GROWTH AND MORPHOGENESIS OF SUN AND SHADE PLANTS

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STELLINGEN

1. Voor de voortgang van het oecofysiologisch onderzoek naar de effekten van de faktor licht zijn klimaatruimten met ver-rood licht van hoge intensiteit onmisbaar.

2. Het is van groot belang experimenten met sterk in groeisnelheid uiteenlopende objecten periodiek te oogsten, zodat niet alleen even oude, maar ook even grote planten vergeleken kunnen worden.

3. Distributiediagrammen vormen een sterk onderschat hulpmiddel bij de groeianalyse.

4. De maximum relatieve groeisnelheid 'R-max' in het model van Grime & Hunt is geen reëel optredende groeisnelheid en is daarom niet bruikbaar als soortskenmerk.

   Grime, J.P. & R. Hunt (1975): Relative growth rate: its range and adative significance in a local flora. Journal of Ecology 63: 393-422.

5. Het toeschrijven van verschillen in morfologie tussen planten in een kas en planten in een klimaatkamer aan het verschil in lichtintensiteit alleen is absurd en leidt tot onzinnige conclusies

   Tan, G-Y., Tan, W-K. & P.D. Walton (1978): Effects of temperature and irradiance on seedling growth of smooth bromegrass. Crop Science 18: 133-136.

6. Het handhaven van de bladgroei in een verlaagde lichtintensiteit gaat niet ten koste van de stengelgroei.

   Smith, H. (1982): Light quality, photoperception and plant strategy. Annual Review of Plant Physiology 33: 481-518.

7. De methode van Ingestad voor het aanbrengen van een groeibeperkende nutrientenvoorziening is niet geschikt om te onderzoeken hoe snel een plant kan groeien bij een bepaalde beperking en is daarom van weinig waarde voor het oecologisch onderzoek.

   Ingestad, T. (1982): Relative addition rate and external concentration: driving variables used in plant nutrition research. Plant, Cell and Environment 5: 443-453.

8. De conclusie dat geen interactie optreedt tussen de effekten van lichtintensiteit en ammoniumaanbod op de groei van mais is misleidend wanneer daar niet expliciet bij vermeld wordt dat de proefplanten niet reageerden op een verandering van het ammoniumaanbod.

   Chan, W-T. & A.F. McKenzie (1971): Effects of light intensity and nitrogen level and source on growth of corn in a controlled environment. Plant and Soil 35: 173-178.

9. Een ten opzichte van optimaal gegroeide planten verminderde hoeveelheid organisch gebonden stikstof per plant in bij een sub-optimale nitraatvoorziening gegroeide planten is onvoldoende argument voor de veronderstelling dat het nog in deze planten aanwezige nitraat niet voor reductie beschikbaar is.

   Clement, C.R., L.H.P. Jones & M. Hopper (1979): Uptake of nitrogen from flowing nutrient solution: effect of terminated and intermittent nitrate supplies. In: E.J. Hewitt & C.V. Cutting (editors): Nitrate assimilation of plants. pp: 123-134.

10. De in mijn onderzoek gevonden nitraatgehalten van bij sub-optimale nitraatvoorziening en lage lichtintensiteit gegroeide planten geven aan dat een verantwoorde kasteelt van potentieel nitraatrijke groenten in de winter praktisch onmogelijk geacht moet worden.

11. De voorwaardelijke financiering van wetenschappelijk onderzoek zal leiden tot een onverantwoorde trendgevoeligheid in de wetenschap.

12. Dat de overheid niet bereid is haar 'pro deo werkers' te verzekeren voor ongevallen en wettelijke aansprakelijkheid in de werksfeer is een goed voorbeeld van het huidige denken over arbeidsverhoudingen en rechtspositie.

13. Wanneer de vraag 'functional equilibrium: sense or nonsense' niet eenduidig positief beantwoord kan worden loopt het functioneel evenwicht gevaar door ons 'no nonsense' kabinet wegbezuinigd te worden.

    Brouwer, R. (1983): Functional equilibrium: sense or nonsense. Symposium Fysiologische en oecologische aspecten van het functioneel evenwicht tussen de bovengrondse delen en het wortelsysteem. Utrecht, 7 april 1983.

W.J. Corré   Wageningen, 6 januari 1984

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des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen

The investigation was carried out at the department of Vegetation Science, Plant Ecology and Weed Science and the department of Plant Physiological Research of the Agricultural University of Wageningen, The Netherlands

achter iedere deur die wij open doen

trekt de natuur een andere weer dicht

en zo blijft zij verborgen

nooit wordt er meer

dan een tip van de sluier opgelicht

vrij naar Boudewijn de Groot

ABSTRACT

A number of species of sun and shade plants in the vegetative phase were grown in different light intensities, different light qualities (r/fr ratio) and different combinations of light intensity and nutrient supply. Sun and shade species were also grown at various plant densities and in interspecific competition in different light intensities and qualities. All the species examined responded to light intensity strongly, and in very much the same way. Sun species generally responded differently than shade species to a low red/far-re ratio: their stem extension increased markedly and their dark respiration rate was higher. The shade species generally responded similarly, but to a lesser degree. Interactions were recorded between the effects of light intensity and the effects of nutrient supply when nitrate supply was limiting and also when phosphate supply was limiting. To ensure that its limiting effect did not depend on plant size, the nitrate, or phosphate, was supplied in a high concentration intermittently and therefore exponential growth occurred in all combinations of light intensity and nutrient supply. When competing with shade species in higher light intensities, the sun species definitely had greater competitive abilities than their competitors. In lower light intensities the competitive ability of a species seemed to depend more on its weight at the beginning of the experiment. The formation of weaker stems in sun species, however, could be an important disadvantage for these species when competing in lower light intensities, especially when the red/far-red ratio is also low, as occurs in natural shade. It can be concluded that the responses to the red/far-red ratio are crucial in the explanation of the habitat preferences of sun and shade species. Responses to the light intensity may play a supplementary role, but systematic differences between sun and shade species in this respect were not observed.

CONTENTS

GENERAL INTRODUCTION

THE ECOLOGY OF SUN AND SHADE PLANTS

Exposed and shaded habitats

The reduced light intensity is, although the most striking, only one aspect of the complex of environmental changes caused by shading under a tree canopy. Temperature, air humidity, wind speed, water supply and nutrient supply are also greatly influenced by a tree canopy (Daubenmire 1974). Besides, in many shaded habitats, particularly the deciduous forests, the reduction in the light intensity has a seasonal rhythm, being less in winter and in early spring and greater in late spring, summer and autumn (Anderson 1964).

Recently, much attention has been paid to the changes in the spectral distribution of the light under a tree canopy (Morgan & Smith 1981). The changes in the light quality, of which the decrease in the red/far-red ratio seems to be the most important, correlate closely with the reduction in the light intensity (Holmes & Smith 1977).

In exposed habitats the herbaceous plants are exposed to the maximum natural light intensity. This, however, does not mean that shading cannot occur in such habitats. At soil level, the degree of shading can surely be as high as in woodlands. The difference from shaded habitats is that in exposed habitats small differences in height are associated with large differences in light interception, while in woodlands small differences in height do not show noticeable differences in light intensity (Grime 1966).

Sun and shade species

The herbaceous vegetation of exposed and shaded habitats is largely different and this enables sun and shade species to be distinguished. The usual classification into sun and shade species is based on the relative light intensities of the habitats in which the species are usually found. Ellenberg (1979) classified circa 2000 vascular plants, more or less common in Central Europe, on this basis by giving the species 'indicator values' from 1 to 9 (see also table 1). Much researc has been done over the years to elucidate the physiological backgrounds of habitat preferences by looking for differences in the properties of the plants, e.g. in carbon metabolism (e.g. Boardman 1977, Björkman 1981) and their responses to light intensity (e.g. Blackman & Wilson 1951, Evans & Hughes 1961, Loach 1970) and to light quality (e.g. Morgan & Smith 1981, Smith 1982).

Almost 20 years ago, Grime (1965, 1966) tried to fit the available evidence into a conceptual framework. This resulted in the concept of the strategies of 'shade avoidance' and 'shade tolerance'. This concept formed part of the general theory of plant strategies (Grime 1979) and was worked out more definitely after the importance of the red/far-red ratio for the physiology of the sun and shade plants was recognized (Grime 1981, Smith 1981, 1982).

Shade avoidance and shade tolerance

The strategy of shade avoidance coincides with the strategies of competitive and ruderal plants; it is intended to achieve escape from the shade. The strategy of shade tolerance is a variant of the general strategy of stress tolerance, and is aimed at enabling survival in the shade. Stress, in this connection, is understood to be present when growth is strongly limited by an environmental factor ('external stress'). A more adequate physiological definition of stress, however, is that it is a sub-optimal state of the plant ('internal stress'). The paradox in this is that stress tolerance is the ability of a species to avoid internal stress in situations with an obvious external stress, such as growing without symptoms of nutrient deficiency in an environment with a low nutrient supply.

Shade avoidance is based on the habit of a species or genotype to show rapid stem extension under shaded conditions at the expense of the development of leaf area (Grime 1965). This strategy is useful in a dense herbaceous vegetation, where small differences in height are associated with large changes in light intensity. Under a tree canopy, however, this strategy will fail: in this case, stem extension does not result in high light interception, and a long period of enhanced stem extension at the expense of all available energy will weaken the plants, resulting in a high mortality rate (Grime 1966). In herbaceous vegetations too, especially in productive habitats, many individual plants will not be able to reach the upper vegetation layers either, and mortality rates may also be high. At the population level, however, this can be compensated for by large seed production in the individuals that have indeed escaped from the low light intensity of the lower layers of the vegetation (ter Borg 1972).

Shade tolerance is based on the absence of an enhanced stem extension and on the conservative use of assimilates under shaded conditions. In this way a weakening of the stems is prevented and a higher level of energy substrate (soluble carbohydrates) can be maintained. This is the best way to survive under a tree canopy, but it also seems to be a possible strategy for survival under herbaceous vegetations. The reason that shade species are not found under such vegetations may be the competition for water and nutrients (which is very severe in such habitats) or that shade plants are not adapted to the factor (for example grazing) that also prevents trees from becoming established in the vegetation. Another reason could be that competition in herbaceous vegetations starts early in spring, whereas, at least in deciduous woodlands, at that time the herbaceous undergrowth temporarily receives a higher light intensity.

Another strategy that is successful in deciduous woodlands is a genetically fixed growth rhythm, involving the formation of seeds or storage organs and the death of the above-ground parts in late spring. This strategy is typical for woodlands herbs of early spring, such as *Scylla non-scripta* and *Ranunculus ficaria*. In this way a species can survive in woodlands without being shade tolerant. Although these species show the characteristics of shade-avoiding species, their shade avoidance in nature is based on other characteristics and to prevent confusion is probably best described as 'shade avoidance in time'. Here it also becomes clear why most shade-tolerant species are perennials (Ellenberg 1979). Perennials can use their reserves for a rapid leaf expansion in early spring, and in this way they can make better use of the short period with a high light intensity.

AIM OF THE RESEARCH

The research described in this thesis was undertaken to improve our understanding of the ecophysiological background of the specific habitat preferences of sun and shade species. To survive in a habitat, a species must be able to complete its full life cycle, from germination, via vegetative growth and flowering, to the formation of viable seeds. For reasons of time and sheer volume of data it was unpractical to study all aspects of the life cycle of the plants chosen for this research project. Therefore I concentrated on the study of plants in the vegetative stage, because there are detailed methods available for evaluating the results (e.g. classic growth analysis: Evans 1972, Hunt 1978), and because the plant strategies of shade avoidance and shade tolerance may be expected to build up to a clear distinction between sun and shade species during this stage of development (Grime 1981, Smith 1982). The use of the methods of growth analysis as the principal approach implies an integrated study of growth and morphogenesis and their physiological background. Physiological processes, such as photosynthesi and respiration were studied indirectly in relation to the morphology of the entire plant.

The actual incentive to start the research was the discovery that many plant species are able to maintain a fairly similar relative growth rate over a wide range of light intensities. This applied to the relative growth rate of the total plant dry weight (e.g. van Dobben et al. 1981) and of individual leaves and internodes (e.g. Pieters 1974, 1983). It seems that plants can compensate for a lower energy supply by means of morphogenetic adaptations. Then, since the magnitude of these adaptations did not seem to differ between sun and shade species, or was even somewhat more pronounced in sun species (Grime 1965), and since Groen (1973) and Pons (1977) had stated that it is impossible to explain the absence of sun species in shaded habitats in terms of efficiency of utilization of light energy, the question arose what different responses could then explain the habitat preferences. Here it was postulated that the responses of sun and shade species might be different if the low light intensity was coupled with a low supply of nutrients or water. Under these conditions an adequate morphogenetic adaptation is more complex, since a low light intensity leads to a low root weight ratio and a low nutrient or water supply requires a high root weight ratio, according to the functional equilibrium (Brouwer 1963). Moreover, large interactions have been found between the effects of light intensity *vis-à-vis* nutrient supply (e.g. Luxmoore & Millington 1971). It was also postulated that growth in higher plant densities and in competition with other species could elucidate the responses, since small and seemingly insignificant differences in performance may be decisive for survival in a plant community. Finally, soon after the start of the research in March 1979, the importance of the light quality as an ecological factor became clear (Morgan & Smith 1979), and therefore this factor was also studied in the experiments.

The research was principally designed to compare the growth responses of sun and shade species in the vegetative phase to varying degrees of shading as a single factor and to shading coupled with different supplies of nutrients and water. The degree of shading was separated into quantum flux density (light intensity) and red/far-red ratio (light quality), the two important, but principally different, components of shading. Initially the responses of free spaced plants were studied, but experiments with higher plant densities and interspecific competition were also carried out.

