COMPARATIVE BIOLOGY OF SOME FEN PLANTS
(*Filipendula* and *Iris* species)

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by

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ABSTRACT

The autoecology of Filipendula ulmaria (L.)Maxim. and Iris pseudacorus L. was studied in terms of germination, growth behaviour and morphogenetic pattern of growth with special reference to light and nutrition requirements both in laboratory and partly in field conditions. A comparative performance of the species was assessed by examining various parameters of growth.

The germination capacity at varying degrees of temperature under light and darkness was found to be different for each species. It was inferred that Iris pseudacorus L. has a wider range of temperature tolerance compared to Filipendula ulmaria (L.) Maxim. which accords with its extended geographical distribution.

Both species were found to have an efficient dormancy mechanism in their seeds. The results showed that their seeds require a certain period of after-ripening at low temperature pretreatment. The seeds when stratified at low temperature and germinate at an alternate high temperature generally increased their germination capacity. Response to this method was found to be more effective in I.pseudacorus than F.ulmaria. A highest germination was evident in I.pseudacorus after a years stratification.

A preliminary attempt was made to isolate the germination - inhibitor of I.pseudacorus seeds and it seems probable that the inhibitors are located in seed coat. These, may disappear or become synthesized into a growth stimulator during the after ripening period of the seed. The results with seed coat either removed or intact has shown that removal of seed coat frees the inhibitor and increased oxygen tension, thus increasing the germination capacity.

Glass house experiments on seedling behaviour and the growth of species under varying light regimes showed that the species are plastic in form and can make viabel growth under decreasing shade, indicating its tolerance to shaded conditions. Experiments on daylength suggested that the growth is restricted to a limited period of the year as the species are incapable of over-wintering with living leaf suface exposed. However, a light break in the middle of a long dark period generally increased leaf area and dry weight of the plants compared with short photo periods, when all plants received the same total amount of light each day.

The species differ in their mineral nutrition requirements. The differences were also considered to be of importance in determining respective differences of the distribution of species on acid and lime rich soils.

Finally, an assessment has been made of the germination characteristics, pattern of development and their timing, growth form in relation to varied environmental factors and then an attempt has been made at least in part, the way in which the two species come both to similarities and the difference in their individual pattern of ecological distribution.

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CHAPTER I
INTRODUCTION

INTRODUCTION.

Autoecology has a fundamental significance for it provides the basis for the etiology of distribution and of dynamic inter relationship between individuals of a population and the environment. The ecological approach becomes indispensable whenever plant behaviour is studied in relation to the natural or cultural environment of the plant; and these kinds of intergrated biological studies ultimately lead to a better idea of the interaction between species in communities and the factors determing habitats and geographical distribution of species.

During the last few decades, the results of investigations in several botanical fields have contributed considerably to a better understanding of the general principles which determine the type of plant community under any well defined but broad range of environmental conditions. In spite however of the very considerable advance made, precise information on the relative importance of the different environmental factors for any one community and for species are lacking. The principal factors likely to be operative under any given set of condition can be assessed but where several factors are seemingly involved the role of each factor or the interaction between factors has not in general been precisely determined for individual species characteristic of the community.

Watt (1957) is of the view that in the accumulation of data of the biology and ecology of species, the recent increase in experiment is to be welcomed in the study both of plant reaction to change in a graded series of factors of soil and climate, and also of the behaviour of the species in relation to other species. In his view it appears that the study of a comparative biology of species leads to the understanding of its ecological status over a wide range of habitats. Poore (1964) in discussing the question of integration in plant community also emphasises the need of a detailed study of the autocoligy of species under the competitive condition of natural communities.

It would be interesting to compare the social status of species over the whole range of their distribution to see whether the status of the species varied from one community to another. Such an approach would be helpful in distinguishing categoies of species and the value of exclusiveness to be attached to a species.

Recently certain workers for instance, Harper & Chancellor (1960), Harper & Clatworthy (1963) Myerscough & Whitehead (1966) have given certain thoughts on such studies for a better understanding of the interaction between species in a community. By the comparative biological investigations of some typical plant species, Myerscough & Whitehead (1966) have described how such typical plant species of pioneer plant communities come to be found as components of more mature community.

In the present work where two typical species of fen community have been taken into account, it was thought that comparison of these species may offer some explanations of their distribbtion and the difference in the habitat they occupy. The species selected were Filipendula ulmaria (L). Maxim. and Iris pseudacorus L.

Both species are characteristic of the "fen formation", which, is characterised by an assemblage of over a hundred species of woody and herbaceous vascular plants, by a peat soil and by alkaline ground water whose level varies. Tansley (1911) has classified fen formation into two associations i.e. fen association and carr association. (The word "carr" or "car" is applied locally to the fen woods). The vegetation of fen association consists chiefly of herbaceous plants, dominated by grass and sedges, while carr association is a wet type of wood developed on peat. The species under discussion are also found as a ground flora of the ultimate carr (developed by the compostion of wood like Salix spp, Fraxinus excelsior. Alnus sp, Quercus robus, etc.,).

The species differ in their systematic postions, as F. ulmaria is a dicotyledonous species, while I. pseudacorus belongs to monocotyledonous family. They appear to be suitable for this type of investigations and can be seen from the following tabulated similarities and disimilarities.

1. They are found growing in this country and so the material for the study can be easily collected and acquired in order to carry out parallel investigations under more controlled conditions.

2. Both species are perennial, and rhizomatous in their growth forms and the leaves are radical in origin.

3. Their seeds posses an efficient dormancy mechanism.

4. They are shade tolerant and hence shows a considerable adaptability against the diffusing light conditions in the woodland.

5. They are also well suited for transplant experiments for investigations of growth and development since they can be lifted and weighed easily.

Besides some specific characteristics outlined above the species also differ in may respects to their distribution and habitat tolerance. An account of the general biology, ecological and geographical distribution of the two species is given below.

Habitat and distribution.

Filipendula ulmaria (L) Maxim

This species is widely distributed over the northern temperate and colder regions of the old world. In its European distribution extends from Iceland and Artic Russia to N. Portugal, Central Spain, Central Italy, Macedonia and the Caucasus.

It also occurs in temperate zones of Asia to Asia Minor and Mongolia. It is a naturalized garden escape in Eastern North America.

The record shows that it has survived continuously in the British Isles since late glacial time, and its remains have also been found in the still older "artic bed" of the Lea Valley. (Pennington 1969).

Itself a characteristic plant of the drier parts of marshes and fens the habitat of this species is usally where the water contents of soil is considerable rather than excessive (Yapp 1912). Thus, in the British Isles it is found in a wide range of wetness of habitats, varying from edges of marshes, rivers and road side ditches to neglected mowing marshes (Ellis 1965), damper parts of meadows and fens; near sea coast (Yapp 1912). In brackish lagoons of Southern Norway, (Nordhagen 1940) has noted its occurance as a dominant drift line vegetation. It is also found in damp hollows between sand dunes (Moss 1907) and in woods if the shade is not too dense (Admmson 1012).

The species is not normally found in communities growing on acid soils, therefore is absent from the acid peat (Clapham, Tutin & Warburg 1952). It appears to be restricted to those habitats where the soil is calcareous. Thus in Derbyshire it is found in abundance on calcareous soils as a ground flora of ashwood (Tansley 1911).

In its more general distribution in the North, it

appears to be limited to relatively sheltered sites away from cold drying winds. For instance in Scania (N.E. Sweden) it is found on damp calcaeous soil as a ground flora of mixed wood (Clapham 1953). In the mountains of Norway at 1020 - 1100 m. above the sea level it is found in sub-alpine birch plant communities (Nordhagen 1943). It also appears to be restricted to those habitats where mineral status is high. In North West Europe it is found on the sides of streams and ditches on heavy nitrogen rich soil (Tuxen 1937). This species is fairly tolerant of temperature condition occuring throughout the lowland and ascending to nearly 3,000 ft. (Clapham, Tutin and Warburg, 1952., Salisbury 1961).

Iris pseudacorus L.

It is a native of Europe, North Africa and Syria. In Europe its distribution extends to about 68^{0} North in western Norway. It is also found in the Caucasus and Western Asia. The species was introduced sparingly into Canada as a garden ornamental, from there it has escaped to swamps and other wet habitats. In most places the first plants probably have arisen from rhizome discarded or otherwise removed from gardens (Cody 1961). The author has reported this species becoming established in Canada and particularly in Ontario very rapidly in the lowlands and swamps of the County.

It is widely distributed throughout the British Isles occuring in a wide range of habitats, e.g. marshy places, swampy woods, in shallow waters or wet grounds at the edges of rivers and ditches.

In respect to water regime it differs from F.ulmaria since it occurs in those habitats where the water content of the soil is excessive and waterlogged. Thus in Scottish highlands it is quite common in low parts of the high lands occupying the shallow fringes of lochs, the edges of streams swampy places and near the sea coast (Holden 1953). It appears to be tolerant of the conditions of poor mineral nutrition as well as acid and alkaline soil. It is typical flora of wet woodland, and is often locally dominant in the fen carr. In Wheat fen broad, the old plants survive shading by trees and bushes when carr developes on the abandoned mowing marshes (Ellis 1965).

GENERAL BIOLOGY.

F. ulmaria (L.) Maxim.

It is a perennial with a sympodial rhizome which creeps on or just below the surface of the soil with deep striking perennial roots which push down into the muddy soil. The vegetative period is comparatively short (about March to October) so that the coldness of soil scarcely plays a very important part in these latitiudes. The aerial parts, consisting of radical cauline leaves, soon die back in Autumn, leaving the persistant rhizome buried in the soil with its winter buds. The vegatative spread starts up again during March when the vegetative buds begin to unfold and each produces several radical leaves. In a vigorous and strong adult plant some of the winter buds may form am erect flowering stalk of reddish hue bearing the cauline leaves. In young seedlings or buds of less vigour and inflorescence is not found as the shoot does not elongate and continues to form radical leaves until September.

The large pinnate leaves are smooth and green above, but the under surface is covered with a thick white felt-like down. This has been considered by Hatfield (1966) to be a feature of marsh plants to protect them against condensed moisture which would otherwise clog the stomata. The author disagrees with this contention, where in case of F. ulmaria the pubescence appears to be associated with the increasingly

xerophytic environment of these exposed plants with the onset of late spring and Summer. This is discussed further later. There exists an entirely glabrous form of F. ulmaria variety denudata which occurs in nature only in quite sheltered places. This variety when occurs in exposed situations, e.g. wind, appears to suffer more from the exposure than the ordinary forms (Yapp 1907).

The seedlings as well as the leaf formed in the first year of growth, are glabrous. The plant if small and weak may remain in this juvenile glabrous condition for two or more years. Yapp (1912) has discovered a remarkable seasonable periodicity of pubescence in the ontogeny of this species. When a winter bud opens early in March, the first leaves unfold are glabrous. After 3 - 5 glabrous radical leaves have unfolded, are followed by one or two partly hairy leaves towards the beginning of May.

As the flowering shoot elongates by the middle of May the leaves are completely covered with hairs on the lower surface and the degree of hair formation becomes more and more dense with the ascending of flowering stalk. The plant generally flowers towards the end of July (or earlier on drier soils) by which time all the leaves on the shoot are unfolded.

The vegetative leaves of adult plant exhibits even more remarkable periodicity of hairiness. They commence about March by unfolding glabrous leaves in preciesely the same manner as on the erect flowering shoot.

As the season advances the successive leaves are increasingly hairy. This goes on till midsummer (middle of June to middle of July) when the process is reveresed. The new leaves expanded are now decreasingly hairy until finally glabrous leaves are once more produced on the approach of autumn. Similarly marked seasonal differences are exhibited in the stomata of leaves. The lower glabrous leaves have more or less a definite "shade" structure with large epidermal cells, few but relatively large stomata and a loose mesophyll with large intercellular spaces. The exposed hairy leaves which approximate to the "sun" type conversely becomes thicker, with thick cuticle smaller opidermal cells and numerous stomata but smaller and the hair much more abundant. The mesophyll is more compact with a minimum intercellular space.

It blooms in mid-summer when competition is at its peak and only the most vigorous plants which grow well above the others vegetation can hope to attract insects. The stigma matures before the stamens have reached maturity, (Holden 1952). In dull weather when few insects are abroad, self-fertilization takes place. The failure of pollination often results in an immature fruit formation. Probably this is the reason why embryoless sedds are of frequent occurance in this species.

After fertilization the thorn shaped achenos are fitted loosely together with a spinal twist. The light weight seeds (achenes) are often shed by strong wind and may be carried away some distance away

from the parent plant, although the seeds have no definite built in dispersal mechanism. In autumn when most of the seeds are shed, a few seeds may be found germinating either under the shade of surrounding vegetation or the parent plant. Generally, the seeds undergo a certain after-ripening period throughout the winter. At the approach of Spring when the season gets warmer, most germination occurs.

The germination is epigeal. In spring when the radical protrudes out of the seed, it penetrates into the moist ground. After two days a weak and tender plumule elongates up to the height of one inch above the ground bearing expanded cotyledons which remain persistant until the first few pairs of leaves are formed. The tap root is replaced very soon by a number of adventitous roots. As growth advances fairly large rosettes of 4 - 5 basal leaves are formed with distinct terminal and paired leaflets on the petiole. At this time the rosettes are surrounded mainly by rushes, sedges and a similar type of vegetation casting a fair amount of shade, thus maintaining a high humidity in the surrounding atmosphere. The roots at this time usually lie in a very wet condition and the radical leaves in mesophytic condition. With the advancement of season cauline leaves develop and each new leaf tends to be smaller. The fibrous roots become increasingly large. Meanwhile the habitat tends to become drier.

By the middle of Summer when the habitats are quite xeric, the plant itself becomes xeromorphic with development, and the leaves show a considerable difference of form according to position. The lower sheltered leaves are mesophytic while those which are exposed to wind and strong isolation are distinctly more xerophytic in character. This degree of xeromorphy of the upper leaves thus brings about a positive advantage to the plant to survive at least under such unusual desiccation and severe transpiration.

Iris pseudacorus L.

The yellow flag is a perennial and forms extensive colonies. Its main stem is thick, creeping rhizome which lies upon the surface of the mud and is usually immersed several inches in the water. It gives off many thick white roots, which penetrate deeply into the mud. During the winter when leaves die back it remains sunken at the bottom of lakes, rivers, completely in an anaerobic condition. Bouter et al (1963) have shown that the internal atmosphere of rhizomes even when examined during mid-Summer has relatively low concentration of CO_2. In this way the rhizome lying in an aquatic environment has developed a tolerance towards low oxygen and raised CO_2 levels. The principal organic acids i.e. Shikimic, Quinic and Malic acids are reported to be found in abundance in the rhizomes (Henshaw,

Coult and Boulter, 1962). It has been shown that those acids are built up during the late winter months and drop considerably following leaf emergence.

At the approach of spring, the rhizome sends out branches and in the course of time, large areas are colonized by a single plant. In wheat fen broads (Norfolk) where large clumps of rhizome were dug out and examined, showed that the plants were growing for nearly 20 - 30 years in this area. Each years' growth was preserved in a sausage-like stucture and bound together in continuation. Thus a record of each summers growth and flowering performance which is left on the branching rhizome of an old plant may yield some useful information to an ecologist when he is trying to discover the age of the carr in which it is growing (Whitehead; personal communication).

On decay of the intervening portions of the rhizome the daughter plants may become independent of the plant. In spring when weather begins to get warmer a large bud at the extremity of rhizome commences to swell and fed by the starch in the cells and sends up a bunch of radical leaves.

The sword shaped, very acute rather glaucous leaves attain as much as three to four feet in height and remarkable for the fact that they posses no under surface but stands erect. They are very strong and are not likely to be damaged by strong exposure to winds.

Hence they have a large surface area, are very efficient assimilatory organs (Holden 1952).

By the middle of June, one or several tall, stout cylindical stems arise in the midst of the leaves, upon which the flowers are born. The flowering stalk bears very large, leafy bracts very similar to the foilage leaves in form and from the upper two or three of which are produced the large showy flowers. Whilst young the flower bud is safely hidden in the hollow sheathing base of the leaf. In this species a complicated structure of flower has been evolved, which is modified and well adapted to favour an entemophilous pollination, favouring a cross pollination and outbreeding. The anthers are covered under the over arching style which protects the pollen from rain and damp. Neotar is produced by the glandular summit of the ovary and is often fills the perianth tube. The stamens are so placed that the bumble bee, following the black lines of the sepals which point the way to the nectar, is bound to brush against one of the stamens cover its back with the pollen which is then carried to the next flower (Inglis, 1958).

At first, when the fruit has been formed it remains green in colour partially as an assimilating organ, as it has a number of stomata scattered all over the fruit wall, and represents a striking example of stomatal formation extending over a considerable period (Farmer 1890). In the late summer the fruit turns pale in colour dehiscing to display the bright orange red seeds.

The seeds spilled from pods in winter are disposed mainly by floods and found germinating among marshes in the following spring.

The seeds are well adapted to float on the surface of water and hence can be carried away by the current of water to far reaching places. Once settled on the soft mud, which provides a suitable stratified media, remain dormant against the unfavourable weather. Like F. ulmaria the seeds are after ripened and/or most often the seed coat is decayed by the interaction of soil micro-organisms. The after ripening takes from one to several months until the rise of temperature during the spring when the germination takes plaoe, and sporadic germination can continue until the end of August. The germination occur in a wide range of temperatures both in the laboratory and field conditions. The minimum temperature requirement is 14° - 15° C, for the emergence of at least radical.

Being a monocotyledonous species the seedling pattern and behaviour strictly follows a hypogeal germination. At first, a tender but thick white radicle emerges out before the plumule and pushed into the mud helping the developing shoot anchored properly. The plumule is surrounded by a protective sheath (coleop tile).

Within 2 - 3 days the first pair of foilage leaves burst out of sheath and remains persistant until the 8-9 leaf stage which functions as an ancillary assimilatory organ. With the formation first leaf stage a strong fleshy adventitious root system develops from the base of developing rhizome. During the first years growth

the rhizome is a swollen mass of tissues, which in its second years' growth gradually accumulates starch and increases its size. Adventitious buds are developed in the axis of leaves but remain dormant till the plant has achieved its maturity. In an exposed condition, However, several adventitious buds are formed at a time which start growing with the parent plant. The plants in their first 2 - 3 years growth, are mainly vegetative, seldom if ever, flowering. It has been observed inflorescence buds appear only over 2 years vegetative growth and it is probably this factor may be correlated with the critical rhizome size and development and yet needs some proper explainations.

From the literature reviewed on habitats, geographical distribution, and the biology of the species, it appears that the factors determining the distribution of species gives little or no information about their casual or positive relationship to the species under investigations. It was thought, therefore, that the probable external factors, which are important in their ecological role are temperature, light and nutrition requirements and mainly responsible to bring about changes in the internal factors, i.e. seed dormancy, viability, seedling behaviour and the plasticity of forms etc.

The literature on these factors is therefore reviewed and the experimentation was undertaken to claify the ecological status of the species on a physiological basis.

REVIEW

Most of the previous studies have been concerned to distinguishing the different woodland plant communities, their floristic composition and soil and climatic factors controlling such differentiation. Some other studies have been concerned with specific problems such as regenration and on this basis general principles have been formulated as to the main environmental factors governing the distribution of ground flora. Nevertheless, abundance of data appears to lack of precision and an absence of comprehensive information on the autoecology of any individual woodland plant is yet to be thoroughly investigated.

One of the first accounts to stress the importance of light intensity on the distribution of species in woodland has been given by Salisbury (1916). By measuring the light intensity inside the woodland be concluded that the plants like Ficaria verne. Primula acaulis and Anemone nemorosa. which open their foilage by middle of January were found favourably surviving the deep shade in summer owing to active photosynthesis at the beginning of Spring. Since then, a considerable attention has been given to the question of shade tolerance and it was assumed by early workers, that difference in tolerance were mainly due to different light requirements of the species and that competition for water and soil nutrients may also determine the establishment of seedlings beneath their parent strand.

Many attempts have so far been made of the quantitative explainations of the relation between light and growth. The early work of Holsch (1931), Pearson (1936) on some tree species deserves notice.

It is only in the last few decades, that new methods of experimentation or the experimental technique and the analysis of data have made it possible to differentiate the complex of factors concerned in these types of studies. The pioneering work of Blackman and Rutter (1946 - 50) on the typical woodland species Endymion non-scripta (Bluebell) has shown the relative importance of light as a factor in determining the distribution and growth of this species in woodland community and the other communities.

With the developmental concepts in growth analysis, the approach to the problem has become more quantitative in expression. The problem of shade tolerance is becoming clarified when the approach is made by analytic synthetic studies of the growth process or dry matter production of the plants under the given shaded conditions. It is noticeable that Blackman & Wilson, (1953), Blackman, Black & Kemp (1955), and others like Evans & Hughes (1961, 62), Whitehead (1962) etc. have thrown much light on this problem by analysing the effect of light intensities on plant growth, especially on two attributes, i.e. net assimilation rate and leaf area ratio.

A precise review of the developmental concept of growth analysis with special reference to the concept of net assimilation rate, leaf area ratio has already been included in the chapter of materials and methods.

In recent years, some Japanese workers have also undertaken the physiological and ecological appraach in assessing the relative importance of the light factor, and many studies have scored very useful information on this subject. For instance, Monsi (1960) realise the importance of dry matter production as the key function for the elucidation of phytoecological and socialogical problems in plants or plant communities. Accordingly, five sebemata were presented for typical dry matter production system, i.e. annual herb, perennial herb, permanent herb, annual leaf tree and perennial leaf-tree systems.

In analysing the shade tolerance of green grain (Phaseolus aureus) Nomoto, Iwaki and Monsi (1961) showed many attributes which are principal in dry matter economy of the species, especially the F/F ratio (synonym to specific leaf area). In this species, the increased ratio in lower light intensity has been considered as the positive effect of shading and advantageous factor to survival and to make positive dry matter production under deep shade. Importance of specific leaf area as an index to the shade tolerant species has been realised earlier by Evans and Hughes (1961).

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In their work on a typical facultative shade plant, Impatiens parviflora it has been shown that it responds to shading by a remarkable increase in the expansion of its leaf surface. The expansion involved only a spatial distribution of plant material in the leaves and no change in the fraction of the total dry weight was observed in the leaves (this finding differs markedly from that of other species (Myerscough & Whitehead 1967) including the present species under investigation). Despite these structural modification the leaves of the plant at all levels of shading were found to have same assimilatory capacity during a week in the given environment irrespective of the previous treatment. The authors have also laid stress on the several aspects of light regimes to have important influences on growth. It has been shown that the rate of increase of dry weight per unit leaf area is practically proportional to the mean total daily radiation up to about 100cal/cm^2/day and almost independent above 300cal/cm^2/day in which region it is however affected by daylength. Specific leaf area has a marked ontogenetic drift, the form of which is much affected by mean total daily radiation. Leaf weight ratio is practically independent of mean daily total radiation, but is slightly affected by daylength.

The compensatory nature of variation of leaf area together with specific leaf area in response to light level has also been established from the studies of Myerscough & Whitehead (1967) on Epilobium, Chamaenerion and Tussilago species.

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Kurowa et al (1964), have approached to this problem with different angle and have shown that it is the distribution ratio of photosynthate which decides ultimately the performance of plants under shade. They divide the plant into two interdependent systems, i.e. photosynthetic (F) and nnn-photosynthetic (C) and thon C/F ratio was analysed. Thus Hiroi and Monsi (1964) establish in Helianthus annus the causes of shade intolerability because of increased C/F ratio with shading. Using the data of Evans & Hughes (1961) and Hiroi (1961), the comparison of growth among H. annuus Phaseolus aureus and Impatiens parviflora, has showed that the degree of shade tolerance in these species was closely related with the feature of assimilates being distributed into the photo-synthetic system. On these grounds, Impatiens parviflora has been regarded as the highly shade tolerant, while H. annuus being extremely intolerant.

With the knowledge available during the last part of the past century investigations of the physiology of germination has been approached two ways. One is by studying the nearly ubiquitous cessation of embryo growth long before seed maturation. The other is by studying the germination - regulating mechanism, which make the environmental requirements for growth distinct from those of subsequent growth. This inability to germinate except under special environmental conditions commonly termed "dormancy". Though the

significance of this term is inadequate and often misleading because of its indiscriminate use and a lack of established criteria. Barton & Crocker (1948), defined dormancy as a general term, which may be applied to any condition which prevents germination when ordinary requirements of moisture and temperature have been met. Mayer & Poljakoff - Mayber (1963), applies the term to those seeds which are generally regarded as unfavourable to germination i.e. in a suitable temperature, adequate water supply, light and normal composition of the atmosphere and hence should be considered dormant or in a state of dormancy. But whatever the embracement of the term may be, it is a well known fact that ontogeny is not a continuous process of development, but is intersperesed with periods during which development is completely or partially inhibited, for instance the egg cell and the endosperm nucleus before fertilization, the embryo in most ripe seeds, and winter and summer rest periods of trees and shrubs are good examples of such inhibitors belonging to the normal development cycle. Sometimes such inhibition is brought about by environmental conditions, more often by conditions within the plant itself. The main biological function of dormancy is the prevention, by self inhibition, of premature germination and the extension of the germination period over a long time, i.e. an extended distribution in time.

A detailed account of the germination inhibitors has been reviewed by Evenari (1949) who enlisted some hundred of plant

species from different sources in which these inhibitors are of most frequent occurance. They are not only localised in seeds or fruit but in various parts of plants according to species. The pulp of pear, apple, Spinosum., juice of tomato; fruit coat of triticum, Helianthus, Fagopyrum; seed coat of cabbage, lettuce; embryo of Helianthus; endosperm of Iris Sp; leaf asap of Phragmitis; bulb of onion; Garlic, and root of carrot and raddish etc., are just the few examples to quote here.

There are evidences that naturally occuring inhibitors of one species can inhibit the germination of other seeds. Evenari (1942) showed that the tomato juice in a dilution of 1:25 wholly inhibits the germination of Lepidium seeds, whereas wheat grain start to germinate in a dilution of 1:4. Konis (1947) has also shown the inhibitory action of the leaf sap of various plant species on germination and growth of the other species.

The best known inhibitors are either the substances or belong to various chemical groups. Among them Hydrogen Cyanide (Almond seeds); mustard oil, (sinapis alba) Malic acid and citric acid (Fruit pulp of apple), unsaturated lactones (Fruit of Sorbus accuparia) and Coumarine (Lettuce seeds) are the few examples.

Randolph & Cox (1943) in their preliminary attempt of culturing barbed Iris embryos showed apparently that there is some growth inhibiting substance present in the stored food which retard the growth of embryo. In a further approach Randolph (1945).

demonstrated that a germinating inhibiting substance in Iris seeds is at least partially responsible for the erratic behaviour in seedling production. Mature embryos removed from the seeds and placed on nutrient agar developed into strong seedling within two or three weeks. The cycle from seed to flowering was reduced to less than a year, instead of two or three years normally required.

The field of embryo culture is comparatively new and offers a great promise for solving certain problems in genetics and physiology, especially in regard to nutritional requirements of plants and the nature and causes of dormancy. With advancement in techniques of chromatography the nature of inhibiting or growth promoting substances is becoming more revealing than before.

Recently by using these techniques, Villiers & Waering (1960) have shown that the deep dormancy in the fruit of Fraxinus excelsior is imposed by the presence of growth inhibitors in both endosperm and embryo. During chilling this dormancy was overcome by the production of a germinating stimulating substance in the tissue of the embryo. Matsuba(1962) obtained seedlings from Datura Tatula by supplamonting the basal medium with growth promoting substances and referred to as "embryo factor". Among the variety of material tested to examine thier growth promoting effect included diffusates from young seeds of I. pseudacorus but was found ineffective in promoting growth of the seedlings.

Among the various environmental factors which are responsible for activating or inhibiting germination regulating

mechanism, light and temperature has proved to be the most important factors. A detailed account of these factors involving in the dormancy has been given by Koller et al (1962). Light effects have been studied extensively and it has been established that the light mechanism active in germination are the same as those involved in a large array of other photomorphogenetic phenomena (Toole et al 1953). Much of the important data for elucidation of light mechanism have been obtained from work on those other phenomena. Discussion of the effect of light on germination is therefore more profitable within a more broader framework which is outside the scope of this review. For the most part, however, seed which are light-favoured may have thier germination accelerated by light, but light is not absolutely necessary for germination. Kinzel (Crocker & Barton, 1957 ; Mayer & Poljakoff-Mayber 1963) made rather limited studies of 964 species and found 672 of them favoured by light. There are seeds on the other hand, which have their germination inhibited by the presence of light of the total of 96 species Kinzel listed 258 as inhibited by light.

In the field of seed technology the process of after-ripening of the seeds of may species in dry storage as well as in low temperatures has been the subject of many investigations. It has now been established that many seed do not germinate in nature unless they overwinter their seed stage. Even if the embryo seems fully developed and has attained considerable size before germination will proceed (Villiere & Waering 1960).

It has been shown that seeds of may rosaceous forms (Crocker & Barton 1931), and many coniferous forms, Barton (1939)

are delayed in this manner. The problem of after-ripening has been especially treated mainly in the field of forestry and horticulture. A much practical solution to prepare seed for germination was "stratification" - a common practice which has come from nersery, where the seeds are stratified with layers of moist soil or sand or stratifying the seeds for winter treatment of temperate zone forms. Thus the term has come to be applied to the process of planting seeds in or mixing seeds with moist soil, sand, granulated peat or any other moist medium. At Boyce Thompson Institute, N. York, two general methods have been extensive by used in applying low temperature pretreatment. In one seeds have been mixed with moist granulated peat and the mixture placed at various low temperatures. In many cases refrigeration has been employed to approximate conditions (Carleton 1937). Among the various seeds treated also included *iris* seeds. In a report by Giersbach & Barton (1929), it has been demonstrated that stratification of the seeds I. pseudacorus at 0°, 5°, and $10^{\circ}C$, for two and three months hastened the germination. Two months at $5^{\circ}C$ gave 58 percent seedlings production after planting, when seed coat was removed it had also a considerable effect in increasing the germination precentage, at constant temperature of 15°, 20°, and $30^{\circ}C$, and in daily alternating temperature of 15° - $30^{\circ}C$ and 20° - $30^{\circ}C$.

CHAPTER II
MATERIALS AND METHODS

MATERIALS AND METHODS

As the present investigations are mainly concerned with seed germination and the growth behaviour of the species under different environmental conditions, a general description of the sources of materials used, and a common methodology adopted for every experiment is described in detail. The separate experimental procedure adapted for each experiment has also been described separately, as most of the experiments differ in their experimental procedure and techniques.

Seed collection: The seeds of I. pseudacorus and F. ulmaria were mainly collected from the cites of "wheatfen broad", Surlingham, Norwich, Norfolk in late summers of 1966 and 1967. These seeds were mainly used for the purpose of germination studies, the remainder being used in the growth experiments.

Seeds were also collected from the vacinity of Silwood Park, Sunninghill, Ascot. I. pseudacorus grows abundantly along the borders of the lake "Virginia water", and the running streams merging into the lake. A very few plants of F. ulmaria are found in this locality. Therefore the seeds of F. ulmaria were mainly collected from Norfolk.

One difficulty in collecting the seeds of I. pseudacorus is that the fruiting stalk falls down on the ground soon after the seeds are ripe, due to a large number of big capsules which puts some weight on the solitary fruiting stalk of the plant. As a result one may think for some time as if the plants have remained sterile, but by examining the surrounding vegetation and the ground it can be found that the part of

the fruiting stalk is either buried in the muddy soil or plunged into the water where some capsules are found to be dehisced partially, some completely empty because of the total dehiscence which set free the seeds. It was found that the ideal period for collecting the seeds of I. pseudacorus is between August and September (late Summer), when the large number of pale green coloured capsules are formed on the erect fruiting stalks. At this condition the seed coat appearance turns from milk to pale brown colour. Capsules were not picked up individually from the fruiting head but the whole fruiting stalk was taken out. The seeds (achenes) of F. ulmaria were taken out in a similar way. The fruiting branches along with the capsules or achenes were immediately kept for drying in the green house. In about 20 to 25 days capsules were completely dehisced and most of the seeds were shed off.

The keeping quality of seeds depends upon its storage conditions. In other words the better the storage for keeping the seeds viable, the better the chance of survival when they are removed to an unfavourable environment. Seeds were kept for storage in a cold ventillated room where the temperature varied between $10^{\circ}C$-$15^{\circ}C$ during most of the storage period. This low temperature is found to be superior to higher temperatures for the maintenance of the germination capacity by many workers. Large polythene bags were selected for the storage of seeds, ensuring a free gaseous exchange and less chances of contamination by mould. Some seed lots were also stored dry in an electric refrigerator for its cold treatment.

Storage in moist medium at low temperature

As discussed in the previous chapter and the succeeding pages both seeds of I. pseudacorus and F. ulmaria possess dormant embryos. Perhaps no other method for breaking dormancy has been more widely used than that of keeping the seeds in moist medium and placing them at a low temperature usually between 1°C and 10°C for a period of several weeks. Under these conditions the seeds after ripen so that they germinate almost immediately upon transfer to an alternate higher temperature. A series of experiments carried out on germination and growth proved itself the validity of this method of pretreatment of seeds in moist medium for breaking the dormancy.

The process of preparing the seeds for germination by giving them low moist temperature pretreatment has been commonly known as "stratification". This comes from the nursery practice of alternating layers of seeds with layers of moist soil or sand or stratifying the seeds for winter treatment of temperate zone forms. Thus stratification has come to be applied to the process of planting seeds in or mixing seeds with moist soil, sand granulated peat moss, or any other moist medium provided a period at low temperature is given. In other words the seeds must be imbibed with water before after ripening of this type can proceed. In the light of this practice it seems that the choice of moist medium a suitable low temperature and the period of storage are the main components of seed storage to bring about a complete after ripening and long term viability of seeds. Many lots of seeds were stored in glass

beakers of 250 ml capacity. These containers proved to be suitable and convenient to remove the seeds when necessary and to examine the water contents from time to time. For stratification, distilled water was used as a moist medium. Before cold storage the seeds were allowed to remain partially submerged in the water medium for 24 hrs. During this time the seeds were completely soaked and imbibed with water. The excessive amount of water was then drained out and the soaked seeds were now stored for cold treatment. The cold treatment was given in an electric refrigerator with a temperature around 41°F. The beakers were covered with filter papers or the musclin cloth held in place by rubber bands. The containers were labelled properly with date of storage.

Germination

The choice of suitable containers to carry out the germination studies created some basic problems, when a large number of seeds had to be germinated in a single petri dish. The use of a general size petri dish of 4" diameter has long been the common practice by many workers, particularly when seeds are of small size. It was convenient to use a 4" diameter petri dish, where about 100 seeds of F. ulmaria can be germinated and counted very easily. In I, pseudacorus where the seeds are considerably large a petri dish of 4" diameter was insufficient to accommodate 100 seeds at a time, Therefore large size petri dishes of 6" diameter with 1" wall were selected for the seed germination studies of I. pseudacorus.

Thick sterilized mats (Steromats) of 4" and 6" diameter were used

as the substratum to fit in the respective sizes of petri dishes. These steromats had a greatest capacity to retain the water for a longer period. Mats were then covered with filter papers of the respective sizes of petri dishes.

Selection of viable and uniform seeds to proceed with the germination studies becomes an obvious task, especially when the seeds show a considerable range of variation in size and viability. The seeds of I. pseudacorus and F. ulmaria in one way or other, and the seeds of the same kind. The capsule-born seeds of I. pseudacorus show much variability in size. In a spindle-shaped capsule, the seeds towards the tapering end are apt to be smaller than the central one. The variation of seed size in F. ulmaria is not so severe, but seedless achenes are of frequent occurance. It has been observed that in every lot of 100 seeds chosen randomly, about 25% seeds were without embryos. The nature of fertility could only be observed when the achenes were soaked in water for at least 12 hours, which made the wall translucent. The after ripened achene in a moist medium were the best samples to detect the presence of seeds.

In case of I. pseudacorus only large seeds were selected for uniformity of size, the remainder being discarded. In F. ulmaria only the achenes containing seeds were used for germination purpose.

In each subsequent experiment on germination, four replicates of petri dishes were used containing 100 seeds in one petri dish. Before sowing the steromats were soaked in water for an hour, then the seeds were

placed on the mats, and petri dishes were now covered with lids. Distilled water was added frequently to keep the seeds moist.

The appearance of radicle was taken to indicate that germination has occurred. In F. ulmaria successful germination was scored in terms of the seedlings with fully expanded cotyledons, when the treatment was given in light. Where the seeds were germinated in the dark the emergence of the long hypocotyl was taken as an indication of germination. In I. pseudacorus, however, germination was scored in terms of the seedlings with emerged coleoptiles.

Primary data on germination for each treatment was recorded in the form of the daily counts of seeds germinated per total number of seeds sown. These seedlings were later on expressed as percentage of the number of seeds sown.

For assessing the effects of treatment two parameters were basically used - number of seeds that finally germinate (germination capacity) and the rate of germination of the seeds, the latter generally being expressed in reciprocal form, i.e. days to reach 50% of germination capacity. The estimate of germination capacity is useful where the differences appease with extremes of treatments. Germination was regarded as being complete when five daily counts showed no significant increase in number of seedlings. A critical period of five days was estimated because the rate of germination was found to be slower in both the species.

Experiments on growth: In majority of experiments on growth under varying levels of environment, the plants were cultured in soil. In fact water culture could have been used for this purpose, but it was restricted only where the experiments were designed to study the comparative dilutions of the nutrient solution.

Many workers preferred water culture to soil culture in majority of their experimental investigations on growth, when the experiments were mostly concerned with the soil-water relations of the plants, e.g. uptake of macro and micro elements, hydrogen ion concentration, deficiency levels of nutrients etc.

The best performance of a plant grown in a semi natural condition of a green house can only be expected when maximum possible conditions of nature are provided for its normal growth. In the present investigations, where the experiments are concerned with the light factors e.g. photo period, light intensity etc., an artificial uniform homogenous soil of high nutrient status was used and thus would not likely to be limiting in growth.

The soil used was a mixture of 2 parts sand and one part peat. The peat used was Irish moss peat. The coarse peat was riddled through a $\frac{1}{2}$" sieve and made to its finest grade and the remainder was rejected. Fine peat and sand were then mixed thoroughly to make a homogenous soil.

