 cm. (128 cm.S + 58 cm.R) and carried on the main stem about 39 pairs of leaves and expanded floral bracts and up to 24 well developed side shoots. The plants started to flower on the 46th day after transplantation and by the time of the last harvest the inflorescence was 55 to 60cm. long on the main stem and up to 30 cm. on the side shoots with innumerable flowers produced in whorls.

At the S/10 dilution the average plant length was

58 cm. (31 cm.S + 27 cm.R) with 14 pairs of leaves. In some plants 3 to 4 cm. long shoots developed in the axils of the lower leaves. By the time of the last harvest there was no inflorescence initiation but two weeks later it started developing and in another three weeks it was 7 cm. long with sparsely arranged floral whorls.

At the S/50 dilution, the root was much longer than the shoot and in the total plant length of 31 cm. the root measured 20 cm. and the shoot only 11 cm. Almost all the plants had developed 7 pairs of leaves of which the lower one to two pairs of leaves turned red then yellowish and were dry by the time of the last harvest. The plants did not develop any inflorescence even five weeks after the last harvest, on the contrary without any appreciable increase in the shoot the root stock became very thick and conspicuous with numerous roots arising from it.

At the S/100 dilution there was a great reduction in shoot compared with that in the S/50 plants, and in the total length of 18 cm. the shoot was 4 cm. long and the root 14 cm. Leaf size was greatly reduced and only 3 to 4 pairs of leaves were present. There was a still greater reduction in the S/200 dilution and plants were minute in the S/300 but proportionately root was better developed. The leaves were narrow and minute. Only 3 to 4 pairs of leaves developed

and most of the lower leaves had fallen away in the S/300 dilution at the time of the last harvest. In the S/200 dilution the plants were 14 cm. ^{long} ~~high~~ and only 9 cm. in length in the S/300 dilution.

It is clear that in the increased dilutions of nutrient solution, in Epilobium both shoot and root were equally affected but in Lythrum although there was a decline in the total dry weight the shoot was more affected than the root. In other words Lythrum responds to low nutrient levels by a diversion of assimilates to root production at the expense of shoot but this does not happen in the case of Epilobium.

Results

The results of various growth estimates were as follows.

1. Increase in dry weight

Progressive curves of increase in dry weight with time in both species are shown in Fig. 39. The general pattern of reduction in the gain of dry weight with the increase in dilution is similar in each species. Relatively speaking there was a greater reduction in Epilobium in the S/10 and S/50 dilutions than in Lythrum when compared with their controls. But Fig. 39 also shows that at the three lower dilutions Epilobium is relatively better than Lythrum.

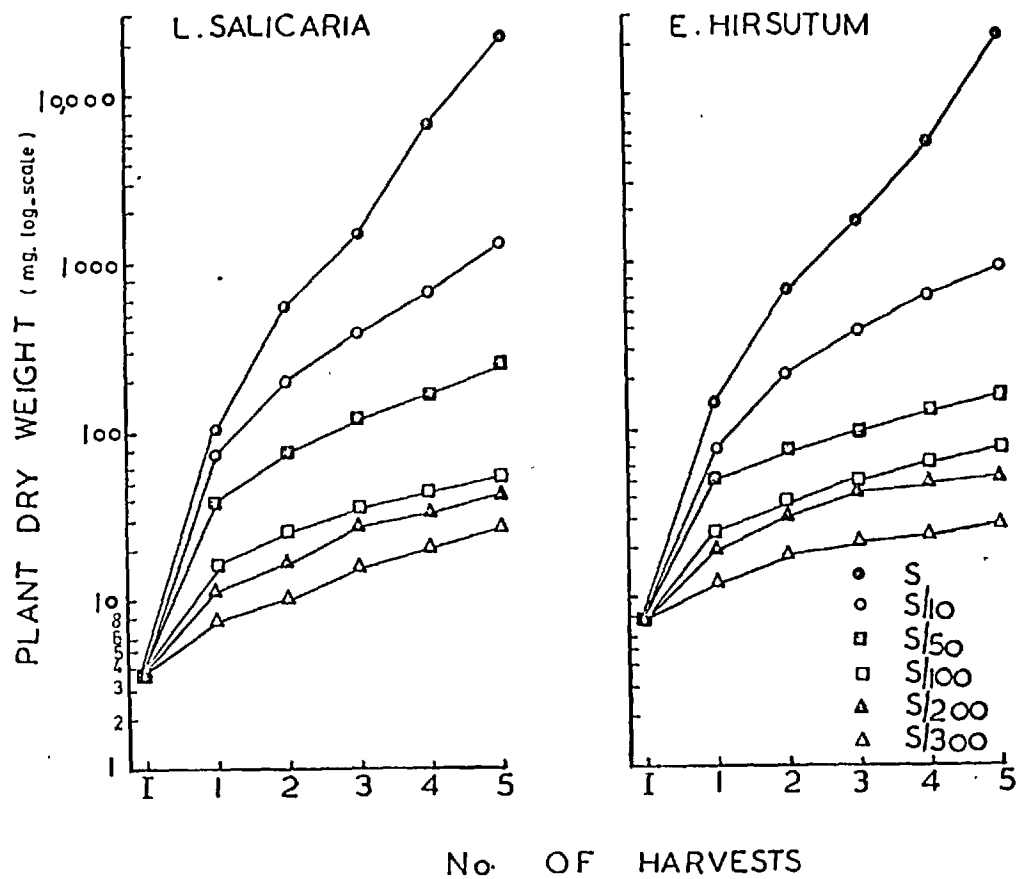


FIG. 39. Effect of different dilutions of a nutrient solution on increase of plant dry weight with time.

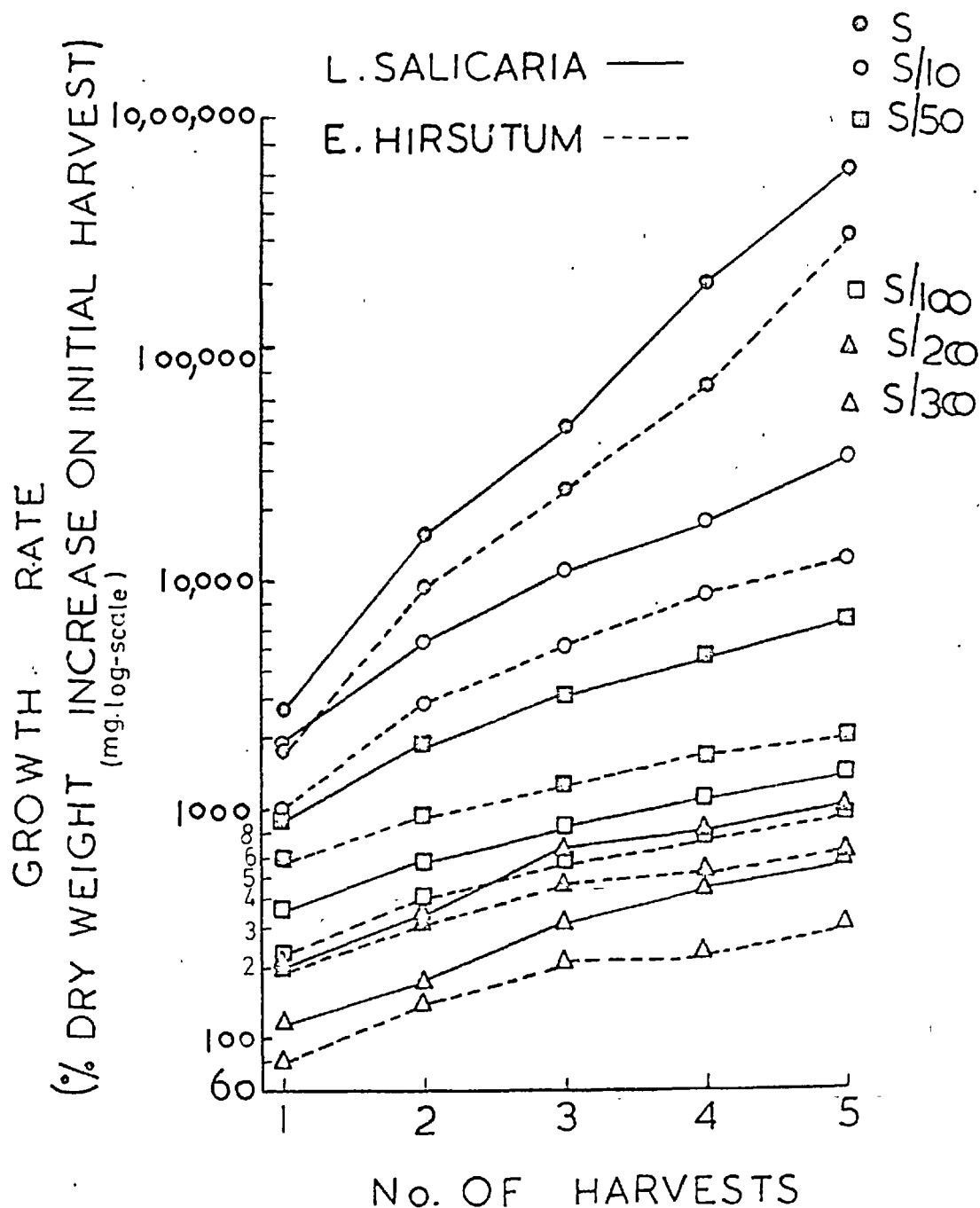


FIG. 40. Effect of different dilutions of a nutrient solution on growth rate. Percentage increase dry weight time from an initial harvest to each successive harvest (i.e., $H_1 - H_I$, $H_2 - H_I$, $H_n - H_I$).

It can also be seen that in the initial harvest Epilobium seedlings have a higher dry weight. This difference is such that the dry weight of Epilobium is double that of Lythrum in the initial harvest, (Epilobium - 7.48 mg., Lythrum - 3.76 mg.). To eliminate this initial advantage in Epilobium, growth rates were calculated in a different way, i.e. the percentage increase in dry weight over the initial harvest, and is presented graphically in Fig. 40. The data presented in this way become more revealing. Although the growth rate of Lythrum in the standard solution is higher than that of Epilobium the trend is very similar in the two. The difference in the growth rate is very marked in the S/10 dilution and the gap between the two species is very large at the S/50 level. At this dilution while there is still a significant progressive increase in dry weight in Lythrum in the last two harvests, in Epilobium this is not so. In the lower dilutions there is a substantial reduction in the growth rate of both species but comparatively Lythrum is much better than Epilobium and very significantly so at the S/300 dilution in the last two harvests.

2. Increase of leaf area

The general pattern of the increase of leaf area with time can be seen in Fig. 41. Like the dry weight there are similar large successive decreases of performance with the

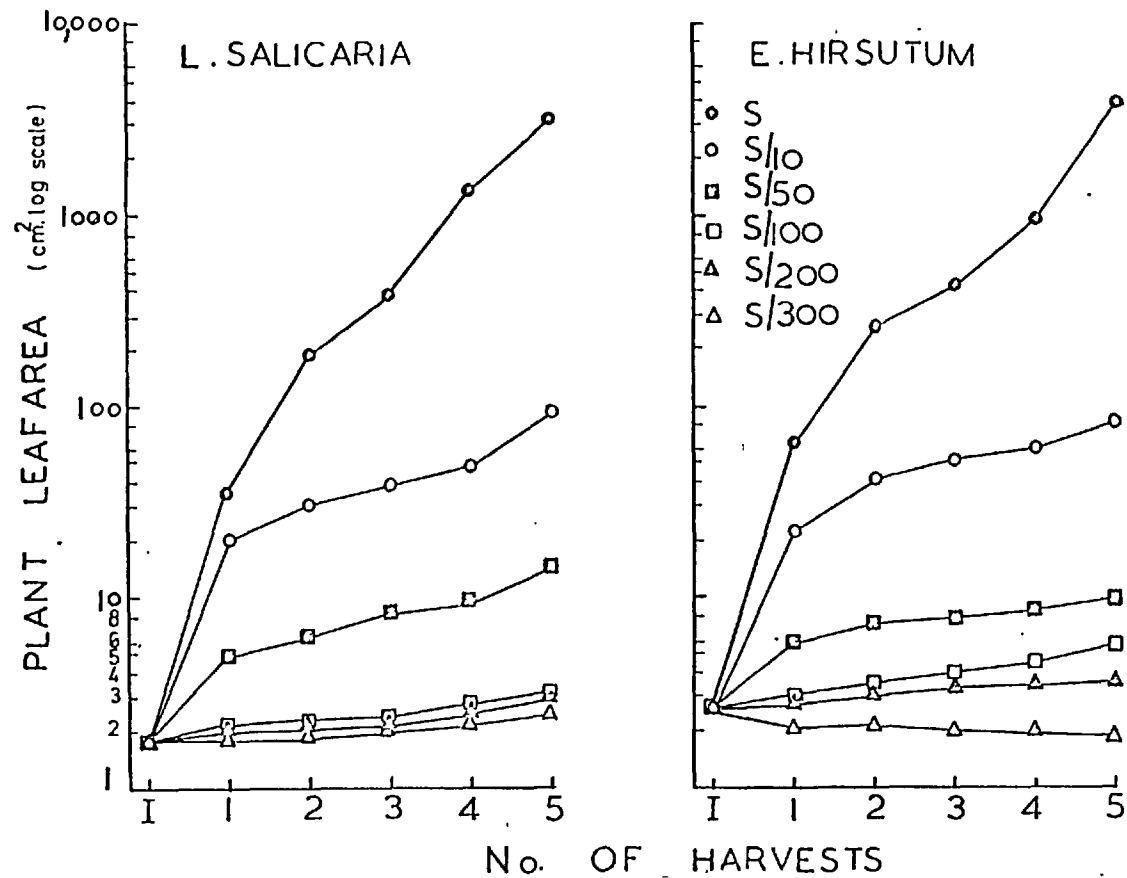


FIG. 41. Effect of different dilutions of a nutrient solution on increase of plant leaf area with time.

increased dilutions. Leaf area at the S/50 dilution is severely affected in Epilobium but below this dilution there is a sudden and greater fall in Lythrum and this, again, can be attributed to the higher initial leaf area in Epilobium.

3. Mean unit leaf rate

These values are presented graphically in Fig. 42. It can be noted that dry weight gain per unit of leaf surface is higher in Lythrum than in Epilobium with the increase in the nutrient dilution. These values have been calculated for intervals between successive harvests. ~~The values calculated between the initial to the final harvest are shown in Fig. 43.~~ The difference between the two species in the 'S', S/10 and S/50 treatments is very marked.

4. Root/shoot ratio

The root/shoot ratios for both species are shown in Fig. 44. It can be noted that Lythrum responded to the series of increased nutrient dilutions by an increase in the root/shoot ratio at all levels, but this response is completely lacking in Epilobium although in the S/10 dilution the plants show a tendency to increase the root/shoot ratio in the last two harvests.

5. Percentage proportions of leaves, stem and root

These proportions for Epilobium and Lythrum can be seen in Fig. 45 and Fig. 46 respectively. The values have

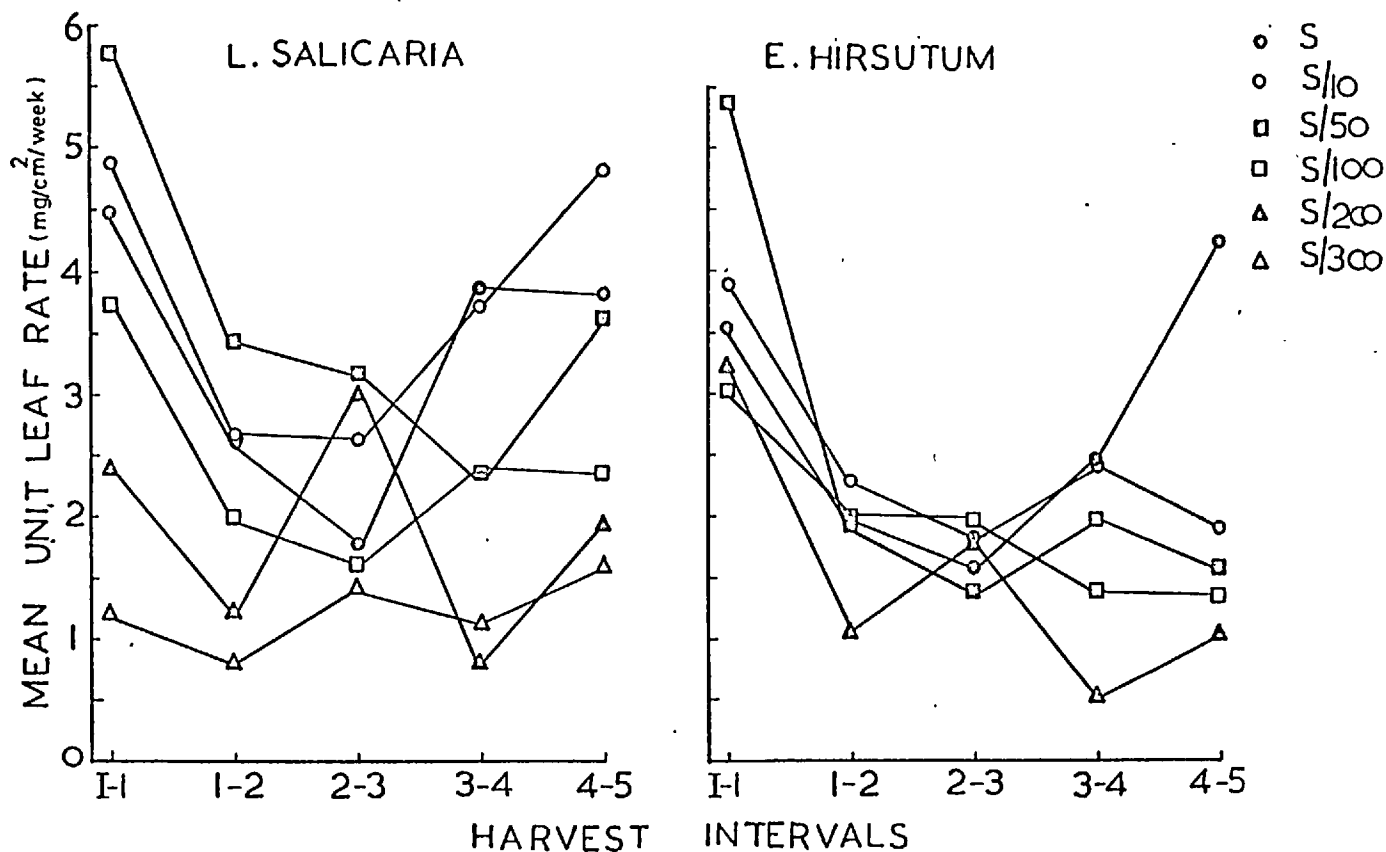


FIG. 42. Effect of different dilutions of a nutrient solution on mean unit leaf area. (For intervals between successive harvests) (I = initial harvest)

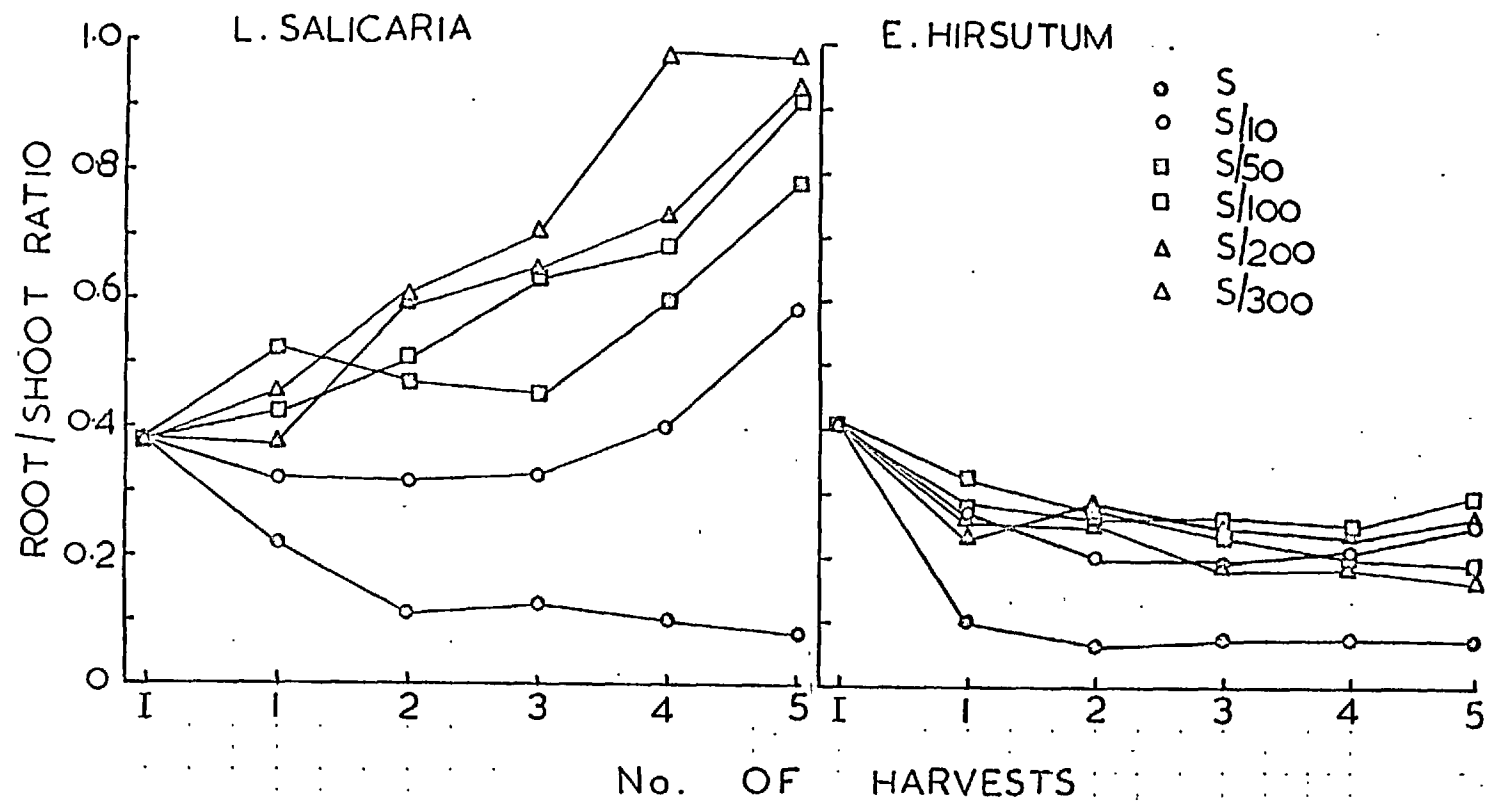


FIG. 44. Effect of different dilutions of a nutrient solution on root/shoot ratio.

been shown only for the initial, first, third and fifth harvests. In Epilobium the pattern of root at all levels of nutrient dilution remains similar from the first to the final harvest but the pattern of leaves and stem undergoes changes with time so that at the fifth harvest the plants in the standard solution are relatively more stemy but the nutrient deficient plants tend to be leafy. It can be seen that there is a gradual increase in the root and leaf proportions at the expense of the stem proportions with the increase in nutrient dilutions. With the change from the 'S' to the S/10 dilution there is a large diversion of dry weight from the stem to the root but in the later dilutions any loss in the stem proportion goes to increase the proportion of leaf. There is a breakdown in the pattern of leaf, stem and root at the S/300 dilution with an abrupt fall in the leaf and root proportions and a sharp rise in the proportion of stem. It should be noted that in the final harvest the root constitutes the lowest proportion in all the dilutions and the leaves the highest (except at the S/10 level) but the differences between the leaves and stem are not very large.

On the other hand, in Lythrum the pattern of leaf, stem and root in the nutrient deficient plants is in complete contrast to those of Epilobium. In the final harvest (fifth harvest) while the plants in the standard solution become

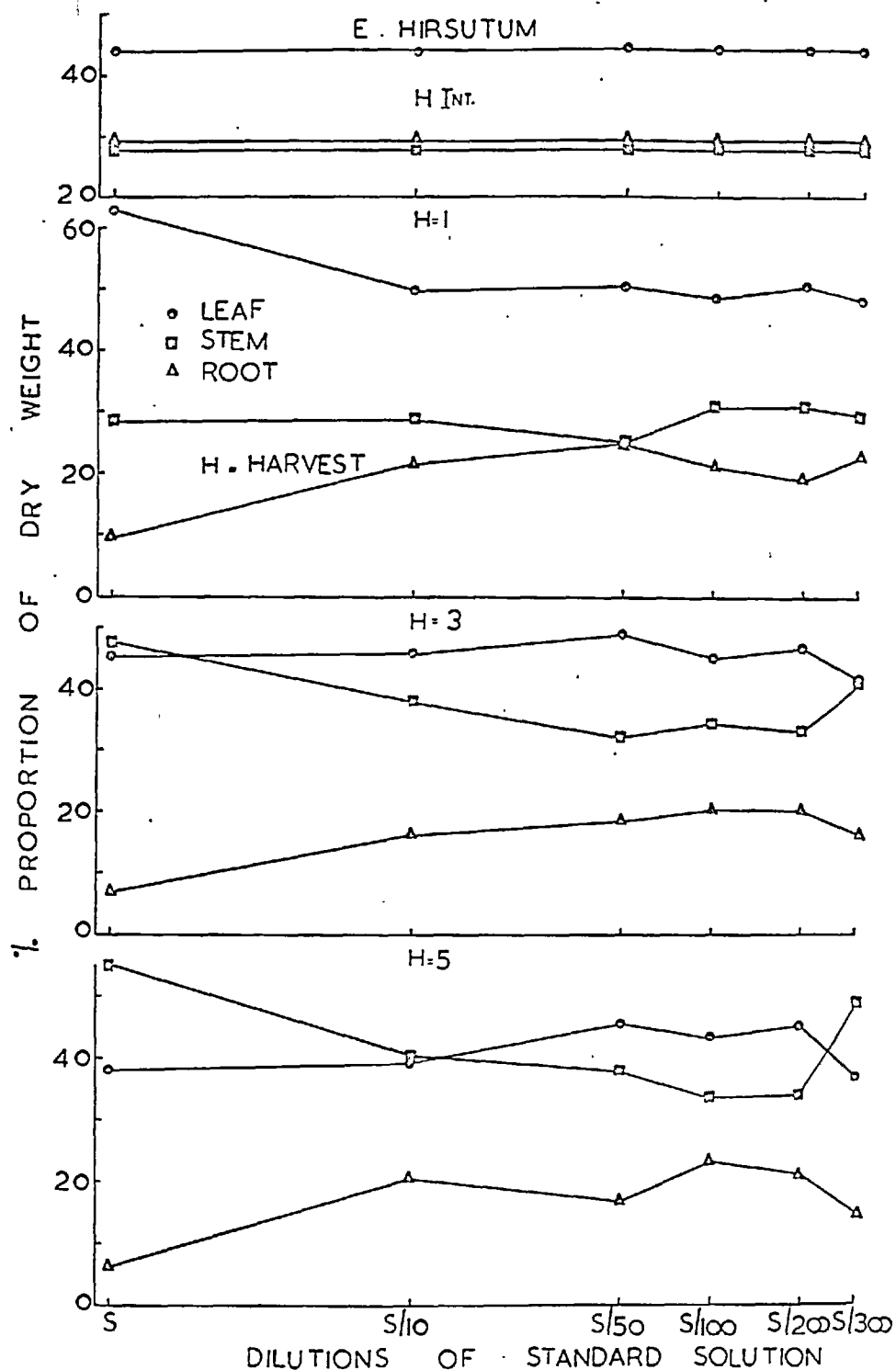


FIG. 45.

Effect of different dilutions of a nutrient solution on percentage proportional distribution of total dry weight to leaves, stems and roots. (Harvests: initial, one, three and five)

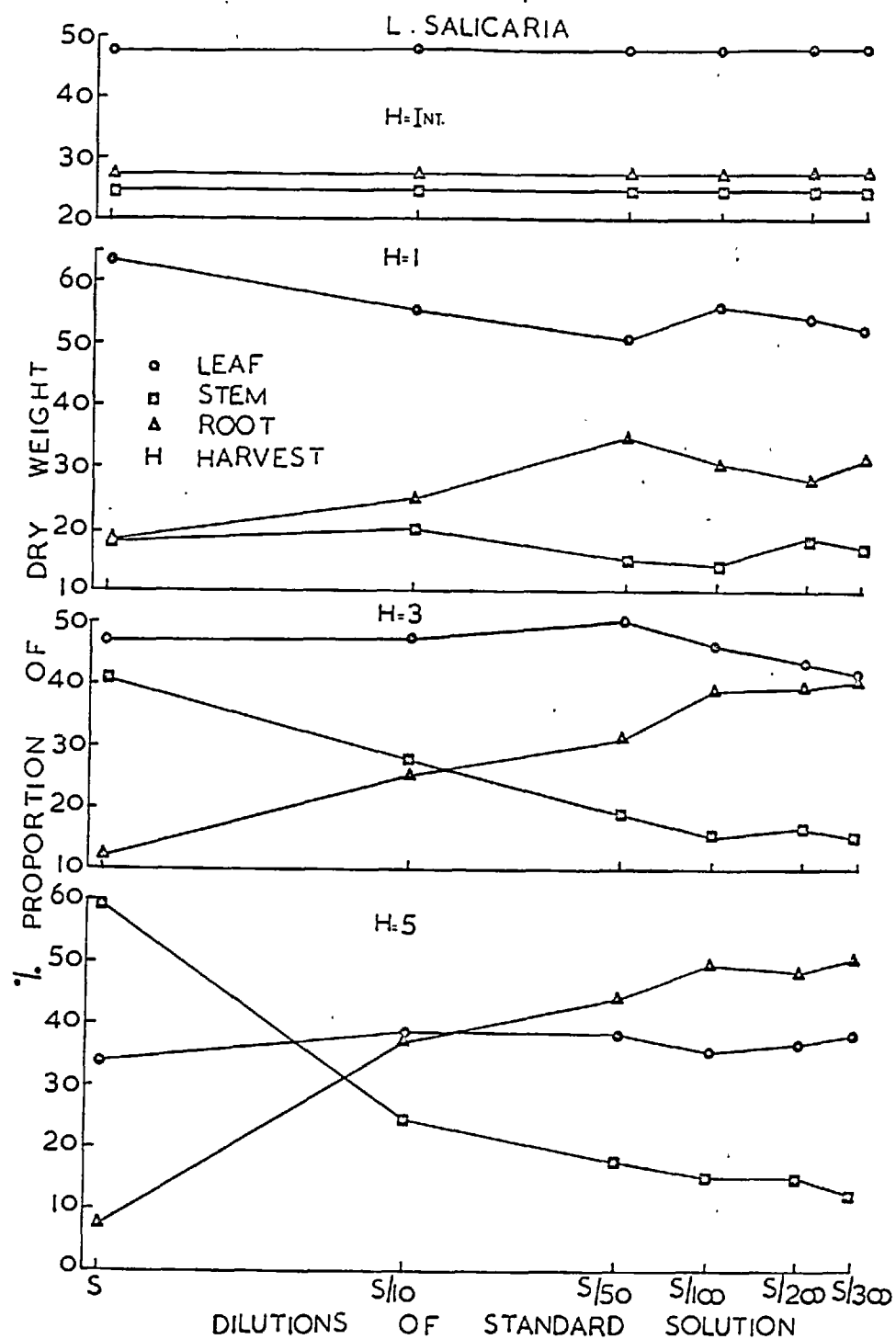


FIG. 46. Effect of different dilutions of a nutrient solution on percentage proportional distribution of total dry weight to leaves, stems and roots. (Harvests initial, one, three and five.)

excessively stemy the nutrient deficient plants tend to become more rooty and this tendency is very marked in the higher dilutions. It can be noted that the leaf proportions in the final harvest remain more or less similar from the standard to the S/300 dilution, and the increase in the root proportions in all dilutions is entirely at the expense of the stem proportions. Unlike Epilobium, in Lythrum there is no breakdown in these patterns in the S/300 dilution. In complete contrast to Epilobium, in Lythrum in the final harvest of the nutrient deficient plants the stem constitutes the lowest proportion while the ^{roots}~~leaves~~ constitute the highest proportion except in the S/10 dilution where the values of leaves and root are very close. It is pointed out that in Epilobium at all levels of nutrient dilution the root constitutes about 20% of the total dry weight but in Lythrum at the S/10 dilution the root is 37% and up to 50% in the later dilutions.

General Discussion

The data presented show that as the solution became weaker, i.e. the dilution was increased, there was a marked falling off in the total dry weight attained by the individual plants. Relatively speaking, reduction in the dry weight gain was greater in Epilobium than in Lythrum. That Lythrum was more efficient and accumulates a higher amount of dry matter

in conditions of nutrient stringency was also shown. from their mean unit leaf rates. Although the dry weight gains of Lythrum at the standard and the S/10 dilution were higher than those of Epilobium the growth in the S/50 dilution seemed to be of critical importance. At this dilution there was no appreciable dry weight increase in Epilobium in the last two harvests but Lythrum showed a continuous progressive dry weight increase throughout the experiment.

Despite the falling off in the dry weight with the increase of dilution it was found that Lythrum responded by an increase in the root proportionately to the shoot so that there was an increase in the root/shoot ratio, such as recorded by Vose (1962); Troughton (1967); Myerscough and Whitehead (II 1967) and Davidson (1969) and many others. This change in the proportionality of root to shoot is such that in teleological terms, it would appear that available assimilates are being employed in a manner which could be considered as compensating to some extent for the lack of mineral nutrients. In other words as the nutrient stress becomes greater a proportionately larger root system capable of exploiting larger volumes of substrate was produced. On the other hand Epilobium did not show any marked tendency to increase the root/shoot ratio in response to nutrient stringency.

It has been shown that this extra proportion of root was obtained mainly at the expense of the proportion of stem. Again, regarded teleologically, it can be considered advantageous to the plant that this should be so. If leaf area was sacrificed the photosynthetic adaptabilities would be affected and material for root building be less available. While in Lythrum this phenotypic plastic response to the nutrient stringency increases with the increase in dilution, in Epilobium there was a breakdown at the S/300 dilution and the plants did not make much growth persisting in the same state for some weeks and eventually dying. The S/200 dilution, therefore, can be regarded as the "critical dilution" for Epilobium, beyond which the compensating mechanism fails and plants make no growth. On the other hand, the "critical dilution" for Lythrum appeared to be much higher than the S/300 dilution.

Troughton (1967) showed that shoot growth in plants growing in low nutrient conditions depends more on the number of roots produced rather than the mass of the roots. In other words the greater the number of root meristems in the nutrient solution the higher will be the nutrient uptake and consequently the better the shoot growth. In this context the difference in the root systems of the two species is very important. In Lythrum it is an organised tap root system with

profusely branched primary and secondary roots while in Epilobium the root system is composed of fewer, relatively less branched, adventitious roots. Thus the root system in Lythrum is a better competitor for the minerals than that of Epilobium. In poor nutrient status soils this could be considered as exploring a correspondingly larger volume of soil leading to a greater net uptake of nutrients. It can be inferred from the above that in the event of competition between the two species, under conditions of low nutrient supply, Lythrum would have an advantage over Epilobium. In this sense the "competitive" nature of the root system in Lythrum can be regarded as an adaptation to low nutrient supply.

In attempting to assess the relative probability of establishment of the two species in sites of low nutrient supply, account must be taken of the amount of growth each species is committed to making before it can switch from growing entirely as an assimilating entity to the production of organs of reproduction as well as its ability to grow under conditions of such stringency. In this experiment, even at the S/10 dilution, both the vegetative and reproductive growth of Epilobium was severely curtailed as the plants failed to produce rhizomes and flowers. Because of the ability of Lythrum to maintain itself as an efficient photosynthetic

entity at this dilution for a longer time with an earlier turnover to the production of flowers it is probably capable of establishment and of making adequate growth in sites with a higher stringency of available nutrients than those in which Epilobium can become established.

The commitment of Epilobium to the making of much leafy growth in the early stages of its establishment and the elaborate morphology, i.e. production of large numbers of rhizomes before it can produce any surplus dry weight required for flowering etc., probably adds to its incapacity to become established and make adequate growth in sites of similar high levels of stringency of available nutrients.

Experiment XI

Chemical analysis of plants grown in different dilutions of nutrient solution.

The results of Experiment X showed that there was a relatively greater reduction in the dry weight gain and the leaf area increase in Epilobium than in Lythrum as the nutrient solution became weaker. It was also suggested that the larger root proportion in Lythrum in nutrient stringency enabled it to absorb greater amounts of nutrients. While it may be correct to assume that this is the case, the possibility that other factors may also be involved exists. In

this connection the "nutrient status" of the two plants is important. The satisfactory growth of Lythrum in weaker solutions may be a reflection of "low nutrient requirements" of this plant. For these reasons investigations of the nutrient uptake in the two species in the solutions of unlimited nutrient supply (standard solution) and limited nutrient supply are imperative. By co-ordinating the results of these findings with those of growth responses under these conditions, it may be possible to determine whether one or both of these factors (i.e. nutrient uptake and nutrient requirements) are in operation.

On the other hand, many and varied examples of differential responses to mineral nutrients in flowering plants recorded in literature do not account for these differences.

In this experiment the uptake of nitrogen, potassium, phosphorus and calcium in plants of the two species, grown in the standard solution and in a series of its dilutions, was determined. The distribution of these elements in the various tissues of the plants, i.e. leaves, stem and root was investigated and its impact on the survival of the species was assessed.

Materials and Methods

Forty day old seedlings of the two species were grown in the standard culture solution and seven of its dilutions, designated as 'S', S/10, S/50, S/100, S/200, S/300 S/400 and S/500, following the same procedure as in Experiment X.

Fifty seedlings per species were grown in the 'S', S/10 and S/50 dilutions and in the rest of the dilutions two hundred plants per species were used. Because of the great reduction in plant size in the higher dilutions it was important to grow more plants in order to have enough material for chemical analysis. The experiment was started on 25 October, 1968. Only the initial harvest, at the time of transplantation, and the final harvest after eight weeks of growth were made. The primary data in terms of the dry weights of leaves, stems and roots were recorded as in the previous experiments.

The amounts of nitrogen, potassium, phosphorus and calcium were determined in the leaves, stems and roots separately in the plants of each species from each dilution. Automatic methods for the determination of these elements have been described in Chapter IV. Determinations of these elements were also made on the seedlings of the initial harvest since they were fed on the nutrient solution before their

transplantation.

Results

The dry weights of the two species in the initial and final harvests are shown in Fig. 47. The general pattern of increase in the dry weight in the two species is similar to that in the previous experiment, and since the difference in the seedling dry weights of the two species was not very large, in the final harvest in the higher dilutions the dry weight of Lythrum is higher than that of Epilobium. The percentage proportion dry weights of the leaves, stem and root are shown in Fig. 48. The patterns of dry weight proportions of these organs follow the same course as those described in Experiment X (Figs. 45 and 46).

NITROGEN

The total amounts of nitrogen per plant in each species for the initial and final harvests are shown in Fig. 49. In plants grown in the standard solution the amount of nitrogen per plant is higher in Epilobium than in Lythrum although the dry weight of the latter is higher than the former. On the other hand, in the increasing series of dilutions the amount of nitrogen per plant is higher in Lythrum than in Epilobium and very markedly so at the S/10 and S/50 dilutions. Fig. 50 shows the amount of nitrogen as percentage dry weight of the plants both for the initial and the final harvests.

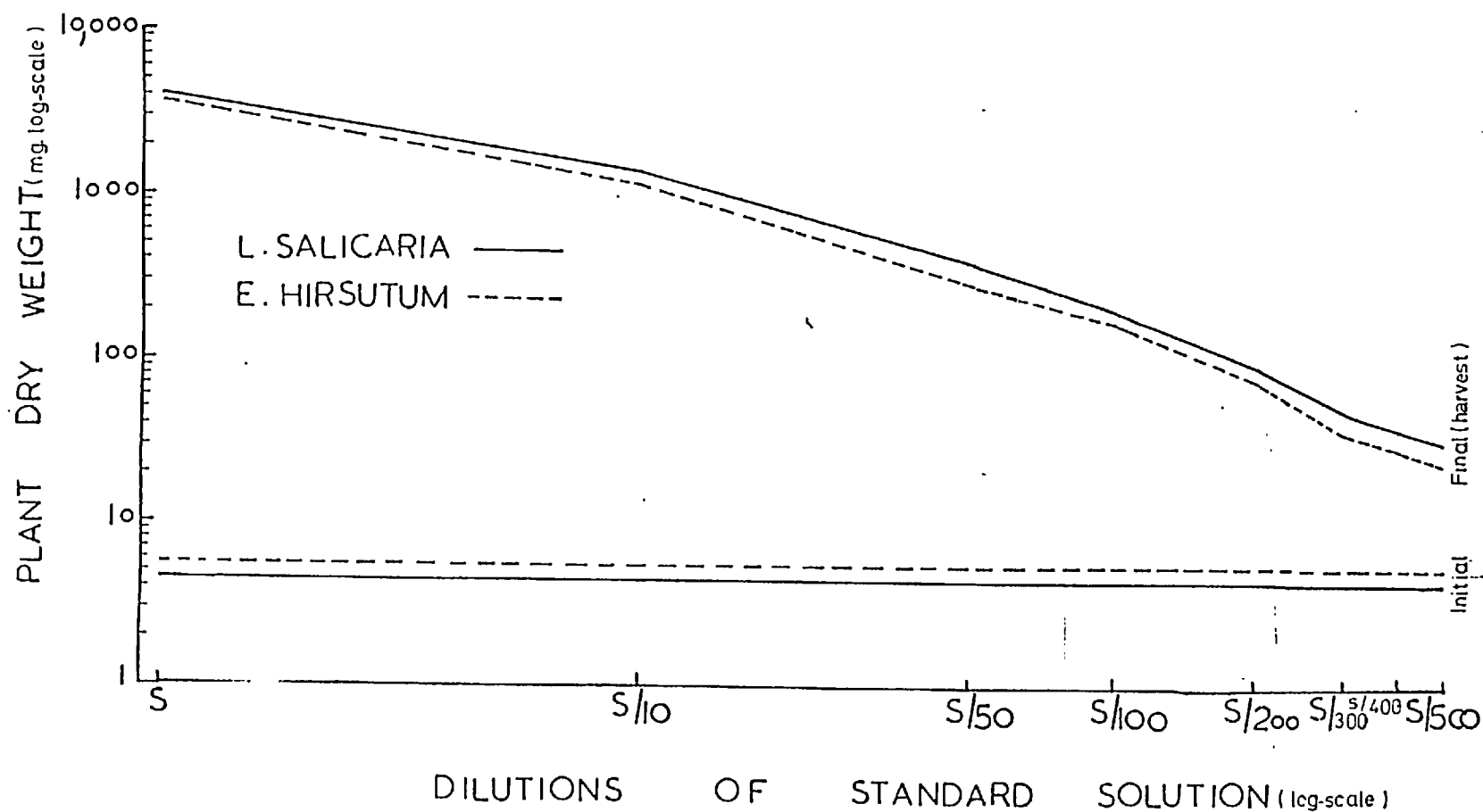


FIG. 47. Effect of different dilutions of a nutrient solution on increase of plant dry weight in final harvest. (Straight lines = initial harvest)

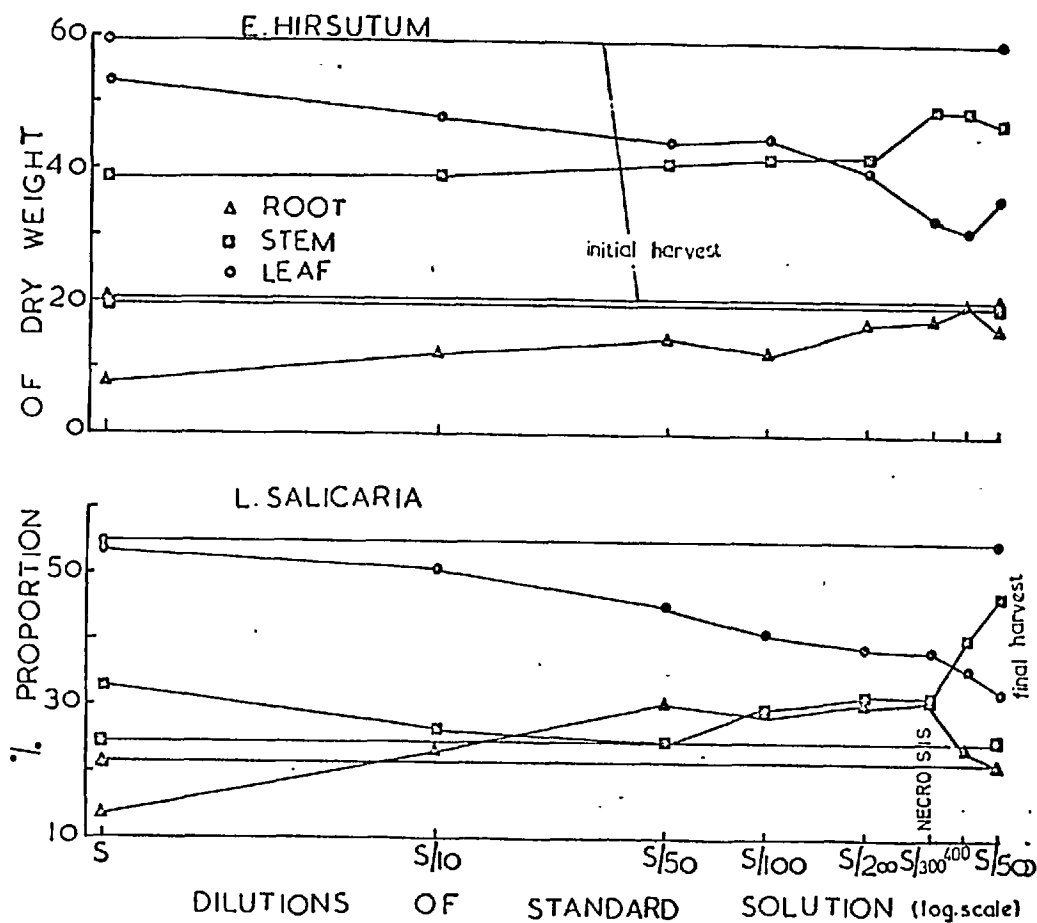


FIG. 48. Effect of different dilutions of a nutrient solution on percentage proportional distribution of total dry weight to leaves, stems and roots in the final harvest. (Straight lines = initial harvest)

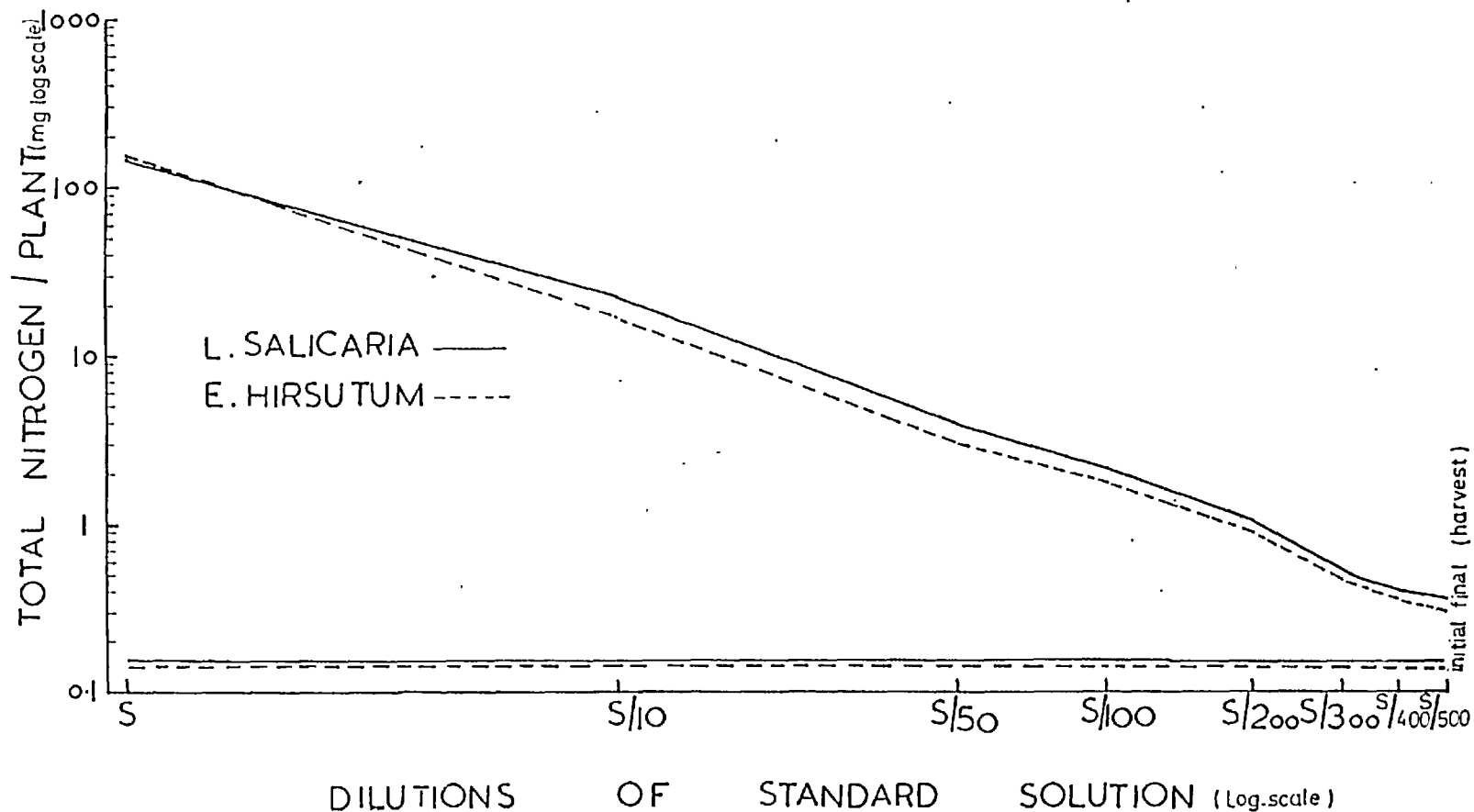


FIG. 49. Effect of different dilutions on a nutrient solution on the uptake of nitrogen. Total amount of nitrogen per plant.
(Straight lines = initial harvest)

It can be noted that the dry weight percentage of nitrogen in the Lythrum seedlings is much higher than in the Epilobium seedlings. In the final harvest again the dry weight percentage of nitrogen is higher in Epilobium in the standard solution but at the S/10 dilution and three others (i.e. up to the S/200 dilution) it is higher in Lythrum than in Epilobium. In the last three dilutions (i.e. S/300, S/400 and S/500) the percentage of nitrogen is again slightly higher in Epilobium. This irregularity can be attributed to the excessive development of necrotic tissue in Epilobium in these dilutions. Fig. 50 also shows that there is a great fall in the dry weight percentage nitrogen contents of the plant with the dilution of the solution from the standard to S/10, later, in all the dilutions, values are more or less similar in Lythrum but in Epilobium there is a slight rise in the values in the last four dilutions. The fall in the percentage amount of nitrogen in the series of dilutions in the two species from their controls is shown in Fig. 51.

It is clear that the fall in the percentage amount of nitrogen is greater in Epilobium than in Lythrum. This would mean that the uptake of nitrogen is more affected in Epilobium than in Lythrum in conditions of nutrient stringency. The dry weight percentage of nitrogen in the individual plant parts, i.e. leaves, stem and root, is shown in Fig. 52. In

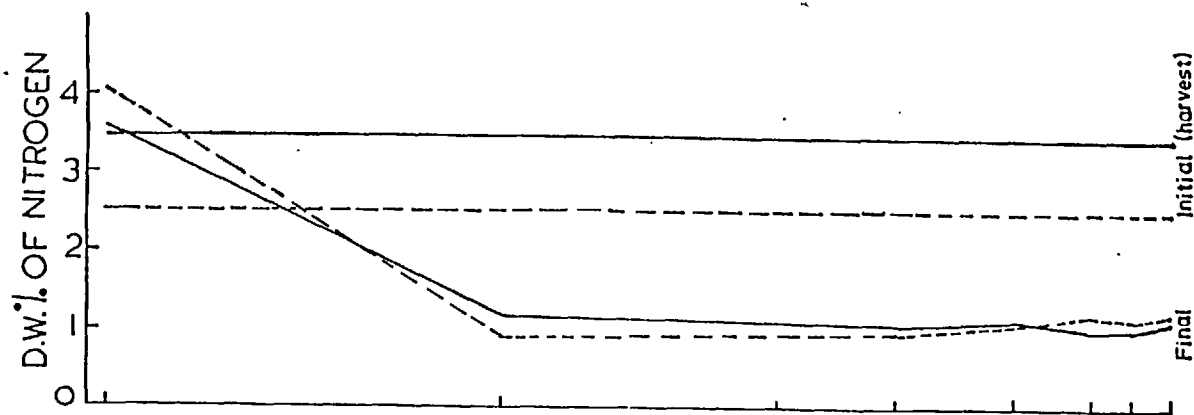


Fig. 50.

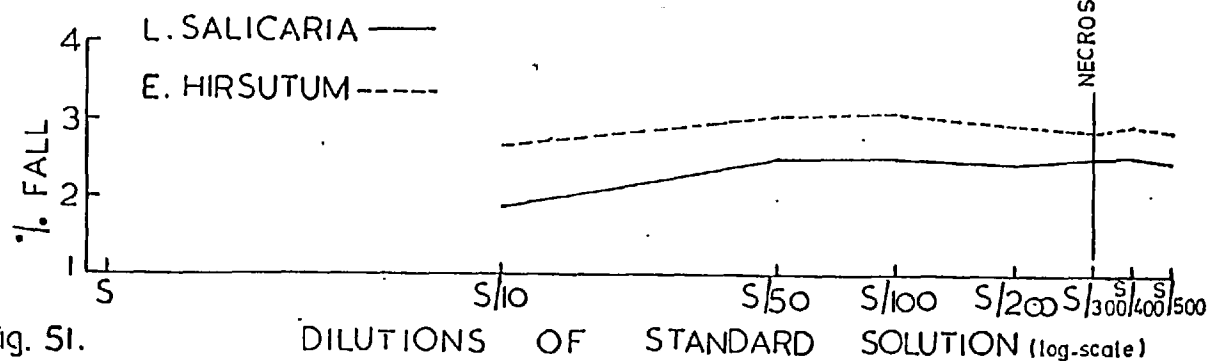


Fig. 51.

Effect of different dilutions of a nutrient solution on the uptake of nitrogen.

FIG. 50. Dry weight percentage of nitrogen per plant (Straight lines = initial harvest)

FIG. 51. Fall in the dry weight percentage of nitrogen in the series of dilutions from the standard treatment.

both species the stem has the lowest percentage of nitrogen at all levels of dilutions. In Epilobium the percentage of nitrogen in the root is higher than in the leaf in the standard solution and in all the dilutions, but at the S/50 dilution and the later dilutions there is a gradual increase in the dry weight percentage of nitrogen in the root and a corresponding reduction in the nitrogen percentage of the leaf. In Lythrum in the standard solution and the S/10 dilution the percentage of nitrogen in the leaves is higher than in the root, but in the later dilutions, like Epilobium, there is an increase in the root contents at the expense of that of the leaves.