The present thesis deals with the results of 17 experiments, and is divided into 4 chapters, each of which was originally published separately.

CHAPTER I describes the effects of the light intensity as a single factor, and also includes a more detailed introduction to this subject.

CHAPTER II deals with the effects of the light quality, especially of the red/far-red ratio, and with the effects of very low light intensities.

CHAPTER III deals with the results of the experiments on the combined effects of light intensity and nutrient supply. Special attention was paid to the existing models describing the relations between the partitioning of dry matter over shoots and roots and the activities of shoots and roots, as functions of the light intensity and the nitrogen supply.

CHAPTER IV describes the effects of light intensity and light quality on plants growing in higher densities or in competition.

A fifth group of experiments, dealing with the combined effects of light intensity and water supply, did not produce usable results, because of problems in the experimental procedure. This subject will be discussed briefly in the general discussion.

SPECIES

It was decided to test a number of herbaceous sun and shade species, in order to be able to draw conclusions that could be generally applicable. Only phanerogams were chosen to represent shade plants, although the most typical shade species are cryptogams. This was for practical reasons, the most important of which was that large numbers of equally sized seedlings had to be available for reliable experiments with a species. This requires large seed production and good germination, preferably at any desired time of the year, or ample simultaneous germination in the natural habitat. For sun species a large assortmen of usable species is available, but for shade species the assortment is limited. Thus, the experiments included seven more or less shade-tolerant species that were reasonably easy to obtain and grow, and six sun species were chosen for comparison. The species that were used are listed in table 1, which also shows that the division into sun and shade species is not absolute but only gradual. With respect to the 'light figures' of Ellenberg (1979) it should be noted that these are based on the relative light intensity of the habitat in summer, and give no information about a possibly higher light intensity that a species might receive in spring. Furthermore, it is striking that the species I used are not classified as full shade species or even as shade species (light figure 1, 2 or

TABLE 1. Sun and shade species used in the different experiments

species	'light figure'	used in expts. of chapter I	II	III	IV
Plantago major	8		+		+
Galeopsis tetrahit	7	+			
Galinsoga parviflora	7	+	+	+	+
Urtica urens	7		+		+
Poa pratensis	6	+			
Polygonum lapathifolium	6		+		
Poa nemoralis	5	+			
Circaea lutetiana	4		+		+
Geum urbanum	4	+	+		+
Impatiens parviflora	4	+	+		+
Scrophularia nodosa	4	+	+		
Stachys sylvatica	4	+	+	+	+
Urtica dioica	X	+	+	+	+

'light figures': (after Ellenberg 1979)

9 full light plant , rarely receiving less than 50% relative light intensity
8 light plant , rarely receiving less than 40% relative light intensity
7 half light plant
6 (between 5 and 7)
5 half shadow plant, mostly receiving more than 10% relative light intensity
4 (between 3 and 5)
3 shadow plant , mostly receiving less than 5% relative light intensity
2 (between 1 and 3)
1 full shadow plant, often receiving less than 1% relative light intensity
X indifferent , occurring both in fully exposed and densely shaded habitats (this implies, however, a great shade tolerance)

3). The latter groups of species, however, include only a small number of species, most of which are not seed plants or do not commonly produce seed in considerable, collectable amounts.

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CHAPTER I

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GROWTH AND MORPHOGENESIS OF SUN AND SHADE PLANTS
I. THE INFLUENCE OF LIGHT INTENSITY

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SUMMARY

A number of herbacious sun and shade plants were grown at different light levels to investigate their adaptations in morphology and growth to light intensity. All species examined respond to low light intensity strongly, but very much the same. It is concluded that shade tolerance is not based on different adaptations in morphology or growth rate.

1. INTRODUCTION

For an understanding of the differences in growth between sun and shade plants carbon metabolism and morphogenesis are considered the two major fields of research. Although only one minor experiment in this study deals with photosynthesis and the principal part concerns morphogenesis, both aspects will be reviewed briefly.

1.1. Photosynthesis and respiration

It seems plausible that the ability of a plant species to tolerate shading has its origin in photosynthesis, viz. in the efficiency of the utilization of light energy. Various authors have compared photosynthesis in sun and shade species or ecotypes. It was shown that the photosynthesis per unit leaf area at high light intensities was appreciably lower in shade adapted ecotypes of *Solidago virgaurea* (BJÖRKMAN & HOLMGREN 1963), *Rumex acetosa* (BJÖRKMAN & HOLMGREN 1966) and *Solanum dulcamara* (GAUHL 1976) grown at high intensity than in sun adapted ecotypes grown in the same light intensity. On the other hand the initial slope of the rate/intensity curve of plants grown at a low light intensity was seemingly somewhat steeper in shade adapted ecotypes, at least in *Solidago virgaurea* (BJÖRKMAN & HOLMGREN 1963), but there were no significant differences in light compensation points, nor in dark respiration. Besides, a comparison of species, like *Plantago lanceolata* and *Lamium galeobdolon* (BJÖRKMAN & HOLMGREN 1966), *Calendula officinalis* and *Impatiens parviflora* (GROEN 1973) and *Cirsium palustre* and *Geum urbanum* (PONS 1977), did not show any difference in photosynthesis of plants grown in lower light intensities in favour of the shade species. Groen and Pons concluded that it is not possible to explain the absence of sun plants in shaded habitats in terms of efficiency of utilization of light energy.

Another possible difference between sun and shade plants lies in the rate of respiration in very low light intensities. MAHMOUD & GRIME (1974) showed that *Deschampsia flexuosa, Festuca ovina* and *Agrostis tenuis* (in order of decreasing shade tolerance) have only negligible differences in light compensation points and in net photosynthesis, based on whole plant dry weights, at low light intensities. However, at very low light intensities, beneath the compensation point, the respiration losses, calculated from weight losses of the whole plant during a period of four weeks, differed widely, the most shade tolerant species showing the smallest losses. The same phenomenon is shown in the experiments of WILLMOT & MOORE (1973) with *Silene alba* and *S. dioica* grown in high and low light intensity, where the shade tolerant *S. dioica* showed the smallest dark respiration rate. In addition to this, LOACH (1967) found much higher dark respiration losses in *Populus tremula* grown in a low light intensity than in some tolerant trees, and HUTCHINSON (1967) showed that seedlings of shade tolerant plant species could survive in absolute darkness much longer than sun species could, which also points to differences in respiration. Moreover a low respiration rate may lead to the maintainance of a higher soluble carbohydrate content, which gives the plant a higher resistance to fungal attack, a very important cause of death in shaded habitats (HUTCHINSON 1967; VAARTAJA 1962).

1.2. Morphogenesis

The major adaptation to a lower light intensity is the formation of thinner leaves with a higher water content, resulting in a higher specific leaf area[1]. Another important adaptation is the decrease of the root weight ratio in low light. This will have no detrimental effect on the plant because of the lower transpiration rate under low light intensities. Also important with regard to this is the increase in diffusion resistance of the leaves, due to a decrease in either number or size of stomata (GAY & HURD 1975, resp. WILSON & COOPER 1969). Mostly, the dry matter not used in root growth will benefit the stems and petioles and not the leaf blades, so this does not contribute to the relative size of the photosynthetic apparatus, although it may contribute indirectly by saving carbohydrates since root respiration in general exceeds stem respiration. On a unit weight basis the leaf weight ratio can remain constant over a wide range of light intensities.

An increasing specific leaf area combined with a generally equal leaf weight ratio leads to an increasing leaf area ratio and this relative increase in leaf area can compensate, at least partially, for a lower photosynthesis per unit leaf area. It seems possible that shade species do better in this respect than sun species. In accordance with this BLACKMAN & WILSON (1951) suggested that the shade

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[1] The expressions and the formulas of growth analysis are used in accordance with HUNT (1978).

plant should be redefined as "a species for which a reduction in light intensity causes a rapid rise in the leaf area ratio from an initial low value in full daylight". This definition, however, has never been confirmed and is even contradicted by GRIME (1965) who supposes that many sun plants even show a more pronounced adaptation to low light intensities than shade plants do. This is supported by the experiments of LOACH (1970) who found a greater adaptation of the leaf area ratio to the light intensity in the non-tolerant *Liriodendron tulipifera* than in three shade tolerant tree species, while the leaf area ratio in high light intensity was about the same in all species. In addition Jackson (cited by LOACH 1970) found that several shade tolerant tree species show much less adaptation in terms of leaf thickness than non-tolerant species do. On the other hand, there are examples of sun species that do not show a good adaptation to a low light intensity, such as *Helianthus annuus,* which shows a strongly decreasing leaf weight ratio in low light intensities (HIROI & MONSI 1963). KUROIWA et al. (1964) found a greater decrease of the leaf weight ratio in some sun plants than in the shade tolerant *Cryptotemia canadensis* var. *japonica,* but LOACH (1970), on the contrary, found a small increase in leaf weight ratio in *Liriodendron tulipifera,* and a small decrease in leaf weight ratio in the shade tolerant *Fagus grandifolia* and *Quercus rubra.*

1.3. Growth

It has been known for some time (BLACKMAN & WILSON 1951; EVANS & HUGHES 1961; HUXLEY 1967) that many plant species do show a rather constant relative growth rate over a wide range of irradiation when they are grown from the beginning in different light intensities and that this is achieved through adaptations in the morphology. VAN DOBBEN et al. (1981) confirmed this reaction in the bush bean *(Phaseolus vulgaris).* This latter study was undertaken to explain the fact that notwithstanding a similar RGR, plants grown in a lower light intensity show a retardation in growth in comparison to high light intensity plants. As expected, this retardation occurs in the phase of seedling development, before the morphological adaptations to weak light are accomplished. At light intensities under about 60 W.m^{-2} (VAN DOBBEN et al. 1981; HUNT & HALLIGAN 1981) the relative increase in leaf area cannot compensate for the lower productivity any longer, and the relative growth rate will decline. Clearly differing reactions to light intensity between sun and shade plants, with respect to the relative growth rate, were not reported.

In the present study a series of experiments was conducted to investigate the morphogenetic adaptations of a number of sun and shade species in the vegetative stage to light intensity and light quality (i.e. r/fr ratio) and the consequences of these adaptations on the relative growth rate. Special interest was directed to the effects of light intensity interacting with nutrient supply, or competition. This first paper deals with the effects of light intensity only and will be more or less an introduction to the problem.

2. MATERIALS AND METHODS

2.1. Plant materials

The following species, having a supposed increasing shade tolerance (after Ellenberg 1979), were used: *Galinsoga parviflora* Cav. (in experiment 1, 3, 4), *Urtica urens* L. (3), *Galeopsis tetrahit* L. (1), *Poa pratensis* L. (2, 3), *Poa nemoralis* L. (2, 3), *Urtica dioica* L. (3, 4), *Geum urbanum* L. (1, 3), *Impatiens parviflora* (L.) DC. (1), *Scrophularia nodosa* L. (4), and *Stachys sylvatica* L. (3). Seeds, collected from plants in their natural habitats, were germinated in a climatic room at 20°C under fluorescent light (40 W/m^2). Only *Galeopsis tetrahit* and *Impatiens parviflora* were collected as seedlings in the field.

2.2. Growth conditions and harvest procedures

In all experiments the plants were grown on an aerated nutrient solution (pH 6.5) containing 6.0 $me.l^{-1}$ NO_3^-, 0.5 $me.l^{-1}$ $H_2PO_4^-$, 3.5 $me.l^{-1}$ SO_4^{--}, 3.5 $me.l^{-1}$ K^+, 4.5 $me.l^{-1}$ Ca^{++}, 2.0 $me.l^{-1}$ Mg^{++} and the trace elements: 2.0 ppm Fe, 0.5 ppm B, 0.7 ppm Mn, 0.05 ppm Mo, 0.1 ppm Zn and 0.02 ppm Cu. The solution was changed once a week.

Experiment 1, with *Galinsoga praviflora, Galeopsis tetrahit, Impatiens parviflora* and *Geum urbanum,* was carried out in a glasshouse in May 1979. The light intensity in the glasshouse was about 65% of the natural light intensity. At noon in full sunshine about 175 $W.m^{-2}$ (400–700 nm) was measured in the glasshouse. This light level (level A) was reduced with white cheesecloth to 80% (level B), 60% (level C) and 40% (level D) respectively. The red/far red ratio was about 1.1 at all light levels. The night temperature was 20°C, the day temperature rose to about 25°C on cloudy days and sometimes to over 30°C on sunny days. In the shaded compartments the night temperature, and on sunny days also the day temperature, usually was about 2°C above the glasshouse temperature. The maximum relative humidity was about 60%, the minimum about 30%, in the shaded compartments this was about 90% and 40% respectively. These climatic differences, however, were assumed to cause no significant effect on growth (VAN DOBBEN et al. 1981). Twice a week ten plants of each species at each light level were harvested, fresh and dry weights of leaf blades, stems with petioles and roots, were recorded and leaf area and leaf thickness were measured.

Experiment 2, with *Poa pratensis* and *Poa nemoralis,* was carried out in the same glasshouse in August 1979. In this period the light intensity at level A was approximately the same as in experiment 1. The same holds for temperatures, whereas the air humidity tended to be slightly higher. The light intensity in the shaded compartments was further reduced to 65% (level B^1), 30% (level C^1) and 20% (level D^1); the red/far red ratio remained about 1.1. Every five days ten plants of both species at each light level were harvested. Since the young *Poa* plants had not yet developed a stem and had very narrow leaves, only fresh and dry weights of shoots and roots were measured.