The containers for the experiments were plastic and clay pots of different sizes depending upon its availability. In some experiments

both types of pots were used at a time. The plastic pots are provided with a number of small drainage holes whereas the clay pots with a single large hole at their bases. In any case the holes were covered by some broken pieces of clay from inside the pot to check the excessive drain . e of water and the root emergence through the holes. The soil was poured in, sheared flat at the top when full, shaken down to settle and filled agair The surface was once more sheared flat and was then made firm with . derate pressure from the fingers, leaving an inch space from the top of the rim. Pot mixture of soil was soaked properly by adding it with water and nutrient solution and then the seedlings were transplanted.

Mass culture of seedlings: In order to proceed with the experiment on growth, considerably large number of seedlings are required when a multiple of replicates per treatment and harvest are involved in a particular set of experiments. With this aim seeds were sown in a number of large wooden trays of 15"x12"x4" sizes. The trays were filled with fine sand up to the top giving a 2" space from the top. The seeds were covered by a fine layer of sand. Nutrient solution of ten times dilution was showered gently over the sand, trays were covered with transparent polythene or the clear glass panels. Water was added frequently to prevent the dry out of sand.

Later a water culture method for the mass culture of seedlings was developed and this was by far the most effective from all points of view. This method was based on the floating technique used by Myerscough (1962) and Hackett (1962) in their germination experiments.

The nutrient solutions were held in a number of baking trays, which

had been painted with cellulose acetate paint and was chemically inert to the solution used (Hewitt 1952). Each tray held 1½ l. of solution. Seeds were supported on the surface in contact with the free solution. The support consisted of a rectangular thick rigid glass fibre matting floated on small narrow strips of ceiling polyvinyl foam. The seeds were spread over the surface of the glass fibre matting which gave the best contact between seeds and solution. The trays were covered by polythene sheets and panels of glass. The seedlings were mostly raised in green house conditions where a minimum temperature of about 20°C was available, otherwise the seeds were germinated in controlled temperature room of 25°C with 16 hours of illumination and no relative humidity control.

With the appearance of seedlings with expanded cotyledons (F. ulmaria) and the first foliage leaves (I. pseudacorus) they were carefully pulled out from the fibre matting or picked up from the sand, whatever the case may be, and immediately transplanted to the pots.

The seedlings were selected for their uniformity of size and development and sown 2 to 3 seedlings per pot at a distance of 1" apart. The seedlings were left under uniform condition of green house for 15-20 days prior to the treatments. In practice it was observed that this was the most suitable period of seedling establishment, during this period the seedlings enter into a 2 leaf stage. At this stage the seedlings were again selected for the uniformity of size and development leaving one seedling per pot and the rest were weeded out.

In an experiment, the sample size ranged from 100 to 120 replicates of plants per species per treatment, depending upon the type of

experiment. Harvest was made at a regular interval of 15 days. In all a maximum of six harvests were made including the"initial harvest". The seedlings selected for an initial harvest were from those established seedlings with 2 leaf stage prior to the treatment. Initial harvest was regarded as the token of unaffected plants and the starting point in the further growth of plants. About 10 to 20 plants were randomly selected and harvested from each treatment per species.

Plants were carefully removed from the pots by inverting the whole pot upside down. Roots were washed under tap water. In the early harvests the root system was not so compact and it was easy to get rid of the peat particles clinging to roots. In the later harvests however, it became difficult to remove the peat from the roots because of the massive root growth. This difficulty was overcome by soaking the roots in water for 2 to 3 hours before washing. A scheduled harvest at a particular date was completed within 12 hours by taking the representative samples from each treatment. Every possible effort was made to measure the leaf area of the samples on the same day, however at the later harvests, where the plants were fully grown, the measurements were not possible on the same day. Therefore the rest of the unmeasured plants were kept in a refrigerator for the other day.

Leaf, stem and root were cut separately and wrapped in filter papers. By leaf means the leaf blade only, as in I. pseudacorus the leaf blades arise directly from the junction of the stem, they were cut directly from the junction of the stem. In F. ulmaria the terminal and lateral

leaflets (pinnae) were cut off from the petioles (rachis). The petioles were included with stem. Leaf area was measured photoelectrically with the help of a planimeter. The plants were dried in a ventillated oven at 80°C to 100°C for forty eight hours. The dried material was then cooled and stored in desiccators until weighing. The dried parts were then weighed in gm/mg on a Stanton balance.

Primary data was scored in terms of leaf area in cm^2 and the separate dry weights of leaf, stem and root. Later on total dry weights of all the parts was calculated. The tables on primary data are given in "Appendix".

Analytical methods

Growth analysis is a customary way of studying the performance of plants in terms of various processes in relation to the factors of environment. In this way primary data provides the basic tools in explaining and investigating these vital processes in relation to environmental complex. Besides the progress curves of the dry weight and leaf area, which only shows in simplest term the performance of plants, a number of parameters can be derived from the primary data.

As pointed out by Evans & Hughes (1961) the estimates falls in two types, on which estimate the morphogenetic conditions of the plant at a series of points in time. The second type is based on an elucidation of the estimates concerning the rates of growth processes of the plants.

These two types, together with an addition of some parameters used by Myerscough & Whitehead (1967), and Whitehead (unpublished) are listed as follows:-

1. Estimates of the morphogenetic conditions.

(a) Relating to the whole plant

i Percentage proportion of the distribution of gross production into various parts of the plant i.e. The dry weight of various morphological categories expressed as a percentage of the total dry weight.

e.g. leaf dry weight as a percent of total dry weight
stem dry weight as a percent of total dry weight
root dry weight as a percent of total dry weight
(see page 107 for discussion)

ii Leaf area ratio i.e. the area of the leaf to the total plant weight (cm^2/mg)

iii Root/shoot ratio, i.e. the root dry weight to the shoot dry weight

(b) Relating to parts of the plant.

i Specific leaf area, i.e. the area of the leaf to the dry weight of the leaf (cm^2/mg)

ii Leaf/shoot ratio, i.e. the leaf dry weight to the shoot dry weight.

iii Root/leaf area ratio, i.e. the root dry weight to the leaf area (mg/cm^2)

iv Root/leaf ratio, i.e. root dry weight to the leaf dry weight.

2. Estimates of the course of growth processes.

i Mean relative growth rate, i.e. the increase of plants dry weight over a time interval (mgs/mgs/week)

ii Mean relative rate of leaf area increase i.e. the increase of leaf area over a time interval (cm^2/cm^2/week)

iii The ratio of the mean relative growth rate to the mean relative rate of leaf area increase over a time interval ~~(mgs/cm^2/week) or~~ $\alpha = \frac{\bar{R}}{\bar{R}_{LA}}$

iv Mean unit leaf rate (net assimilation rate) i.e. the increase in total dry weight per unit of leaf area over a time interval (mgs/cm^2/week)

In the present investigation, the use of these parameters varied from experiment to experiment depending upon its magnitude in the framework of a particular experiment. The main purpose was to express growth processes and morphology in numerical and/or relative terms so that qualitative differences etc. cou'd be demonstrated in quantitative terms.

Theoretical considerations of some parameters of growth used in the present investigation.

Blackman (1919), Briggs, West & Kidd (1920), and Fisher (1920) have shown that various estimates of growth processes over a period of time can be derived from primary growth data. Their estimates of growth processes are usually considered separately and rarely used together in considering growth processes. In the course of investigations involving

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the comparative growth of several species over a range of environmental conditions, Whitehead & Myerscough (1962), pointed out that interpretation of experiments is made easier and more revealing when α values are used instead of the more usual parameters of growth analysis, i.e. mean relative growth rate ($\bar{R}$) and mean relative rate of leaf area increase ($\bar{R}_{LA}$). Either of these two parameters taken separately can only indicate a change of one of the important processes resulting in an ultimate plant form.

The mean relative growth rate $\bar{R}$ over a time interval t_1-t_2 is derived from R the relative growth rate at any instant as follows:-

$$R = \frac{dW}{dt} \cdot \frac{1}{W}$$

where W= total dry weight of plant at time t

$$\bar{R}\,(t_2 - t_1) = \int_{t_1}^{t_2} R\,dt = \int_{W_1}^{W} \frac{dW}{W} = \log_e W_2 - \log_e W_1$$

Fisher has shown this required no assumption regarding the change of W with time.

Similarly the mean relative rate of leaf are increase over an interval of time $t^2 - t^1$ can be derived from R_{LA} the relative rate of leaf area increase at a given instant as follows:-

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$$R = \frac{dW}{dt} \cdot \frac{1}{W}$$

where W = total dry weight of plant at time t

$$\bar{R} = \int_{t_1}^{t_2} R\,dt = \int_{W_1}^{W_2} \frac{dW}{W} = \log_e W_2 - \log_e W_1$$

Fisher has shown this required no assumption regarding the change of W with time.

Similarly the mean relation rate of leaf area increase over an interval of time $t^2 - t^1$ can be derived from $\bar{R}_{LA}$ the relative rate of leaf area increase at a given constant as follows:-

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$$R_{LA} = \frac{dLA}{dt} \cdot \frac{I}{LA}$$ where LA = leaf area of plant

$$\bar{R}_{LA}\,(t_2 - t_1) = \log_e LA_2 - \log_e LA_1$$

Thus the expression for deriving the values of the index α becomes

$$\alpha = \frac{\log W_2 - \log W_1}{\log LA_2 - \log LA_1} = \frac{\log_e W_2 - \log_e W_1}{\log_e LA_2 - \log_e LA_1} = \frac{\bar{R}}{\bar{R}_{LA}}$$

The mean unit leaf rate

The term is synonymous with net assimilation rate (Gregory 1926). The choice of the term "mean unit leaf rate" is in accordance with the arguments of Coombe (1960) and Evans & Hughes (1961). The mean unit leaf rate ($\bar{E}$) over a period of time $t_1 - t_2$ is derived from the rate of increase of weight per unit leaf area E at a given instant.

$$E = \frac{dW}{dt} \cdot \frac{I}{LA}$$

$$\bar{E}\,(t_2 - t_1) = \int_{t_1}^{t_2} E\,dt = \int_{W_1}^{W_2} \frac{dW}{LA}$$

It is usual practice to express $\bar{R}$, $\bar{R}_{LA}$ and $\bar{E}$, in units of weight and leaf/area/week. To integrate the expression of $\bar{E}$ it has been the practice to assume an arbitrary relationship between W & LA irrespective of time. The most useful assumption is that of linearity when

$$\bar{E}\,(t_2 - t_1) = \log_e LA_2 - \log_e LA_1) \frac{W_2 - W_1}{LA_2 - LA_1} \qquad \text{----------(1)}$$

$$R_{LA} = \frac{dLA}{dt} \cdot \frac{1}{LA}$$ where LA = leaf area of plant

$$\bar{R}_{LA} = \log_e LA^2 - \log_e LA^1$$

Thus the expression for deriving the values of the index α becomes

$$\alpha = \frac{\log W_2 - \log W_1}{\log LA^2 - \log LA^1} = \frac{\log_e W_2 - \log_e W_1}{\log_e LA^2 - \log_e LA^1} = \frac{\bar{R}}{\bar{R}_{LA}}$$

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$$\bar{E} = \frac{dW}{dt} \cdot \frac{1}{LA}$$

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$$\bar{E} = \log_e LA_2 - \log_e LA_1 \quad \frac{W_2 - W_1}{LA_2 - LA_1} \qquad \text{----- (1)}$$

Where W_1 , LA_1 , W_2 and LA_2 represent respective values at the first and the second harvest.

Briggs has shown that if it is assumed that W is related to LA_2 (Briggs, unpublished),Coombe (1960) then

$$\bar{E} = \frac{2(W_2 - W_1)}{LA_2 + LA_1} \qquad \text{----- (2)}$$

In the development of concept of growth analysis several formulae have been proposed to estimate the mean unit leaf rate but none of these can claim universal or general applicability. However, in the present investigations, the formula 1 given above has been used frequently, and it has proved to give significantly different values, when species were subjected to different sets of environmental conditions.

The values of $\bar{E}$ are calculated on the basis of leaf area as well as on leaf weight. To get $\bar{E}$ values on the basis of leaf weight the values of leaf area were replaced by the values of leaf weight in the given formula.

CHAPTER III
STUDIES ON GERMINATION

Effect of temperature, light and darkness on the germination of species

Different seeds have different temperature tolerances within which they germinate. The precise temperature requirement is very different according to species. At very low temperature and at high temperatures the germination of all seeds is inhibited. An increase in temperature does not necessari mean an increase in either the rate of germination or the germination capacity. Germination as a whole is therefore not characterised by a simple temperature coefficient. In the range of temperature within which seeds germinate, there is usually an optimum temperature, below and above which germination is delayed but not prevented (May er & Mayber 1963). The optimum temperature may be taken to be that at which the highest percentage of germination is attained in the minimum period.

The effect of temperature on germination is not independent of other factors of the environment. The instances of inter dependance between temperature and light and/or darkness are known for a variety of seeds where for example light may promote germination at unfavourable high termperature but not at low ones etc.

It has been observed that the germination and establishment of the seedlings of F. ulmaria and I. pseudacorus in nature takes place only in a restricted range of season. In Autumn where the temperature is very low germination of these two species does not occur. Thus the establishment of

seedlings and the temperature range under which germination does or does not occur becomes one of the fundamental environmental factors when considering the distribution of these species in nature.

In the present investigations an attempt has been made to determine the precise temperature requirements for the germination and the seedling establishment of the species under investigations.

Experimental procedure

The experiments were carried out in controlled temperature rooms. A range of five temperatures i.e. 10°, 15°, 20°, 25° and 30° C were selected. A controlled temperature room with 10° C was not available therefore a separate arrangement was made available in an electric regrigerator where temperature was regulated to 10° C. Illumination was provided with a 150 watt bulb. The sources of illumination used in C.T. rooms was from a bank of fluorescent tubes hanging over the benches. The illumination varied from room to room, but in any case the range measured was from 500-700 ft candles. Illumination was provided 16 hours a day. The seeds were germinated in petri dishes and followed the same general methods described in material and methods. At each temperature four replicates were provided for each species for germination in both light and dark. Each replicate consisted of 100 seeds, where the seeds were kept in darkness, the petri dishes were covered with round biscuit tins painted black inside and outside. The bottoms were punched with holes to make a proper ventillation inside the tins, then the tins were inverted over the petri dishes.

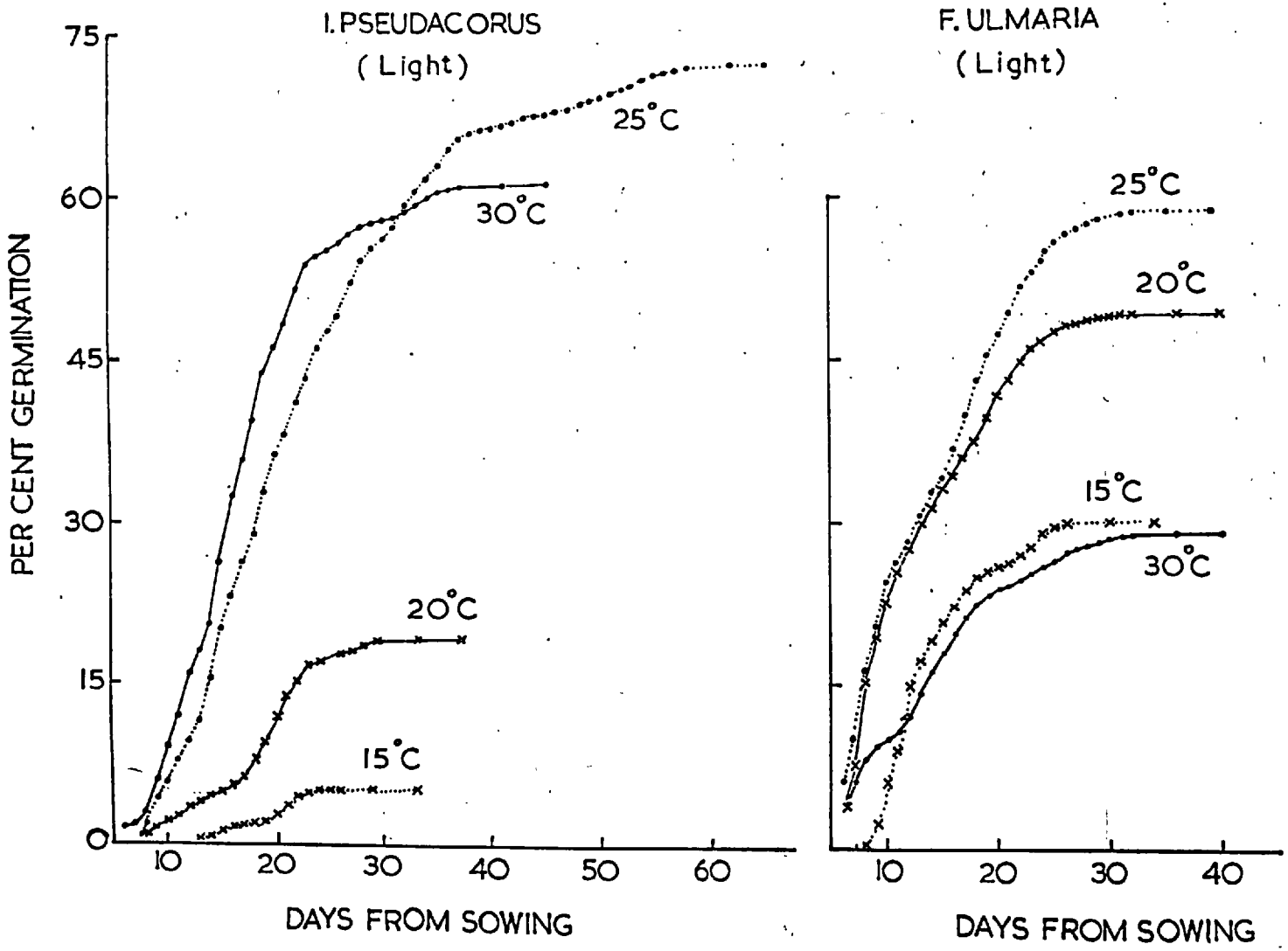


FIG. 1. Effect of differing temperature levels on seedling emergence in light.

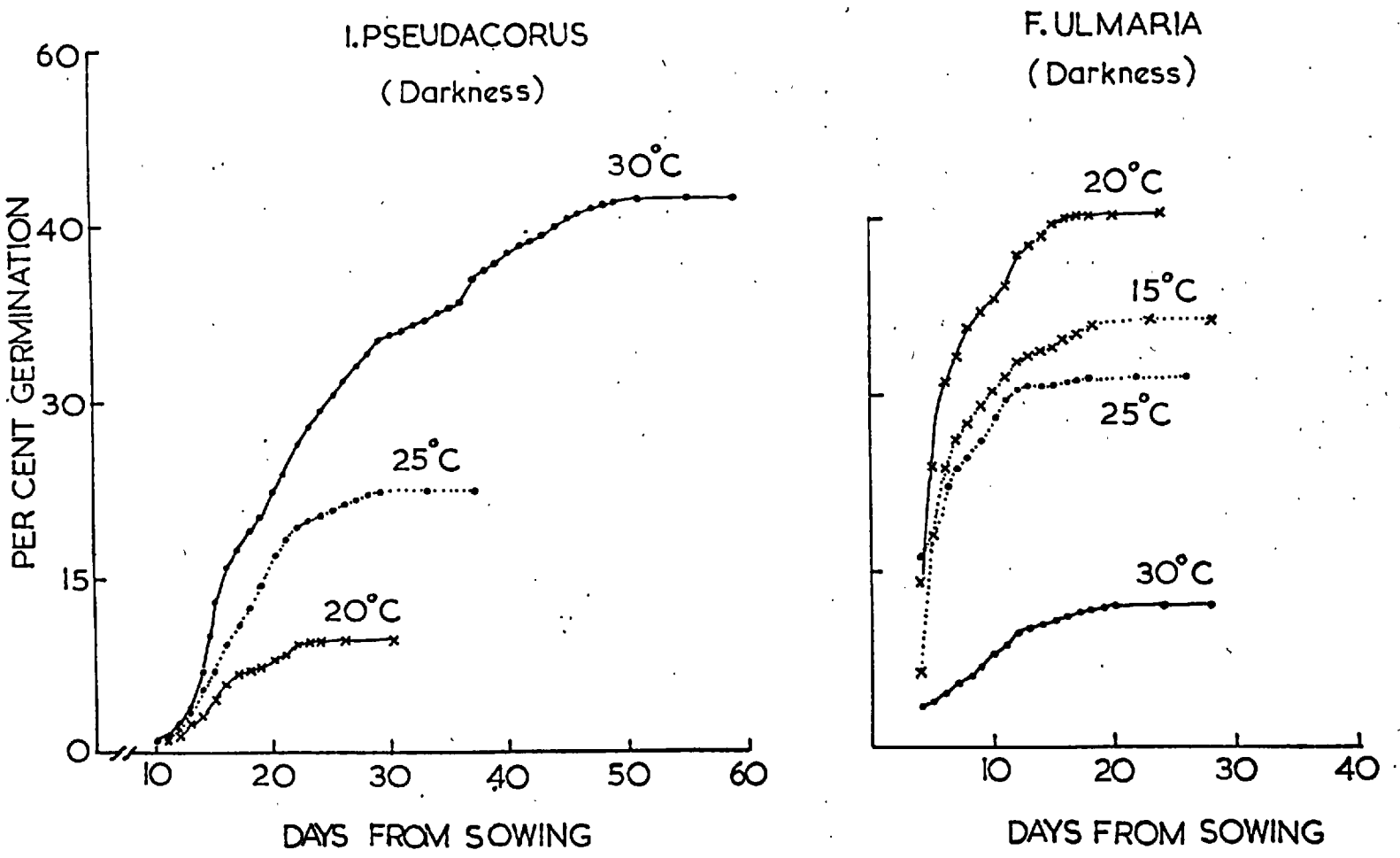


FIG. 2. Effect of differing temperature levels on seedling emergence in darkness.

Results and discussion

With both the species germination did not occur at 10°C either in light or darkness. Some germination occured at 15°C in F. ulmaria both in light and dark but with I. pseudacorus no germination was observed in darkness but about 5% in the light.

The time courses of germination in the light and dark for the different temperatures are shown in Fig. 1 and Fig. 2. With I. pseudacorus it can be seen tha· ·ith the increase in temperature the percentage germination also increased ith time. At 30°C in light good germination, 60% occurs, but the optimum of about 75% seedlings emerged per total of the seed sown occurs at 25°C. It can be seen that with I. pseudacorus the extent of germination in the dark was dependent on temperature. In case of F. ulmaria optimal germination capacity was recorded at 25°C in the light, whereas at 30°C there was a large decrease in the percentage germination, both at light and darkness. It can be seen that in light at 15°C and 30°C there was no significant difference in the total germination capacity. In contrast to I. pseudacorus the extent of germination in darkness is not totally dependent on the temperature, where the optimal germination capacity was scored at 20°C.

In the comparative assessment of the species in terms of germination both species differ markedly in their temperature requirements. F. ulmaria showed a wide range of temperature tolerance ranging from 15° - 30°C, and can germinate well within this range, whereas with I. pseudacorus only a high

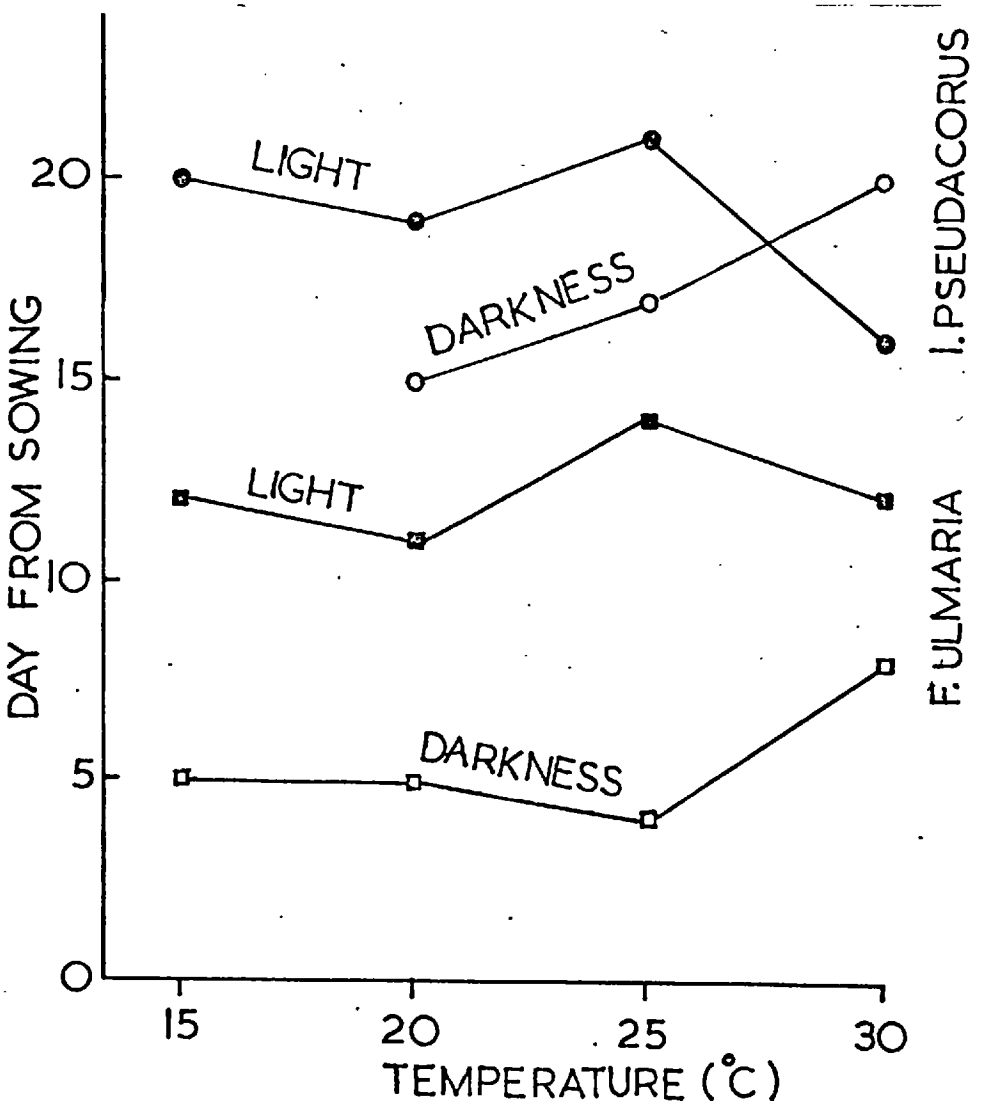


FIG. 3. Effect of differing temperature levels on the time taken to reach half the percentage emergence in light and darkness.

temperature can ensure good germination capacity, occuring in the narrow range of between $25^{o}C$ - $30^{o}C$.

From these findings it can be inferred that the establishment of the seedlings in nature is restricted within certain limits of seasonal periodicity, as these temperatures are only available during and after the Spring. The absence of seedlings during Autumn is self explanatory on the basis of the results discussed.

Effect of various time periods of stratification of seeds in moist madium at low temperature on the germination and seedling behaviour

In very many species of plants, the seeds when shed from the parent plants will not germinate. Such seeds will germinate under natural condition if they are kept for a certain period of time. This delayed germination is of value to the plant especially in the temperate zone where winters are apt to be severe, Seeds must be protected against germination where they fall to the ground in Autumn. If growth proceeded at that time, the young seedlings would be killed by the cold weather which followed. Thus dormant embryos have been developed. Here nature provides the proper conditions for after ripening during the winter months. The seeds are kept moist in the ground by leaf mulch rains and snows. With the advent of warm weather following spring, after ripening has been completed and the young seedlings appear above ground. However, the uncertainties and variations of the weather coupled with other destructive factors permits only a small percentage germination in nature.

The necessity for a period of after ripening may be due to a number of factors. Various kinds of changes may occur during this process. In the case of an immature embryo further anatomical and morphological changes may occur. In some seeds chemical changes must occur in the seed before it can germinate. They may and normally do include an increasing acidity and altered enzyme activity within the tissue of the embryo. Also there may be

chemical as well as chemical or physical changes within the endosperm or stored food of the seed, as well as chemical or physical changes within the seed coat during this after-ripening period. The period required for such embryo to reach maturity varies from a few days to several months. Therefore it becomes important to know the specific time and temperature required for a particular species for after ripening.

The best known cases of seeds requiring low temperature pretreatment for germination are found among the Rosaceae and among various conifers. However, in other families too, such requirements are known as for instance in Juglans nigra (Juglandaceae), Asters (compositae), Adonis and Anemone (Ranunculaceae), Iris (Iridaceae) as well as many others including aquatic plants. Crocker & Barton (1957) have listed a number of plants requiring stratification giving details and time and temperatures used.

The seeds of I. pseudacorus and F. ulmaria have been tested in laboratory conditions for their specific time and temperature requirements for after ripening, by means of a series of experiments to ascertain their particular needs. The aim was to find out how these seeds in nature remain dormant during the autumn and germinate at the advent of spring. An attempt has also been made to correlate the laboratory results with the performance in nature of a limited season of germination with subsequent effect on distribution.

Experimental procedure

In applying a low temperature pretreatment, the same routine procedure employed at "Boyson Thompson Institute", New York, has been adapted to carry out the present experiment. At this institute seeds had been mixed with moist peat moss and the mixture was placed at various temperatures of 33°, 41° and 50°F. An ordinary electric refrigerator was employed to regulate the desired temperature. After regular intervals of weeks and months a counted sample of seed were removed from each temperature and transferred to a high temperature in the green house. A high percentage of seedlings germination in the green house was taken as an indication of the specific time and temperature required for complete after ripening.

In the present work, the seed samples were stored in water medium (distilled water) instead of moss peat. In some instances attempts were made by using peat moss, but it was found that after the seeds were transferred to a high temperature, most of the seeds were destroyed by mould growth on the seeds. Therefore the seeds imbibed with pure distilled water proved to be a good sterilizer media to insure a healthy germination.

Seed samples were stored in an electric refrigerator where a constant temperature of 41°F was maintained throughout the experimental period. Whenever an alternate high temperature had to be given, it was provided in the controlled temperature room of 25°C. The condition of the C.T. room has already been described in the previous pages. This temperature was selected because in the experiment on temperature effect it was found

that at this temperature optimum percentage germination occured with both the species. In the first instances, samples of stratified seeds were removed from the refrigerator at various time periods of one week, 15 days and one month, but the results showed a high degree of discrepancy from one replicate to another. Therefore, some additional samples were removed after one month, 6 months and one year or even longer. A high percent seedlings germination was taken as an indication of the specific time required for complete after ripening. Seeds were sown in four replicates of petri dishes for every treatment, containing 100 seeds per petri dish. The methods used in general were to germinate the seeds on the surface of a suitable substratum in petri dishes illuminated at 500-700 foot candles from fluorescent bars. The primary data recording on germination followed the same general methods discussed in material and methods. For the comparative assessment of the germination capacity some seeds from dry storage were also germinated in petri dishes. These seeds from dry storage will be referred as "control" wherever necessary.

Results & discussion

The daily counts of the seed germinate expressed in terms of percentage in every treatment for both the species is plotted in graph 4 . It is evident that the species showed an increased germination capacity with the increase time periods of stratification. However, with both the species maximum germination capacity is scored at 6 months period of after ripening i.e. 80% (I. pseudacorus) and 58% (F. ulmaria), whereas at one months treatment the germination was not marked as compared to the "control." In F. ulmaria however, no significant difference was observed between control and one month treatment. On the contrary there was a marked increase in the percentage germination of I. pseudacorus with the increase time periods of moisture pretreatment. It should be emphasised therefore, that I. pseudacorus require a very wide range of after ripening period which may range from one month to almost a year.

The beneficial effect of a long period of low temperature pretreatment can also be judged in terms of the days to reach half the germination capacity. Especially in I. pseudacorus it can be seen in table 1. that a prolonged after-ripening period i.e. from "control" to one years treatment had not only increased the germination capacity but had also hastened the germination process, such that the days to reach 40% optimum germination after a six months after ripening have shortened to 12 days compared to one month treatment where it took about 17 days to reach only a 10% germination capacity.

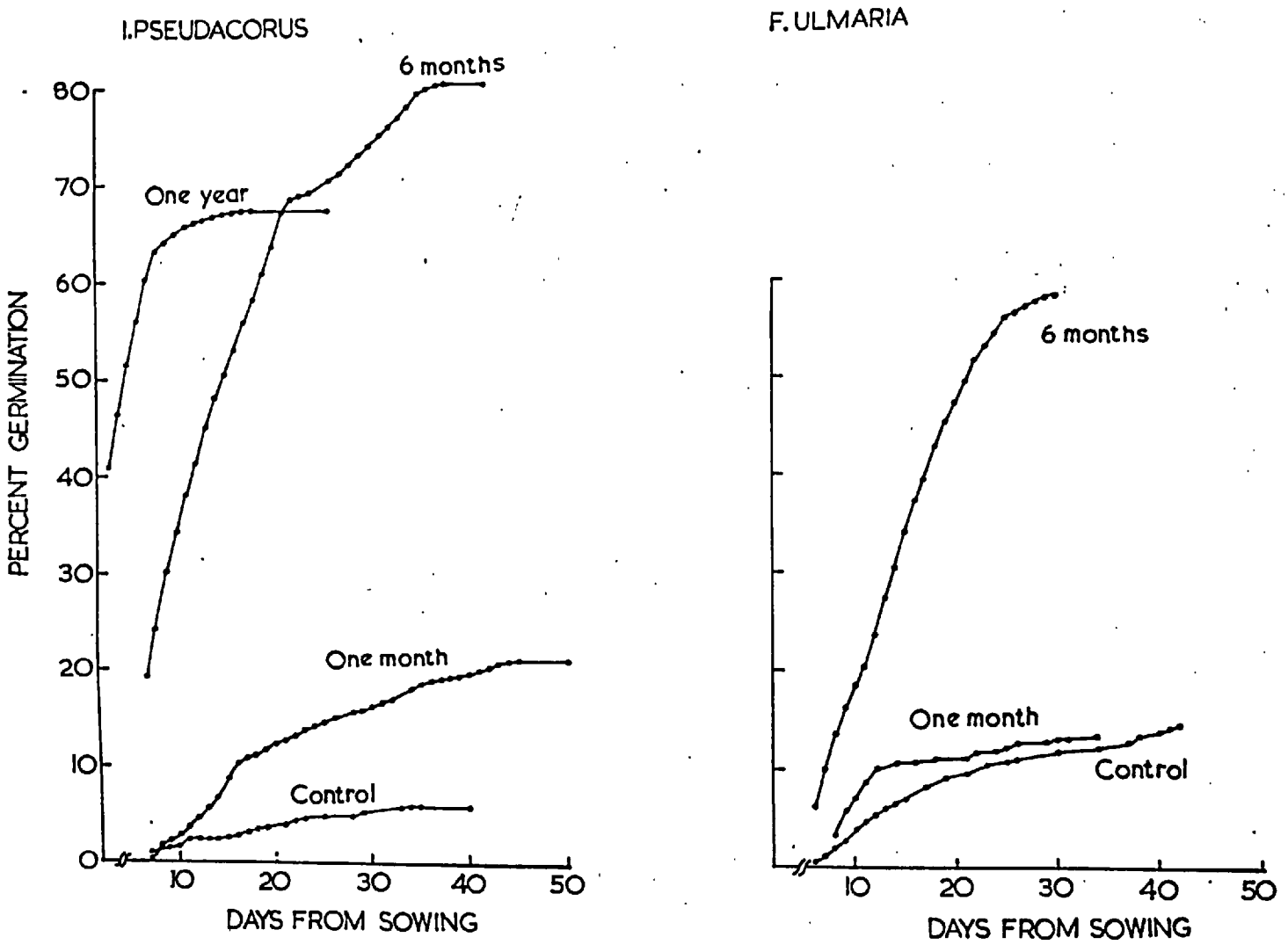


FIG. 4. Effect of various time periods of stratification on seedling emergence.

Table. 1

Time periods of after ripening	I. pseudacorus		F. ulmaria	
	Days	Half%	Day	Half%
control	17	3%	14	7%
one month	16	10%	9	6.5%
6 months	12	40%	13	28%
12 months	2	34%	-	-

An investigation on the germination inhibitors present in the seeds of *I. pseudacorus*

The presence of germination inhibiting substances inhibiting germination has long been realised in many seeds, and inhibiting substances in great variety have been isolated from various seeds and fruits. These substances are usually found in the seed coat or in the tissues of the fruits. Tomato Juice for instance contain a powerful germination inhibitor. If is assumed that these inhibitors act by interferring in some enzyme reaction necessary for growth. Some of them are essential oils and are volatile, while others such as Coumarin, the substance responsible for the smell of new-mown hay are gradually destroyed by enzyme action, so that the seeds are eventually able to germinate. There are the few examples quoted here; a detailed account of the germination inhibitors is discussed Chapter 1.

There are instances when it is also possible to force seeds requieing stratification to germinate by other means, e.g. by complete removal of the seed coat or by removal of the cotyledons (Flemion & Prober 1960.) Such experiments carried out by many workers at Boyce Thompson Institute, Yonkers, New York, particularly on Rosaceous seeds. Seeds forced to germinate in this way did not form normal seedlings, the seedlings being either dwarfed or otherwise deformed. (Barton & Crocker 1948). However cold treatment of the seedlings again resumed a normal growth. It seems probable that this could have happened as a result of the disappearance of substances which inhibited growth or the

formation of substances stimulated the germination. Luckwill (1952) found that growth promoting substances appeared in the embryos of seeds which had completed their after ripening but were absent in seeds kept in dry storage. Valliers and Waering (1960) working on Fraxinus seeds have brought more evidence for the function of growth stimulator in these processes. In Fraxinus seeds a germination inhibitor was found during stratification. It was assumed that dormancy was due to an inhibitor and that dormancy breaking was the result of the counter action of the inhibitor by stimulator. A germination inhibitor substance in Iris seeds had been held at least responsible for the erratic behaviour in seedling production (Randolph 1945). Mature embryos removed from the seeds and placed on nutrient agar developed into strong seedlings within two or three weeks, at that time they could be transplanted to soil.

In the present investigations, where the aim was mainly focused on a particular aspect of the problem of dormancy in the seeds of I. pseudacorus, it was not possible to deal with all the aspects of germination inhibiting substances. Therefore a preliminary approach was made to the problem on limited lines in order to cope with the shorter time available for experiments.

To start with the experiments, one basic assumption was made that the presence of an inhibitory substance is vital in the seeds of I. pseudacorus. Now the aim was to locate these inhibitors either in embryo or in the seed coat, or both within the embryo and seed coat. Secondly, an attempt has also been made to establish the fact that

possibly these germination inhibitors disappear during the period of stratification which makes the seeds ready to germinate or some growth promoting substance are formed during the after ripening period which again triggers the embryos to germinate.