The internal distribution of nitrogen per plant in the leaves, stem and root as a proportional percentage of the total amount of nitrogen is shown in Fig. 53. The contrast in the percentage proportion of stem in the two species is very striking as the proportion is markedly higher in Epilobium than in Lythrum. It can be seen that in both species with the increase in the dilutions there is an increase in the proportion of root ^{nitrogen}, principally at the expense of the proportion of leaf ^{nitrogen}. In Lythrum this increase in the root proportion is very marked compared with Epilobium, it is such that in the S/10 dilution and all the other major dilutions the root proportion is considerably higher than the stem proportion whilst it is

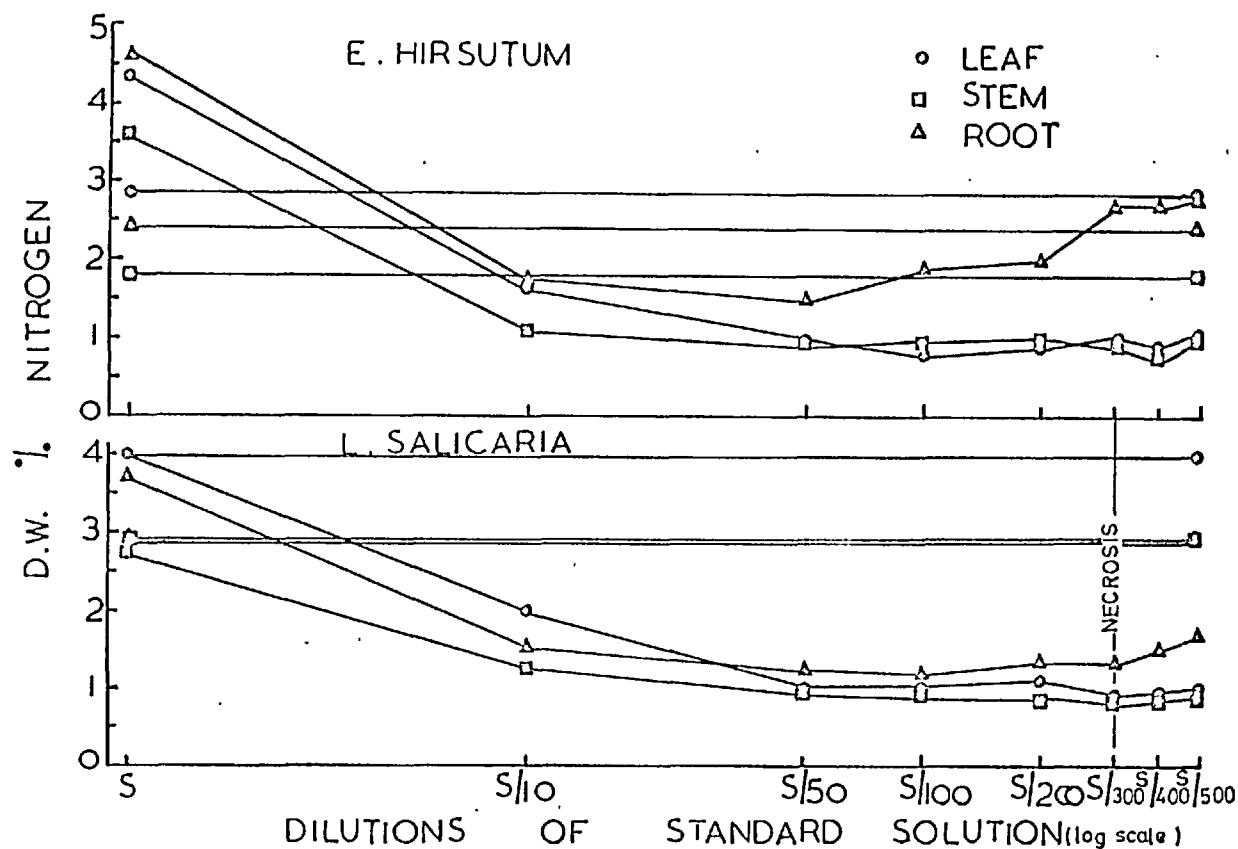


FIG. 52. Effect of different dilutions of a nutrient solution on the uptake of nitrogen. Dry weight percentage of nitrogen in leaves, stems and roots. (Straight lines = initial harvest)

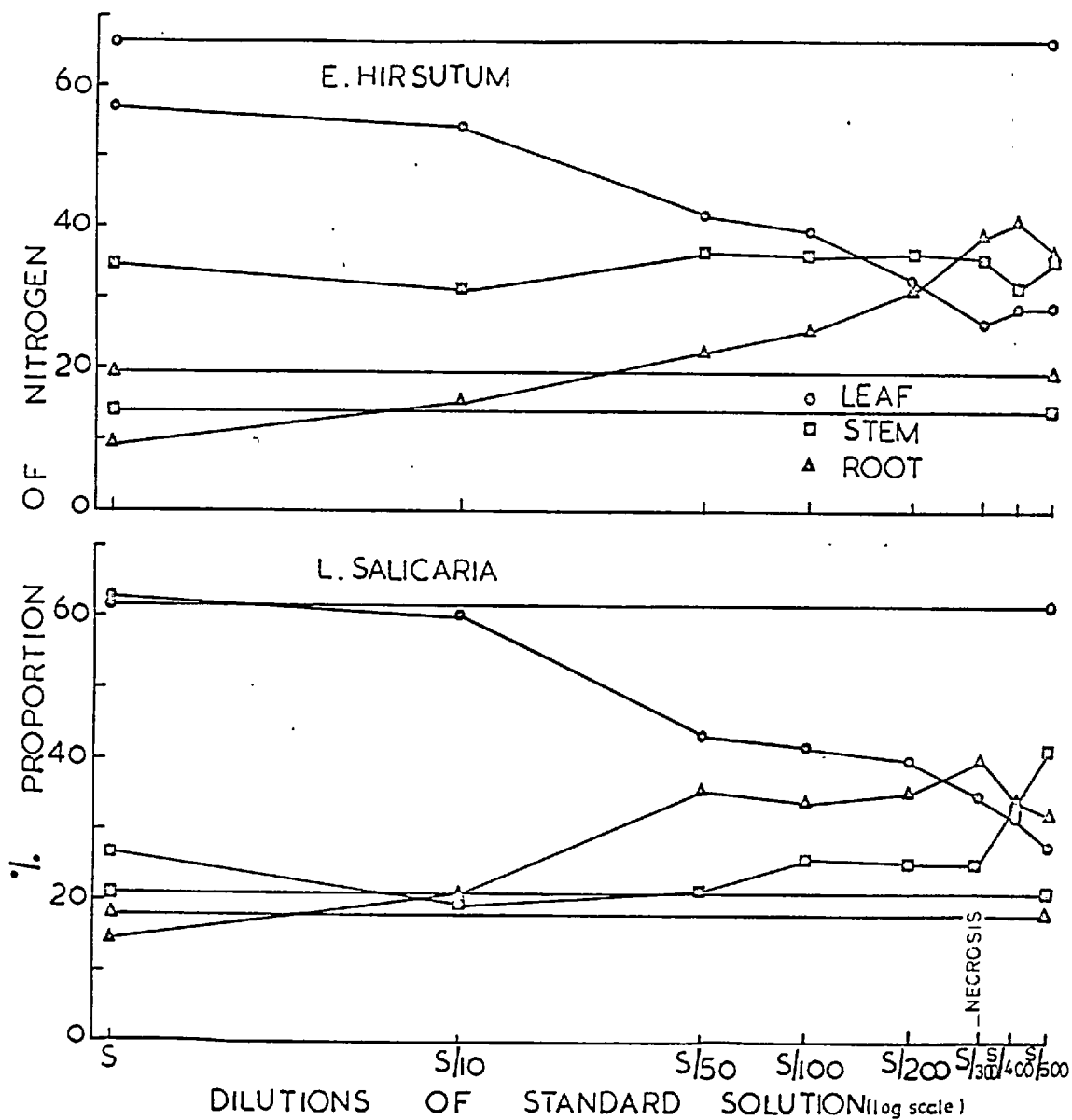


FIG. 53. Effect of different dilutions of a nutrient solution on the uptake of nitrogen. Percentage proportional distribution of the total amount of nitrogen to leaves, stems and roots. (Straight lines = initial harvest).

the reverse in Epilobium. Moreover, the proportion of leaf shows a greater reduction in Epilobium than in Lythrum. Irregularities in the patterns of these proportions in the last three dilutions can be attributed to the excessive development of necrotic tissue in the plants of both species.

Discussion

The results presented show that, of the two species grown in standard solution, the nitrogen contents of Epilobium were higher than those of Lythrum. On the other hand, in the weaker solutions this was reversed and the contents were higher in Lythrum than in Epilobium. This would mean that under conditions of nitrogen stringency there would be a greater reduction in the nitrogen uptake capacity of Epilobium when compared with Lythrum.

In addition to the ability of Lythrum to absorb nitrogen more efficiently in the stringency conditions, its internal distribution in the leaves, stem and root was such that it could be considered advantageous for the growth of the plant. Greater diversion of nitrogen to the root would ensure its healthier growth and efficient functioning. Comparatively less reduction in the leaves means that its photosynthetic adaptabilities would be less affected. In Epilobium the major part of the nitrogen, in deficient conditions, was diverted to the stem, and this lack of available

nitrogen to the leaves and root (vital centres of physiological activity) would result in the decreased absorption capacity, and consequently a greater reduction in the dry weight gains of the plants.

It is clear that Lythrum is not only a plant of comparatively low nitrogen requirements for its normal growth but is also more efficient in its nitrogen uptake capacity under conditions of nutrient stringency. This dual advantage would enable Lythrum to grow as an efficient photosynthetic entity in sites of low nitrogen supply, whilst the high nitrogen requirements and low absorptive capacity would probably exclude the establishment and growth of Epilobium in such nitrogen deficient sites.

POTASSIUM

The total amounts of potassium per plant in the initial and final harvest are shown in Fig. 54. In both species there is a reduction in the potassium contents with the increase in dilutions. Like nitrogen, the potassium contents of Epilobium plants in the standard solution are markedly higher than those of Lythrum, but in the increasing series of dilutions the amount of potassium per plant in Lythrum is higher than in Epilobium. The amount of potassium expressed as a percentage of the dry weight can be seen in Fig. 55. The results are similar to those of Fig. 54.

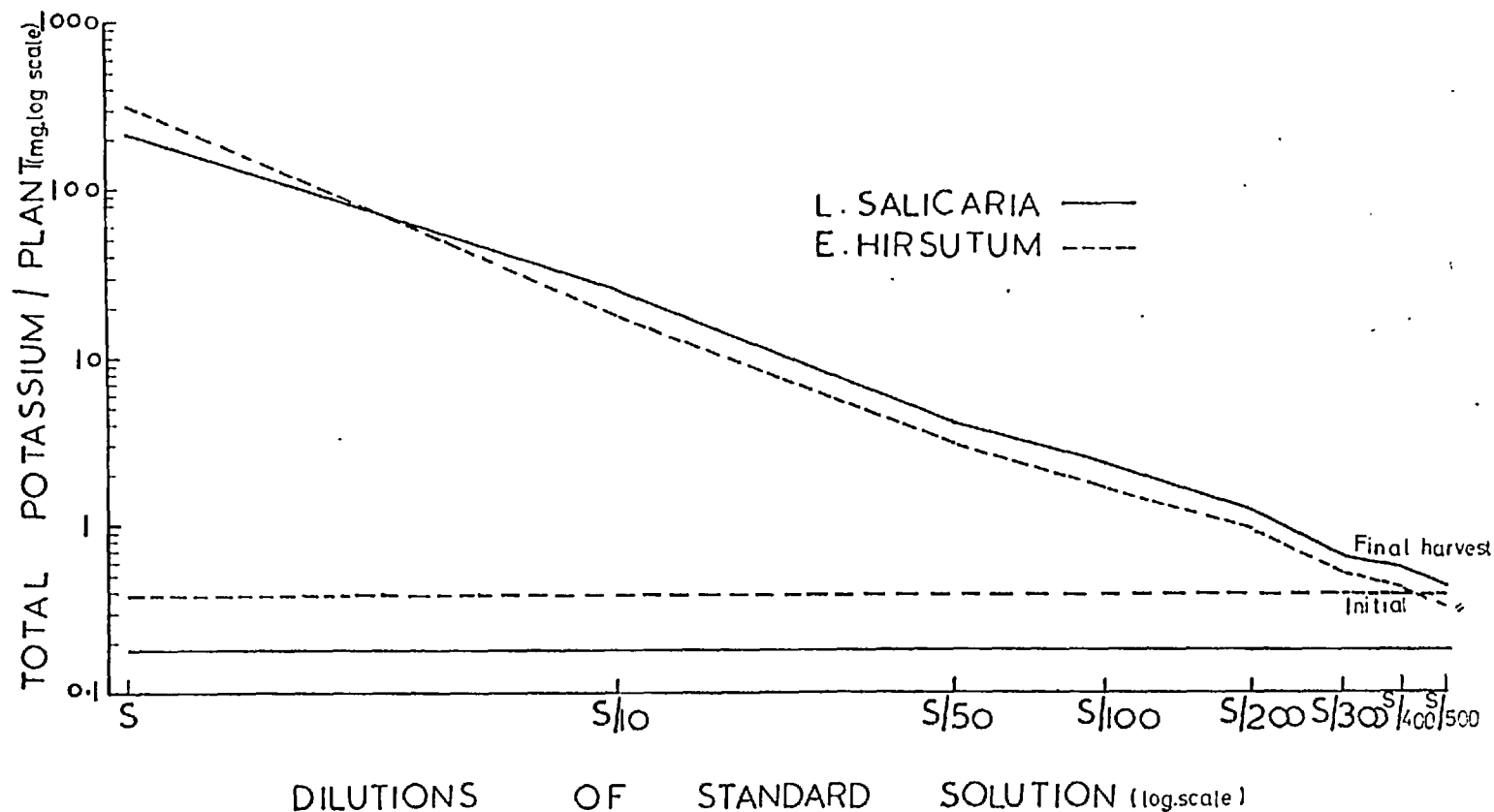


FIG. 54. Effect of different dilutions of a nutrient solution on the uptake of potassium. Total amount of potassium per plant.
(Straight lines = initial harvest)

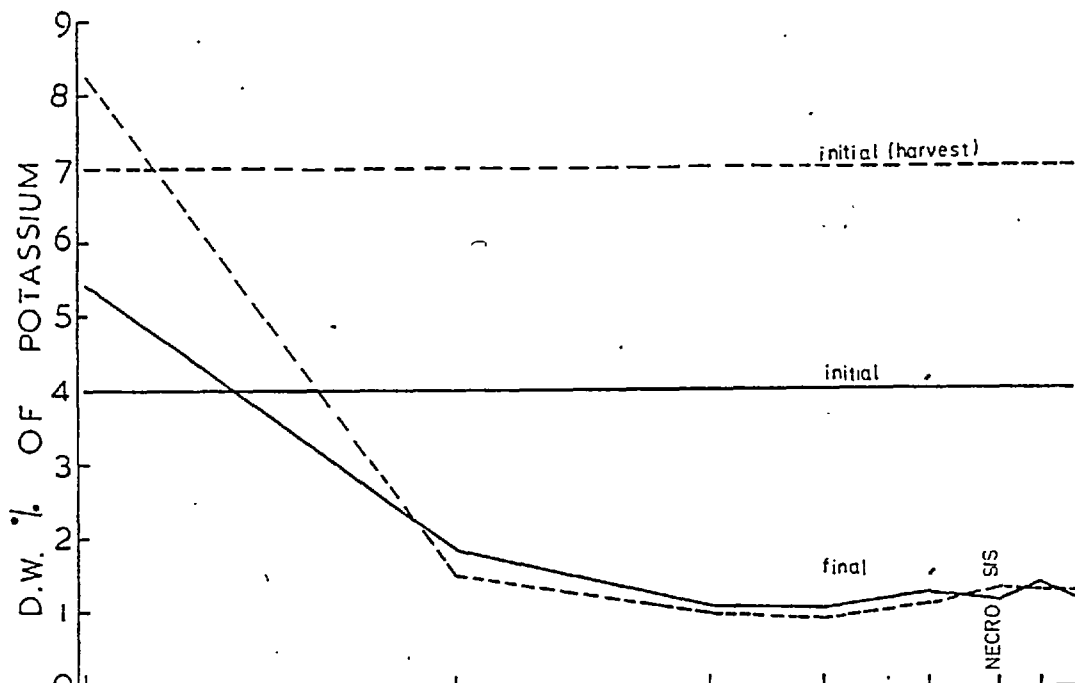


Fig. 55.

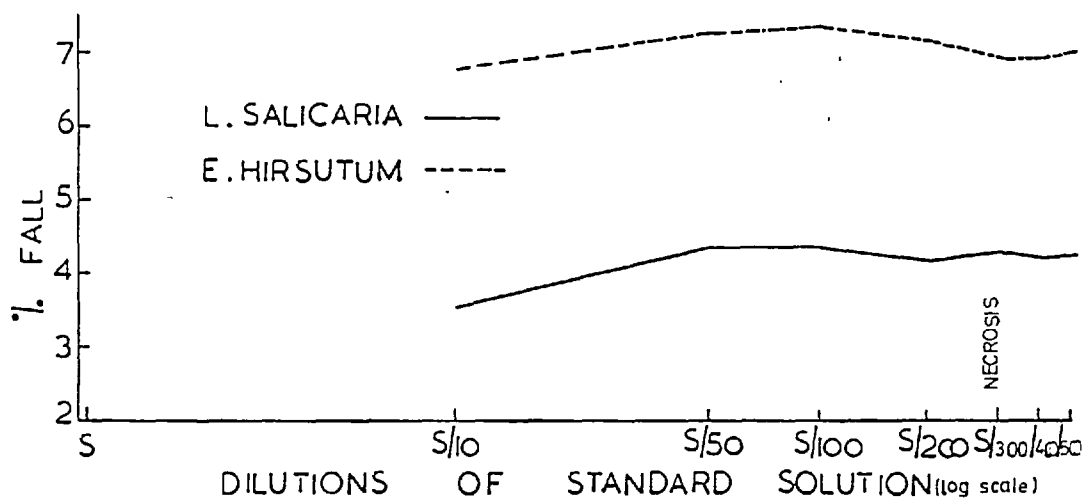


Fig. 56.

Effect of different dilutions of a nutrient solution on the uptake of potassium.

FIG. 55. Dry weight percentage of potassium per plant. (Straight lines = initial harvest)

FIG. 56. Fall in the dry weight percentage of potassium in the series of dilutions from the standard treatment.

Irregularities in the last three dilutions may be because of the development of necrotic tissue in these plants. From Fig. 55 it can also be seen that there is a sharp decline from the 'S' to the S/10 dilution and it is more so in Epilobium than in Lythrum. This fall in the percentage uptake of potassium in various dilutions is shown in Fig. 56. It can be inferred that there is a far greater reduction in the potassium uptake ability in Epilobium than in Lythrum in the series of decreasing potassium supply.

Fig. 57 shows the dry weight percentage of potassium in the leaves, stem and root. In both species the highest dry weight percentage of potassium is in the root and the lowest in the leaves except in the standard Epilobium where the percentage of the leaf is higher than that of the stem.

The proportional distribution of the total amount of potassium to leaves, stem and root, shown in Fig. 58, follows the same pattern as that of nitrogen, i.e. in Lythrum there is a gradual increase in the root proportion at the expense of both leaf and stem proportions, but in Epilobium a greater amount of leaf potassium is being diverted to the stem and the root gains very little. The pattern of the stem proportion is contrasting in the two species. The leaf proportion shows a great reduction at the S/10 and S/50 dilutions in Epilobium; in contrast, in Lythrum reduction at these

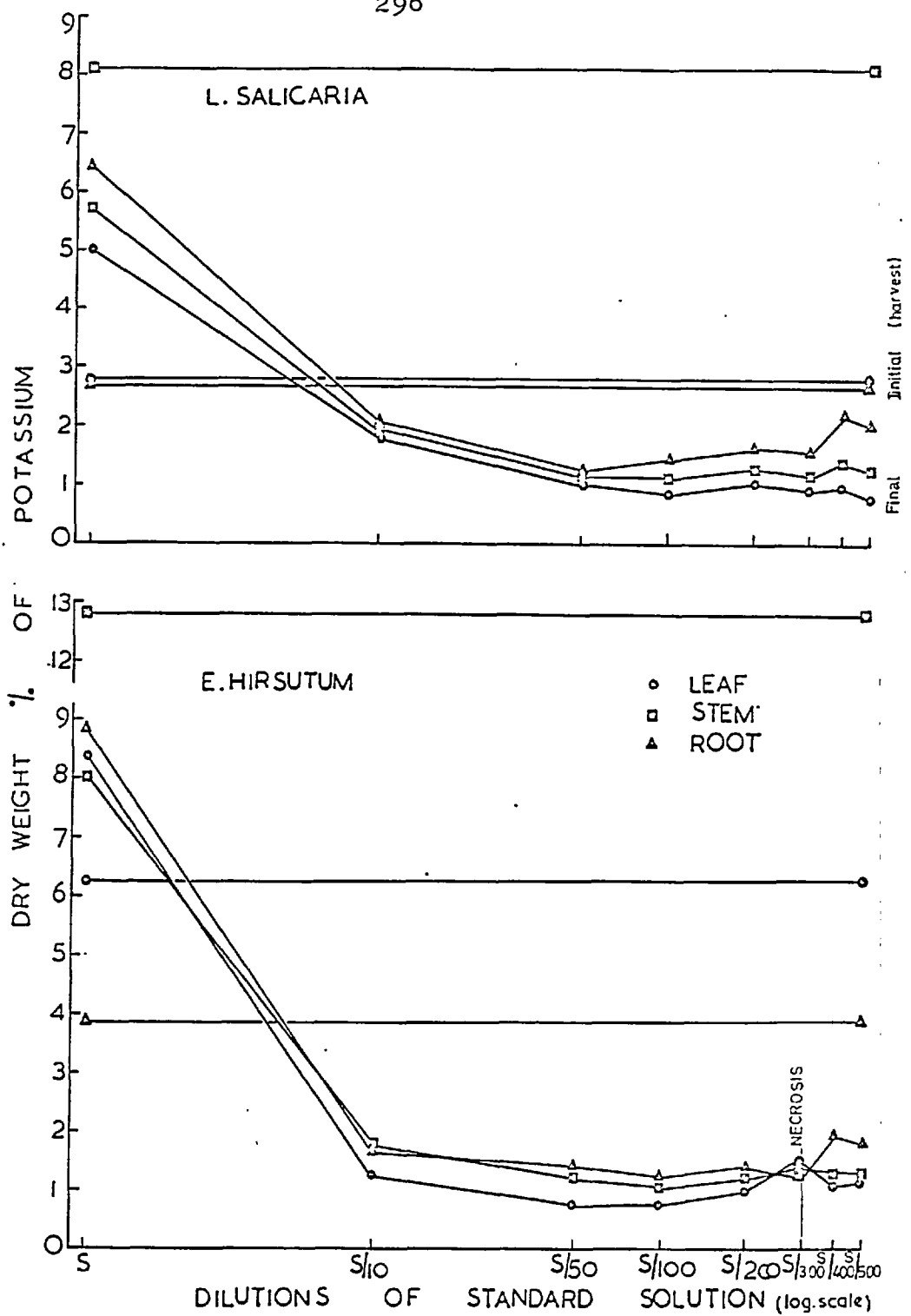


FIG. 57. Effect of different dilutions of a nutrient solution on uptake of potassium. Dry weight percentage of potassium in leaves, stems and roots. (Straight lines = initial harvest)

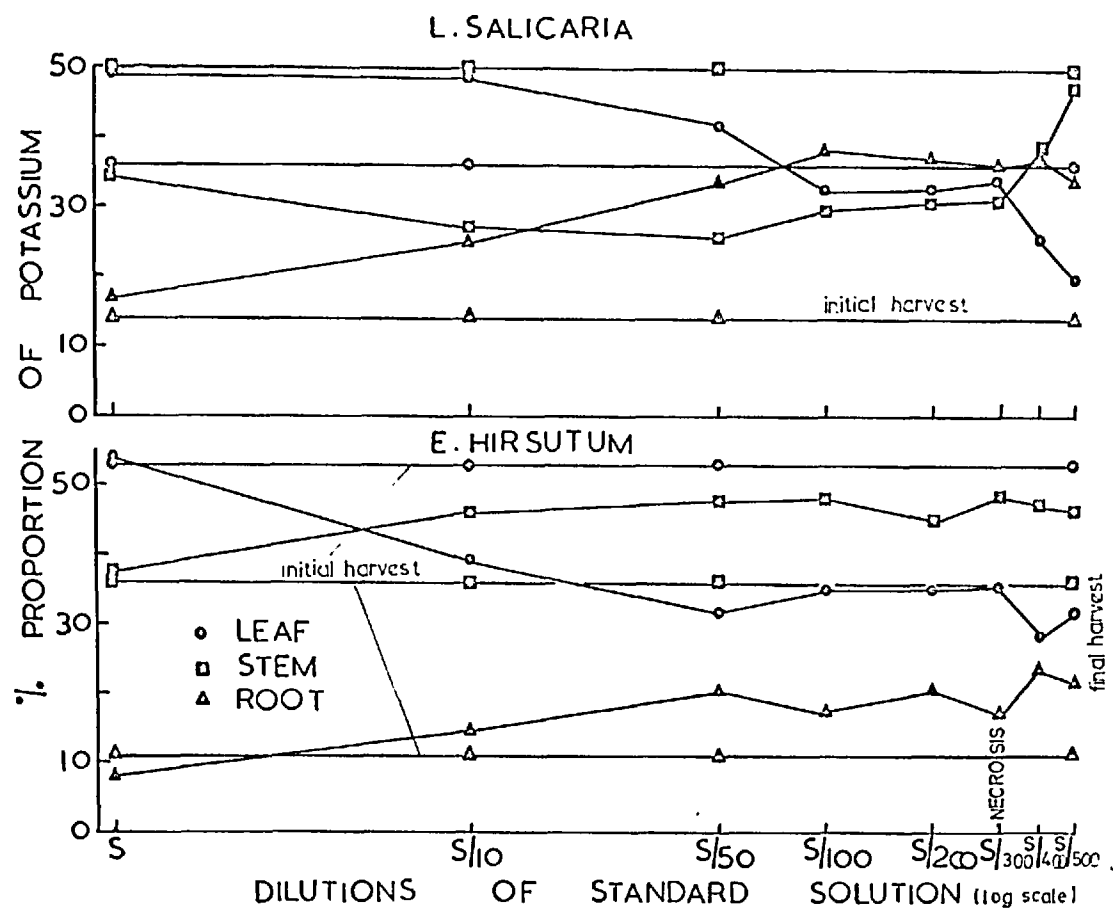


FIG. 58. Effect of different dilutions of a nutrient solution on the uptake of potassium. Percentage proportional distribution of the total amount of potassium to leaves, stems and roots. (Straight lines = initial harvest)

dilutions is not very marked. Further, it can be seen from Fig. 58 that while in Epilobium the stem has the largest proportion of potassium at all levels of dilution, there is a great reduction in the leaf and the root has the lowest proportion. In Lythrum in the first two dilutions the largest proportion of potassium is diverted to the leaves and the increase in the root proportion is mainly at the expense of the proportion of stem, but in the later dilutions the root has the largest proportion of potassium at the expense of the leaf proportion.

Discussion

It is clear from these results that the potassium requirements of these plants are greater than the nitrogen requirements, especially in Epilobium, and the reduction in the potassium uptake capacity in the weaker solutions was greater in Epilobium than in Lythrum.

Potassium is known to be the most mobile of all the nutrients in a plant and the greatest proportion of the absorbed potassium is translocated to the leaves. This mobility of potassium was not greatly affected in Lythrum, especially at the S/10 and S/50 dilutions and at these dilutions while the major part of the absorbed potassium was still being diverted to the leaves there was also an adaptive increase in the root contents at the expense of the stem, and

this tendency became more pronounced in the later dilutions. On the other hand, in Epilobium this translocation of potassium to the leaves was drastically cut down in the S/10 and S/50 dilutions while there was no appreciable increase in the root proportion; the major part of the potassium under conditions of stress was translocated to the stem. Thus in Epilobium supplies of potassium to both centres of physiological activity, i.e. root and leaf, were severely affected by the potassium stringency. This would, consequently, result in a relatively greater reduction in the dry weight gain in Epilobium than in Lythrum.

PHOSPHORUS

The total amount of phosphorus per plant is shown in Fig. 59. The results follow the same pattern as in nitrogen and potassium, i.e. with the fall in the concentration of the solutions there is a decrease in the phosphorus contents of the plants. Although in the standard plants the phosphorus contents of Epilobium are higher than in Lythrum this relationship is reversed in all the dilutions. The dry weight percentage of phosphorus per plant is shown in Fig. 60.

It can be seen that there is very little reduction in the phosphorus uptake from the 'S' to the S/10 dilution, and in the later dilutions the values of dry weight percentage are very similar in both species throughout the series

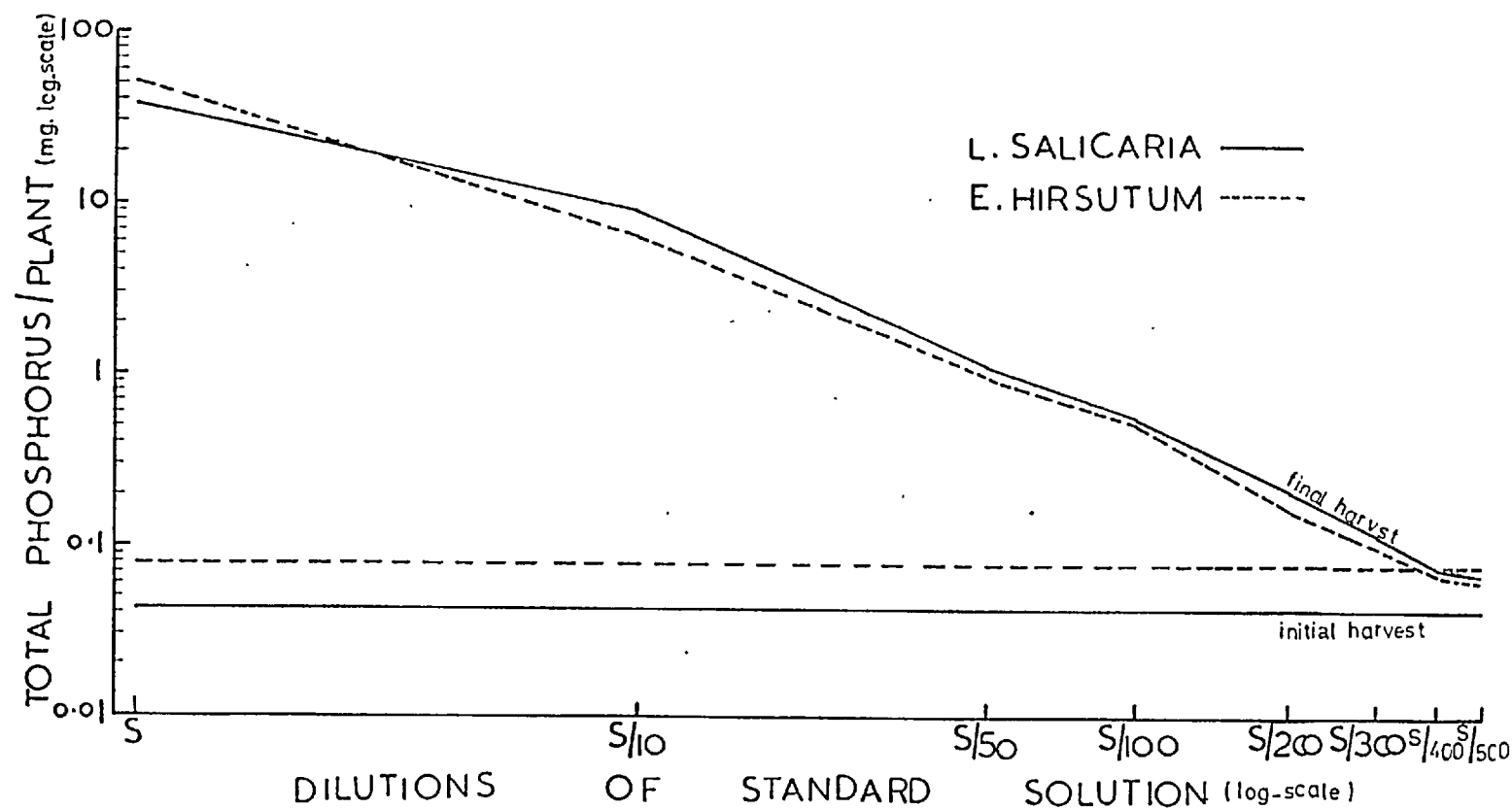


FIG. 59. Effect of different dilutions of a nutrient solution on the uptake of phosphorus. Total amount of phosphorus per plant. (Straight lines = initial harvest)

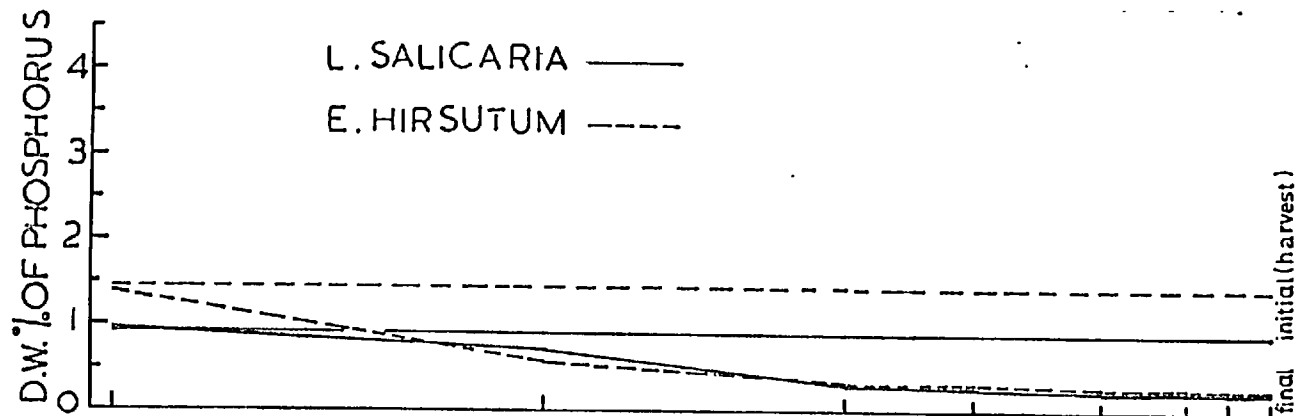


Fig. 60.

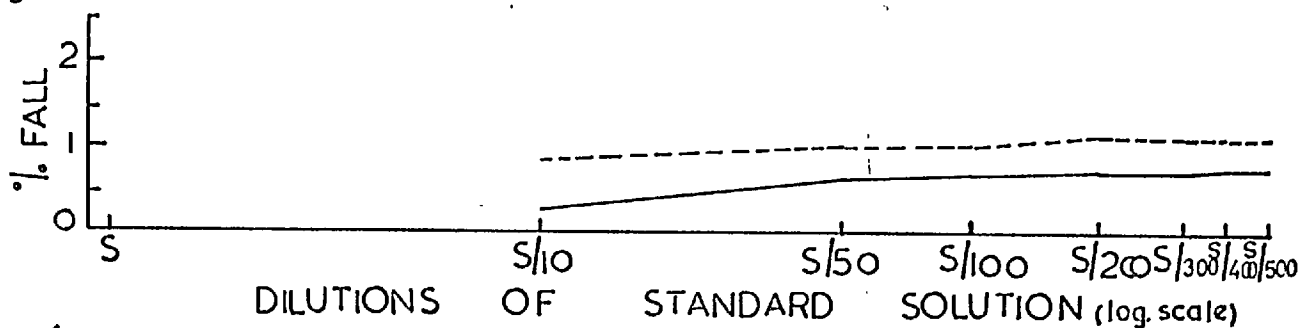


Fig. 61.

Effect of different dilutions of a nutrient solution on the uptake of phosphorus.

FIG. 60. Dry weight percentage of phosphorus per plant. (Straight lines = initial harvest)

FIG. 61. Fall in the dry weight percentage of phosphorus in the series of dilutions from the standard treatment.

with Epilobium slightly higher than Lythrum. There is a greater reduction in the uptake capacity in Epilobium than in Lythrum, as shown by the fall in the percentage of phosphorus in the nutrient deficient plants compared with their controls (Fig. 61). Fig. 62 shows the changes in the dry weight percentage of phosphorus in the leaves, stem and root in both species. In Epilobium the root has the highest phosphorus dry weight percentage in all the dilutions, especially in the standard and S/10 dilution. But in Lythrum, at these levels the leaves have the highest percentage of phosphorus and in the later dilutions values become similar in all the three components.

Again the general pattern of internal distribution of the total amount of phosphorus in the leaves, stem and root follows the same course as that of nitrogen and potassium. This is shown as the percentage proportionate distribution in the various parts in Fig. 63. The important difference is that in both species at the S/10 dilution there is practically no reduction in the leaf proportion, and there is an increase in the root proportion at the expense of stem proportion, but in Lythrum, in the later dilutions, there is a greater diversion of phosphorus from the leaves to the root. On the other hand in Epilobium all the phosphorus from the leaves is diverted to the stem and none to the root in the major

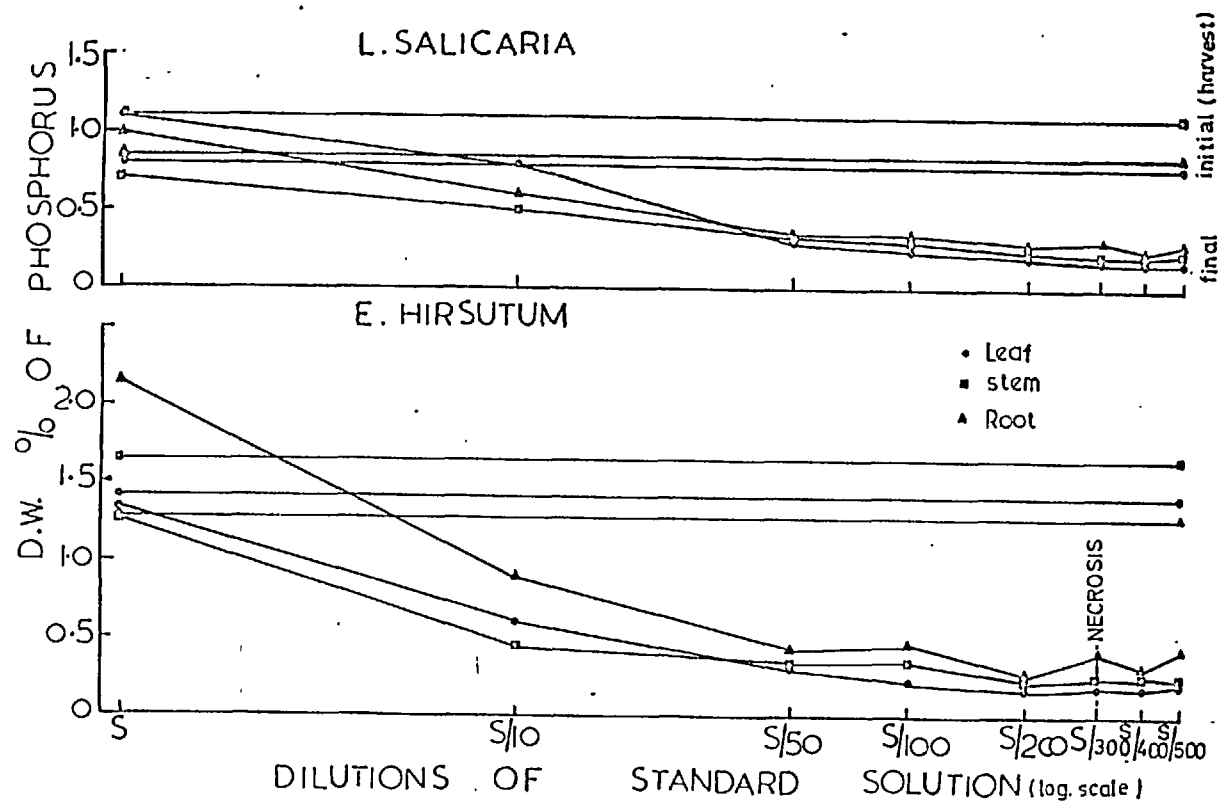


FIG. 62. Effect of different dilutions of a nutrient solution on the uptake of phosphorus. Dry weight percentage of phosphorus in leaves, stems and roots (Straight lines = initial harvest)

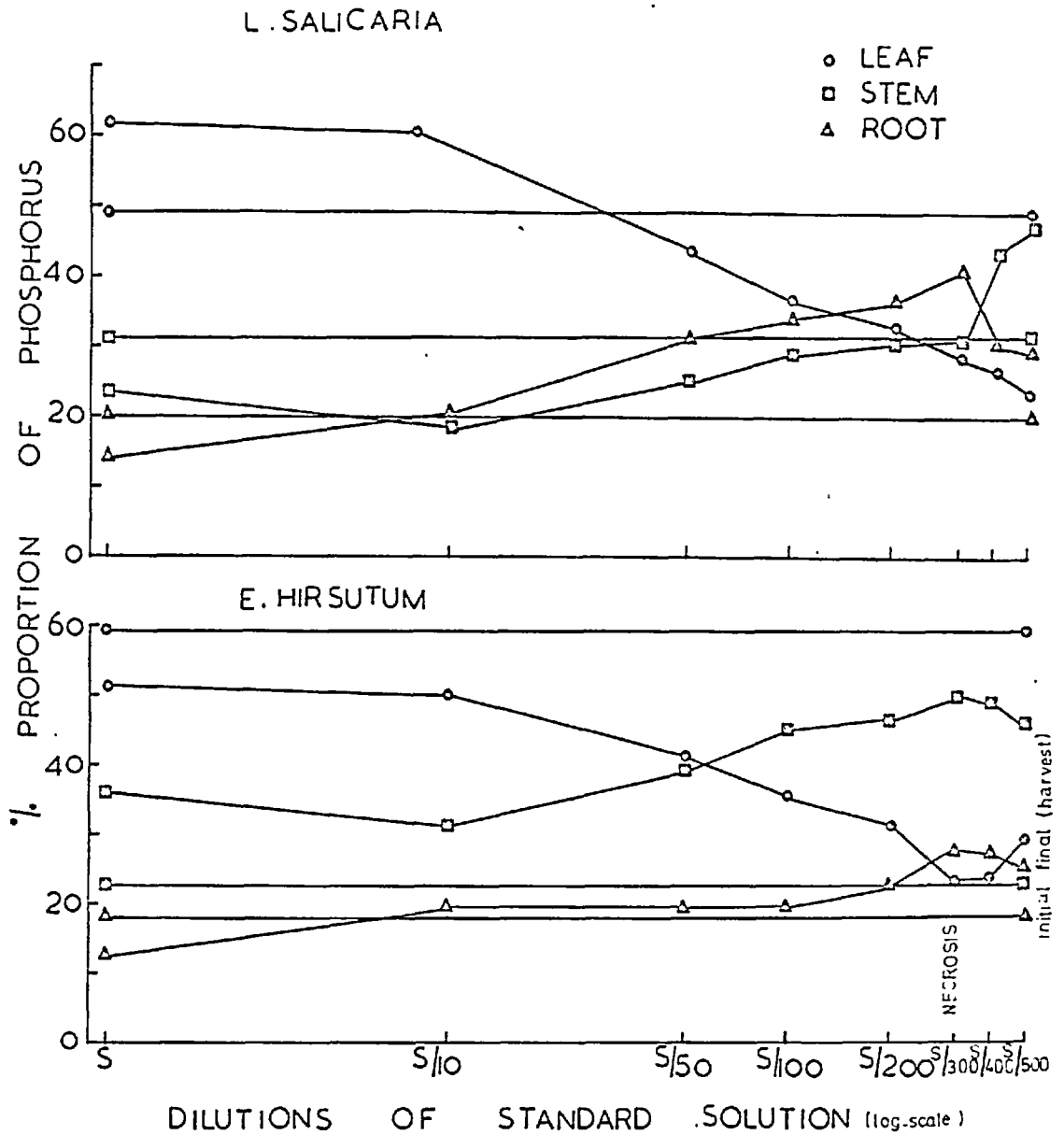


FIG. 63. Effect of different dilutions of a nutrient solution on the uptake of phosphorus. Percentage proportional distribution of total amount of phosphorus to leaves, stems and roots. (Straight lines = initial harvest).

dilutions of the series. Irregularities in these patterns in the last three dilutions in plants of both species can be attributed to widespread necrosis in these plants.

Discussion

It is clear from these results that the uptake of phosphorus was more severely curtailed in Epilobium than in Lythrum under conditions of stress. Under these conditions, in Lythrum there was an adaptive increase in the phosphorus proportions of the root and at the same time there was less reduction in the leaf proportion; but in Epilobium there was no adaptive increase in the root proportion and most of the phosphorus from the leaves was translocated to the stem. This greater loss in the uptake capacity and the disadvantageous internal distribution would lead to a greater reduction of growth in Epilobium under stress conditions when compared with Lythrum.

CALCIUM

In both species there is a decline in the total amount of calcium per plant with the increase in the dilutions (Fig. 64). Unlike nitrogen, potassium and phosphorus, Lythrum has higher calcium contents than Epilobium in the standard solution.

Fig. 65 shows the dry weight percentage of calcium per plant. The percentage contents in both species are much

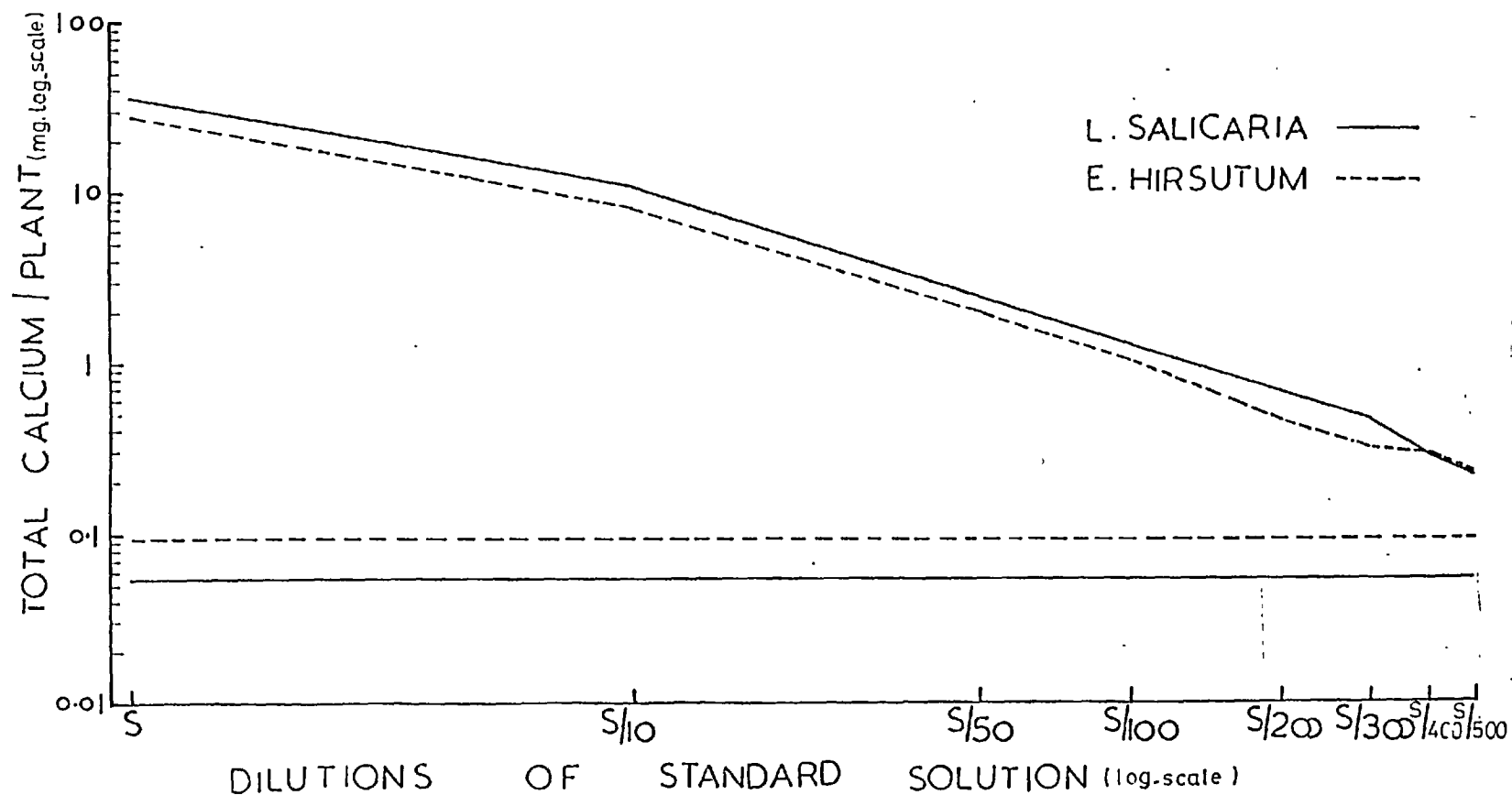
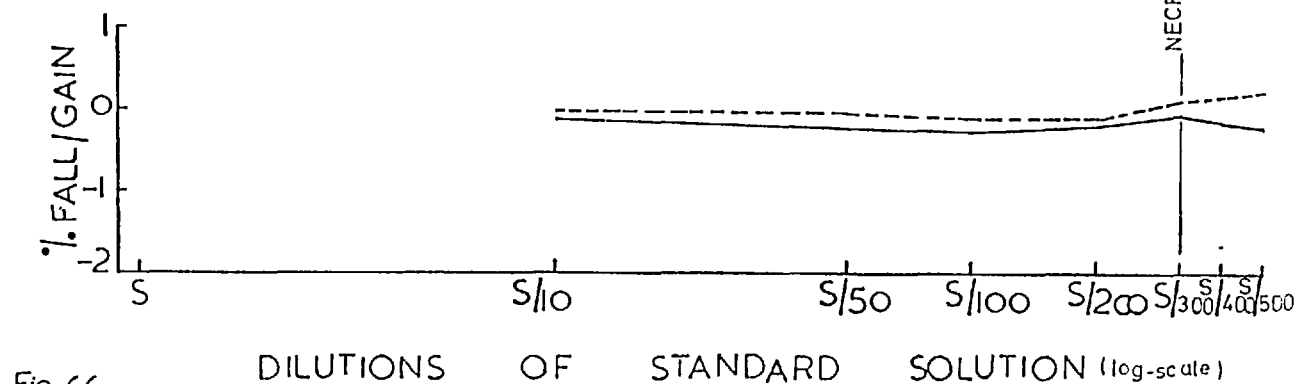
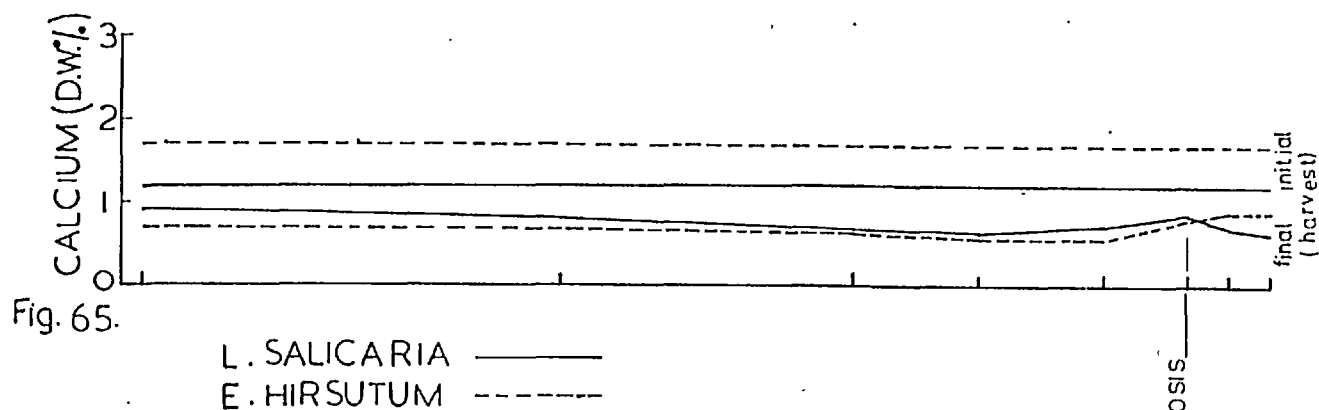


FIG. 64. Effect of different dilutions of a nutrient solution on the uptake of calcium. Total amount of calcium per plant.
(Straight lines = initail harvest)



Effect of different dilutions of a nutrient solution on the uptake of Calcium.

FIG. 65. Dry weight percentage of calcium per plant. (Straight lines = initial harvest)

FIG. 66. Fall in the dry weight percentage of calcium in the series of dilutions from the standard treatment.

lower in the final harvest compared with the initial harvest. There is a negligible decrease in the uptake of calcium, in both species, under conditions of stress. On the other hand in the extreme conditions (i.e. in the last three dilutions) there is an increase in this uptake capacity. At all levels of nutrient dilutions the calcium percentage of Lythrum is higher than that of Epilobium except in the last two dilutions. This apparent increase in Epilobium may be because of the extreme reduction of its dry weight in these dilutions. Similarly, the general increase in the percentage contents of calcium in both species, in the extreme conditions (i.e. S/300 dilution and others) may be a reflection of greater reduction in the dry weight in these dilutions rather than higher absorption rates. It can be seen from Fig. 66 that the fall in the calcium uptake under stringency conditions, in both species, is not very high when compared with the controls. Of the two species, reduction in the uptake capacity is slightly greater in Lythrum than in Epilobium.

The pattern of the dry weight percentage of calcium in the leaves, stem and root is very different in the two species, as shown in Fig. 67. In Lythrum the leaves have the highest percentage and the root the lowest percentage in all the dilutions. In Epilobium, on the other hand, the leaves have the highest percentage, as in Lythrum, but in all the

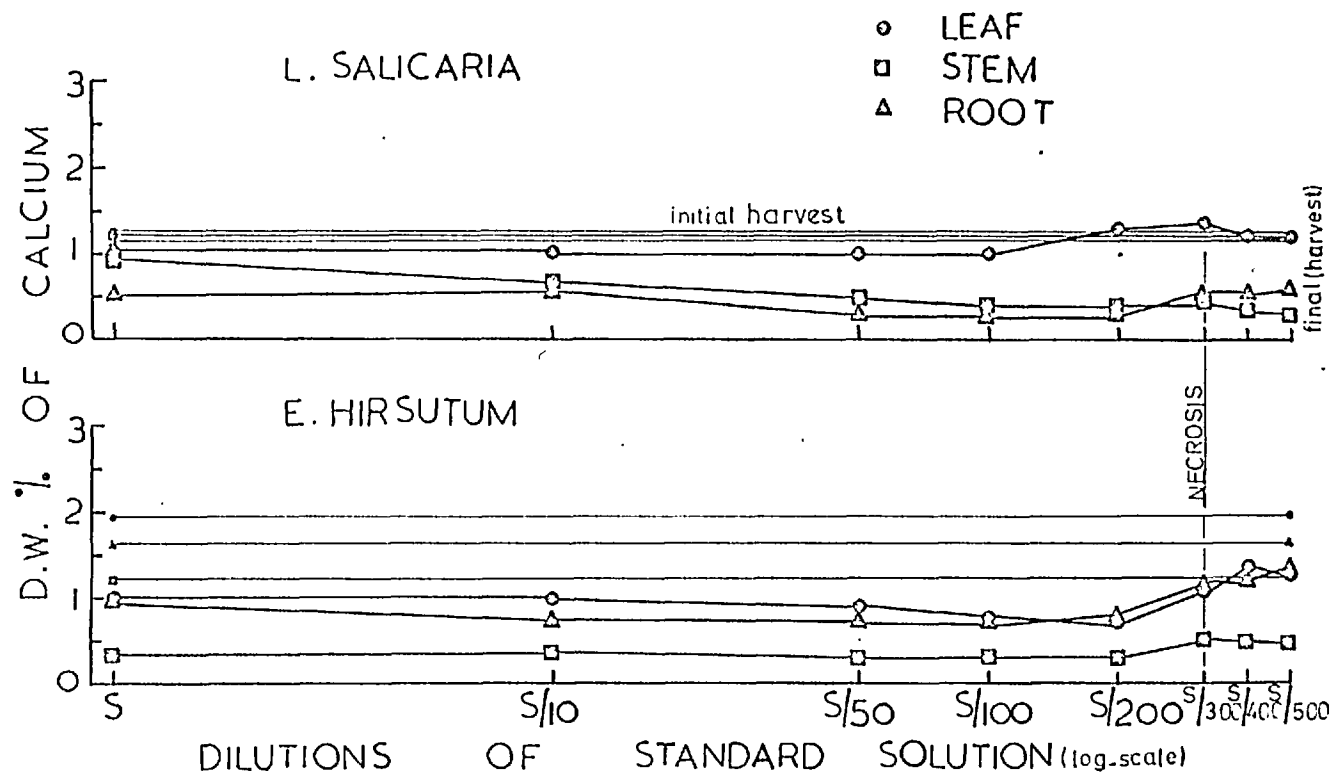


FIG. 67. Effect of different dilutions of a nutrient solution on the uptake of calcium. Dry weight percentage of calcium in leaves, stems and roots. (Straight lines = initial harvest)

dilutions the stem has the lowest percentage. There are some irregularities in both species in the extreme conditions.

The percentage proportional distribution of the total amount of calcium to the leaves, stem and root is shown in Fig. 68. Again the pattern is dissimilar in the two species. In Lythrum the general tendency is that of diversion of calcium to the leaves, but in Epilobium there is a diversion of calcium from the leaves to the stem and root. However, in both species the leaves have the highest proportion of calcium and there is no marked adaptive increase in the calcium proportions of the roots.

It is concluded from these results that the uptake of calcium in both species was affected to a negligible degree under stress conditions, and under these conditions the pattern of translocation to various plant parts remained similar to that of the controls, i.e. the maximum proportion was diverted to the leaves while the stem and root contained only small proportions.

The above evidence suggests that calcium stringency, within limits, would not greatly affect the photosynthetic adaptabilities of the two species. This probability is greater in Lythrum than in Epilobium.

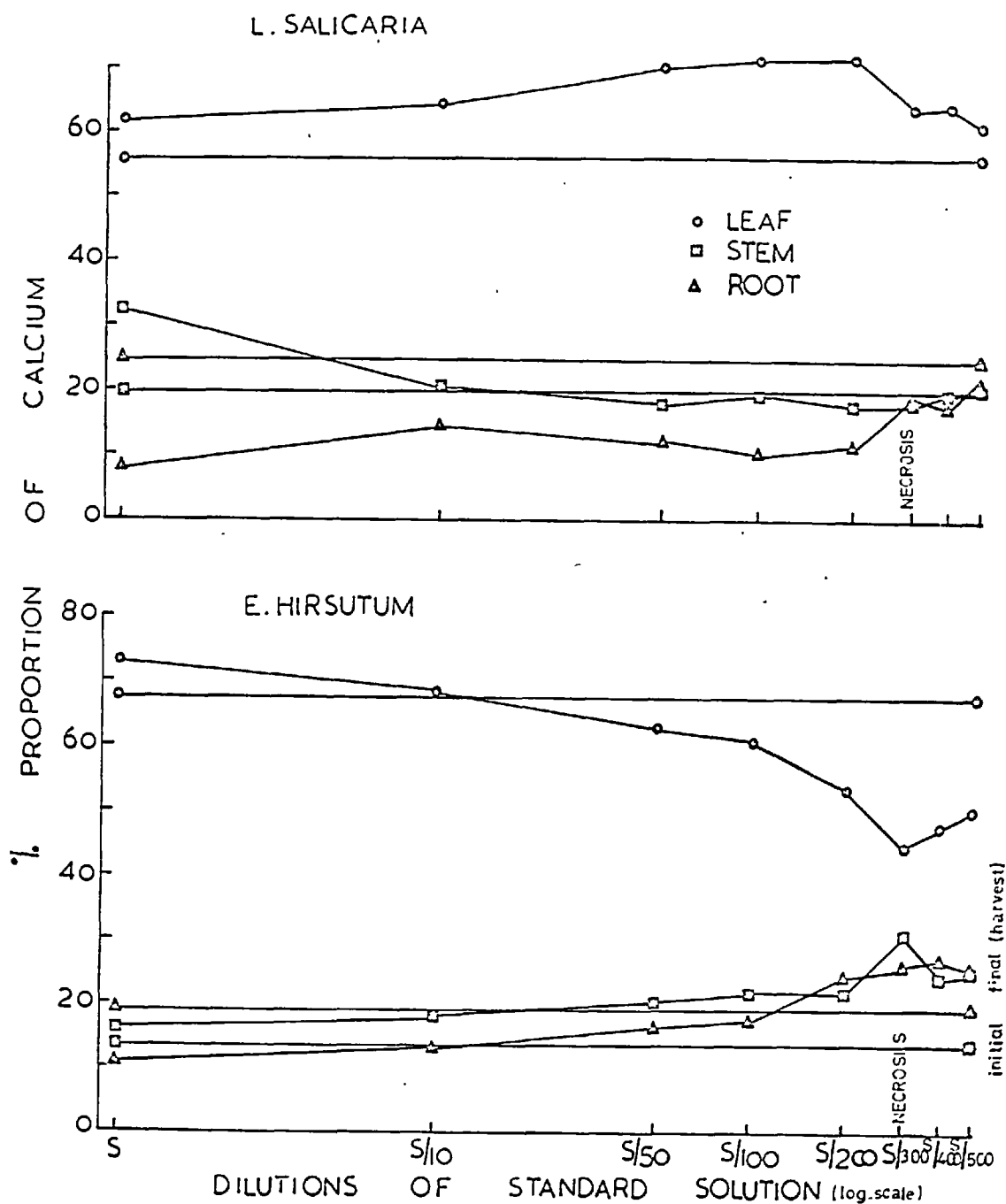


FIG. 68. Effect of different dilutions of a nutrient solution on the uptake of calcium. Percentage proportional distribution of total amount of calcium to leaves, stems and roots. (Straight lines = initial harvest)

General Discussion

The results of the uptake of potassium, nitrogen, phosphorus and calcium, for the two species, in the final harvest are summarised in Fig. 69. It can be seen that, for the same amount of dry weight, the potassium contents are the highest and calcium contents the lowest with nitrogen and phosphorus inbetween, in plants of both species in the standard solution. The difference is such that the potassium contents of Epilobium are eleven times higher than its calcium contents, but in Lythrum potassium is only six times higher than calcium. Although the potassium contents of both species are almost twice that of their nitrogen contents in the standard solution, in the rest of the dilutions the values of the two elements are similar in either species.