In experiment 3 *Galinsoga parviflora, Urtica urens, Poa pratensis, Poa nemoralis, Urtica dioica, Stachys sylvatica* and *Geum urbanum* were grown in a climatic room. Here it was possible to maintain exactly equal temperatures and air humidities at all light levels, on the other hand it is impossible to reach a high light intensity. Three light levels were established: 50 $W.m^{-2}$, 25 $W.m^{-2}$ and 12.5 $W.m^{-2}$, the light source was Philips TL 33 fluorescent tubes, of which the red/far red ratio is 7.0. Daylength was 16 hours, temperature was 20°C and relative humidity was 60%. Plants were harvested every five days, measurements were made according to the procedure described for experiment 1, except for leaf area and leaf thickness, which were only measured in *Galinsoga parviflora* and *Stachys sylvatica*. In these two species internode length was also recorded.

Experiment 4, with *Galinsoga parviflora, Urtica dioica* and *Scrophularia nodosa*, was also carried out in a climatic room. Five light levels were established: 72 $W.m^{-2}$, 28 $W.m^{-2}$, 11 $W.m^{-2}$, 7 $W.m^{-2}$ and 2.5 $W.m^{-2}$. Fluorescent light (Philips TL 33) was complemented with incandescent light to lower the red/far red ratio to about 2.2. Daylength was 16 hours, day temperature was 20°C, night temperature was 15°C and relative humidity was 65% all day. The harvest procedure was as described for experiment 3, internode length was measured in all species, but leaf thickness was not measured.

3. RESULTS

3.1. Morphogenesis

The development of the leaf thickness with time is shown in *fig. 1*. All species show a good adaptation to the light intensity, the differences between species are rather small in experiment 1, in experiment 3 the adaptation in *Galinsoga parviflora* is clearly greater than it is in the shade tolerant *Stachys sylvatica*. It is remarkable that in both experiments the most shade tolerant species has the thickest leaves in lower light intensities. Since leaf thickness is hard to measure, especially in the very soft leaves of plants grown in a low light intensity, and since, within species, it appeared to be closely negatively correlated with the specific leaf area, the leaf thickness was only measured in the experiments 1 and 3. The values of the SLA of the plants of the final harvest are presented in *fig. 2*. As is expected from the leaf thickness, the increase in SLA with decreasing light intensity is in the same direction. Quantitative differences do not seem to be strongly correlated with the supposed shade character of the species. There is a tendency for shade plants even having a somewhat lower SLA.

The dry matter distribution *(fig. 3)* shows generally the same pattern for all species (except for the grasses): in a lower light intensity the root weight ratio decreases in favour of the stem weight ratio, while the leaf weight ratio remains relatively unaffected. In a very low light intensity (expt. 4, *fig. 3*) the leaf weight ratio cannot be maintained at a constant level, it is now decreasing in all species, remarkably most of all in the most shade tolerant species *(Scrophularia nodosa)*. In all species in all experiments no rhizomes or other storage organs were developed during the experimental period. In *fig. 4* the dry matter distribution of

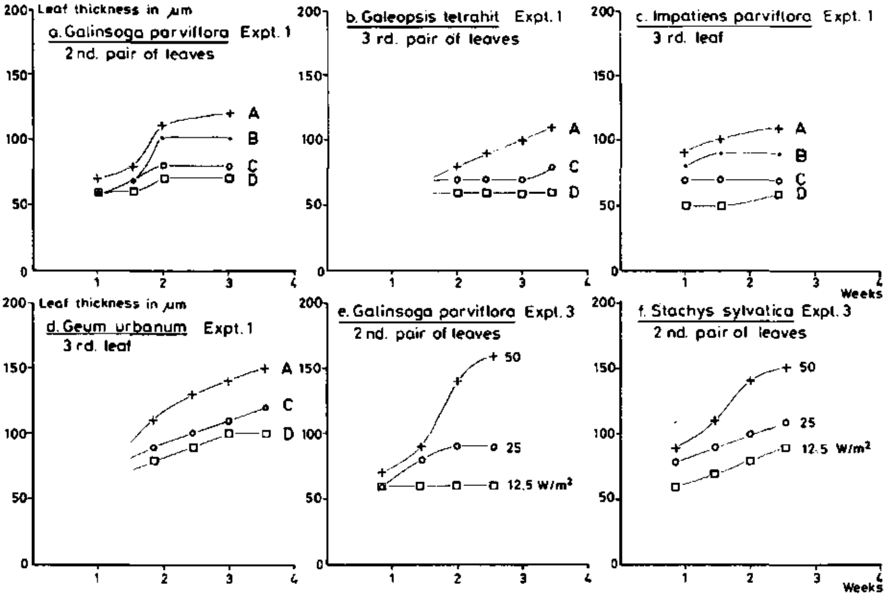

Fig. 1. Development of leaf thickness with time in different light intensities in expts. 1 and 3. Light level A = 100%; B = 80%; C = 60%; D = 40%.

Galinsoga parviflora and *Stachys sylvatica* grown at two light intensities is illustrated in distribution diagrams, in which the weights of the separate organs are plotted against total plant weight. In these diagrams a straight line indicates that the increase in weight of the organ is proportional to the increase in total plant weight. When this line is parallel to the 45° diagonal the weight ratio also remains constant. As is expected in a phase of exponential growth, the dry matter distribution is proportional over the whole growth period. The only exception is the portion that is invested in the roots of *Galinsoga parviflora*, the root weight ratio slowly decreases down to a constant value.

The product of SLA and LWR is the leaf area ratio, the relative size of the photosynthetic apparatus of the plant. Since the LWR is mostly not influenced very much by the light intensity, the increase in LAR in lower light intensities

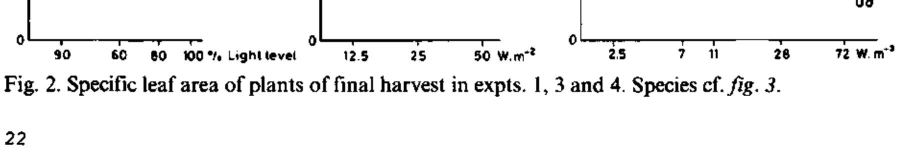

Fig. 2. Specific leaf area of plants of final harvest in expts. 1, 3 and 4. Species cf. *fig. 3*.

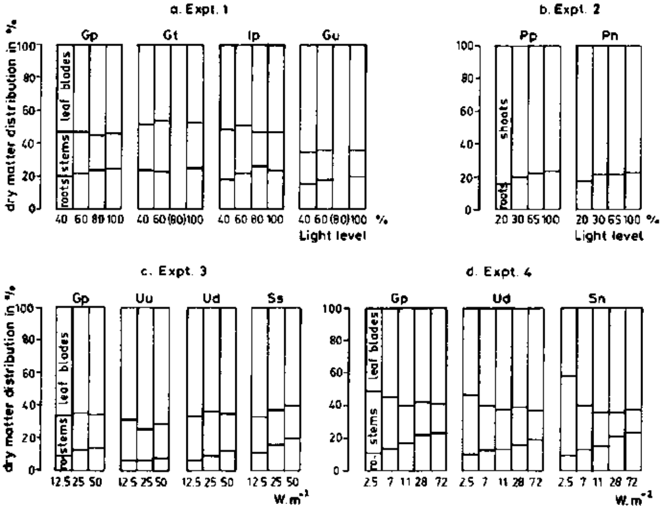

Fig. 3. Dry matter distribution of plants of final harvest in expts. 1, 2, 3 and 4. Species: Gp: *Galinsoga parviflora*, Gt: *Galeopsis tetrahit*, Gu: *Geum urbanum*, Ip: *Impatiens parviflora*, Pn: *Poa nemoralis*, Pp: *Poa pratensis*, Sn: *Scrophularia nodosa*, Ss: *Stachys sylvatica*, Ud: *Urtica dioica*, Uu: *Urtica urens*.

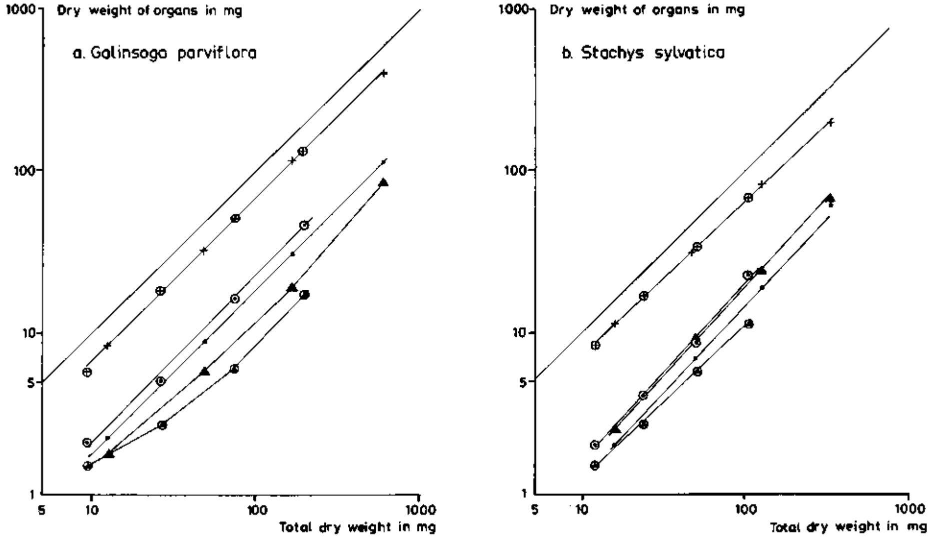

Fig. 4. Dry weight of plant organs plotted against total dry weight for two species and two light intensities in expt. 3 on logarithmic scale. + ⊕ : leaf blades, · ⊙ : stems and petioles, ▲ Ⓐ: roots; ⊕ ⊙ Ⓐ: 12.5 W.m^{-2}, + · ▲ : 50 W.m^{-2}.

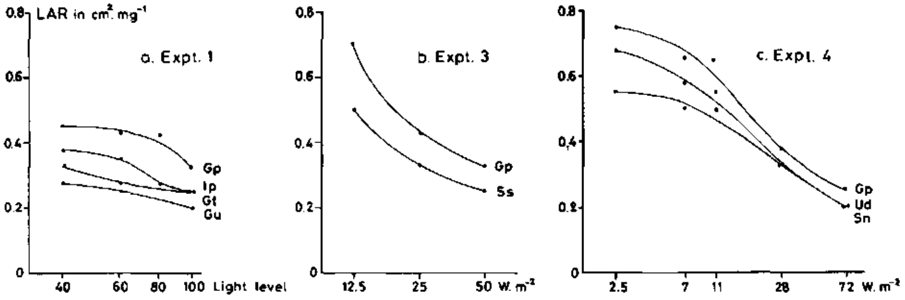

Fig. 5. Leaf area ratio of plants of final harvest in expts. 1, 3 and 4. Species cf. *fig. 3*.

will roughly follow the increase in SLA. It is quite clear that all species show very much the same trend in reaction of the LAR to the light intensity, the adaptation not depending on shade tolerance *(fig. 5)*.

The previous calculations were all made on dry weights, but the water content is also influenced by the light intensity. In a lower light intensity the dry matter content will decrease in leaves and stems. This decrease is shown for leaves in *fig. 6*. The dry matter contents of the leaves vary appreciably with species and with light intensity. There seems to be no correlation between shade tolerance and the extent of decrease in dry matter content at low light intensity. The dry

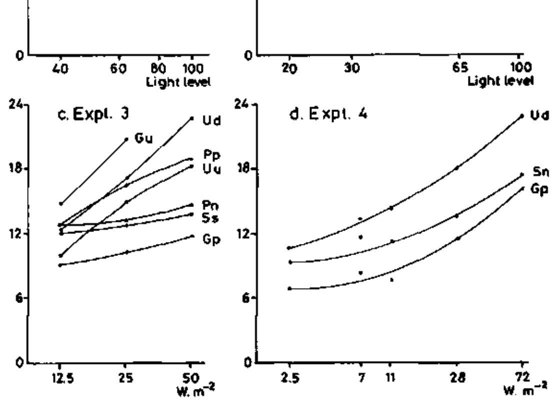

Fig. 6. Dry matter content of leaf blades of plants of final harvest in expts. 1, 2, 3 and 4. Species cf. *fig. 3*.

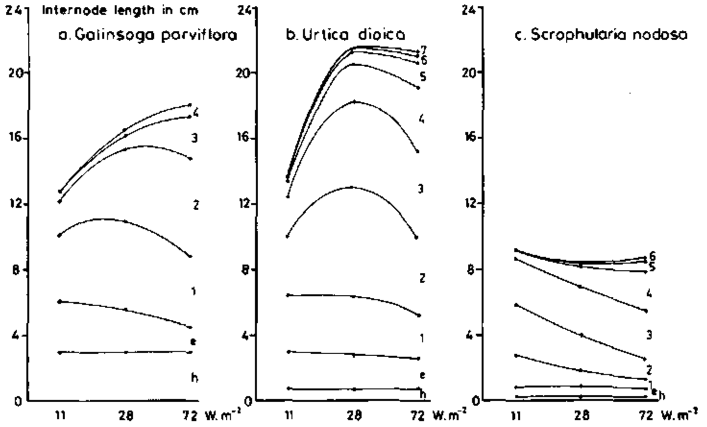

Fig. 7. Length of successive internodes of plants of final harvest in three light intensities in expt. 4. h = hypocotyl, e = epicotyl, 1, 2, ... = successive internodes.

matter content in stems and petioles, for which no data are shown, is always lower than it is in leaves, but it shows very much the same differences between species and pattern of light intensity dependence. This means that the fresh matter distribution will be different from the dry matter distribution; the fresh stem weight ratio is higher at all light intensities and the fresh root weight ratio decreases even more with decreasing light intensity than the dry root weight ratio does. However, since the species do not show any differences with respect to the water content, the fresh matter distribution cannot alter any conclusion drawn from the dry matter distribution.

The internode length is influenced by light intensity, as in shown in *fig. 7*, but probably not in a direct way. In high light intensity the lower, fully grown internodes are somewhat shorter. The upper internodes are longer because of the further state of development of the plants.