Experimental procedure

The seed lots used in the experiments differ in their periods of stratification from experiment to experiment. In a first set of experiments the seed lot used were treated for a period of approximately 10 months, while in the second set of experiments a much longer peiod of 14 months stratified seed were used. A prolonged period in the latter case has no doubt effected considerably the viability of seeds but as no other seeds with a shorter period of stratification were available, a constant factor of the loss of viability of seeds was taken into consideration for all the treatments equally. However, the length of storage period was the same for each treatment in a particular experiment.

The seed coats were carefully removed by hand, first by making an incision on the seed coat and then by a gentle pressure of fingers, then seed coats were threshed out leaving the grains of endosperm and the embryo. The removed seed coat shells were carefully collected and preserved for a further treatment to the naked seeds.

Some 800 seeds were selected for their uniformity of size and the seed coats were removed in the manner described above. The shells were kept for drying in open laboratory conditions for overnight, and then a fine powder was obtained by grinding these shells in an electric grinder.

The powder was weighed, and the weight was found to be about 5.6 gms. A mean weight required for each of 100 seed lot was calculated. It was approximated that the powder obtained from each of 100 seed coats is about 700 mgs.

In the first series of experiments, where only naked seeds without the seed coat were used, two treatments were applied in light and dark. In the second series three treatments were applied i.e. Seeds with intact seed coat, naked seeds, and the naked seeds with the addition of seed coat powder. When the naked seeds were provided with seed coat powder, a separate arrangement was made inside each petri dish. The steromats were punched in the centre by making a 1" diameter hole. A plastic ring with 1" diameter and $\frac{1}{2}$" wall was inserted in each hole, thus making a well in the middle of the petri dish. A measured quantity of 700 mgs. seed powder was added to each "well". Enough distilled water was added equally in every petri dish to dissolve the contents of powder and to keep the steromats moist. The naked seeds were then placed around the "well" over the surface of steromats. The rest of the treatments with intact seed coat and naked seeds followed the same procedure described in materials and methods. In each treatment 4 replicate petri dishes were used containing 100 seeds in each petri dish. Seeds were germinated in a constant temperature room of 25°C. All the treatments received the same illumination. In a second set of experiments no dark treatment was applied.

Primary data on germination was scored in terms of both the no. of

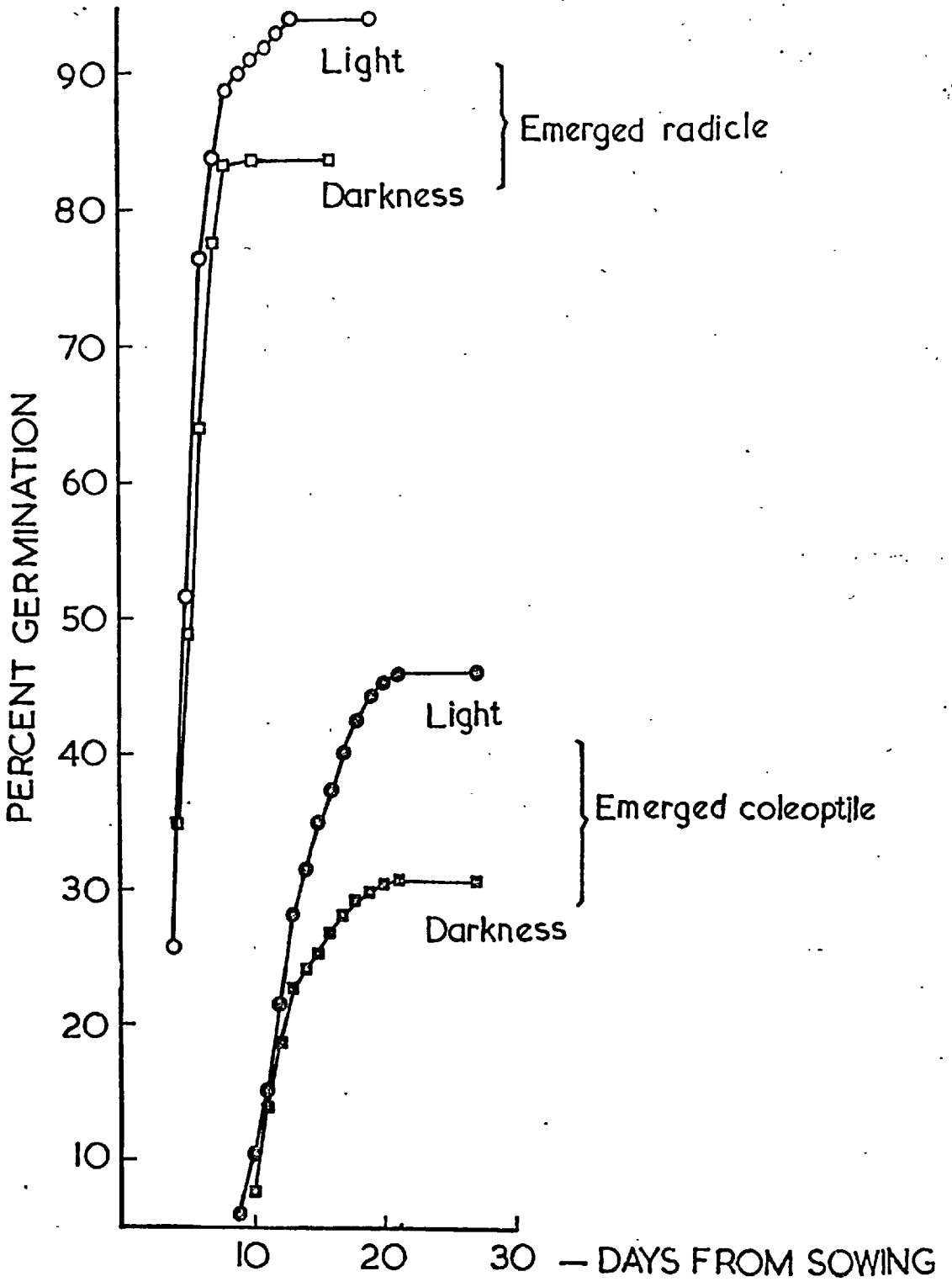


FIG. 5. Effect of removal of seed coat on the seedling emergence in light and darkness.

radicles and the no. of coleoptiles emerged per total of replicates. Later percentage of seedlings with emerged radicles and the emerged coleoptiles were calculated separately.

The term "naked seeds" has been applied to the seeds with removed seed coat, consisting of endosperm and the embryo only. This term will be referred in future whenever necessary. Intact seed coat would only mean the seeds with seed coat intact to the seeds.

Results and discussion

In the first set of experiments where only "naked seed" were used, the aim was to see whether the seeds when freed from seed coat containing inhibitors would germinate successfully or not. It can be seen in Fig.5 that a highest percentage (94%) of seedlings with emerged radicle was obtained in light while in darkness it reduced to 84% seedlings with emerged radicles. In light it was remarkably the highest percentage seedlings ever recorded throughout the experimental period. At the same time it is also interesting to see that the germination capacity in terms of coleoptile emergence was greatly reduced to 46% in the light and 30% in darkness. However, it seems that darkness had a much depressing effect on both the germination capacity in terms of radicle and coleoptile emergence. It could be said that light had a definite stimulatory effect on the germination of naked seeds. The reason for a low percentage seedlings in terms of the emerged coleoptiles in comparison to a high no. of emerged radicles, required some explanations. The question arises why all the seedlings with emerged radicles had failed to give rise

coleoptiles? It seems probable that the naked seeds while exposed to light and atmosphere and freed from the seed coat would have received more oxygen for the continuously respiring embryos, resulting in the emergence of radicles in a shortest period. It is also worth to mention that soon after the radicles emerged, they ceased to grow and started decaying except where the seedlings developed coleoptiles, showed a slow process of deterioration of their radicles.

The germination capacity in terms of emerged coleoptiles when expressed as a percentage to the no. of seeds with emerged radicles, showed that about 50% seedlings failed to give rise the coleoptiles.

It can be concluded that in the absence of the seed coat, the embryo could develop radicles and even a considerable percentage germination with coleoptiles may occur, yet a full germination capacity to reach á 94% level of germination with emerged coleoptiles needs some external stimulator. This stimulation probably lies in the seed coat. In a second set of experiments where the treatments have been extended, this assumption seems to be justified upto some extent.

In a second set of experiments, three treatments were applied. The three types of seed used were:

1. Seeds with intact seed coat.
2. Naked seeds, i.e. the seeds, without seed coat.
3. Naked seeds + seed coat. i.e. Seeds without seed coat with the addition of seed coat powder.

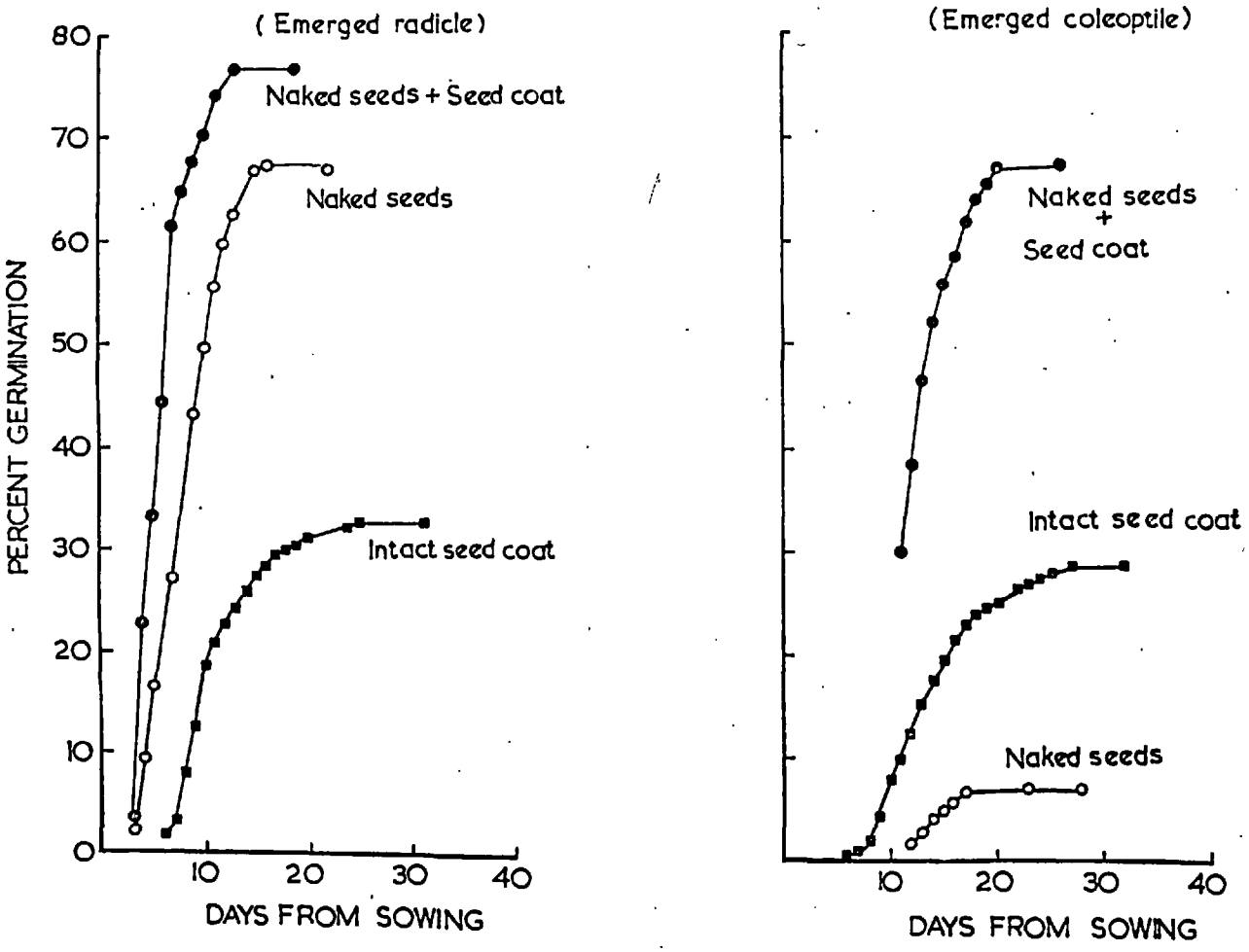


FIG. 6. Seedling emergence with different status of seeds.

The method for germinating these seeds followed the same practice described earlier in the preceding pages. The primary data is given in "appendix" and the graphs are exhibited in Fig. 6 , where percentage seedlings are plotted in terms of emerged coleoptiles and emerged radicles separately against the no. of days from sowing.

It is evident from the figures that a highest percentage seedlings with emerged radicles and emerged coleoptiles was recorded in the treatments where the naked seeds were added with seed coat powder. In the treatments with intact seed coat and naked seeds the germination capacity in terms of emerged radicles and emerged coleoptiles was quite reciprocal to each other, i.e., highest no. of radicles emerged from the naked seeds formed a lowest percent of emerged coleoptile, and the lower percent radicles emerged from intact seed coats showed a higher percent seedlings with emerged coleoptiles. (table II)

Treatments	Emerged radicles	Emerged coleoptiles
Nakes seed + seed coat	76%	67%
Intact seed coat	33%	28%
Nakes seeds	67%	7%

It is also interesting to see that when the percentage of emerged coleoptiles was calculated over the no. of emerged radicles about 90%, 16% and 12% seedlings failed to form the coleoptile with the treatment of naked seeds, intact seed coat, and naked seeds + seed coat respectively.

A highest percentage of seedlings which failed to form coleoptiles in naked seeds treatment could be accounted for the loss of viability of seeds with time. It should be noted that the seeds used in this experiment were those which had received a very long period of stratification. In comparing this treatment with the first set of experiments, it becomes clear that in the previous experiment the naked seeds which recorded about 50% germination capacity in terms of emerged coleoptiles was mainly the factor of loss of viability of seeds. The period of after ripening was about ten months in the first set of experiments while in the existing experiment the seed had received about 14 months period of stratification.

The stimulatory effect of seed coat treatment to the naked seeds resulting a highest percentage of healthy seedlings both in terms of radicles and the coleoptile emergence, leads to so many arguments.

It could be argued here, that during the period of stratification, an after ripening of the embryo was not only sufficient to bring about the germination; yet some chemical changes were also necessary in the seed coat. An assumption could be that with stratification some inhibiting substances might have disappeared and a growth promoting substance was formed, which later on forced the embryo to germinate. The change of an inhibitor to a growth promoting substance could have occurred as a result of the low temperature moist pretreatment. During this time the enzymes under moisture and low temperature becomes active bringing about a positive chemical change by forming a growth

promoting substance.

Although an attempt has been made to establish some facts on an experimental basis, a further elaborate experimental work is highly desirable to explain such findings which unfortunately is not possible in the present investigation.

CHAPTERS IV & V
STUDIES ON GROWTH

IV.

Effect of artificial shading on the growth and morphology of the species.

Shade tolerance has long been treated mainly in the field of forestry, where the term tolerance itself refers to the ability of plants to survive under deep shade, and much practical information has been obtained on the tolerant and intolerant species. A further ecological and physiological approach to this aspect has been made by a number of workers. Most of them discussed the shade tolerance on the basis of a comparison among plant species of certain characteristics; the minimal light for survival or the light compensating point of CO_2 - gas exchange; yet others for instance Blackman & Wilson (1951), have thrown much more light on this problem by analysing the light intensities on plant growth, especially on two attributes, mean unit leaf rate and leaf area ratio. Evans & Hughes (1961) while working on Impatiens parviflora, a typical facultative shade plant, have shown "its growth in full daylight is high and it responds to shading by a remarkable increase in the expansion of leaf surface. This expansion involves only a change in the spatial distribution of plant material within the leaves; there is no change in the fraction of the total dry weight to be found in the leaves. Despite these structural modifications, the leaves of plant at all levels of shading were found to have the same assimilatory capacity".

Recently Myerscough & Whitehead (1967) in their studies on certain shade tolerant species, have shown that the species can make viable growth over a range of light levels. Variations in leaf area occurred

with associated changes in specific leaf area in such a way that similar growth is made over a wide range of different radiation incomes per unit area.

In the present investigations, an experiment has been designed to clarify the physiological and ecological response of the plants of F. ulmaria and I. pseudacorus species to varying degrees of shade. Special attention is focussed on some factors or characteristics which are principal in dry matter production under shaded conditions. Finally, the comparative performance of the species, under shading has been assessed by employing several parameters of growth.

Experimental procedure

The experiment was carried out in early May of 1968. It was expected that the weather would be suitable for the ideal growth of the plants, but because of the overcasted sky during most of the days the natural light was supplemented by 250 watts mercury vapour lamps one outside each tent. This improved the light conditions. The daily illumination was provided for 16 hours a day at late spring values at 100% treatment.

A series of light intensity regimes was created under muslin and terylene screens. The screens were mounted upon wooden lattices of 4' x 3' x 3' dimensions. They were then placed in the wooden benches in the western ridge of the glasshouse. The tents were placed side by side in the manner that the lower light intensity tent was followed by the medium one and the unscreened treatment (100% day light) so that it

was not at any time shaded by either treatments.

The surface of the bench was completely covered by black polythene sheets to cut off the light coming from below the surface of the bench. About 2" thick coarse sand was spread over the polythene. This method proved to be effective as it not only checked the excessive evaporation of water from the pots, but also retained and distributed the water uniformly inside each pot.

The light intensity in terms of the percentage of light in open condition was measured inside each tent using an Eel type Lightmeter at noon on both a sunny day and a day with apparently uniform overcasted sky. By evaluating the values of light it was found that the three light regimes were approximately 100%, 70% and 40% respectively. These percentages of light intensity will be referred as an index of the treatments in the foregoing pages. The methods used for raising the seedlings and transplantation followed the same common methodology described in Chapter 2.

Three to five seedlings of each species were transplanted per pot of 3" diameter. In the early phases of the experiment the seedlings were grown in a 3" diameter plastic pots, but in the later stages 5" diameter clay pots were used. This situation was unavoidable as the number of replicates used in this experiment was very high and the pots could not be accommodated in the tents simultaneously. In all 50 small pots per species were randomised inside each tent, and in every pot 2 seedlings were kept at a distance of 2" apart.

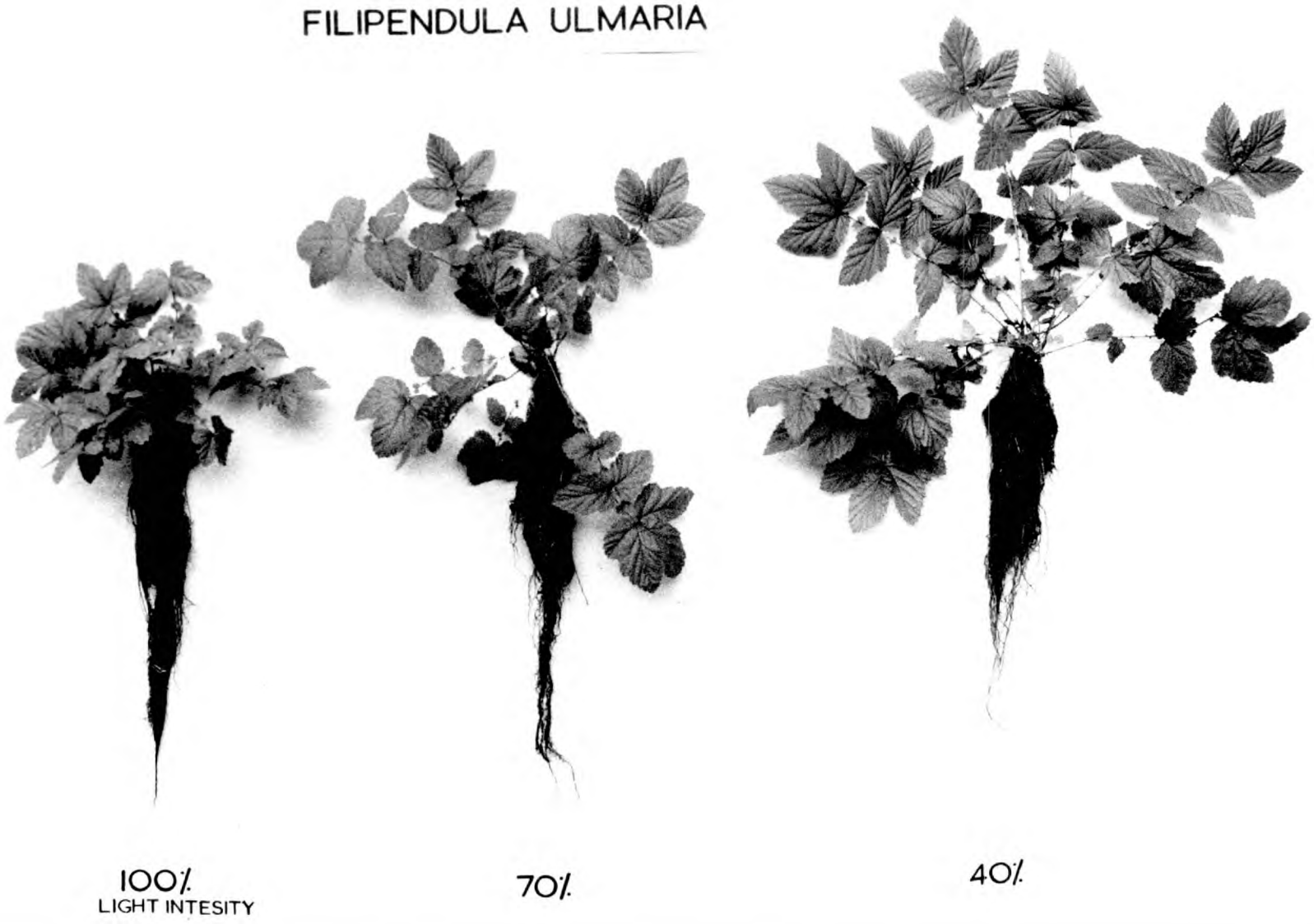
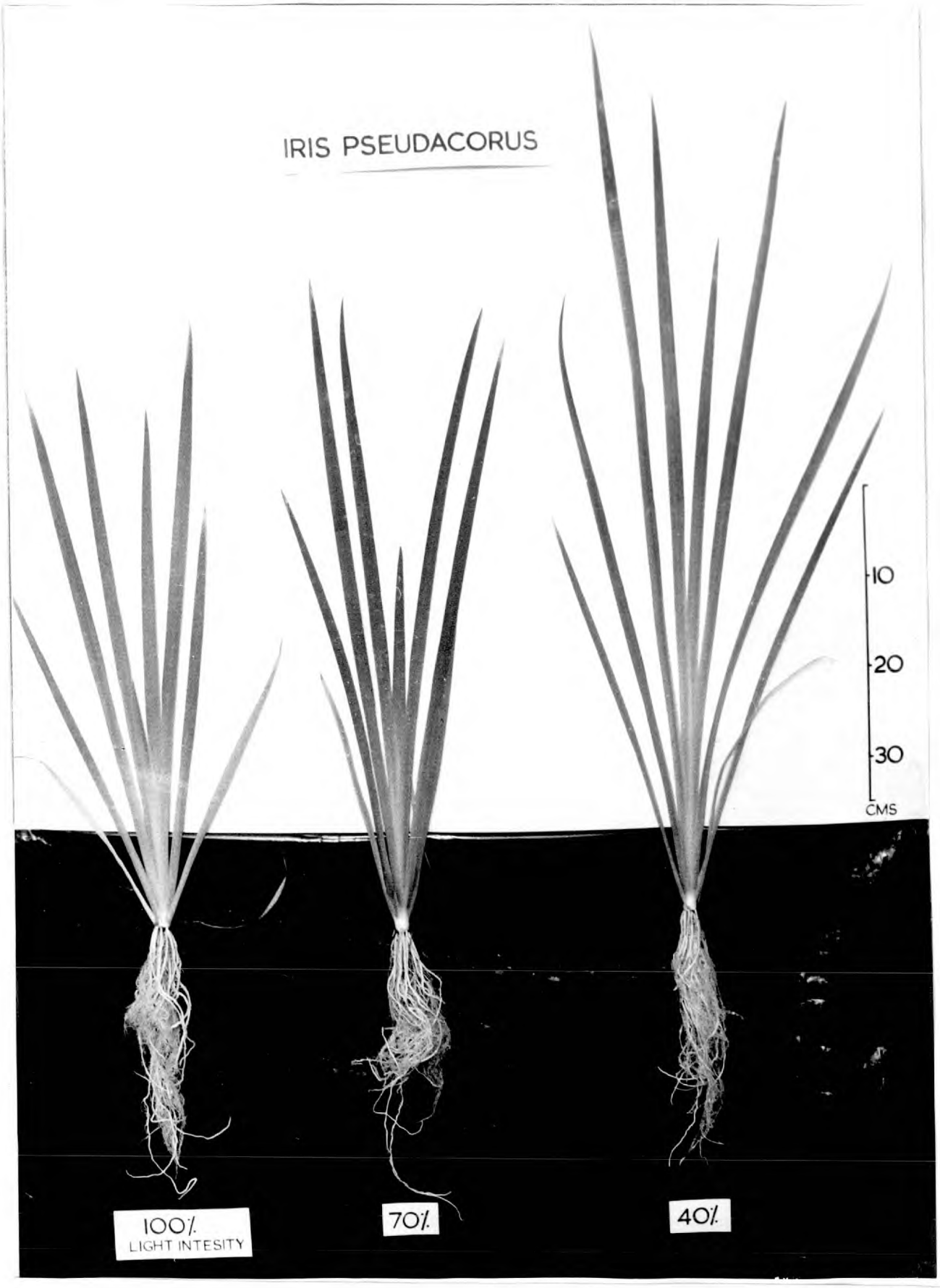


PLATE 1. F. ulmaria grown under a range of light intensity levels. (90 days)



(90 days)

PLATE II. I. pseudacorus grown under a range of light intensity levels.

In the later harvests the plants were thinned to one plant per pot of 5" diameter.

The seedlings were kept for 2 weeks in the glasshouse under uniform conditions of light. When a two-leaf stage was attained, the pots were randomised inside each tent. The pots were rotated frequently every 2 days and re-randomised weekly. Watering was done every day and care was taken not to injure the aerial shoots by heavy showering. Nutrient solution was supplied regularly twice a week.

In all 6 harvests were taken including the initial harvest. For F. ulmaria 20 plants per treatment were harvested at initial, first and second harvest, while in the third harvest 15 were taken out, but for the fourth and the final harvest only 10 plants per light regime were left for harvesting. In Iris pseudacorus from initial to fourth harvest 20 plants were harvested for each light intensity, except in the final harvest, were only 10 plants were taken for harvest.

Results and discussion.

The effect of varying levels of light intensity or shade effect on the growth of the species which has been recorded in the form of primary data and the mean values of several parameters of growth derived from it are given in the "appendix" of the thesis. The graphic representation of these parameters is shown in the accompanying pages whenever necessary. The photomorphogenetic response of the plants at varying levels of light intensity is exhibited in plates I and II.

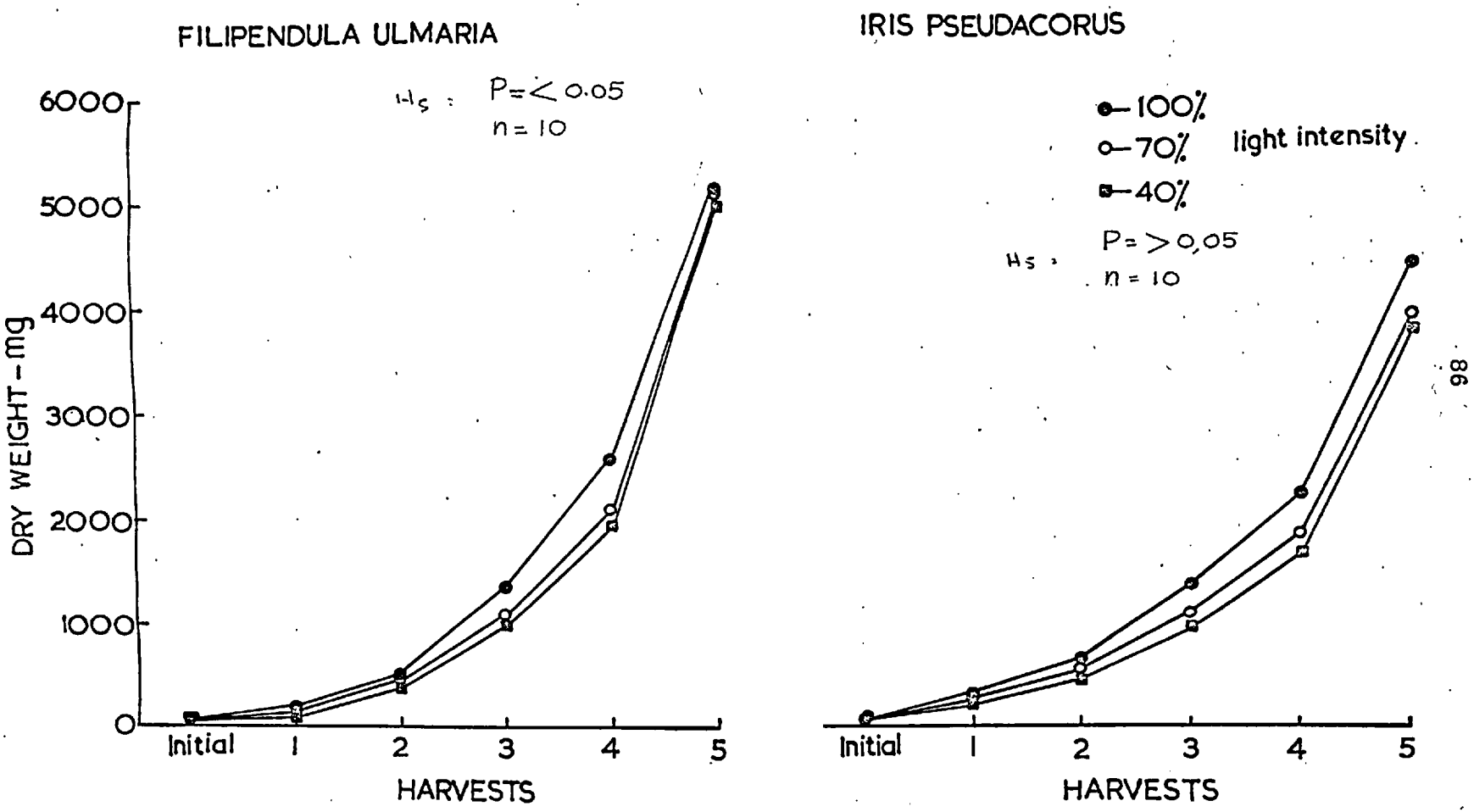


FIG. 7. Effect of varying levels of light intensity on increase of plant weight with time.

Growth in plant weight.

Fig. 7 on page 86 shows the increasing weight of the two species at three levels of light intensity. It can be seen that the general pattern of increase of dry weight with time is very much alike in both species at 100, 70 & 40% light levels. Depressing effect of shade in plants dry weight was evident in 40% light intensity, while the growth in 70% light followed closely the growth in full light. In the first harvest, after 40 days of sewing I. pseudacorus showed the dry weight average of 292, 268 and 228 mgs. for 100, 70, & 40% light levels respectively; the relative percentage being 100, 91, 78, while in F. ulmaria the average was 143, 139, and 101 mgs. for 100% - 40% light intensity. The relative percentage being 100: 97: 70. At intermediate harvests the difference between the light level was significantly increased, which again diminished at the final harvest. Especially in F. ulmaria, no significant difference of dry weight was observed from 100% - 40% light intensity. On the contrary I. pseudacorus still seems to be in a state of adjustment until the final harvest.

It should be noted that under the conditions of the experiment e.g. light and nutrition etc. which were the same for both species, F. ulmaria has a faster growth rate than I. pseudacorus (5100 mgs. in 100 days for

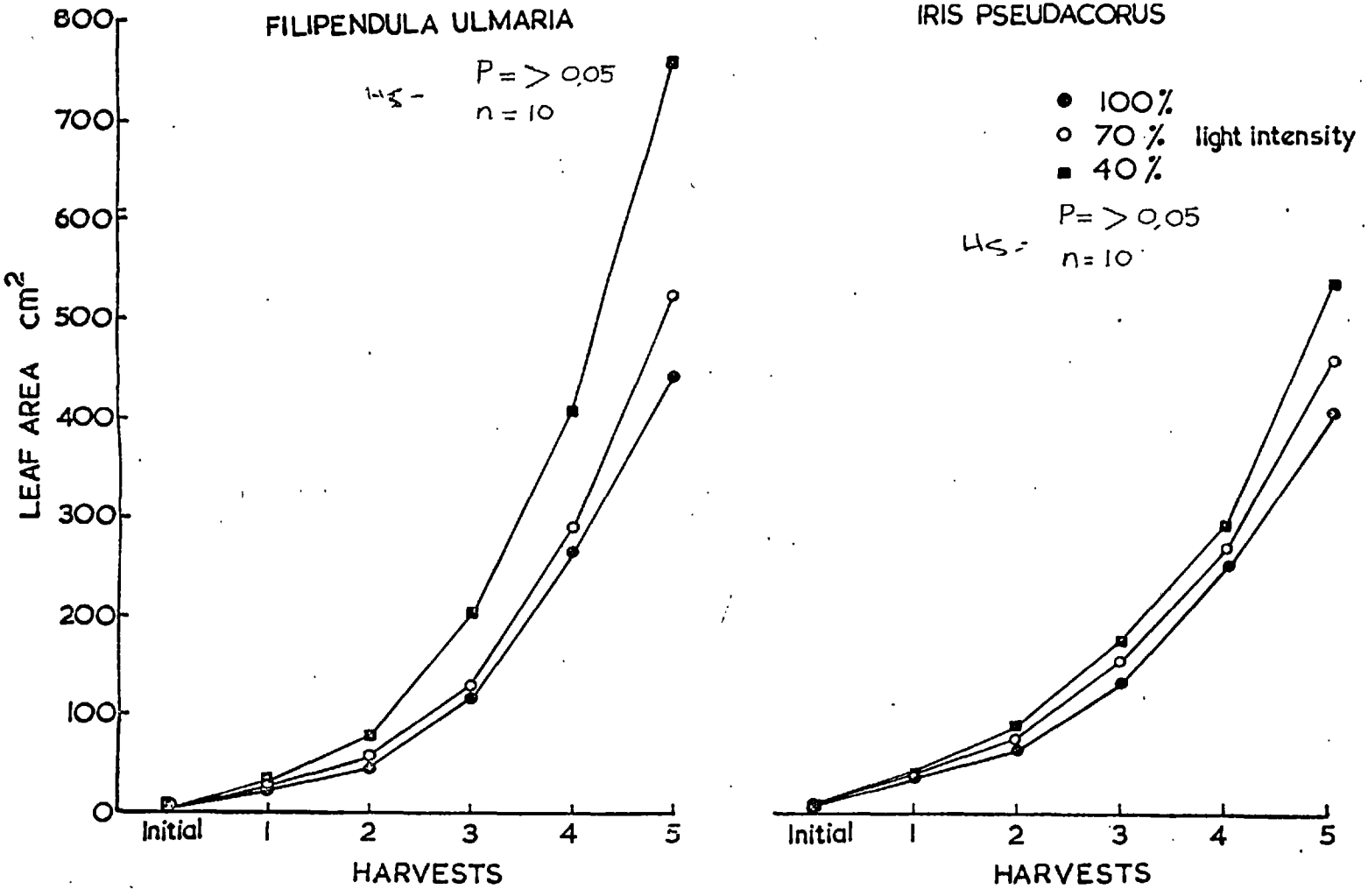


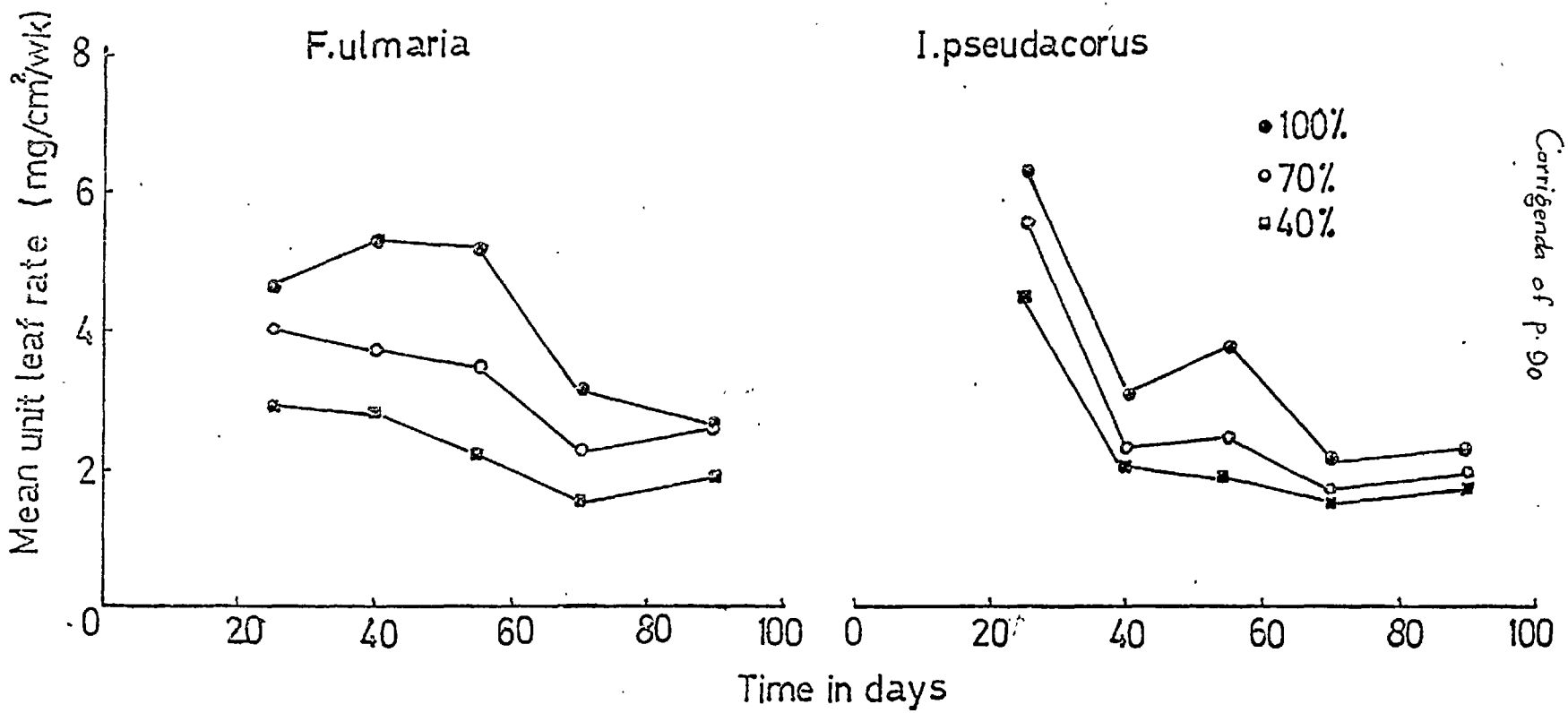
FIG. 8. Effect of varying levels of light intensity on increase of plant leaf area with time.