In Epilobium, in the standard solution, the quantity of phosphorus is twice that of calcium and is more or less similar in Lythrum; but in the series of dilutions, in both species, the calcium contents are almost twice that of the phosphorus contents. In general, in both species, in stress conditions the potassium and nitrogen contents are the highest and phosphorus the lowest while calcium is inbetween. Of the two species, in the standard solution, for an almost similar dry weight all the nutrients, except calcium, are much higher in Epilobium than in Lythrum. But in all the dilutions all

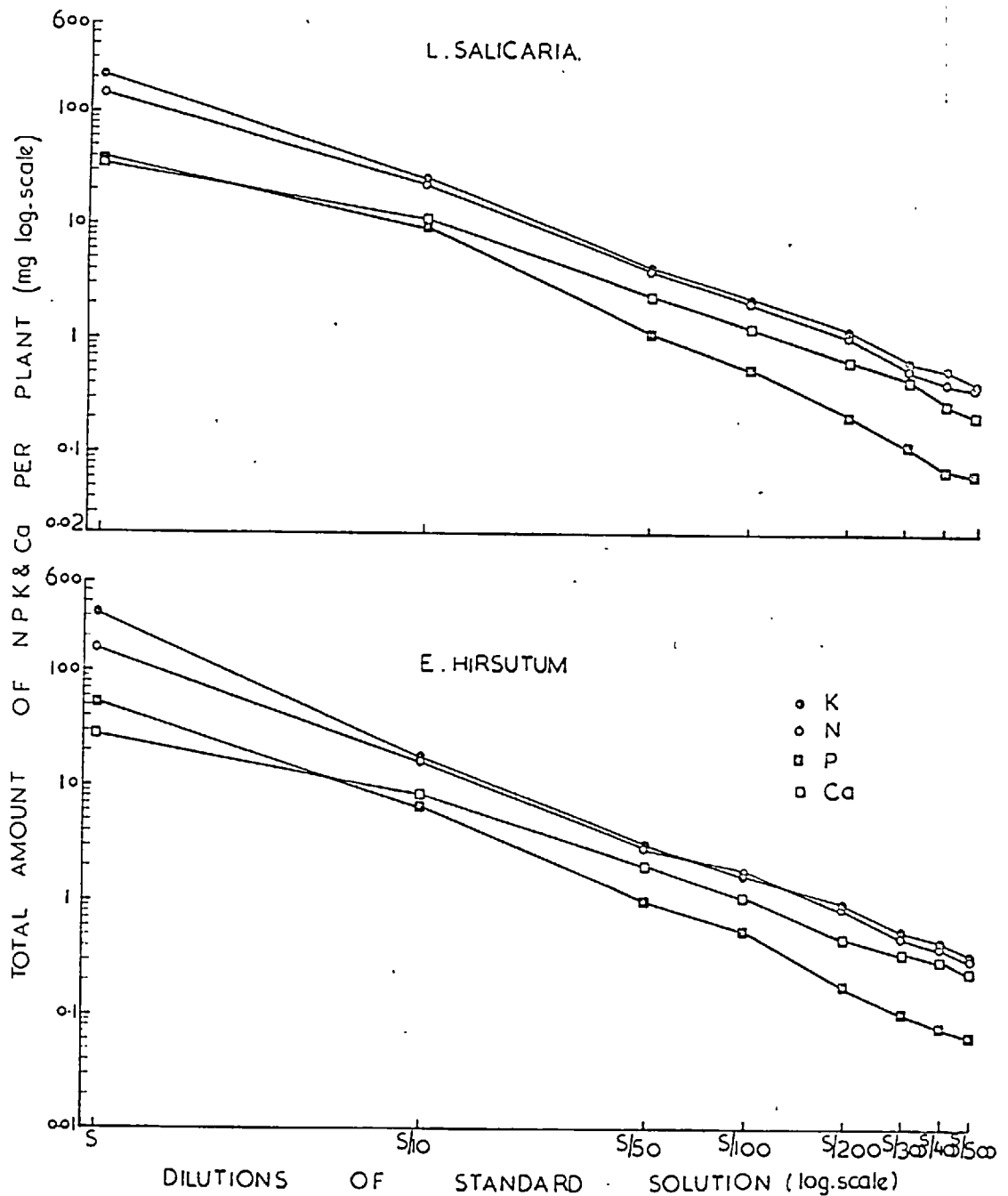


FIG. 69. Effect of different dilutions of a nutrient solution on the nutrient uptake. Total amounts of potassium, nitrogen, phosphorus and calcium per plant.

these elements are considerably higher in Lythrum than in Epilobium.

Although potassium contents are the highest in all the dilutions, at the same time there is greatest reduction in the uptake of potassium and least in the calcium uptake, when compared with the controls, in both species. However, of the two species, reduction in uptake is relatively greater in Epilobium than in Lythrum except in the case of calcium. It can be inferred from this that growth would be most affected by the stringency of potassium and nitrogen, comparatively less in phosphorus stringency and least in calcium stringency. Of the two species, growth would probably be more affected in Epilobium than in Lythrum.

The internal distribution (percentage proportions) to the leaves, stem and root elements under stress conditions is very different in the two species. In Lythrum a larger proportion of nitrogen, potassium and phosphorus is diverted to the root at the expense of the leaves and stem proportions. In calcium deficiency the increase in the root proportion is not so marked and the leaf proportion increases at the expense of the stem proportion. On the contrary, in Epilobium there is no marked adaptive increase in the root proportion and the major proportion of all these nutrients, especially potassium, is diverted from the leaves to the stem. Thus, in Epilobium

the highest amounts of these nutrients are present in the stem, followed by the leaves and root, but in Lythrum the highest amounts are present in the leaves and root and the lowest in the stem. In other words, both the absorptive and photosynthetic adaptabilities of Epilobium would be more severely curtailed by nutrient stringency than those of Lythrum. Consequently this would result in a greater reduction of growth in Epilobium than in Lythrum.

It is concluded from the above discussion that Lythrum is not only a plant of comparatively low nutrient requirements for its normal growth, but also has a high nutrient uptake ability under conditions of stringency. ~~Considering, teleologically~~ The internal distribution of the nutrients to the leaves, stem and root is advantageous for the growth of the plant as an efficient photosynthetic entity. On the other hand, the high nutrient requirements of Epilobium and the decreased uptake capacity under stress conditions, coupled with the complete absence of any advantageous redistribution of the nutrients, results in a greater reduction of growth in this plant.

There is thus a greater probability of the establishment and growth of Lythrum in soils of low nutrient status but the chances of survival of Epilobium in such sites are very remote. The low nutrient requirements of Lythrum ~~may be~~

~~regarded as an adaptation~~ ^{fit it} to grow in soils of low fertility.

Experiment XII

Effect of different dilutions of phosphorus, nitrogen and potassium on growth.

The results of the chemical analysis of the previous experiment showed that there was a great reduction in the potassium and nitrogen uptake capacity, compared with the phosphorous uptake, in the plants growing in various dilutions of the nutrient solution. There was very little reduction in the uptake of calcium under similar conditions. Of the two species, reduction in uptake was relatively greater in Epilobium than in Lythrum. In this experiment the effects of phosphorus, nitrogen and potassium stringencies on the growth of the two species are investigated.

Experimental procedure

The layout of the experiment consisted of three separate series of standard solutions.

- (1) Series of different dilutions of phosphorous.
- (2) Series of different dilutions of nitrogen.
- (3) Series of different dilutions of potassium.

Each series consisted of six treatments, designated as:

- (1) Phosphorus series: P/S, P/10, P/50, P/100, P/200 and O/P

(2) Nitrogen series: N/S, N/10, N/50, N/100, N/200 and O/N

(3) Potassium series: K/S, K/10, K/50, K/100, K/200 and O/K.

Details of the preparations of the various series are given in Chapter IV. P/S, N/S and K/S refer to the same standard solution designated differently in each series, while O/P, O/N, O/K refer to the complete absence of the particular element in the respective series.

Three sets of polythene lined wooden tanks, each composed of ten units, and each unit of the 30 litre capacity were used for the P, N and K series. The plants in the standard solution, common to all the series, were grown in two separate wooden tanks of 50 litre capacity each with perspex tops. Each set of ten tanks had a common black polythene top mounted on a wooden frame with holes pierced through the polythene at appropriate places. The tanks in each series were properly labelled for the species and the dilutions, and were later filled with their respective solutions. Other details of aeration, length of illumination and temperature were similar to those of Experiment X.

Forty-day-old seedlings of each species were selected for uniformity of size. Sixty seedlings per species per treatment were transplanted in the phosphorus and nitrogen series, and eighty seedlings per treatment in the potassium series (due to the high rate of mortality in this

series). In addition to the initial harvest, a series of five other harvests at fortnightly intervals were also made. Ten plants per treatment, per species, were taken at random at each harvest and the data collected as before.

Observations and results are described separately for each series.

Series 1

The effect of various dilutions of phosphorus on growth.

The general morphology of plants of the two species after harvest four can be seen in ^{Plate}~~Fig.~~ 11 (a and b). There was a great reduction in their size and in extreme conditions of stress the plants did not branch. However, the extent of development at the time of the final harvest was as follows.

Epilobium hirsutum

In the standard solution the plants were some 107 cm. tall, with twenty-five pairs of nodes and up to twenty fully developed side shoots. There were almost ten repeatedly branched rhizomes per plant. The plants started flowering on the fifty-first day after transplantation, and by the time of the last harvest had, on average, 168 fruits per plant.

At the P/10 solution the plants did not show any visible departure in their morphology from the standard plants except that they were relatively smaller. The plants were



PLATE 11 (a) Epilobium hirsutum

Plants grown in a standard nutrient solution and at different levels of phosphorus in the solution. (Photographed after 75 days in the treatments, i.e. at the time of Harvest V).

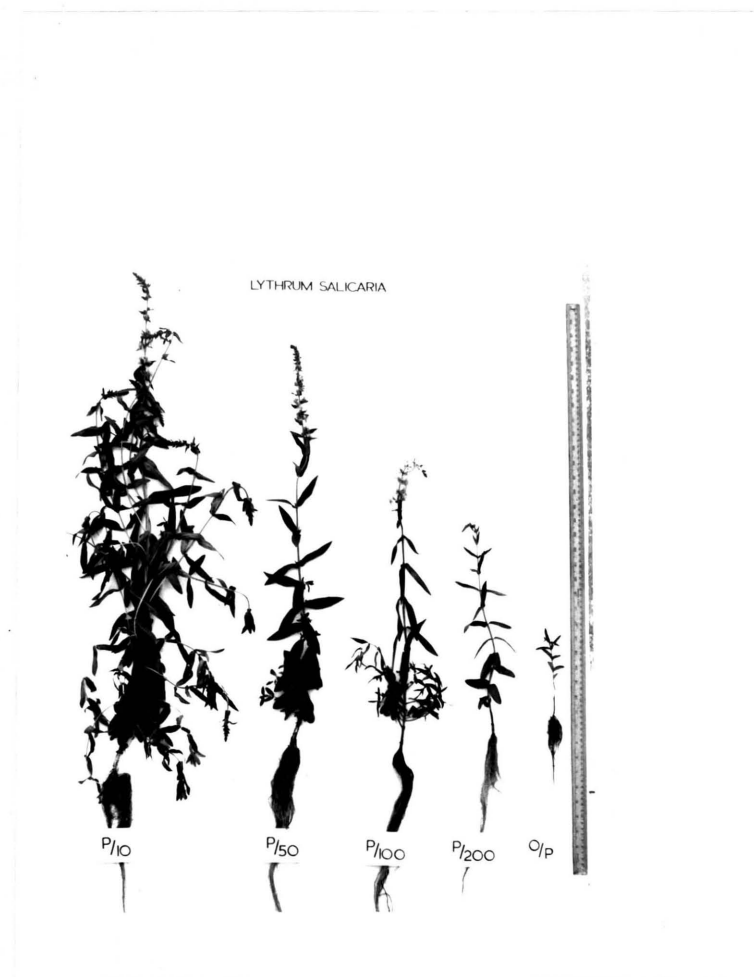
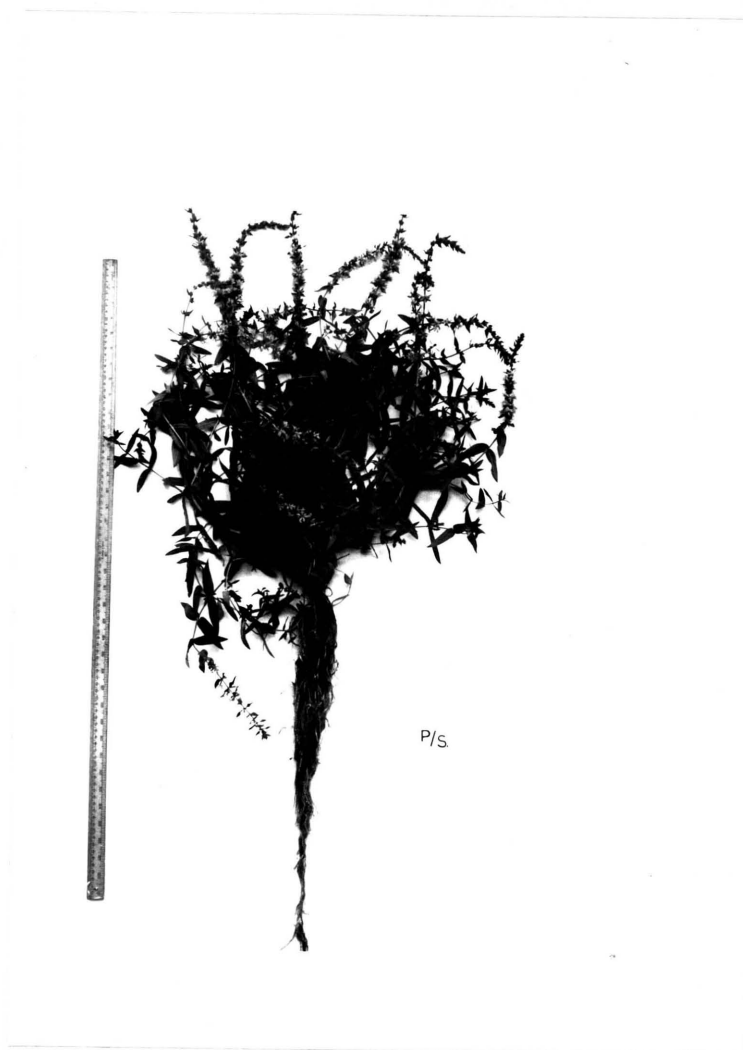


PLATE 11 (b) Lythrum salicaria

Plants grown in a standard nutrient solution and at different levels of phosphorus in the solution. (Photographed after 75 days in the treatments, i.e. at the time of Harvest V).

some 98 cm. long and carried, on the main stem, about twenty pairs of leaves or floral bracts. There were up to seventeen side shoots, the longest measuring 30 cm. in length. The plants had also developed eight to nine slender, relatively less branched, rhizomes. Although, like the standard solution plants, these plants also started flowering on the fifty first day after transplantation there was a great reduction in the number of flowers produced. On average there were twenty-eight fruits per plant by the time of the last harvest.

The plants in the P/50 solution showed a great reduction in size and measured only up to 52 cm. in length. None of the plants developed any side shoots, and on the main stem there were only up to twelve or thirteen pairs of nodes with fully expanded leaves of which the lower two to three pairs became extremely yellowish in the last two harvests. There were four unbranched stolons per plant, and the plants started to flower on the sixty-seventh day after transplantation, however, these did not develop into fruits.

In the P/100 treatment the plants were 50 cm. high and carried, on the main stem, up to twelve pairs of nodes, but the leaves were rather small and narrow. After harvest three the lower four to five pairs of leaves started to become yellow and crumpled. All the plants produced flower buds but only one plant was in flower two days before the

final harvest. All the plants produced two slender unbranched rhizomes.

In the P/200 solution there was a still greater reduction in plant size. The plants were only 17 cm. tall with eleven to twelve pairs of small coriaceous and hairy leaves. In the last harvest most of the lower leaves had become excessively crumpled and necrotic. Only one to two extremely small rhizomes per plant were developed and some of the plants produced abortive flower buds.

The O/P treatment plants showed a further reduction as they were only 9 cm. high with eleven pairs of very small leaves. The lower five pairs of leaves at the final harvest were crumpled and necrotic. None of the plants produced any flower buds or rhizomes.

Lythrum salicaria

The plants grown in the standard solution attained a length of 122 cm., with thirty-five pairs of nodes and up to twenty-three side shoots the longest of which was 82 cm. The plants started flowering on the thirty-ninth day from transplantation and by the time of the final harvest the inflorescence on the main stem was 56 to 60 cm. long with 900 flowers, most of which were developing into fruits.

The shoots of the plants in the P/10 treatment were some 92 cm. in length with seventeen to nineteen nodes bearing

expanded leaves and up to fourteen side shoots, the longest measuring 70 cm. in length. The plants started flowering at the same time as those in the standard solution. The inflorescence was greatly elongated with sparsely placed floral whorls and only up to 195 flowers per plant.

The plants in the P/50 solution showed a rapid growth in the beginning and the stem became very hard and woody. The shoots of the plants were about 90 cm. long and had fifteen nodes with expanded leaves and up to nine slender side shoots. There were about 150 flowers per plant.

The plants in the P/100 solution had broad leaves and were very similar to those in the P/50 solution. They were 80 cm. long with twelve pairs of nodes and only six to seven thin, small side shoots. The flowering took place at the same time as in the other treatments and 120 flowers per plant were present in the final harvest.

The P/200 treatment plants were greatly reduced. They were some 50 cm. long with twelve pairs of leaves and four to five side shoots. The plants developed thick, small and compact inflorescences and the flower buds did not open for a long time. At the time of the last harvest twenty flowers per plant on the average were present.

In the O/P treatment there was an extreme reduction in size, the plants being only 14 cm. high with ten to eleven

pairs of dark green, small, oblong leaves.

The symptoms of phosphorus deficiency, in all these treatments, were not as marked as in Epilobium except that in the P/200 and O/P treatment veins on the underside of the leaves became red and big red patches also developed on the lower portion of the stem.

Results

1) Dry weight and leaf area increase

The general patterns of the increase of dry weight gains and increase of leaf area with time can be seen in Fig. 70 and Fig. 71 respectively. There were similar large successive decreases of performance in each species with the increase in the phosphorus deficiency. Growth rates, calculated as percentage dry weight increase over the initial harvest (Fig. 72), show that although at the P/10 level the percentage dry weight gain was similar in both species, in the later solutions there was a relatively greater reduction in Epilobium than in Lythrum.

2) Root/shoot ratio

Fig. 73 shows the changes in the root/shoot ratio for the duration of the experiment. In the standard and the P/50 solutions there is a gradual fall in the values with time, but in the rest of the treatments there is an adaptive increase in the root/shoot ratio which is very marked in

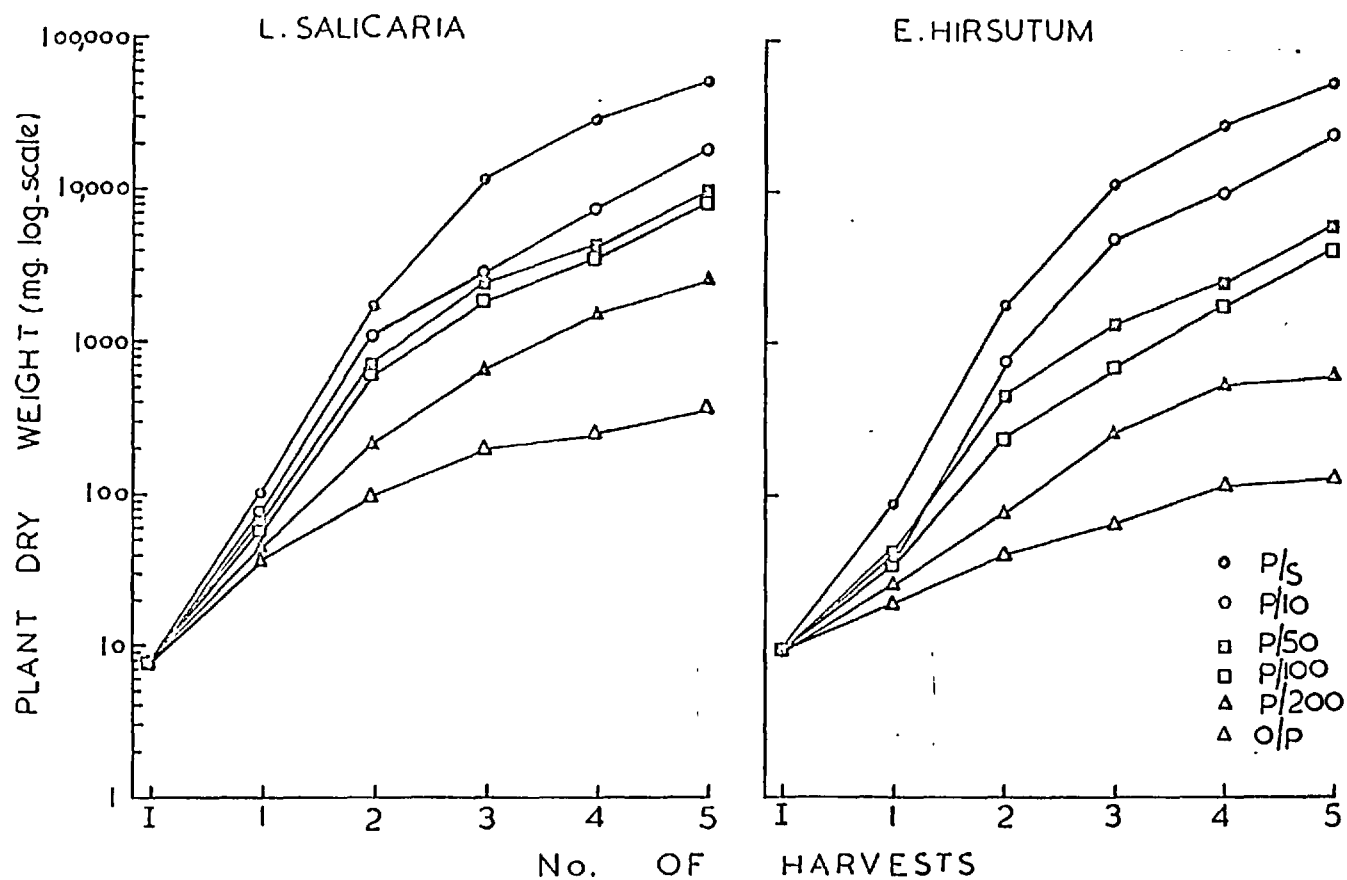


FIG. 70. Effect of different levels of phosphorus on increase of plant dry weight with time. (I = initial harvest)

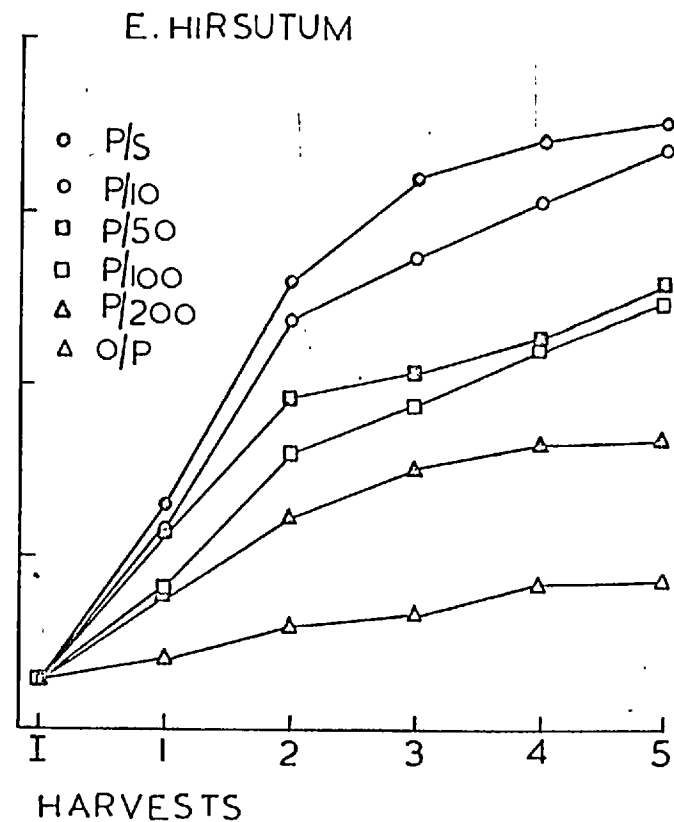
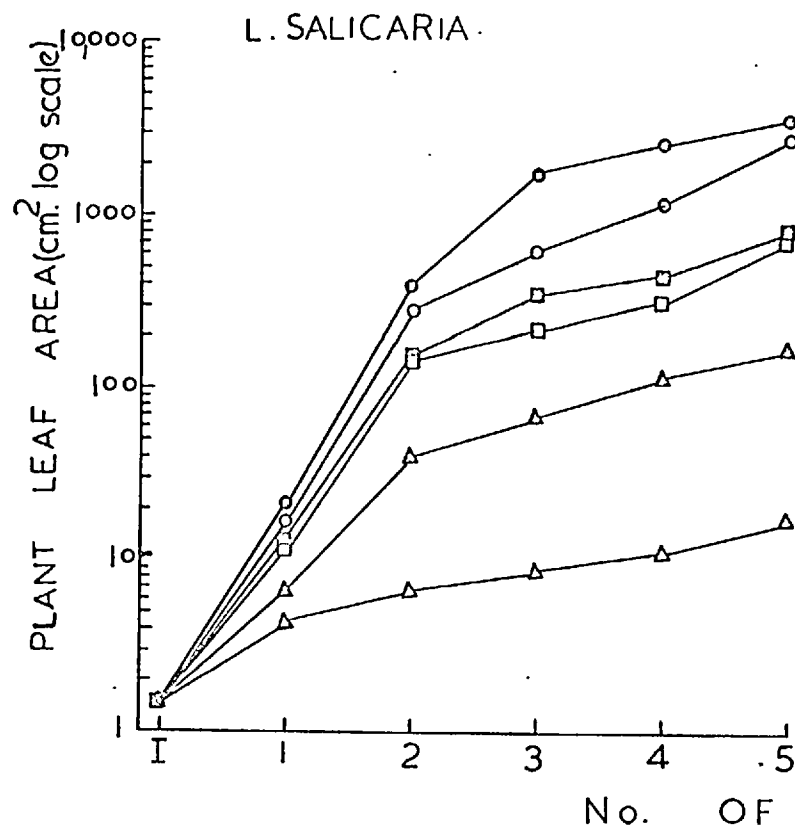


FIG. 71. Effect of different levels of phosphorus on increase of plant leaf area with time. (I = initial harvest)

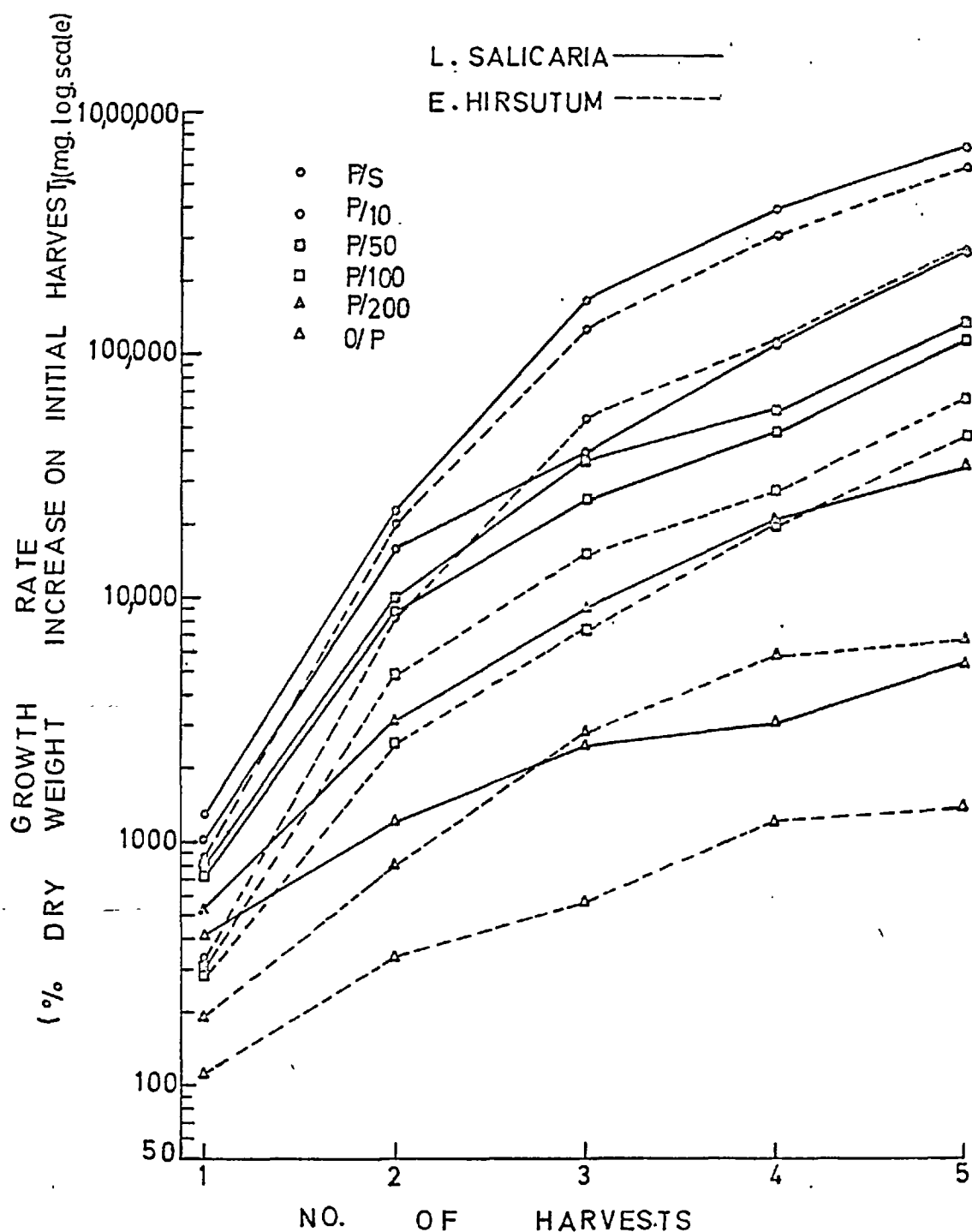


FIG. 72. Effect of different levels of phosphorus on the growth rate. Percentage increase dry weight time from an initial harvest to each successive harvest ($H_1 - H_I$, $H_2 - H_I$, $H_n - H_I$).

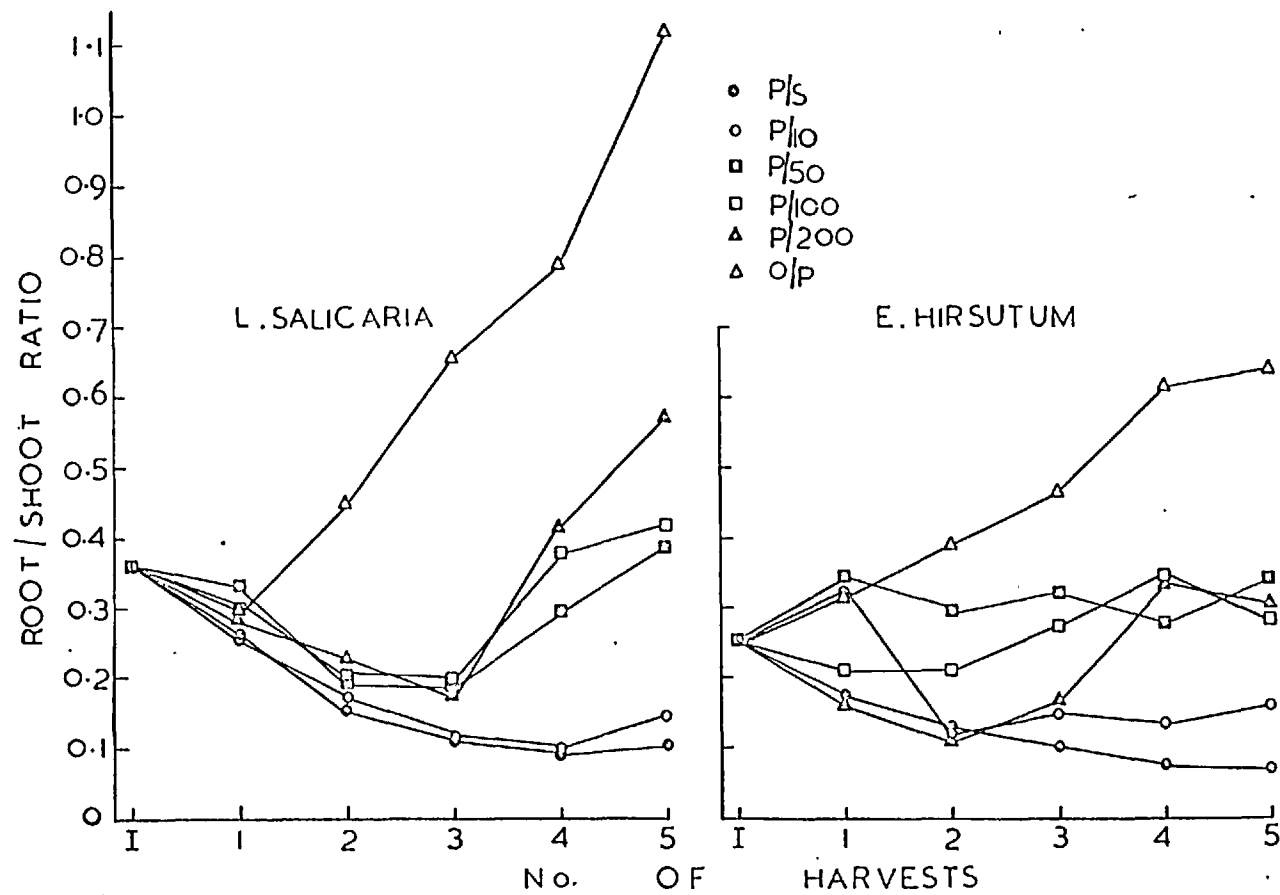


FIG. 73. Effect of different levels of phosphorus on root/shoot ratio.

Lythrum but less marked and irregular in Epilobium.

3) Percentage proportionate distribution of dry matter

The proportional distribution of the total dry weight to leaves, stem and root can be seen in Fig. 74 and Fig. 75 for Lythrum and Epilobium respectively. Only the initial, first, third and fifth harvests are shown. In both the species, the patterns of leaf, stem and root proportions are similar. It can be noted that in both species there is an increase in the root proportion at the expense of the stem proportion with the increase in phosphorus stringency. This increase in the proportion of root is continuous and well developed in Lythrum at all levels, but in Epilobium after the P/50 treatment there is a slight decline. At the O/P level this tendency of increased root proportion is also less marked in Epilobium than in Lythrum.

Discussion

The data presented show that there was relatively greater reduction in Epilobium than in Lythrum both in terms of dry weight gains and leaf area increase. Although in the standard solution and at the P/10 level plants of both species attained similar dry weights, at the P/50 level and in the other solutions the dry weights of Lythrum were double those of Epilobium. Also, at the P/50 level and other solutions, there was a greater adaptive increase in the root/shoot

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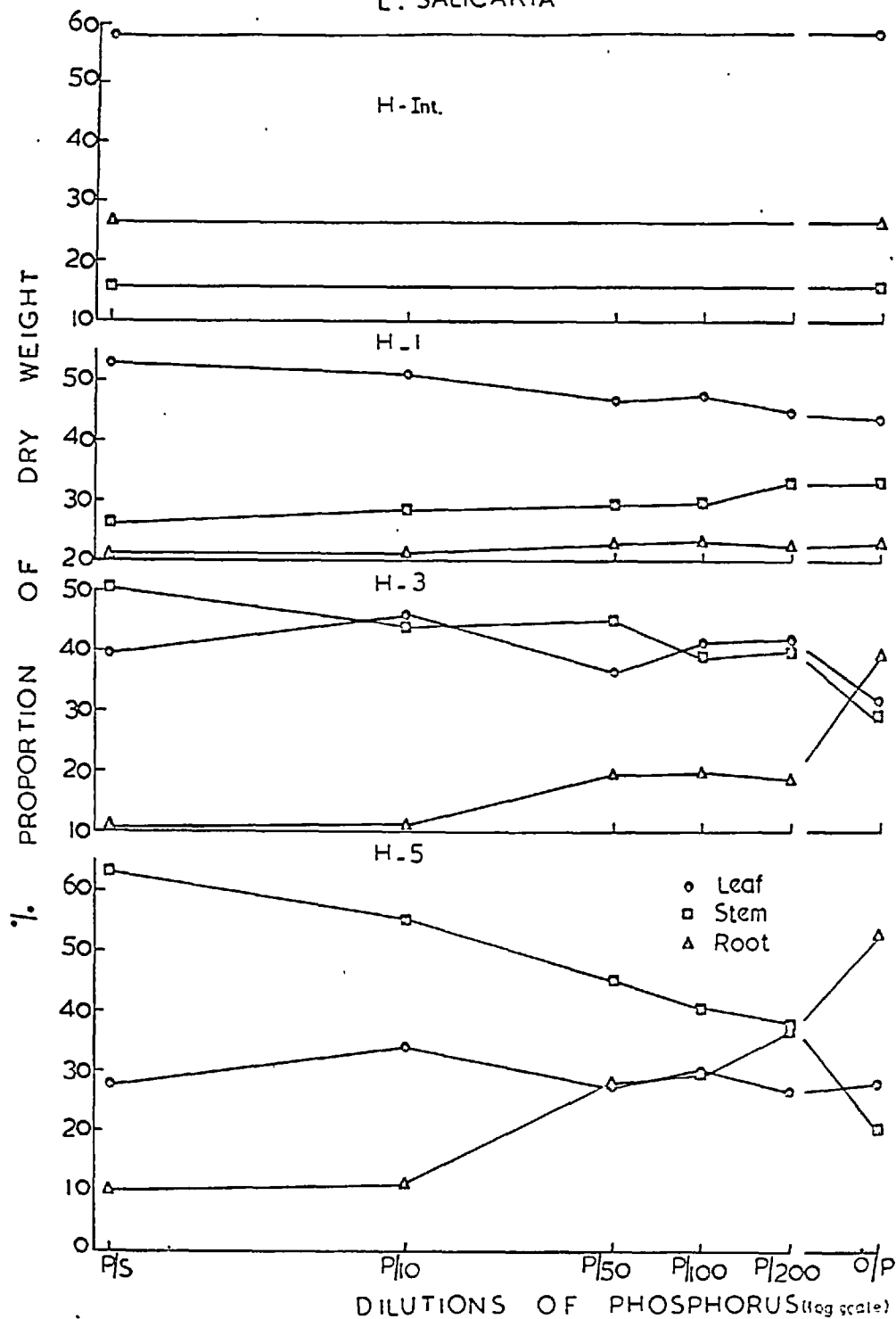


FIG. 74. Effect of different levels of phosphorus on percentage proportional distribution of total dry weight to leaves, stems and roots. (Harvests, initial one, three and five.)

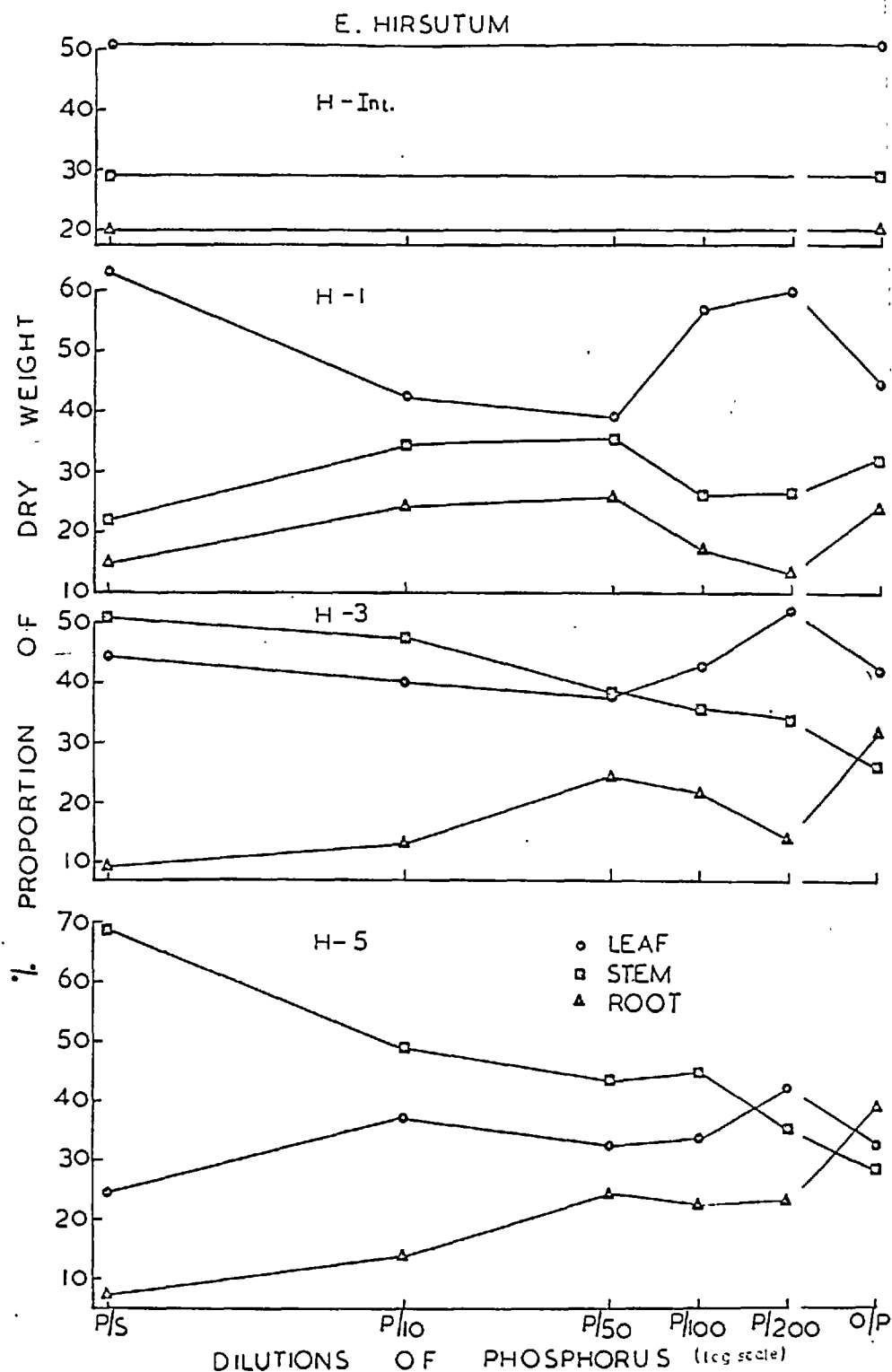


FIG. 75. Effect of different levels of phosphorus on percentage proportional distribution of total dry weight to leaves, stems and roots. (Harvests = initial, one, three and five)

ratio in the case of Lythrum compared with that of Epilobium. This marked increase in the root/shoot ratio in Lythrum was due to the greater diversion of dry matter to the root at the expense of the stem rather than the leaves which also showed an increase.

It can be concluded that, because of these better developed compensatory mechanisms, the dry weight gain in Lythrum is not as severely curtailed as in Epilobium by the phosphorus stringency. It was also suggested in the last experiment (chemical analysis) that because of comparatively less reduction in the phosphorus uptake capacity in Lythrum under stringent conditions, its growth would also be less affected by the phosphorus stringency than that of Epilobium.

Series II

The effect of various dilutions of nitrogen on growth.

The appearance of the plants towards the end of the experiment is shown in Plate 12 (a and b). In general there was a greater reduction in both the species by nitrogen stringency than by phosphorus stringency. The extent of development of the plants at the final harvest was as described below. The standard plants of both species were as described in Series I.

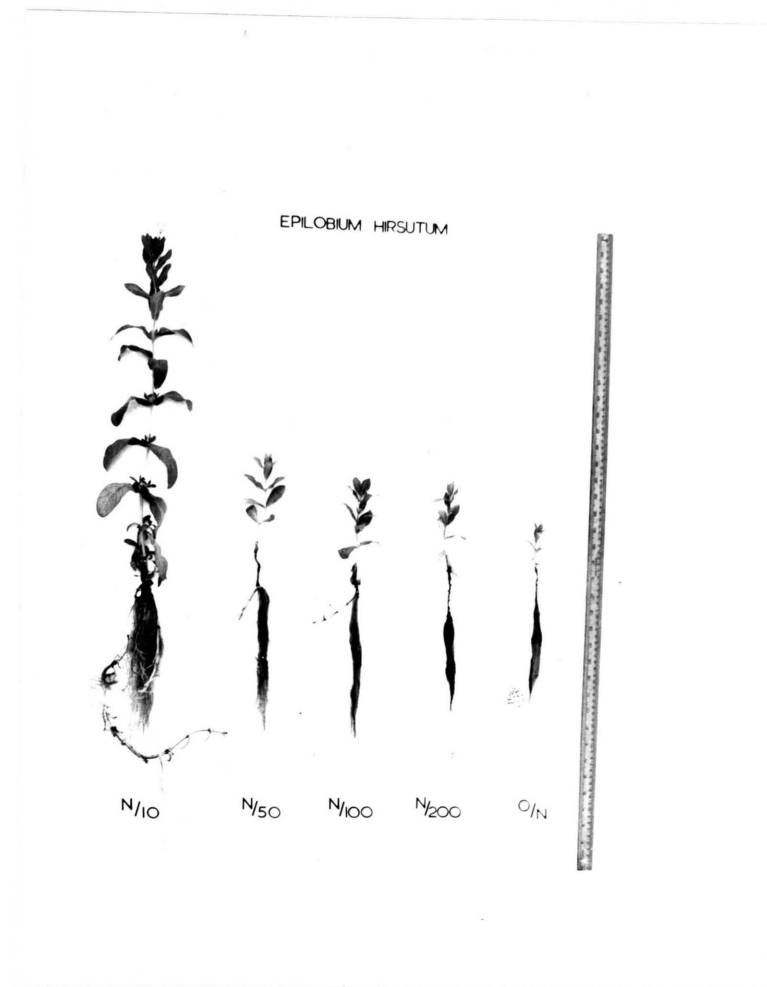


PLATE 12 (a) Epilobium hirsutum

Plants grown in a standard nutrient solution and at different levels of nitrogen in the solution.

(Photographed after 75 days in the treatments, i.e. at the time of Harvest V).

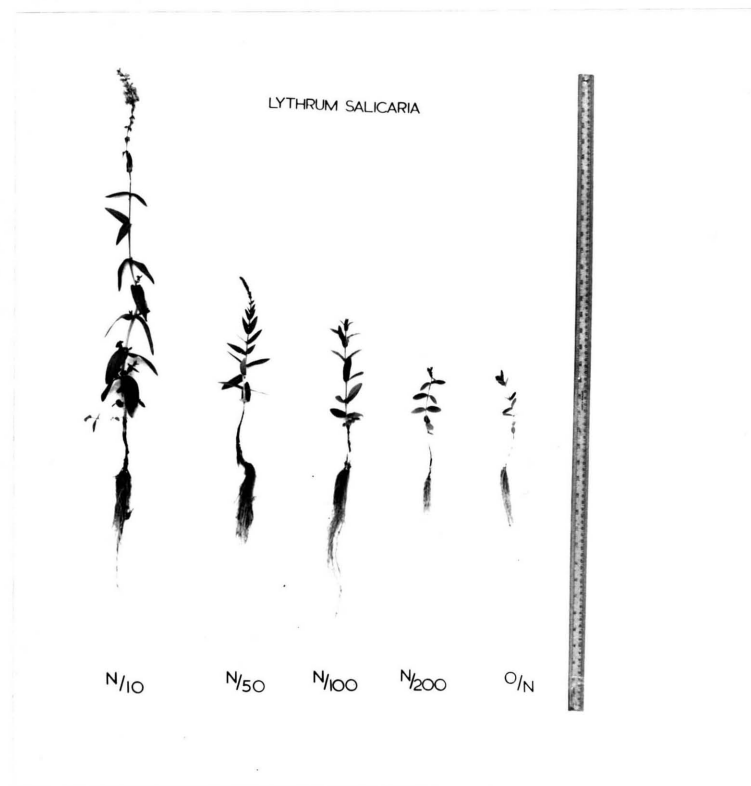


PLATE 12 (b) Lythrum salicaria Plants grown in a standard nutrient solution and at different levels of nitrogen in the standard solution. (Photographed after 75 days in the treatments, i.e. at the time of Harvest V).

Epilobium hirsutum

The plants grown in the N/10 solution showed a greater reduction in size as they were only 60 cm. high and carried, on the main stem, twelve to thirteen pairs of nodes with fully expanded leaves. Side shoots, produced in the axils of most of the leaves, had suppressed elongation as none of them was longer than one inch. However, the plants had developed three long rhizomes by the time of the last harvest. The plants started flowering on the fifty-sixth day from transplantation and had formed three capsules per plant at the final harvest.

The plants in the N/50 solution were only 20 cm. in length, with one well developed rhizome and three rhizome initials per plant. The main stem had developed twelve to thirteen pairs of leaves.

At the N/100 and N/200 levels the plants were similar to the N/50 plants except for their thinner stems and reduced rhizomes. In each of these treatments none of the plants had developed any side shoots or flower buds.

At the O/N level the plants were only 10 cm. high with ten to eleven pairs of very small leaves and did not develop any rhizomes or flower buds.

On the whole there was no reduction in the number of nodes per plant at the various levels of nitrogen stringency,

but the length of the internodes was greatly affected after the N/10 level. The leaves of the same plastochrone showed a gradual reduction in size with the increase in nitrogen deficiency. In all these treatments the leaves were pale green, and the lower four to five pairs of leaves became increasingly red with age and started dying off towards the end of the experiment.

Lythrum salicaria

Although in the N/10 solution the plants showed a great reduction in size compared with their controls, these plants were still better than those of Epilobium in this treatment. The shoot was, on average, 74 cm. long and had developed some sixteen to eighteen pairs of leaves including large, fully expanded, bracts. In the beginning growth was very slow and elongation of the axillary shoots was somewhat curtailed. Later, after harvest four, about eight axillary shoots started elongating and by the time of the last harvest the longest shoot was 35 cm. in length. The inflorescence on the main axis was 32 to 35 cm. long and major side shoots also produced 13 to 15 cm. long inflorescences. The plants flowered from the fifty-fourth day after transplantation and had, on average, developed 340 flowers per plant at the final harvest.

In the N/50 solution the plants were up to 38 cm.

in length and had sixteen pairs of leaves on the main stem. Elongation of the side shoots was suppressed. A compact, small, inflorescence was produced towards the end of the experiment, but only about eight to ten flowers per plant were present at the final harvest.

At the N/100 and N/200 levels the plants were 28 cm. and 25 cm. in length respectively and showed the development of fourteen to fifteen pairs of leaves on the main stem. No flower buds were produced, but in the N/100 treatment suppressed axillary shoots were present.

At the O/N level the shoot was only 16cm. high with a very long root system. There were only twelve pairs of leaves on the stem.

In general, leaves of the same plastochron became extremely narrow and reduced with the increase in nitrogen stringency. Although leaves were pale green in all the treatments, unlike Epilobium they remained thick and glabrous and did not show any sign of crumpling or drying towards the end of the experiment. At the N/10 level symptoms of nitrogen deficiency were not very marked, but in the later treatments the lower leaves and lower parts of the stems became extremely red.

Results

The general pattern of dry weight gain and leaf area

increase, as shown in Fig. 76 and Fig. 77 respectively, is similar in both species. There is a marked reduction in the dry weight and leaf area in solutions with decreased nitrogen concentration compared with the controls. Of the two species, again, there is comparatively less reduction in the case of Lythrum than that of Epilobium, as shown in Fig. 78. Fig. 79 shows the adaptive increase in the root/shoot ratio in response to the nitrogen stringency. In Epilobium the pattern of the root/shoot ratio is irregular and there is a decline in the values in the last two harvest in some of the treatments.

The percentage proportional distribution of the dry matter to the leaves, stem and root is shown in Fig. 80 for Lythrum and Fig. 81 for Epilobium. A comparison of the two species shows that in Lythrum there is a great reduction in the stem proportion with the increase in nitrogen stringency (especially at the N/50 and following treatments), but in Epilobium this reduction is marked only in the N/100 and other treatments. In Lythrum most of the loss from the stem is diverted to the root and some to the leaf. In Epilobium this diversion of dry weight to the root is not so marked as in Lythrum at the final harvest. However, at the O/N level there is a stronger diversion of dry matter to the root and the values of the leaves, stem and root are very similar in both

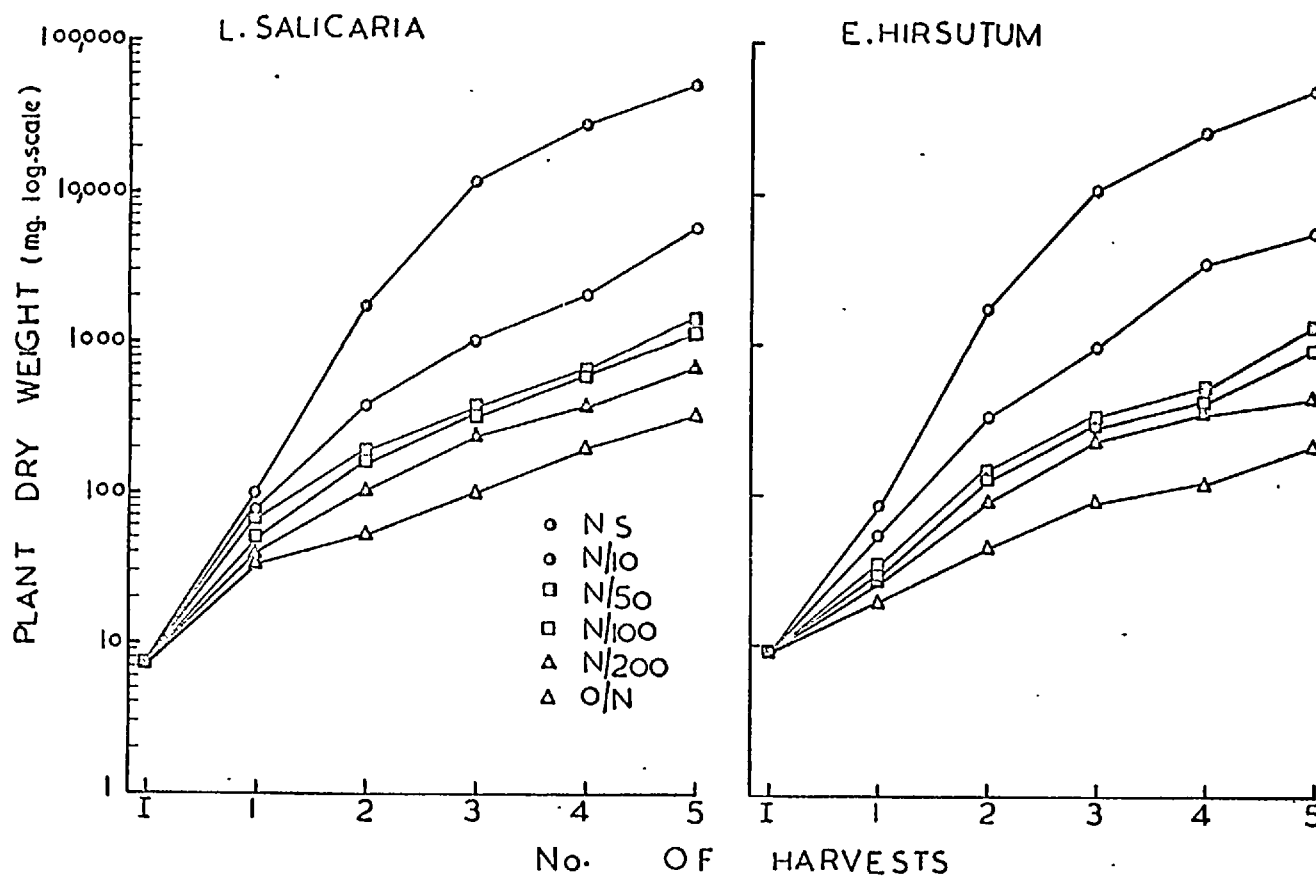


FIG. 76. Effects of different levels of nitrogen on increase of plant dry weight with time. (I = initial harvest)

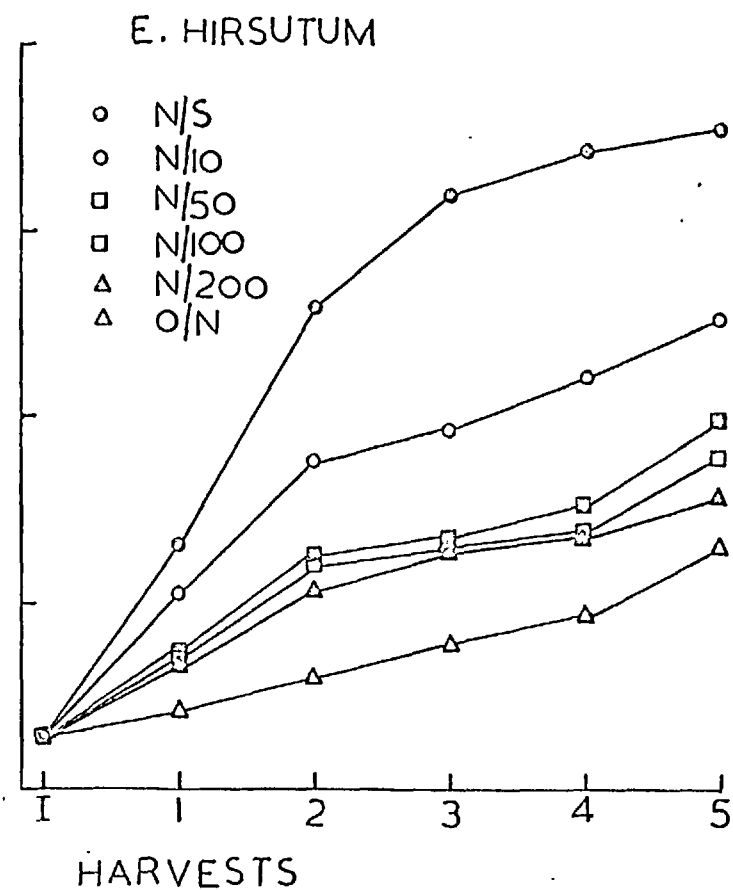
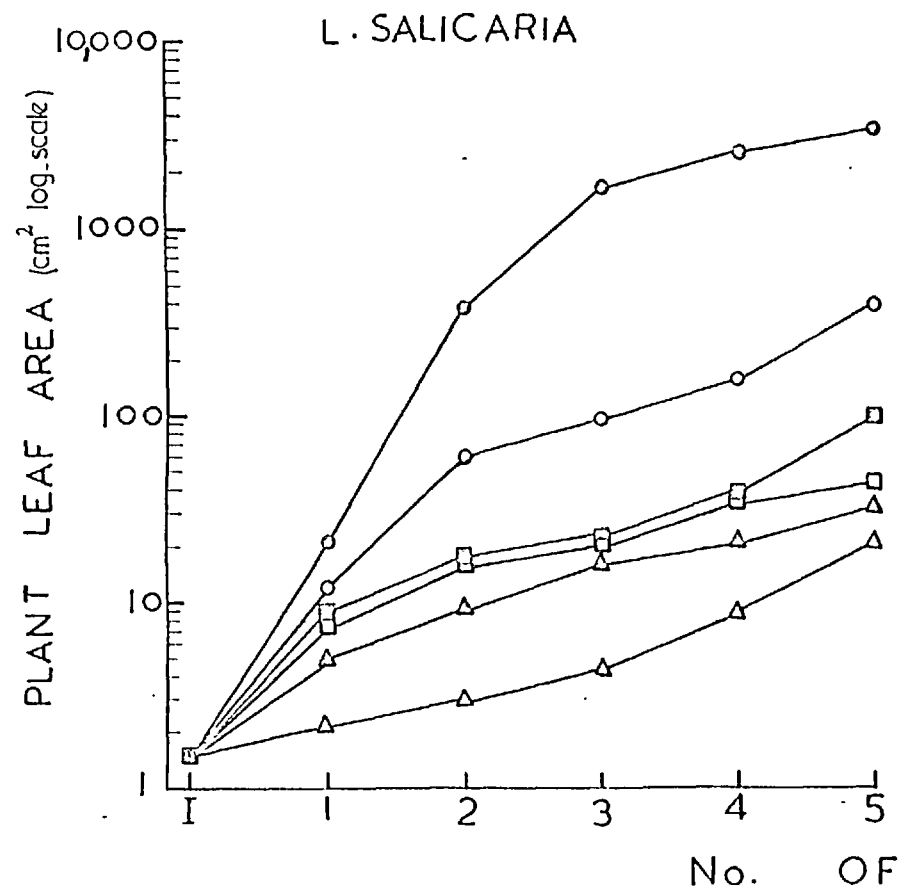


FIG. 77. Effect of different levels of nitrogen on increase of plant leaf area with time. (I = initial harvest).