3.2. Growth

The growth is the product of a morphological character (LAR) and the net productivity (NAR) of the photosynthetic apparatus of the plant. The productivity will decrease in a lower light intensity, as is shown in *fig. 8*. The slopes of the curves do not seem to be correlated with the shade tolerance of the species. As both characters contributing to growth do not show any different adaptation to light intensity for sun and shade plants it is not at all surprising that the relative growth rate shows also the same dependence on light intensity in both sun and shade plants. This is shown once more in *fig. 9*. The only detail in favour of a better adaptation of shade plants to low light intensities is that in a very low light intensity the RGR of *Urtica dioica* is higher than that of *Galinsoga parviflora,* while it is lower in all other light intensities. The RGR of *Scrophularia nodosa,* however, is very low in this light intensity. In all species in all experiments growth was exponential during the whole growth period. A growth retardation could occur in the first few days because it can take some time before the morphology of the plants is properly adapted to the light intensity *(fig. 10)* or because of damage done to the plants at the moment of planting.

4. DISCUSSION

4.1. Morphogenesis

In a low light intensity two major adaptations are observed in both sun and shade species: a decrease in leaf thickness and a decrease in root weight ratio. The decrease of the root weight ratio can be understood as the result of a change in the competitive ability of roots and tops for energy, water and nutrients, leading to a functional equilibrium (BROUWER 1963). The decrease of the leaf thickness asks for a supplementary explanation. This may be found in the special dependence of the development of leaf thickness on energy supply. The contents of non-structural carbohydrates are much lower in a low light intensity (ALBERDA 1965; DEINUM 1966; THORNLEY & HURD 1974). Leaf area and stem length are apparently relatively independent with respect to this value, while root weight, stem thickness and leaf thickness are strongly affected. That the development of leaf thickness depends on energy supply and not directly on the light intensity has been shown in the experiments of HUGHES & EVANS (1963) on the influence of different combinations of light intensity and daylength with equal light quantities. In their experiments the SLA of *Impatiens parviflora* was much more closely related to the NAR than to the light intensity. Recently KEMP (1981) found a very close relationship between the relative growth rates of emerging leaves and the hexose concentration in the extension zone of wheat shoots which had been shaded for different periods, while length growth was not affected. The assumption that the energy supply is a controlling factor is not in accordance with the results of LAMBERS & POSTHUMUS (1979)), who found equal contents of soluble carbohydrates and starch in both shoots and roots of *Plantago lanceolata* grown in high (60 W.m^{-2}) or low (10 W.m^{-2}) light intensity.

The somewhat shorter stem internodes and individual leaves occurring at high light intensities could be reactions to the less favourable water relations (DAU-

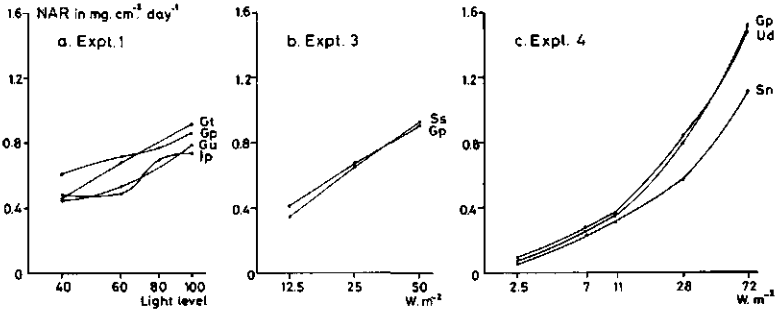

Fig. 8. Net assimilation rate of plants in expts. 1, 3 and 4. Species cf. *fig. 3.*

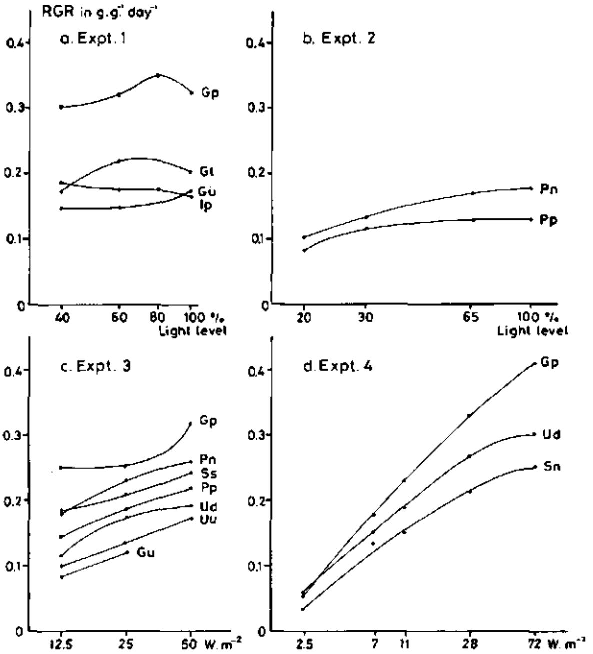

Fig. 9. Relative growth rate of plants in expts. 1, 2, 3 and 4. Species cf. *fig. 3*.

BENMIRE 1974), since at least stem extension is not affected by the light intensity as such (MORGAN & SMITH *1981*).

The dry matter distribution is not only altered by the light intensity, it can also show an ontogenetic drift. The differing leaf weight ratios of *Stachys sylvatica* in the final harvest of experiment 3 *(fig. 3)* are not caused by light intensity but by the ontogenetic drift. In *fig. 4* it is shown that the leaf weight ratio slowly decreases with increasing plant weight, independent of the light intensity.

4.2. Growth

In experiments 1 and 2 the overall relative growth rate was rather independent of the light intensity at light intensities over about 60 W/m^2, conform to the results of VAN DOBBEN et al. (1981) and HUNT & HALLIGAN (1981). So it is evident that at higher light intensities carbohydrate supply is not likely to limit the growth rate. When water and nutrient supply are also optimal, as expected in water cultures, it seems correct to suppose that the plant itself is limiting its own growth. Probably the rate of cell growth in the extension zones is limiting (PIETERS 1974). This theory is supported by the experiments of HUNT & HALLIGAN (1981) with *Lolium perenne*, where during growth the leaf area ratio decreased and the net assimilation rate increased, resulting in a constant relative growth rate at high light intensity. The same principle is seen in the experiments of VAN DOBBEN et al. (1981) where the relative growth rates at the highest light levels become constant from the second day of the experiment, when the leaf

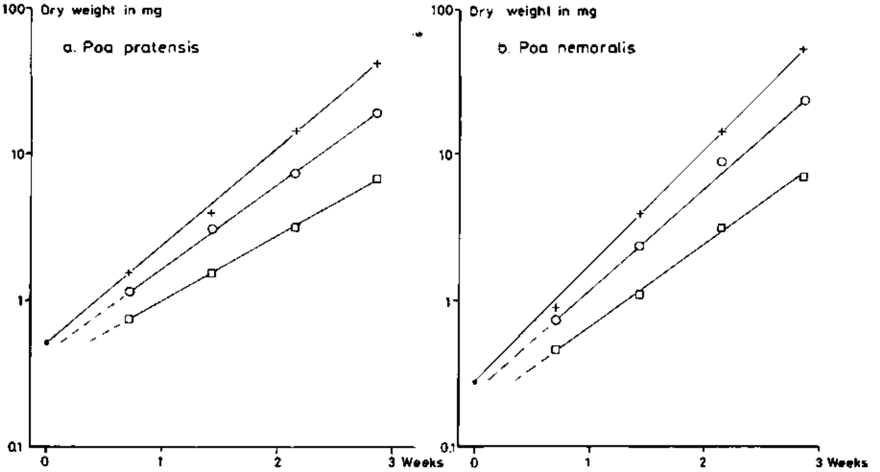

Fig. 10. Logarithmic total weight plotted against time for two species in expt. 3. □ : 12.5 W.m^{-2}, ○ : 25 W.m^{-2}, + : 50 W.m^{-2}.

area ratio is not yet higher than 60% of its later value. In the experiments in climatic rooms the light intensities were never high enough to maintain a constant RGR over some radiation range. That energy supply is involved here has been shown by THORNLEY & HURD (1974), who found a linear relationship between the relative growth rate and the starch availability in tomato plants, grown in a range of light intensities.

This leads to retardation of the growth of plants grown in lower light intensities, which appears during the time the morphogenetic adaptations are not yet accomplished (VAN DOBBEN et al. 1981). This is shown in *fig. 10* for two species from experiment 3. That the plants grown in high light intensity grow exponentially from the first day on, although the pre-treatment was at a lower light intensity, can be explained by the energy supply not being limiting; these plants do reach their maximum relative growth rate well before the ultimate morphogenetic "adaptations" are performed, conforming to the results of HUNT & HALLIGAN (1981) cited above.

5. CONCLUSIONS

All species examined respond to a lower light intensity with a

- decreasing leaf thickness
- increasing leaf area ratio
- decreasing root weight ratio
- decreasing dry matter content in leaves and stems
- decreasing net assimilation rate
- decreasing relative growth rate in lower light intensities
- comparable relative growth rates in a rather broad range of higher light intensities.

All species respond to about the same extent, no systematic differences can be seen between sun and shade plants. It seems plausible that the morphogenetic adaptations to a low light intensity are caused by limiting energy supply and there are no direct light effects. Different responses of sun and shade plants to natural shade seem to be based not on light intensity, but on light quality only. This will be discussed in a following paper.

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CHAPTER II

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GROWTH AND MORPHOGENESIS OF SUN AND SHADE PLANTS II. THE INFLUENCE OF LIGHT QUALITY

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SUMMARY

Some herbaceous sun and shade plants were grown under two red/far-red ratios to investigate their adaptation in morphology, growth and net photosynthesis to the light quality component of shade light. All species reacted in the same way to a low red/far-red ratio, but the sun species reacted more, showing more stem elongation, a lower leaf weight ratio and a lower relative growth rate. It can be inferred that photosynthetic functions are not influenced by the red/far-red ratio, but dark respiration increases, and probably to a greater extent in sun species.

1. INTRODUCTION

In a previous paper (CORRÉ 1983), in common with most publications on the effect of shading on plant growth it was assumed that shading was synonymous with a decreased intensity of light: the changes in the spectral distribution that occur in natural shade and the effects of light of different spectral quality on plant growth were ignored. Advances in the techniques of simulating natural light spectra have meant that extensive research on the physiological and ecological significance of the spectral quality of shade light have recently become possible. The first reviews on this subject were published very recently (MORGAN & SMITH 1981a; SMITH 1982).

The spectral composition of light is changed in a leaf canopy, mainly as a consequence of the light being absorbed by chlorophyll (WOOLLEY 1971). Thus, by comparison with sunlight, shade light is relatively poor in blue and red light and relatively rich in green, and especially rich in far-red light (COOMBE 1957; FEDERER & TANNER 1966; HOLMES & SMITH 1977). Two wavelengths important in photomorphogenesis, namely 660 nm and 730 nm – the absorption maxima of phytochrome – are absorbed in very different proportions, and therefore shade light is often characterized by the red/far-red ratio. This is the ratio between the light intensities (photon fluence rates) at 660 nm and at 730 nm, measured with a band width of 10 nm. At latitude 53° N the red/far-red ratio varies between 1.15 in open habitats (HOLMES & SMITH 1977a) to approximately 0.10 in dense shade, where the light intensity is less than 1 per cent (FEDERER & TANNER 1966; HOLMES & SMITH 1977b). The elevation of the sun and atmospheric conditions also influence the red/far-red ratio, but these changes are only of minor importance, compared with the changes that occur in shade light (HOLMES & SMITH 1977a).

There are two generally recognized photoreceptors that are involved in photomorphogenesis: the phytochrome system, and a blue light receptor. The exact nature of the latter is not yet known. Chlorophyll is presumed to have only indirect effects on morphogenesis via energy transduction (MORGAN & SMITH 1981a). The blue light receptor shows no photoreversibility and is unable to compare the relative magnitude of two wavelengths, as the phytochrome complex can, so it could only be useful in detecting the quantity and not the quality of the light (MORGAN & SMITH 1981a). WILD & HOLZAPFEL (1980) presume that phytochrome is also involved in the photomorphogenetic effects of blue light, and therefore it is very difficult to assess whether the low proportion of blue light in shade light is of physiological or ecological importance. It is also difficult to assess whether the quantity of light has a direct influence on plant growth, or acts only indirectly via energy supply, as I assumed in an earlier paper (CORRÉ 1983). The phytochrome system can, by means of its photoreversibility, act as an indicator of light quality and of the degree of shading (MORGAN & SMITH 1981a). Therefore, research on light quality in relation to shade tolerance focusses on the red/far-red ratio. The red/far-red ratio is very useful for this, because in its natural range it is almost linearly related to the Pfr/Ptotal ratio, the physiologically relevant quantity in the phytochrome photo-equilibrium (SMITH & HOLMES 1977).

One of the most striking effects of the red/far-red ratio is its influence on the stem elongation of many growing plants. Stem elongation can be clearly stimulated in a low red/far-red ratio (e.g. see FRANKLAND & LETENDRE 1978; HOLMES & SMITH 1977c; MCLAREN & SMITH 1978; MORGAN & SMITH 1978). In all plant species stem elongation occurs in natural or simulated shade light, but to very different extents. The elongation is very marked in sun species such as *Chenopodium album* and *Senecio vulgaris*, while it is only weak in shade-tolerant species such as *Circaea lutetiana, Mercurialis perennis* and *Teucrium scorodonia* (FRANKLAND & LETENDRE 1978; MORGAN & SMITH 1979). Like internodes, petioles also elongate more in a low red/far-red ratio in sun plants than in shade plants (MORGAN & SMITH 1979). Concomitant with the stem elongation, the stem weight ratio increases and the leaf weight ratio decreases. This shift in dry matter distribution is much weaker in shade-tolerant species too (MORGAN & SMITH 1979). A decrease in the leaf weight ratio in a low light intensity will greatly reduce dry matter production (see, for example, MCLAREN & SMITH 1978). Not surprisingly, this too is species-dependent. FITTER & ASHMORE (1974) showed that a low red/far-red ratio caused a large decrease in dry matter production in *Veronica persica* (not a shade-tolerant species) and only a moderate decrease in *V. montana* (a shade-tolerant species). The effect of a lower light intensity on dry matter production was equal in both species.