F. ulmaria, as opposed to 4350 mgs. approximately for I. pseudacorus in a similar period). However, I. pseudacorus appears relating to be as efficient as F. ulmaria at the later harvest, compensating for lower light intensity by increased leaf area (see Fig. 8) so that eventually same dry weight is achieved by all three light regimes.

Growth in leaf area.

Since leaves generally function as an organ for photosynthesis, it is quite obvious in the analysis of shade tolerance of plants to consider the leaf area with particular reference to light intensity levels. The effect of shading on the leaf area growth with time is shown graphically in Fig. 8, where the total plant leaf area is plotted against harvest intervals. The general pattern of progressive increase in leaf area is very much similar for both species at 100% - 40% light intensities. Optimal leaf area increase was observed over the whole growing period under 40% light intensity. However, the increase of leaf area with time is converse of that of the total plant weight, where the dry weight was optimal at full light. In F. ulmaria the difference of leaf area is such that at final harvest it is about twice that of full light intensity.

It seems likely that F. ulmaria shows a greater response to low light levels by more rapid leaf area increase than I. pseudacorus. This response is evident from harvest two to onward, whereas in I. pseudacorus



Corrigenda of P. 90

Fig 9. Mean unit leaf rate. Values of $\bar{E}$ were calculated between initial harvest and one; one and two, etc. Each value is plotted as a point at the end of the harvest interval over which it was calculated.

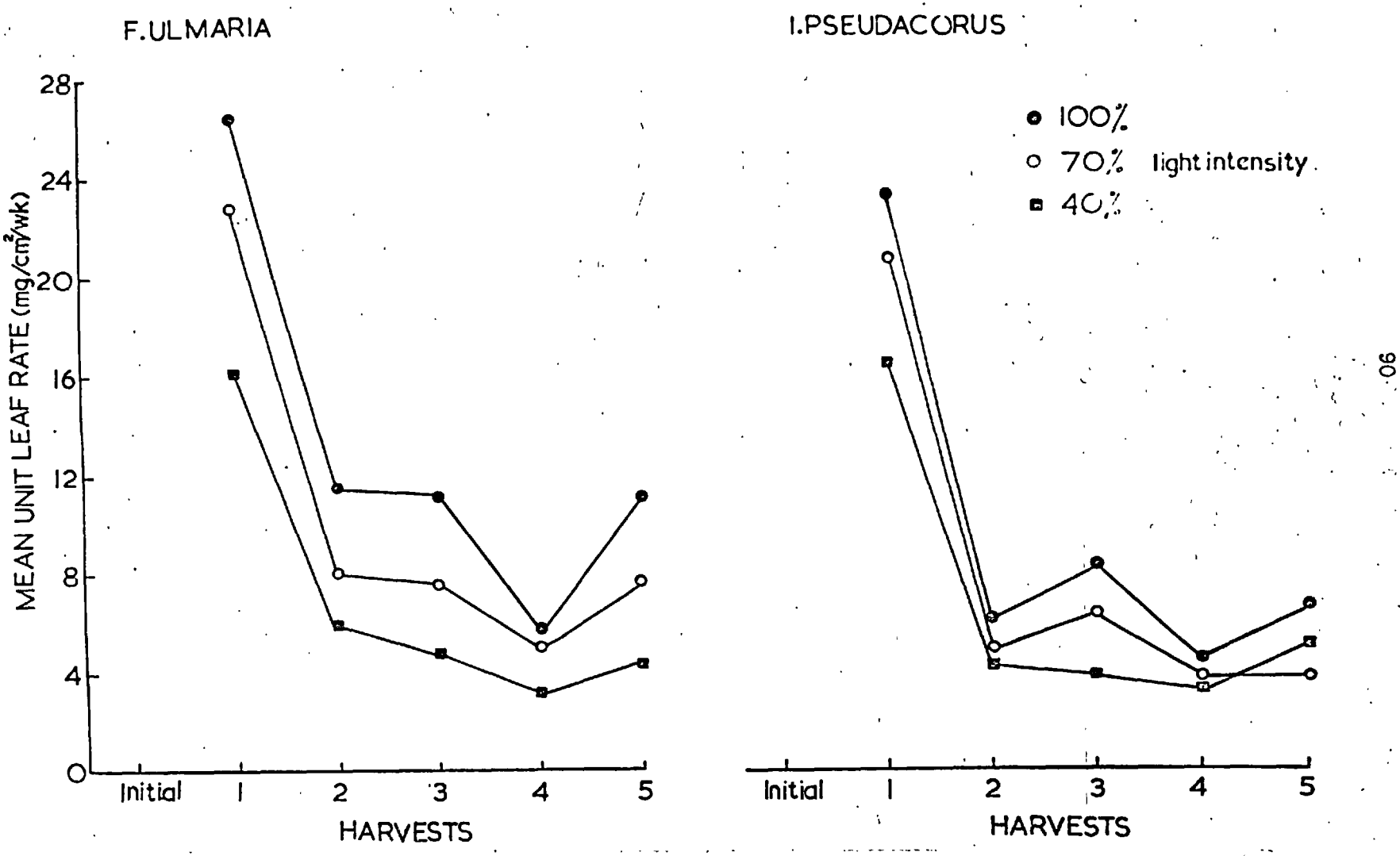


FIG. 9. Effect of varying levels of light intensity on mean unit leaf rate (mgs/cm^2/week). The values were calculated between initial harvest and one; one and two; two and three etc.

the significant difference appears considerably later after fourth to the final harvest. Moreover, the greater leaf area in terms of dry weight is evident by fifth harvest for F. ulmaria, whereas in this experiment at final harvest, I. pseudacorus does not show a greater leaf area in terms of dry weight. The other repeated experiment on light intensity showed that non significant differences in dry weight for I. pseudacorus does not occur until 7th to 8th harvest. The faster growth rate coupled with the larger leaf area in low light levels shows that F. ulmaria has a more rapid response to changes in environment.

The mean unit leaf rate.

The photosynthetic activity of the plant is mostly carried on by the leaves, resulting in an addition of dry matter to the plant body. The usual parameter to estimate this activity is the mean unit leaf rate or net assimilation rate i.e. the increase in plant weight per unit area of leaves over a given time. The values of $\bar{E}$ on the basis of leaf area are shown in Fig. 9 and table 9 . It is apparent that the mean unit leaf rate at any given harvest gradually increased with increasing light intensity. Therefore light mean unit leaf rate must be a positive factor in the dry matter production of the plants that grow under high levels of illumination or in other words, lower mean unit leaf rate to be expected in lower light intensity so that lower dry weight must follow, unless there is a significantly large increase in leaf area to compensate for the lower mean unit leaf rate. Examination of Fig. 7 and Fig. 8 shows that the plants grown at full and 70% light intensities had similar dry weight compared to 40% light level. However at 40% light

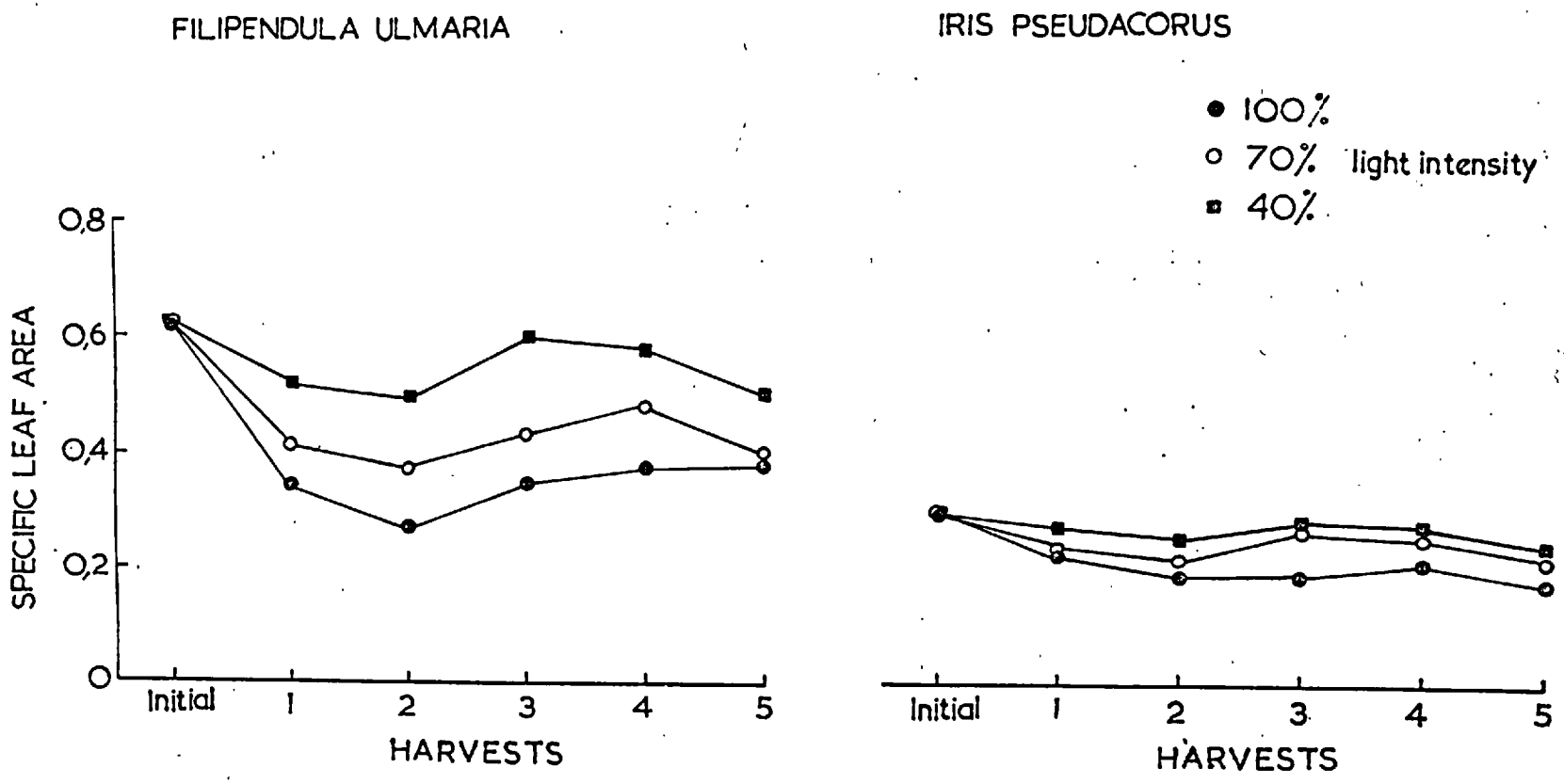


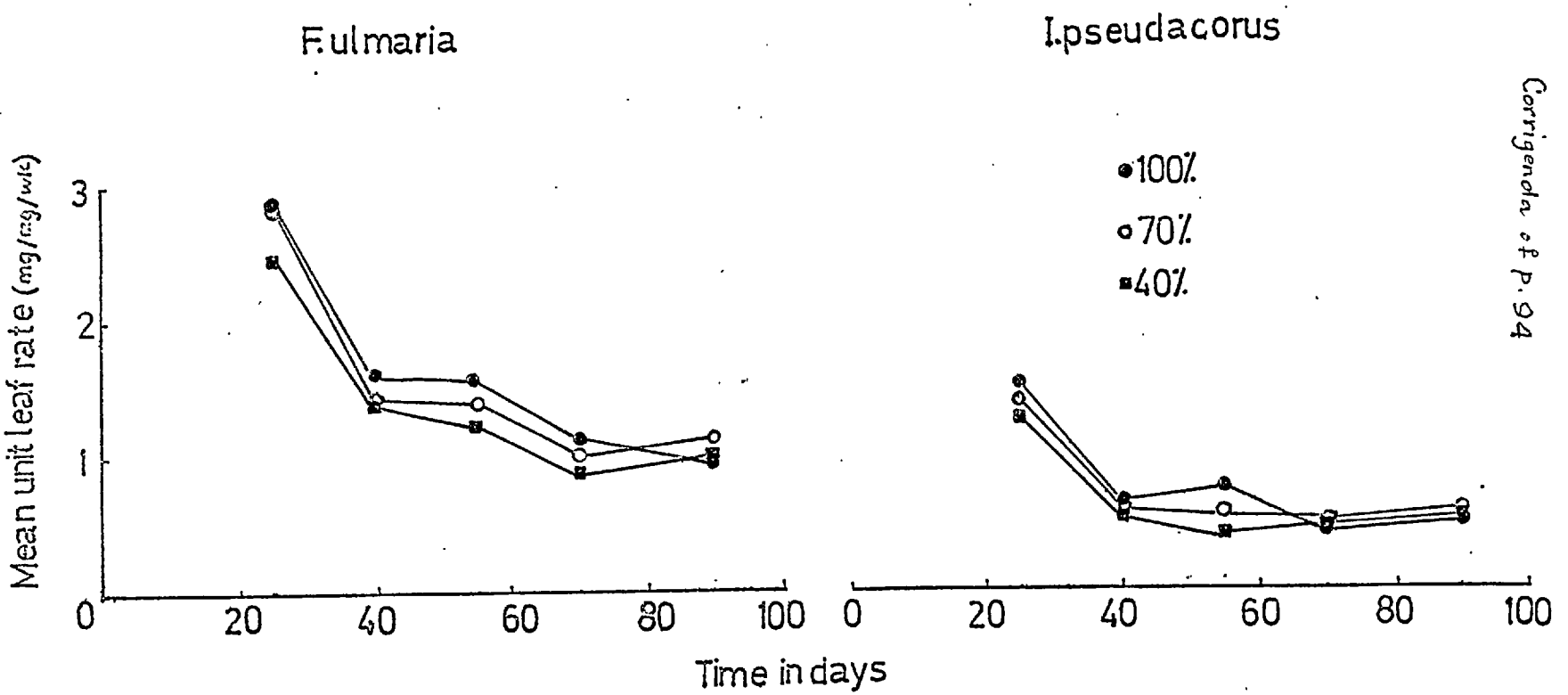
FIG. 10. Effect of varying levels of light intensity on specific leaf area (cm^2/mg)

plant had conversely larger leaf area and smaller weights compared to full and 70% light intensities. At the final harvest insignificant difference in dry weight followed with increased leaf areas at the lower light levels. Therefore the plants growing in shade had smaller mean unit leaf rates compared to full light.

Comparing the rates of the two species it appears that F. ulmaria is more efficient in its photosynthetic activity at all the levels of light. This plant despite its lower initial bonus of seed weight gained a rapid dry weight accomplished by the enhanced rate of the expansion of leaf area through the compensating mechanism by the leaves. It seems likely that in I. pseudacorus despite its larger bonus of seed weight a comparatively smaller dry weight was added coupled with relatively greater leaf area increment so that decreased values of mean unit leaf rate were evident at all the light levels.

Specific leaf area.

In Fig. 10 are represented the growth curves of specific leaf area (cm^2/mg) i.e. the area of the leaves per unit weight of the leaves. It can be seen that with the depression of light intensity the values of specific leaf area are increased. The higher values under low light intensity levels in these plants is achieved through an adaptive mechanism by the expansion of leaf area to a greater extent in the spreading of assimilates over a greater leaf area so that the plants growing under high light levels exhibited small thick leaves of dark green colour and large and thin light green coloured leaves at the lower light intensity.



Corrigenda of P. 94

Fig 11. Mean unit leaf rate. Values of $\overline{E}$ were calculated between initial harvest and one; one and two, etc. Each value is plotted as a point at the end of the harvest interval over which it was calculated.

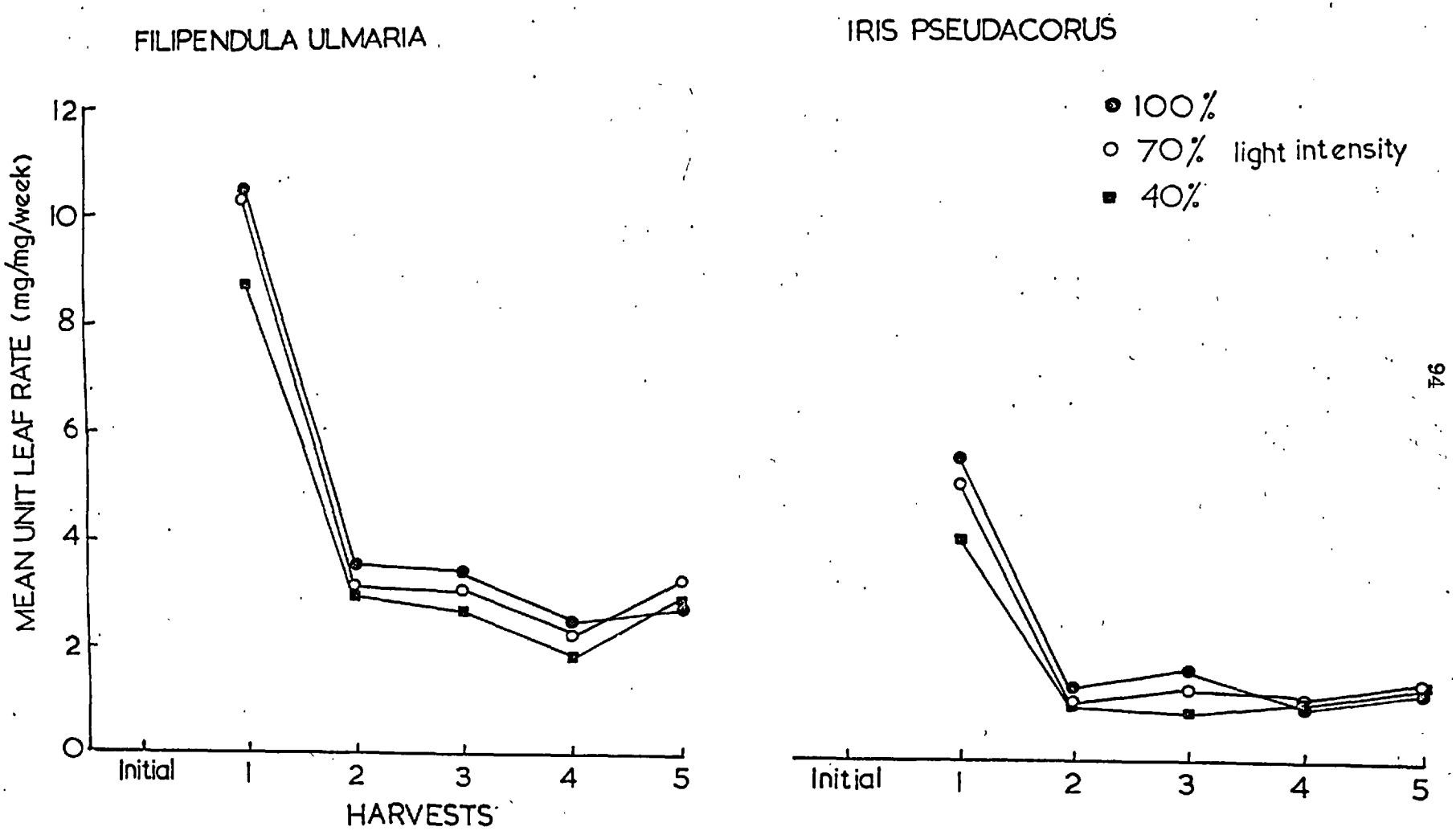


FIG. 11. Effect of varying levels of light intensity on mean unit leaf rate (mgs/mgs/week). The values were calculated between initial harvest and one; one and two; two and three etc.

Although both species show adaptive mechanism by the leaf expansion the extent of leaf area at the expense of dry matter is greater with F. ulmaria than in I. pseudacorus. The values at the third harvest being 0.341, 0.426 and 0.598, cm^2/mg at 100, 70 and 40% light intensity respectively. Here the increased leaf area under lowest light intensity was almost at the same expense of dry matter about twice as large as that of full light. Thus this adaptive mechanism brings about an advantageous effect on the dry matter production under shade and the high values of specific leaf area under lower light intensities becomes an important factor for the plants to survive and to make positive dry matter production. This ability of plants showing high ratios of specific leaf area in response to light levels undoubtedly plays a positive role in shade tolerance of the plants under investigation. The general compensatory nature of this variation of leaf area, together with specific leaf area in relation to lower light level is now well established from studies of several species as for instance in Endymion non-scriptus (Blackman and Rutter 1948) Impatiens parviflora (Evans and Hughes 1961), Phaseolus aureus (Nomoto, Iwaki and Monsi 1961) and in Tussilago, Chamaenerion and Epilobium species (Myerscough and Whitehead 1967). In those levels of light in which this adaptive mechanism compensates fully for the reduction of light intensity a similar mean unit leaf rate expressed in a leaf weight basis is expected. In Fig. 11 are represented the values of mean unit leaf rate on a leaf weight basis as opposed to leaf area. It is evident that for any given harvest interval

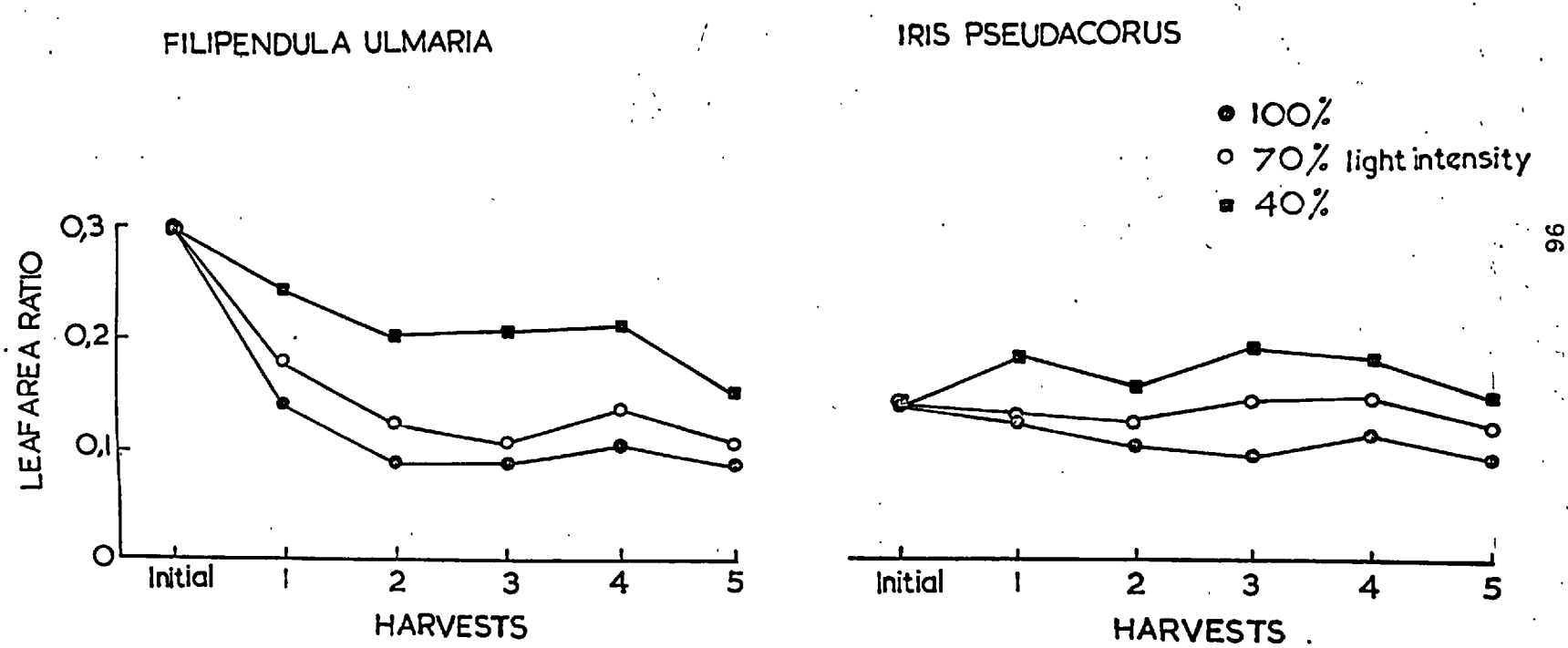


FIG. 12. Effect of varying levels of light intensity on leaf area ratio. (cm^2/mg)

at 100, 70 and 40% light levels the rates are much alike for each of the two species. However in F. ulmaria the mean unit leaf rate decreased considerably with time at all the levels of light intensity.

With age the plant becomes progressively less leafy and this is probably the most important internal factor which can be observed especially in F. ulmaria. The decreasing leafy condition of the plant can also be judged from leaf area ratio (Fig. 12), which is the ratio of total plant leaf area to the plant dry weight. It can be seen that the ratios at all the levels of light decreases gradually. The extent of decrease in leaf area ratio was marked upto the seeded harvest but from second to the final harvest it was considerably slower. This decreasing leafiness of plant with time implies that respiratory tissue is increased relative to photosynthetic tissue so that a fall in the mean unit leaf rate was also obvious at all the levels of light. In I. pseudacorus, it seems likely that these ratios are almost held constant at all the levels of light, which implies that ageing could not effect this plant resulting in an increasing leafiness. In other words with F. ulmaria increase in dry weight was accompanied by diminishing leafiness, ~~whereas~~ In I. pseudacorus increase in dry weight was followed by greater leafiness.

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

The gross differences of morphogenetic conditions and the comparative performance of the species can only be judged by the use of α index. (Whitehead and Myerscough 1962) i.e., the ratio of mean relative growth rate to the mean relative rate of leaf area increase (~~mgs/cm^2/week~~). The values of α are shown in Fig. 13 where these values are calculated from initial to the successive harvests. It can be seen that F. ulmaria showed the values greater than unity, with increasing light intensity and time, whereas in I. pseudacorus the values are always smaller than F. ulmaria. However at 100% and 70% light intensity the values are slightly above 1, whereas at 40% light level the values could not reach to the level of unity upto the fourth harvest except at final harvest where it is exactly 1. It can be argued wherever these values exceeded above the unity, the adoptive mechanism by the expansion of leaf area, was fully compensated for the reduction of light intensity and the plants were already maintaining as an efficient "photosynthetic entity". Especially this compensating point was never achieved in 40% light intensity except at the final harvest. It implies that in I. pseudacorus the plants were not fully adjusted in the shade because of the greater leaf area increase as compared to the relative growth rate.

As pointed out by Whitehead and Myerscough (1962) that the successful performance of an individual plant usually depends on a surplus of assimilates above that needed to maintain the "photosynthetic entity".

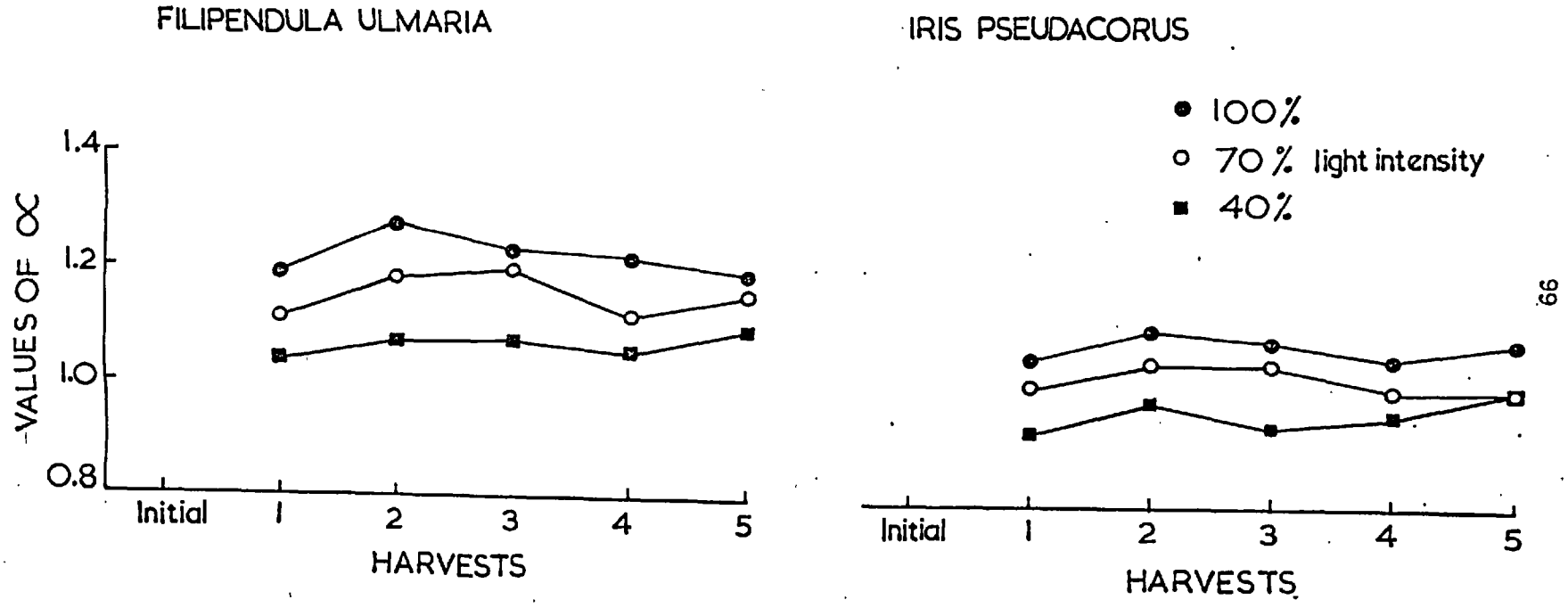


FIG. 13. Effect of varying levels of light intensity on the ratio of mean relative growth rate to the mean relative rate of leaf area increase ~~(mg/cm²/week)~~. Values of α were calculated from Initial harvest and one; initial harvest and two; initial harvest and three etc.

It can be seen in F. ulmaria the values of α remain greater than unity from the beginning of the experiment at all the levels of light intensity, and the plants were already forming a "surplus dry weight".

It was therefore expected that the surplus dry weight might have had brought about the early sexual maturity leading to the formation of reproductive organs, but neither of these species produced flowers and remained vegetative throughout the experimental period. As the plants under investigation are the perennial species, it seems probable that this 'surplus' might have had employed in the vegetative spread of the plants. The estimates of surplus weight expressed as $\overline{W}(\alpha - 1)$ are shown in table III . It can be seen that in full light intensity at the

TABLE III . Surplus dry weight $\overline{W}(\alpha - 1)$

Light intensity	F. ulmaria			I. pseudacorus		
	Initial 3	Initial 4	Initial 5	Initial 3	Initial 4	Initial 5
100%	290.1	534.4	917.8	111.1	110.7	437.1
70%	213.9	226.7	755.9	53.7	Nil*	Nil*
40%	69.0	55.2	449.2	Neg.*	Neg.*	Nil*

* Nil = when α is 1; Neg = when α is below 1

final harvest, Filipendula ulmaria had about 20% surplus weight of the total plant weight whereas in I. pseudacorus it is 15% only. The degree of leafiness in this species is self explanatory on the basis of surplus weight.

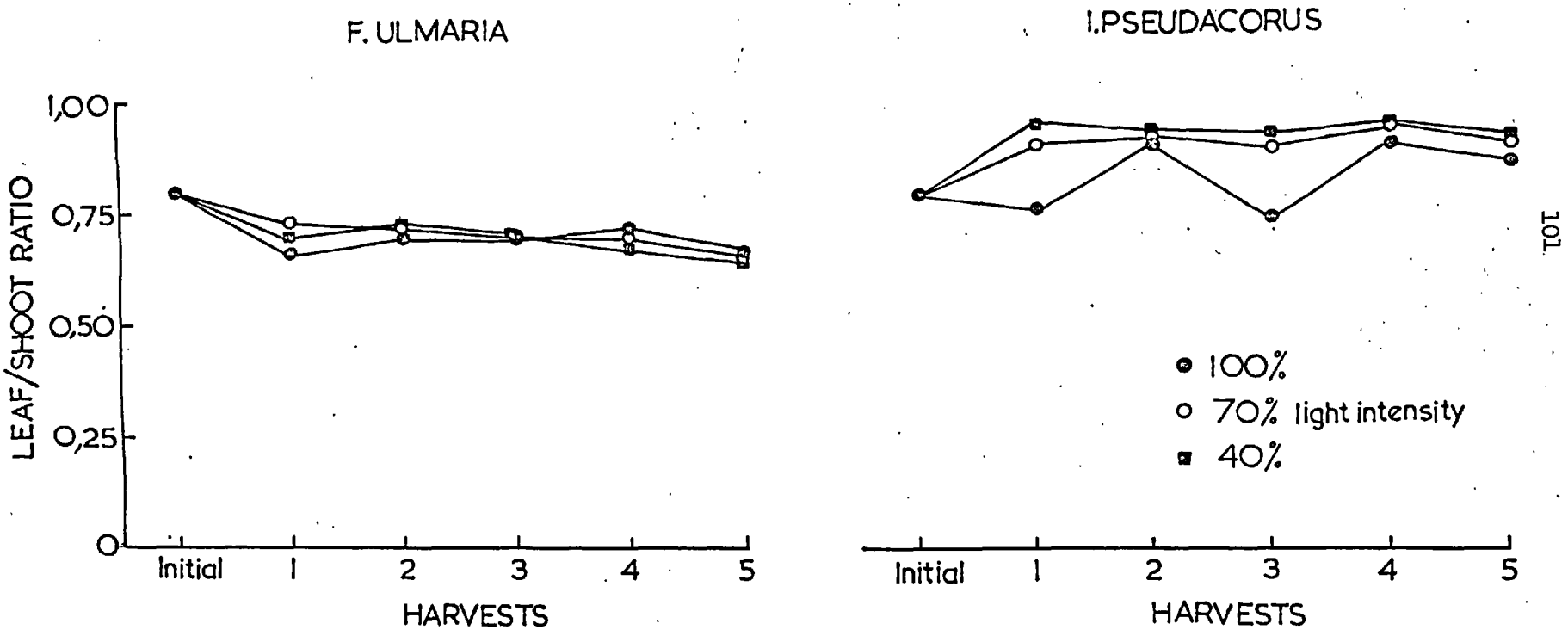


FIG. 14. Effect of varying levels of light intensity on leaf/shoot ratio.

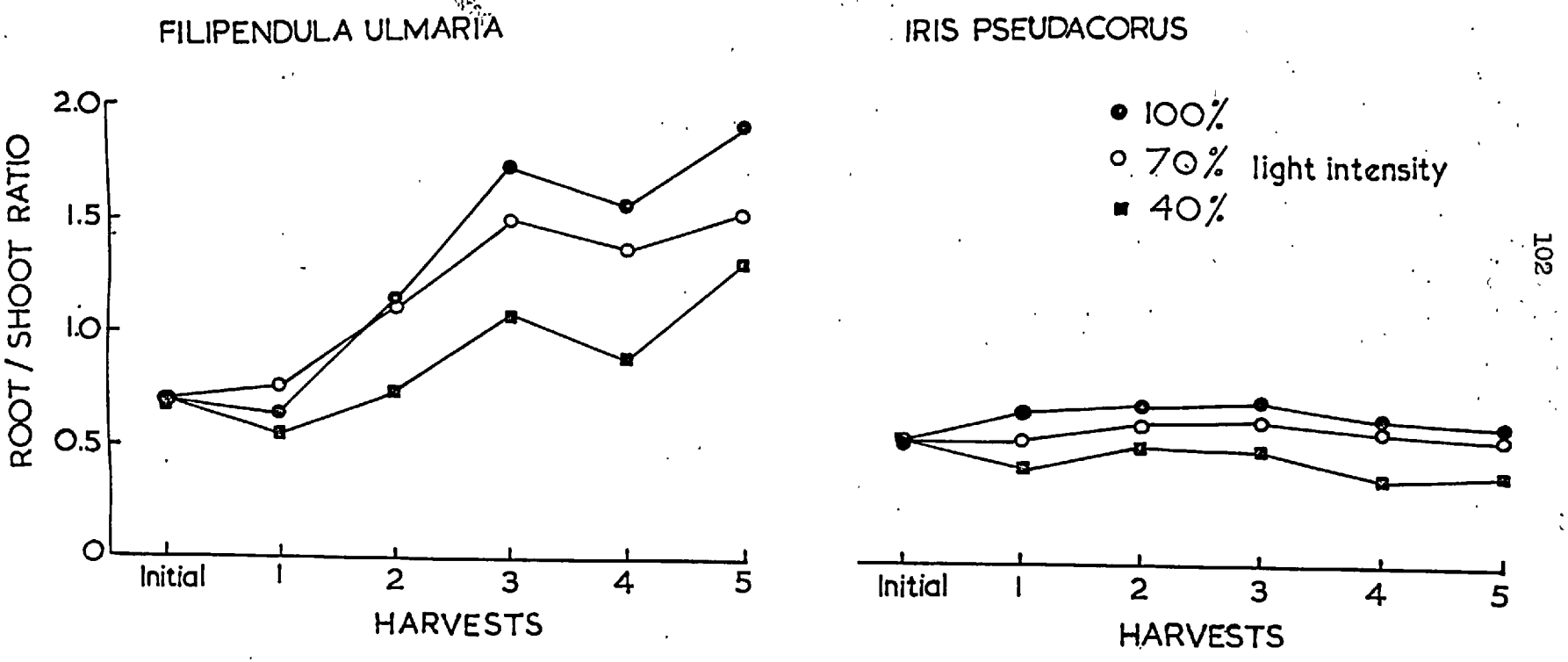


FIG. 15. Effect of varying levels of light intensity on root/shoot ratio.

Leaf/Shoot ratio

In Fig. 14 are represented the values of leaf/shoot ratio i.e. the ratio of leaf dry weight to the shoot dry weight. The degree of leafiness in each species can also be seen in the final performance of the plants, where Iris pseudacorus apparently showed a constant ratio at all the levels of light. In earlier harvests, the leaves constituted about 77% of the shoot weight, while in the final harvest it ranged from 84% - 89% for 100% - 40% light levels. In contrast F. ulmaria showed a decrease fall of leaf weight with time being 65% inclusively for all the light regimes at the final harvest. However, it is worth to point out that in F. ulmaria the least decrease of mean unit leaf rate with time is observed in contrast to I. pseudacorus. The higher mean unit leaf rate may probably be accounted for by the root/shoot ratio and root/leaf ratio on the basis of area and weight of leaf.