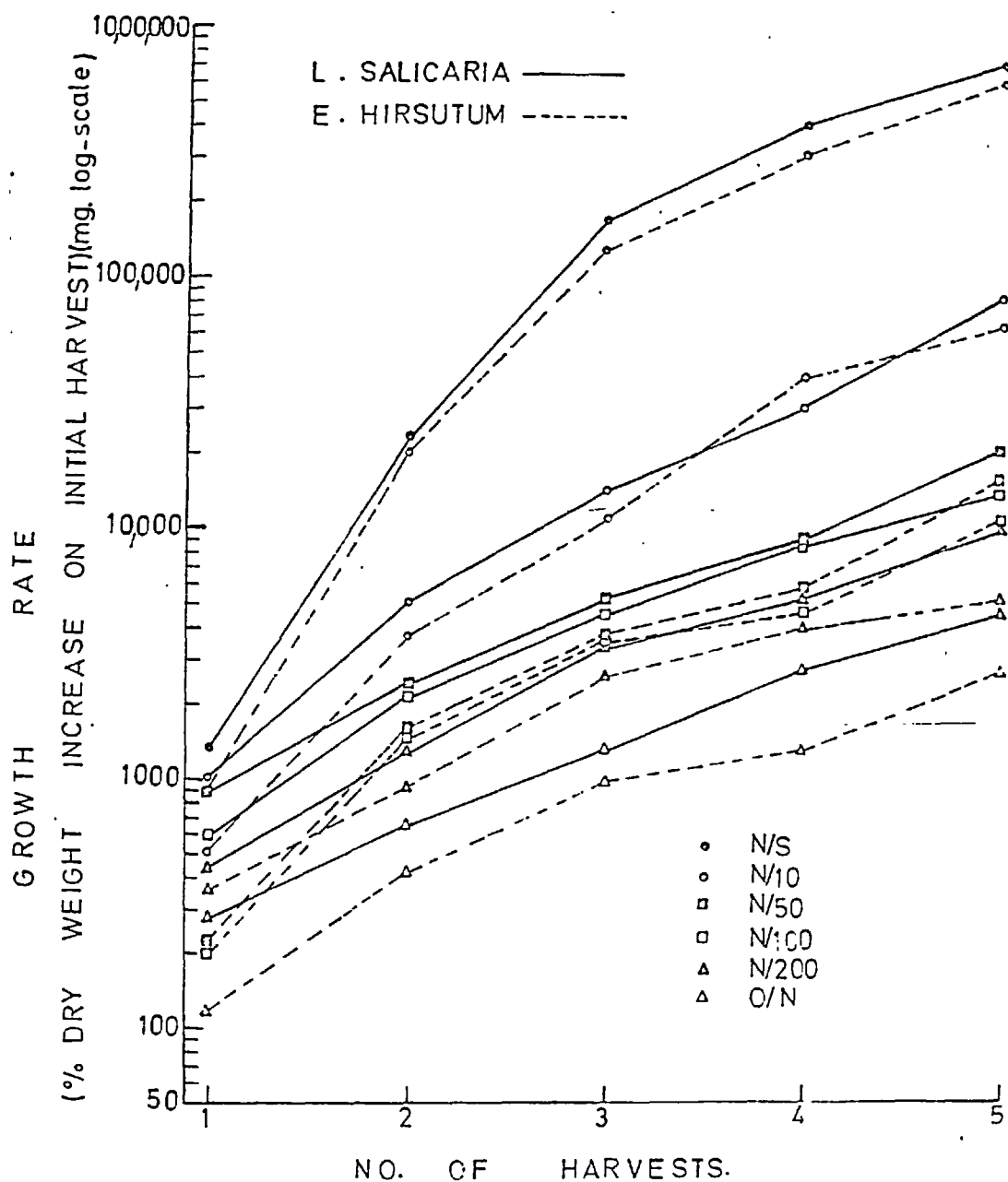


FIG. 78. Effect of different levels of nitrogen on growth rate. Percentage increase dry weight time from an initial harvest to each successive harvest ($H_1 - H_I$, $H_2 - H_I$, $H_n - H_I$)

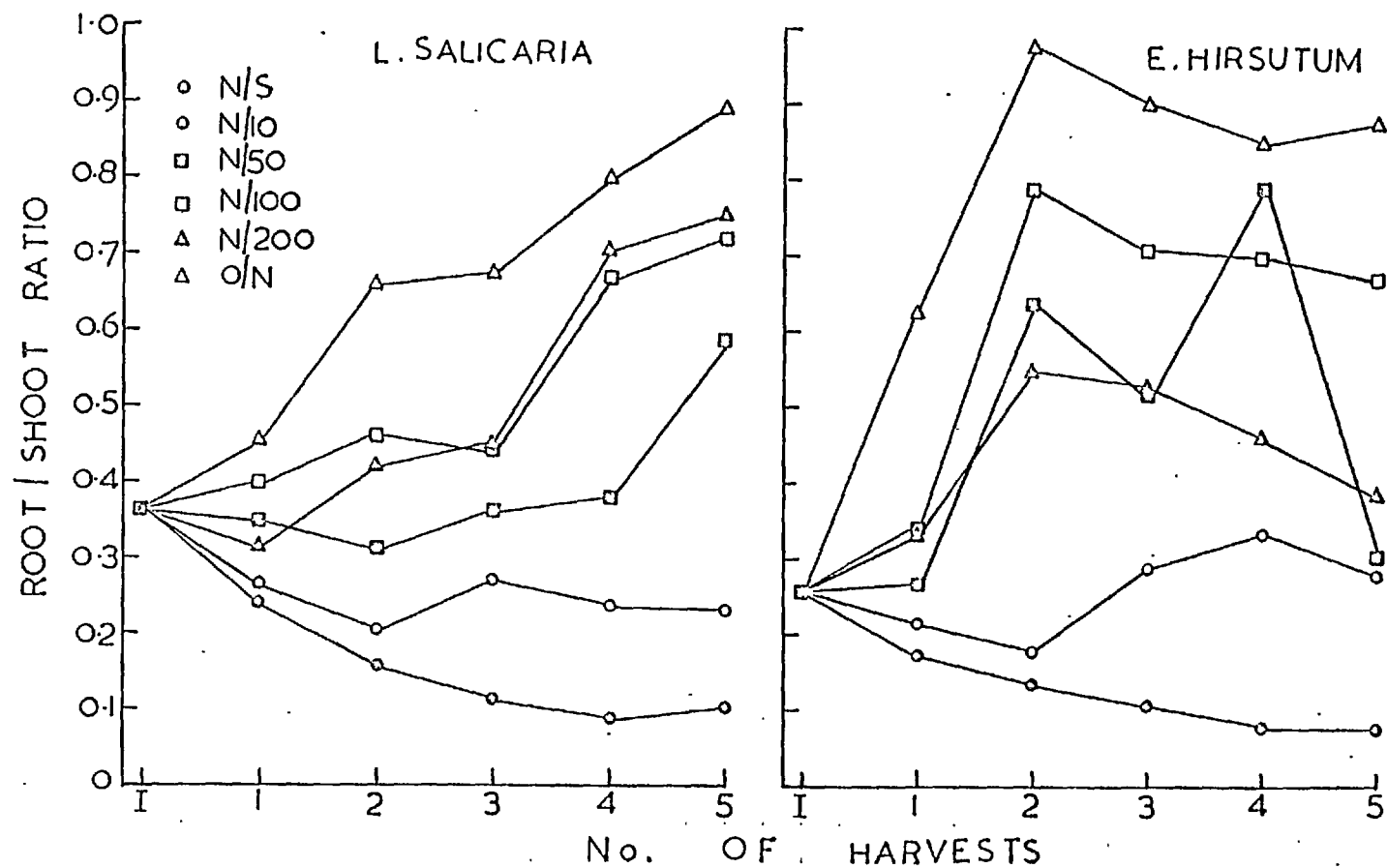


FIG. 79. Effect of different levels of nitrogen on root/shoot ratio.

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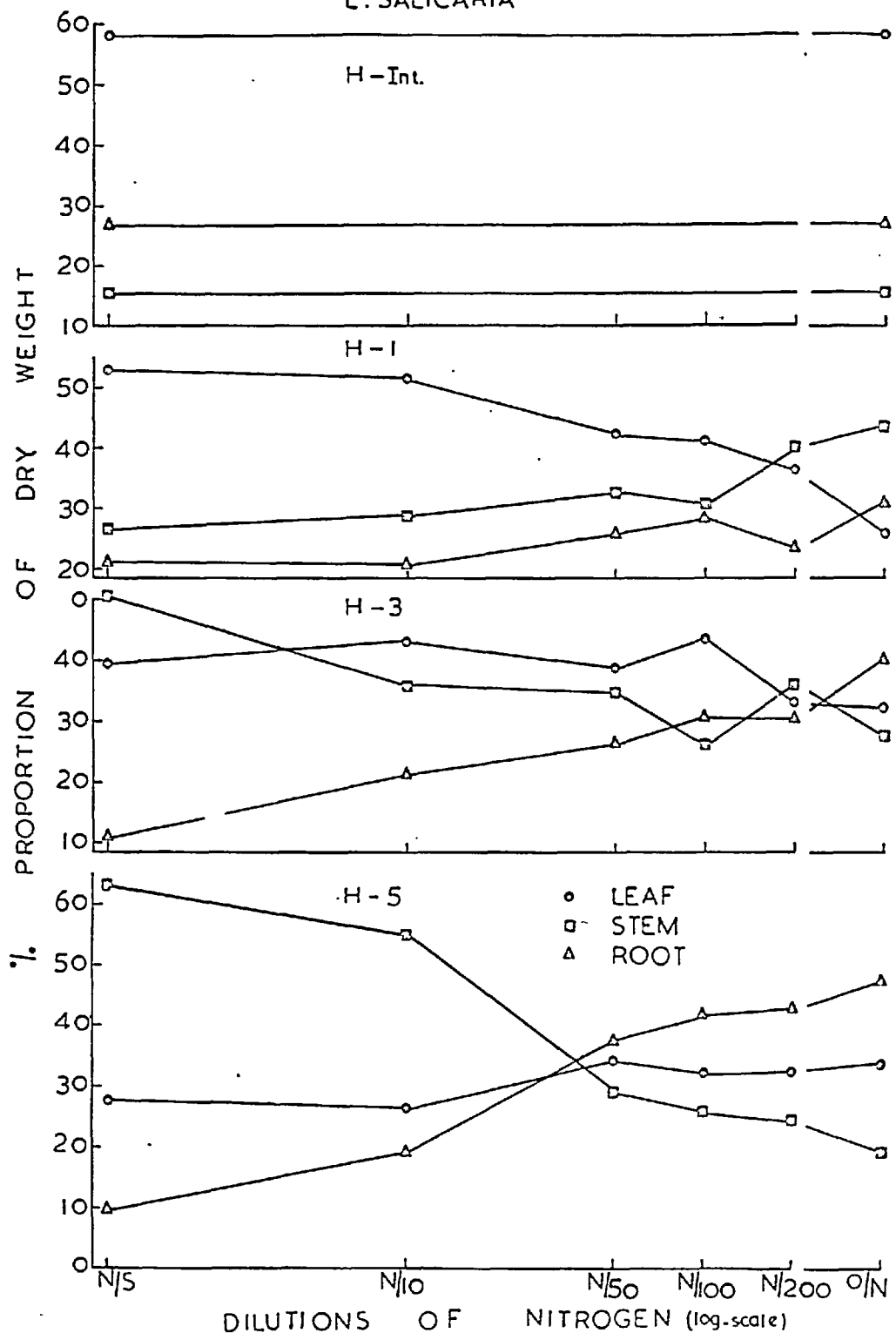


FIG. 80. Effect of different levels of nitrogen on percentage proportional distribution of total dry weight to leaves, stems and roots. (Harvests: initial, one, three and five)

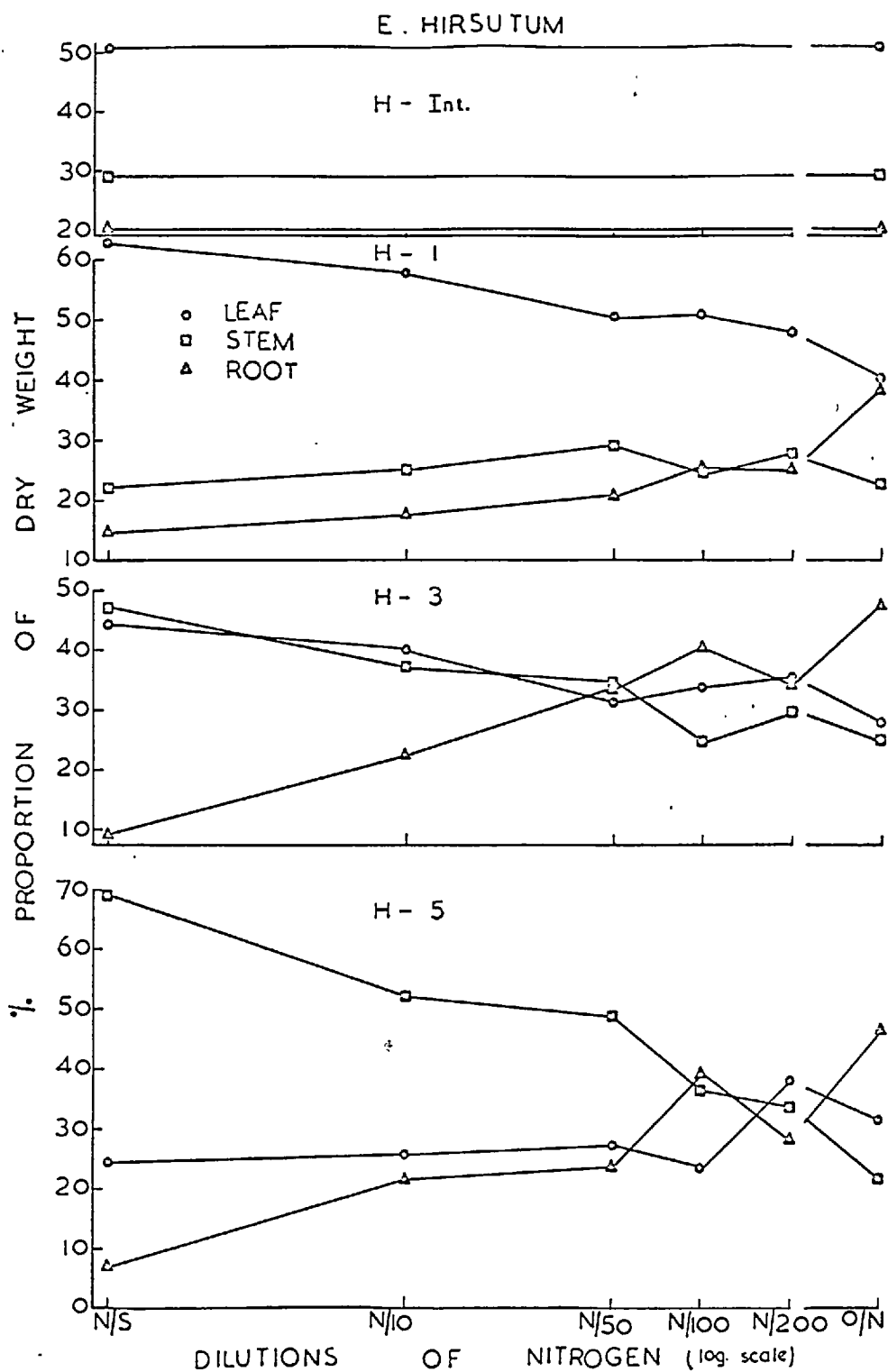


FIG. 81. Effect of different levels of nitrogen on percentage proportional distribution of total dry weight to leaves, stems and roots (Harvests: initial, one, three and five)

the species.

Discussion

The results presented show that, despite the severely diminished gain in dry weight, both species responded to the nitrogen stringency in this nutrient regime by an adaptive increase in the proportion of root to shoot. It should be noted that Epilobium showed a marked decline in the root/shoot ratio in the N/50 and other treatments in the last harvests, but in Lythrum this response was continuous throughout the experiment and was very well marked in all the treatments. The extra, or the larger, proportion of root in Lythrum was gained at the expense of the stem rather than the leaves.

From a survival point of view, it is clearly of value to be able to increase the absorptive and photosynthetic capabilities, as Lythrum does, at times when nitrogen supplies are very low. It is suggested that the greater growth in this species was due to its capability to adapt at a greater level of nitrogen stringency than Epilobium. This conclusion also confirms the suggestion made in Experiment XI (chemical analysis) that because of the higher nitrogen uptake capacity in Lythrum under stringent conditions, its growth would be less affected by nitrogen deficiency than that of Epilobium.

Series IIIThe effect of various dilutions of potassium
on growth

Plate 13 (a and b) shows the appearance of the plants at the end of the experiment. In general, the establishment and early growth of seedlings of both species were very poor. In Epilobium there was 20% mortality in the K/10 and K/50 solutions, and up to 32% in the later treatments. The plants of both species grown in the standard solution were the same as in Series I.

The extent of growth and development in the various dilutions of potassium in the final harvests was as follows.

Epilobium hirsutum

The plants in the K/10 solution were some 72 cm. long with eighteen pairs of nodes on the main stem. The early growth was very slow and elongation of the side shoots was suppressed. After harvest four about ten shoots had started elongating and the longest in the final harvest was 20cm. in length. Even at this dilution the leaves showed marked symptoms of potassium deficiency. After harvest two most of the mature leaves were pale green; thereafter, rapid yellowing of the lower leaves, starting with the oldest, was apparent in all the plants. By the time of the fourth harvest most of the leaves on the main stem were dry, yellow and crumpled but

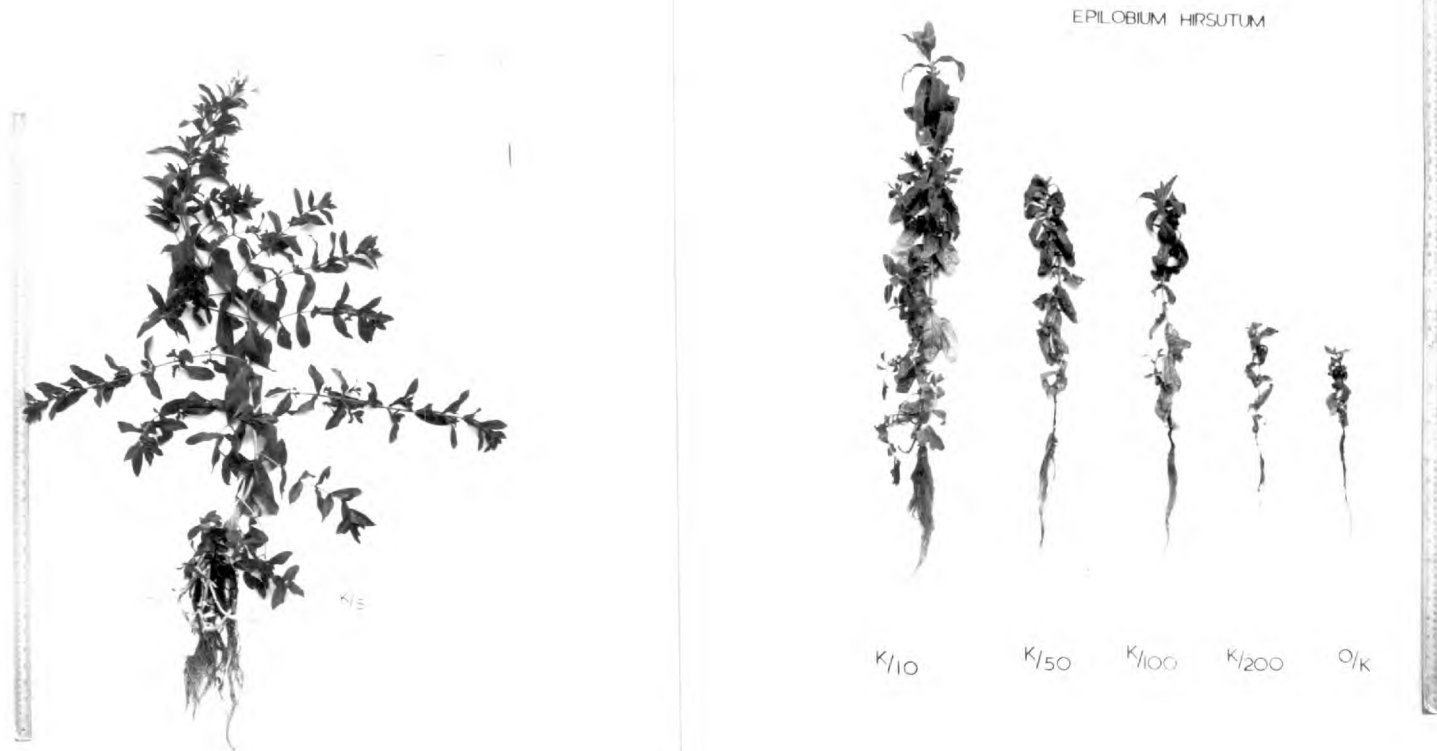


PLATE 13 (a) Epilobium hirsutum

Plants grown in a standard nutrient solution and at different levels of potassium in the solution. (Photographed after 75 days in the treatments, i.e. at the time of Harvest V).

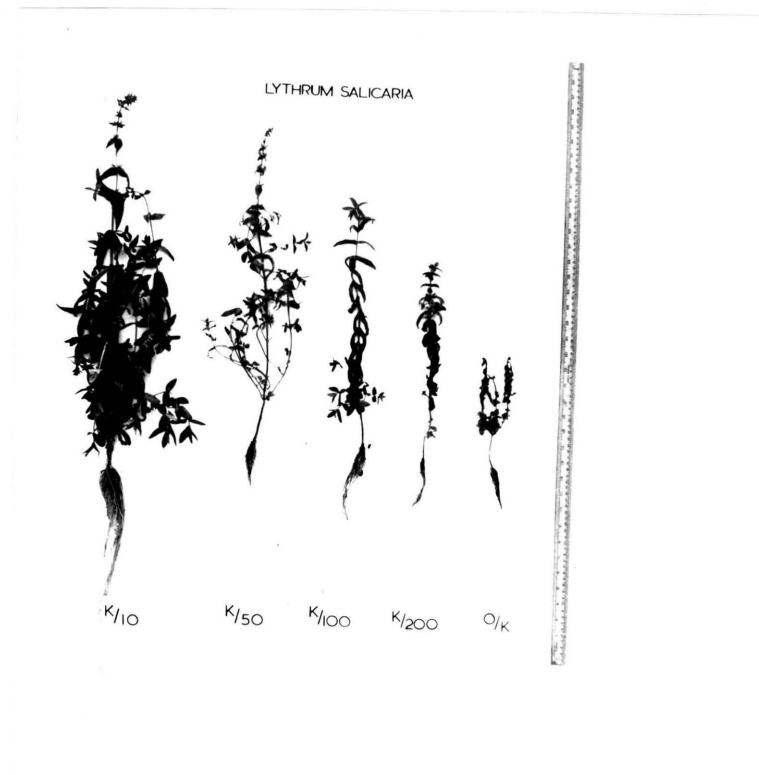
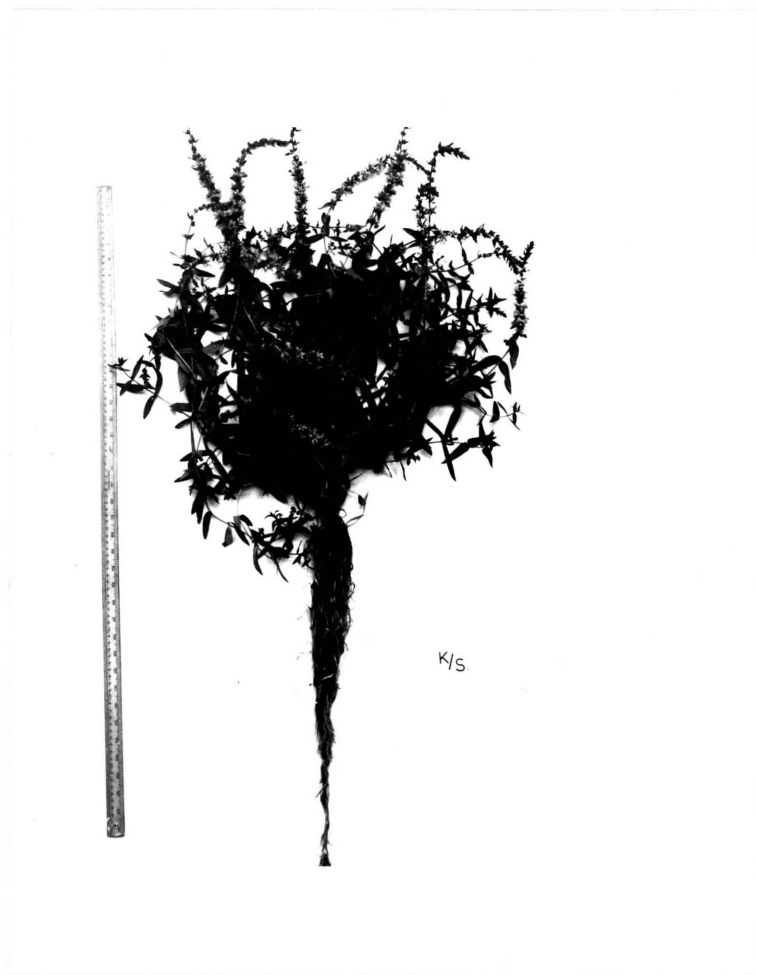


PLATE 13 (b) Lythrum salicaria

Plants grown in a standard nutrient solution and at different levels of potassium in the solution. (Photographed after 75 days in the treatments, i.e. at the time of Harvest V).

did not fall off. However, at the same time these leaves were being gradually replaced by the numerous small, bright green leaves of the young side shoots and even some of these, by the time of the last harvest, started showing similar symptoms. None of the plants developed any rhizomes, except one with two small rhizome initials. Some plants also produced a few abortive flower buds.

In the K/50 and K/100 treatments the average plant length was 50 and 45 cm. respectively and in both cases the stem had developed eighteen pairs of nodes with expanded leaves and suppressed shoots. No rhizome initials or abortive flower buds were produced in any of the ten plants. Leaves were severely affected in these treatments and by the time of harvest three most of the upper leaves showed increasing signs of chlorosis and all the lower leaves became yellow, necrotic and started drying up from the edges inwards. The root system of these plants was also very poorly developed and by the end of the experiment the tips of many roots were blackened and abortive.

At the K/200 and O/K level there was a still greater reduction in the plants and main stem had developed only fourteen pairs of leaves. From the very early stages deficiency symptoms were well marked and the necrosis was widespread towards the end of the experiment. The root system

in both treatments was very poorly developed and, with time, became completely malformed and blackened. At the O/K level the whole of the shoot was completely dried up by the time of the last harvest.

Lythrum salicaria

In the K/10 solution growth was slow in the first three weeks after transplantation but later, after the second harvest, the plants started growing very fast. In the final harvest side shoots were well developed and profusely branched and the general appearance of these plants was very similar to the standard plants. The plants were some 92 cm. high with twenty-two pairs of leaves (including large, fully expanded floral bracts) on the main stem, and the longest side shoot was 68 cm. in length. The leaves were soft, thin and glaucous, mostly narrow, elongated and bright green. Deficiency symptoms were not apparent up to harvest two but later on most of the older leaves developed black spots on their under surfaces which, later on, also spread on to the upper surfaces followed by the drying up of the leaves from the margin inwards and a complete falling off two weeks later. By the time of the final harvest most of the older leaves on the main stem were lost. The plants started flowering on the fifty-fourth day after transplantation. Inflorescence was lax. and the floral whorls sparsely arranged with two to

three flowers in each whorl. On average a plant produced up to 350 flowers.

The plants in the K/50 treatment were 48 cm. high with sixteen pairs of leaves on the main stem and numerous profusely branched side shoots, the longest of which was 25cm. in length. The necrotic effect of potassium deficiency on the leaves was much more marked than in the K/10 treatment. Many plants showed the development of abortive flower buds in the last harvest. In the K/100 and K/200 treatments there were still further reductions but the degree of development was similar as the plants were more or less 30 cm. high with fourteen pairs of nodes on the main stem and were profusely branched. There was a pre-mature die-back of the lower leaves in the early stages of growth, starting with the oldest leaves and becoming extensive with time. By the time of the last harvest almost all the leaves belonged to new young shoots especially in the K/200 treatment. These leaves were small, narrow and pale green.

At the O/K level the plants were extremely soft, succulent and pale green. The main axis was profusely branched with small, narrow oblong leaves. After the first harvest there was a yellowing and drying up of the leaves and a week later most of the leaves showed a pre-mature die-back. They were replaced by young leaves on the new branches which

also behaved in the same way. However, new leaves were continuously being produced on both the old and new shoots, so that during the course of the experiment leaves in each plant were re-newed at least four times.

It can be concluded that the greatest development of plants in both species was in the standard solution! Even in the K/10 treatment both vegetative and reproductive growth was severely affected, more so in Epilobium than in Lythrum. In the K/50 and K/100 treatments the necrotic effect of potassium stringency was still more marked in Epilobium. In Lythrum in the K/200 and O/K treatments, although the leaves showed repeated pre-mature senescence and the pattern of development was less clear in the final stages, still there was an appreciable amount of growth. In Epilobium, in these treatments, growth and development were severely curtailed, roots were completely malformed and blackened, and the whole shoot dried up by the end of the experiment in the O/K treatment.

Results

Fig. 82 shows that with the increase in potassium stringency there is a marked falling off in the total dry weight attained by individual plants. Further, the difference in the total dry weight between the plants at any dilution increases with time.

It can be seen from Fig. 83 that there is a greater reduction in the dry matter production in Epilobium than in Lythrum. The reduction is such that although in the standard solution both species attained similar dry weights, even in the K/10 treatment the dry weight of Lythrum was more than double that of Epilobium and in the later treatments it was three to four times that of Epilobium.

Similarly, in Fig. 84 a relatively greater reduction of leaf area in Epilobium compared with Lythrum can be seen. In Epilobium in the K/100 and following treatments there is a steady decline in the leaf area in the last two harvests while Lythrum shows the usual steady increase.

Fig. 85 shows the changes in the root/shoot ratio for the duration of the experiment. It is particularly noticeable that in both species there is no adaptive increase in the root/shoot ratio in response to potassium stringency unlike the nitrogen and phosphorus stringency.

The percentage proportional distribution of the dry matter to the leaves, stem and root for the various harvests is shown in Fig. 86 for Lythrum and Fig. 87 for Epilobium. There is no increase in the root proportion and it follows the same pattern in both species in all the treatments except at the O/K level in Epilobium where it completely breaks down. The patterns of leaf and stem are different in the two species.

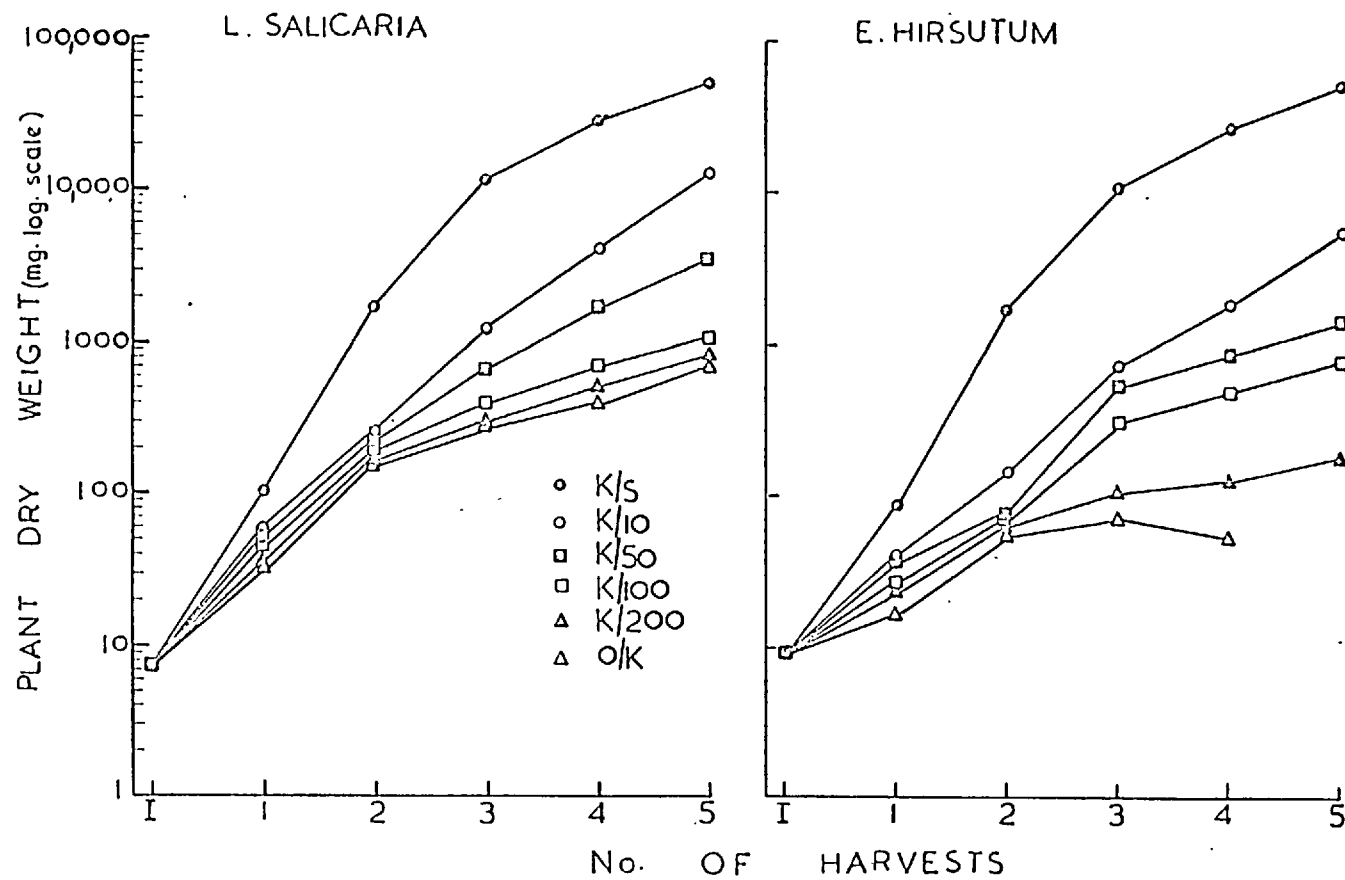


FIG. 82. Effect of different levels of potassium on increase of plant dry weight with time. (I = initial harvest)

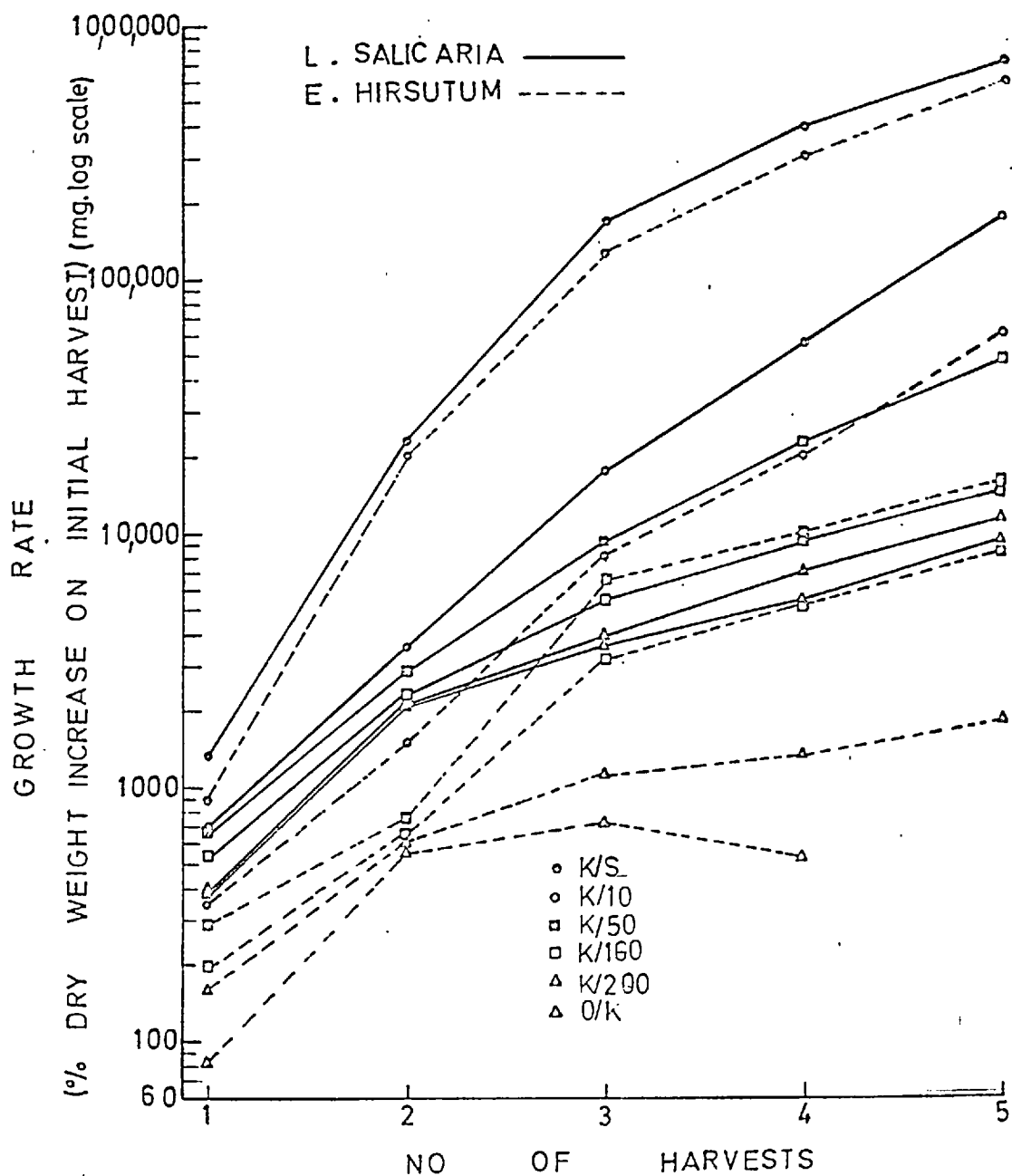


FIG. 83. Effect of different levels of potassium on growth rate. Percentage increase dry weight time from an initial harvest to each successive harvest ($H_1 - H_I$, $H_2 - H_I$, $H_n - H_I$)

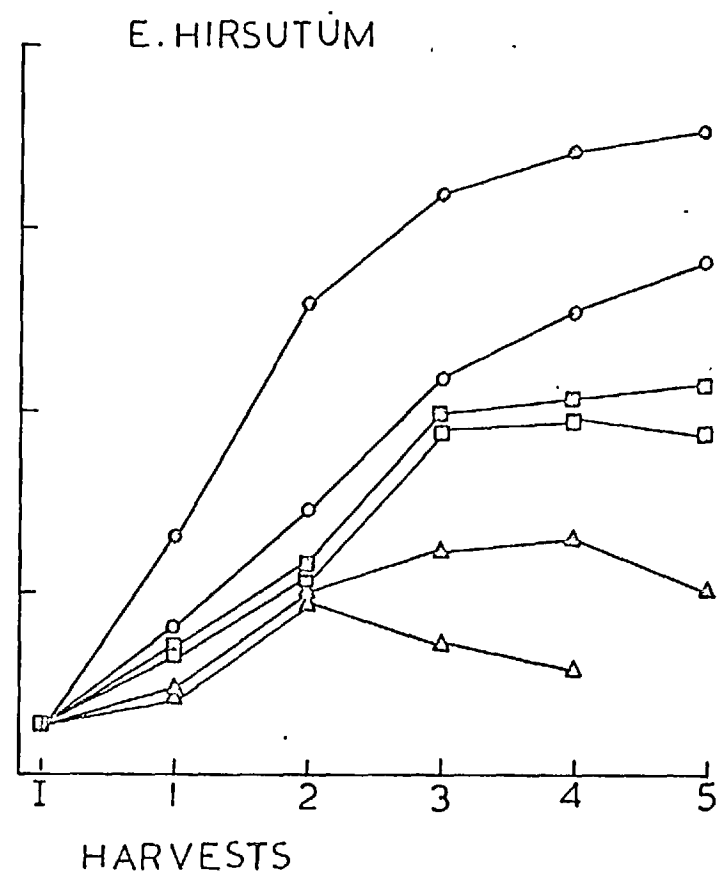
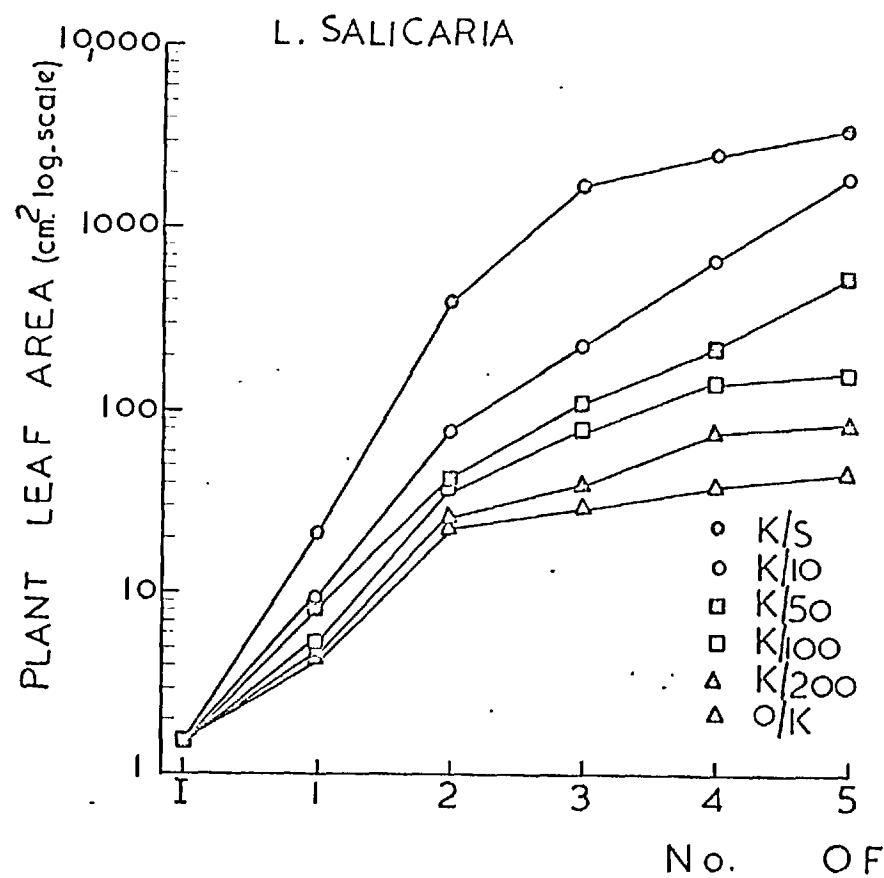


FIG. 84. Effect of different levels of potassium on increase of plant leaf area with time. (I = initial harvest)

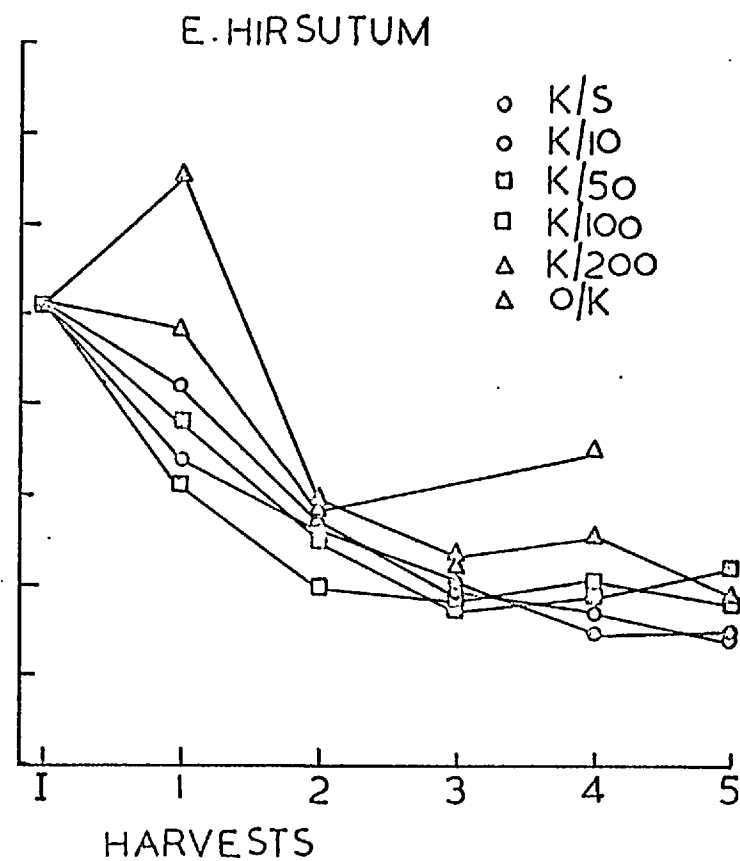
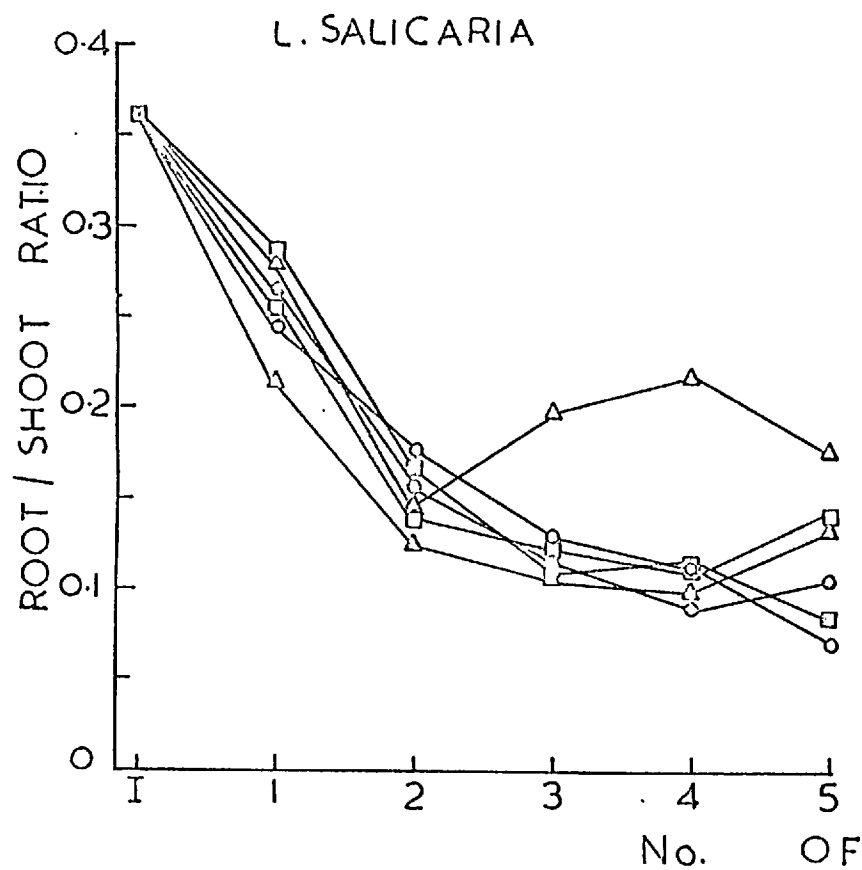


FIG. 85. Effect of different levels of potassium on root/shoot ratio.

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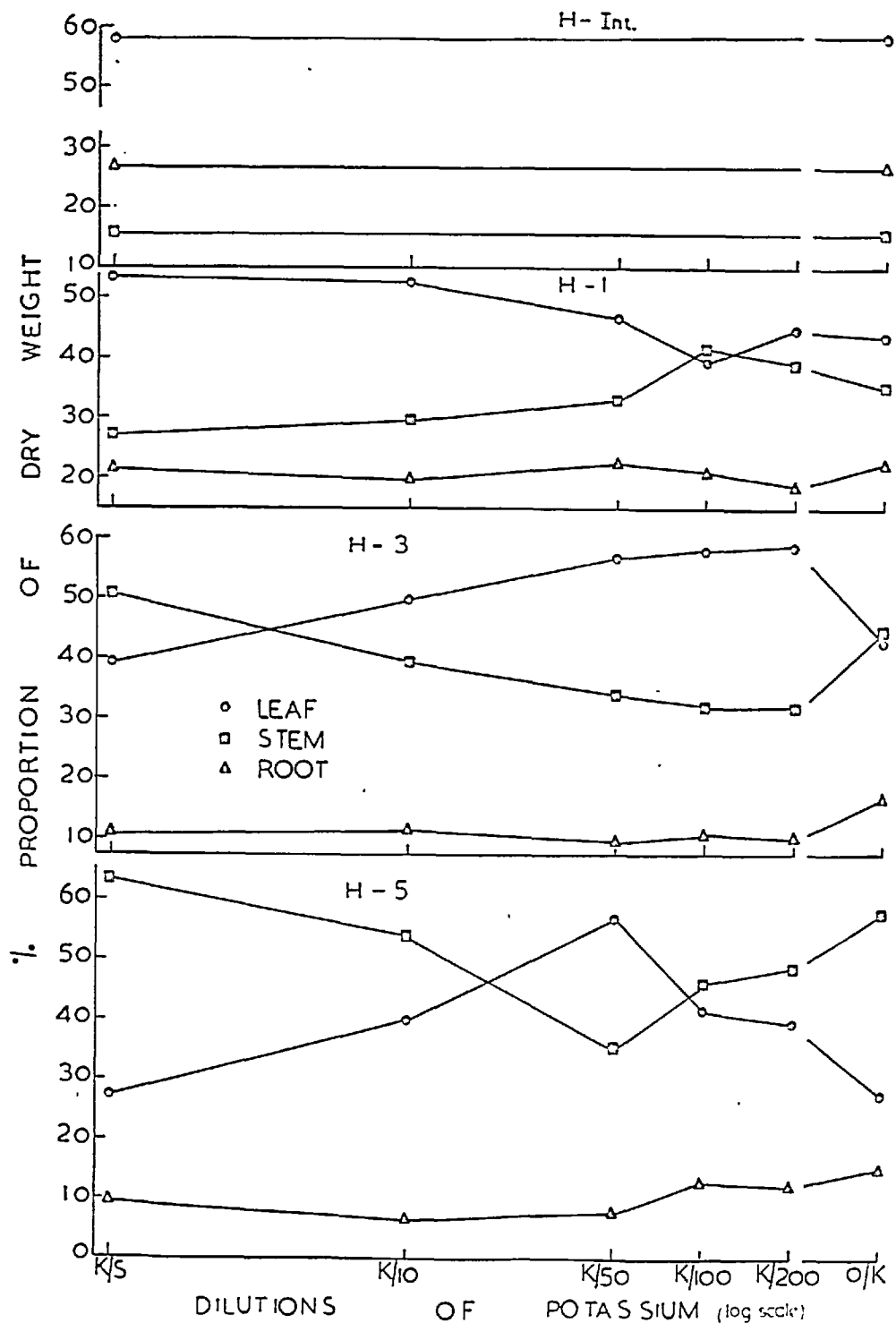


FIG. 86. Effect of different levels of potassium on percentage proportional distribution of total dry weight to leaves, stems and roots (Harvests: initial, one, three and five)

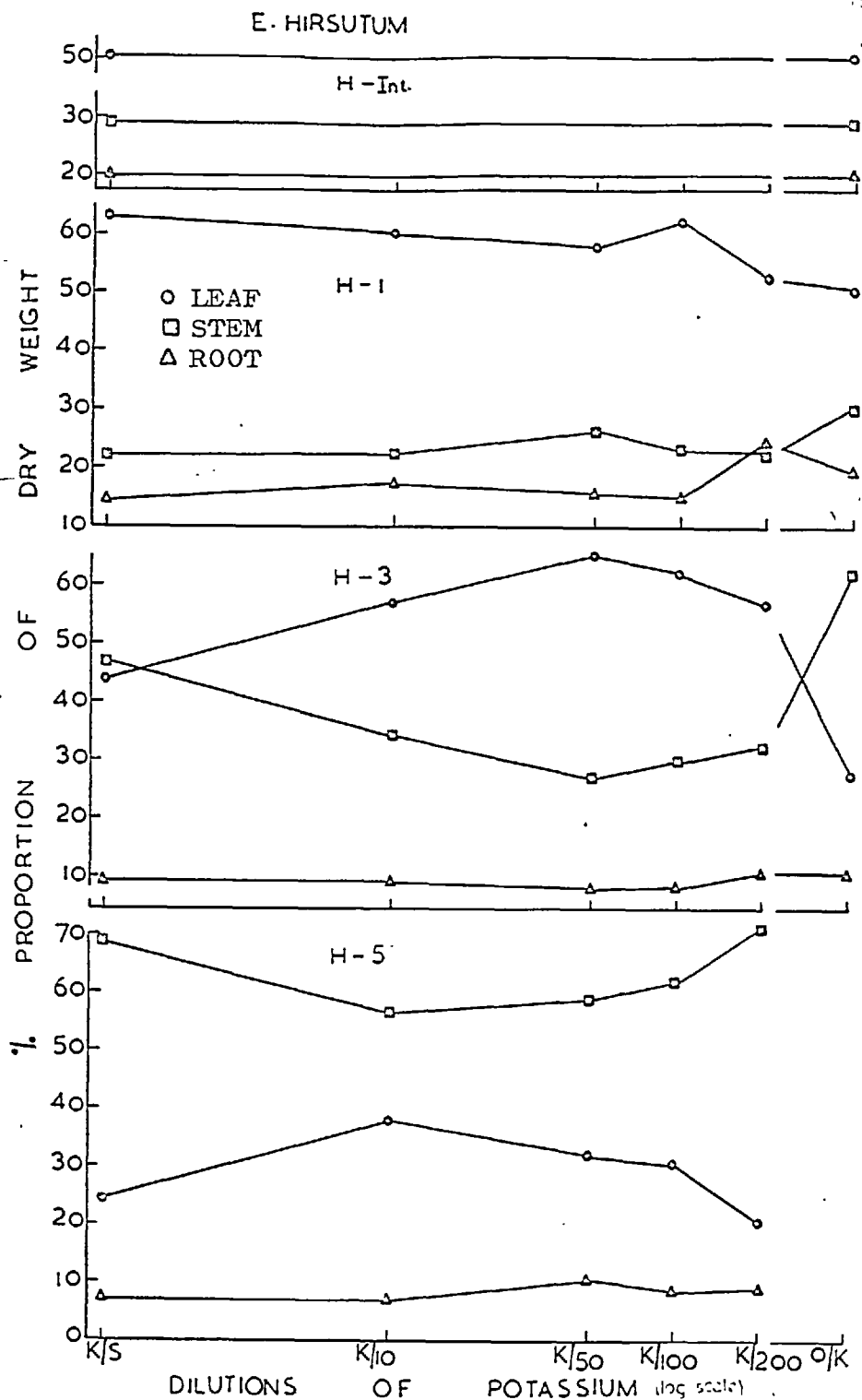


FIG. 87. Effect of different levels of potassium on percentage proportional distribution of total dry weight to leaves, stems and roots (Harvests: initial, one, three and five)

Both species show an increase in leaf proportion at the expense of stem proportion, with time, from the K/S to the K/10 treatment. In Epilobium there is a gradual decline afterwards and the stem gains proportion at the expense of the leaves, but in Lythrum this tendency is very marked at the K/50 level, where the leaves constitute 57% of the total dry weight, followed by a gradual decline.

Discussion

These results show that, whilst the extent of development and dry weight gain were greatly diminished by potassium stringency in both the species, Epilobium, relatively, was far more affected than Lythrum especially in the extreme conditions of deficiency. Necrosis and root malformation were very extensive in Epilobium. Similar effects of potassium stringency have also been found in two other species of Epilobium i.e. E. adenocaulon and E. montanum (Myerscough and Whitehead, II 1967). There was no adaptive increase in the root/shoot ratio in response to potassium stringency in either species. On the other hand, in Lythrum there was an adaptive increase in the leaf proportion at the expense of the stem proportion. In Epilobium (except at the K/10 level) there was an increase in the stem proportion at the expense of the leaves and root. It is considered probable that the much better growth in Lythrum was because of the increased

proportion of photosynthetic tissue in the stringent conditions.

The results agree with the conclusions of Experiment XI (chemical analysis) that a greater potassium uptake ability in Lythrum, in stringent conditions would result in better growth than that of Epilobium.

General Discussion

The results of this experiment showed that the greatest development of the plants, in both species, was in the standard nutrient solution, and in all the three deficiency series there was a marked reduction in the extent of development and growth. The results of dry matter production in the final harvest in all three series are summarised in Fig. 88. It should be noted that in all the series (except at the P/10 level) Epilobium was more affected by the stringency than Lythrum.