The effect of the red/far-red ratio on leaf thickness is not yet clear. Thinner leaves under a low red/far-red ratio were reported by HOLMES & SMITH (1977c), MCLAREN & SMITH (1978) and KASPERBAUER (1971), but no effects were found by MORGAN & SMITH (1981b). FITTER & ASHMORE (1974) found a lower specific leaf area in artificial shade in *Veronica persica* than in *V. montana*, but a much higher specific leaf area in an experiment with natural shade. Other important well-known effects of a low red/far-red ratio are the maintenance of apical dominance, a decrease in the nitrate reductase activity, and the inhibition of germination, at least the latter being very species-dependent (MORGAN & SMITH 1981a; SMITH 1982).

Much less is known about any possible involvement of phytochrome in photosynthesis or respiration. In a previous paper (CORRÉ 1983) I assumed that photosynthesis in low light intensity did not differ systematically between sun and shade plants, but that respiration could be lower in shade plants. The experiments cited in the references of the latter paper, however, mostly used artificial shade, and very little is known about any influence the red/far-red ratio might have. KASPERBAUER & PEASLEE (1973) found that in tobacco, a short red or far-red illumination at the end of the light period did not have any influence on the net photosynthetic rate on the basis of leaf area, although there were marked differences in morphology, for example in leaf thickness. To date, no evidence is available on the possible effects of long-term illuminations with light with a low red/far-red ratio. On the other hand, there is evidence that respiration can be influenced by the red/far-red ratio. LEOPOLD & GUERNSEY (1954) found that under red light, dark respiration decreased in the oat mesocotyl and the pea stem, and that there was a concomitant decrease in cell extension, whereas under far-red light, dark respiration and cell extension increased. Moreover, in red light the dark respiration in leaves of barley (a long-day plant) increased, but in leaves of *Xanthium commune* and soybean (both short-day plants) it decreased: far-red light had the opposite effect. HOCK & MOHR (1964) found that the dark respiration in leaves of *Sinapis alba* was stimulated under both red and far-red light. This increase was larger under red light after a short illumination, but it was larger under far-red light after the illumination exceeded approximately 10 hours. Although not indisputable, it seems reasonable to suppose that the red/far-red ratio has no direct effects on respiration rates, but only indirect effects through its influence on energy-demanding processes, such as stem elongation.

In this paper, four experiments set up to study the effects of the red/far-red ratio during growth on several sun and shade species will be discussed. In experiments 5, 6 and 7 the effects on growth and morphogenesis were investigated and compared with the effects of light intensity, and in experiment 8 the net photosynthesis and dark respiration of entire plants were measured. Experiments 1, 2, 3 and 4 were described in a previous paper (CORRÉ 1983).

2. MATERIALS AND METHODS

2.1. Plant materials

In sequence of increasing shade tolerance (after ELLENBERG 1979) the species *Plantago major* L. (in experiment 8), *Galinsoga parviflora* Cav. (5, 7, 8), *Urtica* *urens* L. (7, 8), *Polygonum lapathifolium* L. (6), *Urtica dioica* L. (5, 7, 8), *Circaea lutetiana* L. (6), *Geum urbanum* L. (8), *Impatiens parviflora* (L.) DC (7), *Scrophularia nodosa* L. (5), and *Stachys sylvatica* L. (6, 8) were grown. Seeds collected from plants in their natural habitats were germinated in a climatic room at 20 °C under fluorescent light (40 $W.m^{-2}$). The experiments were started one or two weeks after germination.

2.2. Growth conditions

In all experiments the plants were grown on an aerated nutrient solution (pH 6.5) containing 6.0 $me.l^{-1}$ NO_3^-, 0.5 $me.l^{-1}$ $H_2PO_4^-$, 3.5 $me.l^{-1}$ SO_4^{--}, 3.5 $me.l^{-2}$ K^+, 4.5 $me.l^{-1}$ Ca^{++}, 2.0 $me.l^{-1}$ Mg^{++} and the trace elements 2.0 ppm Fe, 0.5 ppm B, 0.7 ppm Mn, 0.05 ppm Mo, 0.1 ppm Zn and 0.02 ppm Cu. The solution was changed once a week.

All experiments were carried out in a climatic room. Daylength was 16 hours, day temperature 20 °C, night temperature 15 °C and relative humidity was 65% all day.

2.3. Light treatments

In experiments 5, 6 and 7, three light treatments were administered: a moderate light intensity with a normal red/far-red ratio (treatment C), a very low light intensity with a normal red/far-red ratio (B) and a very low light intensity with a low red/far-red ratio (A). In experiment 8 only two light treatments were administered: one (moderate) light intensity with either a normal (C) or a low red/far-red (C') ratio. The exact values of light intensities and red/far-red ratios are listed in *table 1*. A normal red/far-red ratio was attained with a combination of fluorescent (Philips TL 33) and incandescent lamps. For a low red/far-red ratio, fluorescent light was supplemented with far-red light, by filtering incandescent light (8 × 100 W) through one 3 mm layer of red "502" plexiglass and two 3 mm layers of blue "627" plexiglass (Röhm & Haas). Since the light intensities were measured as energy fluence rates (400–700 nm), and incandescent light is rich in low energy radiation, the light treatments with a low red/far-red ratio had lower photon fluence rates than the normal red/far-red ratio treatments

Table 1. Light treatments in the different experiments. Energy fluence rates (400–700 nm) and red/far-red ratios (photon fluence rates).

treatments	expt. 5		expt. 6		expt. 7		expt. 8	
	$W.m^{-2}$	r/fr	$W.m^{-2}$	r/fr	$W.m^{-2}$	r/fr	$W.m^{-2}$	r/fr
A	2.5	0.14	1.1	0.08	1.4	0.11	–	–
B	2.5	1.15	2.5	1.30	1.5	1.15	–	–
C¹	–	–	–	–	–	–	8	0,11
C	7	1.15	15	1.15	14	1.50	8	1.00

with the same energy fluence rates. Red/far-red ratios were measured with an EG&G 585 spectroradiometer (band width 10 nm).

2.4. Harvest procedures

In experiments 5, 6 and 7 ten plants of each species were harvested every seven days (treatments A and B) or five days (C). The fresh and dry weights of leaf blades, stems plus petioles, and roots were recorded. Leaf area and internode length were also measured. In experiment 8, only four plants of each species were harvested from both treatments after the photosynthesis and dark respiration had been measured. In this experiment the same variables were measured as in the other experiments, but the leaf thickness was also measured in *Plantago major*, *Galinsoga parviflora*, *Geum urbanum* and *Stachys sylvatica.*

2.5. Measurement of photosynthesis and dark respiration

Whole plants with their roots in small flasks containing a nutrient solution, were placed in an assimilation chamber 15 cm in diameter and 30 cm high. The temperature was 24°C (for *Urtica urens* and *U. dioica*) or 19°C (for the other species), the air flow was 40 l.hr^{-1}. The CO_2 contents of incoming (330 ppm) and outcoming air were measured by infrared gas analysis. As a light source an AB Deltalux MS 3540 lamp with a red/far-red ratio of 7.5 was used. The maximum light intensity (400–700 nm) at plant level was 48 W.m^{-2}. Lower light levels were achieved by shading with white cheese cloth; dark respiration was measured under black plastic. In order to determine the direct effects of the red/far-red ratio, the net photosynthetic rates of the plants of *Plantago major* and *Geum urbanum* in light treatment A were also measured at their original growing place, under a red/far-red ratio of 0.11 and with a maximum light intensity of 8.7 W.m^{-2} at plant level.

3. RESULTS

3.1. Morphogenesis

The influence of light quality and light quantity on stem extension is shown in *table 2* (for some species the internode length is shown in *fig. 1*). Because of the very different rate of development in the treatments, instead of comparing plants at the final harvest, plants from the final harvest of the slowest-growing treatment (usually treatment A) were compared with plants of approximately the same total dry weight from the other treatments. These plants were at the same state of development, as can be seen in *fig. 1* which shows that the number of internodes formed was always the same in the three light treatments. *Fig. 1* shows that the internode length was increased in a low red/far-red ratio, and that this increase was large in the non-tolerant *Galinsoga parviflora* and only moderate in the shade-tolerant species. In addition, light intensity influenced internode length, at least in *Galinsoga parviflora* and in *Scrophularia nodosa.*

Stem extension, shown as total stem length or as internode length, has two aspects: the length of stem that is formed per unit dry matter invested in the

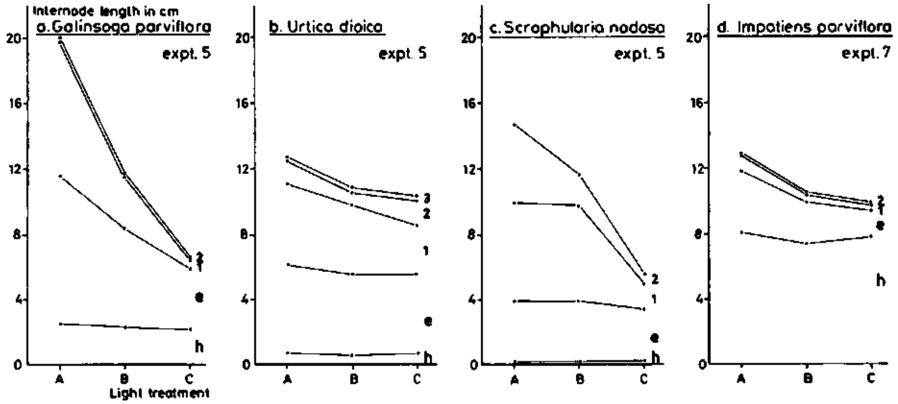

Fig. 1. Stem length of 4 species from experiments 5 and 7, divided into internodes. h = hypocotyl, e = epicotyl, 1, 2, .. = successive internodes.

stem and the part of the total accumulated dry matter that is invested in the stem. *Table 2* shows relevant data on this. Stem weight includes the weight of petioles, but since petiole length is influenced by the red/far-red ratio in the same way as stem extension (MORGAN & SMITH 1979), this will hardly have affected the results. Furthermore, stems and petioles have the same function. From *table 2* it can be seen that a low red/far-red ratio resulted in stem elongation (in mm stem per mg total dry weight); in sun plants this elongation was greater than in shade plants. The increase in stem extension in mm stem per mg stem dry weight, however, was much less marked in all species. Thus it can be concluded that the increased stem extension under a low red/far-red ratio is more the result of a change in the distribution of dry matter between plant organs than of a reduction in stem thickness.

The dry matter distribution is shown for all species in *table 2*. In general, the stem weight ratio in sun species increased greatly under a low red/far-red ratio, but in shade species the increase was slight. The increases in *Polygonum lapathifolium* (experiment 6) and in *Urtica urens* (experiment 7) were only slight, because the very poor growth of these two sun species in the very low light intensity did not enable them to adapt normally to the light treatment. In experiment 8, *Urtica urens* did show a great increase in stem weight ratio under a low red/far-red ratio. Of the shade species, *Stachys sylvatica* was exceptional; its stem weight ratio showed an adaptation comparable with that of the sun species. The increase in stem weight ratio was achieved at the expense of the leaf weight ratio; the root weight ratio remained largely unaffected. A lower light intensity also caused the stem weight ratio to increase, but independent of shade tolerance and at the expense of both leaf weight ratio and root weight ratio. In *fig. 2* the dry matter distribution of four species is shown in distribution diagrams, in which the weight of the different organs is plotted against total plant weight, both on a logarithmic scale. In these diagrams the adaptations in the dry matter distribution during growth can easily be seen. The huge changes

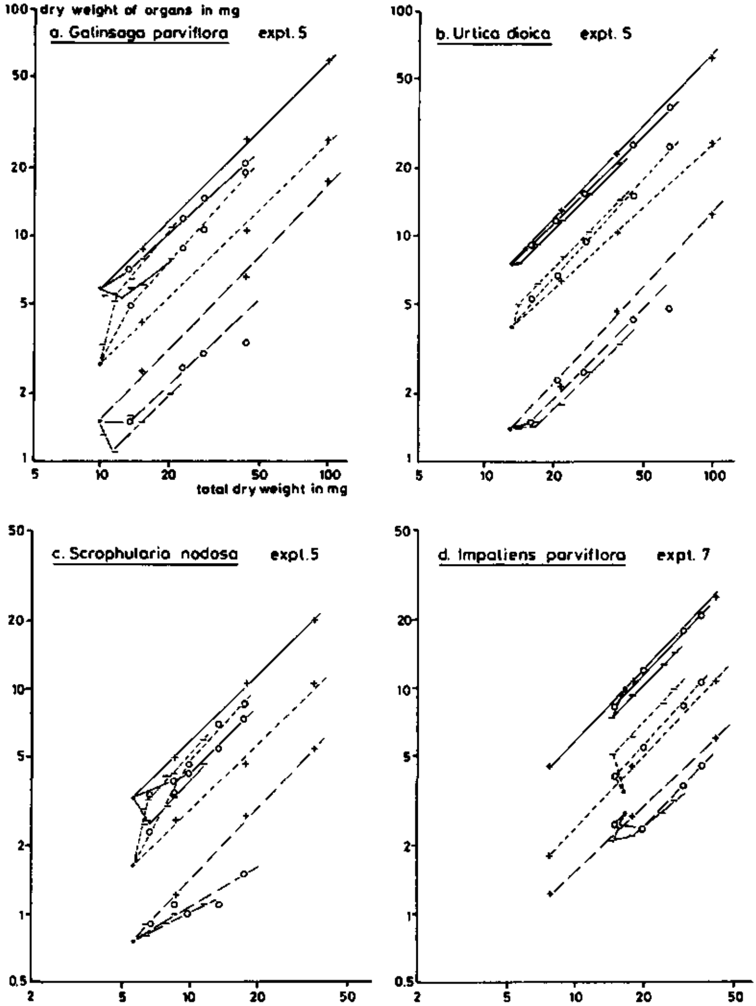

Fig. 2. Dry weight of plant organs plotted against total dry weight for 4 species from experiments 5 and 7, on a logarithmic scale. Light treatment: -: A, o: **B**, + C; —: leaf blades, ---- stems and petioles — — —: roots.

in the dry matter distribution in a low light intensity in *Galinsoga parviflora* and *Scrophularia nodosa*, and in a low red/far-red ratio in *G. parviflora* are obvious. The adaptations took place very rapidly; within one week in all species the dry matter distribution had adapted well to the light treatment, although growth was slight or even negative (in *Impatiens parviflora*) in this period. The new dry matter distribution was not only achieved by a different distribution of the newly produced dry matter: the dry matter from leaves and roots was also redistributed to the stem. *Urtica dioica* had a fractionally higher growth

Table 2. Stem length in relation to plant dry weight and to stem dry weight, and dry matter distribution in the different light treatments. For species cf. *fig. 3*.