These are shown in Figs. 14, 15 and 16. It can be seen that with each of the two species growth in the higher light intensity shows both higher root/shoot (Fig. 15) and root weight/leaf area ratios. (Fig. 17) In I. pseudacorus, the root/weight/leaf area ratio, at each of three light regimes, was most nearly constant with time, whereas the root weight/leaf weight ratio (Fig. 16) fails to show significant differences in their ratios between the light intensity levels. In this species the differences in the root weight/leaf area ratio, may be fully accounted for by difference in specific leaf area ratio (Fig. 10) In F. ulmaria, this is not so, for both the root weight/leaf area ratio and root weight/leaf weight ratio (Fig. 16) progressively increase with time over all

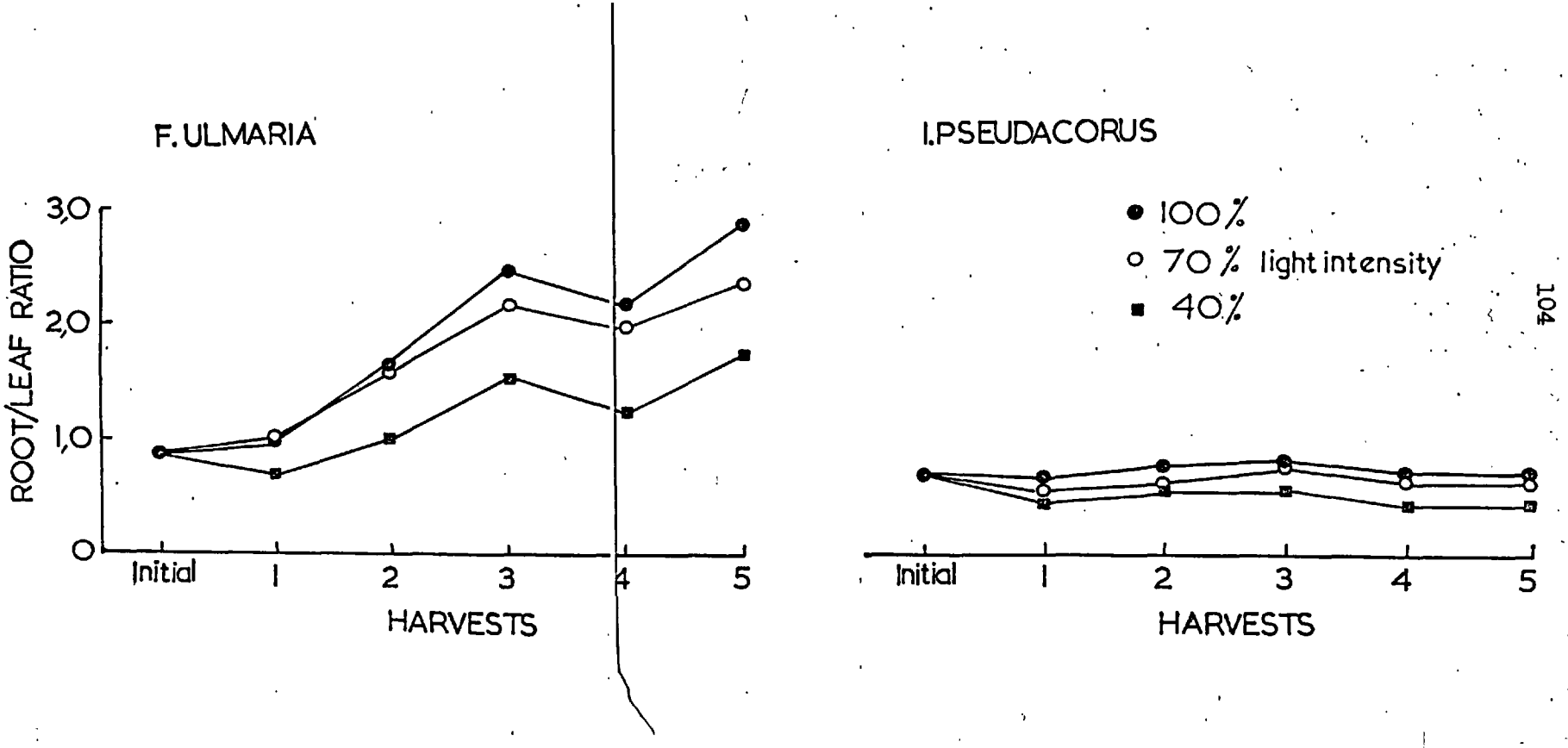


FIG. 16. Effect of varying levels of light intensity on root/leaf ratio.

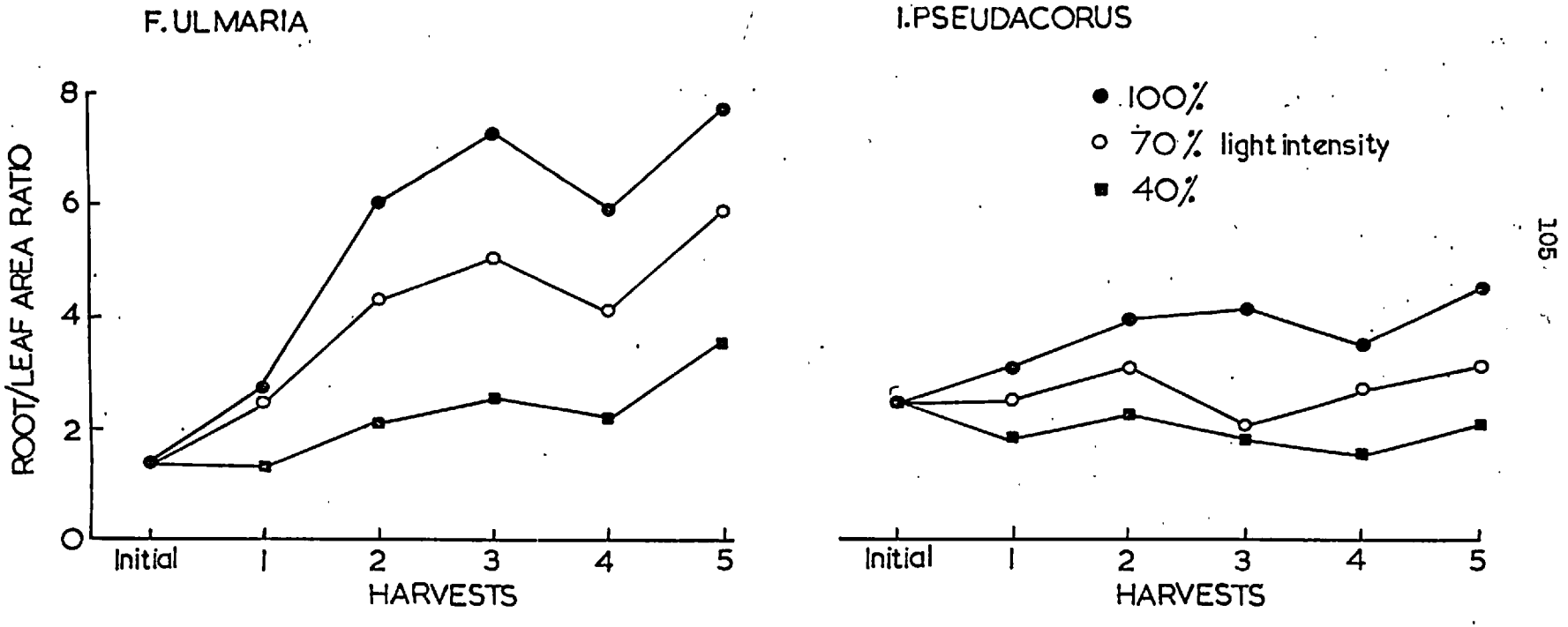


FIG. 17. Effect of varying levels of light intensity in root/leaf area ratio (mgs/cm^2).

the levels of light. The difference between the species can be correlated with a difference in the intrinsic pattern of growth in relation to their habitats. The progressive increase in root/shoot ratio and root/leaf ratio, whether expressed on an area or weight basis, with time implies that as time progresses the plant becomes less "leafy" and increasingly "rooty" whereas the stem remains relatively unchanged. It can be seen clearly in Fig. 18 and is discussed in the succeeding pages.

The percentage proportions of gross production into various morphological categories of the plant.

In elucidating the dry matter economy of the plants in terms of its ~~gross~~ production i.e. the total plant weight, it seems obvious to consider the distribution of ~~gross~~ production in terms of the shares going to each part.

It was thought use of this parameter of growth, might yield some useful information regarding the ontogenetic pattern of growth of the species. The distribution of ~~gross~~ production (dry weight in mgs.) has been worked out for leaf, stem and root separately, expressed as a percentage of the ~~gross~~ production. The values are represented graphically in Fig. 18. The general pattern of growth curves in each morphological category is very much similar from 100% - 40% light intensities. However the growth at 70% light closely followed the full light level.

The species differ markedly in respect of the leaf and root proportion. In F. ulmaria, the root constituted the highest proportion of the plant weight, than the leaves in its final harvest, whereas in I. pseudacorus these proportions are conversely different, i.e. highest proportion is found in leaves compared to roots. In both the species, however stem had the least proportion of the plant, ~~where it ranged from an optimum of 10% - 17% for F. ulmaria and I. pseudacorus respectively.~~ Another distinguishing feature which differs the species, is the time trend of the growth curves of root and leaf separately. In I. pseudacorus it can

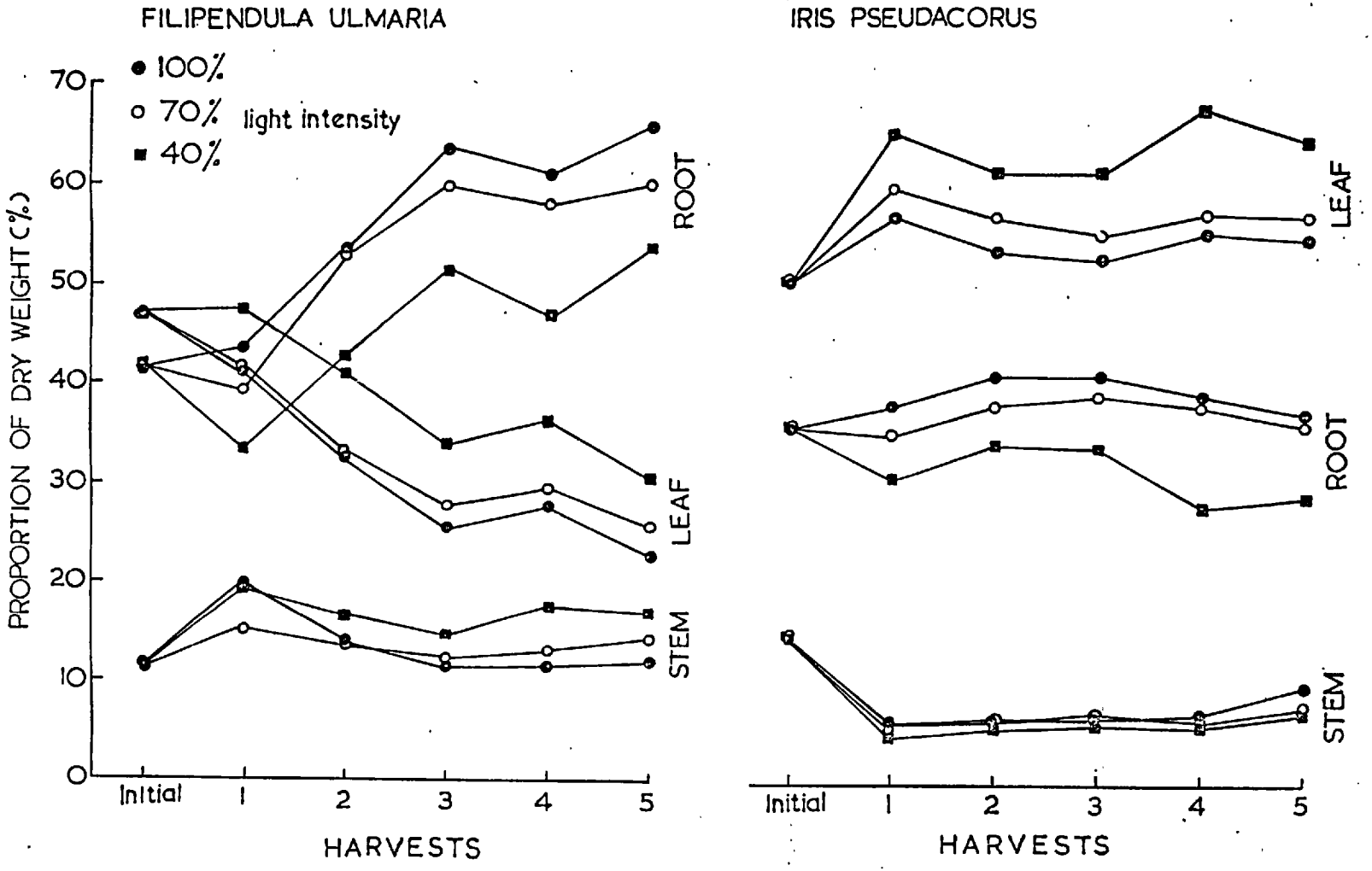


FIG. 18. Effect of varying levels of light intensity on the distribution of gross production into various morphological categories of the plant at successive harvests.

be seen that the proportion of the individual parts of the plant are almost held constant with time from the start of the experiment, whereas in F. ulmaria these proportions of root and leaf changed conversely with time. With age the shifting of highest dry matter proportion in roots at the expense of leaves is very much evident in the late harvests. From the above discussion two basic assumptions could be made. Firstly, the general shape pattern of the growth curves for each morphological category, i.e. leaf, root and stem, for any one species appears to be independent of the variation of light intensity. Secondly the effect of variation of treatments appears to alter only the actual values for each morphological category for any one species. This can be explained as follows:-

1. Each species develops in accordance with an intrinsic genetic developmental pattern over time, so that a general overall proportionality of parts is predetermined and fixed.

2. Within the intrinsic developmental pattern some variations of actual proportionality is possible in response to environmental differences.

In these experiments (and in subsequent experiments dealing with other factors) it can be seen that these environmentally induced changes in proportionality increase the chances of survival and must be considered advantageous. Further advantage from this method of presenting data comes from an examination of the general (genetically induced) developmental pattern.

In case of F. ulmaria it can be seen that as time progresses the plant becomes increasingly less "leafy" and increasingly "rooty", whereas the stem proportion remains relatively unchanged. This might be expected from its type of habitat. It starts off in the Spring with fairly large rosette of basal leaves growing mainly amongst rushes, sedges and similar vegetation tending to cast a fair amount of shade, but maintaining a high humidity in the surrounding atmosphere. The roots at this time are usually in very wet or water logged ground.

As the season progresses cauline leaves develop and each new leaf tends to be smaller. At the same time the root system relatively and absolutely becomes increasingly larger. The habitat meanwhile has tended to become drier. In fact some of these habitats can be quite xeric by mid summer and the plant can itself be seen to be increasingly xeromorphic with development. These changes are achieved by an increasing proportion of current assimilates being used in root development, whilst a corresponding moeity of assimilates is not used in leaf increase.

It is of particular interest to note that the environmentally induced changes follow a coherent pattern to the overall changes i.e. the relative increase of leaf area is achieved at the expense of material which otherwise would be used for root growth. Since such shaded plants occur in regions of less water stress than those exposed to full daylight, this change of proportionality is usually successful, i.e., the increased leaf area permits a satisfactory photosynthetic activity and the increased state of desiccation due to potentially unfavourable root/shoot

ratio (Fig. 15) which does not arise because in the shade high humidities and soil water contents usually occur.

On the contrary in I. pseudacorus at germination seeds are settled often on unstable habitats (mud and stream side etc.,) and therefore is advantageous to make rapid root growth for anchoring purposes. Once it is established leaf production follows and plants become much leafy with time. The xeric environments however does not bring about the xeromorphic changes in the species as was found in F. ulmaria. The increased leafiness follows with decreased root formation and at this time the increased leafiness is at the expense of roots.

V.

Photoperiodic influence on the growth and morphology of the species

Since the classical work of Garner and Allard (1923) who recognised the influence of daylength on the flowering as well as on the vegetative development of plants, many studies on plant growth have been concerned with the induction or inhibition of flowering. It has now generally been recognised that irrespective of the flowering response of plants, the growth form changes with different photoperiods and may also be of great importance in survival. Went (1941), and Stuckey (1942) reported the effect of light on stem and leaf growth. They cited the inhibition of stem elongation as the simplest evidence of photoperiodism. The photoperiodic influence on many aspects of vegetative growth of the plants has also been studied by a number of workers for instance, tillering, leaf size and rate of leaf production (Friend, Helson and Fisher, 1962; Newton, 1963; Aspinall and Paleg, 1964; and Ryle, 1966), cell size cell number and petiole length (Guttridge and Thompson 1963). However many plant responses to light particularly to variation in photoperiod or spectral contents are derived from other reaction systems. The action of these more direct photomorphogenetic pathways such as the phytochrome system has been shown to control such vegetative growth responses as cotyledon expansion and hypocotyl extension. (Mohr 1962)

Although some of these responses may depend on the spectral distribution of the light or change in daily radiation, it seems likely

that in natural conditions photoperiod may affect the form and array of vegetative growth within the plant independently of its influence on the light energy available for photosynthesis.

Recently Ryle (1966) working on some perennial grasses has shown that when short photoperiods of eight hours are extended by a "light break" in the middle of a long dark period the response generally produced is a long day effect shown by an increased rate of expansion of leaf surface, but decreased rate of leaf production and tillering. Similarly the total dry weight of plant material was greater in long than short photoperiods.

In the present investigations the plants of the two species were grown under contrasting photoperiods and the growth analysis was carried on in terms of gross morphogenetic responses and the dry matter economy of the plants. In this connexion two experiments were carried on to determine the differential photoperiodic influence on the growth and the results were compared and discussed. The treatments in each experiment were as follows:-

Experiment 1.

Plants were grown under

a) 9 hours of continuous light + 15 hours of darkness.

b) and 8 hours of continuous light + 15 hours of darkness with a one hour light halfway through the dark period.

Experiment 2.

Plants were grown under

a) 9 hours of light + 15 hours of darkness

b) and 16 hours of light + 8 hours of darkness.

In future the two experiments described would be referred as photoperiod and daylength experiments respectively.

The methods and design of these experiments differed in many respects, therefore a separate experimental procedure and technique has been adapted for each experiment, which would be discussed separately.

Experiment 1. Effect of 9 hours photoperiod of continuous and intermittent light on growth.

Experimental procedure.

Photoperiods were provided in growth cabinets erected in the green house. Two separate cabinets were prepared for the respective treatments. Each cabinet was supported by steel bars measuring 6' x 5' x 4' in dimension. The cabinets were then covered with big sheets of thick black polythene on top and each of three sides, so that the light coming from outside was completely cut off. The face of the cabinets were covered with black out curtains of polythene sheets, so that it could be raised and dropped accordingly. The cabinets were also provided with ventillation fans, one in each cabinet. Fans were supported on a rigid hard board and faced in such a direction that the surrounding air could be propelled inside the cabinet. Illumination used was from the bank of white warm fluorescent bars hanging over the roof of each

chamber. Provisions were made for adjusting the height of the lights according to the size of the plants. Daily period of illumination was controlled by means of Venner's automatic time switches. The exhaust fans (Ventillation fans) were also connected to automatic time clocks so that it could be turned on and off with the lights simultaneously.

As no separate arrangement was possible for the control of temperature inside the cabinets, the temperature was partly dependent on the glass house temperature and mostly on the warm fluorescent bars, which generated a considerable heat for raising the temperature. As an equal light intensity level was maintained in each chamber, the temperature also remained uniform for both treatments. However, when lights were put off, particularly at night the temperature also fell off considerably. In any case the temperature varied between 20 - 25°c at daytime and 15° - 18°C during the period of darkness.

The particulars of temperature, light intensity and the daily photoperiods compared were as follows:

a) 9 hours of light from 7 a.m. - 4 p.m. (intensity: approx. 2000 ft.c., temperature, between 20°-25°C) plus 15 hours of darkness (temperature between 15°-18°C.)

b) 8 hours of light, from 7.0 a.m. - 3 p.m. (intensity: approx. 2000 ft.c., temperature between 20°-25°C) plus 15 hours of darkness (temperature 15°C - 18°C) with an intermittent light break of one hour (intensity, approx: 2000 ft.c.) halfway through the dark period.

As no changes were made in the light intensity and the daily period of illumination, all the plants received the same total amount of light each day, when 100 ft.c. = 0.00499 g - cal/cm^2/min. The light measurements are in accordance with the data of Ryle (1966).

The working area on the floor of each cabinet measured to 6 x 4 feet. On the floor a thick layer of sand was spread over the polythene, the method which is already discussed in "Light intensity experiment". Seeds of F. ulmaria and I. pseudacorus were germinated in early April of 1967, and 2-3 seedlings were transplanted into 3" pots, containing peat and sand mixture. Seedlings were kept in an unheated glass house in natural daylengths until late April, when two leaf stage was fully attained. The pots were then moved to the chambers. All plants equally received nutrient solution twice a week. Watering was done daily to check the excessive evaporation of water through the pots.

Harvesting was made in early May of 1967, when plants showed gross morphological differences in between the treatments. There were ten replicates per treatment. In all six harvests were made including the initial one. Measurements of growth, recording of primary data and the derivation of parameters for growth analysis followed the same general methodology, discussed in Chapter 2.

Experiment 2. Effect of 9 and 16 hours of daylength on the growth.

The existing experiment was carried on simultaneously with the previous experiment on photoperiodism. The aim was in the first instance to evaluate the ecological significance of the species in response to

contrasting daylengths of 9 and 16 hours of duration corresponding to Winter and Summer daylight and to elucidate and evaluate the morphogenetic changes in terms of various parameters of growth. Secondly an attempt was also made to explain some of the findings of the earlier experiment in the light of the existing experiment. It was expected that the species would flower under long photoperiods but neither of the species flowered and remained vegetative all over the experimental period.

Experimental procedure.

It was mentioned earlier that the experiment was started simultaneously with the photoperiod experiment. A separate arrangement was made in an other green house because of the inavailability of growth cabinets in the same green house.

A central bench in the green house was occupied to perform the exisitng experiment. A growth chamber for 9 hours daylength was constructed at the northern ridge of this bench supported by wooden lattices, measuring 7' x 6' x 6' feet in dimension. The top and the two northern and southern sides of the chamber were completely covered with black polythene sheets, while the western and eastern sides were covered with black out curtains, which could be raised and dropped accordingly. The space adjacent short day chamber was used for long day treatment. As the experiment was started in early May of 1967, the natural light available ranged from 11-12 hours a day. Control of required photoperiod was achieved by extending natural light to the long photoperiod of 16 hours with 400 w. mercury lamps (type MBFR/U).

For the uniformity of treatments short day growth chamber was also supplemented with mercury lamps so that both long and short day treatments received a mixture of natural light supplemented with artificial light. No record of light intensity measurement was kept as light intensity varied considerably with and within the treatments during most of the experimental period. Temperature was also not strictly controlled. However the glass house temperature was not allowed to fall below $15^{\circ}c$. Thus temperature ranged between $15^{\circ}c$ - $25^{\circ}c$ during most of the experimental period. The control of required long and short photoperiods with artificial illuminated was achieved by automatic time clocks as described earlier in the "photoperiod experiment". Daily control of natural light duration inside the 9 hours daylength chamber was achieved by raising and dropping the curtain daily at 9 a.m. and 6 p.m.

Seeds of F. ulmaria and I. pseudacorus were germinated in early April of 1967 and the seedlings were transplanted into 5" diameter pots containing peat and sand mixture. Seedlings were raised in an unheated glass house. When two leaf were fully expanded the pots were randomised inside each respective treatments. The plants were equally supplied with nutrient solution twice a week. Watering was done every day.

Harvesting was started in early May 1967. Ten replicates plant per treatment were selected for each harvest. In all six harvests were made including the initial one. Measurements of growth in terms of leaf area and separate dry weight of different parts of plants were made according to the methods discussed earlier in the previous experiment.

FILIPENDULA ULMARIA

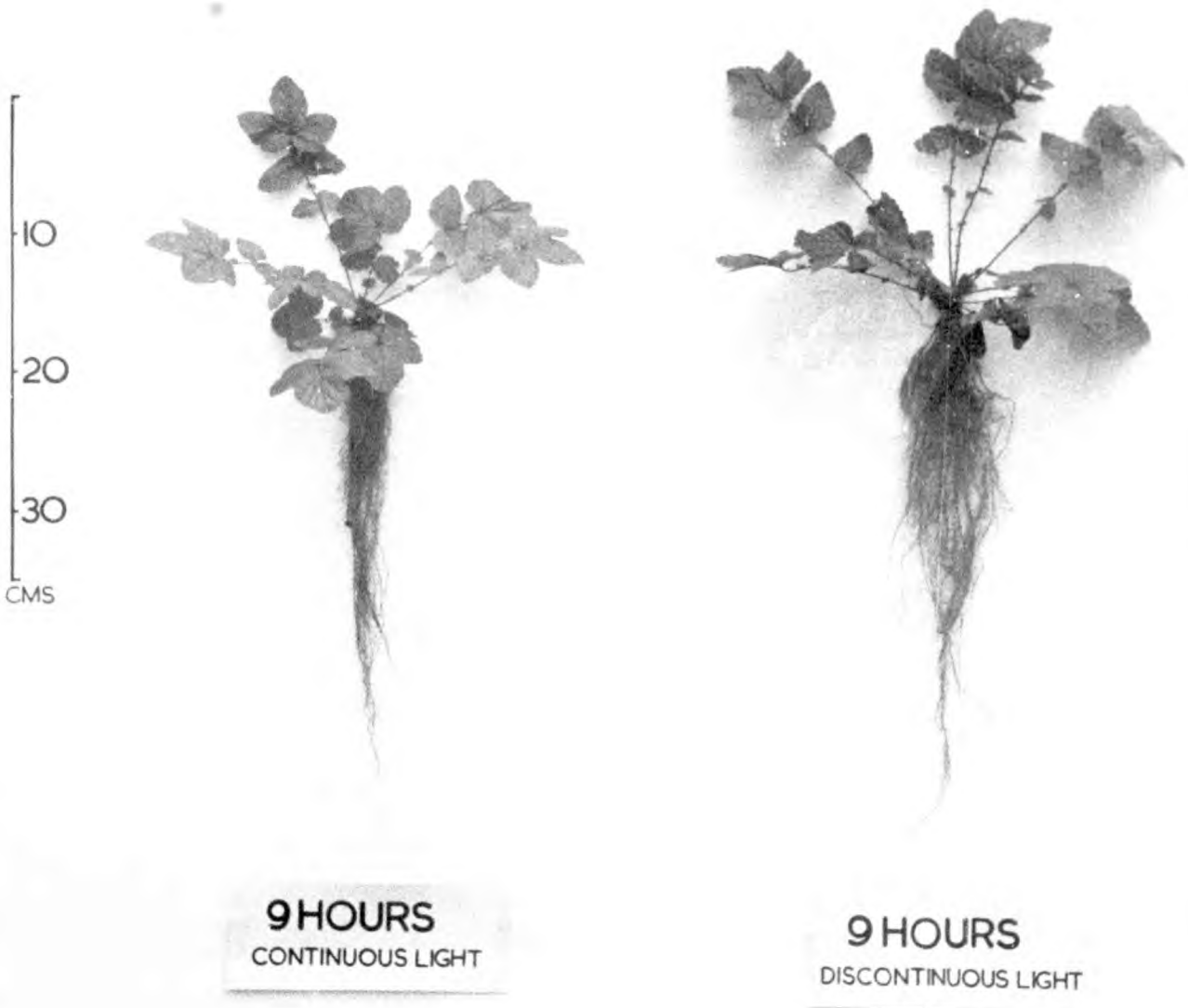


PLATE III. F. ulmaria grown in a photoperiod of 9 hours continuous light and in a photoperiod of intermittent light.

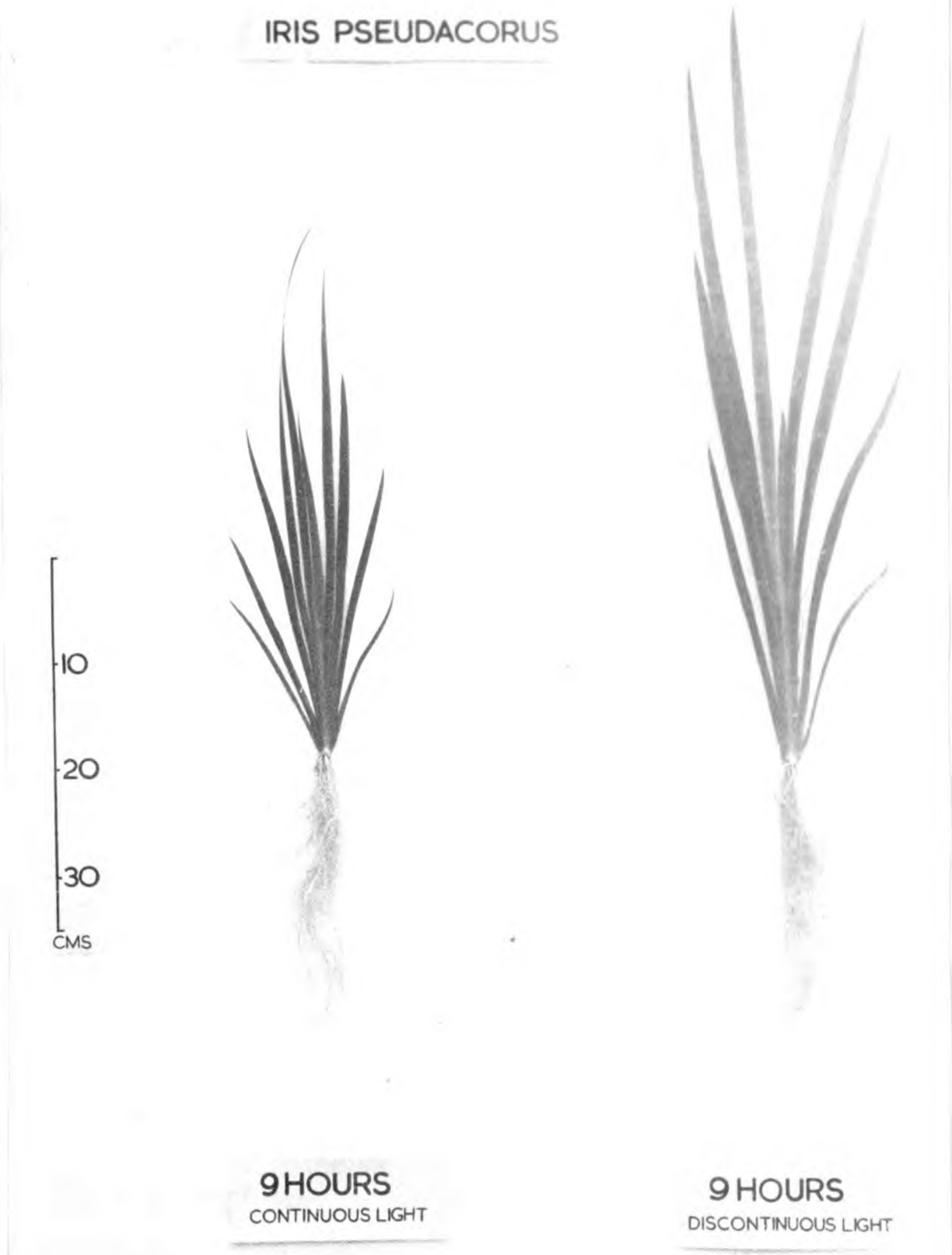


PLATE IV. I. pseudacorus grown in a photoperiod of 9 hours continuous light and in a photoperiod of intermittent light. (Sodo.)



PLATE V. F. ulmaria grown in a daylength of 9 hours light and in a daylength of 16 hours light.

(80 days)

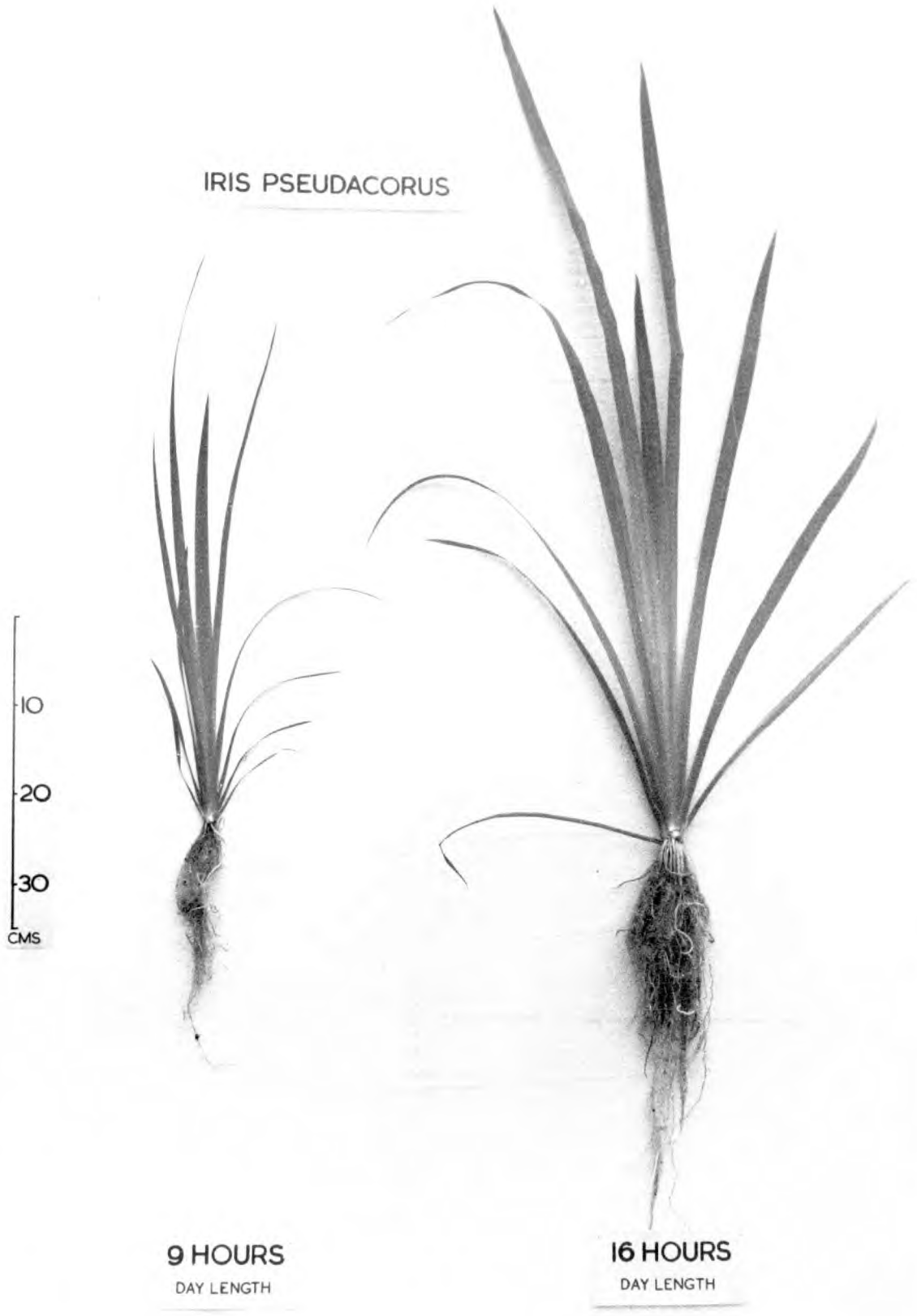


PLATE VI. I. pseudacorus grown in a daylength of 9 hours light and in a daylength of 16 hours light. (80 days)

The growth analysis was carried on similar to that of the "photoperiod experiment".

Results and discussion.

Results have not been discussed individually for each experiment as it was more convenient to discuss the results of the two experiments together. A joint discussion on the experiments is followed in the succeeding pages. The appearance of plants at the final harvest is exhibited on plate III - VI inclusive.

Leaf Production and the expansion of leaf surface:

The counts of live leaves per plant were recorded at each harvest per treatment. Only the active green leaves were counted, whereas senescent leaves were not taken into account. It can be seen in Fig. 19&20 and table IV that the leaf production in I. pseudacorus was slightly greater in short days than in either of a long day or "light break" treatment. Whereas in F. ulmaria a slightly decreased number of leaves were observed in long day and/or "light break" than the short days.

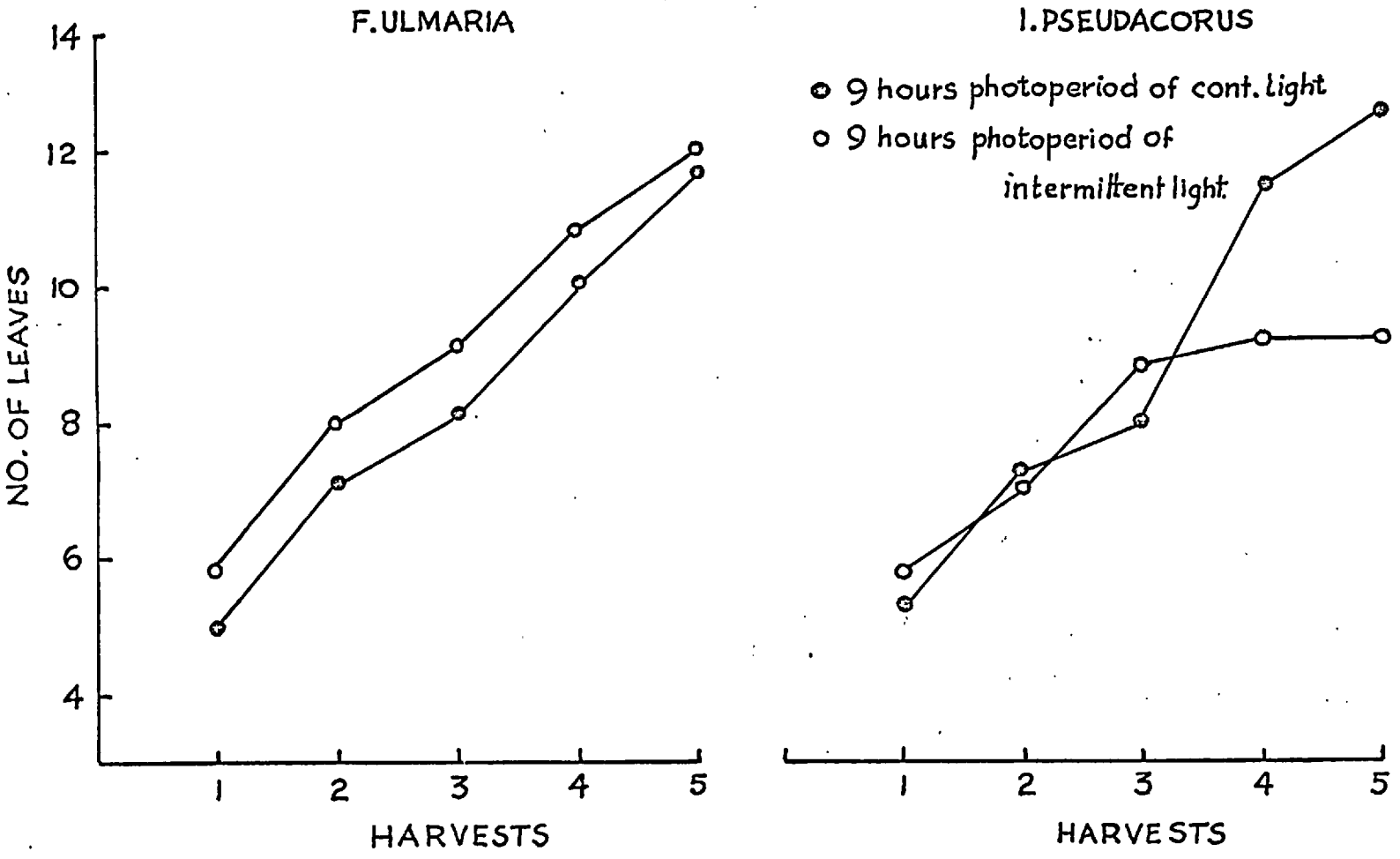


Fig 19. Effect of 9 hours photoperiod of continuous and intermittent light on leaf production.