Considering all these series separately, it can be seen that in Lythrum growth was comparatively less affected by the phosphorus deficiency than the nitrogen deficiency, and growth in the potassium deficiency was inbetween these two extremes. In contrast, in Epilobium although growth was less affected by the phosphorus deficiency, as in Lythrum, nitrogen and potassium deficiency had an equally depressing

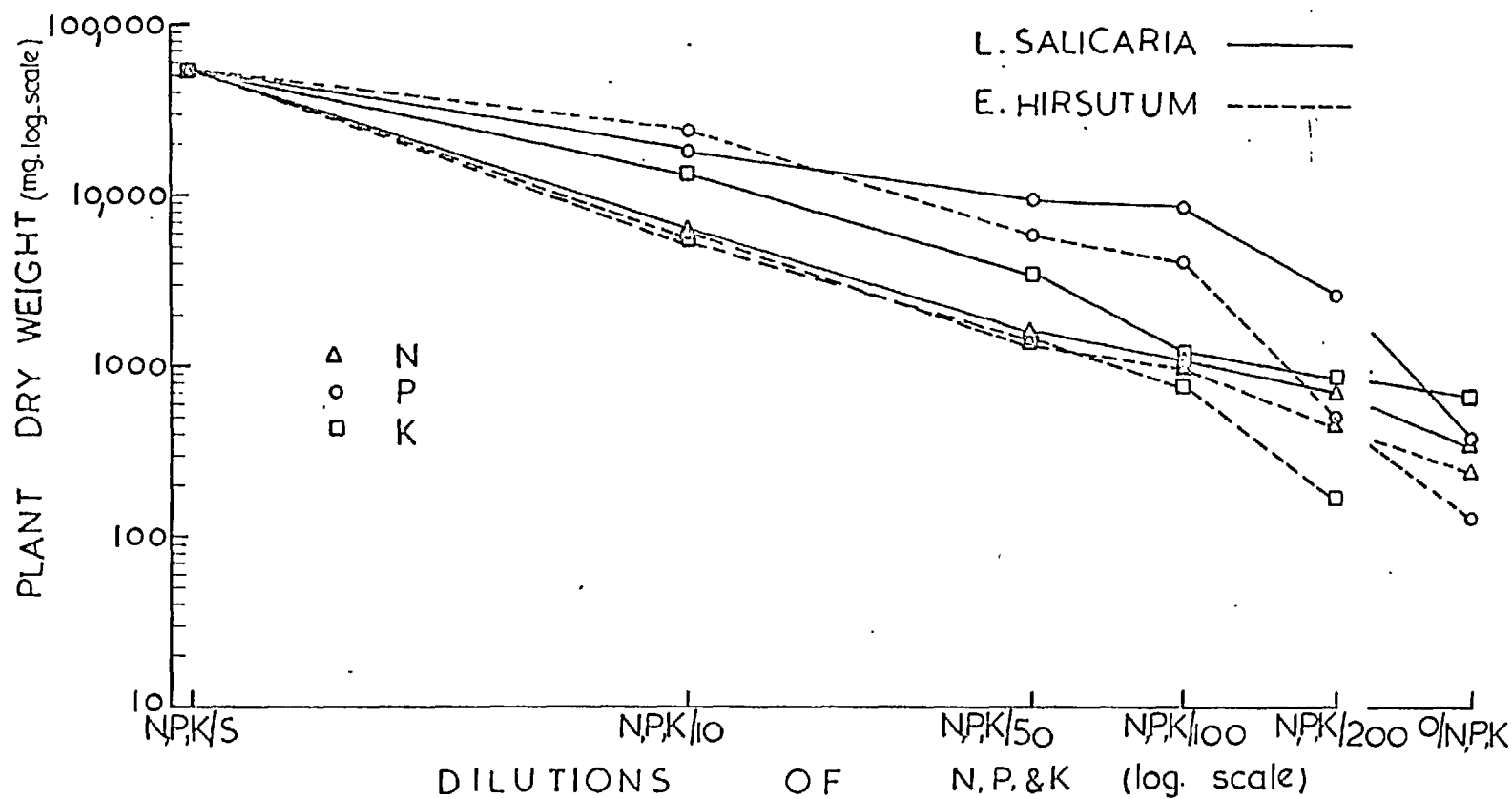


FIG. 88. Effect of different levels of phosphorus, nitrogen and potassium on growth. Total plant dry weight in final harvest.

effect on the dry weight gain, and the effect of potassium deficiency was even more marked in the extreme conditions.

The reproductive growth was also differently affected in the two species. In the phosphorus deficiency series Lythrum produced flowers at all levels of stringency, whilst in Epilobium flower buds opened very rarely at the P/100 level and were abortive in the P/200 treatment. However, rhizomes were produced in all the treatments. In the nitrogen stringency, the flower and fruit production was greatly reduced in Epilobium even at the N/10 level, and no flower buds were produced at the N/50 level, however the plants continued rhizome production even in the N/200 treatment. In contrast Lythrum did not show any great reduction in flower production at the N/10 level and, unlike Epilobium, flowers were also produced in the N/50 treatment. In Epilobium reproductive growth was severely affected by the potassium deficiency and even at the K/10 level there was no flower or rhizome formation. In contrast, Lythrum produced a normal inflorescence and flowers in the K/10 treatment and abortive flower buds were also produced in the K/50 solution.

It would appear that in Lythrum, in general, the flower formation depends upon the amount of dry weight attained by the plant irrespective of phosphorus, nitrogen or potassium deficiency. (In this connection it is noteworthy

that the dry weight gain in the P/100 treatment was similar to that of the N/10 treatment, see Fig. 88). This also seems to be the case in Epilobium in the phosphorus and nitrogen stringency but the potassium stringency appears to interfere with the flower formation. It should be noted in this connection that although the plants attained similar dry weights in the K/10 and N/10 treatments, there was no flower or rhizome formation in the former treatment. It is suggested that in Epilobium potassium is directly involved in the production of reproductive organs and any deficiency in the amount from the standard requirement results in the complete suppression of these organs. Moreover, the internal balance of the plant is completely upset by any potassium deficiency, resulting in a widespread necrosis of leaves and malformation of the roots.

It has been shown that, despite great reductions in the dry weights, both species responded to the stringency of phosphorus and nitrogen by an increase in the proportion of root to shoot. It is considered that this increase of root relative to shoot is an example of an adaptive compensating mechanism. It can be argued that if for a given weight of shoot tissue the area of root surface is increased, the greater would be the probability of uptake of any available nutrient present. This shift in the balance of growth towards

an increased root/shoot ratio in response to phosphorus and nitrogen stringency appears to be a fairly general response of flowering plants; Brouwer (1962), Bradshaw et al. (1960 and 1964), Myerscough and Whitehead, II (1967) indicated that an increase in the root/shoot ratio is a common growth response under nitrogen as well as under phosphate stringency. The work of Parker (1927), Tidmore (1930) and Williams (1936) also showed the increase in the root/shoot ratio in response to phosphorus stringency. However, it is pointed out that this tendency of an increase in the proportion of root to shoot is much better developed and consistent in Lythrum compared with Epilobium.

On the other hand, none of the species showed any adaptive increase in the root/shoot ratio in response to potassium stringency. Of the four species studied by Myerscough and Whitehead II (1967) only in one species, i.e. Tussilago farfara, an adaptive increase of root/shoot ratio was made in response to potassium stringency. However, the much better growth in Lythrum was due to the diversification^{align} of a greater proportion of dry weight from the stem to the leaves, ~~and considered biologically it~~^{which} is advantageous to the plant as the photosynthetic adaptabilities are enhanced and, in the absence of any adaptive increase in the root proportion, a much better growth and survival of the plant is ensured.

Conversely, in Epilobium both the leaves and roots are severely affected by potassium stringency and in the absence of any compensatory mechanism the growth and development of the plant were severely curtailed by this deficiency.

It is suggested that of the three nutrient elements investigated here, i.e. phosphorus, nitrogen and potassium, it is the deficiency of potassium which would play a crucial and decisive role in determining the establishment and growth of the two species in the soils of low nutrient status.

In any attempt to consider the results of this experiment in relation to the probability of the establishment of these two species in sites with comparable phosphorus stringency, the amount of growth needed before the production of reproductive organs must be taken into account. It has been noted that in the P/100 treatment flower buds did not open in Epilobium whilst, in contrast, Lythrum was in flower even in the P/200 treatment. Since it showed normal growth at the P/10 level, it is probable that Epilobium is capable of becoming established and making adequate growth in sites with a moderately low level of available phosphorus, but Lythrum would be able to grow efficiently even in extremely low levels of phosphorus supply.

In attempting to assess the relative probability of the species becoming established in sites with a comparable

stringency of available nitrogen, account should be taken of the amount of growth, as an assimilating entity, the seedling of each species is committed to making before it can produce organs of reproduction. In Epilobium nitrogen stringency, even at the N/10 level, depressed the dry weight gain of the plant at an early stage and, although this tended to disappear in the final harvest with the appearance of rhizomes etc., still there was a great reduction in the number of flowers produced (only six to seven flowers per plant). In comparison, in Lythrum not only was the growth much better in the N/10 solution but also a large number of flowers per plant were produced. Flowers were also present at the N/50 level in Lythrum, while Epilobium failed to produce even the flower buds.

It is, therefore, considered probable that Epilobium is not capable of becoming established in sites with as low a level of available nitrogen as Lythrum because of its commitment to making much leafy growth in its earlier stages before it can form the appreciable dry weight surplus required for its maintained growth as an assimilating entity for the production of rhizomes and flowers.

With regard to the relative probability of the establishment of the species in sites of comparable stringency of potassium, assessment should be made solely in terms of the

ability to grow, the quality of growth made and the presence or absence of any compensating mechanism in each species under such stringency conditions. Of the two species Lythrum is more likely to make adequate growth in sites of low potassium supply. In this species, unlike Epilobium, growth and flowering at the K/10 level was quite normal; development and growth did not become unbalanced in the K/50 treatment and flower buds were produced; at still higher levels of potassium stringency the necrotic effect on the plants was less marked than in Epilobium. Also, in this species there was an adaptive increase in the leaf proportion of the plants at the expense of the stem proportion under such stringency.

Mineral nutrition in relation to
the biology of the species

The edaphic habitats affect the growth, distribution and competition of plant species by exerting their influence through the deficiency or abundance of certain major or minor plant nutrient elements. Such a description is prompted by the observations that some species are confined to nutrient-rich soils, making high demands on the nutrient supplying power of the soil, and are unable to grow on nutrient deficient soils or grow so poorly that they are unable to compete successfully with other plants. This reasoning may also give rise to the assertion that species which grow in nutrient-

poor soils have, also, low nutrient requirements. Besides this, there are several ways in which plants might adapt themselves to life in nutrient-poor soils, such as differential nutrient uptake capacity, life form and phenotypic response to the environment.

In the present investigations of the nutrient relations of the two species these hypotheses have been tested.

Summarising the conclusions based on the results of the experiments described in this chapter, it is clear that Lythrum has relatively lower nutrient requirements for its normal growth, whilst Epilobium is a plant of high nutrient requirements. The confinement of Epilobium to base rich fens and the silted banks of hedgerows, and its complete exclusion in less fertile sites speaks of its high demand rate on the nutrient supplying power of the soil. The results of chemical analysis interpreted in connection with the establishment of the two species in natural sites of low fertility, would suggest that besides the high nutrient requirements, the uptake of major nutrients like potassium, nitrogen and phosphorus is more severely curtailed in Epilobium than in Lythrum under nutrient deficient conditions. On the contrary the dual advantage of Lythrum, i.e. low nutrient requirements and high uptake capacity under stringent conditions would enable

it to become established and grow on nutrient-poor soils. It is suggested that in terms of the logistics of supply and demand, Lythrum would have a natural advantage over Epilobium in the event of competition on nutrient-poor soils.

In addition to this, logistics, phenotypic plastic response to the environment, life form and growth rate also affect the competition and survival of the plants under stress conditions. Of the two species, Epilobium has an elaborate morphology and a slow growth rate which means that not only would it make high nutrient demands but the length of time taken to complete its life cycle would also cause a greater strain on the nutrient supplying capacity of the soil. This commitment of the plant to an extensive morphological structure and the lack of any compensatory mechanism (increase in root/shoot ratio) to cope with the unfavourable conditions, leads to its exclusion from soils of low nutrient status. On the other hand, Lythrum is a less elaborate plant morphologically, with a faster growth rate and it completes its life cycle in a very short time compared with Epilobium. Although the nutrient uptake under stress conditions is higher in Lythrum, the overall strain on the nutrient supplying power of the soil would not be as high as in Epilobium. It seems possible, however, that in the evolution and adaptation of this species to nutrient-poor situations, it has been able to

combine a low rate of demand on the nutrient supplying power of the system and a greater efficiency of uptake by changes in its morphological balance. It is probable that the selective processes caused an overall decline in the plant size and elaboration, with a corresponding increase in the competitive and survival value. Phenotypic plastic response to the changed environment in terms of increased root/shoot ratio is the greatest asset of this plant in its survival and competition. The proportionately larger root system would lead to higher nutrient uptake by exploring correspondingly larger volumes of soil and, on top of this, in the reduced shoot it is not the leaves but the stem which undergoes reduction. Considered teleologically, it is again advantageous for the plant that it should be so, as the photosynthetic processes are not affected and the adaptability, at least on a short-term basis, to the nutrient stringent conditions is ensured.

However, it must be remembered that the selective pressure against the establishment and survival is greatest at the young seedling stage and Epilobium, because of its commitment to making more and elaborate growth at this early stage of development, would suffer a great loss in terms of the number of individuals eliminated. Later on those succeeding in establishing themselves would be handicapped by

the low nutrient supply, and the lack of any compensating mechanism would curtail their growth and competitive ability. On the other hand, Lythrum has no great growth commitments in its early stages; investment in terms of root growth is greater than the expected dividends, again teleologically advantageous at this stage of growth. Again, the mature plant is not only less elaborate morphologically, but is also biologically well equipped to cope with the stress conditions by changes in the morphological balance as a result of differential utilization of the assimilates. These changes have great survival value as they produce growth forms epharmonic with the environment. The growth forms, well adjusted to their environment even on a short term basis, would not only grow as efficient photosynthetic entities, but would also be successful in competing with other plants.

It is emphasized, however, that of all the mineral nutrient deficiencies, potassium stringency would be the decisive factor in excluding the establishment of Epilobium from sites of low fertility.

In increasing stringency of major nutrient elements (N,P,K,) there is a corresponding reduction in the level of reproduction and yield especially in the case of Epilobium. It is known that a large number of seeds are wasted in nature during the establishment of a species. Thus a drastic cut in the seed production due to nutrient deficiency from generation to generation may have long term effects on the survival and continuation of these plant communities, as potentially a lower contribution is made to population and hence to population dynamics.

VIII. THE EFFECT OF TEMPERATURE ON GROWTH

While discussing the geographical distribution of the two species in Chapter III, it was pointed out that their altitude and temperature relations affect their distribution, as Epilobium is mostly confined to higher altitudes and mountainous regions while Lythrum preferably inhabits low-lying, warm, coastal areas. The abundance of Epilobium in northern Europe at high altitudes as opposed to the dominance of Lythrum in the warm zones of central and southern Europe and hot Mediterranean, indicates that temperature may be an important factor in controlling the geographical distribution of the two species.

Temperature is one of the most important of the complex environmental factors; described by Lunde●gårdh (see Environment and Plant Development, Translated by Ashby, 1931) as a master factor which exerts more or less a direct effect on the growth and development of the terrestrial plants, and indirectly may control the establishment and distribution of different plant communities. As Turrill (1948) pointed out, every plant function has temperature limits above or below which it ceases, sometimes very abruptly, and that these temperature limits vary from species to species. Respiration

and photosynthesis are directly affected by temperature changes, but they are less easy to measure in natural habitats than growth and, to a considerable degree, growth summates the physiological activities of a plant. This affect of temperature on the physico-chemical processes may also change the course of morphologic differentiation in plants.

However, in the estimation of the action of temperature on the geographical distribution of these two species the interference by other factors, such as light, water and mineral nutrients, cannot be overlooked. Only the experimental studies of the effect of each of these factors can reveal to what extent distribution depends upon temperature and to what degree upon water, nutrition and light.

Most of the information in the literature deals with the effects of temperature on growth alone, or in conjunction with light as by Mitchell (1953); Davidson and Milthorpe (1965); Morley (1958); Eagles (1967); Humphries (1967); Broue et al (1967); and Silsbury (1969). The concept of temperature influences on growth has been enormously expanded by the work of F. W. Went in the Earhart Laboratories, California (see, Experimental Control of Plant ~~Control~~ by Went, 1957). His major contribution to this area of knowledge was finding that low night temperatures were of increasing benefit to many plants as the overall plant size increased.

On the other hand, there is no information in literature of the existence of any direct experimental evidence of the significance of the temperature effect on the ecological distribution of the plants.

The varied pattern of occurrence and distribution of the two species in Britain and on the Continent cannot be fully understood in terms of light or mineral nutrient requirements, which can account for only the localised distribution. While the exact nature of the environmental factors influencing these patterns of distribution are not clearly known, observations on the distribution show that temperature may be an important controlling factor. The germinability of Epilobium at low temperatures is indicative of its low temperature requirements, which is further manifested by its ability to grow, in nature, in cold months and for most parts of the year, compared to the very short active growing period of Lythrum. In the light of these results it is pertinent to compare the growth responses to different temperatures in these two species, as a first step in elucidating the role of this factor in influencing the pattern of their geographical distribution in nature.

Experiment XIII

Growth responses of the species to different temperature regimes.

This experiment was conducted in controlled environment growth cabinets (Fison's Phytotrons) at Silwood Park, to study the growth response of the two species to 8°C. and 18°C. temperature regimes. These temperature levels could have relevance to the autumn-winter-spring growth cycle of the species in Britain.

Experimental procedure

Seedling plants were raised to the third leaf stage (L.3) in sand culture, in 45 days at a temperature of 20°C. and a photoperiod of 16-hours in the controlled temperature rooms. Just after the L.3 stage the seedlings were transplanted, separately, into blackened plastic boxes with perforated tops and of 600 ml. capacity. Ten seedlings per box per species, and ten boxes of each species were used in the phytotron set at 8°C., so as to provide one hundred plants per species in this treatment, while there were only seventy plants of each species in the 18°C. treatment. It was necessary to use a higher number of seedlings in the 8°C. treatment due to the expected mortality of the seedlings, especially

those of Lythrum. It is pointed out that before this setting up the whole experiment was started with young seedlings in the second leaf stage. The mortality rate was very high in the 8°C. treatment, as high as 80% in Lythrum and up to 30% in Epilobium, while only 5 to 6% in the 18°C. treatment. The whole set-up was discarded and the experiment started again with seedlings in a more advanced stage of growth.

All the conditions were similar in both the phyto-trons, i.e. 80% relative humidity, 16-hour photoperiod and 1200 F.C. light intensity, except that one was set at 8°C. and the other at 18°C. temperature. Standard nutrient solution used in the experiment was replaced every two days in the 8°C. treatment, but in the 18°C. treatment the boxes were topped up after every 24 hours because of excessive loss due to plant size and the high transpiration rate. In addition to the initial harvest at the time of transplantation, a series of six other harvest were made with ten replicates per species, per treatment, per harvest and the data were collected as in the previous experiments.

The experiment was started in May 1967.

Observations

The morphology of the plants was studied at each harvest. The extent of development of the plants at harvest two and harvest five is shown in Plate 14 and Plate 15.

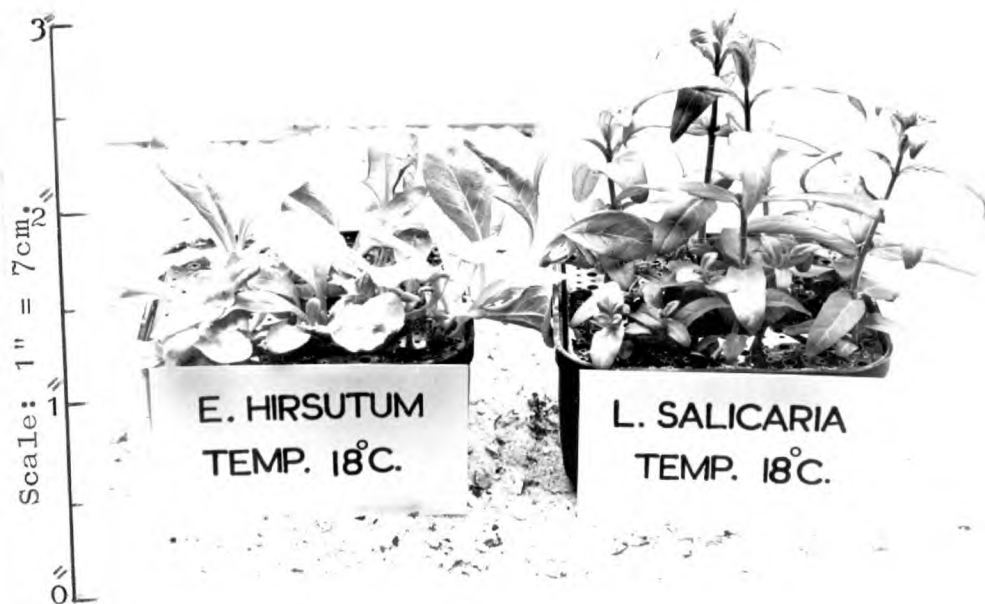


PLATE 14. Effect of different temperature regimes on growth form of the plants. (Harvest II. i.e. after 30 days in treatment.)



PLATE 15. Effect of different temperature regimes on growth form of the plants. (Harvest V..i.e. after 75 days in treatment.)

respectively.

At the final harvest Epilobium, in the 8°C. treatment developed into characteristic overwintering, prostrate rosette forms, though much smaller than those produced in the short-day treatment; and the normal long-day forms (though much smaller in size) were developed in the 18°C. treatment. Lythrum plants in the 8°C. treatment were extremely reduced, deformed and crumpled, but in the 18°C. treatment normal flowering plants were produced.

The two species responded differently to the low temperature. While growth was suppressed in Lythrum there was a great reduction in growth in Epilobium, as shown in the plates. In most of the Lythrum seedlings the leaves became yellowish after a week's treatment and growth was negligible in the first harvest, while Epilobium was well adjusted after the first week of treatment and the growth response was well marked in the first harvest, and in the later harvests growth was very regular and uniform. At the third harvest the plants were prostrate and extremely leafy. The stem at this stage was weak and greatly reduced with all the leaves crowded on it. The sub-sessile leaves had their petioles twisted in such a way as to expose their oblongly-rounded blades to the light. The mature leaves were broadly oblong, thick, soft, fleshy, devoid of hairs and a very light green. At the time

of the final harvest the stem was also thick, fleshy and 8.4 (± 0.6) cm. long with ten pairs of fully expanded leaves, of which the lower most was completely decayed, and some other leaves showed signs of chlorosis (Plate 15). The rhizome initials were visible at the time of harvest four and at the time of the final harvest two to three thick, small rhizomes per plant were present. Some plants had also developed one to two reduced axillary shoots in the axils of the lower leaves.

Growth was very slow in Lythrum in the 8°C. treatment. The stem did not show any elongation over the initial stage and was 3.6 (± 0.8) cm. long with six to seven pairs of leaves at the final harvest. The leaves were thick, green irregularly enlarged and variously contorted and almost all the leaves showed restricted chlorosis, (Plate 15). The primary root was very thick at this time.

In the 18°C. treatment growth was very slow in Epilobium. At the final harvest the plants were 40 (± 3.6) cm. long and the main stem had developed fifteen to sixteen pairs of fully expanded leaves. Axillary shoots were reduced and suppressed, however, the plants had developed four to five long, slender rhizomes. The leaves were thick, coriaceous, hairy and bright green. The lower two pairs of leaves were completely crumpled and yellow at the time of the last harvest, and many of the pairs of lower leaves had whitish, chlorotic

spots on their surface. The stem was also comparatively soft and hairy. None of the plants produced any flower buds in the duration of the experiment.

Lythrum, on the other hand, had nineteen to twenty pairs of leaves and fully expanded floral bracts on the main stem of the 64 (± 3.8) cm. long plant with up to eight fully developed side shoots in the axils of the lower leaves, while those in the axils of the upper leaves were reduced and suppressed, (Plate 15). The leaves were thin, soft and green.

While Epilobium did not produce any flowers during the course of the experiment in the 18°C. treatment, in Lythrum, at the time of the last harvest, 120 flowers per plant, on average, were present. In addition, the course of morphogenetic differentiation was very different in the two species in the early stages of development. It can be seen from Plate 14 that in the 18°C. treatment, up to the third harvest, Epilobium plants were prostrate with reduced, weak stems and large leaves, while the Lythrum plants were upright with moderately long stems. Moreover, it is noteworthy that Epilobium plants, in both the treatments, passed through similar phases of development, i.e. a prostrate, rosette growth form in the early stages.

Results

Dry weights and leaf area

Fig. 89 shows that in both the species there is an increase in dry weight with time in each temperature treatment. It can be noted that there is, relatively, a much greater reduction in the dry weight gain in Lythrum than in Epilobium in the 8°C. treatment when compared with their respective controls in the 18°C. treatment. The contrast is such that the Epilobium plants in the 18°C. treatment have a dry weight double that of those in the 8°C. treatment, but in Lythrum it is 24 times higher in the plants in the 18°C. treatment when compared to their 8°C. treatment forms. Of the two species in the 8°C. treatment, the dry weight in Epilobium is ten times that of Lythrum. Conversely, in the 18°C. treatment, after an initial advantage in Epilobium, there is a gradual increase in the dry weight of Lythrum, which is very marked in the final harvest.

The increase in leaf area with time (Fig. 90) follows a similar pattern to that of the dry weight increase. It is noteworthy that at the lower temperature the reduction in leaf area is more marked than the reduction in dry weight. In Lythrum it is 45-times less and only 3-times less in Epilobium when compared with their respective forms at the high temperature. But, at the high temperature, after an

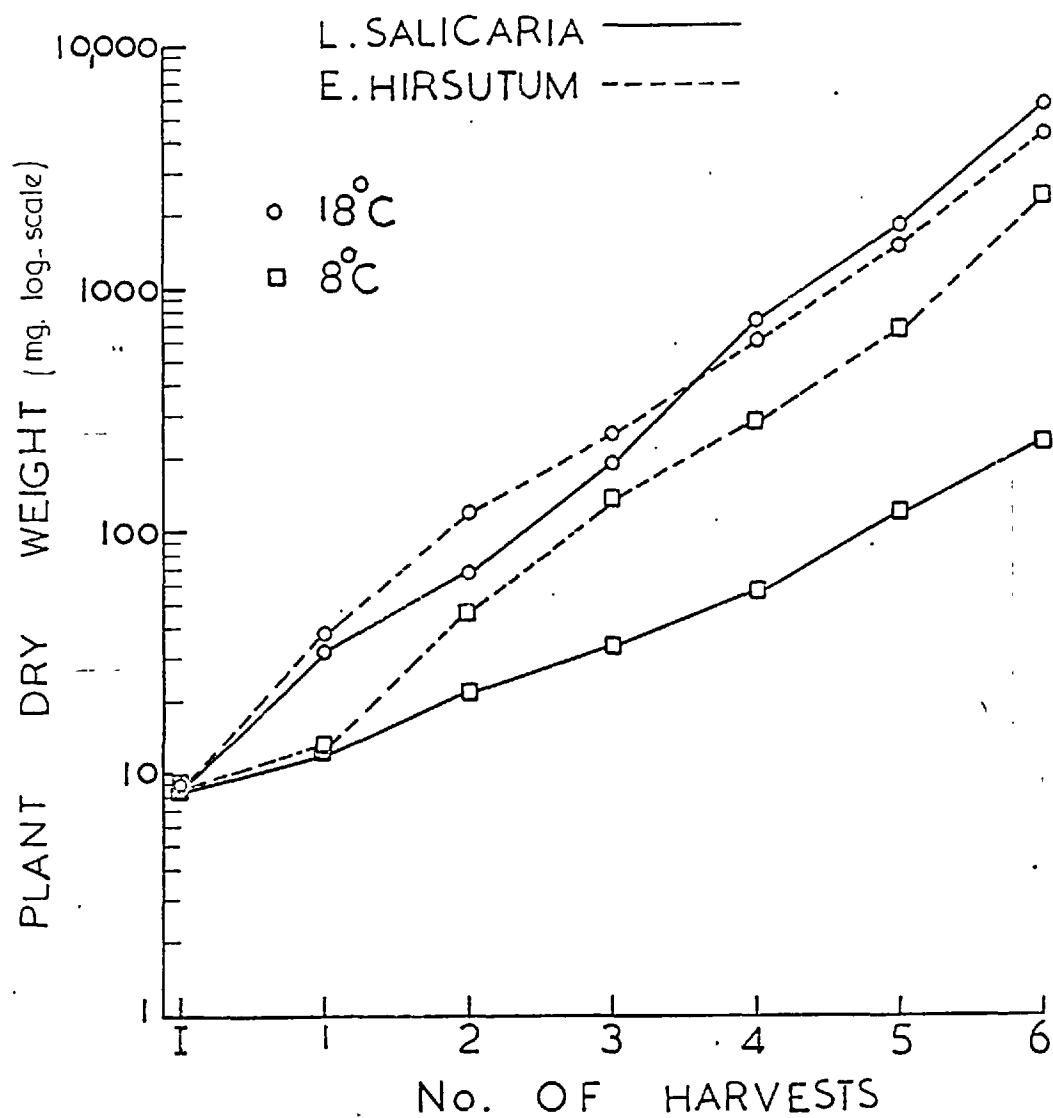


FIG. 89. Effect on increase of plant dry weight with time of different temperature regimes. (I = initial harvest)

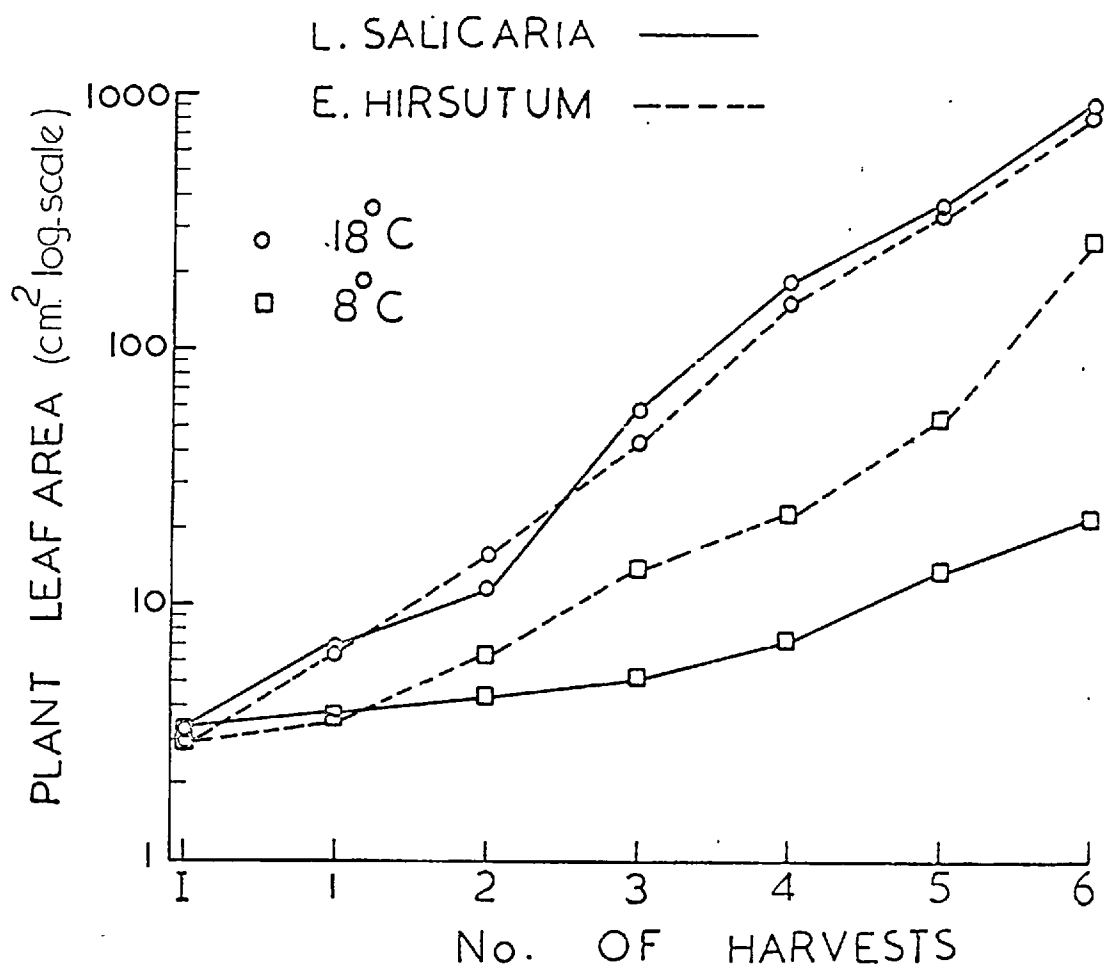


FIG. 90. Effect on increase of plant leaf area with time of different temperature regimes.
(I = initial harvest)

initial adjustment, Lythrum maintains a higher leaf area than that of Epilobium.

This trend, of a great reduction in Lythrum at a low temperature and a better performance at a high temperature when compared with Epilobium, can also be seen from the study of comparative growth rates (Fig. 91) calculated as the percentage dry weight increase over the initial harvest.

Mean unit leaf rate

The mean unit leaf rates, calculated for between harvest intervals (Fig. 92), show a tendency of marked increase in unit leaf rate in Lythrum, compared with Epilobium, in the last interval in the 18°C. treatment. On the other hand, in the 8°C. treatment the values of Epilobium are markedly higher than those of Lythrum at all the intervals except the first one, and in the last four intervals the values are also higher than those of Epilobium in the 18°C. treatment.

~~The values of mean unit leaf rate calculated from the initial to each successive harvest (Fig. 93) show the contrasting response of the two species to different temperatures. In Epilobium, after the second interval, the values are markedly consistently higher in the 8°C. treatment than those of the 18°C. treatment. Conversely, in Lythrum the values are markedly higher in the 18°C. treatment than those of the 8°C. treatment.~~

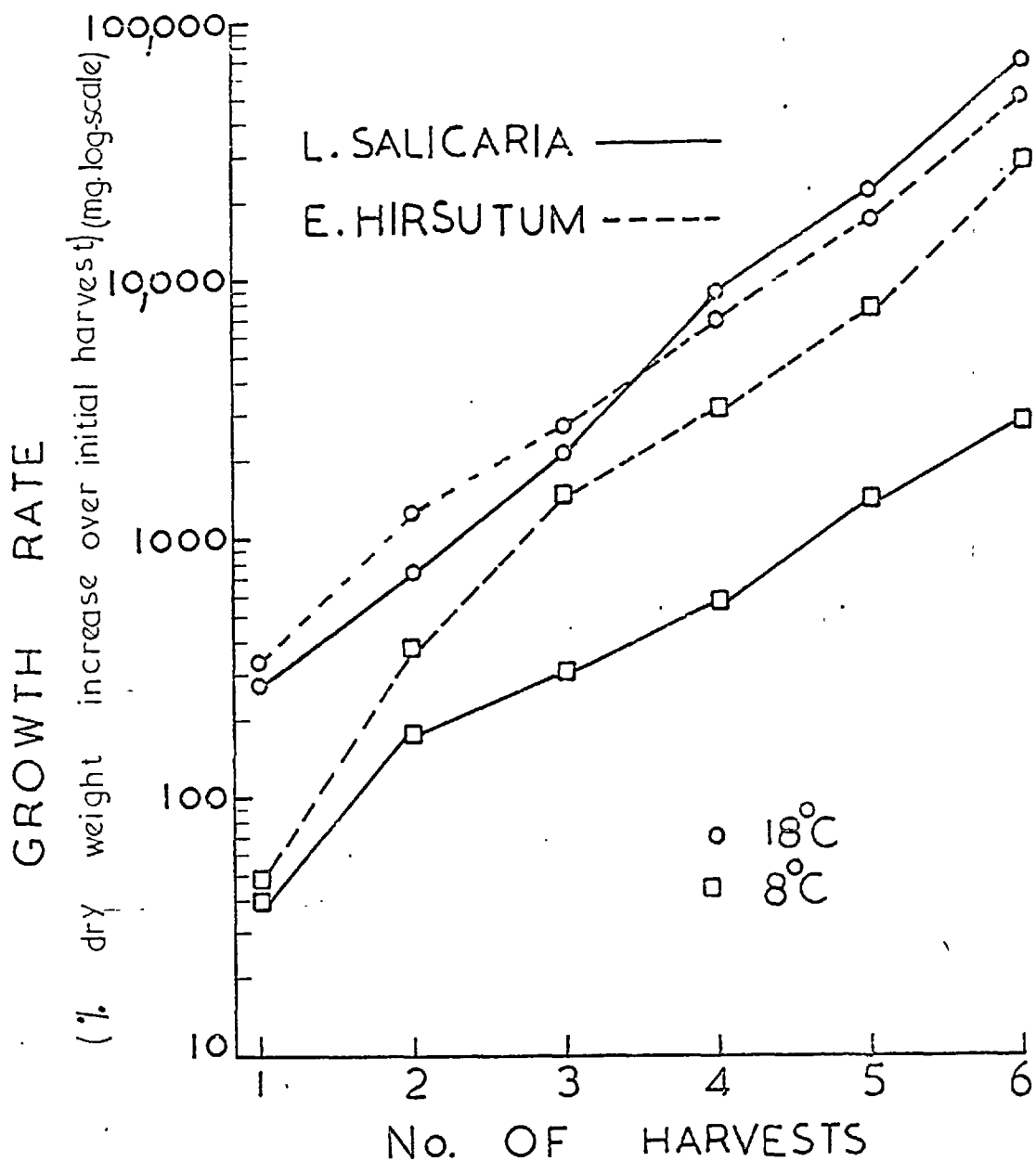


FIG. 91. Effect of different temperature regimes on growth rate. Percentage increase dry weight time from an initial harvest to each successive harvest (i.e., $H_1 - H_I$, $H_2 - H_I$, $H_n - H_I$)

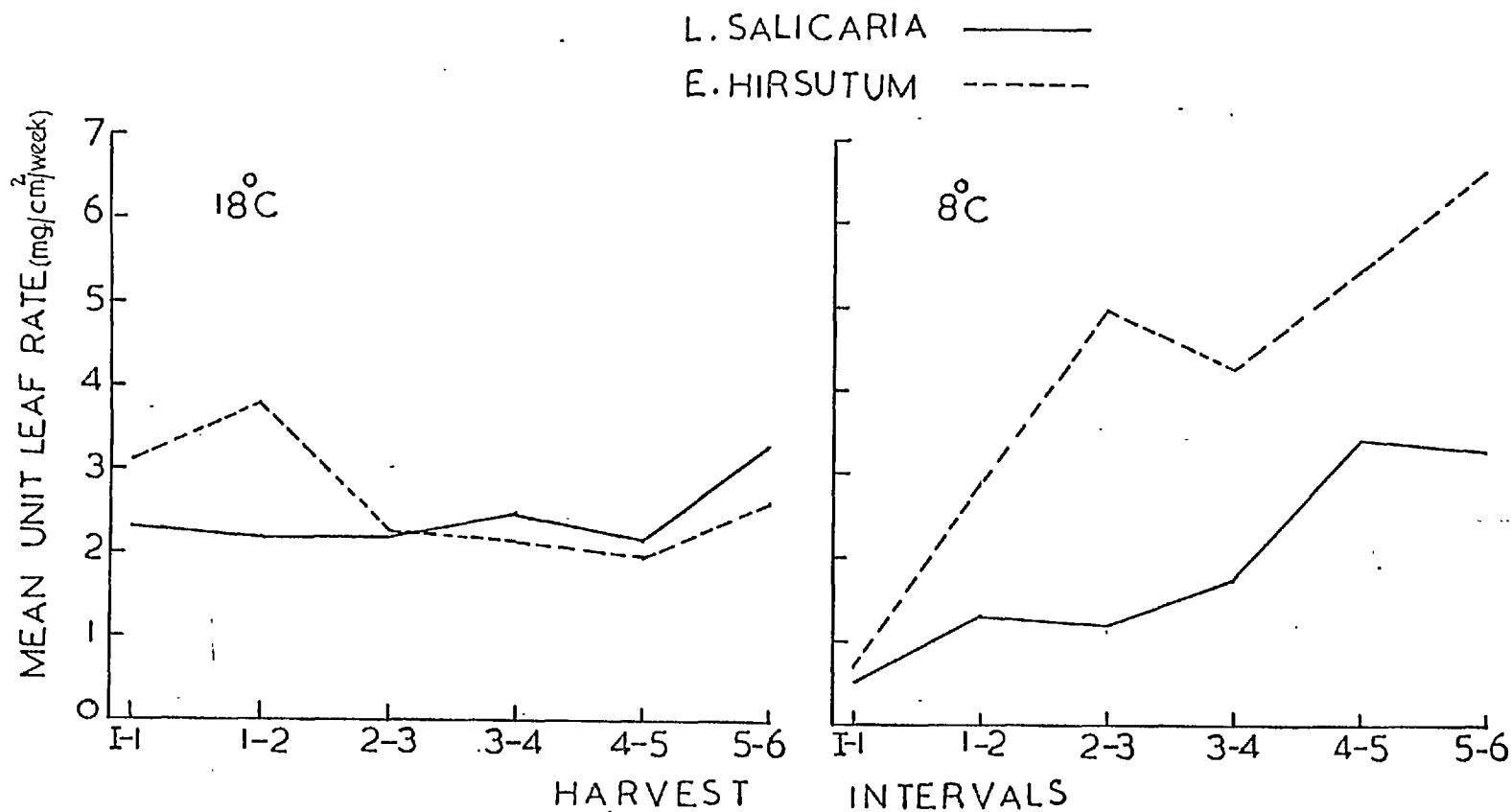


FIG. 92. Effect of different temperature regimes on mean unit leaf rate calculated for between the harvest intervals. (I = initial harvest)

Ratio of mean relative growth rate to mean
relative rate of leaf area increase

Fig. 94 shows that in the 18°C. treatment both species follow a similar pattern of α values. In the beginning there is a relatively greater leaf area increase than dry weight increase so there is a decline of α values, but later there is a gradual rise in the values because of a relatively greater increase in dry weight than of leaf area. On the other hand, in the 8°C. treatment in Epilobium there is a continuous and gradual decline of α values due to the relatively greater increase of leaf area compared with the dry weight increase. But in Lythrum, after an initial rise in the values, there is a sharp decline after which the values become more or less constant in the last two intervals.

Root/shoot ratio

Fig. 95 shows that the pattern and, to some extent, the values of the root/shoot ratio are similar in the two treatments of Epilobium, but in Lythrum they follow different patterns. While there is a gradual decline in the values in the 18°C. treatment there is an irregular rise in the 8°C. treatment. The pattern of the root/shoot ratio is also contrasting in the two species at the low temperature. It seems probable that the increased root proportion in Lythrum in the 8°C. treatment is not of an adaptive nature but because

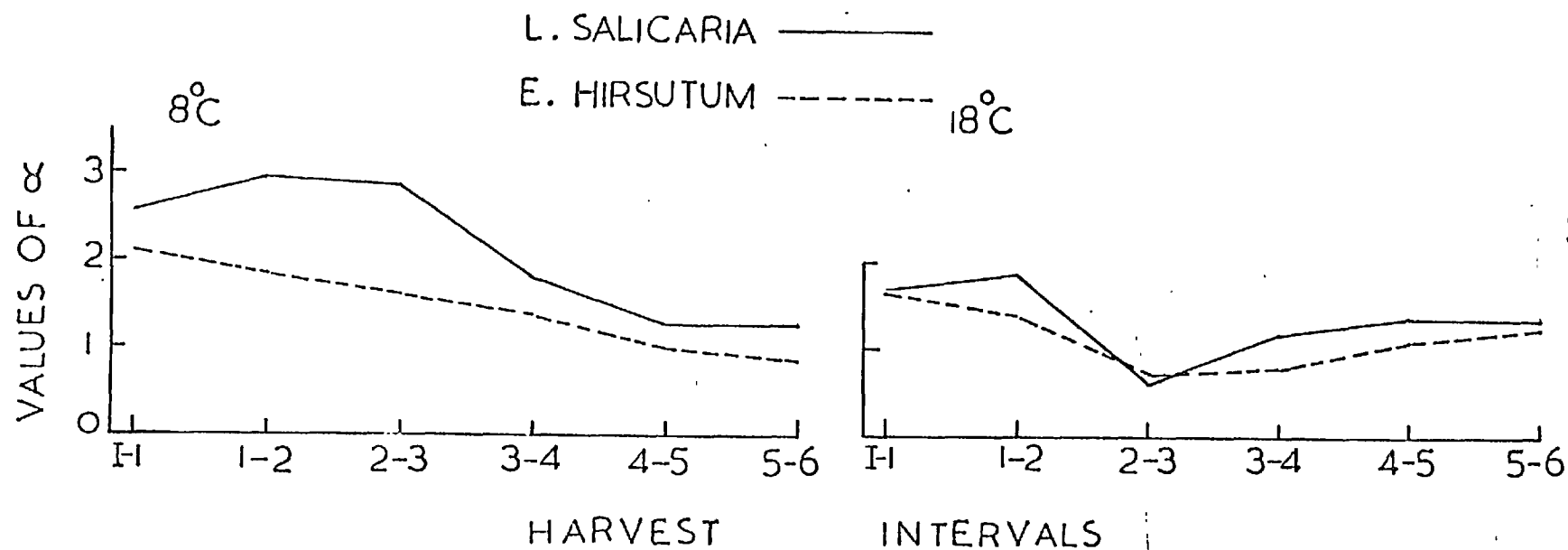


FIG. 94. Effect of different temperature regimes on ratio, mean relative growth rate to mean relative rate of leaf area increase (α).
 (I = initial harvest)

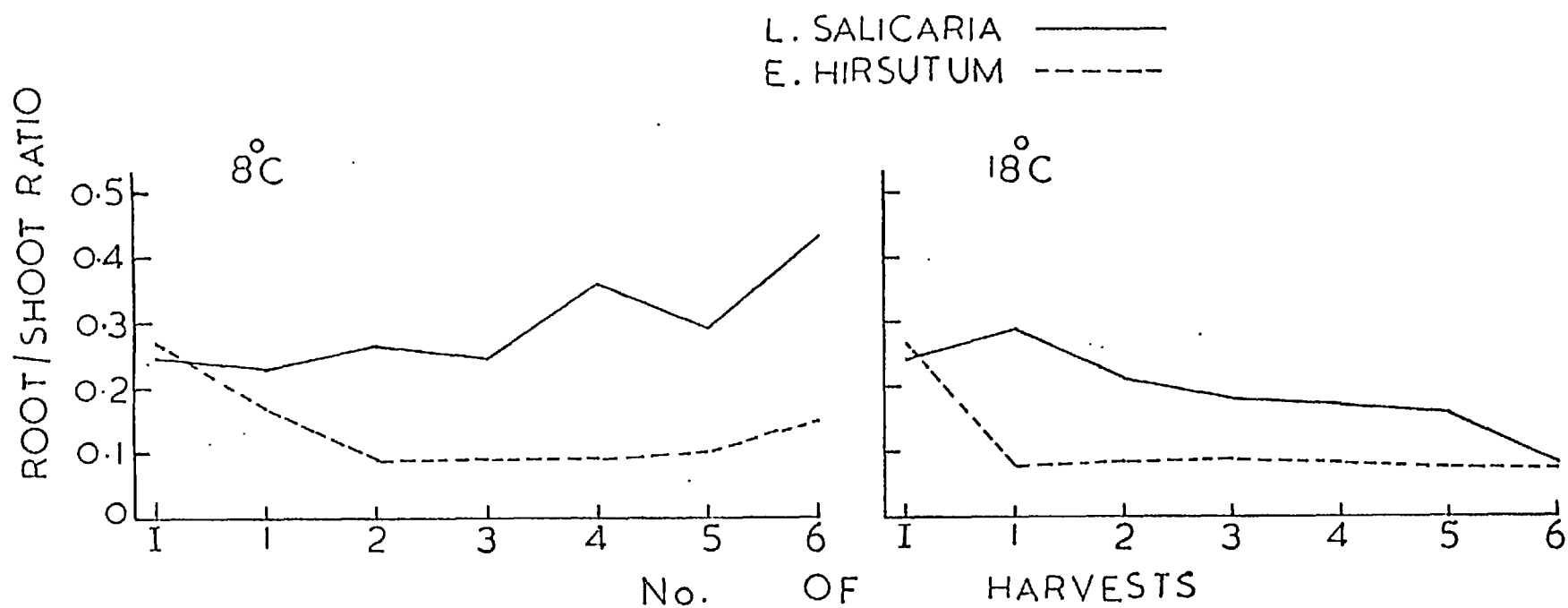


FIG. 95. Effect of different temperature regimes on root/shoot ratio.
 (I = initial harvest)

of the extreme reduction of shoot.

Percentage proportional distribution of
the dry matter

Fig. 96 shows that in the 18°C. treatment the percentage proportional distribution of dry matter to root, stem and leaves is very similar in both the species. The roots constitute the lowest proportion in both plants although the values of Lythrum are almost twice those of Epilobium except in the last harvest. With time there is an increase in the stem proportion principally at the expense of the leaf proportion. This increase in stem proportion is very regular in the case of Lythrum but irregular in Epilobium.

In the 8°C. treatment the percentage proportion of leaves remains similar in both the species with time, but not for Lythrum in the last harvest. While in Epilobium there is an increase in the stem proportion at the expense of the root proportion, in Lythrum it is the reverse as root proportion increases at the expense of the stem proportion and in the last harvest the leaves also contribute to the increase in the root proportion.

Discussion

The results presented here show that there was a marked difference in the two species in their growth response to the low temperature. The contrast in the response was

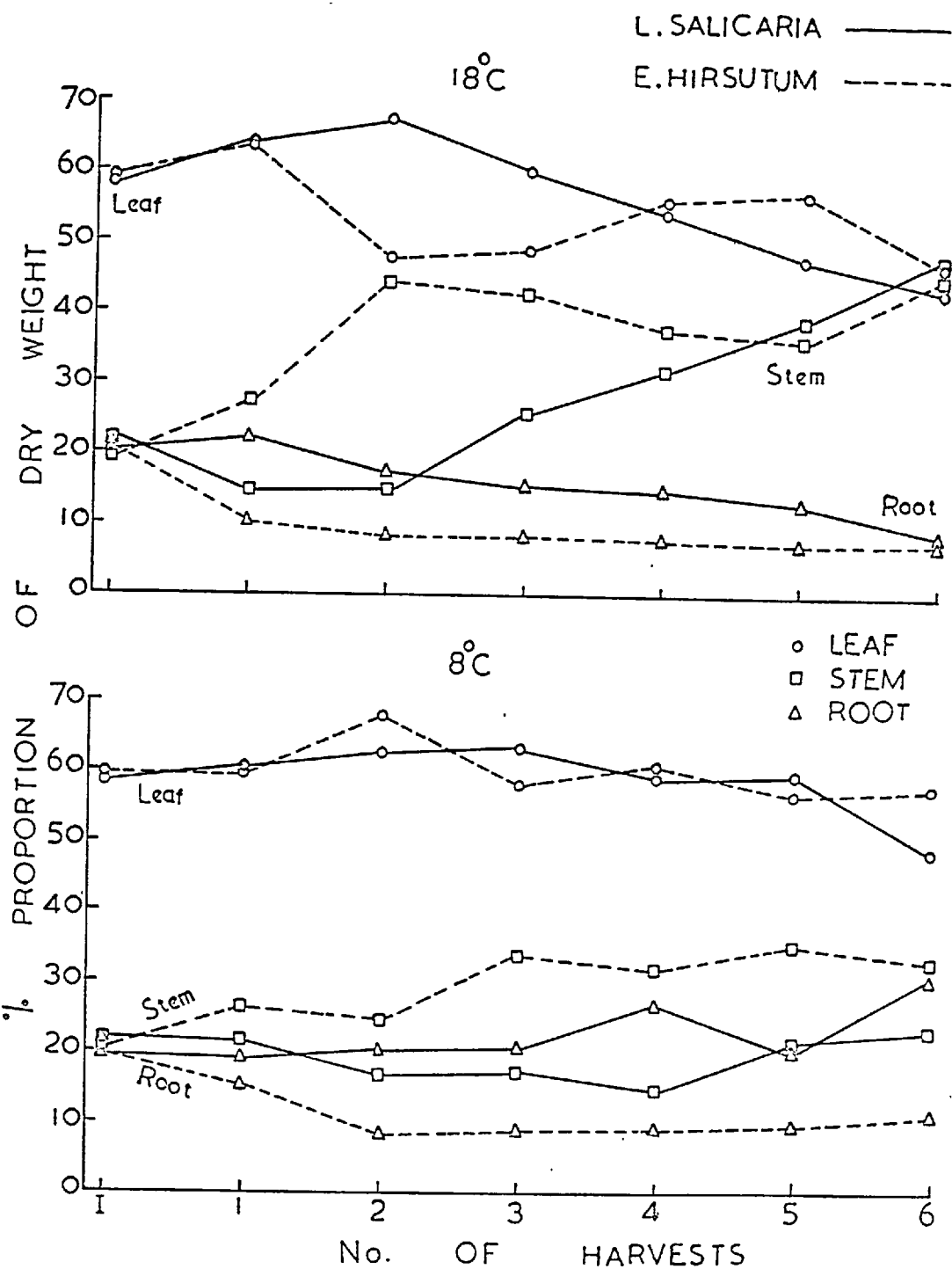


FIG. 96.

Effect of different temperature regimes on percentage proportional distribution of dry matter to leaves, stems and roots.
(1 = initial harvest)

such that there was an extreme reduction or suppression of growth in the case of Lythrum while Epilobium developed into small rosettes. In Lythrum both the leaf expansion and stem elongation were severely curtailed, but in Epilobium the leaves were relatively less affected by the low temperature and only the stem elongation was suppressed. On the other hand, in the 18°C. treatment growth was much better in the case of Lythrum compared with that of Epilobium in terms of dry weight gain, growth rate and mean unit leaf rate.

It is interesting to point out that in Epilobium, although growth was much better in the 18°C. treatment than in the 8°C. treatment in terms of dry weight gain and growth rate, the mean unit leaf rate was markedly higher in the 8°C. treatment. Also, it was the highest unit leaf rate in both species in all the treatments.

It is clear from these results that although there is an overall reduction in the performance of Epilobium at the low temperature, the plant is most efficient in terms of mean unit leaf rate; conversely, at the high temperature, Lythrum in comparison with Epilobium, is the most efficient in all respects.

From the above discussion it is suggested that the Q10 of growth is far higher in the case of Lythrum compared with Epilobium, as the dry weight in Lythrum was 24-times

higher in the 18°C. treatment than the 8°C. treatment, while in Epilobium the dry weight in the 18°C. treatment was only double that of the 8°C. treatment. Furthermore, it is worthy of note that, associated with the increase of growth rate with the 10°C. rise in temperature, is a shortening of the duration of the growth period, as shown by the flower formation in Lythrum, thus completing the whole life-cycle in the duration of the experiment, while Epilobium failed to produce flowers. Conversely, the low Q₁₀ of Epilobium would imply a much better growth of this plant at the low temperature compared with Lythrum.

On the basis of these results it can be concluded that there is a greater probability of Epilobium being capable of growing as a reduced, leafy, prostrate, plate-like plant in winter, in nature, while Lythrum would not make any growth at all. On the other hand, at the high temperature Lythrum would show much better, quicker and efficient growth than Epilobium. Thus, in the event of competition at high temperatures Lythrum will have an advantage over Epilobium and may completely suppress its growth and development.

This ability of Epilobium to grow at low temperatures is also reflected by the history of natural adaptation of this plant. It can be said that growth habit plays an important part in determining the influence of temperature

upon each species. While Epilobium, for countless generations, is adapted to certain extremes of cold and heat as well as to a seasonal sum of temperatures during the completion of its life-cycle, Lythrum is adjusted to growing only in high temperature conditions. It would seem that these temperature adjustments became so deeply impressed in the protoplasm of a species that the result is a more or less fixed habit as regards the temperature. Thus, the much better growth in Epilobium at a low temperature is because of its adaptation to grow at low temperatures, but Lythrum, adapted to grow at high temperatures, fails to grow at a low temperature.

Because of the great efficiency of growth at the low temperature, it seems probable that the growth and development in Epilobium is a gradual, phased and integrated process, in that the plant develops to a particular stage at a particular temperature, after which temperature becomes a limiting factor. Any further increase in temperature would increase growth, and the temperature for flower and fruit formation is much higher than 18°C. It is interesting to note that there is a parallel between the temperature control of growth and the photoperiod control of growth described in Experiment VI, and this is in accordance with the habitat adaptation of this plant, as it passes through extremes of

minimum and maximum temperatures during its life-cycle in Britain.

On the other hand, in the case of Lythrum growth is abrupt and fast. Like germination and photoperiod responses, the response to temperature is again an all or nothing phenomenon as in the unfavourable temperature there is complete suppression of growth, but in the lowest favourable temperature full growth and development of the plant takes place.

It is probable that in Epilobium winter growth is a necessary phase to be endured, and may be a stimulation to renewed growth, but in Lythrum winter is a recurrent catastrophe. Since temperature influences the plant growth by affecting various physico-chemical and physiological processes, so any decrease in the temperature would slow down the rate of these processes rather than altering the course of physiological reactions. Thus the temperature is related to the inherent growth rate of the plant in the case of Epilobium, and efficient growth at low temperatures involves some obscure protoplasmic characters which result in the low cardinal points of various processes. Daubenmire (1959) pointed out that the succulent nature of the leaves and stem in many young plants (as is the case of Epilobium in this experiment) is an adaptation to low temperature growth as the

protoplasm develops low structural viscosity. The free water contents decrease and, at the same time, soluble proteins and sugars increase. Similarly, Turvill (1948) also pointed out that the majority of plants retaining green foliage during the winter have sugar and not starch as their main carbohydrate food reserve.

Lastly, it is pointed out that in the 18°C. treatment Epilobium passes through a leafy prostrate stage of growth similar to that of the final stage of growth in the 8°C. treatment. Most probably this prostrate growth form is an inherent phase in the growth of Epilobium at all temperatures. Since, under natural conditions a plant passes through extremes of temperature, it would seem that this form of growth is an adaptation to grow at low temperatures, as it is of considerable advantage to allow a plant to exploit the warm ~~sub~~stratum of air which lies next to the earth's surface and thus carry on photosynthesis at times when taller shoots would be too cool for this function.

Experiment XIV

Competition and survival of the species in
high and low nutrient regimes at a constant
temperature of 25°C.

It was suggested in the previous experiment that in the event of competition between the two species at a high temperature, Lythrum would be more successful than Epilobium due to its faster rate of growth. Similarly, a suggestion was made in Experiment X (Effect of different dilutions of a standard nutrient solution on growth) that if Lythrum and Epilobium were to grow together on the nutrient-poor soils, Lythrum would show a better growth than Epilobium and might even suppress the growth of the latter leading to its elimination.

Harper (1964) has shown already the danger of such assumptions unsupported by experiment so that this experiment was designed to verify these two hypotheses under controlled conditions, and as an attempt at understanding the mechanisms of competition and survival when the species are grown singly or mixed together. The experiment was carried out in the heated greenhouse of the "Chelsea Physics Garden", London, at a carefully controlled constant temperature of 25°C.

Experimental procedure

The seedlings of both species were raised to a third

leaf stage, as in the previous experiment. Two sets of wooden tanks, each consisting of six black polythene lined units, were laid out on the central and side bench of the greenhouse. Each unit had internal dimensions of 2ft. x 1ft. x 1ft. and a capacity of 40 litres. A common wood-mounted black polythene top was used for each set and in each unit 1152 (24 x 48) holes, $\frac{1}{2}$ in. apart, were pierced through the polythene. One set was filled with the standard nutrient solution and the other with a x20 dilution of the same solution (S/20). There were four, 400 watt, Philip bulbs on the top of each set of tanks and the illumination was controlled for 16-hours a day. In each unit 1000 seedlings were transplanted. The seedlings were transplanted into three different categories, i.e., two categories, one each of pure species and the third of mixed. The mixed unit consisted of 500 seedlings of each species (500 + 500 = 1000) transplanted alternately. Thus, in each treatment of nutrient solution there were two replicates of each category of transplantation. The units with pure and mixed transplantations alternated with one another. These three types of transplantations, in each treatment, will be referred to as the pure stands of each species and the mixed stand.