Expt. 5	G. parviflora			U. dioica			S. nodosa		
	A	B	C	A	B	C	A	B	C
stem length mm	200	129	60	127	110	93	147	135	50
plant d.w. mg	21	23	20	39	39	38	12	12	12
stem d.w. mg	11	9	5	15	14	11	6	6	3.5
mm stem/mg plant	9.5	5.6	3.0	3.3	2.8	2.4	12	11	4.2
mm stem/mg stem	18	14	12	8.5	7.9	8.5	24	22	14
leaf weight ratio	.40	.50	.55	.54	.55	.60	.39	.41	.53
stem weight ratio	.50	.40	.30	.37	.35	.28	.52	.50	.34
root weight ratio	.10	.10	.15	.09	.10	.12	.09	.09	.13

Expt. 6	P. lapathifolium			C. lutetiana			S. sylvatica		
	A	B	C	A	B	C	A	B	C
stem length mm	59	54	38	52	42	19	87	35	17
plant d.w. mg	5	6	6	20	21	19	18	23	20
stem d.w. mg	1.7	1.9	1.7	5.6	4.7	2.8	6.7	5.4	3.5
mm stem/mg plant	12	9.0	6.3	2.6	2.0	1.0	4.8	1.5	0.9
mm stem/mg stem	35	28	22	8.9	8.9	6.8	13	6.5	4.9
leaf weight ratio	.52	.58	.60	.54	.52	.58	.49	.62	.60
stem weight ratio	.34	.32	.24	.28	.30	.24	.36	.28	.28
root weight ratio	.14	.10	.16	.18	.18	.18	.15	.10	.12

Expt. 7	G. parviflora			I. parviflora			U. urens			U. dioica		
	A	B	C	A	B	C	A	B	C	A	B	C
stem length mm	171	106	56	129	104	70	36	28	14	53	44	26
plant d.w. mg	11	11	11	28	30	30	1.7	1.7	1.7	5.3	5.6	5.5
stem d.w. mg	5.1	3.8	2.7	9.9	8.4	7.6	0.5	0.4	0.3	1.7	1.5	1.1
mm stem/mg plant	16	10	5.1	4.6	3.5	2.3	21	16	8.2	10	7.9	4.7
mm stem/mg stem	34	34	21	13	12	9.1	72	70	47	31	29	24
leaf weight ratio	.43	.53	.60	.52	.60	.60	.49	.50	.65	.58	.60	.63
stem weight ratio	.47	.38	.25	.36	.28	.25	.28	.24	.17	.32	.27	.23
root weight ratio	.10	.09	.15	.12	.12	.15	.23	.26	.18	.10	.13	.14

Expt. 8	G. parviflora		S. sylvatica		U. urens		U. dioica	
	C′	C	C′	C	C′	C	C′	C
stem length mm	180	96	102	59	148	75	110	101
plant d.w. mg	23	114	30	70	38	47	50	54
stem d.w. mg	11	27	12	20	15	11	15	15
mm stem/mg plant	7.8	0.8	3.4	0.8	3.9	1.6	2.2	1.9
mm stem/mg stem	16	3.6	8.5	3.0	9.9	6.8	7.3	6.7
leaf weight ratio	.45	.64	.52	.64	.48	.63	.59	.68
stem weight ratio	.46	.23	.38	.29	.40	.27	.28	.27
root weight ratio	.09	.13	.10	.07	.12	.10	.13	.15

Table 3. Some data on morphology, photosynthesis and dark respiration of plants in experiment 8. For species see *fig 3*.

	U. urens		U. dioica		G. parvifl.		S. sylvat.		P. major		G. urbanum	
	C′	C	C′	C	C′	C	C′	C	C′	C	C′	C
leaf thickness mm	–	–	–	–	.080	.095	.085	.100	.135	.145	.085	.090
specific leaf area $cm^2.mg^{-1}$	.86	.98	.87	.85	1.41	1.28	1.16	1.15	.65	.59	.69	.72
leaf weight ratio	.48	.63	.59	.58	.45	.64	.51	.64	.56	.67	.62	.64
stem weight ratio	.41	.23	.29	.27	.47	.23	.39	.29	.37	.20	.27	.23
leaf area ratio	.42	.60	.51	.51	.64	.83	.60	.73	.36	.40	.43	.47
photosynthetic capacity mg $CO_2.dm^{-2}.h^{-1}$	14	13	11	12	9	12	8	10	13	15	10	12
photosynthetic efficiency mg $CO_2.dm^{-2}.h^{-1}.W^{-1}.m^2$	.74	.74	.77	.76	.57	.59	.57	.55	.57	.64	.64	.62
dark respiration mg $CO_2.dm^{-2}.h^{-1}$	2.5	1.9	1.4	2.3	1.4	.2	.7	.2	.5	.1	.3	.2
dark respiration mg $CO_2.g$ $plant^{-1}.h^{-1}$	10.5	11.4	7.1	11.7	9.0	1.7	4.2	1.5	1.9	.4	1.3	.9
light compensation point $W.m^{-2}$	3.5	2.7	2.0	3.3	2.5	.3	1.3	.4	.9	.2	.5	.3

C′: r/fr ratio 0.11
C : r/fr ratio 1.00

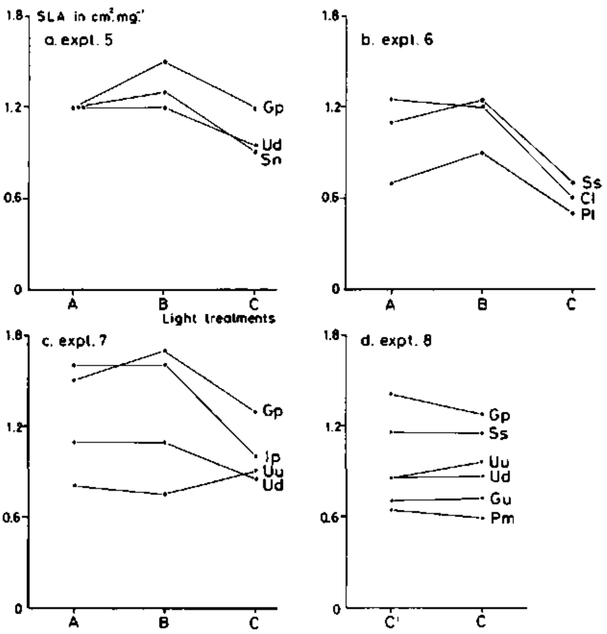

Fig. 3. Specific leaf area of plants in experiments 5, 6, 7 and 8. Species: Cl: *Circaea lutetiana*, Gp: *Galinsoga parviflora*, Gu: *Geum urbanum*, Ip: *Impatiens parviflora*, Pl: *Polygonum lapathifolium*, Pm: *Plantago major*, Sn: *Scrophularia nodosa*, Ss: *Stachys sylvatica*, Ud: *Urtica dioica*, Uu: *Urtica urens*.

rate than the other species and this enabled it to make its minor adaptations to this light treatment without redistributing dry matter.

Leaf thickness was only measured directly in four species in experiment 8 (*table 3*). In all four species the leaves were thinner in a low red/far-red ratio and this did not seem to depend on shade tolerance. No clear concomitant increase in specific leaf area occurred. In the other species and in the other experiments the influence of the red/far-red ratio was inconsistent (*fig. 3*). As expected, the influence of light intensity on the specific leaf area was clear; the leaves of all species were much thinner in low light intensity, except in *Urtica urens* in experiment 7, where again poor growth inhibited a proper adaptation.

As it is the product of leaf weight ratio and specific leaf area, the leaf area ratio also showed a clear response to the light treatment (*fig. 4*). Under a low red/far-red ratio the leaf area ratio decreased greatly in sun species but only weakly in shade species, with *Stachys sylvatica* as an exception. This response was most marked in experiments 5 and 8, where all species had a reasonable growth rate. In general, in a low light intensity the leaf area ratio increased markedly, independent of shade tolerance.

The dry matter content of leaf blades and stems showed some variation under the influence of the red/far-red ratio (*fig. 5*). In experiments 5, 6 and 7 no trend emerged. In experiment 8, however, the influence was clear. Under a low red/far-

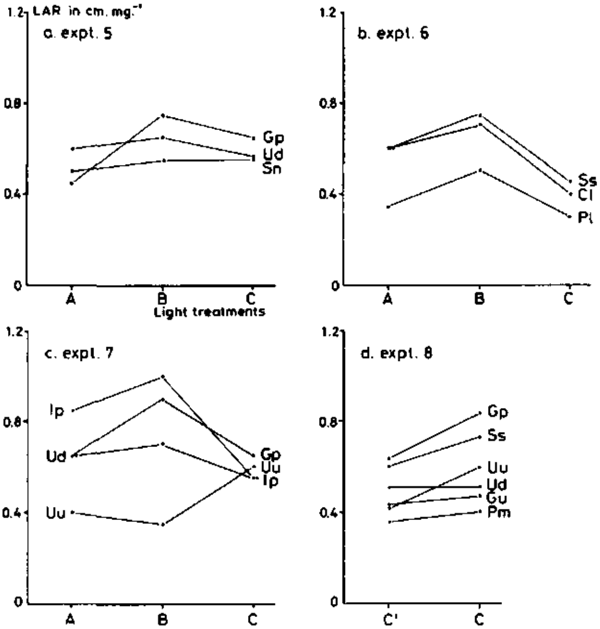

Fig. 4. Leaf area ratio of plants in experiments 5, 6, 7 and 8. For species, see *fig. 3*.

red ratio the dry matter content of leaf blades increased in all species. This increase may have been caused by a higher leaf temperature that resulted from the additional infra-red radiation from the far-red light sources. The effect of leaf temperature could only be of minor importance in the other experiments, because they experienced lower light intensities. The dry matter content of stems increased to a varying degree in the shade-tolerant species, but decreased in the sun species. This difference between sun and shade species was inexplicably striking.

3.2. Growth

As the net assimilation rate in very low light intensities is very sensitive to small differences in light intensity, temperature etc., this rate can only be compared within experiments, for species that were grown simultaneously. Two sun species, *Polygonum lapathifolium* and *Urtica urens,* appeared to have a very low net assimilation rate under a low red/far-red ratio, while the third sun species, *Galinsoga parviflora*, showed approximately the same decrease as shade species. The net assimilation rate decreased in all species, but this could have resulted from differences in light intensity: this was evident in experiment 6 but might also have operated in the other experiments, which had approximately the same energy fluence rates, but in which photon fluence rates were lower under a low red/far-red ratio. Also, small differences in leaf temperature, resulting from more infra-red radiation under the low red/far-red ratio, might have caused the net assimilation rate to decrease slightly. As expected, a lower light intensity resulted

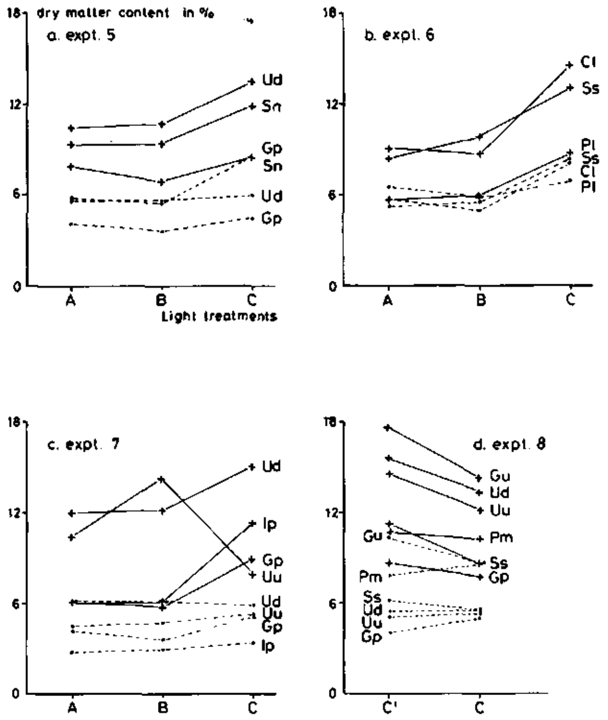

Fig. 5. Dry matter content of leaf blades and of stems and petioles of plants in experiments 5, 6, 7 and 8. +: leaf blades, •: stems and petioles. For species, see *fig. 3*.

in a marked fall in the net assimilation rate and in the relative growth rate. It is notable, however, that the relative growth rate of *Polygonum lapathifolium* and of *Urtica urens* declined drastically, much more than the decrease in the third sun species, *Galinsoga parviflora*, and in the shade-tolerant species. Under a low red/far-red ratio the relative growth rate decreased in all species, because of a lower net assimilation rate, but in the sun species the decrease also occurred because of a lower leaf area ratio. Thus the decrease in relative growth rate was much greater in sun species, some of which even stopped growing, whereas all shade-tolerant species continued to grow healthily, albeit slowly.