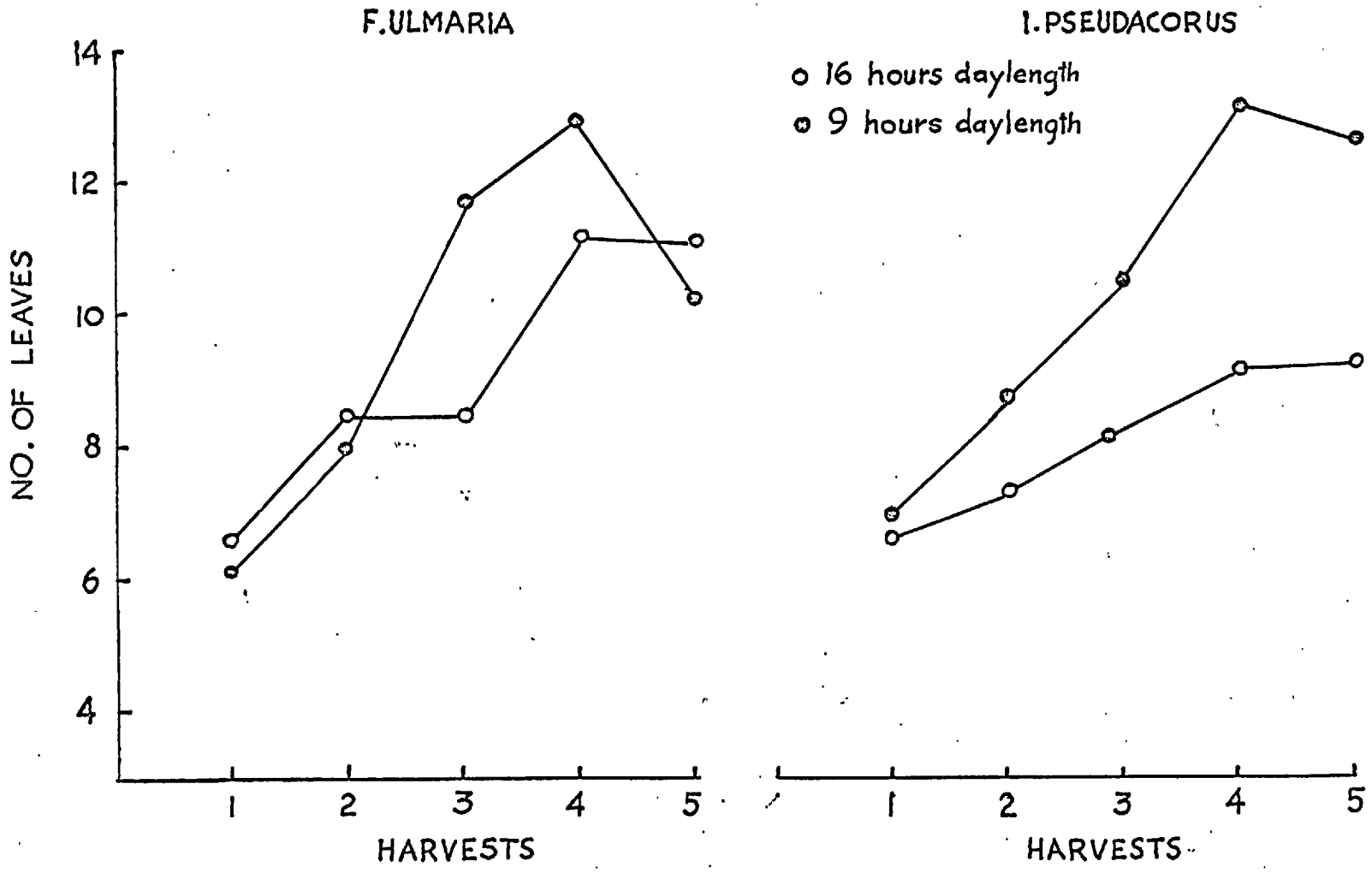


Fig 20. Effect of long and short daylengths on leaf production.

Table IV. No. of live leaves per plant at successive harvests and contrasting photoperiods

F. ulmaria

Harvest No.	Photoperiod experiment: 9 hours cont. light	Photoperiod experiment: 9 hours intermit. light	Daylength experiment: 9 hours daylength	Daylength experiment: 16 hours daylength
1.	5.0	5.8	6.1	6.6
2.	7.2	8.0	8.0	8.5
3.	8.2	9.2	11.8	8.5
4.	10.1	10.7	13.0	11.2
5.	11.7	12.0	10.2	11.6
	I. pseudacorus			
1.	5.2	5.7	7.2	6.7
2.	7.2	7.0	8.7	7.3
3.	8.0	8.7	10.5	8.1
4.	11.5	9.2	13.2	9.2
5.	12.5	9.2	12.8	9.2

With I. pseudacorus increased leaf production in short days was not generally sufficient to overweight the larger leaves in long day so that the rate of expansion of new leaf surface per plant still appeared to be greater in long day. As it can be seen in Fig. 21 and table 28 in the appendix, that the increase in photoperiod whether by a light

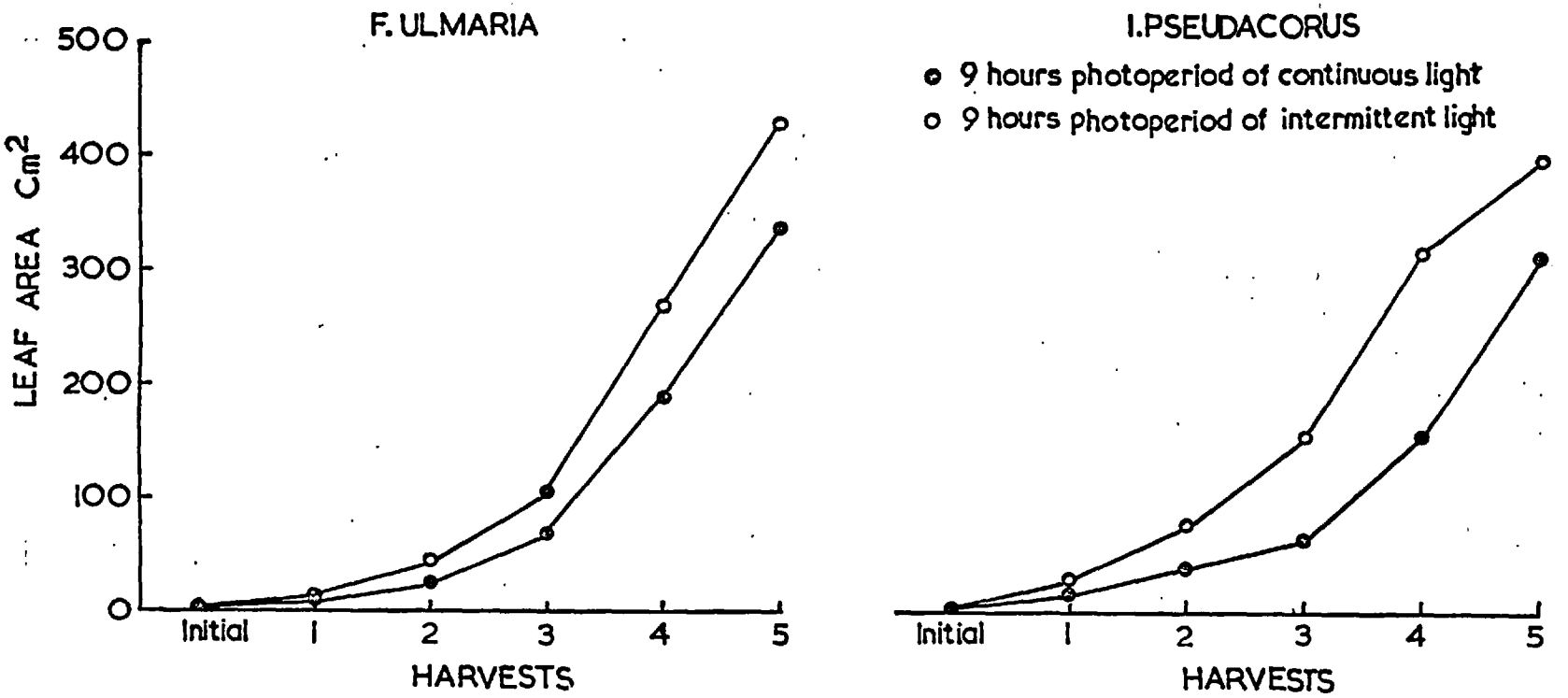


FIG. 21. Effect of 9 hours photoperiod of continuous and intermittent light on increase of plant leaf area with time.

break in the middle of long dark period or by extending the basic short photoperiod generally increased the leaf area. Thus with both the species a "light break" (Exp. 1) appeared more effective in increasing leaf area than a short photoperiod and had effects similar to that of a long photoperiod (Exp. 2). Ryle (1966) reached a very similar conclusion while working on some perennial grasses. In exp. 1 it seems likely that with I. pseudacorus the extent of larger leaf area in long day and/or with "light break" was greater than short photoperiods, whereas with F. ulmaria a long photoperiod seems to be less effective compared to short photoperiod.

The effect of photoperiod on the dry weight of plant parts in exp. 1 were more or less similar to those in exp. 2. Thus the final dry weight per plant of I. pseudacorus was obviously larger in long and/or in "light break" than in short photoperiod, because the weight of individual part was much increased (Fig. 22 and table 28. in the "appendix"). With F. ulmaria in exp. 1 it can be seen that very little differences in the total dry weight appeared between the treatments. With F. ulmaria an insignificant difference in dry weight could be accounted for the increase of root dry weight in short photoperiods. The increased dry weight of root was such that the total plant weight was also increased at the final harvest in a short photoperiod of continuous light (Fig. 22).

From overall performance of the species in terms of dry weight and leaf area increment, it seems likely that the changes in relationship between plant leaf area and dry weight must be understood properly then

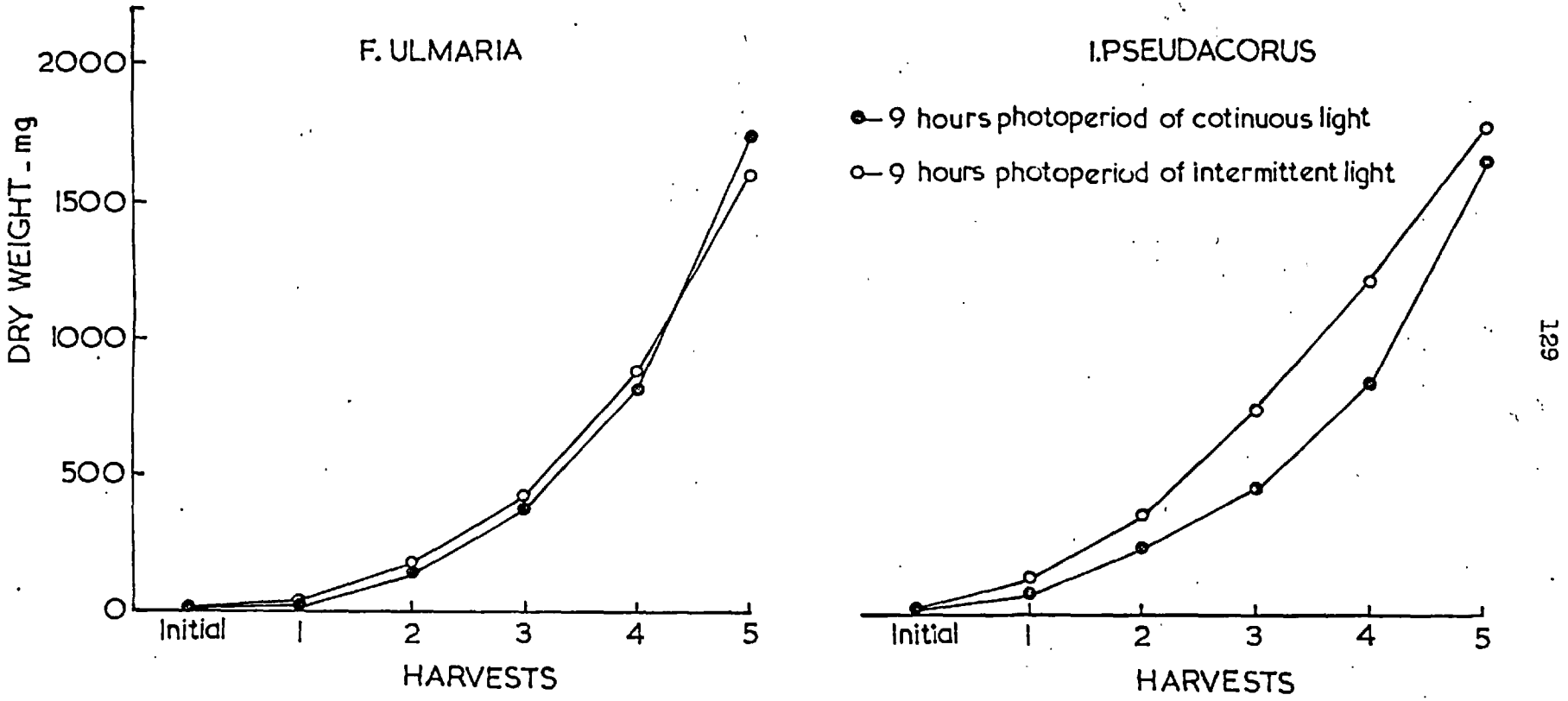


FIG. 22. Effect of 9 hours photoperiod of continuous and intermittent light in increase of plant weight with time.

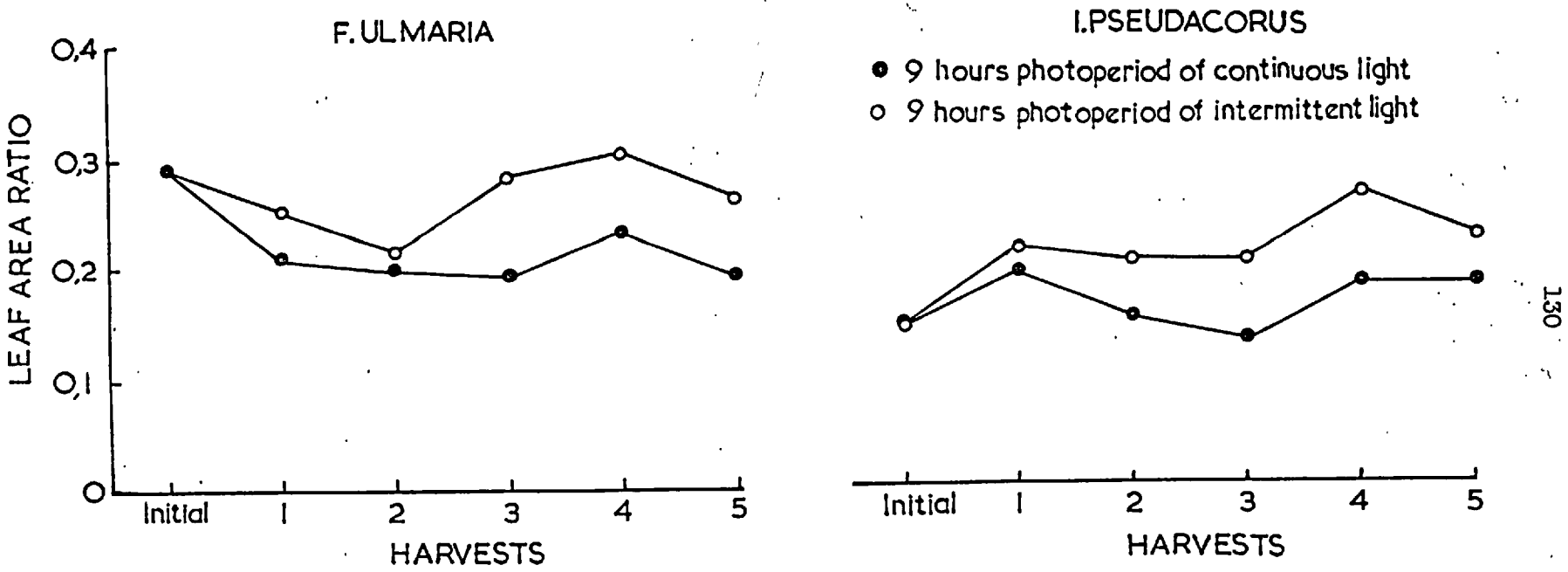
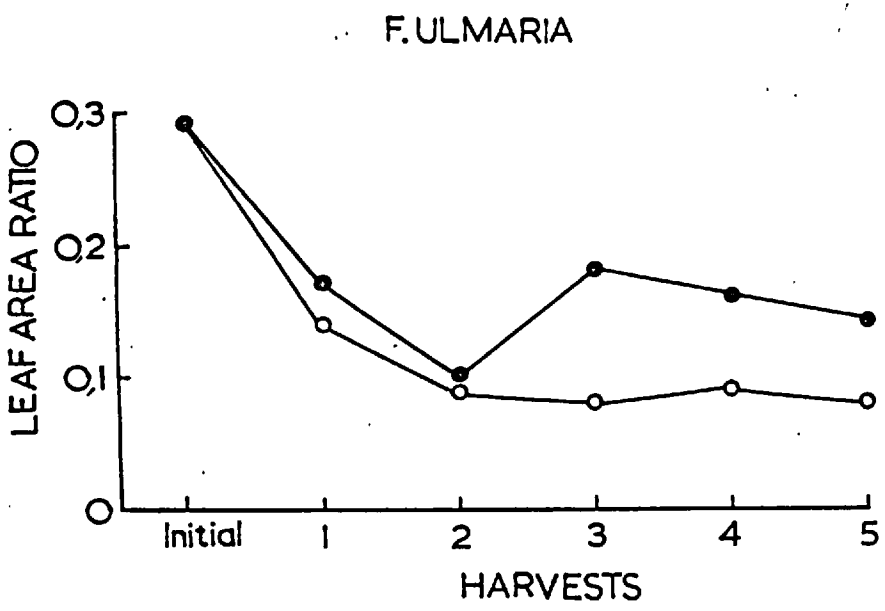


FIG. 23. Effect of 9 hours photoperiod of continuous and intermittent light on leaf area ratio (cm^2/mgs).



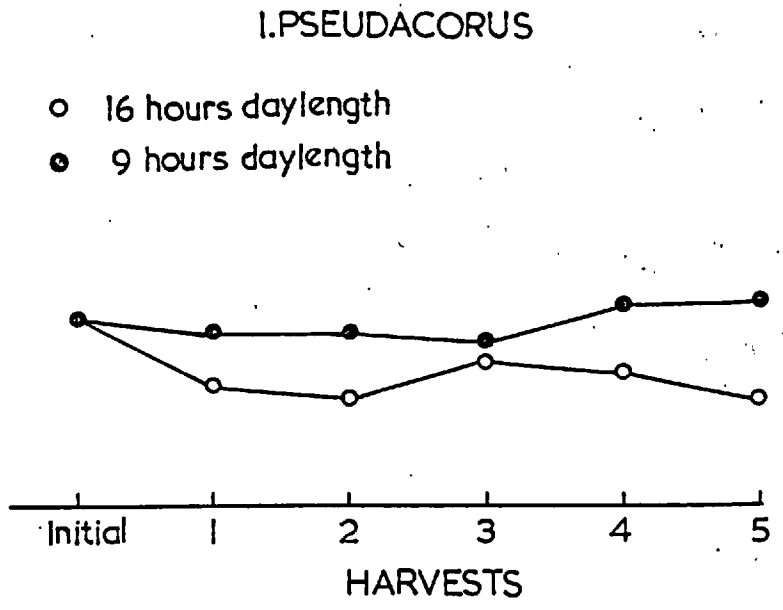


FIG. 24. Effect of long and short daylengths on leaf area ratio (cm^2/mgs).

various photoperiodic influences on plant growth could be explained. Amongst several parameters of growth, leaf area ratio seems to be a suitable parameter for the comparative assessment of the species in response to contrasting photoperiods. In Figs. 23 and 24 on page 130 and 131 are represented the values of leaf area ratio for both species under different levels of photoperiods and successive harvests. It can be seen that with both species lowest leaf area ratio was found in the plants grown at 16 hours daylength whereas highest ratios were found amongst the short day and/or photoperiod with light break in the middle of dark period. The decrease of leaf area ratio in contrasting photoperiods of Exp. 1 and 2 could be summarised as follows:

16 hours daylength < 9 hours photoperiod < 9 hours photoperiod with intermittent light (light break).

It is to be noted that in exp. 2 the ratio in F. ulmaria decreases slowly with time at 16 hours daylength. This was because of the "age factor" which has been discussed earlier in experiment on "light intensity". The effect of a "light break" in the middle of a 15 hours dark period in promoting leaf area ratio, compared to short and long photoperiods was very consistent and significant in both species. In other words plant weight per unit area of leaf was greatly reduced with "light break" treatment, so that the expansion of leaf area was almost at the expense of total plant weight. It may be argued that the gross production of plant was mainly consumed in the construction of leaves throughout the experimental period. Thus a higher degree of leafiness was evident in both species. The effect of a 9 hours continuous

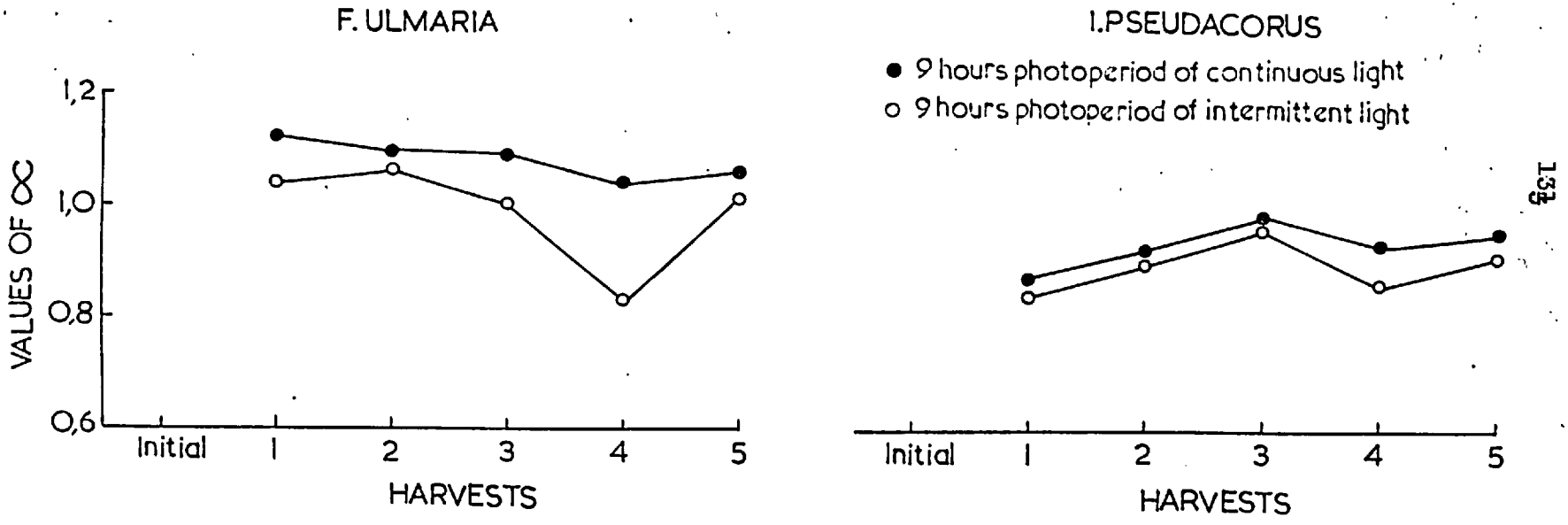


FIG. 25. Effect of 9 hours photoperiod of continuous and intermittent light on the ratio of mean relative growth rate to the mean relative rate of leaf area increase (mgs/cm^2/week). The values of α are calculated from Initial harvest and one; initial harvest and two; initial harvest and three etc.

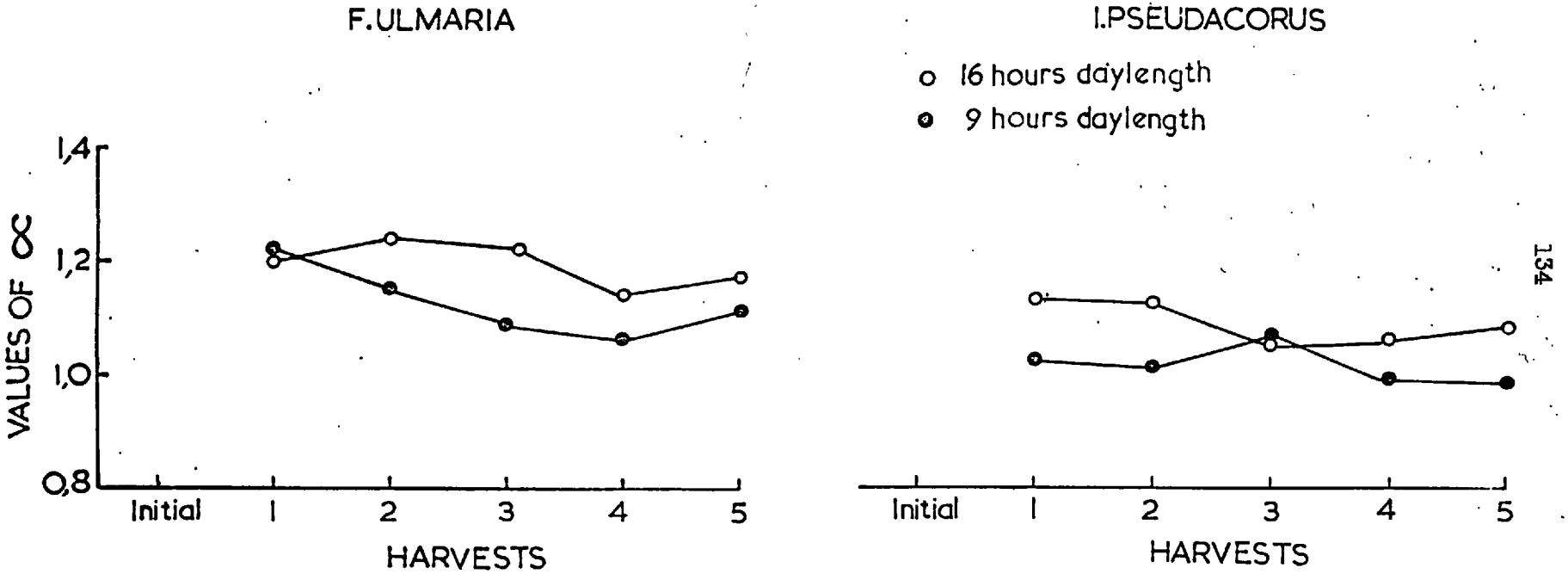


FIG. 26. Effect of long and short daylengths on the ratio of mean relative growth rate to the mean relative rate of leaf area increase (mgs/cm^2/week). The values were calculated from initial harvest and one; initial harvest and two; initial harvest and three etc.

photoperiod was also consistent in increasing the leaf area ratio but was less than that of a "light break", so that a comparatively less leafiness was also evident in short photoperiod.

The comparative performance of the species in both experiments at contrasting conditions of photoperiod could only be assessed when the increment of plant weight is compared with increment of leaf area at a specific time, then a relationship between these could be held on plant weight/leaf area basis.

The use of α index again seems to be an appropriate and suitable parameter of growth. The values of α calculated from initial to the successive harvests in Exp. 1 and 2. for both species is represented in Figs. 25 and 26 on page 133 and 134 and the tabulated form is shown in table 25 and 33 on page 221 and 231 of appendix. It can be seen that in 16 hours daylength both species shows highest values of α at such successive harvest, compared to short photoperiod of 9 hour and/or lightbreak in the middle of theperiod of darkness. The sequence of increased values of α for both species in Exp. 1 and 2 may be indicated as follows:

16 hours daylength $>$ 9 hours photoperiod $>$ 9 hour photoperiod with intermittent light.

In other words the plants in long photoperiods were not only adjusted but also surviving as an efficient photosynthetic entity. However, the effect of a "light break" considerably decreased the values, so that lowest values were found with both species. The reason could be that in the latter case the greatest expansion of leaf area was followed by

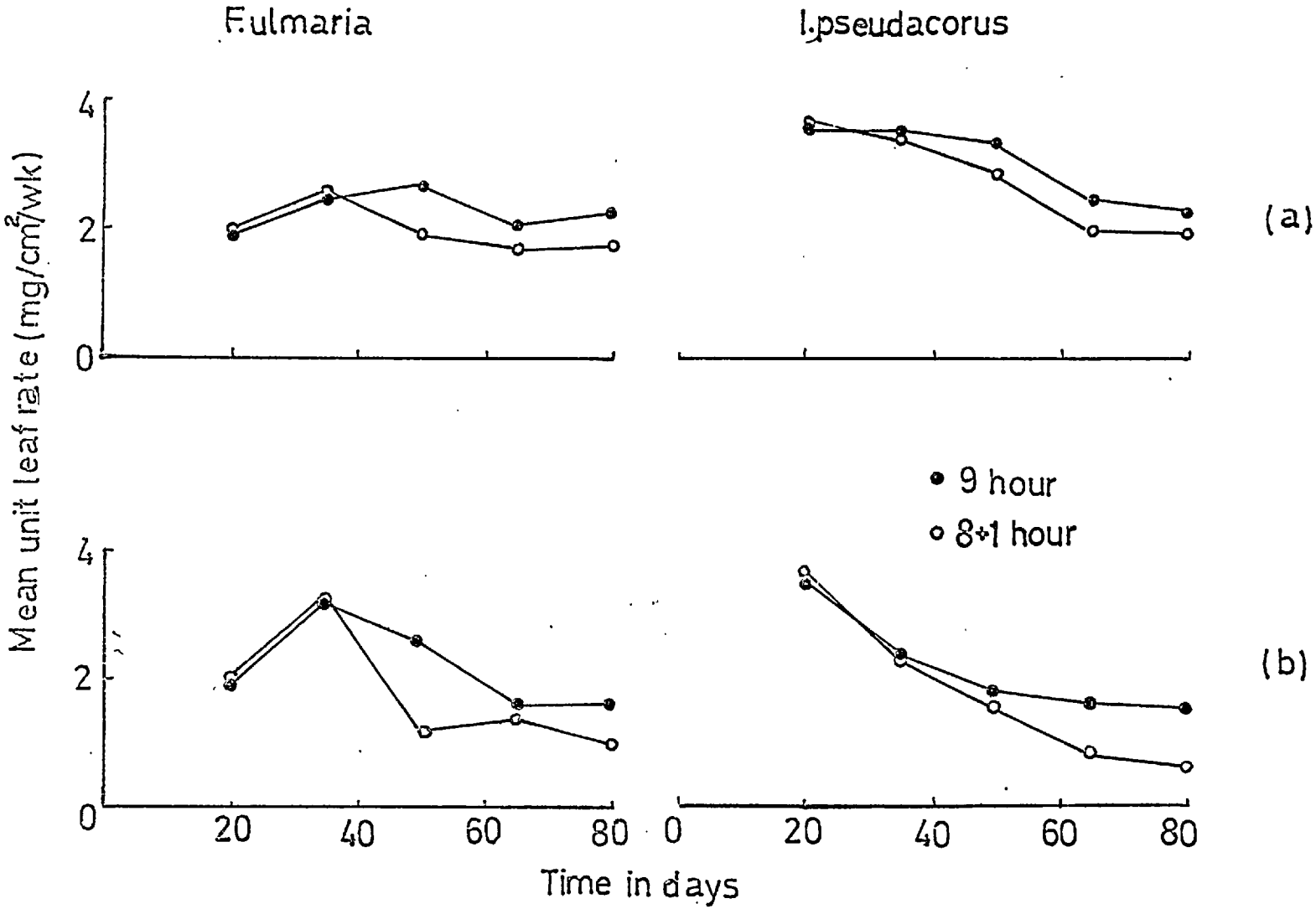


Fig 27. Each value is plotted as a point at the end of the harvest interval over which it was calculated. (a) Values of $\bar{E}$ between initial harvest and one; Initial and two, etc. (b) between Initial and one; one and two, etc.

Corrigenda to p. 136

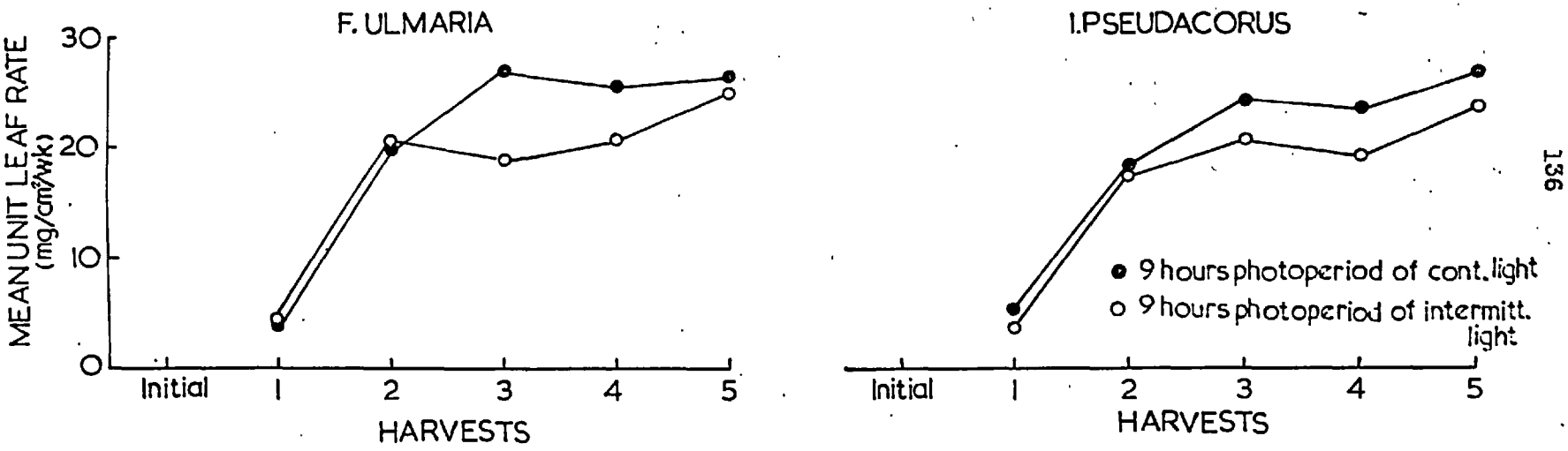


FIG. 27. Effect of 9 hours photoperiod of continuous and intermittent light on mean unit leaf rate (mgs/cm^2/week). The values are from initial harvest and one; initial harvest and two; initial harvest and three etc.

relatively lower relative growth rate, as a result decreased values of α were observed.

In the comparative performance of the species under contrasting levels of photoperiod and/or daylength, F. ulmaria again proves to be a successful species which yet shows higher values of α indicating its highest photosynthetic efficiency in comparison to I. pseudacorus. It should be pointed out that in "photoperiod" experiment, I. pseudacorus shows remarkably decreased values of α, below the "unity" at each treatment. It can be argued here that this species was not adjusted to either of the treatments, therefore an increased leafiness was evident all over the experimental period.

The mean unit leaf rate:

The values of $\bar{E}$ were also calculated on the basis of leaf area, as discussed in Chapter 2 of "Material and Methods". These values are calculated in between the initial to the successive harvests and are shown in Fig. 27 and Table 33 on page 232 of "appendix".

The photosynthetic efficiency of the species in contrasting levels of photoperiod of Exp. 1 and 2 could be well judged from the values of $\bar{E}$. It can be seen that the increase in daylength has generally increased the mean unit leaf rate indicating its highest photosynthetic efficiency. However a "light break" in the middle of a period of darkness had no consistent effect to overweight the highest mean unit leaf rate in long day, so that both species showed lowest mean unit leaf rates. When the rates are compared in between the species, it seems likely that F. ulmaria, especially in Exp. 2 had highest photosynthetic efficiency

compared to I. pseudacorus. However in Exp. 1 the rates were similar for both species.

Root/shoot ratio:

A pronounced effect of different levels of photoperiod in Exp. 1 and 2 on the root/shoot ratio of the two species can be seen in Figs. 28 and 29 on page 139 and 140. It should be noted that a "light break" treatment has considerably decreased the root/shoot ratio with either of the species. In other words a greater proportion of plant weight was employed in the construction of shoots, resulting in a decreased root weight. As the stem (rhizome) constitute a fraction of shoot weight in both species, a greater proportion of shoot weight was also employed in the construction of leaves. As a result increased leafy conditions was found in a "light break" treatment. It can be seen that the degree of increased leafiness in F. ulmaria is less than that of I. pseudacorus, where comparatively lower root/shoot ratio are observed.

In I. pseudacorus the effect of a long day was similar to that of a "light break", so that highest root/shoot ratios were found in a short photoperiod, whereas in F. ulmaria grown in long days had highest root/shoot ratio compared to short days irrespective of 9 hour continuous and/or intermittent light.