In the standard treatment, tanks were refilled with nutrient solution every week and in the S/20 treatment the

whole solution was replaced every fortnight. A system of aerating tubes was passed through the various tanks as in the previous experiments. The number of survivors were noted at fortnightly intervals, in each treatment, in each replicate and the means were calculated. In addition to the initial harvest at the time of transplantation only one final harvest was made at the end of the experiment. The data were collected in terms of the mean number of survivors, the mean biomass of each category of transplantation and the dry weight of shoot and root.

The setting up of the experiment was completed on 15 November, 1968 and the final harvest was made six months later on 15 May, 1969.

Observations

The general appearance of the plants, in both the treatments, after eight weeks ^{from} of transplantation is shown in Plate 16. Plate 17 shows details of the three different categories of transplantations in the S/20 treatment. Two weeks after transplantation seedlings of both species, in each treatment, showed a favourable response and started growing equally, although growth was less marked in the S/20 treatment. A few weeks later, in the standard solution the plants started to show differential growth, so far as their height was concerned. At this stage the Epilobium plants



"Standard"
solution

(Only 3
of the 6
tanks are
visible
in the
photo-
graph.

Epilobium

Lythrum



"S/20"
Dilution

PLATE 16. Inter and intraspecific competition in a standard solution and its S/20 treatment. (Photographed after 8 weeks from transplantation).

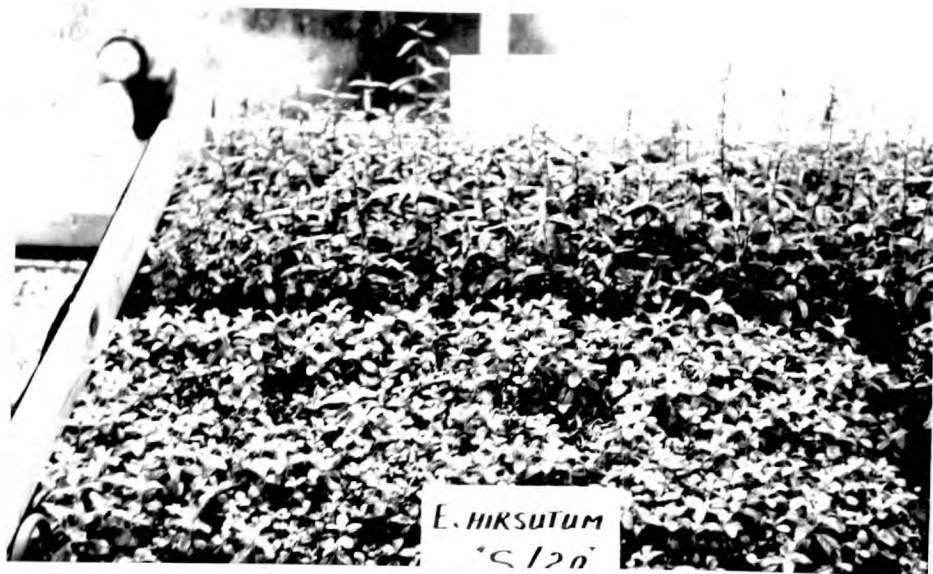


PLATE 17. Interspecific competition of *Epilobium hirsutum* and *Lythrum salicaria* in the S/20 dilution of a nutrient solution. (Photographed after 8 weeks from transplantation).



PLATE 17 (cont.) Intraspecific competition
between E. hirsutum and L. salicaria
in the "S/20" dilution of a nutrient
solution. (Photographed after 8 weeks
of transplantation).

showed a tendency of increasingly prostrate growth with large, oval leaves, while the Lythrum plants were erect with slender, upright stems.

Almost at this stage, many Epilobium plants in the pure stand started decaying. Decay was very prominent in the centre of the stand from where it started spreading outwards. Conversely, in the pure Lythrum stand the plants showed more or less uniform growth and, unlike Epilobium, there was no decay of plants in the centre of the stand. But, since the growth was very unequal there was extreme reduction in the growth of some seedlings, especially in the centre where these consisted of only a small, pale green weak stem and reduced leaves, while a few other plants were very well developed and became conspicuously dominant in the stand.

In the mixed stand the Lythrum plants were much bigger than those in the pure stand, while the Epilobium plants were conspicuously prostrate and in the centre of the tank the majority of them were decaying fast. Eight weeks after transplantation almost all the Epilobium plants were completely wiped out (except for two to three plants towards the open side of the tanks) by the aggressive, fast growing Lythrum plants. The soft shoots of Epilobium were rotten due to fungal attack and were buried under the Lythrum plants.

By this time, Lythrum plants in the pure stands

were also enormously developed and had started spreading laterally towards the adjoining stands, thus shadowing and covering the low-lying Epilobium plants. In each tank a few plants had a commanding lead over the other plants, being highly developed and profusely branched and tall; but the majority of the plants consisted of only one tall, unbranched, flowering shoot. There were also many short to medium sized brown shoots, completely devoid of leaves except for a few old ones, buried among the tall flowering shoots. A few weeks later Lythrum had completely spread all over the area and the whole set of six units in the standard treatment appeared to consist of one, big Lythrum stand with a few surviving Epilobium plants towards the periphery, as shown in Plate 18.

All the tall shoots of Lythrum in the pure and mixed stands flowered. The number of flowers was highly variable, depending upon the plant size i.e. from 1245 to only 89, and most of these developed into fruits.

All the surviving Epilobium plants also flowered (up to 18 flowers with 11 fully ripened fruits), but developed only a few side shoots in the upper half, while all the leaves and branches in the lower half were completely decayed due to fungal attack. The tall dominant Lythrum plants had, on average, a height of 112 cm. with up to fifteen side shoots, and amongst the rest the majority of the plants had an average



Lythrum
salicaria

Epilobium
hirsutum

PLATE 18. Lythrum salicaria spreading over the whole area with a few surviving Epilobium hirsutum plants towards the periphery of the tank.
(Photographed 15 weeks after transpl^antation).

height of 65 cm. with a few suppressed side shoots. The surviving Epilobium plants were some 80 cm. tall.

In the S/20 dilution Lythrum seedlings of the pure stand grew very uniformly in the first three weeks after transplantation, but later there was a gradual reduction in the number as many plants started dying due to overcrowding. Usually, it was the alternate or every third plant that died, so most of the plants showed quite uniform growth except for some, rare, tall plants. The range of size in general was 30 to 36 cm. The plants produced twelve to thirteen pairs of leaves on average, and of the survivors seventeen plants (the mean of two replicates) had developed flowers by the end of the experiment. There were 8 to 22 flowers per plant.

In the mixed stand, in this treatment, Lythrum plants were much bigger than those in the pure stand. Up to three weeks after transplantation Epilobium seedlings showed a quite normal growth. Later on, the Lythrum seedlings started out-growing and over-shadowing them, so the growth of Epilobium was restricted and curtailed and most of them started dying. Their leaves became red, then yellow and gradually the whole plant dried up. With time, as the Lythrum plants grew bigger, the Epilobium plants started drying up very rapidly and twelve weeks after transplantation all the Epilobium plants were completely dried up and dead (Plate 19).



(a)



(b)

PLATE 19. Competition and survival under low nutrient (S/20) conditions.

- (a) Dominant L. salicaria in the mixed stand.
- (b) Patches of dead E. hirsutum plants in the pure stand.

(Photographed 24 weeks after transplantation.)

At the end of the experiment i.e. six months after transplantation, 28 plants (the mean of two replicates) were in flower and, on average, the plants were 38 cm. tall and produced up to 36 flowers per plant. However, there was no fruit formation.

In the pure Epilobium stand, a few weeks after transplantation, patches of seedlings at various spots started to decay. With time the lower four to five pairs of leaves started yellowing and drying up, and twelve weeks after transplantation more than two-thirds of the plants were dead. Most of the surviving plants had a height of 25 cm., on average, with ten to eleven pairs of leaves and, in almost all the survivors, up to eight lower pairs of leaves were reddish and decayed. There were big patches of dead plants in this stand by the end of the experiment, as shown in Plate 19. Plate 20 shows the complete set of six tanks in the S/20 treatment fourteen weeks after transplantation, and the marked difference between the Epilobium and Lythrum stands is noteworthy.

The root system of the Lythrum plants in the pure and mixed stands was well developed and the primary root was thick, swollen and woody at the base. In contrast, the root system of Epilobium in the pure stand was very poorly developed.

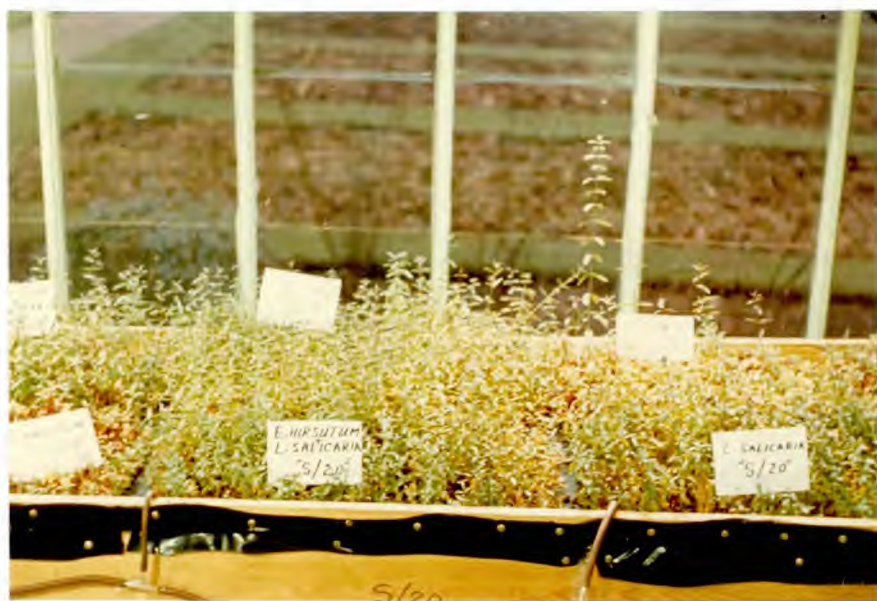


PLATE 20. Competition and survival under low nutrient (S/20) conditions. General view of 6 tanks of pure and mixed transplantations of L. salicaria and E. hirsutum, 14 weeks from transplantation.

Results

The mean number of survivors

The mean of the survivors of the two replicates, in both the species and each treatment, was taken at fortnightly intervals and is presented graphically in Fig. 97. It can be seen that in the standard solution the decline in the number of Epilobium plants in the pure stand is very rapid compared with that of Lythrum; this is also true in the case of the mixed stand.

In the S/20 treatment also, the decline in the number of individuals with time is much higher in Epilobium than in Lythrum. In the mixed stand the loss in the Lythrum plants with time is small, but twelve weeks after transplantation all the Epilobium plants perished.

The total number of survivors in both species in each treatment, along with the number of seedlings transplanted initially, is presented in the form of a histogram in Fig. 98. The percentage survival of the two species in each stand of both the treatments is also shown graphically in Fig. 99.

The Biomass

The biomass of the pure and mixed stands of both species in each treatment, along with the initial biomass is shown in the form of a histogram in Fig. 100. It is clear

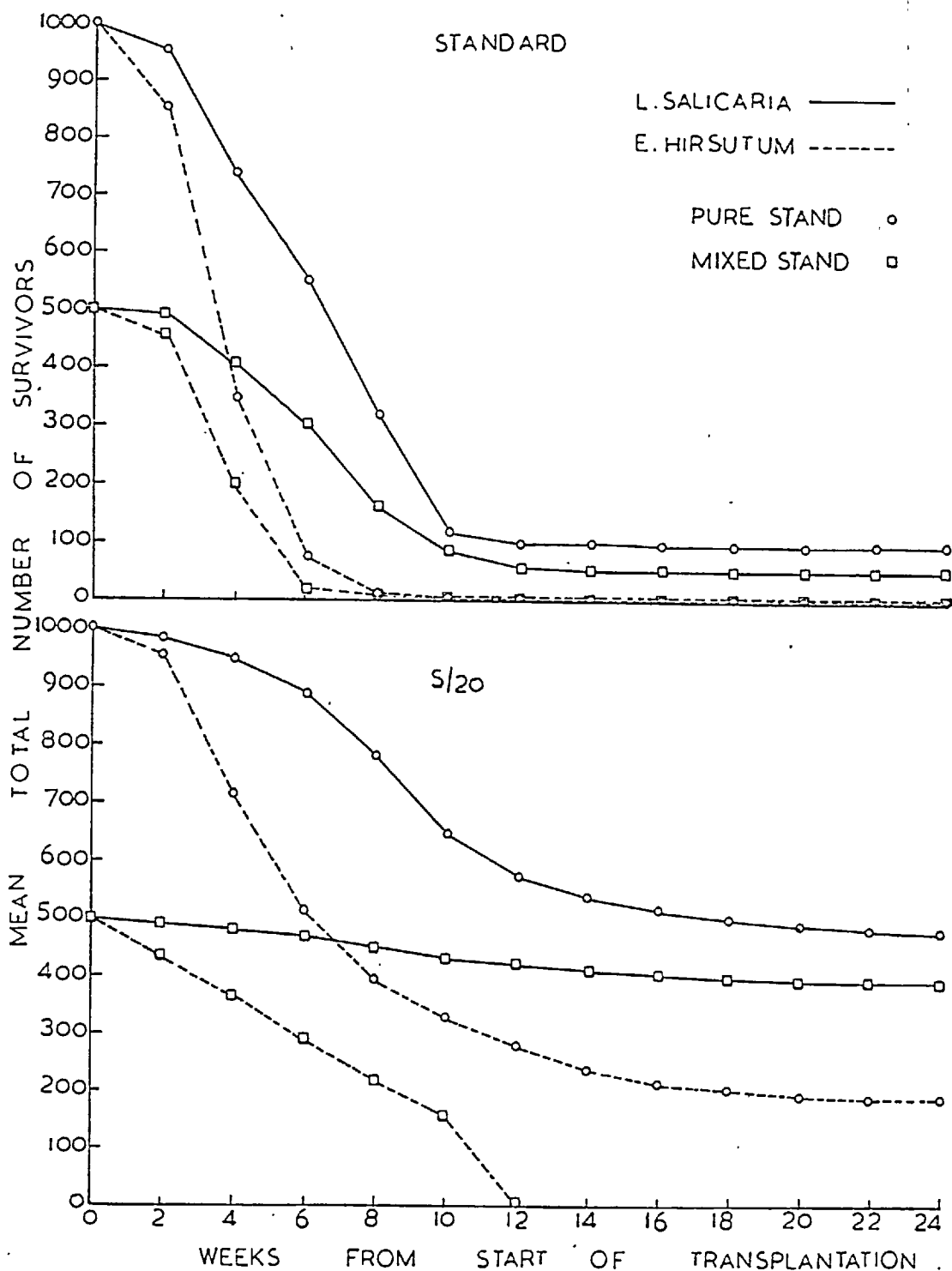


FIG. 97. Mean total number of survivors in pure and mixed species stands under low (S/20) and high (Standard) nutrient conditions at a constant temperature of 25°C. (Initial no. in pure stands = 1000; initial no. in mixed stands = 500 of each species)

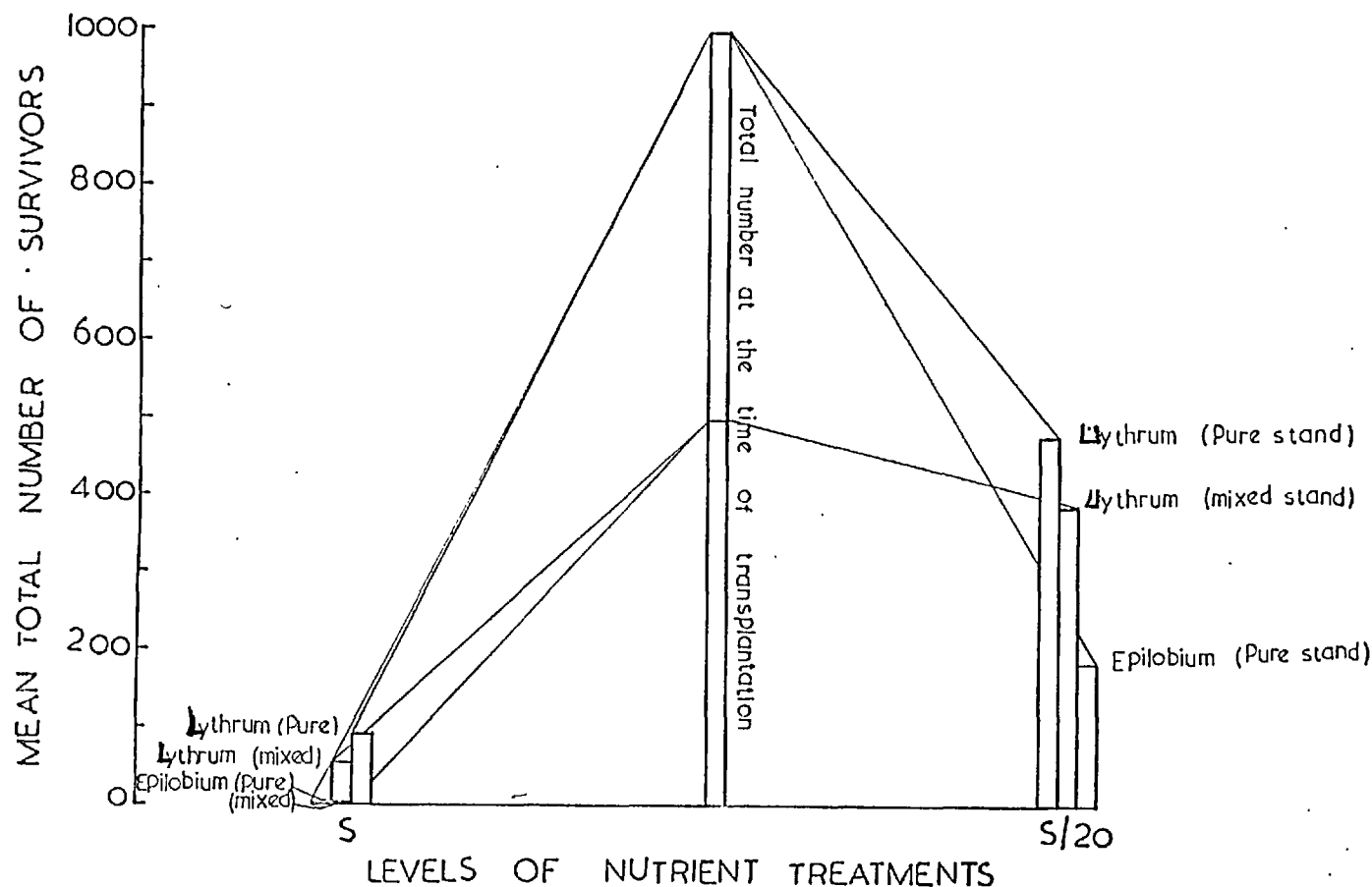


FIG. 98. Mean total number of survivors in pure and mixed species stands under low (S/20) and high (S) nutrient conditions at a constant temperature of 25°C. (Initial no. in pure stands = 1000; initial no. in mixed stands = 500 of each species)

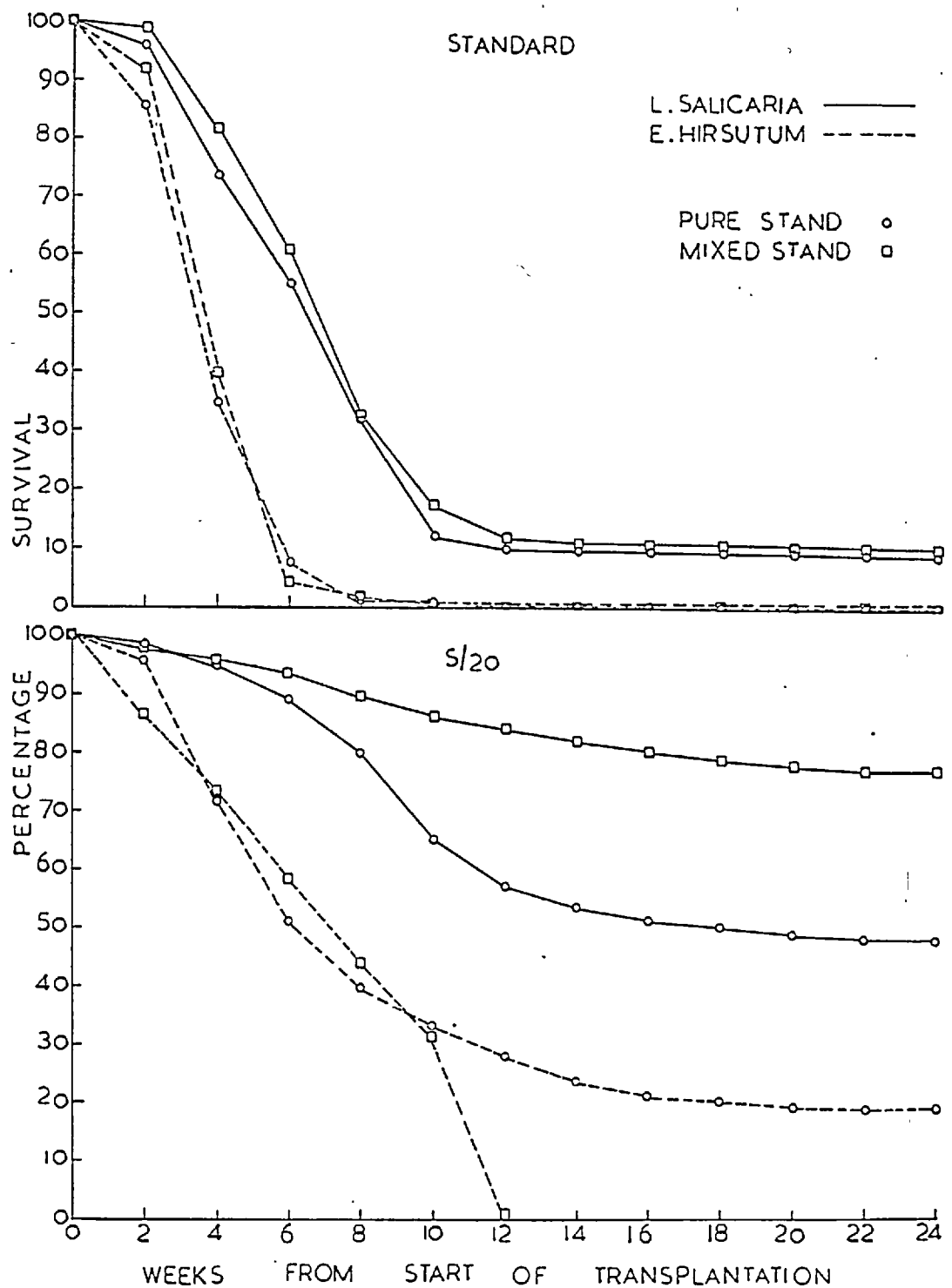


FIG. 99. Percentage survival in pure and mixed species stands under low (S/20) and high (S) nutrient conditions at a constant temperature of 25°C.

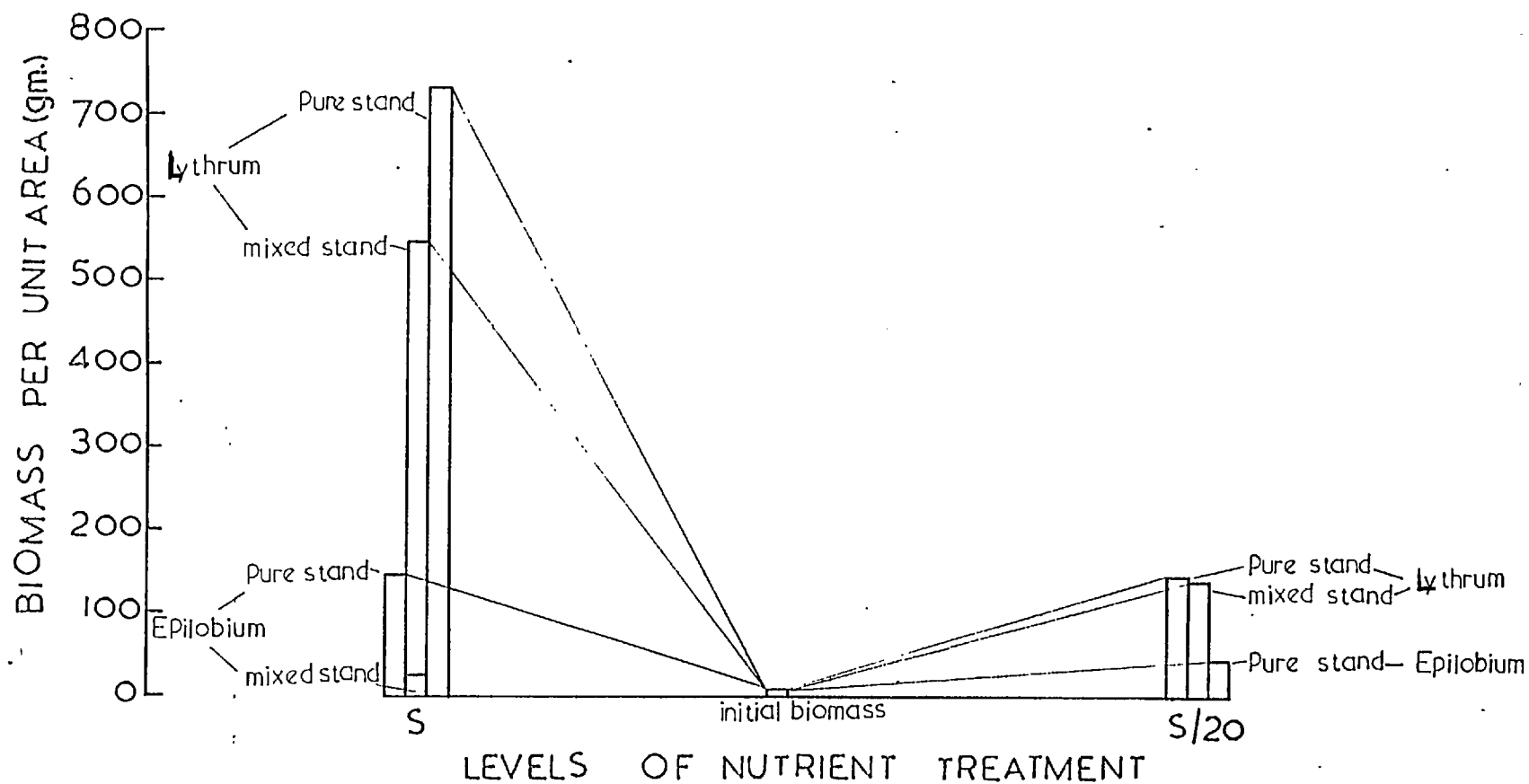


FIG. 100. Biomass of pure and mixed species stands after six months of growth in 2' x 1' area under low (S/20) and high (S) nutrient conditions at a constant temperature of 25°C.

that although the number of survivors in Lythrum is much higher in the S/20 treatment than in the standard treatment, the biomass in the unit area in the S/20 treatment is four to five times less than that in the standard treatment.

It is noteworthy that in the standard treatment the number of survivors of Lythrum plants in the mixed stand is little more than half that of the pure stand, but proportionately the difference in the biomass is not very marked. (The ratio between the mixed and pure stand is 3:4.) In the case of Epilobium the biomass of the pure stand is almost six times that of the mixed stand. Similarly, in the S/20 treatment although there are 91 more Lythrum survivors in the pure stand than in the mixed one, the biomass in the two is almost the same (being 13753gm. in the mixed, and 14415gm. in the pure stand). In this treatment the biomass of the pure stand of Lythrum is almost three times that of pure Epilobium.

The proportionately higher biomass of survivors in the case of Lythrum, in the mixed stands of both the treatments, can be attributed to the better development of the individuals, as they were more adequately spaced compared with the pure stands.

In the standard treatment, because of the overcrowding of Lythrum plants in the pure and mixed stands, some plants were dominant over others. So, three different

categories of plants were recognised, i.e. large, medium and small. The number of individuals and their dry weights, in each category, are given in Table 13.

TABLE 13. Total Number and Dry Weights of Lythrum Plants of Three Different Sizes in the Standard Solution.

(a) Pure Stand

Category	No. of Plants	Total dry Weight (gm)	Dry weight/ Plant (gm)
Large	6	259.65	43.27
Medium	36	410.40	11.40
Small	<u>51</u>	<u>61.20</u>	<u>1.20</u>
Total	93	731.25	7.86

(b) Mixed Stand

Large	4	158.80	39.70
Medium	24	329.14	13.71
Small	<u>26</u>	<u>34.06</u>	<u>1.31</u>
Total	54	522.00	9.67

It is clear that the average dry weight/plant is markedly higher in the plants in the mixed stand.

In Table 14 are given the number of survivors and their dry weights for the Epilobium plants in the pure and mixed stands in the standard solution.

TABLE 14

Plant	Stand	Total Survivors	Biomass (gm)	Weight/plant (gm)

<u>Epilobium</u>	Pure	4	144.00	36.00
<u>Epilobium</u>	Mixed	1	24.00	24.00

The higher dry weight per plant of Epilobium in the pure stand is due to the production of a large number of big rhizomes by all the surviving plants, whereas in the mixed stand, apart from small rhizome initials, the plants did not produce any rhizomes. This was probably due to the great development of the roots of the surviving Lythrum plants which filled the whole tank.

In the S/20 treatment the surviving Lythrum plants, both in the pure and mixed stands, were also variable but the large plants were not so distinct as to be recognised as a separate category.

Table 15 shows the number of survivors, biomass and average weight per plant of Lythrum and Epilobium for the

various stands.

TABLE 15 GROWTH IN $S/20$ SOLUTION.

Plant	Stand	Total Survivors	Biomass (gm)	Weight/ Plant (gm)
<u>Lythrum</u>	Pure	478	144.15	0.30157
<u>Lythrum</u>	Mixed	387	137.53	0.35537
<u>Epilobium</u>	Pure	185	46.25	0.25000
<u>Epilobium</u>	Mixed	-	-	-

It can be seen from the table that in the case of Lythrum the dry weight per plant is higher in the mixed stand than in the pure stand. The dry weight per plant in the case of Epilobium is markedly less than that of any type of Lythrum.

Root/shoot ratio

Root/shoot ratios for various stands in both the treatments as well as at the time of the initial harvest are presented in the form of a histogram in Fig. 101. It can be seen that Lythrum, in the $S/20$ treatment, shows an adaptive increase in the root/shoot ratio, while the value in the case of Epilobium remains similar to that in the initial harvest. The slight increase in the ratio can be attributed to the decay of leaves on the shoot rather than to an increase in the

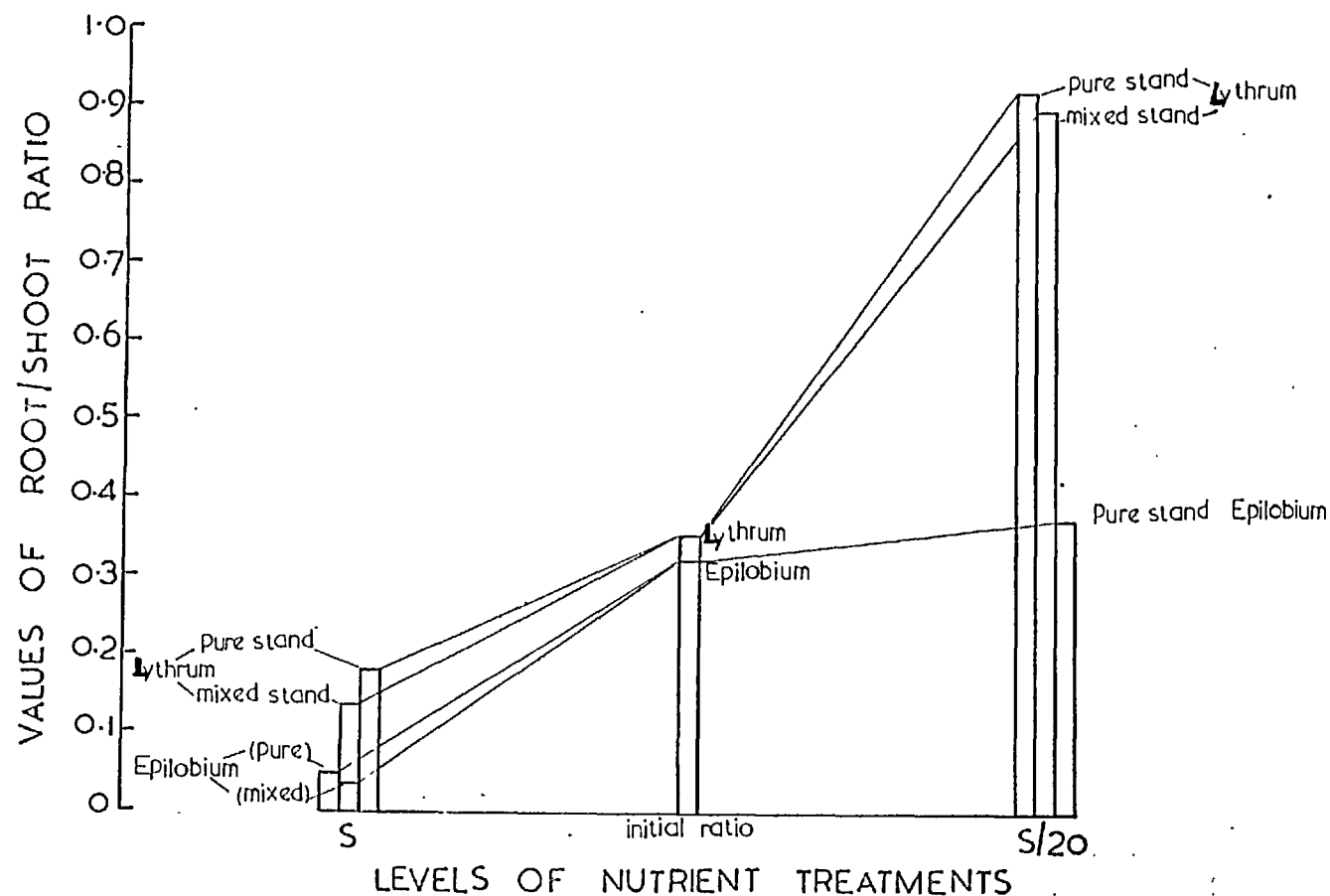


FIG. 101. Values of root/shoot ratio for initial and final harvests of pure and mixed species stands after six months of growth in a 2' x 1' area under low (S/20) and high (S) nutrient conditions at a constant temperature of 25°C.

root. Similarly, in the standard solution the value of the root/shoot ratio of Lythrum is also twice that of Epilobium.

Discussion

The results presented show that there was a greater reduction in the number of individuals in the case of Epilobium than that of Lythrum when 1,000 seedlings of each species were transplanted separately, or mixed, in unit areas in the standard solution. In the pure stands there was a 9.3% survival rate in Lythrum and only 0.5% in Epilobium. In the mixed stand there was almost 11% survival in the case of Lythrum and only 0.1% in Epilobium. It can be said that, under the conditions in which this experiment was performed, most of the elimination of Epilobium plants in the pure stand was due to the lateral spread of the fast growing, aggressive, Lythrum plants which started spreading over the adjoining tanks, so that only a few Epilobium plants towards the periphery on the open side could survive.

On the other hand, in the S/20 dilution the survival of Lythrum in the pure and mixed stands was far higher than those in the standard solution. It was 48% in the pure and 77% in the mixed stand. In the case of Epilobium all the plants were eliminated in the mixed stand and only 18.5% survived in the pure stand.

The results also showed that, in the standard

solution, in the case of Lythrum the biomass of a unit area depends upon the number of survivors rather than the percentage of survival. So, although the percentage survival rate was higher in the mixed stand, the actual number of survivors was almost doubled in the pure stand. Conversely, the average dry weight per plant was markedly higher in the mixed stand. In other words, the plants show less effect from competition on the dry weight gain when they are adequately spaced. This tendency is also shown in the S/20 treatment where the Lythrum plants in the mixed stand are much better and heavier than those in the pure stand. Again, here the biomass and the number of survivors is higher in the pure than the mixed stand, but the difference between the biomass is negligible compared with the difference between the survivors in the two treatments.

It would appear that although, apparently, the biomass of a unit area depends upon the number of individuals in it, proportionately a unit area with fewer individuals shows a tendency to have a higher biomass, and this is more so in the S/20 treatment than the standard treatment. Obviously, in the standard treatment a few individuals take a lead, suppressing the growth of other individuals around them, and the effect of competition on their growth is very marked. In the S/20 treatment growth of the plant in terms of dry

weight gain is also limited, so a few plants cannot take a commanding lead and interfere or suppress the growth of adjoining plants. So, although there is a difference between the number of survivors in the pure and mixed stands, the biomass becomes more or less similar.

In other words, the effect of competition on the survival and growth of the plants depends upon the number of individuals in a unit area as well as the fertility status of the substratum in which they are growing, as the number of survivors in the S/20 treatment is many times that in the standard treatment.

Both the survival and the biomass in a unit area is much less in the case of Epilobium than in Lythrum in the S/20 dilution, and when the two species are mixed together Lythrum completely eliminates Epilobium. Similarly, in the standard solution Lythrum eliminates Epilobium when the two are mixed together.

In the S/20 dilution, although many Epilobium plants managed to survive, after the initial growth of the first few weeks they did not show any further growth and, also, the plants did not flower. On the other hand, although growth was very slow in the case of Lythrum it was continuous and progressive, and after a prolonged treatment many of the plants produced flowers. This better growth in Lythrum is

due to an adaptive increase in the root proportionately to the shoot.

Mechanisms of Competition

It is clear from the results that when both species are crowded together in a unit area, either separately or mixed, they show acute competition for growth and survival. The results of this experiment have shown that Lythrum is very successful in competition and survival both in the standard and the S/20 treatment; whereas, Epilobium is a complete failure. The nature of both the interspecific and intraspecific competition is discussed below.

In the pure Epilobium stand, the great reduction in the number of individuals in the standard solution is primarily due to the growth habit of the plant. In the beginning, during the prostrate stage of growth when large and fleshy leaves are overlapping one another in several layers, there is acute competition for light and many plants are eliminated due to fungal rot. The few surviving plants spread over the surface of the tank as their stems are weak and they cannot stand upright. At the same time Lythrum is growing very fast in the adjoining tanks and, sometimes, later there is lateral invasion of the Epilobium plants by Lythrum, thus covering the low lying Epilobium and completely cutting off the light and causing their death. Only a few Epilobium plants towards

the open side of the tank managed to survive.

The nature of the interspecific competition in Lythrum is very different. Since the plants have an erect growth habit and leaves of an appropriate size, in the beginning there is little interference amongst the plants. Later on a few individuals take the lead and suppress the growth of others by cutting off their light. Thus, although the plants show great variations in size and dry weight the number of survivors is many times that of Epilobium.

The very high survival of Lythrum in the S/20 treatment can be attributed to the limitations imposed on the plant growth and the extent of its development by the nutrient stringency. The S/20 dilution of the nutrient solution is strong enough to keep the plants going but not to let them develop to the extent of interfering with one another. Thus, the competition for light is not as acute as in the case of the standard solution and there is 47.8% survival. It is quite possible that some reduction in the number of individuals may be due to nutrient stringency. In the case of Epilobium there is a still greater reduction in the number of individuals as the plants have to compete both for nutrition and light.

In the mixed stand, in the standard solution, Lythrum has a dual advantage of a fast growth rate and an erect growth habit so that in the early stages of growth,

while Epilobium is passing through the prostrate phase of growth, Lythrum outgrows it, cutting off the light and thus suppressing its growth. Due to the excessive moisture and high temperature the Epilobium plants develop a fungal rot and are soon eliminated. In the S/20 treatment Lythrum also outgrows Epilobium, thus cutting off the light, and at the same time nutrient stringency is also operative. Thus the growth and development are suppressed in the early stages and later all the Epilobium plants are completely eliminated.

It is pointed out that the high percentage survival of Lythrum in the mixed stand (77.4%), compared with that of the pure stand (47.8%) is because the plants are overcrowded in the pure stand and, due to competition for light and nutrients, there is a great reduction in the percentage survival although the actual number of survivors is higher than that in the mixed stand.

The success of Lythrum, in competition and survival in the standard and diluted nutrient solution at a high temperature of 25°C., can be summarised as follows:

1. Life form

The life form of the two species seems to have an important bearing on their competitive abilities. The erect, tall plants of Lythrum, with strong woody stems, have an inherent advantage over the weak stemmed, prostrate, low

growing, large leaved Epilobium plants, especially in the early stages of growth as they can intercept the light from above.

2. Earliness of starting growth

The quick and early response of Lythrum to start growth after transplantation, and the proportionate development of root, stem and leaves, confer on it a great competitive advantage at the temperature used in this experiment: in that the light and nutrient supplies are pre-empted by the shoots getting the advantage of height and spread, and the root system growing to its full capacity. In the standard solution, interception of light by the fast growing tall, Lythrum shoots is the main factor in eliminating Epilobium, and in the S/20 dilution the faster and better root growth in Lythrum in the early stages of development is principally responsible for knocking out Epilobium.

3. Rapid growth rate

It has been shown in the previous experiments that Lythrum has a faster growth rate at a high temperature and also in the low dilution of nutrient solution. This differential growth rate is also very important in the suppression of the growth of Epilobium.

4. Efficient uptake of nutrients

Under conditions of low nutrient supply Lythrum is

quick to incorporate most of the nutrient solution supply in its tissue, due to its faster growth rate and larger size, while Epilobium is critically weakened during the early period of growth and later growth is completely suppressed.

5. Phenotypic plasticity

The ability of Lythrum to accommodate ^{to} nutrient stringency by developing an increased root proportionately to the shoot, while still maintaining the photosynthetic efficiency, gives it a great advantage in competition. On the other hand, Epilobium completely lacks any such phenotypic plasticity, which ~~in teleological terms~~, could be considered of any advantage in the competition and survival of the plant.

Any assessment, in terms of competition and survival of the two species when growing together in nature, should take into consideration the five points outlined above. It can be concluded from the results of this experiment that, under the high temperature conditions, there is a greater probability of the successful survival of Lythrum both in the nutrient-rich and nutrient-poor soils, and that Lythrum would form large, monospecific stands. Again, under the high temperature conditions, there is a great probability that Epilobium plants would not be able to establish themselves in the vicinity of any fast growing species, such as Lythrum or any other plant. In this connection, it is pointed out

that the lateral invasion by the fast growing Lythrum of the adjoining tanks completely wiped out the Epilobium plants except those towards the open side of the tank.

Temperature in relation to the biology of the species

The results of the two experiments described here have shown that the two species react differently to low and high temperatures in terms of their growth, competition, and survival. In the case of Lythrum, low temperature has an extremely suppressive effect on growth, which would exclude its establishment under these conditions. On the other hand, in Epilobium although there is reduction in the size at the low temperature, the plant grows very efficiently. The whole situation is reversed in the high temperature. Here, Lythrum grows more efficiently and completes its life cycle in a much shorter time compared with Epilobium. It has also been shown that Lythrum is very successful in the inter and intraspecific competition, both in the high and low nutrient supply under the high temperature conditions.

While light and nutrition factors may affect the localised distribution of the two species in the same habitat (apart from the effect of light duration), the temperature appears to be the principal factor controlling the geographical distribution of the two species. On the basis of

the results of this experiment it is possible to get a better understanding of the different patterns in the geographical distribution of the two species.

In the British Isles, being located within the north temperate zone on the Atlantic edge of Europe, there are no extremes of summer heat or winter cold, as experienced by many of the north temperate Continental land masses or even by some coastal districts. Moreover, due to the influence of the prevalent "Westerlies", together with the warmer ocean drifts, these Isles have a more equable, oceanic type of climate than many other lands in approximately the same latitude.

Climatically, two isotherm belts have been recognised in the British Isles. The southern part of Ireland, the south-west of England and Wales lie in the northern part of the 60°- 50°F. average annual isotherm belt and the rest of the northern and north-western parts of England and Scotland are within the 50°- 40°F. belt (Turrill, 1948; see '~~the~~ British Plant Life'). It is worthy of note that Lythrum is mostly confined to Ireland and south-west England, from where it moves upwards to the north, with a general decrease in the frequency of occurrence, and is totally absent in Scotland (see Chapter III, "Distribution in Britain"). On the other hand, Epilobium is abundant in Scotland, from where it spreads

downwards, less frequent in Wales and rare to absent along the warm west coast of Ireland, where Lythrum is found in abundance, (Personal comm., Dr. W. D. Hamilton).

On the Continent the distance from the sea and the altitude affects the temperature relations of a habitat. In this connection, the luxuriant growth and dominant presence of Lythrum along the low lying coastal areas of the Balkan peninsula and Dalmatian coast and gradual reduction at higher altitudes and in northern Europe, in contrast to the restriction and abundance of Epilobium in these regions, is a reflection of the temperature control of the different geographical distribution of the two species.

In spite of the limitations imposed by the temperature requirements of the two species on their growth and occurrence, it seems probable that the pole-ward ecesis of Lythrum, in the suitable temperature zones, is much more successful than that of Epilobium towards the equator. This possibility is attributable to their growth rates and competitive abilities. Because of its faster growth rate and ability to complete its life cycle in a much shorter period of time, Lythrum can avail itself of the most favourable period of the high temperatures of summer, in the colder regions of the world, for its successful growth and occurrence (at least, it does so in Britain).

On the other hand, the growth and establishment of Epilobium in the warmer regions of the world would not only be affected by its slower growth rate and the competitive pressure from other plants, but would also be complicated by its water and nutrient relations. In most parts of southern and central Europe, and the warm coastal area, high temperatures are also accompanied by summer droughts (Turrill, 1929, The Plant Life of the Balkan Peninsula), which may be detrimental to the establishment of Epilobium. However, in Britain water is available throughout the year and the fens are never dry, thus growth is possible all the year round in the nutrient-rich sites. It is quite possible that on the Continent many factors, including climate, edaphic factors etc., frequently prevent Epilobium from attaining its theoretical maximum range with respect to temperature requirements.

The following generalised hypothesis is put forward in an attempt to explain the occurrence of the two species in different parts of the world as controlled by their temperature relations.

In Britain (Wheatfen Broad, Norfolk) Epilobium is dominant over Lythrum, mostly occurring as a large, one-species stand. Seeds of Epilobium can germinate at a very low temperature ($7 - 10^{\circ}\text{C.}$) and the seedlings can also grow, persist and become established at this low temperature. Due

to continued growth during winter and early spring, plants may develop to a formidable size and may also start vegetative multiplication, while the Lythrum seeds have not even germinated. By the time the Lythrum seeds start to germinate in the summer (due to their high temperature requirements of 15 - 20°C.), the tall, well grown Epilobium plants would make the edaphic and environmental conditions unfavourable for their germination and later would suppress their growth. Thus, the Epilobium plants, once established, would persist and grow in the same area from year to year forming a dominant, single species stand and encroaching upon new territory due to the rhizomatous habit of growth and completely eliminating Lythrum from the start.

On the other hand, in Yugoslavia Lythrum grows as a dominant plant in nature and often as a one species stand in the Neretva Estuary, near Metkovic (Personal comm. Dr. F. H. Whitehead). Turrill^{*} recorded it in the Struma plain of South Macedonia, growing luxuriantly along the banks of the rivers where Epilobium has not been recorded. The great abundance of Lythrum in these places can be attributed to the warm spells occurring at intervals during the winter (Turrill). The temperatures may go very high, thus providing Lythrum seeds an equal opportunity to germinate and become established alongside the Epilobium seeds. Unlike Britain, spring sets in

* 1929.

abruptly with a sudden change of temperature. This gives Lythrum an opportunity to grow at a faster rate and thus be able to eliminate most of the slow growing Epilobium seedlings.

In Czechoslovakia winter temperatures are below $-20^{\circ}\text{C}.$, preventing the germination of either species, and therefore no pre-emption of space. In the spring, because of the abrupt change from winter conditions, both species start to germinate almost together. Both species, therefore, tend to occur as individuals (no one-species stands) with Lythrum being the most frequent, (personal comm. Dr. Whitehead). Possibly, the reduction in the frequency of Epilobium may be due to the competition between the two plants.

It can be concluded that, nutrition being similar, the differing behaviour of these two species in Britain, Yugoslavia and Czechoslovakia is due to their differing temperature requirements for germination and their subsequent differing growth responses to temperature.

IX. FIELD EXPERIMENTS

The experiments described so far were carried out in controlled conditions and certain conclusions have been reached. It was suggested in Chapter V (Germination) that since Epilobium seeds are capable of germinating at a temperature far lower than that required by the Lythrum seeds ($15 - 20^{\circ}\text{C}.$), so in nature, in Britain, Epilobium seeds would be able to germinate and establish themselves as young plants in the autumn or late winter, while Lythrum would still be waiting for its germination to start in the summer when the temperature would be quite high.

Again, it was suggested in Chapter VIII (The effect of temperature on growth) that since Epilobium can grow very efficiently at a low temperature ($8^{\circ}\text{C}.$), so early establishment in autumn with some growth during winter, since many days exceed $8^{\circ}\text{C}.$, and the resumption of full growth very early in the spring would give it an advantage over Lythrum (still in germination stages), suppressing its growth and leading to the establishment of monospecific stands in Britain. Winter establishment in the case of Epilobium is further ensured by its ability to grow in short-day conditions (see Experiment VI The effect of different day lengths on germination and growth).

On the other hand, it was also suggested that if the two species start their germination and growth together at a high temperature (as in South Yugoslavia (Dalmatia) and southern Europe), Lythrum, because of its faster growth rate, would out-grow and suppress the growth of Epilobium and may possibly lead to its elimination thus establishing pure Lythrum stands. It was also suggested in Chapter VI (The effect of light on growth) that of the two species, Lythrum would be able to grow and establish itself in relatively shady conditions compared with Epilobium; also, that Epilobium would fail to establish and grow in nutrient-poor soils, (Chapter VII - The effects of mineral nutrient conditions on growth) and that in the event of competition between the two species on such sites Lythrum would suppress the growth of Epilobium.

Before these conclusions can be accepted with confidence, information is required of the germination and growth of these species in different seasons and in soils of variable nutrient status, under field conditions, so that the performance of the plants can be judged in their proper context. Accordingly, a series of field experiments were carried out.

The areas used for these experiments were located at Silwood Park (College Field Station) and at Wheatfen Broad in Surlingham, Norfolk. The experimental areas at Silwood

Park were located in the valley of a woodland consisting of oak, beech and chestnut on the slopes surrounding an open valley, with dominant Pteridium aquilinum in the open dry ground, and dominated by Juncus effusus and Scirpus sylvaticus in the swamps at the head of the lake. The valley, as a whole, is a clayey extension of Bagshot sands mixed with pebbles and gravel drift, receiving drainage mainly from the springs coming off very poor nutrient status Bagshot sands, (see - The Flora of Berkshire, by Druce, 1897). Towards the relatively drier margins of the marsh, various species of Viola, Ranunculus, Stellaria, Hypericum, Digitalis, Veronica, Dactylis and Deschampsia were the most common plants. Patches of Chamaenerion angustifolium and shrubs of Rosa canina were scattered frequently in the open on the margins of the marsh, and a big patch of Epilobium hirsutum in the middle of the marsh. In the Wheatfen Broad the area selected for the experiment was surrounded by the dominant Glyceria and Phragmites with scattered plants of various species of Epilobium, Lythrum, Equisetum, Myosotis, Digitalis, Convolvulus, Ranunculus and various grasses, i.e. Poa, Agropyron and Dactylis.

Experiment XV

The effect of density on the competition and survival of the two species in field conditions, on a dry site at high temperatures. (1967)

This experiment was carried out at Silwood Park in the summer of 1967.

Two relatively dry sites were selected, one in the open sun and the other in the shade of a chestnut tree, about 15 feet away from the margin of the swamp. In each site a 10ft. x 10ft. area was cleared of vegetation by removing all aerial shoots and as much living, underground, material as possible, and the thick, clayey substratum was dug or chopped to a depth of about 50cm. to reduce it to a more or less uniform consistency. Each ^{area} was fenced with wire netting to protect it from trespassing or grazing animals especially rabbits, quite frequent in the valley. Three plots, each of 2ft. x 2ft. were marked out at 9in. intervals. The substratum in these plots was thoroughly homogenised and all the fibrous roots and underground remains of grasses were removed.

The seedlings of both species were raised on standard nutrient solution in sand culture as in the previous experiment, to a very advanced stage of growth when the fourth pair of leaves was visible. In both sites, i.e. sun

and shade, all the plots were planted with 2,304 seedlings each $1/2$ in. apart, in such a way that there was one pure plot of each species and a mixed plot with seedlings of the two species planted alternately. The whole operation was completed on 30th May, 1967.

The summer, in 1967, was exceptionally dry and hot, and the temperature for some parts of the months of June and July was as high as 30°C . The plots in the open, sunny site became very dry and were watered artificially for five weeks. No harvest was made, only the survivors were counted at intervals.

Observations and Results

A week after transplantation, the older leaves and the lower parts of the stems of the Epilobium seedlings started to develop a red colouration and did not make any appreciable growth even two to three weeks later. The Lythrum seedlings, on the other hand, started responding after the first week and a few weeks later were fully established as large plants. In the mixed plot the reddening and drying up of the Epilobium seedlings started even earlier than in the pure plots both in the sun and shade.

In the pure Epilobium plots, about three weeks after transplantation Juncus effusus seedlings started to come out amongst the Epilobium seedlings and, as they

grew rapidly, the growth of Epilobium was greatly suppressed, thus most of these seedlings started to die and were eliminated. Similarly, many Juncus seedlings replaced Epilobium seedlings in the mixed plot but there was no growth of Juncus in the pure Lythrum plot. In the shade the site was relatively wet and seedlings of both species were green in the first few weeks after transplantation. Because of heavy rains and high temperatures in July, humidity was very high and, due to very low light intensity, brown rot started developing in the middle of the pure Epilobium plot and most of the plants still in the prostrate stage of growth were eliminated. In the mixed plot, most of the Epilobium and some of the Lythrum plants also decayed due to rot and there was some rot effect in the pure Lythrum plot as well. The number of survivors at monthly intervals was recorded and is shown in Table 16 (A) and (B).

The mean monthly maximum and minimum temperatures recorded at the main meteorological site at Silwood Park, about 400 yards away from the experimental site, are also given, in Table 17.

TABLE 16(A) Plots in the Open Sun

	<u>Date</u>	<u>Lythrum</u> (pure)	<u>Epilobium</u> (pure)	<u>Lythrum + Epilobium</u> (mixed) (mixed)			
1.	30. 5.67	2304	2304	1152	+	1152	= 2304
2.	29. 6.67	1568	1105	711	+	418	= 1129
3.	1. 7.67	872	318	518	+	72	= 590
4.	31. 8.67	517	68	392	+	-	= 392
5.	30. 9.67	402	-	371	+	-	= 371
6.	28.10.67	402	-	312	+	-	= 312

(B) Plots in the Shade

1.	30. 5.67	2304	2304	1152	+	1152	= 2304
2.	29. 6.67	1792	1208	718	+	308	= 1026
3.	1. 7.67	815	112	389	+	-	= 389
4.	31. 8.67	368	-	192	+	-	= 192
5.	30. 9.67	292	-	185	+	-	= 185
6.	28.10.67	268	-	185	+	-	= 185

TABLE 17

Mean Monthly Temperatures °C.

<u>Month</u>	<u>1967</u>		<u>1968</u>	
	<u>Maximum</u>	<u>Minimum</u>	<u>Maximum</u>	<u>Minimum</u>
May	14.9	6.2	14.9	5.4
June	19.5	8.5	19.9	10.0
July	22.7	11.7	20.3	10.7
August	20.3	10.9	19.7	11.2
September	17.3	9.7	18.0	10.0
October	14.2	7.6	15.8	9.7

It is clear from Table 16 that while Epilobium does not survive in sun or shade conditions, survival in Lythrum is much higher in the sun than in the shade. ~~conditions~~. The effects of density on the growth of the plants were very marked in the sun plots compared with the shade ones. Most of the Lythrum plants, in pure and mixed plots, in the sun varied in height from 20 to 45cm., and only 20 plants measured up to 80cm. and flowered in September. In the shade growth was severely curtailed, survivors, as a whole, grew uniformly and none was more than 20cm. in height. Leaves in these plants

were very small and the stems weak and fragile; the growing points were reduced and there was no flowering.

Discussion

The failure of establishment and elimination of Epilobium can be attributed to many factors. In the beginning the dry and hard nature of the substratum might have made the penetration of its soft adventitious roots difficult, thus preventing the plant meeting the greater growth commitments in the earlier stages of growth. At the same time the seedlings were also confronted with the poor nutrient conditions of the soil as they showed typical deficiency symptoms, similar to the S/50 plants in Experiment X (The effect of different dilutions of a standard nutrient solution on growth). Furthermore, the rapid growth of Juncus seedlings made both the soil and aerial environments unfavourable for Epilobium growth. On the other hand, the tap root system is very strongly developed in Lythrum and grows very deep into the soil, thus exploiting a correspondingly larger volume of soil in terms of water and nutrient supply and therefore being more successful in survival. In the mixed plot the elimination of Epilobium was still quicker, probably due to the better growth of Lythrum and the development of Juncus. It is pointed out that in the pure Epilobium plot, Juncus plants were tall and much better developed compared to those

in the mixed plot. It is clear that Lythrum not only eliminated Epilobium but also successfully competed with Juncus.

Under the shade conditions, although the survival of Lythrum was very high, the plants showed poor growth and development.

Observations on these plots were made again in the years 1968 and 1969. In May, 1968 most of the Lythrum plants in the pure and mixed plots had started their growth (Plate 21). A count of the survivors was made in September. In the sunny site, in the pure plot there were 162 plants of which 70 were large and flowering and a few small Juncus plants were also present in this plot. The survival and growth of the species were very much affected by Juncus in the mixed plot where only 87 Lythrum plants survived and only 35 of these flowered. The growth and survival in the shade was again very poor. There were 118 plants in the pure and 69 in the mixed plot and again there was no flowering.

By the summer of 1969 the whole of the experimental area in the open sun was grown over by the tall, well established Juncus; but there were still only a few Juncus plants in the pure Lythrum plot and 158 Lythrum plants were very well established, but there were only 25 flowering plants as most of the young plants had been eaten away in a rabbit attack, (Plate 22). In the mixed plot Juncus showed

Plate 21L. salicariaJ. effususPlate 22L. salicariaJ. effusus

PLATE 21. L. salicaria plants surrounded by the dominant J. effusus plants in the pure sunny plot (June 1968)

PLATE 22. Flowering L. salicaria plants in the pure sunny plot surrounded by dominant J. effusus plants (Sept. 1969)

luxuriant growth with tall Lythrum plants scattered inbetween. There were only 30 tall Lythrum plants here and all the other plants were completely eliminated by the fast growing Juncus plants. In the shade site, the plots were grown over by various grasses especially Deschampsia and Dactylis and only a few Lythrum plants had survived, 78 in the pure and 25 in the mixed plot.