3.3. Photosynthesis and dark respiration

The net photosynthesis/light intensity curves for the species of experiment 8 are shown in *fig. 8*. Moreover, photosynthetic capacity (light-saturated photosynthetic rate at 330 ppm CO_2), photosynthetic efficiency at non-saturating light intensities, and dark respiration (all on the basis of area and of weight) are given in *table 3* together with light compensation points. The photosynthetic capacity was reached at about 30 $W.m^{-2}$ in all species and tended to be higher in the sun species. It was lower in plants that were grown under a low red/far-red ratio,

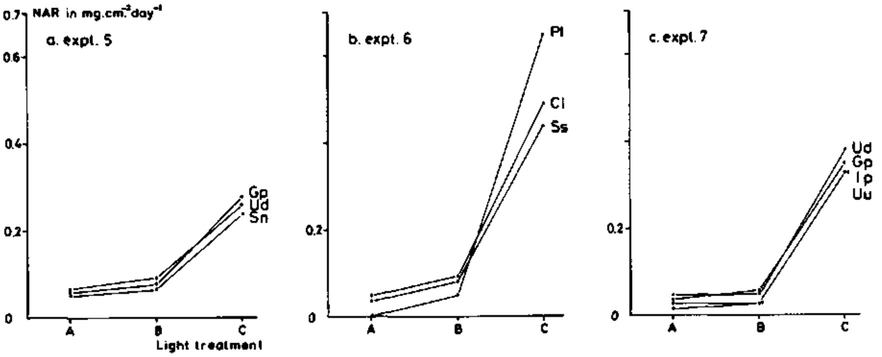

Fig. 6. Net assimilation rate of plants in experiments 5, 6 and 7. For species, see *fig. 3*.

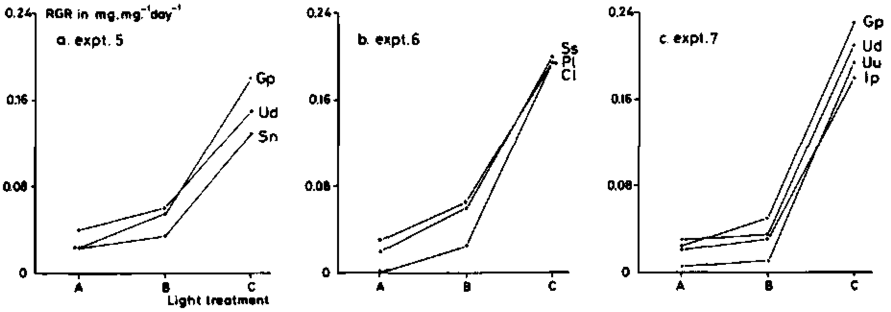

Fig. 7. Relative growth rate of plants in experiments 5, 6 and 7. For species, see *fig. 3*.

except for *Urtica urens,* in which it was slightly higher. The photosynthetic efficiency varied appreciably with species: this may have been caused by the different angles of the leaf blades or by internal shading. The efficiency was not influenced by the red/far-red ratio in which the plants were grown, except in the case of *Plantago major,* where it was lower in the plants grown under a low red/far-red ratio, probably because the leaves grew more upright under the low red/far-red ratio.

The dark respiration was much higher in the *Urtica* species because temperatures were higher during the measurements. When grown under a high red/far-red ratio the dark respiration of sun and shade species was similar. On the basis of leaf area, dark respiration increased when the plants were grown under a low red/far-red ratio, except in *Urtica dioica,* where dark respiration was lower. In general, the increase in dark respiration was clearly greater in the sun species than in the shade species. This difference partly resulted from different adaptations in the leaf area ratio. The dark respiration on the basis of total plant weight showed a smaller increase in the low red/far-red ratio plants, but nevertheless it was still an increase and was also clearly greater in the sun species. Since the

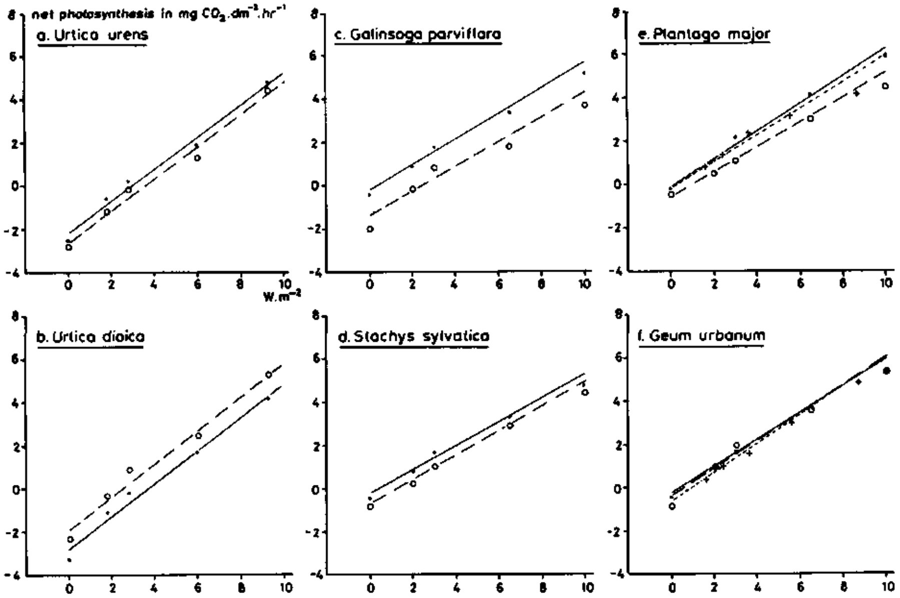

Fig. 8. Net photosynthesis/light intensity curves of plants in experiment 8. –•–: high r/fr ratio, —O—: low r/fr ratio, – – + – – low r/fr ratio, measured at growing place.

photosynthetic efficiency was not influenced by the red/far-red ratio, the light compensation points depended totally on dark respiration. Thus in these experiments the light compensation points were generally higher when plants were grown under a low red/far-red ratio, with the sun species having the greatest increase in light compensation point. The photosynthesis measured at the growing place, under light of a low red/far-red ratio did not differ greatly from the photosynthesis measured under light with an unnaturally high red/far-red ratio (7.5). The differences in photosynthesis in *Geum urbanum* were negligible, but in *Plantago major* the photosynthetic efficiency increased. This might have resulted from the more diffuse light source which was used at the growing place, and which probably favoured the plants with more upright leaves.

This experiment must be regarded as preliminary. The results were fairly reproduceable and therefore relative differences are reliable. The absolute values, especially those of dark respiration rates, are, however, less reliable and need to be confirmed by further research.

4. DISCUSSION

As expected from the earlier series of experiments (CORRÉ 1983), the effects of a decreased light intensity with a constant red/far-red ratio were very much the same in all species, resulting in approximately the same decrease in relative growth rate in both sun and shade species. In the very low light intensity used in light treatment B of experiments 5, 6 and 7, however, some sun species showed a much greater decrease in relative growth rate than others and than the shade species; *Urtica urens* grew especially poorly. Although no differences in dark respiration rates were found between sun and shade species when grown in 8 $W.m^{-2}$ and under a normal red/far-red ratio, it is possible that differences can occur at very low light intensities, as MAHMOUD & GRIME (1974) found in three grass species with differing tolerance to shade. It can be concluded that the effects of light intensity might also be important in shade tolerance, when very low light intensities are involved.

A low light intensity can stimulate stem elongation appreciably. The individual fully-grown internodes became longer (cf. GRIME & JEFFREY 1965; LECHARNEY & JACQUES 1980; HOLMES et al. 1982), but because of a lack of assimilates, fewer nodes are produced when the light intensity is low (cf. GRIME & JEFFREY 1965; VIRZO DE SANTO & ALFANI 1980), resulting in shorter plants in a very low light intensity. This increased elongation of the internodes was not stronger in sun species than in shade species. In the species where internodes elongated appreciably in a very low light intensity, a concomitant increase was found in the stem weight ratio.

Plants from treatments with a low red/far-red ratio showed an increased stem extension and a higher stem weight ratio. Stem thickness was usually only slightly affected. Since the dry matter distribution in low light intensities must be regarded as the result of the ability of the different plant parts to compete for energy, it is reasonable to explain the higher stem weight ratio as resulting from the extra demand for energy made by the rapidly elongating stem (CORRÉ 1983). This view agrees with the results obtained by LEOPOLD & GUERNSEY (1954) on the influence of red and far-red light on the dark respiration rates of oat mesocotyles and pea stems. The greater increase in dark respiration rates in sun species, and in *Stachys sylvatica*, when grown under a low red/far-red ratio confirms that the rapidly elongating stem has a larger energy demand. However, leaf thickness, which is very dependent on energy supply, showed no clear difference between sun and shade species. It may be that leaf thickness primarily depends on the amount of energy that is fixed in the leaves, and therefore it could depend much more on the intensity than on the quality of the light.

The different morphogenetic adaptations of sun and shade plants to the low red/far-red ratio led to differences in the extent to which the relative growth rate decreased. Differences in the net assimilation rate were of minor importance. This was confirmed in experiment 8, in which it was shown that the photosynthetic efficiency in a low light intensity is not influenced by the red/far-red ratio during growth.

In these experiments, the different adaptations of sun and shade plants to light quality corresponded very well with Grime's model of plant strategies (GRIME 1979; 1981) and with his earlier concept of shade-avoiding and shade-tolerating plants (GRIME 1965; 1966). According to SMITH (1981; 1982), sun species have a strategy for avoiding shade by mobilizing all available carbohydrates (high respiration rates) and by greatly increasing stem extension at the expense of the development of leaf area. This strategy will be successful in herbaceous vegetations, where increased stem extension may result in the plants reaching a higher light intensity but it will be fatal in woodland, where the plant cannot escape from the low light intensity. The shade species, on the other hand, show a typical example of stress toleration: a conservative use of assimilates (low respiration rates), resulting in a slow-growing, but strong plant, and only a slight reaction to the light quality component of shade. The reactions to light intensity are the same in both strategies, sometimes even more pronounced in sun species (see GRIME 1979). This proves once more that the red/far-red ratio is used by plants to detect the degree of shading and not the light intensity. The red/far-red ratio is indeed much more critical; it varies much less with weather conditions and also with time of day, so a rapid functional response is possible (SMITH 1982). The smaller increase in dark respiration rate that occurred in the shade species grown under a low red/far-red ratio, tended to confirm the hypothesis of plant strategies outlined above. On the other hand, the very large increase in the respiration rate, i.e. a five-fold increase in *Galinsoga parviflora*, cannot, at the moment, be explained. Thus, before definitive conclusions can be drawn from the results of this experiment, more extensive research will have to be done on this subject.

To sum up: a low red/far-red ratio can be expected to increase respiration more in sun species, because the energy demand of the rapidly elongating stem is higher (cf. LEOPOLD & GUERNSEY 1954). The changes in respiration rates may be more complex, because the photoperiodic effects of the red/far-red ratio may also influence energy-demanding processes (cf. LEOPOLD & GUERNSEY 1954). Energy supply is important in stem extension, as can be seen in the experiment done by LECHARNEY & JACQUES (1979), where the stem extension after a short end-of-day illumination with far-red light was greater in plants that had been grown in a light intensity of 140 $W.m^{-2}$ than in plants that had been grown in 85 $W.m^{-2}$.

5. CONCLUSIONS

All the plant species investigated responded strongly to light intensity. There were no systematic differences between sun and shade species. In a very low light intensity, however, some sun species showed a much greater decrease in relative growth rate than others and than shade species.

Sun and shade species reacted systematically differently to a low red/far-red ratio, sun species showing much more stem elongation, a higher stem weight ratio, and correspondingly lower leaf weight and leaf area ratios. Because of their large morphogenetic adaptations, the sun species showed an appreciable decrease in relative growth rate. Differences in net assimilation rate seemed to be small.

Photosynthetic efficiency did not seem to be influenced by the red/far-red ratio. In most species dark respiration increased in a low red/far-red ratio; this increase seemed to be greater in sun species.

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CHAPTER III

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GROWTH AND MORPHOGENESIS OF SUN AND SHADE PLANTS

III. THE COMBINED EFFECTS OF LIGHT INTENSITY AND NUTRIENT SUPPLY

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SUMMARY

In three experiments the effects of light intensity and nutrient supply (nitrate or phosphate) and their combined effects on the growth and morphogenesis of two shade-tolerant plant species and a non-tolerant species were studied. Nutrient supply was limited by placing the plants on a standard nutrient solution for a limited period each day and placing them on a nitrogen-free or phosphate-free solution for the rest of the day. The effects of light intensity and nitrate supply on growth and morphogenesis showed a marked interaction: low nitrate supply caused a much greater decrease in the relative growth rate under high light intensity, because of much larger changes in the dry matter ditribution; the net assimilation rate was only slightly affected by nitrate supply. The effects of light intensity and phosphate supply on the dry matter distribution and the net assimilation rate both showed interaction, but the effects on the relative growth rate were independent. Low phosphate supply caused greater changes in the dry matter distribution under high light intensity and a greater decrease in the net assimilation rate under low light intensity; the relative growth rate decreased to the same extent under both high and low light intensities. The experimental data were compared with the balanced quantitative model for root/shoot ratios proposed by THORNLEY (1972). The results were very satisfactory, but it was concluded that the model must be used in its exact form and that the use of approximations cannot be allowed.