It should be stressed that in F. ulmaria with the increase in photoperiod there is an increase in root/shoot ratio with time, whereas a "light break" has brought about a considerable decrease in the ratio with time. In this species the variation in root/shoot ratio in response

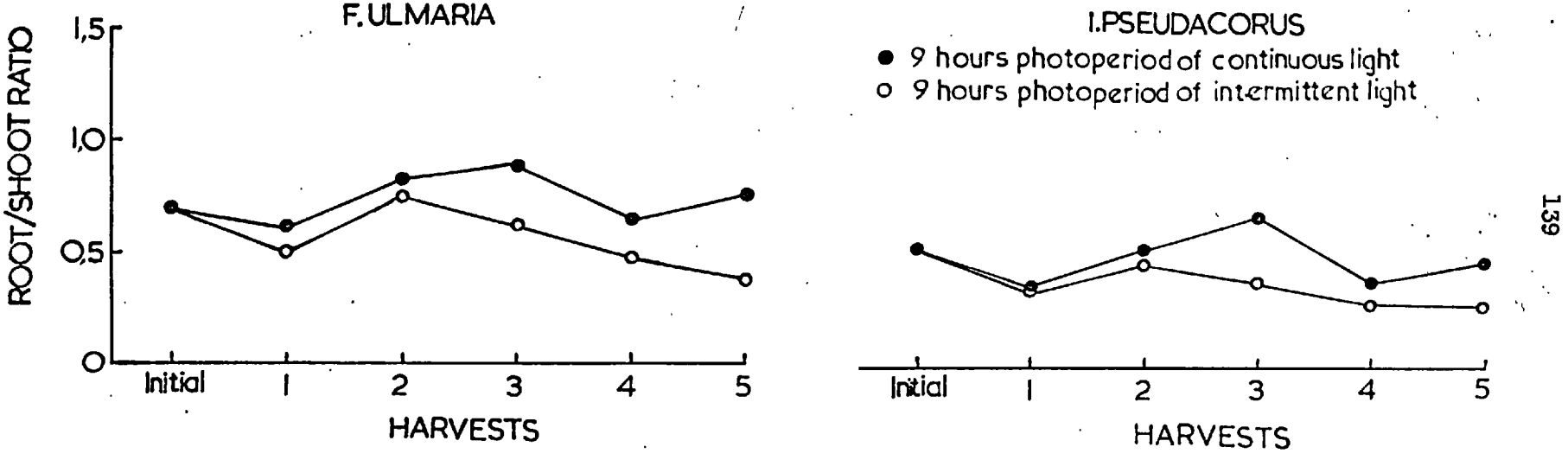


FIG. 28. Effect of 9 hours photoperiod of continuous and intermittent light on root/shoot ratio.

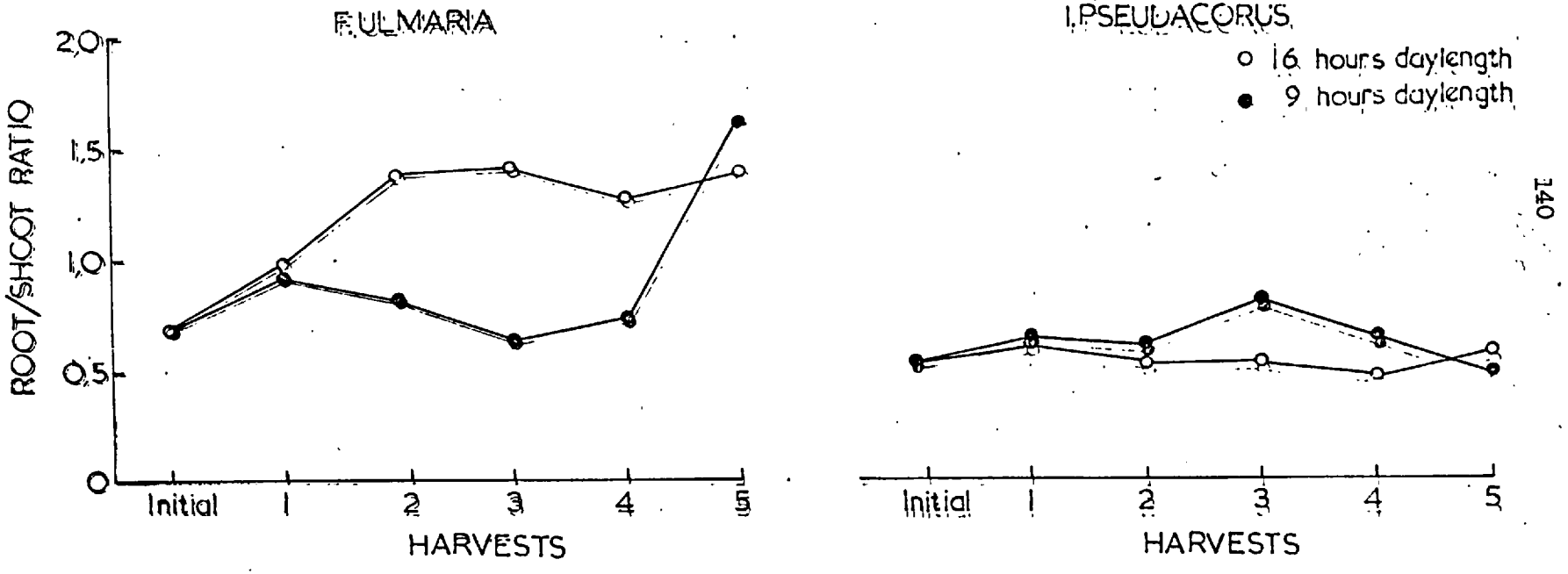


FIG. 29. Effect of long and short daylengths on root/shoot ratio.

to contrasting photoperiods could be accounted for its intrinsic pattern of growth, which can be referred back in the experiment of "Light intensity" on page 107 •

CHAPTER VI
FIELD EXPERIMENT

Field Experiment.

The use of lime to improve crop growth on acid soils has been the subject of extensive investigations; yet there is a little agreement today as to the fundamental causes of the poor growth of plants on acid soils.

The problem here, considered, is the ecological adaptation of the species under investigation to "rich" and "poor" soils; in the former case with calcium occuring in calcium carbonate. Initially, a plant geographic topic, it has now advanced far into a physio-ecological interpretation of how the species react to the calcium contents of the soil. Why are certain plant species preferably bound to calcareous soils, whereas other thrive on calcium poor organogenous soils. The correct term for the two types of plants are "calcareous" and "calcifuges" respectively. It is not so much that there are two sharply defined types of plants but that there is a continuous degree of sensitivity to or against the contents of $CaCO_3$ in the soil, because the species are not constant in their behaviour either (Burström 1968). There are evidences that a species appears as a calcicole in one region but not in other climatic conditions. It is emphasized that the physiological differences between ecotypes must also be taken into account (Shaydon & Bradshaw, 1961). Such observations often led to a desire to consider calcium carbonate as of no direct importance for the vegetation and it was stated some decades ago that whatever the explaination of lime problem might be calcium as an element has no part in it. All kinds of conditions connected with a lime content of the soil have been advanced as

explanation of the soil preference of calcifuge, that would explain the difference between acid soil plants from localities of pH value 6.0 and 8.0. The nutrient status has alos been often adduced and there are frequent references in the literature to "rich" and "poor" soil without specification of what nutrients are in mind but it usually means calcareous and acid soils. All such conditions may be of importance for any one plant species in the field but now, it is established that they are of decisive importance. A difficulty may be encountered in taxonomically determined physiological characters, when it is not known whether they are of any importance for the ecological adaptation of the plants is not (Hou & Merkle 1950).

It is pointed out by Burstrom (1968) that the competition between species for water mineral nutrients and light as well as chemical interaction between the species should also be taken into account. Competing power may be bound to a growth pattern and morphology and a small advantage of one plant may be sufficient under strained conditions to keep out another species. Little information on competition is availble. Rorison (1960) has demonstrated poor competing power of the calcifuge Holcus Mollis in acid soil condition but it turned out a better competitor with very changed morphology in high pH, high calacium conditions.

Thus the investigation follows two lines; one is a comparative study of the characteristics of the two plant types,

another is a study of the characteristics which might be decisive for the reaction of plants against lime. The literature thus contains a rather heterogenous collection of data not easy to sumarise here and is beyond the scope of the present work. Schmehl and the co-workers (1950) have thrown much light on the causes of poor growth of plants on acid soils and the beneficial effects of liming. In their studies many factors have been evaluated which are responsible for acid soil injury to the plants. Burstrom (1968) has fully revived the literature on this problem.

The field experiment carried out was designed to determine the differences in response of the species when subjected to its natural situation in the field. A further aim of the study was to investigate how far the distribution of species can be interpreted in terms of (1) rich and poor status of soil (2) the calcicolous and calcifugous nature of the species (3) the independent tolerance of the species and interference between the species. As it was pointed out that the two species concerned may frequently be found living together, a struggle for existence might reasonably be expected to occur between them (the species cohabit, sensu Harper & Chancellor 1 5) and a competition for the available nutrients, light, etc., may occur. The intensity of competition is determined by the amount in which the demands exceeds the supply and the chances may arise for eliminating the other species, but yet in a mature community the number of individuals and the species may naturally adjusted by competitive damands to use the available environment (Oosting 1948) and thus species coexist.

Layout of plots.

The site for experiment was situated in the vicinity of Imperial College field station, Silwood Park. It was started in May 1968 and continued till September 1968. The area selected was by the side of a small running stream. Here colonies of I. pseudacorus are also found in abundance all along the sides of stream. Two sites were selected at different places. At each site a big plot of 10' x 10' was marked out. These plots were situated on low lying ground and much wetter. This situation was considered suitable the idaal growth hence the species are moisture loving plants. One of these plots was laid out under the shade of a big Sycamore tree, (Aces pseudoplantanus). Here the soil was much wetter than the other one, because of its close proximity to the stream.

The soil in this area was found to be acidic and very poor in nutrient status. The pH measured ranged from 5.0 to 5.5. The existing vegetation covering the area of experiment, mainly consisted of sedges, rushes and grasses. This was all deeply uprooted and the soil surface exposed completely. Each plot was sub-divided into six 2' x 2' sub plots of leaving a 3' path between the two rows of 3 sub plots. In each row only a foot space was left in between each of the three sub plots.

A week before the transplantation of seedlings, fertilizer treatments were applied. A single treatment being given to a single row of 3 sub plots. The treatment was applied with fertilizer (Fisons Top growth 8), plus crystalline form of $CaCo_3$.

The rest of the sub plots were lef untreated. The sub plots with fertilizer plus calcium carbonate treatment and without treatment would be referred to fertilized and unfertilized respectively. Firstly the fertilizer and then after two days $CaCo_3$ was spread over the surface of plots. By the time of transplantation a considerable amount of $CaCo_3$ was leached out which was again boosted by a second application before the day of transplantation of seedlings. The pH measurements were made twice which ranged between 6.5 - 7.5.

Seedlings were raised in the green house following mass water culture tenhnique, described in materials and methods. Seedlings with their first pair of leaf expanded were selected for their uniformity of size and development and taken to the field. In each sub-plot a total of 196 seedlings were planted at a distance of 1" apart. Thus in a plot where the two species were sown together consisted of 98 plants per species alternating each other. The sub-plots consisting of one species only, would be referred to "Intra Specified" whereas, the plots with mixed seedlings as "inter specific".

The complete transplantation of seedlings took about 15 days. It was tried whenever possible to prepare at least one plot in a day. This long interval of transplantation was considered negligible for the growth of the plants, as the plant response to treatments was not evident during this period. The plots were fenced all around for protection against animal grazing. Weekly visits were made to the field. The weeds were uprooted and the shoots originating from the buried rhizome of Carex sp. beneath the plots were cut out from time



PLATE VII. Plants grown on fertilised soil
(a) F.ulmaria (b) I.pseudacorus
(c) F.ulmaria + I.pseudacorus



PLATE VIII. Plants grown on unfertilised soil
(a) F.ulmaria (b) I.pseudacorus
(c) F.ulmaria + I.pseudacorus

to time.

In the middle of July, there was excessive rainfall and the whole plot under shade was in most of the parts overflooded, thus uprooting most of the seedlings. Especially seedlings of F. ulmaria could not withstand the waterlogged conditions and were either buried in the mud or washed away. The shade plot, therefore is excluded from the experiment and only the "open" plot would be discussed.

Harvest was made on the 20th September, 1968, when plants were fully grown. The plants were carefully uprooted by digging out the whole plot, and washed under tap water. Roots and shoots of individual sub plots were cut separately and wrapped in big perforated envelopes. The material was oven dried at 100°C, for 48 hours and then taken out for weighing. Data was recorded in terms of the counts of the total number of plants survived per sub plot and the total plant weight of roots and shoots separately for the plants survived in each sub plot, and then main dry weight per plant was calculated. Final appearance of the plants in field is exhibited in plates VII & VIII.

Results and discussion.

Fertilizer and calcium had a pronounced effect on the growth and survival of F.ulmaria. whereas plants grown on unfertilized soil showed a poor and chloritic growth with few seedlings survivings. It was considered therefore, that the nutrient regime of the soils of these sites was too low for F. ulmaria. seedlings to become established and make adequate growth, but on the contrary the low nutrient status

was adequate for I. pseudacorus to continue its growth almost on every sub plot irrespective of low and high nutrition regime.

The survival value of F. ulmaria. can also be appreciated both in terms of fertilized and unfertilized plots. It can be seen from table V that the percentage survival of F. ulmaria. is highest on fertilized soil (76.5 - 79.4%) compared to unfertilized soil (47.9 - 48.9%). In case of I. pseudacorus low nutrition had also a marked effect on the survival but the effect was to such an extent that on unfertilized soil the percentage survival was higher (67.8 - 68.5%) compared to F. ulmaria. (47.9. - 48.9%). It can be inferred that I. pseudacorus is more tolerant to the stringency of mineral nutrition and can make an adequate growth with time. The lowest survival of I. pseudacorus. in a fertilized plot with a pure strand of the seedlings could be accounted for the elimination of plants due to some biotic factors.

Table V.

Treatments	No. of seedlings sown/sub plot	F. ulmaria		I. pseudacorus	
		no. of seedlings survived	Percentage survival	no. of seedlings survived	Percentage survival
Fertilized Soil	Intra-specific 196	150	76.5%	108	55.2%
	Inter-specific 98	78	79.4%	84	85.1
Unfertilized soil	Intra-specific 196	94	47.9%	133	67.8
	Inter-specific 98	48	48.9%	67	68.5

Corrigenda of page 151

Apart from the survival value, performance of species can also be interpreted in terms of dry weight gain during the 5 months spring and summer growth period. It is evident from table VI that F. ulmaria could not make a viable growth in the plots with unfertilized plots and there was a many time greater dry weight found in the plots with fertilizer treatment. This finding gives further weight to the conclusion that this species is very much intolerant to the lack of available nutrition of soil. In I.pseudacorus, dry weight gain can be appreciated both in fertilized and unfertilized plots.

Table VI.

Treatment	competition	F. ulmaria		I. pseudacorus	
		Total * weight of the survived seedlings	Mean weight* per plant	Total weight* of survived seedling	Mean Weight per plant
Fertilized soil	Intra-specific	99450.0	663.0	89650.0	830.0
	Inter-specific	19100.0	244.8	131800.0	1569.0
Un-fertilized soil	Intra-specific	6533.3	69.5	191150.0	1437.2
	Inter-specific	3645.9	75.9	54900.0	819.4

* weight expressed in mgs.

The root/shoot ratio which has been calculated from the individual dry weight of roots and shoots from a single plot shows also many attributes of the competence of species in response to low and high nutrition status of soil. It can be seen in table VII.

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The root/shoot ration which has been calculated from the individual dry weight of roots and shoots from a single plot shows also many attributes of the competence of species in response to low and high nutrition status of soil. It can be seen in table VII.

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that where both species were growing independently they show a highest root/shoot ratio with the fertilizer treatment compared to other plots with or without competition. However, with F. ulmaria compared to I. pseudacorus has the highest values with all the plots. In this species proportionally high root formation against the shoot is the factor which may be attributed to its intrinsic pattern of growth. This has been discussed earlier in the foregoing pages.

Table VII.

Treatment	Competition	F. ulmaria Root* d.wt.	F. ulmaria Shoot* d.wt.	F. ulmaria Root/ Shoot	I. pseudacorus Root* d.wt.	I. pseudacorus Shoot* d.wt.	I. pseudacorus Root/ Shoot
Fertilized Soil	Intra-Specific	500.33	162.66	3.07	349.53	480.55	0.72
	Inter-Specific	162.82	82.05	1.98	523.80	1045.23	0.50
Unfertilized soil	Intra-Specific	51.75	17.74	2.91	325.18	1112.03	0.29
	Inter-Specific	56.14	19.79	2.83	228.35	591.04	0.38

* weight expressed in mgs.

In both types of treatments competition in between and within the species has also a marked effect on survival and yield. It should be pointed out (table V.) that where the species were grown together (Interspecific competition) either with fertilized or unfertilized plots the percentage survival was higher for I.pseudacorus indicating its dominance over F.ulmaria. It can also be seen that higher values of percentage survival in this species is directly proportional to the gain of dry weight both in fertilized or unfertilized soil (table VII).

that where both species were growing independantly they show a highest root/shoot ratio with the fertilizer treatment compared to other plots with or without competition. However, with F. ulmaria compared to I. pseudacorus has the highest values with all the plots. In this species proportionally high root formation against the shoot is the factor which may be attributed to its intrinsic pattern of growth. This has been discussed earlier in the foregoing pages.

Table VII.

		F. ulmaria			I. pseudacorus		
Treatment	Competition	Root* d.wt.	Shoot* d. wt.	Root/ Shoot	Root* d.wt.	Shoot* d. wt.	Root/ Shoot.
Fertilized Soil	Intra-Specific	75.05	24.4	3.07	37.75	51.9	0.72
	Inter-Specific	12.7	6.4	2.9	44.0	37.8	0.29
Unfertilized soil	Intra-Specific	4.86	1.66	2.0	43.25	147.9	0.52
	Inter-Specific	2.69	0.95	2.8	15.3	59.6	0.38

*weight expressed in mgs.

In both types of treatments competition in between and within the species has also a marked effect on survival and yield. It should be pointed out (table V.) that where the species were grown together (Interspecific competition) either with fertilized or unfertilized plats the percentage survival was higher for I. pseudacorus indicating its dominance over F. ulmaria. It can also be seen that higher values of percentage survival in this species is directly proportional to the gain of dry weight per plant both in fertilized or unfertilized soil (table VII).

It seems probably that the cohabitation of I.pseudacorus, not only affected the survival of F. ulmaria but also decreased the weight considerably. It can be said, where the two species compete together, I. pseudacorus tends to be more dominant in eliminating the seedling establishment of F.ulmaria particularly when there is a lack of available nutritients in the soil. This is probably one of the reaons why F. ulmaria is absent from the sites of I. pseudacorus growing in a poor nutrition regime.

CHAPTER VII
GENERAL DISCUSSION AND CONCLUSIONS

General Discussion & Conclusions.

In the foregoing pages, results discussed individually shows some attributes of the speices investigated, which make it possible to evaluate and elucidate the role of both internal and external factors in determining the ecological and geographical distribution of these species. Plants occupying different habitats and ecological niches are morphological and physiological expression of the relationship of their gene complex and its environments itself the interaction of variable factors. Therefore in an autecological study of a particular species, the task is to discover the internal as well as the external factors interacting most powerfully with the organism. It is therefore, not claimed that each and every factor has been taken into account, but rather that factors most important in determining the distribution of the species have been selected and discussed.

Seed size and dispersal mechanism.

The species differ markedly in their seed size. The seeds of *I. pseudacorus* despite their large size and weight can be easily carried to the far distant sites of running streams, rivers, fens etc. This ready dispersal and its tolerance to low nutrient status enables rapid colonizations of a large range of new sites. The small seed size of *F. ulmaria* together with its large nutrient requirements for establishment and its poor dispersal mechanism tend to limit the rate of its spread and confine it to sites of high nutrient status.

Seed dormancy and germination

Both species have dormancy mechanism in their seeds which necessitate overwintering before germination. Thus the after-ripening of the seeds which takes place before the approach of spring ensures a viable seedling growth during summer period of the year. Seeds of I. pseudacorus after shedding, either remain buried in the mud or settle to the bottom of the water, where possibly the germination inhibitors are either washed out or converted into growth promotors. Soil micro-organism may also play some part in destroying the seed coat thus increasing oxygen tension.

Germination & Temperature.

Difference between the species can also be accounted for the differences in temperature tolerance of the seeds. However, the differential germination response to light and darkness is also enough to allow seeds of the species to germinate at different sites or time. The narrow temperature range for the germination of the seeds of F.ulmaria. suggests in part for its restricted distribution in the colder parts of the northern hemisphere. With I. pseudacorus highest germination capacity between the range of 25° - 30°C shows that the germination in this species may occur even at high temperature of the year and permit a greater southernly range of distribution.

Growth form and vegetative spread.

The dispersive mechanisms of rhizome and aerial shoot of the species appears to be of considerable importance in determining

the exploitation of area. Thus an efficent dispersive vegetative propagation of the species become more advantageous in a rapid colonization of the suitable sites. Winter buds along the length of the extended rhizome of F. ulmaria may give rise to new plants from year to year. I. pseudacorus also has the capability but the shorter rhizomatous growth restricts the new shoots appearing to near the same spot from year to year.

Growth pattern and light intensity.

Both species are shade tolerant and can make viable growth under a range of light regimes. The species exhibits a marked adaptive ability by increasing their leaf surface with the reduction of light intensity. This compensating mechanism operating in the leaves appears to be more efficient in F. ulmaria. so that almost the same dry weight is achieved at all the radiation level. This appears to be more important in accounting the distribution of these species in certain woodlands where F.ulmaria may be quite active whilst I. pseudacorus in the same situation appears to be more or less static.

In evaluating the ecological role of the species with respect to radiation differences several parameters of growth shows many attributes; for instance the difference in the distribution of gross production into various morphological catogories of the plants appears to be important in explaining the different growth pattern of species with associated changes in the environment. The results discussed earlier shows than in F. ulmaria associated changes in environment brings about some positive advantages on the survival and gross morphology.

At the time of establishment of the seedlings which have glabrous leaves develops a high degree of hariness with time, showing its xeromorphic characteristics in association with xeric environment which follows. The nature of xeromorphy in this species had been questioned several years ago by Yapp (1912). He while questioning the xeromorphy in this species seems to be unsccuesful in relating the xeromorphy of this kind with environment and the peculiar intrinsic pattern of growth. Such xerophytic adaptation is not exhibited by I. pseudacorus. The pattern of growth in this species, however follows an increment in the assimilates at the expense of roots. The simple root system in this species probably be related to its type of habitat, which are either waterlogged or muddy soild and suitable for the proper anchorage of the developing roots. The difference in habit of each species also seems to be important in determining the type of habitat they occupy and the parameter discussed appears to be the most practical approach in accounting the differences in both habit and habitat of the species.

Vegetative growth and daylength.

The seedlings of both species are unable to overwinter the long cold season with its living leaf surface exposed . During this period probably the daylength as well as temperature decrease considerably. At the approach of spring when temperature and daylengths are favourable the dormant vegetative buds at the apices of rhizome emerges out of the ground and in no time develops into large rosettes (F. ulmaria), or tall blades (I. pseudacorus). The maximun period of leaf area exposure following germination or perennation in the two speacies is therfore achieved in spring established seedlings and/or plants. The result either of daylength and / or

photoperiod experiments showed that a maximum surface area is achieved only in long photoperiods.

Growth and nutrition.

The species were found to be different in their nutrition requirements and in part to the soil acidity. The field experiment showed that F. ulmaria is more sensitive to stringency of nutrition and calcium. The elimination of F. ulmaria from the sites of acid peat soil has been reported by Clapham et al (1952) and the experiment confirms the possibility of F.ulmaria being restricted to lime-rich soil. In the two species concerned here, this species appears to be highly calcicolous in nature. I. psuedacorus. on the contrary appears to be ~~tolerant to both low and high mineral status of soil~~ less exacting in its mineral requirements and therefore ~~is more ambiguient in its~~ has a wide range of distribution, being found from ~~an~~ high to low nutrient status and acid to base rich soils.

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APPENDIX

Temperature: 15°C — primary data On Germination and Temperature — F. ulmaria

Table 1.

LIGHT				DARKNESS		
No. of observations	Days from start of sowing	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.	No. of observations	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.
-	4	-	-	1	25	6.25
-	5	-	-	2	72	18.0
-	6	-	-	3	95	23.75
-	7	-	-	4	105	26.25
1	8	1	0.25	5	110	27.5
2	9	10	2.5	6	116	29.0
3	10	26	6.5	7	121	30.25
4	11	37	9.25	8	125	31.25
5	12	60	15.0	9	131	32.75
6	13	69	17.25	10	132	33.0
7	14	76	19.0	11	134	33.5
8	15	85	21.25	12	135	33.75
9	16	90	22.25	13	139	34.75
10	17	96	24.0	14	140	35.0
11	18	101	25.25	15	144	36.0
12	19	102	25.5	-	-	-
13	20	104	26.0	-	-	-
14	21	105	26.25	-	-	-
15	22	109	27.25	-	-	-
16	23	112	28.0	-	-	-
17	24	117	29.25	-	-	-
18	25	119	29.75	-	-	-
19	26	120	30.0	-	-	-

Temperature: 20°C F. ulmaria

Mean no. or percent seedlings/day to the total no. of seeds sown

LIGHT				DARKNESS		
No. of observations	Days from start of sowing	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.	No. of observations	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.
-	4	-	-	1	57	14.25
-	5	-	-	2	88	22.0
1	6	16	4.0	3	124	31.0
2	7	30	7.5	4	132	33.0
3	8	63	15.75	5	143	35.75
4	9	79	19.75	6	148	37.0
5	10	91	22.75	7	152	38.0
6	11	104	26.0	8	156	39.0
7	12	110	27.5	9	167	41.75
8	13	119	29.75	10	169	42.25
9	14	126	31.5	11	173	43.25
10	15	133	33.25	12	177	44.25
11	16	141	35.25	13	178	44.5
12	17	150	37.5	14	178	44.5
13	18	158	39.5	15	179	44.75
14	19	166	41.5	-	-	-
15	20	172	43.0	-	-	-
16	21	179	44.75	-	-	-
17	22	184	46.0	-	-	-
18	23	186	46.5	-	-	-
19	24	190	47.5	-	-	-
20	25	192	48.0	-	-	-
21	26	193	48.25	-	-	-
22	27	194	48.5	-	-	-
23	28	196	49.0	-	-	-
24	29	196	49.0	-	-	-
25	30	299	49.75	-	-	-

Temperature: 30°C

F. ulmaria

LIGHT				DARKNESS		
No. of observations	Days from start of sowing	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.	No. of observations	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep
-	4	-	-	1	13	3.25
-	5	-	-	2	14	3.25
1	6	16	4.0	3	18	4.5
2	7	24	6.0	4	22	5.25
3	8	33	8.25	5	23	5.75
4	9	37	9.25	6	27	6.75
5	10	41	10.25	7	31	7.75
6	11	44	11.0	8	33	8.25
7	12	58	14.5	9	39	9.75
8	13	65	16.25	10	40	10.0
9	14	72	18.0	11	41	10.25
10	15	79	19.75	12	42	10.5
11	16	86	21.5	13	44	11.0
12	17	89	22.25	14	45	11.25
13	18	93	23.5	15	46	11.5
14	19	94	23.5	16	47	11.75
15	20	94	23.5	17	48	12.0
16	21	98	24.5	-	-	-
17	22	101	25.25	-	-	-
18	23	104	26.0	-	-	-
19	24	105	26.25	-	-	-
20	25	108	27.0	-	-	-
21	26	110	27.5	-	-	-
22	27	111	27.75	-	-	-
23	28	114	28.5	-	-	-
24	29	115	28.75	-	-	-
25	30	116	29.0	-	-	-

Temperature: 25°C F. ulmaria

LIGHT				DARKNESS		
No. of observations	Days from start of sowing	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.	No. of observations	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep
-	4	-	-	1	64	16.0
-	5	-	-	2	72	18.0
1	6	25	6.25	3	90	22.25
2	7	38	9.5	4	95	23.75
3	8	55	13.75	5	98	24.5
4	9	65	16.25	6	104	26.0
5	10	74	18.5	7	112	28.0
6	11	81	20.25	8	118	29.5
7	12	96	24.0	9	121	30.25
8	13	111	27.75	10	122	30.5
9	14	123	30.75	11	122	30.5
10	15	137	34.25	12	122	30.5
11	16	150	37.5	13	123	30.75
12	17	158	39.5	14	124	31.0
13	18	172	43.0	15	125	31.25
14	19	182	45.5	-	-	-
15	20	190	47.5	-	-	-
16	21	198	49.5	-	-	-
17	22	207	51.75	-	-	-
18	23	212	53.0	-	-	-
19	24	217	54.25	-	-	-
20	25	224	56.0	-	-	-
21	26	225	56.25	-	-	-
22	27	228	57.0	-	-	-
23	28	229	57.25	-	-	-
24	29	231	57.75	-	-	-
25	30	232	58.0	-	-	-
26	31	232	58.0	-	-	-
27	32	232	58.0	-	-	-

Temperature 15°C

Table 2.

I. pseudacorus

LIGHT				DARKNESS		
No. of observations	Days from start of sowing	No. of seedlings emerged/ per total of seeds sown	Mean no. or per cent seedlings per rep.	No. of observ.	No. of seedlingsemerged /per total of seeds sown	Mean. no. or percent seedlings per rep.
1	13	2	0.5	-	-	-
2	14	2	0.5	-	-	-
3	15	5	1.25	-	-	-
4	16	6	1.5	-	-	-
5	17	7	1.75	-	-	-
6	18	7	1.75	-	-	-
7	19	7	1.75	-	-	-
8	20	11	2.75	-	-	-
9	21	14	3.5	-	-	-
10	22	17	4.25	-	-	-
11	23	18	4.5	-	-	-
12	24	20	5.0	-	-	-

Temperature: 20°C

I. pseudacorus

LIGHT				DARKNESS		
No. of observations	Days from start of sowing	No. of seedlings emerged/ per total of seeds sown	Mean no. or percent seedlings per rep.	No. of observations	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.
1	10	6.0	1.5	1	5	1.25
2	11	9	2.25	2	7	1.75
3	12	11	2.75	3	7	1.75
4	13	14	3.5	4	11	2.75
5	14	15	3.75	5	12	3.0
6	15	18	4.5	6	19	4.75
7	16	19	4.75	7	23	5.75
8	17	25	6.25	8	27	6.75
9	18	32	8.0	9	28	7.0
10	19	38	9.5	10	29	7.25
11	20	47	11.75	11	32	8.0
12	21	55	13.75	12	37	9.25
13	22	60	15.0	13	38	9.5
14	23	66	16.5	-	-	-
15	24	67	16.75	-	-	-
16	25	70	17.5	-	-	-
17	26	71	17.75	-	-	-
18	27	74	18.5	-	-	-
19	28	76	19.0	-	-	-

Temperature: 25°C

I. pseudacorus

LIGHT				DARKNESS		
No. of observations	Days from start of sowing	No. of seedlings emerged/ per total of seeds sown	Mean no. or percent seedlings per rep.	No. of observations	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.
1	8	3	0.75	-	-	-
2	9	4	1.0	-	-	-
3	10	20	5.0	1	4	1.0
4	11	27	6.75	2	5	1.25
5	12	32	8.0	3	5	1.25
6	13	38	9.5	4	14	3.5
7	14	45	11.25	5	22	5.5
8	15	62	15.5	6	27	6.75
9	16	80	20.0	7	37	9.25
10	17	93	23.25	8	47	11.75
11	18	105	26.25	9	58	14.5
12	19	116	29.0	10	68	17.0
13	20	131	32.75	11	73	18.25
14	21	146	36.5	12	77	19.25
15	22	152	38.0	13	80	20.0
16	23	164	41.0	14	82	20.5
17	24	173	43.25	15	83	20.75
18	25	184	46.0	16	85	21.25

cont'd...

Temperature: 25°C — I. pseudacorus

19	26	191	47.75	17	86	21.5
20	27	195	48.75	18	88	22.0
21	28	206	51.5	19	90	22.5
22	29	217	54.25	20	91	22.75
23	30	225	56.25	-	-	-
24	31	231	57.75	-	-	-
25	32	237	59.25	-	-	-
26	33	242	60.5	-	-	-
27	34	246	61.5	-	-	-
28	35	252	63.0	-	-	-
29	36	257	64.25	-	-	-
30	37	261	65.25	-	-	-
31	38	262	65.5	-	-	-
32	39	263	65.75	-	-	-
33	40	266	66.50	-	-	-
34	41	266	66.5	-	-	-
35	42	267	66.75	-	-	-
36	43	270	67½5	-	-	-

cont'd...

Temperature: 25°C — I. pseudacorus

37	44	270	67.5	-	-	-
38	45	270	67.5	-	-	-
39	46	271	67.75	-	-	-
40	47	271	67.75	-	-	-
41	48	273	68.25	-	-	-
42	49	275	68.75	-	-	-
43	50	276	69.0	-	-	-
44	51	277	69.25	-	-	-
45	52	279	69.75	-	-	-
46	53	280	70.0	-	-	-
47	54	283	70.75	-	-	-
48	55	284	71.0	-	-	-
49	56	285	71.25	-	-	-
50	57	285	71.25	-	-	-
51	58	288	72.0	-	-	-

Temperature: 30°C

Iris pseudacorus

LIGHT				DARKNESS		
No. of observations	Days from start of sewing	No. of seedlings emerged/ per total of seeds sown	Mean no. or percent seedlings per rep.	No. of observations	No. of seedlings emerged /per total of seeds sown	Mean no. or percent seedlings per rep.
1	6	6	1.5	-	-	-
2	7	6	1.5	-	-	-
3	8	12	3.0	-	-	-
4	9	24	6.0	-	-	-
5	10	36	9.0	-	-	-
6	11	47	11.75	-	-	-
7	12	63	15.75	-	-	-
8	13	72	18.0	-	-	-
9	14	82	20.5	-	-	-
10	15	105	26.25	1	4	1.0
11	16	129	32.25	2	6	1.5
12	17	143	35.75	3	9	2.25
13	18	157	39.25	4	16	4.0
14	19	175	43.75	5	27	6.75
15	20	184	46.0	6	51	12.75
16	21	193	48.25	7	63	15.75
17	22	206	51.5	8	69	17.75
18	23	216	54.0	9	76	19.0

cont'd...

Temperature: 30°C — Iris pseudacorus

19	24	216	54.0	10	80	20.0
20	25	219	54.75	11	90	22.5
21	26	223	55.75	12	98	24.5
22	27	226	56.5	13	105	26.25
23	28	229	57.25	14	112	28.0
24	29	228	57.25	15	116	29.0
25	30	231	57.75	16	121	30.25
26	31	232	58.0	17	127	31.75
27	32	235	58.75	18	131	32.75
28	33	237	59.25	19	136	34.0
29	34	240	60.0	20	142	35.5
30	35	242	60.5	21	142	35.5
31	36	242	60.5	22	143	35.75
32	37	244	61.0	23	147	36.75
33	38	-	-	24	147	36.75
-	-	-	-	25	150	37.75
-	-	-	-	26	152	38.0
-	-	-	-	27	157	38.0

cont'd...

Temperature: 30°C						Iris pseudacorus
-	-	-	-	28	162	40.5
-	-	-	-	29	164	41.0
-	-	-	-	30	166	41.5
-	-	-	-	31	171	42.75
-	-	-	-	32	173	43.25
-	-	-	-	33	174	43.5
-	-	-	-	34	176	44.0
-	-	-	-	35	179	44.75
-	-	-	-	36	181	45.25
-	-	-	-	37	183	45.75
-	-	-	-	38	185	46.25
-	-	-	-	39	185	46.25
-	-	-	-	40	186	46.5
-	-	-	-	41	187	46.75
-	-	-	-	42	187	46.75
-	-	-	-	43	188	47.0

Control (Dry Storage) F. ulmaria

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds	Mean no. of percent seedlings per replicate
1	6	3	0.75
2	7	5	1.25
3	8	8	2.0
4	9	11	2.75
5	10	15	3.75
6	11	18	4.5
7	12	21	5.25
8	13	24	6.0
9	14	25	6.25
10	15	28	7.0
11	16	31	7.75
12	17	32	8.0
13	18	36	8.75
14	19	36	9.0
15	20	36	9.0
16	21	38	9.5
17	22	41	10.25
18	23	41	10.25
19	24	42	10.5
20	25	42	10.5
21	26	44	11.0
22	27	46	11.5
23	28	46	11.5
24	29	46	11.5
25	30	46	11.5
26	31	48	12.0
27	32	48	12.0
28	33	48	12.0
29	34	48	12.0
30	35	50	12.5
31	36	50	12.5
32	37	50	12.5
33	38	53	13.25
34	39	53	13.25
35	40	55	13.75
36	41	56	14.0
37	42	58	14.5

Table 3.

PRIMARY DATA

Germination after various time periods of stratification of seeds.

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds sown	Mean no. of percent seedlings per replicate
1	8	1.75	3.5
2	9	3.0	6.0
3	10	3.5	7.0
4	11	4.25	8.5
5	12	5.0	10.0
6	13	5.25	10.5
7	14	5.25	10.5
8	15	5.25	10.5
9	16	5.25	10.5
10	17	5.5	11.0
11	18	5.5	11.0
12	19	5.5	11.0
13	20	5.5	11.0
14	21	5.75	11.5
15	22	5.75	11.5
16	23	5.75	11.5
17	24	6.00	12.0
18	25	6.25	12.5
19	26	6.25	12.5
20	27	6.25	12.5
21	28	6.25	12.5
22	29	6.5	13.0
23	30	6.5	13.0
24	31	6.5	13.0
25	32	6.75	13.5

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds sown	Mean No. of percent seedlings per replicate
1	6	25	6.25
2	7	38	9.5
3	8	55	13.75
4	9	65	16.25
5	10	74	18.5
6	11	81	20.25
7	12	96	24.0
8	13	111	27.75
9	14	123	30.75
10	15	137	34.25
11	16	150	37.5
12	17	158	39.5
13	18	172	43.0
14	19	182	45.5
15	20	190	47.5
16	21	198	49.5
17	22	207	51.75
18	23	212	53.0
19	24	217	54.25
20	25	224	56.0
21	26	225	56.25
22	27	228	57.0
23	28	229	57.25
24	29	232	58.0
25	30	232	58.0
26	31	232	58.0
27	32	232	58.0

Control (dry storage) I. pseudacorus

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds sown	Mean no. of percent seedlings per replicate
1	7	4	1
2	8	7	1.75
3	9	7	1.75
4	10	7	1.75
5	11	9	2.25
6	12	9	2.25
7	13	9	2.25
8	14	9	2.25
9	15	10	2.5
10	16	11	2.75
11	17	12	3.0
12	18	14	3.5
13	19	14	3.5
14	20	15	3.75
15	21	15	3.75
16	22	17	4.25
17	23	18	4.5
18	24	19	4.75
19	25	19	4.75
20	26	19	4.75
21	27	19	4.75
22	28	19	4.75
23	29	20	5.0
24	30	20	5.0
25	31	20	5.0
26	32	21	5.25
27	33	21	5.25
28	34	21	5.25
29	35	21	5.25
30	36	22	5.5
31	37	22	5.5
32	38	22	5.5
33	39	23	5.75
34	40	23	5.75
35	41	23	5.75
36	42	24	6.0

Table 4.