From the foregoing observations and results it can be concluded that Lythrum showed much better growth and survival, especially in the open sunny conditions, and not only succeeded in eliminating Epilobium but also successfully competed with Juncus. It seems quite probable that the elimination of Epilobium is due to the scarcity of water and the poor nutrient supplying capacity of the soil, rather than any direct suppressive effect of the Lythrum or Juncus plants, as the Epilobium plants in the pure plot also did not survive.

On the other hand, Lythrum showed a great tolerance to dry soil and a low nutrient supply in so far as it showed good growth, survival and successful competition with Juncus. It is noteworthy that Lythrum, once successfully established on a dry site, persisted from year to year and endured the competitive pressure of the early growing plants, such as Juncus, although its own growth starts in May when the temperature is quite high. The experiment also showed that of

the two species Lythrum can survive better in the shade although growth was very poor.

Experiment XVI

The effect of fertilizer on density survival, at a high temperature, on wet soil. (May to October, 1968)

In this experiment the area selected was on the muddy banks of the swamp both in the sun and shade, and at places the mud was almost 2ft. in depth. A 15ft.x 15ft. area was cleared by removing Scirpus and Juncus species in both the sites, and the area was properly fenced. In each site six plots, of 16in.x 16in. dimensions, were marked out at 9in. intervals in two rows. One row of three plots was sprinkled with Fison's granulated "Topgro 8" fertilizer at the rate of 2oz. per plot. The granules were absorbed in the mud a few hours later. This fertilizer is rich in N.P.K. present in a 3:2:3 ratio. Below are given their percentages in the composition of the fertilizer. (Table 18).

TABLE 18

Total	Total	Water Soluble	
<u>Nitrogen</u>	<u>Phosphate</u>	<u>Phosphate</u>	<u>Potash</u>
N%	P ₂ O ₅ %	P ₂ O ₅ %	K ₂ O%
13.5	9.0	8.5	13.2

1024 seedlings were planted 1/2in. apart in each plot in both sites, so that in each treatment there was one pure plot of each species and one with the two species mixed together. (In addition to the above setting up, 1000 seedlings of each species were planted separately in two 16in. x 16in. plots, one treated with fertilizer and the other left untreated to study the continuation of growth and survival in the following years).

Monthly counts of the survival of the two species in all the treatments were made. The mean pH of the mud in the open sun site was 5.2 and in the shade 4.8. The setting up of the experiment was completed on 5th May, 1968, and the plants were harvested five months later in October. The total number of survivors, their heights and dry weights in each plot were recorded.

Observations and Results

In the shade, seedlings of both species showed a good response a few weeks after transplantation, but due to heavy rains in June most of the plants while still in the seedling stage were washed away, and others showed brown fungal rot, especially in the fertilized plots. Only 13 plants survived in the pure Lythrum stand. In the sunny site the plants were quite well established and tall at the time of the rains and floods and, moreover, this site was located

at a higher level compared with the shade site, so there was no loss due to the rains.

Comparatively there was a greater reduction in the number of individuals in the case of Epilobium than in Lythrum in the pure plots, with time. In the mixed plots Lythrum completely eliminated Epilobium a few weeks after transplantation. The survival and growth was better in the fertilized plots than in the unfertilized ones, (Plate 23). The number of survivors in each treatment, at approximately monthly intervals, is shown in Table 19.

In the unfertilized mixed plot there was some growth of Juncus inbetween the Lythrum plants. The surviving Lythrum plants in the fertilized plots showed a variation in size from 60 to 120cm. while those in the unfertilized plots varied between 40 and 90cm. A greater number of plants in the fertilized plots showed flowering compared to the unfertilized ones. In the fertilized plots Epilobium plants were much bigger and up to 30cm. in height compared to the unfertilized plots where the height varied from 11 to 18cm.

The total survival, biomass, percentage survival and mean dry weight per plant are given in Table 20.

It is clear from the results that in both the species the survival, biomass and dry weight per plant are higher in the fertilized than in the unfertilized plots.



(a)

L. salicariaJ. effusus

(b)

L. salicariaJ. effusus

PLATE 23. Survival and growth of Lythrum salicaria in the open sunny plots. (a) Treated with fertilizer
 (b) No fertilizer treatment.
 (Photographed on 8 September, 1968, i.e. 4 months after transplantation.)

TABLE 19

Number of Survivors in Each TreatmentPlots in the Open Sun

(A)

Without Fertilizer

	<u>Dates</u>	Pure <u>Lythrum</u>	Pure <u>Epilobium</u>	Mixed <u>Lythrum + Epilobium</u>			
1.	5.5.68	1024	1024	512	+	512	= 1024
2.	2.6.68	915	711	467	+	293	= 760
3.	6.7.68	609	519	393	+	20	= 413
4.	5.8.68	501	378	365	+	-	= 365
5.	8.9.68	492	363	348	+	-	= 348
6.	4.10.68	492	359	348	+	-	= 348

With Fertilizer

1.	5.5.68	1024	1024	512	+	512	= 1024
2.	2.6.68	953	793	502	+	315	= 817
3.	6.7.68	685	627	473	+	-	= 473
4.	5.8.68	573	502	453	+	-	= 453
5.	8.9.68	550	470	439	+	-	= 439
6.	4.10.68	550	465	439	+	-	= 439

TABLE 19 (cont.)

Plots in the Shade

(B)

Without Fertilizer

	<u>Date</u>	<u>Pure Lythrum</u>	<u>Pure Epilobium</u>	<u>Mixed Lythrum + Epilobium</u>			
1.	5.5.68	1024	1024	512	+	512	= 1024
2.	2.6.68	476	391	182	+	50	= 232
3.	6.7.68	106	83	41	+	-	= 41
4.	5.8.68	13	-	-	+	-	= -
5.	8.9.68	13	-	-	+	-	= -
6.	4.10.68	13	-	-	+	-	= -

With Fertilizer

1.	5.5.68	1024	1024	512	+	512	= 1024
2.	2.6.68	308	209	82	+	20	= 102
3.	6.7.68	93	11	-	+	-	= -
4.	5.8.68	-	-	-	+	-	= -
5.	8.9.68	-	-	-	+	-	= -
6.	4.10.68	-	-	-	+	-	= -

TABLE 2Q Total survival, Biomass, % Survival and mean
Dry weight per plant.

Initial number at the time of transplantation = 1024
in the pure plots, and $512 + 512 = 1024$ in the mixed plots.

	<u>Without Fertiliser</u>			<u>With Fertiliser</u>		
	Pure	Pure	Mixed	Pure	Pure	Mixed
	* <u>L.S.</u>	<u>E.H.</u>	<u>L.S.</u>	<u>L.S.</u>	<u>E.H.</u>	<u>L.S.</u>
Total survivors	492	359	348	550	465	439
Biomass (gm)	942.0	225.4	487.0	1705.0	697.5	1485.0
% Survival	48.05	35.06	67.97	53.71	45.41	85.74
Dry Wt/Plant(gm)	1.915	0.628	1.399	3.10	1.50	3.38

*L.S. = Lythrum salicaria

E.H. = Epilobium hirsutum

(No survival of Epilobium in the mixed plots with, or without, fertilizer treatment)

Also, the density of plantation has definite effects on the growth and survival of Lythrum. It can be seen that the percentage survival of Lythrum is much higher in the mixed plots than in the pure ones, especially in the fertilized treatment. Similarly, the dry weight per plant is also higher in the mixed, fertilizer treated, plot. In the unfertilized plot the relatively lower plant dry weight can be attributed to the growth of Juncus in the plot, whereas there was no Juncus growth in the fertilized plot.

In the case of Epilobium both survival and biomass are very poor compared with Lythrum, both in the treated and untreated plots. Although yield and survival improved with the application of fertilizer still the plants in the fertilized plot did not attain a normal height and there was no flowering.

In the four additional plots the survival of Lythrum and Epilobium in the treated and untreated plots, for the two successive years, is as follows.

TABLE 21

Initial number at the time of transplantation = 1024

	<u>LYTHRUM</u>		<u>EPILOBIUM</u>	
	<u>Fertilized</u>	<u>Unfertilized</u>	<u>Fertilized</u>	<u>Unfertilized</u>
September 1968	539	468	421	372
September 1969	507	413	-	-

While Lythrum maintained a high degree of survival in the year 1969 none of the Epilobium plants survived in 1969. Despite the heavy fertilization and the abundance of water, the failure of Epilobium to establish fully in the first season and the lack of survival in the second season can be attributed to the acidic nature of the soil. On the

other hand, Lythrum is not only tolerant of the acidic conditions but shows a good growth in the first year of establishment which is further improved by the application of fertilizer, and in the second season the plants are relatively much better and vigorous.

It is noticeable that, although Lythrum plants showed good flowering, setting large quantities of seeds every year, there were no new seedlings visible around the plots. It is also pointed out that the whole experimental area, except the plots with Lythrum, was over-grown by Juncus. The most probable explanation for the absence of new Lythrum seedlings is that Juncus starts its growth very early in the spring and by the time that the Lythrum seeds have the suitable germination temperature of summer, both the edaphic and environmental conditions are unfavourable due to the growth of Juncus which suppress the germination or growth of Lythrum from the very beginning.

It can be concluded that although Lythrum is very successful in inter and intraspecific competition when given a good start on a rich or poor substratum under high temperature conditions, and can persist on the same area for many years, it fails to make any territorial advances. This handicap is principally attributable to the delay in its germination as, while its seeds are waiting for the high summer

temperatures, other plants grow to a large size and create conditions unfavourable for the germination of its seeds, thus excluding the establishment of its seedlings from the very beginning. At the same time, the mature, established Lythrum plants lack any means of vegetative multiplication and so fail to increase in number. They may, in fact, undergo gradual reduction in numbers from year to year and may disappear altogether after some time or become reduced to a few individuals.

Experiment XVII

The effect of low temperature and overwintering on the growth, competition and survival in the high temperature of the following summer. (Oct. 1968 to Sept. 1969)

This experiment was carried out in the Wheatfen Broad, Surlingham, Norfolk, in 1968-1969.

Since Epilobium failed to grow and establish successfully in the acidic marsh at Silwood Park in spite of heavy fertilization, it was considered preferable to set up this experiment at the Wheatfen Broad where Epilobium forms dominant monospecific stands, with scattered Lythrum plants in places, thereby eliminating the soil factor, to study the competition and survival of the two species as affected by

the low temperature of autumn and the high temperature of the following summer.

A 15ft.x 15ft. area was selected near the bank of a dyke in the Home Marsh adjoining the River Yare. The surface vegetation was removed, the soft peat was chopped and homogenised, and the area was properly fenced. Soil samples were brought back to Silwood Park and the pH, measured by a Beckman's electric pH meter, was found to be 6.63. Six 16in.x 16in. plots were marked out at 9in. intervals and were thoroughly cleared of the remains of the roots of grasses, rhizomes of Phragmites, etc. As in the previous experiment, 1024 seedlings per plot were transplanted, so that there were two replicates of pure plots of each species and two replicates of mixed plots.

The whole transplantation operation was completed on 21st October, 1968 and the plants were harvested on 27th September, 1969. The temperature was also recorded about 20 yards away from the experimental site. The experimental area was visited at monthly intervals and most of the observations on growth, especially during the winter, were made by the well known naturalist, Mr. E. A. Ellis, owner of the Wheatfen Broad.

Observations

Both species started showing growth responses in

the pure as well as the mixed plots. By mid-November, 1968, although there was a great reduction in the number of plants in all the plots, still growth was very marked especially in the case of Epilobium, both in the pure and mixed plots. During this period of growth Epilobium plants developed into small dwarfs with thick, fleshy, large leaves on reduced stems. In Lythrum the shoots remained very weak with small crumpled leaves. The leaves remained green in the case of Epilobium in December, while in Lythrum they were palish green to yellow by the end of November and were falling off very rapidly by the beginning of December, so that in most cases only defoliated stumps were visible. In the mixed plots, Epilobium showed comparatively better growth than Lythrum and, due to the great suppression and reduction of Lythrum, the plots appeared to be composed only of the Epilobium plants. Towards the end of December, 1968 most of the leaves of the Epilobium plants were also decayed due to snow, etc.

The Epilobium plants started their growth in January and by mid-February, 1969 some plants had their full complement of leaves in both the pure and mixed plots, and their numbers increased with time. At the beginning of May the Lythrum plants also started to develop leaves both in the pure and mixed plots. While the number of plants with leaves

increased with time they remained small owing to slow growth up to the first week of June, whereas the Epilobium plants were much better developed and up to 30cm. in height (see Plate 24). In July the growing tips of most of the Lythrum plants were bitten off in the pure plot and the damage was severe as the plants were still very young. Mr. Russell (Field Assistant) was quite sure that the shoots were bitten off by pheasants or wild pigeons as they usually attack young growing plants. However, the plots were covered, on the top, with wire netting. In contrast, none of the Epilobium plants or Lythrum plants in the mixed stand under the protection of the taller Epilobium plants were damaged by this attack.

The height of the tall flowering Epilobium plants, on average, was some 110cm. both in the pure and mixed plots. The Lythrum plants in the mixed plot were only up to 18cm. tall. In the pure plot a few tall flowering plants attained a height of 60 - 70cm., but most of the plants were hardly 30cm. tall and did not flower. This lack of flowering and full development of the Lythrum plants in the pure plots is principally due to the pheasant attack.

Results

The mean number of survivors in the pure and mixed plots at various intervals is given in Table 22.



PLATE 24. Mixed plot of Epilobium hirsutum and Lythrum salicaria (June 1969)



(a)

E.hirsutum

(b)

L.salicaria

PLATE 24. Pure plots of (a) Epilobium hirsutum and
(b) Lythrum salicaria (June 1969)

TABLE 22 Mean Number of Survivors

<u>Date</u>	Pure	Pure	Mixed			
	<u>Lythrum</u>	<u>Epilobium</u>	<u>Lythrum</u>	+	<u>Epilobium</u>	
21.10.68	1024	1024	512	+	512	= 1024
15.11.68	311	408	69	+	192	= 261
8.12.68	13	56	-	+	31	= 31
Jan. 69	-	-	-	+	-	= -
23. 2.69	-	5	-	+	6	= 6
22. 3.69	-	10	-	+	13	= 13
5. 5.69	-	18	-	+	22	= 22
5. 6.69	125	23	20	+	36	= 56
17. 7.69	134	19	60	+	30	= 90
27. 9.69	66	17	58	+	29	= 87

In Table 23 are given the mean number of survivors at the time of the final harvest (i.e. 27th September, 1969), the biomass and the dry weight per plant.

TABLE 2.3

	Pure	Pure	Mixed	
	<u>Lythrum</u>	<u>Epilobium</u>	<u>Lythrum</u>	<u>Epilobium</u>
Mean no, of survivors	66	17	58	29
Mean biomass (gm)	57.55	67.10	16.20	85.60
Dry wt/plant (gm)	0.872	3.941	0.276	2.952

The mean monthly maximum and minimum temperatures are shown in Table 24.

TABLE 24

	<u>Temperatures °C.</u>	
	<u>Mean Maximum</u>	<u>Mean Minimum</u>
October 1968	12.8	6.8
November 1968	7.2	3.5
December 1968	2.7	-5.5
January 1969	6.3	0.55
February 1969	4.4	-3.5
March 1969	6.8	-1.6
April 1969	11.1	1.2
May 1969	16.8	3.9
June 1969	19.5	2.2
July 1969	22.8	7.4
August 1969	21.0	11.8
September 1969	18.6	9.4

It is clear from the results that the survival of Lythrum in terms of numbers is much higher than that of Epilobium, both in the pure and mixed plots. Also, the

survival of Epilobium is higher in the mixed than the pure plot. On the other hand, the biomass and dry weight per plant are markedly higher in the case of Epilobium than in Lythrum both in the pure and mixed plots.

These results are suggestive of the fact that Epilobium made good growth immediately after transplantation in the autumn of 1968, even when the temperatures were quite low. It has been said before that Epilobium establishes itself as small plate forms by the end of its first season of growth while Lythrum remained much weaker. In the second growing season, in 1969, Epilobium had the dual advantage of making an early start in the low temperatures of February and of exploiting the stored food material (in its rhizomes) from the previous year's growth. On the other hand, Lythrum started its growth in the second season very late (almost ten weeks later) and there does not seem to be any large amount of surplus stored food material from the previous year's growth to boost its growth in the second year.

There is no doubt that the results of the biomass and dry weight per plant in the pure Lythrum plots may not be completely valid due to the damage and curtailment of plant growth caused by the pheasant attack. However, some plants were not damaged in these plots and went on to flower. It is

considered significant that these undamaged plants were not as fully developed (as regards plant size and flowering) as the equivalent plants of Epilobium and that the contention that autumn established plants of Epilobium, in soils of pH.6 and above, and of high nutrient status, have a high competitive advantage over plants of Lythrum established at the same time.

On the other hand, there is clear evidence of the suppression of Lythrum's growth by Epilobium in the mixed plots. Although the number of survivors in Lythrum is twice that of Epilobium the biomass is five times higher and the dry weight, per plant, more than ten times higher in Epilobium. It is clear that Epilobium takes advantage of the seasons; it made better growth in the autumn of 1968 and then had a very early start in 1969. By the time Lythrum resumed its growth in June 1969, both the substratum (due to the rhizomatous growth of Epilobium) and aerial environments (due to the tall shoots of Epilobium) were rendered unfavourable for its full growth and development.

It can be concluded from these results and discussion, that temperature has a profound effect on the relative performance of the two species since the soils in the Surlingham Broads, especially those adjoining the river and

supporting Glyceria maxima and Phragmites communis, are very rich in nutrients (Buttery, Williams and Lambert, 1965). The ability of Epilobium to continue its growth in autumn and its resumption of full growth the next spring gives it a tremendous advantage over Lythrum which depends upon a high temperature for its growth, thus in the event of interspecific competition under these conditions growth and development of Lythrum is greatly suppressed by Epilobium.

On the other hand, the number of survivors is much higher in the case of Lythrum, both in inter and intra-specific competition.

Experiment XVIII

Germination and establishment of the two species on bare areas, in summer, when the seeds are sown in the autumn of the previous year. (October 1968 to September 1969)

This experiment was also carried out at the Wheatfen Broad along with the density survival experiment in the same area. Two plots each 3ft.x 3ft. were cleared of root remains, at the other end of the same experimental area, and the soil was thoroughly homogenised and labelled. 30,000 seeds of each species (by weight, i.e. 1.9gm. of Lythrum and 5.5gm. of Epilobium, fresh weight) were scattered in their respective plots. The hairy Epilobium seeds were thinly

spread over the area, uniformly, and were covered by a thin layer of wet soil. The setting up was completed on 19th October, 1968.

The Epilobium seeds started to germinate towards the end of February, 1969, while there was no sign of germination in Lythrum. In March and April there was very high germination in Epilobium and seedlings were present uniformly all over the plot. By the end of May the Lythrum seeds also started germinating. Counts of seedlings in both species, at various intervals, are given in Table 25.

TABLE 25

<u>Date</u>	<u>Epilobium</u>	<u>Lythrum</u>
22 March 1969	1615	-
5 May 1969	4985	-
5 June 1969	378	6205
17 July 1969	71	1817
27 Sept. 1969	27	487

These results suggest that there is a flush of seedling emergence in both species in the beginning and as time passes there is a great reduction in their number (due

to various factors to be discussed later). This reduction is markedly higher in the case of Epilobium compared with Lythrum. Observations on 5th June showed that some Epilobium seedlings were quite big and produced up to three pairs of leaves. At the same time patches of dead seedlings were also present under the shade of some plants of Ranunculus, Urtica, Convolvulus and Equisetum growing at places in the plot, while along the margin various grasses, Glyceria and Phragmites were showing fast growth. With time most of the seedlings were killed by the shade of these plants. On the other hand, the Lythrum plot was surrounded by tall Phragmites and Glyceria but only one Ranunculus and one small Convolvulus plant were present inside the plot. On 27th September, when the last observation was made, all the Lythrum seedlings were growing uniformly, 5 to 7cm. high with up to five pairs of small leaves. Most of the surviving Epilobium seedlings, by this time, had grown into small sized plants 19 to 24cm. in height with eight to nine pairs of broad, well developed, leaves; there was no flowering but most of these plants had developed two to three long, slender rhizomes.

Discussion

It is clear from these results that the Epilobium and Lythrum seeds, collected in September 1966 and sown at the beginning of winter, 1968, retained their viability

during the snowy winter and readily germinated in the following spring and summer respectively. Although there is a flush of germination in both types of seeds in the beginning, the time of germination is affected by the temperature.

Epilobium seeds start germination by the end of February when the temperature is still very low (the average maximum = $4.4^{\circ}\text{C}.$) and the peak of germination is reached in May, with the average maximum temperature up to $16.8^{\circ}\text{C}.$ Lythrum, however, does not start germinating until the end of May when the temperature is very high and still rising, with the average maximum of $19.5^{\circ}\text{C}.$ in June. After the flush germination there is a great loss in the number of seedlings with time, especially in Epilobium as out of 4985 seedlings counted on 5th May only 27 managed to survive and grow while, comparatively, survival is much higher in Lythrum, 487 seedlings survived out of the 6205 counted on 5th June.

While there is no doubt that the overcrowding of seedlings in both cases led to the elimination of most of them, due to inter^{ra}~~er~~specific competition, those germinating a few days earlier could easily suppress the growth of those germinating later in the same spot. Furthermore, the growth of other herbaceous plants plays an important role in killing and eliminating many seedlings by their shade.

While the above hypothesis may go a long way to

explain the reduction in the number of seedlings with time, the far greater reduction in the number of Epilobium compared with Lythrum cannot be fully accounted for by this hypothesis. There seems to be a possibility that the firmness of the ~~establishment~~ ^{attach} immediately after germination may be an important factor in the successful establishment and survival of the two seedlings. In this connection, the root system of the two species seems to be very important. In Epilobium the tap root is short lived and is replaced by soft adventitious roots. It is possible that because of the relatively hard substratum penetration of these roots is not successful. Thus, in most cases after germination there is no establishment of the seedlings, leading to their death and exclusion. This probability seems convincing as there were large patches of dead seedlings in the cotyledonary stage not firmly attached to the soil.. On the other hand, Lythrum seedlings have long, persistent, tap root systems growing deep into the soil and thus establishing the seedlings firmly into the substratum soon after germination.

Although the establishment and survival of seedlings in the case of Lythrum is many times that of Epilobium, conversely growth is much better in Epilobium in the first season as it can grow into small sized plants with fully developed leaves and rhizomes, while Lythrum does not grow

beyond 5 to 7cm. high in the seedling stage.

Before discussing the ecological significance of the substantial amount of growth accomplished by the Epilobium seedlings during the first season of growth in relation to the density survival experiments, it has been considered better to describe the other field experiments.

Experiment XIX

The effect of spacing on competition and survival of the two species on a dry site at high temperatures.

This experiment was carried out at Silwood Park in June 1967 on a drier site along the margin of the swamp.

Two sites, each of 25ft.x 12ft, were selected, one in the sun and the other in the shade along-side the density survival experiment No. XV. The areas were properly cleared and fenced.

In each site eighteen plots each 30in.x 30in. were marked out at 1in. intervals in three rows, in such a way that there were six sets of plots each composed of three units. Each set was properly labelled for the distance at which the seedlings were transplanted, i.e. 1in., 3in., 5in., 7in., 10in. and 15in. apart, and the corresponding number of seedlings at the different spacings, i.e. 900, 100, 36, 16, 9

and 4. In each set of three plots there was one plot each of the pure species, on the sides, and the central plot with the two species mixed together. In the mixed plot the seedlings were transplanted alternately. All the plots were watered during the summer, as in Experiment XV.

Observations

A few weeks after transplantation the Epilobium seedlings started to develop a red coloration on the mature leaves and the lower parts of the stem. They persisted for some time without making any growth and gradually dried up both in the pure and mixed plots. In the beginning of July Juncus seedlings started to appear in all the Epilobium plots, mixed plots, and in the Lythrum plots where the seedlings were spaced 5in. or more apart. By the end of July all the plots and most of the bare area were full of Juncus plants and almost all the Epilobium plants were eliminated.

In the shady site growth of the Epilobium seedlings was very poor, most of the seedlings placed at 5in., 7in., 10in. and 15in. apart failed to establish and died very quickly, while in other plots (containing 900 and 100 seedlings) there was a gradual elimination of the seedlings. In the case of Lythrum the establishment and growth of seedlings were also poor in the shade and most of the seedlings in all the plots, especially where widely spaced, were eliminated.

In the sunny site Lythrum seedlings started responding two to three weeks after transplantation. In all the pure and mixed Lythrum plots there was growth of Juncus except where planted 1in. apart.

The surviving plants counted on both sites on 23 September, 1968, were as follows:

TABLE 26

The Survival of Lythrum salicaria on Plots of
30in.x 30in. Area on a Dry Site Under
Different Spacing.

	<u>Pure Plots</u>					
Distance apart in ins.	1"	3"	5"	7"	10"	15"
Total no. transplanted	900	100	36	16	9	4
Total no. of survivors in sunny plot	295	28	15	3	2	-
Total no. of survivors in shady plots	73	5	-	1	-	-

(No survival in pure Epilobium plots)

TABLE 26 (cont.)

Mixed Plots

Distance in ins.	1"		3"		5"		7"		10"		15"	
	* LY	EP	LY	EP	LY	EP	LY	EP	LY	EP	LY	EP
No. of seedlings Transplanted	450+450		50+50		18+18		8+ 8		5+ 5		2+ 2	
Survivors in sun	83	-	13	-	8	-	2	-	2	-	1	-
Survivors in Shade	13	-	-	-	-	-	-	-	-	-	-	-

* LY = Lythrum salicaria

EP = Epilobium hirsutum

It can be seen that survival is greatest in the plots with the highest density of plants, but still there is relatively greater reduction in the mixed plots than in the pure ones. This is most probably due to the excessive growth of Juncus in these plots. Both the survival and growth are much better in the sunny than in the shady plots. In the shade the plants were up to 19cm. in height with weak stems and very small leaves. In the sunny plots the plants in the 900 seedling plot showed great variation in size, from 15 to 74cm. and only 10 large plants flowered. In other plots the plants were surrounded by heavy Juncus growth and their size was variable, but still the plants were quite woody with well developed stems and large leaves. Only three plants in the

mixed 900 seedling plot showed flowering.

It can be concluded from these results that the growth and survival of Lythrum is very poor if the plants are widely spaced, especially in the shade. But still, Lythrum can survive much better than Epilobium. Although the most important factor in the elimination of Epilobium is the dryness and low nutrient status of the soil, at the same time the enormous and rich growth of Juncus is also responsible for its elimination. Juncus also affected the growth and survival of Lythrum. In the plots with 100, 36, 16, 9 and 4 Lythrum plants and in the mixed plots with a lot of unused open spaces numerous Juncus seedlings started growing up and in a few days covered the growing Lythrum plants, thus cutting off their light and suppressing their growth, so much so that some plants were only 10cm. in length, buried amongst the tall Juncus plants. Other Lythrum plants in an advanced stage of growth could successfully compete and grew as tall as the Juncus plants.

Experiment XX

The effect of spacing and fertilizer on the yield, competition and survival of the two species on a wet site at a high temperature. (May to October, 1968)

Four 25ft.x 12ft. areas, two in the sun and two in the shade, were selected in the wet, muddy banks of the marsh in the valley at Silwood Park. All the Juncus and Scirpus plants and some herbaceous flora in the shady sites were removed and the areas were properly fenced. Six sets of plots each of three units were marked out in the same pattern as in the previous experiment on the dry site. In both the sites plots in one area were treated with Fison's "Topgro 8" fertilizer at the rate of 4oz. per plot. The seedlings were transplanted in the same pattern as the previous experiment, i.e. at a distance of 1in., 3in., 5in., 7in., 10in., and 15in. apart in pure and mixed forms. The mean pH of the mud in the sun and shade was 5.2 and 4.8 respectively.

The setting up of the experiment was completed on 18 May, 1968. The record of temperature during the period of the experiment is shown in Experiment XV.

Observations

In the shade site seedlings of both species showed some growth and establishment for a period of four weeks

after transplantation. Later, due to heavy rains in July, most of the seedlings in all the plots were washed away. The remaining ones in the high density plots were buried under the mud and eventually decayed due to the extremely low light intensity, high humidity and high temperature.

In the open, sunny site (Plate 25) the growth of Lythrum in all the plots was much faster than that of Epilobium, especially in the fertilizer treated plots. Both species in the treated plots were much healthier than in the untreated plots. The Epilobium plants in the mixed plots died a few weeks after transplantation due to the growth of Lythrum and Juncus. In the pure Epilobium plots, with widely spaced plants, the growth was severely curtailed and suppressed by the fast growing Juncus and after some time most of the plants died. Loss of Lythrum plants was much less than that of Epilobium and most of these plants grew very tall and successfully competed with the Juncus surrounding them. Most of the tall surviving Lythrum plants flowered in September, both in the fertilized and unfertilized plots.

The plants in all the plots and treatments were harvested on 5 October, 1968. At this time the very large plants in the plot with 900 plants (lin. apart) and in some other plots were up to 112cm. high in the treated plots but only up to 92cm. in the untreated plots. Other plants in



Scirpus
sylvaticus

Lythrum
salicaria

PLATE 25. General view of field experiment No.XX.

The effect of spacing and fertilizer on the yield, competition and survival of the two species on a wet, sunny site at a high temperature. (Photographed on 18 September, 1968, i.e. 4 months after transplantation.)

these plots varied between 40 to 70cm. in length. On the whole, plants in the non-treated plots appeared less developed, smaller, had weaker stems and light green leaves and fewer flowers.

Results

The number of survivors, % survival, biomass and the mean dry weight per plant for various plots of the sunny site are given in Table 27.

It is clear that the survival and biomass are much higher in plots treated with fertilizer than in the non-treated ones. In the case of Lythrum, in the pure plots there is a much greater improvement in the biomass and dry weight per plant than in survival by the application of fertilizer.

The density of individuals in a unit area has a great effect on their dry weight gain, as can be seen in Table 27. Where the individuals are spaced 3in. apart (and also at other spacings), the dry weight per plant is five times that of the individuals in the plot spaced 1in. apart. It can also be seen that 3in. is the minimum adequate spacing where both the survival and yield are at their best in a unit area. In the other plots treated with fertilizer, with the increase in spacing there is some increase in the individual plant weight, but at the expense of yield per unit area.

In both the fertilized and unfertilized plots with

TABLE 27LYTHRUM SALICARIAPure PlotsTreated with Fertilizer

Distance in ins.	1in.	3in.	5in.	7in.	10in.	15in.
No. of seedlings Transplanted	900	100	36	16	9	4
No. of survivors	795	90	34	16	9	4
% Survival	88.3	90	94.4	100	100	100
Biomass/plot (gm.)	2464.5	1395.0	578.0	273.6	146.7	72.4
Mean dry wt. per plant (gm.)	3.1	15.5	17.0	17.1	16.22	18.1
Biomass of <u>Juncus</u> /plot (gm.)	-	49.0	129.8	118.7	113.0	158.7

Untreated Plots

No. of seedlings Transplanted	900	100	36	16	9	4
No. of survivors	750	86	30	12	7	3
% Survival	83.3	86.0	83.3	75.0	77.7	75.0
Biomass/plot (gm.)	1215.0	439.0	141.0	54.72	30.66	12.39
Mean dry wt. per plant (gm.)	1.62	5.1	4.7	4.56	4.38	4.13
Biomass of <u>Juncus</u> /plot (gm.)	-	298.0	463.0	578.0	715.0	798.0

TABLE 27 (cont.)

EPILOBIUM HIRSUTUMPure PlotsTreated with Fertilizer

Distance in ins.	1in.	3in.	5in.	7in.	10in.	15in.
No.of seedlings Transplanted	900	100	36	16	9	4
No.of survivors	407	39	12	4	-	-
% Survival	45.2	39	33.3	25	-	-
Biomass/plot (gm.)	732.6	64.35	20.5	6.7	-	-
Mean dry wt. per plant (gm.)	1.8	1.65	1.71	1.67	-	-
Biomass of <u>Juncus</u> /plot (gm.)	533.7	735.15	713.3	972.0	873.0	1011.0

Untreated Plots

No.of seedlings Transplanted	900	100	36	16	9	4
No.of survivors	275	19	7	-	-	-
% Survival	30.5	19	19.4	-	-	-
Biomass/plot (gm.)	137.5	7.8	2.73	-	-	-
Mean dry wt. per plant (gm.)	0.5	0.41	0.39	-	-	-
Biomass of <u>Juncus</u> /plot (gm.)	780.0	903.6	1109.4	1178.3	1183.0	1203.0

TABLE 27 (cont.)

LYTHRUM + EPILOBIUM(Mixed)Treated with Fertilizer

Distance (in)	lin.		3in.		5in.		7in.		10in.		15in.	
	<u>L</u>	<u>E</u>	<u>L</u>	<u>E</u>	<u>L</u>	<u>E</u>	<u>L</u>	<u>E</u>	<u>L</u>	<u>E</u>	<u>L</u>	<u>E</u>
No. seedlings Transplanted	450	450	50	50	18	18	8	8	5	4	2	2
No. survivors	365	-	43	-	15	-	5	-	4	-	2	-
% Survival	81.1	-	86	-	83.3	-	62.5	-	80	-	100	-
Biomass/plot (gm)	766.5	-	550.4	-	244.5	-	87.0	-	58.4	-	22.4	-
Mean dry wt. per plant (gm.)	2.1	-	12.8	-	16.3	-	17.4	-	14.6	-	11.2	-
Biomass of <u>Juncus</u> /plot (gm.)	38.0		109.8		149.3		205.1		212.0		228.7	

Untreated Plots

No. seedlings Transplanted	450	450	50	50	18	18	8	8	5	4	2	2
No. survivors	305	-	38	-	14	-	4	-	3	-	1	-
% Survival	67.8	-	76	-	77.7	-	50	-	60	-	50	-
Biomass plot (gm)	396.5	-	148.2	-	68.6	-	13.2	-	12.3	-	1.6	-
Mean dry wt. per plant (gm.)	1.3	-	3.9	-	4.9	-	3.3	-	4.1	-	1.6	-
Biomass of <u>Juncus</u> /plot (gm.)	178.0		378.4		501.8		715.0		812.0		877.0	

plants spaced lin. apart there was no growth of Juncus, but in the other plots there was a greater growth of Juncus in the ^{un}treated than the ~~untreated~~ plots, as shown by their biomass per plot in Table . It can also be seen that there is less Juncus growth where the density of Lythrum is higher. In the unfertilized plots both the low nutrition and competition with Juncus curtail the growth and development of the Lythrum plants. The plants grow unequally as some are very large and others very small.

Compared with Lythrum, the survival, biomass and dry weight per plant is very low in Epilobium both in the treated and untreated plots. On the other hand, in comparing the two treatments the survival and biomass are much better in the fertilized than the unfertilized plots. Unlike the Lythrum plots, there was a tremendous Juncus growth in the Epilobium plots, both in the treated and untreated ones. While the low dry weight of Epilobium in plots with plants spaced lin. apart may be due to mutual competition as well as the effect of Juncus, in the other plots it is the effect of Juncus which causes the elimination of almost all the Epilobium plants where very widely spaced, and those which survive have their growth and development curtailed. Thus the plants have more or less similar dry weights per plant no matter the distance apart they were transplanted.

In the plots where the two species were mixed together, Epilobium was completely suppressed and eliminated both by the Lythrum and Juncus plants. The surviving Lythrum plants were much better in the fertilized plots compared to the unfertilized plots (Table 27).

Discussion

These results have shown that treatment with fertilizer improved the growth in both the species, but in Epilobium it was not enough as the plants failed to grow into normal flowering plants. It would appear that the pH of the soil may be an important factor curtailing the growth of Epilobium since, despite heavy manuring, plants could not resume normal growth. However, due to manuring both the survival and yield improved in Epilobium, but in Lythrum there was a far greater improvement in the yield when compared with survival.

Most probably, the elimination of Epilobium in the mixed plots is due to its slow growth and delayed establishment, during which time rapidly growing Lythrum and Juncus plants suppressed its growth. Conversely, Lythrum not only showed good growth and survival when present in greater density in a unit area by excluding the invasion of Juncus, but even when the plants were widely spaced they showed quick, vigorous growth and establishment, and also successfully

competed with the Juncus even though greatly outnumbered.

It has already been pointed out that the density of plant^{ing}~~ation~~ greatly affected the dry weight gain of an individual, as plants (Lythrum) that were widely spaced had a much higher dry weight than those closely spaced, and the 3in. spacing is ideal for the maximum dry weight yield per plant and survival in a unit area. Also, in the higher density only a few plants flowered compared to the lower densities where most of the plants flowered.

It is concluded that at a high temperature and under the soil conditions in which the experiment was performed, Lythrum showed good growth and establishment whereas Epilobium failed to grow as well as under more favourable conditions.

The comparative success of Lythrum appears to be due to its tolerance of low pH conditions and its well developed compensating mechanism, by which its proportionately increased root system exploiting a larger volume of soil offsets the low nutrient availability in the soil. Its faster growth rate in particular, together with the nature of its leaf mosaic, enables it to overshadow a number of potential competitors (in this case principally Juncus). Although manuring removed one of the factors lowering the competitive ability of Epilobium, i.e. mineral nutrient requirements, this species was still at a disadvantage compared with Lythrum.

From this and other experiments it seems clear that the lack of tolerance of ~~pH~~^{acid soils} below about pH 6 is responsible for the competitive failure of Epilobium under these conditions. To this must be added the "mechanical" failure in seedling establishment of this species, i.e. the inability to get its root system established in all except a very restricted range of substratum conditions. In competition with Juncus the slower growth rate of Epilobium compared to Lythrum results in a lesser competitive ability of Epilobium. There is, therefore, under comparable conditions a greater elimination of spring germinating Epilobium compared with Lythrum.

It must be emphasised that this experiment clearly demonstrates that a number of factors have determined the result, but that laboratory studies combined with appropriate field experiments can demonstrate the complex interaction of these factors and the way in which competition is operating under the conditions of the experiment.

Discussion and Summary of the Field Experiments

The various conclusions and suggestions reached by the laboratory experiments mentioned in the beginning of this chapter have been proved by these field experiments.

Discussed below are the results of the field experiments in their proper context.

The field germination studies have shown the successful retention of viability of seeds by both the species, after long, dry laboratory storage and exposure to the freezing winter of 1968-1969, in so far as both the species showed a flush of germination in the growing season under suitable temperature conditions. Most of the Epilobium seedlings were eliminated due to lack of establishment and the shade of invading weeds, while the survival and establishment of Lythrum seedlings were very high. On the other hand, Lythrum failed to avail itself of the full growing season due to late establishment in July and did not grow beyond a few centimetres in length, while the few surviving Epilobium seedlings developed into small rhizomatous plants by the end of the growing season. However, growth was not enough to cause flowering in the first growing season.

Due to the accumulation of substantial food material in the rhizomes, Epilobium may grow vigorously into flowering plants in the next season and their number may also increase due to vegetative multiplication. Lythrum, however, would still be handicapped in the next growing season by the lack of reserve food material for an invigorated growth and, due to a late start of its active growth (in June), may be over-

grown and eliminated by early growing Epilobium or any other plants.

The support for this hypothesis comes directly from Experiment XVIII (Effect of low temperature and over-wintering on the growth, competition and survival in the high temperature of the following summer). In the mixed plot Epilobium showed much better growth in the autumn of 1968 and, due to an early start of growth in the spring of 1969, grew into tall flowering plants in the summer, thus succeeding ⁱⁿ ~~to~~ suppressing the growth of Lythrum starting very late in June. Even in the pure plots, Lythrum plants were not as fully developed as the Epilobium plants although the results are not very valid due to the pheasant attack.

Compared to this situation, results are very different in the density survival experiments carried out at Silwood Park directly under the high temperature conditions of summer in 1967 and 1968. Here Lythrum grew to its full capacity both in the fertilized and non-fertilized soils, flowering and setting seeds even in the first year of growth, and once established persisted from year to year. While there is no doubt about the direct suppressive effect of Epilobium on the summer growth of Lythrum in the nutrient-rich soil of the Wheat Fen, the dominance of Lythrum in the mixed plots in the Silwood Park experiments is complicated

by the nutrient status and acidity of the soil. Even in the pure plots Epilobium did not survive on dry or wet soil, and the application of fertilizer did not bring about much improvement. It is emphasized that the soil factor is very important for the growth and survival of Epilobium even when the temperature is suitable for its growth. Most probably the elimination of Epilobium in these experiments is the result of exclusion from establishment rather than suppression by Lythrum. On the other hand, many facts have been categorically proved about Lythrum, i.e. it can survive in shade, shows a luxuriant growth at high temperatures and successfully competes with the most dominant plant of the area (Juncus), and can flourish very well in the dry and nutrient-poor soils.

These two opposite situations, i.e. at Silwood Park and Wheatfen Broad, though complicated by the soil factor, clearly show the influence of temperature on growth. On the basis of the above discussion an attempt is made here to understand the occurrence of these plants in nature in different environments.

It is certain that Lythrum seeds do germinate and seedlings establish in the rich soil of the Wheatfen Broad but make very poor growth. There is uncertainty about the continuation of growth in the next season as the regular hot summers are not guaranteed in the British Isles, and since

the plants start their growth very late in the season, the area may be colonized by other plants leading to the elimination of Lythrum. But the seedlings happening to grow on a freshly created bare area may be able to develop and persist temporarily as monospecific stands, but would never last permanently due to delayed and weak growth in mild summers. At the same time, the gradual infiltration and spread of the early growing plants would gradually increase the momentum of their suppressive influence and, in time, may completely eliminate the restricted weakened Lythrum stand. This reasoning may at least explain the observations of Dr. Whitehead, i.e. the appearance of Lythrum in the fens in the bomb craters during World War II, and that of E. A. Ellis, i.e. the appearance of huge beds of Lythrum flourishing temporarily in freshly created "lows" due to coypus grazing. (For details see Chapter III).

On the other hand, in the rich soil of the Wheat fen Broad's though fewer seedlings of Epilobium become established they make substantial growth in the first season, persist from year to year and, at the same time, multiply vegetatively due to the rhizomatous habit of growth, resulting in the establishment of a small monospecific stand. These stands may expand rapidly in area taking advantage of seasonal

growth of cold spring and short day conditions, avoiding competition with other plants and in time may invade vast territories. Contrarily, in Yugoslavia and other central and southern European countries and along the warm coastal areas, due to the early setting in of spring and the sudden rise in temperature, Lythrum no longer is handicapped by the delay in germination and growth and makes vigorous and substantial growth, successfully competing with other plants and establishing itself as a dominant plant of the habitat.

It is concluded that, given a suitable substratum congenial to the growth of both the species, temperature is the decisive factor, controlling the growth, dominance and persistence of the two species in different environmental regions of the world.

X. GENERAL DISCUSSION AND CONCLUSIONS

It is intrinsically the biology of a species that controls its ecological and geographical distribution. In the preceding chapters an experimental investigation dealing with the various aspects of the biology of the two species i.e. germination, early establishment of seedlings and growth in relation to light, temperature and mineral nutrients, have been described. In this chapter these findings are being appraised collectively in an attempt to elucidate their impact on the growth and adaptations of the species and some of the ways in which competition, interaction and selection restrict the two species to their particular patterns of ecological and geographical distribution.

The two species investigated are perennial herbs of low seed weight capable of being dispersed by wind over long distances. The hairy seeds of Ecilobium hirsutum are particularly adapted ^{to} ~~for~~ the dispersal of the species in wet places - its usual habitat. Germination probably takes place during relatively drier periods when the water level has fallen or seeds settle in a depth of water into which light can still penetrate. In general the light requirement of the seeds is so small that it may be supposed an adequate

stimulus to germination is received under almost all circumstances. The amount of light necessary for the germination of Lythrum salicaria is astonishingly small; Clapham (1956) reported that exposure for one second to light of 730 candlepower at 30°C. raised the percentage germination from 1-2 to 30%. This dormancy mechanism of the seeds of both the species is broken by high temperatures (30°C.) at which dark germination occurs. This, probably, is not a great disadvantage as such temperatures do not occur during the critical autumn, winter, spring, period. The light requirement for germination therefore appears to be ecologically advantageous.

The two species show profound differences in their germination characteristics, especially in regard to temperature and soil type. Harper et al. (1960) have already pointed out that differences in germination requirements allow different species to germinate at different sites or times. Both the species can persist for long periods in suitable sites as dormant seeds because seed viability is of several years and the seeds have efficient dormancy mechanisms. This may explain the sudden appearance of large, almost completely monospecific patches of Lythrum in areas laid bare and disturbed by a coypu attack during winter, as observed by Dr. Whitehead and Mr. E. A. Ellis (1963).

Differences between the two species in respect to

temperature are so marked as to allow their germination at different sites or times. Since Epilobium showed a very high percentage germination at below 10°C . and Lythrum only at 20°C ., it is obvious that in Britain Epilobium seeds can germinate in autumn or early spring while Lythrum only in summer. The field experiments have confirmed this hypothesis. The germinability and successful seedling growth of Lythrum both in alkaline and acidic, nutrient rich and poor soils, is an attribute important in its occurrence in a wide variety of habitats. In the case of Epilobium there is poor germination and seedling establishment in acidic soils, in contrast to a flush of germination in moist, rich, alkaline soils, as in the Wheatfen Broad, and most probably the establishment of seedlings in large numbers can take place only in wet sites, thus confining the species to sites with sufficient moisture at the critical period of germination and early establishment.

Germination having been successfully accomplished in any environmental conditions, favourable or unfavourable for subsequent growth, the successful establishment of seedlings depends upon the biology, growth commitments, growth habit and growth rate of the species in the particular environment.

As the seeds are light, they carry only little stored food reserve. It is important, from the survival view

point, that they must germinate under conditions where photosynthesis occurs very soon after germination. Of the two species Lythrum was found to be more tolerant of moderate shade than Epilobium. Also, Lythrum showed a tendency to a compensatory increase in the leaf area and a high unit leaf rate. These differences are important in their ecological distribution. Pearsall (1918) reported an increase in the frequency, growth and flowering of Lythrum with the increase in light intensity in the "closed carr" at Esthwaite Water where trees have fallen and light intensity risen. Field experiments also confirmed the establishment and survival of Lythrum in shade. Laboratory results also suggested that the potential contribution made by individuals to population survival is reduced by a decrease in the light intensity, as shown by the number of capsules and dry weight 'surplus' $W(x - 1)$ in Lythrum; and by the capsule and rhizome number in relation to $W(x - 1)$ in Epilobium. Although in increasing shade there was a reduced level of reproduction there was no reduction in individual seed weight. In other words the essential character and properties of the seed, shown to be necessary for successful germination, were maintained at the expense of seed number.

Under the laboratory conditions both species showed germination under short-photoperiod, and while the post-

germination growth in Lythrum was completely suppressed, Epilobium developed into rosette form plants. This different response to short-day conditions is very important from the view point of their growing period and occurrence in nature in Britain. Because of high temperature requirements the immediate post-germination growth of the seedlings of Lythrum is restricted to a limited period of late summer in Britain. But there is no such restriction imposed on the growth of Epilobium. As it can germinate in autumn the rosette/plates are capable of overwintering and developing into elongated flowering forms in summer. Thus, the period of time taken by Epilobium to complete its life-cycle is far longer than that of Lythrum.

Although in Lythrum there was suppression of growth under short-day conditions the plant showed a marked response to a short light-break in the long dark period under these conditions of growth. Whereas Lythrum developed into tall, normal, flowering plants, Epilobium did not show any response at all. Also, in Lythrum there was no growth response to any photoperiod except the critical photoperiod. There is a critical photoperiod (14 hours) in the case of Epilobium in respect of its growth form and flowering and, unlike Lythrum, all increments of light either of intensity or duration during the short-day treatment, resulted in a

greater amount of carbon fixation.

In Britain, short-day lengths and low temperatures occur together, while long days are accompanied by high temperatures. Laboratory evidence shows that there is a high mortality rate and very little growth in Lythrum at low temperatures and short days, compared with the efficient growth of Epilobium which develops into short rosette/plate like plants. On the other hand, at high temperatures Lythrum shows a much better performance and growth rate than Epilobium.

The behaviour of the two species in respect of germination and growth to temperature and photoperiod seems to be complementary. In Epilobium the ability to germinate at low temperatures is complemented by an efficient growth of the seedling into a dwarf rosette/plate at low temperatures and short-day conditions. Similarly, in Lythrum the requirement of high temperatures for germination is accompanied by a rapid growth at this temperature and a complete suppression of growth at low temperatures and short-day conditions. Due to these differences in biology, the two species are differently adjusted to environments in Britain. Epilobium is adapted to long exposure to the environment during its life-cycle and passes through

extremes of environment i.e. from lowest temperature and day length to highest temperature and longer day lengths. It would appear that growth in Epilobium is a phasic phenomenon, and that the plant develops up to a particular phase in a given photoperiod and temperature and increases with their increase. Thus, the growth responses of Epilobium to the environments are gradual and diffused. This integrated growth of the plant may be responsible for its slow rate of growth. In contrast, the germination and growth in Lythrum is an all or none phenomenon. The plant is exposed to the environments only for a short period, as it completes its life-cycle in one growing season, exploiting efficiently the short interval of favourable temperatures (summer) and all the various aspects of its biology are well suited towards this end. The adaptation of Epilobium to periodic changes of environments is convincing evidence of the perfection which the genotype constitution of the protoplasm has attained in its ability to change from the latent to the vital condition - an ability upon which its very existence in the British type of climate depends.

This difference in response to the environments underlies the difference in their ecological distribution in the British Isles, as Epilobium is common throughout the

cold northern regions, while Lythrum is less frequent in Scotland and absent from most of the north, (Clapham, Tutin and Warburg, 1952); on the contrary, it is widespread and dominant along the warm west coast of Ireland (Pers. comm. Dr. Hamilton). The general tendency of Lythrum to increase in frequency of occurrence to the south (where it is common along the warm coastal areas of central and southern Europe) and the greater dominance of Epilobium in the northern regions of the world and confinement to higher altitudes, is a reflection of the temperature control of their geographical distribution.

With regard to the mineral status of the soil, different distributions of the species are to be expected not only on grounds of the relative ability of the seedlings of the species to grow and their possession, or not, of an adaptive compensating mechanism of growth in conditions of stringency, but also on their nutrient status and, consequently, their demands on the site, their nutrient uptake ability and the amount of growth each species is committed to making.

A comparison of the two plants with respect to their growth in a series of nutrient dilutions, has shown that Epilobium is not only a plant of high nutrient

requirements but also its uptake of the major nutrients like potassium, nitrogen and phosphorous, is more severely curtailed under nutrient stringency than that of Lythrum. On the contrary, Lythrum has a dual advantage of low nutrient requirements and high uptake capacity under stringent conditions, which would facilitate its growth on the nutrient-poor soils. Thus, in terms of logistics of supply and demand, Lythrum would have a natural advantage over Epilobium in the event of competition. In addition to this, Lythrum responds to nutrient stringency by a phenotypic plastic response in terms of increased root proportionately to shoot. ~~Considered teleologically~~ This compensatory change is an adaptation to low nutrient supply.

Due to the simpler plant structure in Lythrum and the completion of its life-cycle in a short period of time, it would seem that in the course of evolution this species has adapted to nutrient-poor situations by combining a low-rate demand on the nutrient supplying power of the system, and the greater efficiency of uptake, with the changes in its morphological balance. Most probably, the selective process caused an over-all decline in the plant size with a corresponding increase in the competitive and survival value.

In relation to the stringency of supply of individual nutrients, it has been shown that growth in Lythrum is less affected than in Epilobium by the deficiency of potassium nitrogen and phosphorus. Of the three nutrient elements investigated, the response to potassium stringency was markedly different in the two species. Whereas Lythrum showed normal reduction in growth with a decrease in potassium supply, in Epilobium the great reduction in growth was accompanied by physiological disorders, such as the necrosis of leaves and root malformation, which increased in intensity with the increased stringency of potassium. Moreover, there was complete suppression of flower formation and rhizome production even at the lowest level of stringency, (K/10). On the other hand, in Lythrum flower formation depends on the attainment of a certain minimum amount of dry weight irrespective of phosphorus, nitrogen or potassium deficiency. It is suggested that it is the deficiency of potassium which would play a crucial and decisive role in determining the establishment and growth of the two species in soils of low nutrient status.

In increasing stringency of major nutrient elements there is a corresponding reduction in the level of reproduction and yield, thus having long term effects on

the survival and continuation of these plant communities as, potentially, a lower contribution is made to population and hence to population dynamics.

The profound differences in growth responses to light, temperature and nutrients, as exhibited by the two species under investigation, have great impact on their competitive abilities and survival in nature. Various aspects of competition, as studied under laboratory conditions, showed Lythrum to be highly successful in the inter as well as intra-specific competition both in the high and low nutrient levels at a high temperature of 25°C.

At a low nutrient level Lythrum suppresses the growth of Epilobium, due to its efficient nutrient uptake, faster growth rate and by the phenotypic plasticity of its morphological balance, and with time completely eliminates Epilobium. At a high nutrient level, because of its erect life form and rapid growth rate, Lythrum has a great advantage as it out-grows and covers the low, prostrately growing Epilobium at an early stage of growth, thus completely eliminating it later on. These laboratory findings were later confirmed by the field experiments at Silwood Park, where the soil was not only poor in nutrition, but also acidic in nature.

It was suggested that the elimination of Epilobium at high temperatures is primarily due to its life-form. The initial obligate, excessively leafy, prostrate form of its seedlings, while seemingly well adapted to its growth in autumn and spring, proves self-destructive for summer growth compared to the elongate summer form of the seedlings of Lythrum, for as a rosette it will be easily over-topped and eliminated in the intra-specific competition. In the inter-specific competition Lythrum has a very high survival value and the dry weight gain of individuals depends upon their density. On the other hand, if Epilobium is given the seasonal advantage of growth at the low temperature of autumn or early spring, it exerts a strong suppressive influence on the growth of Lythrum in the next summer; (field experiment at Wheatfen Broad). This underlies the success and dominance of this plant in British climatic conditions.

From the various field experiments carried out during this investigation, it is concluded that Epilobium is a good colonizer under the most suitable conditions of soil and temperature. It takes advantage of seasonal growth for its establishment, has a tendency to avoid competition, and spreads in territory due to its rhizomatous habit of growth. Lythrum, on the other hand, is not only an

aggressive colonizer in favourable circumstances of soil and temperature, especially the latter, but also an efficient competitor even in poor soil conditions if given a chance to establish. The occurrence of Lythrum as frequently scattered individuals amongst other plant communities in Britain points to the efficiency of competition and survival of this plant.

Germination characteristics, the pattern of development ^{of its phases} and the ~~the~~ timing, plant form and reaction to temperature, light, and the chemical nature of the substrate have been discussed to give a greater understanding of the various aspects of biology in an effort to explain the mechanisms of competition and survival of the species concerned, in nature.

It is known that the action of the external environment on the plant is very complex, and it is desirable to analyse it into component parts and to experiment with a ^{factor} ~~factor~~, varying its intensity, and keeping other factors constant as far as possible. It is realised that it has its dangers as no factor ever acts in isolation from other factors. In natural habitats, the observed distribution and inter-relationship of the competing species are the outcome of a long period of progressive adjustment. Indeed, Harper (1961) has already emphasized that, to most ecologists, the term "competition" carries this long-term implication and

covers all those forces by which one organism succeeds at the expense of another. Nevertheless, one of the factors often appears to have a predominating influence. In the present investigation of the comparative biology of these two species, it is certain that temperature is a predominant factor, governing the ecological and geographical distribution of the two species, whereas light and nutrient factors are of subordinate nature, affecting the localized distribution of the species in the same climatic region. In other words, the greater dominance of Epilobium in the British Isles and northern regions of Europe and that of Lythrum in Yugoslavia and along the warm coastal, low lying areas of central and southern Europe, is predetermined by the temperature differences.

The above investigations have shown the adaptive nature of phenotypic plasticity of form of the plants in a range of conditions, but do not show how wide the range of genetic variation is within each species nor the importance of this in their distribution. However, Mulligan (1957) suggested that there may be a close relationship between the ploidy, genetic versatility, life form, duration, and wide range of distribution exhibited by Lythrum salicaria in various habitats and ecological niches. Nevertheless,

there is no evidence of different physiological races, (Pers. comm. Dr. Whitehead, who has grown a range of European material) despite differences of ploidy etc. in Lythrum, so that conclusions based on the material used in this study are applicable throughout the distribution of this species. In contrast, Epilobium as it occurs in Britain, has²_A relatively stable genotype and is confined to particular ecological niches, i.e. rich alkaline fens.

In the end, it remains to be said that while no claim is being laid that every factor or aspect of the biology has been considered, nor that a complete explanation is offered, nevertheless it is emphasized that integrated biological studies of the present kind may help to give a clearer understanding of the interaction between the species and environments, the mechanisms of competition and the adaptation of species to their particular habitats.

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Experiment I

The effect of Temperature on germination.

% Mean number of seedlings with expanded cotyledons.