One month — I. pseudacorus

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds shown	Mean No. of percent seedlings per replicate
1	7	1	0.25
2	8	7	1.75
3	9	8	2.0
4	10	12	3.0
5	11	15	3.75
6	12	19	4.75
7	13	23	5.75
8	14	27	6.75
9	15	34	8.5
10	16	41	10.25
11	17	43	10.75
12	18	44	11.0
13	19	46	11.5
14	20	49	12.25
15	21	50	12.5
16	22	52	13.0
17	23	54	13.5
18	24	56	14.0
19	25	57	14.25
20	26	60	15.0
21	27	60	15.0
22	28	61	15.25
23	29	62	15.5
24	30	64	16.0
25	31	65	16.25
26	32	66	16.5
27	33	69	17.25
28	34	70	17.75
29	35	73	18.25
30	36	73	18.25
30	37	75	18.75
31	38	75	18.75
32	39	76	19.0

One month — I. pseudacorus

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds sown	Mean no. of percent seedlings per replicate.
33	40	77	19.25
34	41	79	19.75
35	42	80	20.0
36	43	82	20.5
37	44	83	20.75
38	45	83	20.75

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds sown	Mean No. of percent seedlings per replicate
1	7	77	19.25
2	8	97	24.25
3	9	121	30.25
4	10	137	34.25
5	11	153	38.25
6	12	165	41.25
7	13	181	45.25
8	14	195	48.25
9	15	202	50.5
10	16	212	53.0
11	17	224	56.0
12	18	233	58.25
13	19	244	61.0
14	20	255	63.75
15	21	268	67.0
16	22	270	67.5
17	23	270	67.5
18	24	276	69.0
19	25	279	69.75
20	26	281	70.25
21	27	284	21.0
22	28	288	72.0
23	29	292	73.0
24	30	295	73.75
25	31	300	75.0
26	32	303	75.75
27	33	306	76.5
28	34	311	77.75
29	35	316	79.0
30	36	318	79.5
31	37	320	80.0
32	38	320	80.0

One Year (12 months) — I. pseudacorus

No. of observations	Days from start of sowing	No. of seedlings emerged/per total of seeds sown	Mean no. of percent seedlings per replicate
1	3	164	41.0
2	4	186	46.5
3	5	207	51.75
4	6	224	56.0
5	7	241	60.25
6	8	253	63.25
7	9	258	64.5
8	10	260	65.0
9	11	263	65.75
10	12	264	66.0
11	13	265	66.25
12	14	266	66.5
13	15	267	66.75
14	16	267	66.75
15	17	268	67.0
16	18	268	67.0

Nakes seeds (Light)

EMERGED RADICLE				EMERGED COLEOPTILE		
No. of observations	Days from start of sowing	No. of radicles emerged/per total of seeds sown	Mean no. or percent radicles per replicate	No. of observations	No. of coleoptiles emerged/per total of seeds sown	Mean no. or percent coleoptiles per replicate
1	4	107	25.75	-	-	-
2	5	207	51.75	-	-	-
3	6	307	36.75	-	-	-
4	7	336	84.0	-	-	-
5	8	357	89.25	-	-	-
6	9	361	90.25	1	24	6
7	10	365	91.25	2	43	10.75
8	11	370	92.25	3	60	15.0
9	12	373	93.25	4	86	21.5
10	13	377	94.25	5	113	28.25
-	14	-	-	6	126	31.5
-	15	-	-	7	140	35.0
-	16	-	-	8	150	37.5
-	17	-	-	9	161	40.25
-	18	-	-	10	170	42.5
-	19	-	-	11	178	44.5
-	20	-	-	12	182	45.5
-	21	-	-	13	184	46.0

Table 5.

PRIMARY DATA
Germination inhibitors of I. pseudacorus.

Nakes Seeds (Dark)

EMERGED RADICLE				EMERGED COLEOPTILE		
No. of observations	Days from start of sowing	No. of radicles emerged/per total of seeds sown	Mean no. or percent radicles per replicate	No. of observations	No. of coleoptiles emerged/per total of seeds sown	Mean no. or percent coleoptile per replicate
1	4	140	35.0	-	-	-
2	5	198	49.5	-	-	-
3	6	256	64.0	-	-	-
4	7	309	77.25	-	-	-
5	8	333	83.25	-	-	-
6	9	334	83.5	1	23	5.75
7	10	334	83.5	2	29	7.25
8	11	335	83.75	3	56	14.0
-	12	-	-	4	75	18.75
-	13	-	-	5	90	22.5
-	14	-	-	6	96	24.0
-	15	-	-	7	101	25.25
-	16	-	-	8	108	27.0
-	17	-	-	9	113	28.25
-	18	-	-	10	117	29.25
-	19	-	-	11	120	30.0
-	20	-	-	12	122	30.5
-	21	-	-	13	123	30.75

Table 6.

Naked Seeds

EMERGED RADICLE				EMERGED COLEOPTILE		
No. of observations	Days from start of sewing	No. of radicles emerged/ per total of seeds sown	Mean no. or percent radicles per replicate	No. of observations	No. of coleoptiles emerged/per total of seeds sown	Mean no. or percent coleoptiles per replicate
1	3	10	2.5	-	-	-
2	4	38	9.5	-	-	-
3	5	66	16.5	-	-	-
4	6	96	24.0	-	-	-
5	7	144	26.0	-	-	-
6	8	173	43.25	-	-	-
7	9	199	49.75	-	-	-
8	10	222	55.5	-	-	-
9	11	239	59.75	-	-	-
10	12	250	62.5	1	7	1.75
11	13	265	66.25	2	11	2.75
12	14	268	67.0	3	16	4.0
13	15	269	67.25	4	19	4.75
14	16	269	67.25	5	22	5.5
15	17	270	67.75	6	27	6.75

Intact Seed Coat

EMERGED RADICLE				EMERGED COLEOPTILE		
No. of observations	Days from start of sowing	No. of radicles emerged/ per total of seeds sown	Mean no. or percent radicles per replicate	No. of observations	No. of coleoptiles emerged/per total of seeds sown	Mean no. or percent coleoptiles per replicate
1	6	8	2	1	2	0.5
2	7	13	3.25	2	4	1.0
3	8	32	8.0	3	8	2.0
4	9	50	12.5	4	17	4.25
5	10	74	18.5	5	31	7.75
6	11	82	20.5	6	39	9.75
7	12	90	22.5	7	49	12.25
8	13	96	24.0	8	61	15.25
9	14	103	25.75	9	70	17.5
10	15	109	27.25	10	78	19.5
11	16	113	28.25	11	86	21.5
12	17	118	29.5	12	92	23.0
13	18	119	29.75	13	96	24.0
14	19	121	30.25	14	98	24.5
15	20	125	31.25	15	100	25.0
16	21	125	31.25	16	104	26.0
17	22	127	31.75	17	106	26.5
18	23	129	32.25	18	108	27.0
	24	131	32.75	19	110	27.5
	25	-	-	20	111	27.75
	26	-	-	21	113	28.25
	27	-	-	22	114	28.5

Naked seeds + Seed coat

EMERGED RADICLE				EMERGED COLEOPTILE		
No. of observations	Days from start of sowing	No. of radicles emerged/ per total of seeds sown	Mean no. or percent radicles per replicate	No. of observations	No. of coleoptiles emerged/per total of seeds sown	Mean no. or percent coleoptiles per replicates
1	3	13.0	3.25	-	-	-
2	4	90.0	22.75	-	-	-
3	5	133.0	33.25	-	-	-
4	6	170.0	44.5	-	-	-
5	7	243.0	61.5	-	-	-
6	8	559.0	64.75	-	-	-
7	9	270.0	67.5	-	-	-
8	10	280.0	70.0	-	-	-
9	11	296.0	74.0	1	120	30
10	12	302.0	75.5	2	154	38.5
11	13	305.0	76.25	3	186	46.5
-	14	-	-	4	209	52.25
-	15	-	-	5	223	55.75
-	16	-	-	6	234	58.5
-	17	-	-	7	247	61.75
-	18	-	-	8	256	64.0
-	19	-	-	9	264	66.0
-	20	-	-	10	268	6.0

PRIMARY DATA

Table 7 . Total leaf area and dry weight of different parts of the plant at successive harvests, and varying levels of light intensity

Filipendula ulmaria — 100% light intensity

Harvest No.	Mean leaf area cm^2	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	0.5	0.8	0.2	1.0	0.7	1.7
1	20.21	58.8	28.2	87.0	56.0	143.0
2	43.35	160.9	68.6	229.5	264.0	493.5
3	115.06	337.3	148.9	486.2	832.8	1319.0
4	263.25	706.4	294.9	1000.6	1544.5	2545.1
5	436.25	1164.0	607.6	1771.6	3327.4	5099.0

Filipendula ulmaria — 70% light intensity

Harvest No.	Mean leaf area cm^2	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	0.5	0.8	0.2	1.0	0.7	1.7
1	23.92	53.1	20.9	79.0	60.1	139.2
2	53.0	143.7	58.6	202.3	230.9	433.2
3	126.6	298.9	132.3	431.2	638.4	1069.6
4	286.25	603.9	269.5	873.4	1187.6	2061.0
5	515.725	1298.2	720.3	2018.5	3021.2	5039.7

Filipendula ulmaria

40% light intensity

Harvest No.	Mean leaf area cm^2	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	0.5	0.80	0.2	1.0	0.7	1.7
1	24.63	47.9	19.5	67.4	34.1	101.5
2	75.45	153.8	62.8	216.6	160.1	376.7
3	200.0	334.1	144.0	478.1	508,8	986.9
4	402.75	697.4	331.5	1028.9	892.5	1921.4
5	748.675	1503.3	835.6	2338.9	2652.3	4991.2

PRIMARY DATA

Table 8 . Leaf area and dry weight of different parts of the plant at successive harvests and varying levels of light intensity

Iris pseudacorus — 100% light intensity

Harvest No.	Mean leaf area cm^2	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	2.1	7.2	2.1	9.3	5.1	14.4
1	36.62	166.1	15.6	181.7	110.9	292.6
2	62.7	325.6	39.5	365.1	249.2	614.3
3	130.0	671.4	83.0	754.4	534.4	1388.8
4	249.0	1211.2	150.7	1361.9	852.1	2214.0
5	396.91	2346.1	393.0	2739.1	1603.6	4342.7

Iris pseudacorus

70% light intensity

Harvest No.	Mean leaf area cm^2	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	2.1	7.2	2.1	9.3	5.1	14.4
1	37.65	158.9	16.1	175.0	93.6	268.6
2	63.25	290.1	31.6	321.7	193.4	515.1
3	152.2	582.8	74.0	656.8	411.9	1068.7
4	260.25	1037.4	111.4	1148.8	684.4	1833.2
5	449.1	2167.1	303.8	2470.9	1375.6	3846.5

Iris pseudacorus

40% light intensity

Harvest No.	Mean leaf area cm^2	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	2.1	7.2	2.1	9.3	5.1	14.4
1	40.72	147.8	10.7	158.5	69.5	228.0
2	71.45	283.5	25.2	310.7	159.7	470.4
3	171.6	560.5	54.0	614.5	309.1	923.6
4	286.12	1100.0	90.3	1190.3	453.5	1643.8
5	526.0	2361.5	281.8	2643.3	1075.2	3718.5

Corrigenda of page 202.

Table 9. Mean unit leaf rate

on the basis of leaf area $\overline{E}_{LA}$ = (mg/cm^2/week)

on the basis of leaf weight $\overline{E}_{W}$ = (mg/mg/week)

F. ulmaria

Days	Harvest intervals	100%		70%		40%	
		$\overline{E}_{W}$	$\overline{E}_{LA}$	$\overline{E}_{W}$	$\overline{E}_{LA}$	$\overline{E}_{W}$	$\overline{E}_{LA}$
25	Initial-1	2.870	4.642	2.877	4.079	2.422	2.907
15	1-2	1.617	5.394	1.442	3.753	1.400	2.829
15	2-3	1.610	5.241	1.400	3.510	1.239	2.228
15	3-4	1.141	3.197	1.064	2.366	0.882	1.510
20	4-5	0.973	2.610	1.148	2.673	1.022	1.925
		I. pseudacorus					
25	Initial-1	1.533	6.450	1.449	5.778	1.281	4.591
15	1-2	0.630	3.095	0.525	2.330	0.539	2.069
15	2-3	0.765	3.915	0.609	2.550	0.399	1.849
15	3-4	0.343	2.103	0.448	1.771	0.413	1.501
20	4-5	0.427	2.349	0.455	2.035	0.434	1.843

Table 9 . Mean unit leaf rate

on the basis of leaf area $\overline{E}_{LA}$ = (mgs/cm^2/week)

on the basis of leaf weight $\overline{EL}_W$ = (mgs/mg/week)

in between the successive harvests and at various levels of light intensity

Filipendula ulmaria

Harvest intervals	100%		70%		40%	
	$\overline{E}_W$	$\overline{E}_{LA}$	$\overline{E}_W$	$\overline{E}_{LA}$	$\overline{E}_W$	$\overline{E}_{LA}$
Initial to 1	10.47	26.55	10.28	22.71	8.67	16.12
1 -2	3.465	11.56	3.11	8.042	3.006	6.056
2 -3	3.461	11.20	3.009	7.608	2.659	4.774
3 -4	2.454	4.85	2.287	5.072	1.892	3.225
4 -5	2.787	11.06	3.283	7.638	2.925	4.37

Iris pseudacorus

Initial to 1	5.493	23.03	5.184	20.64	4.592	16.40
1 - 2	1.357	6.633	1.132	4.976	1.159	4.435
2 - 3	1.621	8.390	1.319	5.467	0.866	3.961
3 - 4	0.7491	4.507	0.969	3.796	0.899	3.666
4 - 5	1.237	6.714	1.314	3.811	1.256	5.266

Table 10 . Specific Leaf area

(cm^2/mg)

of successive harvests and varying levels of light intensity

Filipendula ulmaria

Harvest No.	100%	70%	40%
Initial	0.625	0.625	0.625
1	0.343	0.411	0.514
2	0.269	0.368	0.490
3	0.341	0.426	0.598
4	0.372	0.474	0.577
5	0.374	0.397	0.498

Iris pseudacorus

Initial	0.290	0.290	0.290
1	0.220	0.236	0.275
2	0.192	0.218	0.250
3	0.193	0.261	0.280
4	0.205	0.250	0.260
5	0.168	0.207	0.222

Table 11 . Leaf area ratio

(cm^2/mg)

under varying levels of light intensity

Filipendula ulmaria

Harvest No.	100%	70%	40%
Initial	0.294	0.294	0.294
1	0.140	0.178	0.242
2	0.0878	0.122	0.200
3	0.0872	0.118	0.202
4	0.103	0.134	0.209
5	0.085	0.102	0.149

Iris pseudacorus

Initial	0.137	0.137	0.137
1	0.125	0.140	0.178
2	0.102	0.122	0.151
3	0.993	0.142	0.185
4	0.112	0.141	0.174
5	0.091	0.116	0.141

Table 12. Mean relative growth rate (mgs/mgs/week)

$$\overline{R} = (\log_e \overline{W}_2 - \log_e \overline{W}_1)$$

E.ulmaria

Harvest No.	100% $\log_e \overline{W}$	100% $\overline{R}$	70% $\log_e \overline{W}$	70% $\overline{R}$	40% $\log_e \overline{W}$	40% $\overline{R}$
Initial	+0.53063	-	+0.53063	-	+0.53063	-
1	4.96284	4.43221	4.86060	4.32997	4.62002	4.09039
2	6.20152	5.67089	6.07120	5.54057	5.93146	5.40083
3	7.18311	6.65242	6.97542	6.44479	6.89467	6.36404
4	7.84168	7.31105	7.63095	7.10032	7.56269	7.03206
5	8.53205	8.00142	8.52517	7.99454	8.51550	7.98487
*± S.E	*(± 0.008)		*(± 0.008)		*(± 0.008)	
			I. pseudacorus			
Initial	2.66723	-	2.66723	-	2.66723	-
1	5.68018	3.01295	5.59472	2.92749	5.42935	2.76219
2	6.42049	3.75326	6.24436	3.57713	6.15358	3.48635
3	7.16162	4.49439	6.97426	4.30703	6.82872	4.16149
4	7.70247	5.03524	7.51372	4.84649	7.40492	4.73769
5	8.37632	5.70909	8.25493	5.58770	8.22149	5.55426
*± S.E	(± 0.039)		*(± 0.039)		*(± 0.039)	

Table 13 Mean relative rate of leaf area increase (cm^2/cm^2/week)

$$\overline{R}\, L_A = (\log_e L_{A_1} - \log_e L_{A_2})$$

at successive harvests and varying levels of light intensity

Filipendula ulmaria

Harvest No.	100% $\log_e \overline{L}_A$	100% $\overline{R}\, L_A$	70% $\log_e \overline{L}_A$	70% $\overline{R}\, L_A$	40% $\log_e \overline{L}_A$	40% $\overline{R}\, L_A$
Initial	0.69315	-	0.69315	-	0.69315	-
1	3.00617	3.69932	3.17473	3.86788	3.20398	3.89713
2	3.76930	4.46246	3.97029	4.66344	4.32347	5.01667
3	4.74237	5.43552	4.84023	5.53338	5.29832	5.99147
4	5.32935	6.02250	5.65669	6.34984	5.99832	6.69147
5	6.07810 *(± 0.037)	6.77125	6.24514 *(± 0.037)	6.93829	6.61832 *(± 0.037)	7.31147

*± S.E

Iris pseudacorus

Harvest No.	$\log_e \overline{L}_A$	$\overline{R}\, L_A$	$\log_e \overline{L}_A$	$\overline{R}\, L_A$	$\log_e \overline{L}_A$	$\overline{R}\, L_A$
Initial	0.74194	-	0.74194	-	0.74194	-
1	3.60057	2.85863	3.62834	2.88640	3.70672	2.96478
2	4.13836	3.39642	4.14709	3.40513	4.26900	3.52806
3	4.86753	4.12557	5.02521	4.28327	5.14458	4.40264
4	5.51745 *(± 0.034)	4.77551	5.56182 *(± 0.034)	4.81988	5.65635 *(± 0.034)	4.91441

*± S.E

Table 14 . Ratio of mean relative growth rate to the mean relative rate of leaf area increase mg/cm^2/week at successive harvests and varying levels of light intensity

$$\alpha = \frac{\bar{R}}{\bar{R}_{LA}}$$

Filipendula ulmaria

Harvest No.	100%	70%	40%
Ini -1	1.19	1.11	1.04
Ini -2	1.27	1.18	1.07
Ini -3	1.22	1.20	1.07
Ini -4	1.21	1.11	1.05
Ini -5	1.18	1.15	1.09

Iris pseudacorus

Ini -1	1.05	1.01	0.93
Ini -2	1.10	1.05	0.98
Ini -3	1.08	1.05	0.94
Ini -4	1.05	1.00	0.96
Ini -5	1.08	1.00	1.00

Table 15 . Leaf/Shoot ratio

at successive harvests and varying levels of light intensity

Filipendula ulmaria

Harvest No.	100%	70%	40%
Initial	0.80	0.80	0.80
1	0.67	0.73	0.71
2	0.70	0.71	0.71
3	0.69	0.69	0.69
4	0.70	0.69	0.67
5	0.65	0.64	0.64

Iris pseudacorus

Initial	0.77	0.77	0.77
1	0.74	0.90	0.93
2	0.89	0.90	0.91
3	0.72	0.88	0.91
4	0.88	0.92	0.92
5	0.84	0.87	0.89

Table 16 . Root/Shoot ratio

at successive harvests and varying levels of light intensity

Filipendula ulmaria

Harvest No.	100%	70%	40%
Initial	0.70	0.70	0.70
1	0.643	0.762	0.505
2	1.150	1.141	0.739
3	1.712	1.480	1.064
4	1.543	1.350	0.867
5	1.878	1.495	1.133

Iris pseudacorus

Initial	0.53	0.53	0.53
1	0.66	0.53	0.43
2	0.68	0.60	0.51
3	0.70	0.62	0.50
4	0.62	0.59	0.38
5	0.58	0.55	0.40

Table 17 . Root/Leaf area ratio

(mgs/cm^2)

at successive harvests and varying levels of light intensity

Filipendula ulmaria

Harvest No.	100%	70%	40%
Initial	1.4	1.4	1.4
1	2.77	2.51	1.38
2	6.08	4.35	2.12
3	7.23	5.04	2.54
4	5.87	4.14	2.21
5	7.62	5.85	3.54

Iris pseudacorus

Initial	2.42	2.42	2.42
1	3.02	2.49	1.76
2	3.97	3.05	2.23
3	4.11	2.04	1.80
4	3.41	2.62	1.59
5	4.42	3.06	2.04

Table 18 . Root/leaf ratio

at successive harvests and varying levels of light intensity

Filipendula ulmaria

Harvest No.	100%	70%	40%
Initial	0.87	0.87	0.87
1	0.98	1.03	0.71
2	1.64	1.60	1.04
3	2.46	2.13	1.51
4	2.18	1.96	1.28
5	2.86	2.32	1.76

Iris pseudacorus

Initial	0.70	0.70	0.70
1	0.67	0.58	0.46
2	0.76	0.66	0.56
3	0.79	0.70	0.55
4	0.70	0.65	0.41
5	0.68	0.63	0.45

Table 19. Percentage proportion of the distribution of gross production into various parts of the plant at successive harvests and varying levels of light intensity.

Filipendula ulmaria

Harvest No.	100% light intensity			70% light intensity			40% light intensity		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
Initial	47.0	11.7	41.1	47.0	11.7	41.1	47.0	11.7	41.1
1	41.1	19.7	39.4	41.7	15.0	43.3	47.1	19.2	33.5
2	32.6	13.9	53.4	33.1	13.5	53.3	40.8	16.6	42.5
3	25.5	11.2	63.1	27.9	12.3	59.6	33.8	14.5	51.5
4	27.7	11.5	60.6	29.3	13.0	57.6	36.2	17.2	46.4
5	22.8	11.9	65.2	25.7	14.2	59.9	30.1	16.7	53.1

Table 20. Percentage proportion of the distribution of gross production into various parts of the plant at successive harvests and varying levels of light intensity.

Iris pseudacorus

Harvest No.	100% light intensity			70% light intensity			40% light intensity		
	Leaf	Stem	Root	Leaf	Stem	Root	Leaf	Stem	Root
Initial	50.0	14.5	35.4	50.0	14.5	35.4	50.0	14.5	35.4
1	56.7	5.3	37.9	59.1	5.9	34.8	64.8	4.6	30.4
2	53.0	~~34.5~~ 6.05	40.5	56.3	6.1	37.5	60.69	5.35	33.9
3	52.09	7.0	40.83	54.5	6.9	38.5	60.68	5.84	33.4
4	54.7	6.8	38.4	56.5	6.07	37.3	66.91	5.49	27.5
5	54.0	9.5	36.5	56.3	7.8	35.7	63.5	7.5	28.1

PRIMARY DATA

Table 21.a. Leaf area and dry weight of different parts of the plants at successive harvests and two levels of photoperiod

9 Hours continuous light — Filipendula ulmaria

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	0.50	0.8	0.2	1.0	0.7	1.7
1	6.47	15.3	3.6	18.9	11.7	30.6
2	26.03	55.0	15.1	70.1	59.2	129.3
3	69.10	150.6	49.1	199.7	178.6	378.3
4	185.50	360.0	130.2	490.2	312.2	802.4
5	334.75	645.4	293.7	939.1	719.4	1730.5

9 Hours intermittent light

Filipendula ulmaria

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	0.50	0.8	0.2	1.0	0.7	1.7
1	9.06	19.8	4.4	24.2	11.4	35.6
2	42.21	84.5	24.8	109.3	83.2	192.5
3	102.55	172.1	48.8	220.9	134.8	355.7
4	265.56	417.5	174.3	591.8	292.4	884.2
5	428.75	728.7	387.1	1115.8	474.2	1590.0

PRIMARY DATA

Table 21b. Leaf area and dry weight of different parts of the plants at successive harvests and two levels of photoperiod

9 Hours continuous light — Iris pseudacorus

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Rotal
Initial	2.10	7.2	2.1	9.3	5.1	14.4
1	17.87	63.8	4.9	68.7	25.4	94.1
2	38.96	146.2	13.6	159.8	84.9	244.7
3	62.90	246.4	23.6	270.0	182.4	450.4
4	151.50	559.9	47.6	607.5	230.8	838.3
5	308.62	1054.0	96.9	1074.4	510.3	1662.1

9 Hours discontinuous light

Iris pseudacorus

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	2.10	7.2	2.1	9.3	5.1	14.4
1	26.50	84.2	4.8	89.0	32.2	121.2
2	73.30	232.1	16.2	248.3	116.9	365.2
3	151.00	505.4	28.8	534.2	208.9	741.7
4	314.37	896.8	42.8	939.6	268.3	1207.9
5	390.00	1296.3	72.5	1368.8	390.0	1759.2

Table 22 . Leaf area ratio

(cm^2/mg)

at successive harvests and 9 hours
photoperiod of sontinuous and intermittent light

	Filipendula ulmaria		Iris pseudacorus	
Harvest No.	9 hours continuous light	9 hours intermittent light	9 hours continuous light	9 hours intermittent light
Initial	0.294	0.294	0.145	0.145
1	0.209	0.224	0.190	0.218
2	0.201	0.219	0.159	0.200
3	0.182	0.288	0.139	0.203
4	0.231	0.300	0.180	0.260
5	0.193	0.269	0.185	0.221

Table 23. Mean relative growth rate (mgs/mgs/week)

$$\overline{R} = (\log_e \overline{W}_2 - \log_e \overline{W}_1)$$

at successive harvests and 9 hours photoperiods
continuous and intermittent light

Harvests No.	F. ulmaria 9 hours continuous light				I. pseudacorus 9 hours continuous light			
	$\log_e W$	$\overline{R}$	$\log_e W$	$\overline{R}$	$\log_e W$	$\overline{R}$	$\log_e W$	$\overline{R}$
Initial	0.53063	-	0.53063	-	2.66723	-	2.66723	-
1	3.42100	2.55878	3.57235	2.89702	4.54436	2.14008	4.79744	2.53520
2	4.86218	3.95138	5.26010	4.43581	5.49921	2.92009	5.89990	3.55262
3	5.93570	4.92870	5.87353	5.32303	6.00389	3.39961	6.60800	4.27534
4	6.68761	6.15698	6.78469	6.27477	6.68898	4.27853	7.09418	5.00841
5	7.45587	6.92524	7.37149	6.75461	7.41577	4.99305	7.47019	5.22420

Table 24. Mean relative rate of leaf area increase (cm^2/cm^2/week)

$$\bar{R}_{LA} = (\log_e LA_2 - \log_e LA_1)$$

at successive harvests and 9 hours photoperiod
continuous and intermittent light

Harvest No.	F. ulmaria				I. pseudacorus			
	9 hours continuous light		9 hours intermittent light		9 hours continuous light		9 hours intermittent light	
	$\log_e LA$	$\bar{R}_{LA}$	$\log_e LA$	$\bar{R}_{LA}$	$\log_e LA$	$\bar{R}LA$	$\log_e LA$	$\bar{R}_{LA}$
Initial	0.69315	-	0.69315	-	0.74194	-	0.74194	-
1	1.86563	2.89037	2.20387	3.04172	3.27714	1.87713	2.88202	2.13021
2	3.25823	4.33155	3.74266	4.72947	4.29456	2.83198	3.66203	3.23267
3	4.23555	5.40507	4.62988	5.34290	5.01728	3.33666	4.14155	3.94077
4	5.22303	6.15698	5.58162	6.25406	5.75035	4.02175	5.02049	4.32695
5	5.81294	6.92524	6.06146	6.84086	5.96614	4.74854	5.73499	4.80296

Table 25. . Ratio of mean relative growth rate to the mean relative rate of leaf area increase (mgs/cm^2/week) at successive harvests and 9 hours photoperiod of continuous and intermittent light

	Filipendula ulmaria		Iris pseudacorus	
Harvest intervals	9 hours continuous light	9 hours intermittent light	9 hours continuous light	9 hours intermittent light
Ini -1	1.12	1.04	0.87	0.84
Ini -2	1.09	1.06	0.92	0.90
Ini -3	1.09	1.00	0.98	0.96
Ini -4	1.04	0.83	0.93	0.86
Ini -5	1.05	1.01	0.95	0.91

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Table 26. Mean unit leaf rate (mg/cm^2/week)

Days	Harvest Intervals	F. ulmaria		I. pseudacorus	
		9 hours continous light	9 hours intermittent light	9 hours continous light	9 hours intermittent light
20	Ini - 1	1.986	2.094	3.785	3.883
35	In - 2	2.564	2.789	3.648	3.500
50	Ini - 3	2.722	1.911	3.413	2.923
65	Ini - 4	2.111	1.752	2.541	2.061
80	Ini - 5	2.317	1.742	2.348	2.056
20	I - 1	1.986	2.094	3.785	3.883
15	1 - 2	3.279	3.398	2.599	2.475
15	2 - 3	2.636	1.119	1.922	1.634
15	3 - 4	1.678	1.439	1.795	0.976
15	4 - 5	1.711	0.968	1.748	0.734

Table 26 . Mean unit leaf rate (mgs/cm^2/week) at successive harvests and 9 hours photoperiod of continuous and intermittent light

	Filipendula ulmaria		Iris pseudacorus	
Harvest intervals	9 hours continuous light	9 hours intermittent light	9 hours continuous light	9 hours intermittent light
Ini - 1	3.63	3.66	5.33	3.60
Ini - 2	19.74	20.29	18.24	17.50
Ini - 3	27.08	18.46	24.37	20.88
Ini - 4	25.63	20.89	23.59	19.14
Ini - 5	26.05	25.05	26.83	23.49

Table 27 . Root/Shoot ratio

at successive harvests and 9 hours

photoperiod of continuous and intermittent light

	Filipendula ulmaria		Iris pseudacorus	
Harvest No.	9 hours continuous light	9 hours intermittent light	9 hours continuous light	9 hours intermittent light
Initial	0.700	0.700	0.548	0.548
1	0.619	0.471	0.369	0.361
2	0.844	0.761	0.531	0.470
3	0.894	0.612	0.675	0.391
4	0.650	0.494	0.379	0.285
5	0.766	0.424	0.484	0.279

PRIMARY DATA

Table 20.a Leaf area and dry weight of different parts of the plants at successive harvests and two levels of daylength.

9 hours daylength — Filipendula ulmaria

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	0.50	C.8	0.2	1.0	0.7	1.7
1	5.28	11.7	3.7	15.4	14.4	29.8
2	23.22	54.9	14.2	69.1	56.6	125.7
3	70.16	175.9	48.3	224.2	145.2	369.4
4	165.70	430.2	136.9	567.1	425.2	992.3
5	266.00	629.0	218.1	847.1	988.2	1835.5

16 hours daylength

Filipendula ulmaria

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	0.50	0.8	0.2	1.0	0.7	1.7
1	17.81	49.0	13.7	62.7	62.4	125.1
2	54.44	186.7	54.1	240.8	335.4	576.2
3	176.50	624.5	198.9	823.4	1182.5	2005.9
4	350.40	1171.5	459.7	1632.2	2070.3	3701.5
5	550.00	1872.2	808.0	2680.2	3750.5	6430.7

PRIMARY DATA

Table 28 b. Leaf area and dry weight of different parts of the plants at successive harvests and two levels of daylength.

9 hours daylength — Iris pseudacorus.

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	2.10	7.2	2.1	9.3	5.1	14.4
1	40.44	168.0	17.1	185.1	113.1	298.2
2	55.90	229.9	24.8	254.7	151.8	406.5
3	113.71	458.4	56.7	515.1	415.8	930.5
4	298.4	1081.6	102.9	1184.5	748.0	1932.5
5	492.4	1938.4	175.4	2113.8	996.6	3110.4

16 hours daylength

Iris pseudacorus

Harvest No.	Mean leaf area cm^2/plant	Mean dry weight in mgs. Leaf	Stem	Shoot	Root	Total
Initial	2.10	7.2	2.1	9.3	5.1	14.4
1	55.61	335.1	34.4	369.5	226.2	595.7
2	108.77	741.0	69.7	810.7	444.2	1254.9
3	277.77	1430.0	144.2	1574.2	826.8	2401.0
4	469.00	2829.2	266.5	3095.7	1465.9	4561.6
5	729.00	4714.2	593.6	5307.8	2796.0	8103.8

Table 29 . Leaf area ratio

(cm^2/mg)

at successive harvests and daylength

of 9 and 16 hours

	Filipendula ulmaria		Iris pseudacorus	
Harvest No.	9 hours daylength	16 hours daylength	9 hours daylength	16 hours daylength
Initial	0.29	0.29	0.14	0.14
1	0.17	0.14	0.13	0.09
2	0.10	0.09	0.13	0.08
3	0.18	0.08	0.12	0.11
4	0.16	0.09	0.15	0.10
5	0.14	0.08	0.15	0.08

Table 30. Mean relative growth rate (mgs/mgs/week) at successive harvests and daylengths of 9 and 16 hours

Harvest interval	F. ulmaria				I. pseudacorus			
	9 hours daylength		16 hrs. daylength		9 hrs. daylength		16 hrs. daylength	
	$\log_e \overline{W}$	$\overline{R}$	$\log_e \overline{W}$	$\overline{R}$	$\log_e \overline{W}$	$\overline{R}$	$\log_e \overline{W}$	$\overline{R}$
Initial	0.53063	-	0.53063	-	2.66723	-	2.66723	-
1	3.39451	2.86388	4.82832	4.29769	5.70713	3.03390	6.38856	3.72143
2	4.83388	4.30325	6.35639	5.82576	6.00760	3.34037	7.13090	4.46367
3	5.91190	5.38127	7.60377	7.07314	6.83573	4.16850	7.78323	5.11600
4	6.90003	6.36940	8.21649	7.68586	7.56133	4.89410	8.42500	5.75785
5	7.51507	6.9844	8.76881	8.23818	8.04238	5.37515	8.99962	6.33239

Table 31 . Mean relative rate of leaf area increase (cm^2/cm^2/week)

$$\bar{R}_{LA} = (\log_e LA^2 - \log_e LA^1)$$

at successive harvests and daylengths of 9 and 16 hours

Harvest No.	F. ulmaria				I. pseudacorus			
	9 hours daylength		16 hrs. daylength		9 hours daylength		16 hrs. daylength	
	$\log_e LA$	$\bar{R}_{LA}$	$\log_e LA$	$\bar{R}_{LA}$	$\log_e LA$	$\bar{R}_{LA}$	$\log_e LA$	$\bar{R}_{LA}$
Initial	0.69315	-	0.69315	-	0.74194	-	0.74194	-
1	1.65345	2.34660	2.87976	3.57291	3.70982	2.96788	4.01836	3.27642
2	3.14930	3.74245	3.99673	4.68988	4.02356	3.28162	4.68681	3.94487
3	4.25063	4.94378	5.17332	5.76647	4.63185	3.88991	5.62402	4.88208
4	5.10894	5.80209	6.04643	6.73958	5.69843	4.95639	6.15060	5.40866
5	5.58349	6.27664	6.30992	7.00307	6.19929	5.45735	6.59167	5.84973

Table 32 . Ratio of mean relative growth rate to the mean relative rate of leaf area increase (mgs/cm^2/week) at successive harvests and daylengths of 9 and 16 hours.

	Filipendula ulmaria		Iris pseudacorus	
Harvest interval	9 hours daylength	16 hours daylength	9 hours daylength	16 hours daylength
Ini -1	1.22	1.20	1.02	1.13
Ini -2	1.15	1.24	1.01	1.13
Ini -3	1.09	1.22	1.07	1.04
Ini -4	1.06	1.14	0.98	1.06
Ini -5	1.11	1.17	0.98	1.08

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Table 33. Mean unit leaf rate (mg /cm^2/week)

Days	Harvest intervals	F. ulmaria		I. pseudacorus	
		9 hours daylength	16 hours daylength	9 hours daylength	16 hours daylength
20	Ini-1	1.997	5.455	7.663	12.457
35	Ini-2	2.676	7.037	4.783	9.180
50	Ini-3	2.629	7.142	4.587	5.920
65	Ini-4	2.852	5.882	3.455	5.672
80	Ini-5	2.955	5.750	3.015	5.696
20	Ini-1	1.997	5.455	7.663	12.457
15	1 - 2	3.694	6.421	1.058	3.882
15	2 - 3	2.679	6.429	3.003	2.967
15	3 - 4	2.616	3.120	2.442	2.761
15	4 - 5	1.856	2.876	1.419	2.804

Table 33 . Mean unit leaf rate (mgs/cm^2/week) at successive harvests and daylengths of 9 and 16 hours

	Filipendula ulmaria		Iris pseudacorus	
Harvest intervals	9 hours daylength	16 hours daylength	9 hours daylength	16 hours daylength
Ini -1	13.79	35.72	21.90	36.67
Ini -2	20.87	49.96	23.90	45.87
Ini -3	26.09	66.80	31.92	44.03
Ini -4	34.79	71.26	32.08	52.20
Ini -5	43.35	81.93	34.46	57.05

Table 34 . Root/Shoot ratio at successive harvests and daylength of 9 and 16 hours

Harvest No.	F. ulmaria		I. pseudacorus	
	9 hours daylength	16 hours daylength	9 hours daylength	16 hours daylength
Initial	0.70	0.70	0.548	0.548
1	0.934	0.995	0.615	0.612
2	0.818	1.39	0.595	0.547
3	0.647	1.43	0.807	0.525
4	0.749	1.26	0.631	0.473
5	0.160	1.39	0.471	0.592