Lythrum salicaria

(Light)

Days from
sowing

Temperature (°C)

	14°C	15°C	20°C	25°C	30°C
1					
2			3.4 ± 1.14	19.0 ± 1.79	15.0 ± 1.24
3			34.0 ± 1.58	27.8 ± 1.92	38.4 ± 1.69
4			62.8 ± 1.86	46.8 ± 1.78	49.0 ± 1.42
5			69.2 ± 1.47	55.8 ± 1.28	63.6 ± 1.86
6			74.6 ± 1.48	66.4 ± 1.40	71.2 ± 1.92
7		0.8 ± .38	80.4 ± 1.40	69.6 ± 1.58	77.6 ± 2.24
8			83.6 ± 1.57	73.4 ± 1.42	79.4 ± 1.92
9			86.4 ± 1.42	76.0 ± 1.48	81.0 ± 1.42
10			87.8 ± 1.40	77.4 ± 1.62	84.0 ± 1.40
11			89.2 ± 1.62	77.8 ± 1.28	85.0 ± 1.38
12			90.2 ± 1.28	78.6 ± 1.16	85.8 ± 1.42
13			90.4 ± 1.16	79.4 ± 1.22	86.2 ± 1.26
14		1.2 ± .375	91.4 ± 1.7	80.2 ± 1.32	86.4 ± 1.40
15			92.2 ± 1.11	81.0 ± 1.28	86.6 ± 1.42
16			92.2 ± 1.11	81.6 ± 1.42	87.0 ± 1.36
17	0.2 ± .02		92.8 ± 1.03	82.2 ± 1.57	87.0 ± 1.36
18				82.4 ± 1.40	
19				82.8 ± 1.31	
20				83.0 ± 1.62	
21		1.8 ± .51		83.4 ± 1.24	
22				83.4 ± 1.24	
23				83.6 ± 1.35	
25	0.4 ± .025	2.6 ± .51			
34	0.8 ± .02				
35		3.2 ± .68			
40		5.0 ± .84			
41	1.0 ± .49				
45		6.0 ± .175			
46	1.2 ± .375				

Experiment I - Continued

Epilolium hirsutum

(Light germination)

Days from
Sowing

Temperature (°C)

	5	7	8	10	15	20	25	30
4						16.6±1.36	2.8±1.3	
5					7.2±1.32	55.0±2.8	33.8±2.8	9.0±2.13
6					15.0±2.75	78.0±1.42	60.6±2.4	27.2±2.05
7					19.4±3.82	85.8±1.36	70.6±1.78	39.0±1.92
8					25.2±5.68	90.8±1.40	75.0±1.40	61.2±1.40
9					31.4±5.01	94.6±1.45	80.0±1.32	73.6±1.78
10					38.4±4.64	96.0±1.78	82.4±1.42	77.4±1.43
11				0.8±.375	44.0±4.68	96.8±1.52	84.8±1.36	82.0±1.41
12				7.2±1.82	48.4±5.0	97.6±1.43	85.4±1.82	84.6±1.38
13				15.6±3.21	54.6±5.11	98.2±1.46	85.8±1.29	87.6±1.82
14				22.0±4.2	58.0±4.82	99.2±1.28	86.2±1.42	87.6±1.32
15				33.4±5.12	62.6±4.28		87.6±1.40	87.8±1.38
16				43.0±4.72	67.0±5.0		88.0±1.36	88.2±1.29
17				50.6±6.18	71.2±4.78		89.2±1.29	89.0±1.38
18				57.6±5.62	75.0±4.77		89.2±1.29	90.6±1.42
19				65.0±5.15	78.8±3.88		89.4±1.40	92.4±1.48
20				72.0±4.89	83.4±3.92		90.6±1.36	92.8±1.42
21				73.0±4.77	87.0±4.12		91.0±1.22	
22				75.2±5.15	88.6±4.08			
23			0.6±.4	76.4±4.92	91.0±3.13			
24		0.4±.4		79.0±3.92	91.8±2.94			
25				81.2±4.12	92.6±2.26			
26		0.6±.4	1.0±.142	82.0±3.86	93.8±2.82			
27				84.4±4.75	94.6±1.87			
28					95.0±1.42			
31			2.4±.39	85.0±3.92				
32				85.4±3.86				
33				85.6±3.26				
35		0.8±.375		85.8±3.12				
36				86.4±3.02				
37				86.6±3.12				
40	0.4±.025	1.4±.4		87.4±3.08				
41								
42			3.0±.1					
44				88.0±2.98				
45	0.8±.02							
48		1.6±.4						
50	1.0±.49		3.4±.25					
52		2.0±.49						

Experiment I - Continued

Dark Germination

Lythrum salicaria

Days from sowing	Temperature (°C)		
	20°C	25°C	30°C
3			6.4 ± 1.28
4		0.2 ± .02	13.2 ± 2.78
5		0.8 ± .375	16.4 ± 2.68
6	0.2 ± .02	4.4 ± .78	18.6 ± 2.23
7		5.8 ± 1.07	21.0 ± 2.62
8		6.4 ± 1.20	21.8 ± 2.46
9	0.6 ± .4	7.4 ± 1.42	22.0 ± 2.34
10		7.8 ± 1.28	22.2 ± 2.24
11		8.0 ± 1.04	22.2 ± 2.24
12	0.8 ± .375	8.4 ± 1.16	22.4 ± 2.1
13			23.6 ± 2.21
14		8.6 ± 1.28	24.0 ± 1.87
15			24.8 ± 1.62
16			
17			
18	1.0 ± .49		
19			
20			
24		8.8 ± 1.16	
26		9.0 ± 1.05	

Experiment I - Continued

Epilolium hirsutum

(Dark Germination)

Days from sowing	Temperature (°C)		
	20°C	25°C	30°C
5		2.2 ± 1.48	1.2 ± .375
6		11.4 ± 3.87	1.4 ± .4
7	0.4 ± .4	15.2 ± 4.8	1.8 ± .51
8	0.6 ± .4	19.0 ± 5.3	
9	0.6 ± .4	20.8 ± 5.3	
10	0.8 ± .375	21.8 ± 5.5	
11	1.0 ± .49	22.6 ± 5.6	2.0 ± .49
12	1.2 ± .375	23.2 ± 5.30	
13		23.4 ± 5.7	
14		25.0 ± 5.4	3.2 ± 1.1
15		26.8 ± 5.8	4.2 ± .78
16	1.4 ± .4	28.4 ± 5.74	6.0 ± .95
17		28.4 ± 5.74	6.6 ± 1.23
18	1.8 ± .51	28.6 ± 5.64	
19	2.0 ± .49	28.8 ± 5.67	6.8 ± 1.11
20	3.0 ± .1	29.0 ± 5.61	7.0 ± 1.02
21	4.0 ± .82		
22	4.4 ± .78		
23	5.0 ± .84		

Experiment III Germinability of E. hirsutum and L. salicaria in soil and sand.
(In light and at a temperature of 20°C)

Days from sowing	SOIL		SAND	
	<u>Lythrum salicaria</u>	<u>Epilobium hirsutum</u>	<u>Lythrum salicaria</u>	<u>Epilobium hirsutum</u>
7			12.0 ± 1.97	
8			35.0 ± 2.82	10.2 ± 1.48
9			49.8 ± 3.14	39.0 ± 4.72
10			55.0 ± 5.14	51.0 ± 3.18
11			65.2 ± 3.85	55.0 ± 2.11
12	9.2 ± 1.58		69.6 ± 3.14	62.4 ± 3.28
13	18.0 ± 2.5		72.0 ± 2.87	68.0 ± 3.01
14	22.4 ± 2.92		78.0 ± 2.15	72.0 ± 2.92
15	29.0 ± 3.5		80.6 ± 1.86	76.8 ± 2.87
16	35.6 ± 4.8	5.2 ± 1.92		82.4 ± 2.02
17	45.0 ± 5.6			88.2 ± 2.07
18	51.6 ± 4.2	8.8 ± 1.68		92.6 ± 1.42
19	58.0 ± 3.8	16.1 ± 4.10		94.0 ± 1.32
20	62.8 ± 3.92	22.2 ± 3.98		
21	65.2 ± 4.28	24.1 ± 4.2		
22	65.0 ± 4.28	29.2 ± 4.8		
23	67.0 ± 3.92	31.0 ± 4.86		
24	68.0 ± 3.75	31.0 ± 4.86		
25	68.0 ± 3.75	31.0 ± 4.86		

Experiment IV The germinability of seeds of E. hirsutum and L. salicaria after a period of cold dry storage. At 20°C in light

Days from sowing	<u>Lythrum salicaria</u>		<u>Epilobium hirsutum</u>	
	0 year	3 years	0 year	3 years
2	3.4 ± 1.14			
3	34.0 ± 1.58			
4	62.8 ± 1.86	5.0 ± 0.84	16.6 ± 1.36	
5	69.2 ± 1.47	28.0 ± 1.82	55.0 ± 2.8	8.0 ± 2.31
6	74.6 ± 1.48	44.0 ± 1.24	78.0 ± 1.42	30.6 ± 1.98
7	80.4 ± 1.40	56.0 ± 1.40	85.8 ± 1.36	52.0 ± 2.18
8	83.6 ± 1.57	75.0 ± 1.86	90.8 ± 1.40	72.8 ± 3.02
9	86.4 ± 1.42	81.0 ± 1.42	94.6 ± 1.45	84.4 ± 1.40
10	87.8 ± 1.40	82.0 ± 1.58	96.0 ± 1.78	88.6 ± 1.68
11	89.2 ± 1.62	83.0 ± 1.40	96.8 ± 1.52	92.0 ± 1.26
12	90.2 ± 1.28	84.0 ± 1.24	97.6 ± 1.43	95.0 ± 1.64
13	90.4 ± 1.16		98.2 ± 1.46	96.2 ± 1.42
14	91.4 ± 1.70		99.2 ± 1.28	
15	92.2 ± 1.11		100.0	
16	92.2 ± 1.11			97.0 ± 1.38
17	92.8 ± 1.03			

Experiment V The effect of light intensity on the growth and morphology of L. salicaria and
E. hirsutum. Primary Data (Mean dry weights and leaf area)

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	100% daylight Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	0.40	0.287	0.121	0.092	0.500	0.505	0.310	0.120	0.120	0.556
1	1.53	2.77	0.62	1.12	4.51	2.8	5.42	1.36	1.27	8.05
2	10.73	19.15	3.50	6.10	28.75	31.38	73.69	15.91	22.61	112.21
3	53.54	110.60	32.33	55.92	198.85	96.70	272.86	121.94	210.55	605.35
4	118.77	328.97	122.83	142.53	594.33	362.77	896.10	625.54	444.84	1966.48
5	484.60	1130.63	594.08	403.48	2128.19	840.0	2185.98	2005.00	839.50	5030.48
6	888.30	2407.53	3787.46	1707.50	7902.49	1803.3	5542.73	9724.20	2358.66	17625.59
7	1440.0	4091.93	8552.33	2597.93	15242.19	2133.33	6884.66	16419.53	4765.93	28070.12
70% daylight										
Initial	0.40	0.287	0.121	0.092	0.500	0.505	0.310	0.120	0.120	0.550
1	1.54	2.15	0.59	0.76	3.50	3.85	7.40	1.65	1.20	10.25
2	7.16	13.96	2.85	4.46	21.27	17.97	37.14	8.83	8.96	54.93
3	49.60	84.48	26.89	35.14	146.51	77.92	161.02	71.02	78.15	310.19
4	150.90	322.20	134.47	106.85	563.52	318.25	558.91	338.76	171.96	1069.63
5	509.16	977.53	690.30	300.00	1967.83	598.33	1067.93	915.01	268.71	2251.65
6	930.00	2019.60	3460.90	1192.75	6673.25	1480.00	2967.46	3882.33	639.86	7489.65
7	1380.00	3002.60	7016.13	1579.60	11598.33	2216.66	5303.86	8762.82	1775.33	15842.02

Experiment V - Continued

40% daylight

L. salicaria

E. hirsutum

Harvest No.	leaf area cm ²	leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	0.40	0.287	0.121	0.092	0.50	0.505	0.310	0.120	0.120	0.550
1	1.73	2.80	0.47	0.78	4.05	2.80	4.84	1.00	0.74	6.58
2	6.88	11.18	2.25	3.51	16.95	18.78	36.79	10.02	7.51	54.32
3	40.33	69.30	24.80	22.84	116.94	89.83	156.50	87.44	64.67	308.61
4	108.38	237.48	111.01	68.41	416.90	265.20	403.57	292.81	94.11	790.49
5	285.28	509.28	342.21	122.22	973.71	463.00	842.72	683.57	177.47	1703.76
6	826.60	1434.40	1828.06	432.60	3695.06	1475.00	2451.50	3015.13	513.53	5980.16
7	1225.00	2597.40	4794.70	1030.30	8422.40	2021.66	3862.33	5469.86	904.33	10236.52

532

Primary data for harvest eight used only to count the number of flowers and fruits and regression on the surplus dry weight.

Day light levels

100%

70%

40%

	Plant D. weight mgs.	Loge	Plant D. weight mgs.	Loge	Plant D. weight mgs.	Loge
E. hirsutum	92561.7	11.43564	48245.9	10.78406	35965.9	10.49034
L. salicaria	33542.6	10.42059	25816.9	10.15880	15561.4	9.65253
	Plant Leaf area cm ²	Loge	Plant Leaf area cm ²	Loge	Plant Leaf area cm ²	Loge
E. hirsutum	2120.0	7.65917	2040.0	7.62070	2005.0	7.60334
L. salicaria	570.0	6.35713	980.0	6.88766	965.0	6.87213

Experiment V

The effect of light intensity on the growth and morphology of L. salicaria and E. hirsutum.

Mean Dry Weight mgs. (Log₁₀ Values)

No. of harvests	<u>E. hirsutum</u>			Light levels	<u>L. salicaria</u>		
	100%	70%	40%		100%	70%	40%
Int.	-0.59784	-0.59784	-0.59784		-0.69315	-0.69315	-0.69315
1	2.08006	2.32729	1.88403		1.50630	1.25276	1.39872
2	4.72206	4.00606	3.99489		3.35866	3.05729	2.83007
3	6.40581	5.73722	5.73211		5.29261	4.98701	4.76159
4	7.58401	6.97495	6.67266		6.38744	6.33421	6.03285
5	8.52328	7.71943	7.44056		7.66302	7.58469	6.88111
6	9.77712	8.92124	8.69621		8.97493	8.80586	8.21475
7	10.24248	9.67045	9.23369		9.63183	9.35847	9.03865

L.S.D. at 5% level = 0.0936

L.S.D. at 1% level = 0.1245

L.S.D. at 5% level = 0.0690

L.S.D. at 1% level = 0.091770

Initial harvest excluded from the analysis of variance.

Experiment V The effect of light intensity on the growth and morphology of L. salicaria and E. hirsutum.

Mean Leaf area cm^2 (Log_e values)

No. of harvests	<u>E. hirsutum</u>			Light levels	<u>L. salicaria</u>		
	100%	70%	40%		100%	70%	40%
Int.	-0.68320	-0.68320	-0.68320		-0.91629	-0.91629	-0.91629
1	1.02962	1.34807	1.02962		0.42527	0.43178	0.54870
2	3.44618	2.88872	2.93276		2.37304	1.96851	1.92862
3	4.57148	4.35569	4.49792		3.98043	3.90399	3.69709
4	5.89373	5.76286	5.58049		4.77723	5.01728	4.68564
5	6.73341	6.39415	6.13773		6.18335	6.23285	5.65354
6	7.49730	7.29980	7.29642		6.78932	6.83519	6.71732
7	7.66542	7.70375	7.61164		7.27240	7.22984	7.11071
L.S.D. at 5% level = 0.0600					L.S.D. at 5% level = 0.056		
L.S.D. at 1% level = 0.0798					L.S.D. at 1% level = 0.07448		

Initial harvest excluded from the analysis of variance.

Experiment V -Continued
 "Surplus" dry weight $W(\alpha - 1)$

E. hirsutum

Harvest intervals	100%		70%		40%		Light Levels
	Surplus weight mgs	Log _e	S. weight mgs.	Log _e	S. weight mgs.	Log _e	
I - 1	4.5357	1.51182	4.5100	1.506	2.953762	1.082	
I - 2	32.350	3.47661	15.869	2.7645	14.672	2.685	
I - 3	201.4605	4.30527	79.781	4.3795	68.419	4.2256	
I - 4	479.821	6.173	186.864	5.23	127.032	4.844	
I - 5	1156.004	7.053	394.264	5.977	303.951	5.717	
I - 6	4727.183	8.461	1441.009	7.273	984.932	6.89265	
I - 7	8376.124	9.033	3553.366	8.175	1903.991	7.5517	
I - 8	40940.173	10.619	17884.792	9.7915	12156.508	9.4055	

Experiment V - Continued
 "Surplus" dry weight $W(\alpha - 1)$

L. salicaria

Harvest intervals	100%		70%		40% Light levels	
	Surplus weight mgs	Log _e	S. weight mgs.	Log _e	S. weight mgs.	Log _e
I - 1	2.884	1.05779	1.5531	0.444	1.733	0.548
I - 2	6.664	1.89612	6.382	1.85317	4.0388	1.396
I - 3	44.224	3.78917	26.134	3.26301	21.326	3.05971
I - 4	144.790	4.9754	103.874	4.643	83.649	4.42664
I - 5	376.649	5.93121	310.661	5.7388	148.861	5.003
I - 6	2012.609	7.607	1504.417	7.31598	675.28	6.515
I - 7	3962.972	8.28476	2712.965	7.905	1788.749	7.49
I - 8	17710.493	9.782	10068.591	9.217	5104.139	8.538

Experiment VI The effect of daylength on the germination and growth form of Epilobium hirsutum
and Lythrum salicaria. Primary data (Mean dry weights and leaf area).

16 hours daylength

<u>L. salicaria</u>						<u>E. hirsutum</u>				
Harvest No.	leaf area cm	leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	0.14	0.118	0.070	0.078	0.266	0.26	0.174	0.054	0.062	0.290
1	2.20	4.92	0.66	2.12	7.70	6.90	17.00	3.90	3.80	24.70
2	27.00	68.50	12.90	25.40	106.80	127.00	338.80	141.40	112.20	592.4
3	259.00	537.96	195.93	182.90	916.79	595.96	1479.00	1659.00	745.00	3883.00
4	824.44	1955.28	1565.26	897.11	4417.65	1240.00	3047.10	4496.00	1706.10	9249.20
5	1178.36	3060.30	3259.30	1649.60	7969.20	1953.00	5546.20	10433.30	3092.30	19071.80

537

9 hours daylength

Initial	0.14	0.118	0.070	0.078	0.266	0.26	0.174	0.054	0.062	0.290
1	0.75	1.20	0.40	0.60	2.20	2.4	4.60	0.80	0.60	6.00
2	1.53	2.986	0.724	3.413	7.123	20.0	33.00	5.60	5.40	44.00
3	2.89	5.192	2.178	8.500	15.870	74.46	163.0	30.00	32.60	225.60
4	8.44	15.18	5.70	22.00	42.88	237.00	545.20	129.00	126.20	800.40
5	27.00	49.8	14.2	62.00	126.00	449.50	1339.0	333.0	327.0	1999.00

Experiment VI - Continued

Mean Dry Weight mgs. (Log_e values)					Mean Leaf Area cm^2 (Log_e values)			
No. of Harvests	<u>E. hirsutum</u> <u>Log_{10} values</u>		<u>L. salicaria</u>		<u>E. hirsutum</u>		<u>L. salicaria</u>	
	Photoperiods				Photoperiods			
	16-hrs.	9-hrs.	16-hrs.	9-hrs.	16-hrs.	9-hrs.	16-hrs.	9-hrs.
I	-1.4624	-1.4624	-1.32426	-1.32426	-1.34707	-1.34707	-1.96611	-1.96611
1	2.3927	-0.78	2.04122	0.78846	1.93152	0.87547	0.78846	-0.28768
2	2.7723	1.64	4.67088	1.96333	4.84419	2.99573	3.29584	0.49470
3	3.59	2.35	6.82090	2.76449	6.39024	4.30946	5.55683	1.07158
4	3.96	2.90	8.39332	3.75846	7.12287	5.46805	6.71478	2.13298
5	4.28	3.30	8.98339	4.75359	7.57710	6.10925	7.07180	3.29584
L.S.D. at 5% level = 0.1325		L.S.D. at 5% level = 0.17178		L.S.D. at 5% level = 0.1266		L.S.D. at 5% level = 0.12571		
L.S.D. at 1% level = 0.17704		L.S.D. at 1% level = 0.2295		L.S.D. at 1% level = 0.1685		L.S.D. at 1% level = 0.16794		

Initial harvest excluded from the analysis of variance

Experiment IX Effect of light-break on growth in short-photoperiodic conditions.

Primary data (Mean dry weights and leaf area)

8 + 1 hours Photoperiod

<u>L. salicaria</u>						<u>E. hirsutum</u>				
Harvest No.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	0.45	0.35	0.15	0.11	0.61	0.6	0.5	0.18	0.20	0.88
1	1.536	4.40	1.4	1.5	7.3	10.8	22.7	5.74	5.06	28.44
2	15.44	27.74	6.63	7.96	42.33	73.0	191.50	68.70	59.60	319.80
3	133.20	242.44	74.60	53.72	370.76	258.4	632.68	353.82	177.90	1164.40
4	483.00	852.88	573.56	251.36	1677.80	336.66	770.966	573.566	222.866	1567.398
5	799.00	1245.06	957.88	377.68	2580.62	408.60	929.86	671.92	268.06	1869.84
6	1088.3	1808.0	1765.90	471.20	4045.10	444.0	1109.00	751.66	230.46	2091.12
7	1463.0	3216.3	4610.2	3778.9	11605.4					

hrs.

9.00/Photoperiod

Initial	0.45	0.35	0.15	0.11	0.61	0.6	0.5	0.18	0.20	0.88
1	1.27	3.04	1.14	1.05	5.23	6.86	15.486	3.726	3.330	22.545
2	3.544	7.97	3.86	5.84	17.67	44.30	105.89	38.18	28.05	172.141
3	15.5	36.26	13.92	20.62	70.80	242.00	548.58	319.90	169.08	1037.56
4	46.00	78.12	39.70	61.62	179.44	361.16	756.06	327.51	201.58	1285.15
5	150.8	243.70	108.00	213.90	565.60	422.50	1043.80	559.65	262.87	1866.32
6	314.5	542.00	152.00	548.00	1242.00	507.0	1282.72	797.80	373.10	2453.62
7	444.0	817.80	389.30	1952.5	3159.60					

Experiment IX - Continued

No. of Harvests	Mean Dry Weight mgs. ($\log_e$ values)				Mean Leaf Area cm^2 ($\log_e$ values)			
	E. hirsutum		L. salicaria		E. hirsutum		L. salicaria	
	Photo periods		Photo periods		Photo periods		Photo periods	
	9.00 hrs.	8+1 hrs.	9.00 hrs.	8+1 hrs.	9.00 hrs.	8+1 hrs.	9.00 hrs.	8+1 hrs.
Int.	-0.12783	-0.12783	-0.49430	-0.49430	-0.51083	-0.51083	-0.79851	-0.79851
1	3.11530	3.51155	1.65250	1.98787	1.92571	2.37955	0.23902	0.43178
2	5.14836	5.76832	2.87356	3.74550	3.79078	4.29046	1.25675	2.73737
3	6.94532	7.06018	4.25986	5.91620	5.48893	5.55453	2.74084	4.89187
4	7.15856	7.35756	5.18999	7.42526	5.88928	5.81892	3.82864	6.18002
5	7.57490	7.53369	6.33791	7.85578	6.12928	6.01251	5.01728	6.68337
6	7.80537	7.64546	7.12445	8.30524	6.22852	6.09583	5.75257	6.99216
7			8.05804	9.35920			6.09582	7.28824
	L.S.D. at 5% level = 0.07276		L.S.D. at 5% level = 0.0916		L.S.D. at 5% level = 0.09398		L.S.D. at 5% level = 0.136	
	L.S.D. at 1% level = 0.09720		L.S.D. at 1% level = 0.1215		L.S.D. at 1% level = 0.12555		L.S.D. at 1% level = 0.181	

Initial harvest excluded from the analysis of variance

Experiment X Effect of different dilutions of a standard nutrient solution on growth.
 Primary Data (Mean dry weights and leaf area).

Standard Solution

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.70	1.80	0.92	1.04	3.76	2.65	3.26	2.06	2.16	7.48
1	35.04	65.47	18.65	18.68	102.80	63.11	89.10	40.02	13.00	142.12
2	191.60	315.71	208.64	61.29	585.64	258.42	367.36	283.41	41.45	692.22
3	356.50	721.26	620.64	180.47	1522.37	465.11	815.46	854.18	129.36	1799.00
4	1306.00	3144.78	3356.58	689.34	7190.70	934.00	2109.17	2645.98	358.87	5114.02
5	3014.00	7743.70	13673.00	1645.10	23061.80	3792.00	8629.00	12497.20	1460.20	22586.40

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S/10 Dilution

Initial	1.70	1.80	0.92	1.04	3.76	2.65	3.26	2.06	2.16	7.48
1	20.33	42.61	15.43	18.88	76.92	22.45	39.77	22.89	17.20	79.86
2	30.54	100.33	57.55	50.57	208.45	41.35	105.84	77.57	38.36	221.77
3	37.32	182.08	107.18	96.12	385.38	52.50	178.05	147.45	62.42	387.92
4	43.00	299.09	186.69	197.92	683.70	59.70	287.53	259.52	114.77	661.82
5	92.29	505.72	317.12	483.72	1306.56	78.75	358.85	375.73	188.33	922.91

Experiment X - Continued

S/50 Dilution

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.70	1.80	0.92	1.04	3.76	2.65	3.26	2.06	2.16	7.48
1	4.96	19.66	5.81	13.46	38.93	6.03	26.18	12.85	12.78	51.81
2	6.62	39.38	13.89	25.06	78.33	7.21	39.58	21.38	16.32	77.28
3	8.74	63.80	23.67	39.26	126.73	7.80	48.48	31.56	18.66	98.70
4	9.20	74.56	30.92	63.20	168.68	8.10	65.00	43.67	21.39	130.06
5	14.85	96.88	45.43	111.55	253.86	9.50	72.32	60.01	25.50	157.83

S/100 Dilution

Initial	1.70	1.80	0.92	1.04	3.76	2.65	3.26	2.06	2.16	7.48
1	1.93	9.73	2.46	5.16	17.35	3.05	12.03	7.71	5.10	24.84
2	2.00	12.96	3.76	8.52	25.24	3.35	18.08	11.97	7.83	37.88
3	2.11	15.67	5.08	13.31	34.06	4.02	23.37	18.23	10.68	52.28
4	2.33	19.36	7.11	18.07	44.54	4.53	29.36	22.04	12.87	64.27
5	2.67	19.87	8.40	27.07	56.34	5.47	33.83	26.00	18.17	78.00

Experiment X - Continued

S/200 Dilution

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.70	1.80	0.92	1.04	3.76	2.65	3.26	2.06	2.16	7.48
1	1.82	6.58	2.27	3.36	12.21	2.87	12.81	7.87	4.71	25.39
2	1.94	7.39	3.07	6.30	16.76	3.01	15.00	9.45	7.07	31.52
3	2.07	12.60	5.00	11.29	28.89	3.23	20.15	13.91	8.63	42.69
4	2.20	13.02	5.67	13.57	32.26	3.40	21.45	15.73	9.00	46.18
5	2.43	15.16	6.20	19.90	41.26	3.64	24.36	18.10	11.21	53.67

S/300 Dilution

Initial	1.70	1.8	0.96	1.04	3.76	2.65	3.26	2.06	2.16	7.48
1	1.79	4.5	2.56	2.64	8.00	2.00	5.24	3.18	3.30	11.72
2	1.88	6.2	2.84	4.04	10.22	2.05	7.24	6.31	4.60	18.15
3	1.98	7.8	4.49	6.67	15.76	2.08	8.18	8.35	4.28	20.81
4	2.02	8.4	4.81	10.71	20.33	1.92	7.95	9.99	4.47	22.41
5	2.10	10.5	6.26	14.05	26.99	1.90	9.59	12.81	5.06	27.46

Experiment X Growth in different dilutions of nutrient solution

Mean Dry weight mgs. ($\log_e$ values)

Epilobium hirsutum

Lythrum salicaria

Dilutions of a nutrient solution

No. of Harvests	S	S/10	S/50	S/100	S/200	S/300	S	S/10	S/50	S/100	S/200	S/300
Int.	2.01223	2.01223	2.01223	2.01223	2.01223	2.01223	1.32442	1.32442	1.32442	1.32442	1.32442	1.32442
1	4.95667	4.38030	3.94758	3.21248	3.23431	2.46130	4.63282	4.34277	3.66177	2.85362	2.50226	2.07944
2	6.53991	5.40164	4.34744	3.63447	3.45063	2.89866	6.37281	5.33998	4.36093	3.22841	2.81901	2.32435
3	7.49501	5.96082	4.59209	3.95660	3.75401	2.03544	7.32803	5.95429	4.84206	3.52654	3.36353	2.75750
4	8.53973	6.49499	4.86799	4.16312	3.83257	3.10951	8.88059	6.52755	5.12817	3.79639	3.47563	3.01209
5	10.02518	6.82755	5.06157	4.35671	3.98288	3.31272	10.04591	7.17544	5.53676	4.03140	3.71988	3.29584

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L.S.D. at 5% level = 0.0606 and at 1% level = 0.0806

L.S.D. at 5% level = 0.0678 and at 1% level = 0.0902

Mean Leaf Area cm^2 ($\log_e$ values)

Int.	0.97456	0.97456	0.97456	0.97456	0.97456	0.97456	0.53063	0.53063	0.53063	0.53063	0.53063	0.53063
1	4.14483	3.11129	1.79675	1.11514	1.05431	0.69315	3.55648	3.01209	1.60141	0.65752	0.59884	0.58222
2	5.55461	3.72207	1.97547	1.20896	1.10194	0.69559	5.25534	3.41904	1.89010	0.69315	0.66269	0.63127
3	6.14228	3.96081	2.05412	1.39128	1.17248	0.69706	5.87635	3.61952	2.16791	0.74669	0.72755	0.68310
4	6.83948	4.08933	2.09186	1.51072	1.22378	0.65233	7.17450	3.76120	2.21920	0.84587	0.78846	0.70310
5	8.24065	4.36628	2.25129	1.69928	1.29198	0.64185	8.01101	4.52495	2.69803	0.98208	0.88789	0.74194

L.S.D. at 5% level = 0.0522 and at 1% level = 0.069426

L.S.D. at 5% level = 0.0612 and at 1% level = 0.0814

Experiment XI Chemical analysis of plants grown in different dilutions of nutrient solution.
 Total dry weight and amounts of N, P, K & Ca as dry weight percentage (mgs).
 Primary data for the final harvest.

"S" Solution

	<u>L. salicaria</u>				<u>E. hirsutum</u>			
	Leaf	Stem	Root	Plant Total	Leaf	Stem	Root	Plant Total
Total Dry weight mgs.	2118.25	1297.88	551.13	3967.26	2051.67	1491.67	308.33	3851.67
D.W. % of Nitrogen	4.00	2.72	3.72	3.542	4.33	3.63	4.58	4.079
D.W. % of Potassium	5.00	5.7	6.43	5.428	8.37	8.00	8.87	8.267
D.W. % of Phosphorus	1.09	0.68	0.97	0.9394	1.32	1.27	2.16	1.368
D.W. % of Calcium	1.03	0.9	0.5	0.9138	1.0	0.3	0.97	0.7265

S/10 dilution

Total Dry weight mgs.	687.05	353.10	310.00	1350.15	576.24	464.76	150.60	1191.60
D.W. % of Nitrogen	1.97	1.25	1.50	1.674	1.58	1.12	1.70	1.416
D.W. % of Potassium	1.77	1.90	2.00	1.857	1.23	1.77	1.73	1.504
D.W. % of Phosphorus	0.81	0.49	0.62	0.6827	0.58	0.45	0.86	0.5646
D.W. % of Calcium	1.03	0.64	0.53	0.813	1.00	0.33	0.73	0.704

Experiment XI - Continued

S/50 dilution

	<u>L. salicaria</u>				<u>E. hirsutum</u>			
	Leaf	Stem	Root	Plant Total	Leaf	Stem	Root	Plant Total
Total Dry weight mgs.	171.28	95.06	115.06	381.40	134.79	123.55	45.32	303.66
D.W. % of Nitrogen	1.00	0.88	1.22	1.037	0.95	0.92	1.53	1.024
D.W. % of Potassium	1.00	1.07	1.20	1.078	0.73	1.2	1.4	1.021
D.W. % of Phosphorus	0.29	0.30	0.31	0.2986	0.30	0.31	0.42	0.3219
D.W. % of Calcium	1.03	0.47	0.27	0.6613	0.93	0.33	0.73	0.6560

S/100 dilution

Total Dry weight mgs.	84.79	60.97	59.28	205.04	82.97	76.45	23.39	182.81
D.W. % of Nitrogen	1.05	0.88	1.20	1.043	0.77	0.92	1.92	0.980
D.W. % of Potassium	0.83	1.07	1.4	1.066	0.73	1.07	1.23	0.936
D.W. % of Phosphorus	0.25	0.27	0.33	0.2791	0.23	0.32	0.45	0.2958
D.W. % of Calcium	1.07	0.4	0.2	0.6194	0.77	0.30	0.77	0.5733

S/200 dilution

Total Dry weight mgs.	36.73	29.72	27.93	94.38	32.68	34.11	14.11	80.90
D.W. % of Nitrogen	1.13	0.87	1.33	1.107	0.88	0.95	2.00	1.105
D.W. % of Potassium	1.07	1.23	1.6	1.278	1.00	1.2	1.4	1.136
D.W. % of Phosphorus	0.20	0.23	0.29	0.2361	0.16	0.23	0.27	0.2089
D.W. % of Calcium	1.33	0.4	0.27	0.7237	0.77	0.3	0.83	0.5822

Experiment XI - Continued

S/300 dilution

	<u>L. salicaria</u>				<u>E. hirsutum</u>			
	Leaf	Stem	Root	Plant Total	Leaf	Stem	Root	Plant Total
Total Dry weight mgs.	20.58	16.66	16.50	53.70	12.70	19.16	6.90	38.76
D.W. % of Nitrogen	0.93	0.83	1.33	1.023	0.97	0.87	2.66	1.221
D.W. % of Potassium	1.03	1.13	1.33	1.154	1.47	1.33	1.27	1.365
D.W. % of Phosphorus	0.17	0.22	0.30	0.2253	0.18	0.26	0.39	0.2570
D.W. % of Calcium	1.40	0.5	0.53	0.8547	1.1	0.5	1.2	0.8204

S/400 dilution

Total Dry weight mgs.	14.75	16.61	9.55	40.91	10.06	16.04	6.50	32.60
D.W. % of Nitrogen	0.90	0.83	1.50	1.012	0.88	0.70	2.62	1.138
D.W. % of Potassium	1.00	1.33	2.23	1.421	1.03	1.27	1.93	1.327
D.W. % of Phosphorus	0.13	0.19	0.22	0.1755	0.18	0.23	0.32	0.2331
D.W. % of Calcium	1.23	0.33	0.5	0.6942	1.4	0.43	1.23	0.8896

S/500 dilution

Total Dry weight mgs.	10.90	16.02	7.00	33.92	9.20	12.13	4.11	25.44
D.W. % of Nitrogen	0.92	0.97	1.66	1.097	0.97	0.92	2.75	1.234
D.W. % of Potassium	0.73	1.20	1.93	1.20	1.13	1.23	1.73	1.275
D.W. % of Phosphorus	0.15	0.21	0.30	0.2093	0.20	0.23	0.42	0.2500
D.W. % of Calcium	1.2	0.27	0.63	0.6429	1.27	0.47	1.37	0.9041

Experiment XI Chemical analysis of plants grown in different dilutions of Nutrient Solution.
 Initial harvest applicable to all the dilutions.
 Total dry weight and amounts of N, P, K and Ca as dry weight percentage.

	<u>L. salicaria</u>				<u>E. hirsutum</u>			
	Leaf	Stem	Root	Plant Total	Leaf	Stem	Root	Plant Total
Total Dry weight mgs.	2.43	1.12	0.95	4.50	3.31	1.10	1.13	5.54
D.W. % of Nitrogen	3.96	2.92	2.92	3.482	2.83	1.79	2.42	2.539
D.W. % of Potassium	2.70	8.13	2.70	4.051	6.27	12.8	3.87	7.078
D.W. % of Phosphorus	0.81	1.11	0.84	0.891	1.41	1.63	1.26	1.4224
D.W. % of Calcium	1.23	1.17	1.13	1.193	1.93	1.17	1.60	1.71

Experiment XII Effect of different dilutions of Phosphorus, Nitrogen and Potassium on growth.

I Phosphorus series. Primary data (Mean dry weights and leaf area)

Standard Solution

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	21.00	53.6	26.6	21.2	101.4	20.4	54.4	19.2	12.6	86.2
2	380.00	853.6	628.4	230.4	1712.4	393.2	922.4	620.0	203.2	1715.6
3	1685.00	4618.0	5965.0	1212.0	11795.0	1580.0	4866.3	5122.0	1022.3	11010.6
4	2541.00	10146.4	15975.0	2301.0	28422.4	2708.0	9966.7	15386.7	1899.0	27252.4
5	3442.00	14275.0	33078.0	5082.0	52435.0	3482.0	12797.5	36086.5	3630.0	52514.0

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P/10 Solution

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	16.8	39.4	22.2	16.0	77.4	14.4	15.8	13.0	9.2	38.0
2	280.0	596.4	370.4	166.2	1133.0	234.0	448.2	229.8	78.6	756.6
3	595.0	1282.0	1229.0	289.0	2800.0	539.0	1916.3	2279.3	614.7	4810.3
4	1120.0	2676.3	4232.0	664.0	7572.3	1133.0	3460.7	4946.3	1130.0	9537.0
5	2788.0	6346.5	10338.0	2051.5	18736.0	2480.0	8798.0	11602.5	3307.5	23708.0

Experiment XII - Continued

I Phosphorus series

P/50 Solution

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	13.0	29.3	18.5	15.6	63.4	14.00	15.9	14.2	10.3	40.4
2	147.5	376.0	225.0	115.0	716.0	82.00	232.6	107.4	100.0	440.0
3	345.0	947.0	1181.4	501.2	2629.6	118.00	500.0	504.2	318.0	1322.2
4	425.0	1321.3	1917.5	959.5	4198.3	183.00	761.2	1150.3	532.5	2444.0
5	802.0	2624.3	4405.5	2714.0	9743.8	405.00	1892.0	2571.0	1506.0	5969.0

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P/100 Solution

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	11.6	28.2	17.5	13.7	59.4	6.5	19.6	9.0	6.0	34.6
2	144.0	314.0	195.5	104.3	613.8	39.2	126.0	66.0	40.0	232.0
3	225.0	763.0	729.0	362.0	1854.0	75.0	291.0	245.2	145.5	681.7
4	303.0	1069.0	1524.0	981.0	3574.0	163.0	704.0	593.8	450.0	1770.3
5	675.0	2534.5	3398.5	2487.5	8420.5	313.0	1365.0	1868.0	901.3	4134.3

Experiment XII - Continued

I Phosphorus series

P/200

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	6.5	20.0	14.8	10.0	44.8	5.6	15.0	6.7	3.5	25.2
2	39.2	126.6	60.0	42.0	228.6	16.25	48.0	22.1	7.5	77.6
3	65.4	272.0	258.4	118.4	648.8	32.00	130.8	85.0	35.0	250.8
4	110.0	460.0	558.0	421.0	1439.0	45.00	214.5	173.0	128.5	516.0
5	165.0	677.0	973.0	945.0	2595.0	49.00	250.0	208.0	139.5	597.5

O/P

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	4.2	15.5	11.8	8.1	35.4	2.5	8.0	5.7	4.3	18.0
2	6.5	37.0	29.0	30.0	96.0	3.8	17.8	10.4	11.0	39.2
3	8.4	60.0	56.0	76.0	192.0	4.3	25.5	16.0	19.3	60.8
4	10.0	62.0	61.0	97.0	220.0	6.7	42.0	30.0	44.0	116.0
5	17.0	106.0	77.0	205.0	388.0	7.1	42.1	36.5	50.0	128.6

Experiment XII - Continued
I Phosphorus series

Mean Dry weight mgs. ($\log_e$ values)

Lythrum salicaria

Epilobium hirsutum

Different dilutions of Phosphorus

No. of Harvests	P/S	P/10	P/50	P/100	P/200	O/P	P/S	P/10	P/50	P/100	P/200	O/P
Int.	1.97408	1.97408	1.97408	1.97408	1.97408	1.97408	2.18605	2.18605	2.18605	2.18605	2.18605	2.18605
1	4.61905	4.34899	4.14946	4.08429	3.80221	3.56671	4.45667	3.63759	3.69883	3.54385	3.22684	2.89037
2	7.44565	7.03265	6.57369	6.41965	5.43205	4.56435	7.46489	6.62883	6.08678	5.44674	4.35157	3.66868
3	9.37586	7.93737	7.87457	7.52508	6.47518	5.25750	9.30664	8.47851	7.18706	6.52462	5.52179	4.10759
4	10.25492	8.93226	8.34245	8.18145	7.27173	5.39363	10.21288	9.16290	7.80139	7.47889	6.24611	4.75360
5	10.86734	9.83820	9.18511	9.03842	7.86137	5.96101	10.86884	10.07357	8.69436	8.32706	6.39276	4.85678

L.S.D. at 5% level = 0.0744
and at 1% level = 0.0989

Mean Leaf Area cm^2 ($\log_e$ values)

L.S.D. at 5% level = 0.06
and at 1% level = 0.0798

Int.	0.37156	0.37156	0.37156	0.37156	0.37156	0.37156	0.59884	0.59884	0.59884	0.59884	0.59884	0.59884
1	3.04452	3.82138	2.56495	2.45101	1.87180	1.43508	3.01553	2.66723	2.63906	1.87180	1.72277	0.91629
2	5.94018	5.63479	4.99384	4.96982	3.66868	1.87180	5.97381	5.45533	4.40672	3.66868	2.78810	1.33500
3	7.42954	6.38857	5.84355	5.41611	4.18052	2.12823	7.36518	6.28972	4.77069	4.31749	3.46574	1.45862
4	7.84031	7.02108	6.05209	5.71374	4.70049	2.30259	7.90389	7.03265	5.20949	5.09376	3.80666	1.90211
5	8.14381	7.93309	6.68711	6.51472	5.10595	2.83321	8.15537	7.81601	6.00389	5.74621	3.89182	1.96009

L.S.D. at 5% level = 0.0628 and at 1% level = 0.0835

L.S.D. at 5% level = 0.0518 and at 1% level = 0.0689

Experiment XII - Continued

II Nitrogen Series Primary Data (Mean dry weights and leaf area)

Standard Solution

<u>L. salicaria</u>						<u>E. hirsutum</u>				
Harvest No.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	21.00	53.6	26.6	21.2	101.4	20.4	54.4	19.2	12.6	86.2
2	380.00	853.6	628.4	230.4	1712.4	393.2	922.4	620.0	203.2	1745.6
3	1685.00	4618.0	5965.0	1212.0	11795.0	1580.0	4866.3	5122.0	1022.3	11010.6
4	2541.00	10146.4	15975.0	2301.0	28422.4	2708.0	9966.7	15386.7	1899.0	27252.4
5	3442.00	14275.0	33078.0	5082.0	52435.0	3482.0	12797.5	36086.5	3630.0	52514.0

N/10 Solution

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	12.0	40.1	22.5	15.4	78.0	11.3	31.0	13.4	9.4	53.8
2	60.0	193.00	119.6	64.0	376.6	58.4	176.0	115.4	50.2	341.6
3	93.0	443.0	363.0	218.0	1024.0	82.5	396.0	369.0	221.0	986.0
4	126.0	568.0	1207.0	422.0	2197.0	164.5	950.0	1758.0	893.0	3601.0
5	414.0	1538.3	3244.7	1104.7	5887.7	340.0	1506.7	3044.3	1287.0	5838.0

Experiment XII - Continued

II Nitrogen Series

N/50

<u>L. salicaria</u>						<u>E. hirsutum</u>				
Harvest No.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	8.60	29.7	22.6	18.0	70.3	5.5	16.6	9.6	6.8	33.0
2	17.5	75.8	61.2	42.8	179.8	18.0	59.0	29.6	56.4	145.0
3	21.6	146.2	132.4	100.4	379.0	20.0	106.0	115.0	112.5	333.5
4	38.0	232.0	244.0	181.0	657.0	31.5	140.0	151.0	231.0	522.0
5	102.0	479.0	410.3	521.4	1410.7	94.0	379.0	683.0	318.0	1380.0

N/100

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	7.4	20.4	15.1	14.1	49.6	5.20	14.3	6.8	7.1	28.2
2	16.0	72.0	39.0	50.6	161.0	16.00	51.0	24.0	59.0	134.0
3	21.2	143.2	85.4	101.0	329.6	19.50	101.0	73.0	122.5	296.5
4	32.0	225.0	153.0	252.0	630.0	24.00	122.2	124.0	171.2	417.4
5	42.0	330.5	267.5	430.3	1028.3	61.00	226.5	348.7	386.6	961.8

Experiment XII - Continued

II Nitrogen series

N/200

L. salicaria

Harvest No.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2
1	4.8	14.3	15.7	9.2	39.2
2	9.1	38.0	29.4	28.4	95.8
3	16.0	80.0	86.4	73.4	239.4
4	20.4	117.6	105.6	157.4	380.6
5	33.0	225.2	170.8	298.0	694.0

E. hirsutum

Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
1.82	4.5	2.6	1.8	8.9
4.7	12.5	7.1	6.6	26.2
11.7	37.3	21.2	32.0	90.5
18.00	83.7	70.0	80.0	233.7
23.3	121.7	124.3	113.0	359.0
37.0	177.5	156.1	127.8	461.4

O/N

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	2.20	8.30	14.1	10.1	32.5	2.6	7.6	4.4	7.5	19.5
2	2.84	15.0	16.4	21.0	52.4	3.9	15.0	8.0	22.5	45.5
3	4.00	31.0	27.0	39.0	97.0	6.0	25.5	23.0	43.5	92.0
4	8.50	61.0	48.0	87.0	196.0	8.3	35.0	27.0	52.5	114.5
5	21.00	113.6	64.6	159.0	337.2	20.0	77.5	52.7	114.0	244.2

Experiment XII - Continued
II Nitrogen series

Mean Dry Weight mgs. (Log_e values)

Lythrum salicaria

Epilobium hirsutum

Dilutions of Nitrogen

No. of Harvests	N/S	N/10	N/50	N/100	N/200	O/N	N/S	N/10	N/50	N/100	N/200	O/N
Int.	1.97408	1.97408	1.97408	1.97408	1.97408	1.97408	2.18605	2.18605	2.18605	2.18605	2.18605	2.18605
1	4.61905	4.35671	4.25277	3.90399	3.66868	3.48124	4.45667	3.98527	3.49651	3.33932	3.26576	2.97041
2	7.44565	5.93121	5.19187	5.08141	4.56226	3.95891	7.46489	5.83363	4.97674	4.89784	4.50535	3.81771
3	9.37586	6.93148	5.93754	5.79792	5.47818	4.57471	9.30664	6.89366	5.80965	5.69206	5.45405	4.52179
4	10.25492	7.69495	6.48769	6.44572	5.94174	5.27812	10.21288	8.18896	6.25767	6.03405	5.88333	4.74066
5	10.86734	8.68064	7.25624	6.93570	6.54248	5.82069	10.86884	8.67077	7.22984	6.86878	6.13426	5.49799
L.S.D. at 5% level = 0.08068 and at 1% level = 0.1073						L.S.D. at 5% level = 0.060 and at 1% level = 0.0798						

Mean Leaf Area cm^2 (Log_e values)

Int.	0.37156	0.37156	0.37156	0.37156	0.37156	0.37156	0.59884	0.59884	0.59884	0.59884	0.59884	0.59884
1	3.04452	2.48491	2.15176	2.00148	1.56862	0.78846	3.01553	2.42480	1.61939	1.64866	1.54756	0.95551
2	5.94018	4.09434	2.86220	2.77259	2.20827	1.04380	5.97381	4.06732	2.89037	2.77259	2.45959	1.36098
3	7.42954	4.53260	3.07269	3.05400	2.77259	1.38629	7.36518	4.41280	2.99573	2.97041	2.89037	1.79176
4	7.84031	4.83629	3.63759	3.46574	3.01553	2.14007	7.90389	5.10296	3.44999	3.17805	3.14845	2.11626
5	8.14381	6.02587	4.62498	3.73767	3.49651	3.04452	8.15537	5.82895	4.54329	4.11089	3.61092	2.99573
L.S.D. at 5% level = 0.066 and at 1% level = 0.0877							L.S.D. at 5% level = 0.061 and at 1% level = 0.08113					

Experiment XII - Continued

III Potassium series (Primary data) Mean weights and leaf area.

Standard solution

<u>L. salicaria</u>						<u>E. hirsutum</u>				
Harvest No.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	21.00	53.6	26.6	21.2	101.4	20.4	54.4	19.2	12.6	86.2
2	380.00	853.6	628.4	230.4	1712.4	393.2	922.4	620.0	203.2	1745.6
3	1685.00	4618.0	5965.0	1212.0	11795.0	1580.0	4866.3	5122.0	1022.3	11010.6
4	2541.00	10146.4	15975.0	2301.0	28422.4	2708.0	9966.7	15386.7	1899.0	27252.4
5	3442.00	14275.0	33078.0	5082.0	52435.0	3482.0	12797.5	36086.5	3630.0	52514.0

K/10 Solution

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	9.4	29.1	16.3	11.1	56.5	6.40	25.0	9.3	7.2	41.5
2	70.7	150.0	69.2	38.0	257.2	28.60	92.5	31.3	16.9	140.7
3	229.0	618.0	490.0	139.3	1247.3	151.00	413.0	248.0	64.0	725.0
4	666.7	1939.0	1722.0	406.0	4067.0	345.00	857.7	838.2	140.5	1836.4
5	1903.0	5192.3	6992.0	842.0	13026.3	670.00	2086.0	3109.0	369.0	5564.0

Experiment XII - Continued

III Potassium series

K/50

L. salicaria

Harvest No.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2
1	8.0	25.5	18.1	12.3	55.9
2	39.8	119.5	62.2	29.7	211.4
3	112.0	373.0	223.5	62.8	659.3
4	220.0	801.0	679.0	165.0	1645.0
5	534.0	2005.0	1218.0	270.0	3493.0

E. hirsutum

Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
1.82	4.5	2.6	1.8	8.9
5.20	20.0	9.1	5.4	34.5
14.00	45.0	20.1	8.2	73.3
100.00	371.0	154.0	43.0	568.0
115.00	424.0	371.5	74.0	869.5
138.00	453.0	841.0	142.0	1436.0

K/100

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	5.20	17.8	19.0	9.4	46.2	4.80	16.4	6.1	3.7	26.2
2	38.00	94.6	56.0	21.3	171.9	11.00	43.0	16.2	5.8	65.0
3	80.00	227.0	125.0	41.4	393.4	76.00	187.0	90.0	24.0	301.0
4	140.00	352.0	269.0	68.0	689.0	89.00	220.7	208.0	45.0	473.7
5	160.00	447.3	507.7	133.7	1088.7	72.00	231.0	473.0	62.0	766.0

Experiment XII - Continued

III Potassium series

K/200

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	4.60	15.30	13.30	6.10	34.7	2.80	12.0	5.1	5.6	22.7
2	26.00	92.00	50.60	18.00	160.6	10.00	39.0	15.5	7.8	62.3
3	40.00	169.20	92.00	29.00	290.2	17.00	60.0	34.0	11.0	105.0
4	77.50	286.00	182.00	46.50	514.5	19.00	69.7	40.0	14.0	123.7
5	85.00	327.00	398.00	98.00	823.0	10.00	35.0	122.6	15.0	172.6

O/K

Initial	1.45	4.18	1.11	1.91	7.2	1.82	4.5	2.6	1.8	8.9
1	4.60	14.1	11.4	7.1	32.6	2.60	8.1	4.8	3.1	16.0
2	23.00	98.8	41.6	20.1	160.5	8.80	40.0	11.5	7.0	58.5
3	29.00	117.0	110.0	45.0	272.0	5.0	20.0	45.0	7.3	72.3
4	38.00	150.0	172.2	69.5	391.7	3.8	12.3	32.7	8.0	53.0
5	45.00	188.5	397.0	102.0	687.5					

Experiment XII - Continued
III Potassium series

Mean Dry weight mgs. ($\log_e$ values)

Lythrum salicaria

Epilobium hirsutum

Dilutions of Potassium

No. of Harvests	K/S	K/10	K/50	K/100	K/200	O/K	K/S	K/10	K/50	K/100	K/200	O/K
Int.	1.97408	1.97408	1.97408	1.97408	1.97408	1.97408	2.18605	2.18605	2.18605	2.18605	2.18605	2.18605
1	4.61905	4.03424	4.02356	3.83298	3.54674	3.48431	4.45667	3.72569	3.54096	3.26576	3.12237	2.77259
2	7.44565	5.54908	5.35372	5.14738	5.07890	5.07827	7.46489	4.94655	4.29456	4.17439	4.13196	4.06903
3	9.37586	7.12861	6.49119	5.97482	5.67057	5.60581	9.30664	6.58618	6.34213	5.70712	4.65397	4.28082
4	10.25492	8.31069	7.40554	6.53525	6.24320	5.97046	10.21288	7.51559	6.76793	6.16057	4.81793	3.97029
5	10.86734	9.47475	8.15853	6.99355	6.71296	6.53307	10.86884	8.62407	7.26963	6.64119	5.15098	

500

L.S.D. at 5% level = 0.09724 and at 1% level = 0.12933

L.S.D. at 5% level = 0.0636 and at 1% level = 0.08459

Mean Leaf Area cm^2 ($\log_e$ values)

Int.	0.37156	0.37156	0.37156	0.37156	0.37156	0.37156	0.59884	0.59884	0.59884	0.59884	0.59884	0.59884
1	3.04452	2.24071	2.07944	1.64866	1.52606	1.52606	3.01553	1.85630	1.64866	1.56862	1.02962	0.95551
2	5.94018	4.25845	3.68387	3.63759	3.25810	3.13549	5.97381	3.35341	2.63906	2.39790	2.30259	2.17475
3	7.42954	5.43373	4.71850	4.38203	3.68888	3.36730	7.36518	5.01728	4.60517	4.33073	2.83321	1.60944
4	7.84031	6.50234	5.39363	4.94165	4.35028	3.63759	7.90389	5.84355	4.74494	4.48864	2.9444	1.33500
5	8.14381	7.55117	6.28040	5.07518	4.44265	3.30666	8.15537	6.50728	4.92726	4.27667	2.30259	

L.S.D. at 5% level = 0.070 and at 1% level = 0.0931

L.S.D. at 5% level = 0.06833 and at 1% level = 0.09142

Experiment XIII Growth response of the species to different temperature regimes.

Primary Data. Mean dry weights and Leaf area.

AT 18°C

Harvest No.	<u>L. salicaria</u>					<u>E. hirsutum</u>				
	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.	Leaf area cm ²	Leaf wt. mgs.	Stem wt. mgs.	Root wt. mgs.	Plant Total wt. mgs.
Initial	3.20	4.82	1.77	1.64	8.23	2.83	5.17	1.71	1.86	8.74
1	6.95	19.15	4.26	6.79	30.20	6.77	23.47	9.83	3.67	36.97
2	10.65	46.12	9.91	11.89	67.92	15.75	55.90	53.18	9.50	118.58
3	56.70	113.23	47.34	28.89	189.46	43.70	117.72	105.39	19.62	242.73
4	176.50	389.16	224.42	104.42	718.00	148.56	341.69	223.06	46.25	611.00
5	344.00	850.00	695.00	247.00	1792.00	339.34	855.86	549.77	105.40	1511.03
6	898.61	2622.12	2708.50	343.31	5673.93	825.00	2086.68	2006.11	300.77	4393.56

AT 8°C

Initial	3.20	4.82	1.77	1.64	8.23	2.83	5.17	1.71	1.86	8.74
1	3.53	6.94	2.50	2.17	11.61	3.41	7.69	3.37	1.87	12.93
2	4.53	13.85	3.62	4.67	22.14	6.35	27.60	9.78	3.25	40.63
3	5.20	20.66	5.68	6.36	32.70	13.30	77.98	45.59	11.11	134.68
4	7.20	33.10	7.60	15.14	55.84	22.60	171.00	88.25	23.15	282.40
5	13.19	72.89	25.70	24.19	122.78	53.35	380.60	232.45	60.25	673.30
6	21.52	111.29	52.82	70.65	234.76	264.00	1396.47	784.20	257.00	2437.67

Experiment XIII - Continued

	Mean Dry weight mgs. (Log _e values)				Mean Leaf Area cm ² (Log _e values)				
	<u>E. hirsutum</u>		<u>L. salicaria</u>		<u>E. hirsutum</u>		<u>L. salicaria</u>		
	Temperature (C°)				Temperature (C°)				
Harvest No.	8°C	18°C	8°C	18°C	8°C	18°C	8°C	18°C	
Int.	2.16791	2.16791	2.10779	2.10779	1.04028	1.04028	1.16315	1.16315	
1	2.55959	3.51010	2.36178	3.40784	1.22671	1.91250	1.26130	1.93874	
2	3.70451	4.77564	3.09735	4.21834	1.84845	2.75684	1.51072	2.36505	
3	4.90295	5.49222	3.48738	5.24416	2.58776	3.77735	1.64866	4.03777	
4	5.64332	6.41510	4.02249	6.57647	3.11795	5.00102	1.94876	5.17331	
5	6.51219	7.32056	4.81059	7.49115	3.97688	5.82703	2.57980	5.84065	
6	7.79880	8.38800	5.45877	8.64364	5.57595	6.71539	3.06898	6.80084	
L.S.D. at 5% level = 0.088318 and at 1% level = 0.117504					L.S.D. at 5% level = 0.090112 and at 1% level = 0.119849				
(Analysis of variance applicable to both the species)					(Analysis of variance applicable to both the species)				

Experiment XIV Competition and Survival of the species in high and low nutrient regimes at
a constant temp. of 25°C.

"Standard Solution"

Date	Week from trans- plantation	L. salicaria (pure stand) Mean No. of survivors	E. hirsutum (pure stand) Mean No. of survivors	L. salicaria + E. hirsutum (Mixed stand) Mean No. of survivors		Initial Primary data applicable to both treatments
15.11.68	0	1000	1000	500	+	500
1.12.68	2	955	852	493		459
15.12.68	4	735	347	407		197
31.12.68	6	549	73	302		19
15. 1.69	8	319	9	160		7
30. 1.69	10	118	6	86		1
14. 2.69	12	98	4	59		1
28. 2.69	14	98	4	55		1
15. 3.69	16	95	4	54		1
31. 3.69	18	94	4	54		1
15. 4.69	20	94	4	54		1
30. 4.69	22	94	4	54		1
15. 5.69	24	93	4	54		1
Mean shoot wt./stand (gms)						621.44
Mean root wt./stand (gms)						137.37
Mean Total Dry wt/stand (gm)						458.3
Mean Root/Shoot Ratio/stand						23.2
						0.8
						0.176
						0.0483
						0.139
						0.0344
						24.0
						522.0
						24.0

L. salicaria (seedlings)
Mean Total no. transplanted/pure stand: 1000
Mean Total Shoot D.W. (gm) 470/stand
Mean Total Root D.W. (gm) 1.65/stand
Mean Total Dry weight (gm) 6.35/stand
Mean Root/Shoot Ratio 0.351/stand

E. hirsutum (seedlings)
Mean total no. transplanted/pure stand: 1000
Mean total Shoot D.W. (gm) 4.98/stand
Mean total Root D.W. (gm) 1.62/stand
Mean Total Dry weight (gm) 6.60/stand
Mean Root/Shoot Ratio 0.325/stand

In mixed stand 500 seedlings of each species were transplanted.

Experiment XIV - Continued

S/20 dilution of standard solution

Date	Weeks from trans- plantation	L. salicaria (pure stand) Mean no. of survivors	E. hirsutum (pure stand) Mean no. of survivors	L. salicaria + E. hirsutum Mixed Stand	
15.11.68	0	1000	1000	500	500
1.12.68	2	980	955	486	432
15.12.68	4	950	716	479	365
31.12.68	6	890	509	467	290
15. 1.69	8	779	393	449	218
30. 1.69	10	651	330	431	157
14. 2.69	12	570	279	422	5
28. 2.69	14	535	238	410	-
15. 3.69	16	515	213	402	-
31. 3.69	18	499	199	395	-
15. 4.69	20	488	190	390	-
30. 4.69	22	482	186	387	-
15. 5.69	24	478	185	387	-
Mean Shoot wt./stand (gms)		74.80	33.59	72.32	
Mean Root wt./stand (gms)		<u>69.35</u>	<u>12.65</u>	<u>65.21</u>	
Mean Total Dry wt/stand (gm)		144.15	46.25	137.53	
Mean Root/Shoot Ratio/ stand		0.927	0.376	0.902	