1. INTRODUCTION

In shaded habitats, as in unshaded habitats, the nutrient supply in the soil is assumed to be an important factor in determining the distribution of herbaceous plant species (PIGOTT & TAYLOR 1964). This, combined with the existence of major interactions between the effects of light intensity and nutrient supply on growth raises the question of whether shade-tolerant plant species react differently than non-tolerant species to a combination of low light intensity and low nutrient supply. This combination is typical for forests, because there most of the available nutrients are accumulated in the trees and in the leaf litter (GRIME 1979), and there is severe competition for the nutrients from the extensive root systems of the trees. If shade species do react differently to a combination of low light intensity and low nutrient supply, this might contribute to their shade tolerance.

Very few studies have been done to compare the reactions of different herbaceous species to certain combinations of light intensity and nutrient supply, but many studies have dealt with the reactions of single species. The combined effects of light intensity and nitrate supply on agricultural grasses have been described frequently (e.g. by ALBERDA 1965, DEINUM 1966, LEMAIRE 1975, LUXMOORE & MILLINGTON 1971a and 1971b). All these studies clearly showed a larger increase in dry matter production after the addition of nitrate under high light intensity. ROBSON & PARSONS (1978) asserted that the increase in dry matter production after the addition of nitrate under high light intensity is partly caused by an increased shoot weight ratio and partly by an increased rate of photosynthesis per unit area, whereas under low light intensity only the shoot weight ratio increases. ERIKSEN & WHITNEY (1981) compared the reactions of six tropical forage grasses. Under a high light intensity the dry matter production was raised 1.5 to 3 times more by high nitrogen supply than it was raised under a low light intensity. No attempt, however, was made to explain these differences in terms of the ecology or other characteristics of the species.

Much less is known about interactions between the effects of light intensity and other nutrients. In most studies the effects showed the same type of interaction; a greater effect of nutrient supply on growth, under high light intensity (BLACKMAN & RUTTER 1947, phosphate and potassium in *Scilla non-scripta;* PIGOTT 1971, phosphate in *Urtica dioica*). PEACE & GRUBB (1982) used a combination of nitrate and phosphate for *Impatiens parviflora* and found that it produced the same effects as I described above, so the relative importance of phosphate is unclear. Another type of interaction between the effects of light intensity and nutrient supply, an increase in the effect of the nutrient supply under low light intensity, also occurs (BLACKMAN & WILSON 1951, nitrogen, phosphate and potassium combined in *Helianthus annuus*). In view of the well-know interactions between the effects of nitrogen supply and light intensity, nitrogen was probably not the limiting nutrient in that experiment. The authors' conclusion is opposite to mine: they concluded that the effect of nutrient supply was greater under high light intensity, as shown by the absolute decrease in the relative growth rate, while I am interested in relative alterations of the relative growth rate. From their experiments, CHAN & MCKENZIE (1971) concluded that there was no interaction between the effects of light intensity and ammonium supply on the growth, but their experimental species (corn) grew very poorly in the absence of nitrate. Thus the general validity of their conclusion is doubtful.

Studying these relationships between nutrients, light intensity and plant growth is complicated by the fact that the results greatly depend on the methods used. In most of the studies mentioned above, the nutrient supply per plant was the same in alle light intensities, and therefore the shortage of nutrients was felt more strongly under high light intensities, simply because of the faster growth of the plants (INGESTAD 1962). This is particularly true for mobile nutrients such as nitrate, and for nutrient solutions, but sometimes also for less mobile nutrients in soil (e.g. phosphate), when the soil volume is limited. For this reason, in my experiments I chose a method in which the problem of adjusting the nutrient supply according to the size of the plants was avoided: the limiting nutrient was supplied in optimum concentration in a water culture for a limited constant period each day. The use of a water culture implies, however, free access of the nutrients to the surface of the roots. In soil this is more or less assured for nitrate, but not for phosphate. In the case of phosphate, one aspect of the influence of the light intensity on the root weight ratio was ignored. Plants with a lower root weight ratio (low light intensity plants) explore a relatively smaller volume of soil and so the effects of a low phosphate supply could be greater in these plants in the field than in my experiments.

The results of three experiments on the effects of light intensity and nutrient supply on sun and shade plants will be discussed in this paper. In all three experiments (9, 10 and 11) the effects of light intensity and nitrate supply were studied; in experiment 11 the effects of light intensity and phosphate supply were included. Experiments 1 to 8 were discussed in two earlier papers (CORRÉ 1983a and 1983b).

2. MATERIALS AND METHODS

2.1. Plant materials

In experiment 9 the sun species *Galinsoga parviflora* Cav. and the shade-tolerant *Stachys sylvatica* L. were used, and in experiments 10 and 11 *G. parviflora* was compared with the shade-tolerant *Urtica dioica* L. Seeds collected from plants in their natural habitats were germinated in a climate room at 20°C under fluorescent light (40 $W.m^{-2}$). The experiments were started approximately two weeks after germination, except for experiments with *U. dioica*, which were begun circa three weeks after germination.

2.2. Light intensity and nutrient supply

All three experiments were carried out in a glasshouse which had a relative light intensity of 65% of the natural light. This light level (L3) was reduced to 30% (L2) and to 12% (L1) of the L3 level by black plastic shade screens. Experiment 9 was done in June and the beginning of July 1980, an extremely cloudy period. At noon on clear days, a light intensity of 200 $W.m^{-2}$ (400–700 nm) could be measured, but on most days it did not exceed 100 $W.m^{-2}$. Experiment 10 was done in August and the first week of September 1980, a period with many hours of sunshine. The maximum light intensity was circa 180 W.m⁻2 in the glasshouse. The red/far-red ratio was 1.1 at all light levels in both experiments. Experiment 11 was done in September and October 1980. The natural light was augmented with artificial light (Philips HPIT) with an intensity of 10 $W.m^{-2}$ for 16 hours per day. So at noon in full sunshine the maximum light intensity was 75 $W.m^{-2}$. The red/far-red ratio varied from 1.4 to 3.5 at all light levels, depending on the quantity of natural light (r/fr ration natural light 1.1, r/fr ratio HPIT 3.5).

Three nutrient solutions were used: the standard solution, containing 6.0 $me.l^{-1}$ NO_3^-, 0.5 $me.l^{-1}$ $H_2PO_4^-$, 3.5 $me.l^{-1}$ SO_4^{--}, 3.5 $me.l^{-1}K^+$, 4.5 $me.l^{-1}$ Ca^{++}

and 2.0 me.l^{-1} Mg^{++}; a nitrogen-free solution. containing 0.5 me.l^{-1} $H_2PO_4^-$, 5.2 me.$l.^{-1}$ SO_4^{--}, 4.0 me.l^{-1} Cl^-, 3.2 me.l^{-1} K^+, 4.5 me.l^{-1} Ca^{++} and 2.0 me,l^{-1} Mg^{++}; and a phosphate-free solution containing 6.0 me.l^{-1} NO_3^-, 4.0 me.l^{-1} SO_4^{--}, 3.5 me.$l.^{-1}$ K^+, 4.5 me.l^{-1} Ca^{++} and 2.0 me.l^{-1} Mg^{++}. All solutions contained as trace elements 2.0 ppm Fe, 0.5 ppm B, 0.7 ppm Mn, 0.05 ppm Mo, 0.1 ppm Zn and 0.02 ppm Cu. The solutions had a pH of 6.5, were aerated constantly and replaced once a week. In experiments 9 and 10 three nitrate nutrition regimes were established. The plants were placed on the standard solution for 1 hour (N1), 3 hours (N3) or 24 hours (N24) each day. After the nitrate nutrition the roots of the N1 and N3 plants were rinsed with demineralized water and the plants were placed on the nitrogen-free solution for the rest of the day. In experiment 11, three nutrition regimes were established: 2 hours on the standard solution and the rest of the day on nitrogen-free solution (N2); half an hour on the standard solution and the rest of the day on the phosphate-free solution (PO.5); and 24 hours on the standard solution (N24, P24).

2.3. Growth conditions and harvest procedures

In experiment 9 the night temperature was usually circa 20°C, the day temperature was mostly between 20° and 25°C; on the few sunny days it could rise to circa 30°C. In the shaded compartments the night temperature, and on sunny days also the day temperature, was usually circa 2° higher than the glasshouse temperature. The maximum relative humidity was circa 70%, the minimum circa 30%. In the shaded compartments the corresponding values were 90% and 45% respectively. These climatic differences, however, were assumed to cause no significant effects on growth (VAN DOBBEN et al. 1981). In experiment 10 the night temperature was also mostly circa 20°C, but the day temperature frequently exceeded 30°C. The maximum relative humidity was circa 65%, the minimum circa 25%, in the shaded compartments the corresponding values were circa 90% and 40%. In experiment 11 the minimum night temperature was 15°C and the day temperature was mostly between 20° and 25°C. The maximum relative humidity was circa 70%, the minimum circa 35%. In the shaded compartments the corresponding values were circa 90% and 45% respectively.

In experiments 9 and 10, in which the influence of light intensity and nitrate supply on the competition between sun and shade plants was also studied (CORRÉ in preparation), the plants were not grown separately, as usual, but twelve plants were placed in an area of 0.0625 m^2 and harvested simultaneously. Of each species, two replicates of twelve plants from each treatment were harvested 2, 3, 4 and 5 weeks after the start of the experiments. The fresh and dry weights of leaf blades, of stems with petioles, and of roots were recorded, and leaf area was measured. For growth analysis, the only data used were those obtained from plants harvested before exponential growth passed into a more linear growth as a result of mutual shading. In experiment 11 the plants were grown separately and growth was exponential during the whole growth period of 24 days. Every 6 days, 10 plants of each species and from each treatment were harvested, and the same variables measured as in the other experiments. In all experiments, the total nitrogen content of the plants of the final harvest was measured after wet ashing with sulphuric acid and salicylic acid, and the nitrate-nitrogen content was measured after extraction with demineralized water. The organic nitrogen content was calculated by subtracting the nitrate-nitrogen content from the total nitrogen content. In addition, in experiment 11 the phosphate content was measured after the wet ashing.

3. RESULTS

All results from growth analysis and chemical analysis are listed in *table 1* (experiments 9 and 10) and in *table 2* (experiment 11).

3.1. Control series (N24, P24)

The reactions of the three species to light intensity confirmed the results of experiments 3 and 4 (Corré 1983a). In low light intensity the relative growth rate fell, because the decrease in the net assimilation rate greatly exceeded the increase in the leaf area ratio. No fundamental differences could be seen between the species. But the data on chemical composition indicated that light intensity did produce different effects in sun and shade species. In *Galinsoga parviflora*, under low light intensity the total nitrogen content tended to be higher, while the nitrate-nitrogen content was clearly higher and the organic nitrogen content tended to be lower. Surprisingly, in *Stachys sylvatica* and in *Urtica dioica* the levels of the different nitrogen compounds were hardly affected by the light intensity. Even the content of free nitrate was constant, except in *U. diocia* in experiment 10, where it was slightly higher in low light intenstity plants. The phosphate content of *Galinsoga parviflora* was slightly higher under low light intensity; in *Urtica dioica* no trend was visible.

3.2. Nitrate series (N1, N2, N3)

Under conditions of high light intensity, limiting the nitrate supply caused a large decrease in the relative growth rate in all species. A lower leaf area ratio appeared to be largely responsible for this decrease; the net assimilation rate remained unaffected (experiments 9 and 10) or decreased only slightly (experiment 11). As the values of the specific leaf area show, the leaf thickness did not appear to be influenced by the nitrate supply. Thus the decrease in the leaf area ratio was caused by a lower leaf weight ratio. The leaf weight ratio was indeed much lower when the nitrate supply was low, and the root weight ratio increased greatly at the expense of both stem and leaves. Under conditions of low light intensity, the relative growth rate was only slightly lower when the nitrogen supply was low. Mostly this decrease was caused by a small decrease in the net assimilation rate, while the leaf area ratio remained unaffected. The root weight ratio was slightly higher under these conditions too, but a decrease in the stem weight ratio was sufficient to achieve this and the leaf weight ratio remained unaffected. Thus it was concluded that the interaction between the effects of light intensity and nitrate supply on the relative growth rate was major.

Table 1. Data on growth analysis and chemical composition of plants from experiments 9 and 10.

Experiment 9	Galinsoga parviflora									Stachys sylvatica								
	L1			L2			L3			L1			L2			L3		
	N1	N3	N24	N1	N3	N24	N1	N3	N24	N1	N3	N24	N1	N3	N24	N1	N3	N24
SLA $cm^2.mg^{-1}$	1.64	1.69	1.62	1.23	1.25	1.18	0.70	0.73	0.70	1.35	1.34	1.36	0.96	0.98	0.99	0.58	0.58	0.61
LWR $mg.mg^{-1}$	0.54	0.55	0.55	0.47	0.53	0.60	0.41	0.51	0.60	0.57	0.62	0.61	0.54	0.59	0.64	0.46	0.55	0.61
SWR $mg.mg^{-1}$	0.32	0.34	0.37	0.22	0.25	0.27	0.16	0.18	0.18	0.29	0.28	0.31	0.21	0.22	0.24	0.15	0.17	0.19
RWR $mg.mg^{-1}$	0.14	0.11	0.08	0.31	0.22	0.13	0.43	0.31	0.22	0.14	0.10	0.09	0.25	0.19	0.12	0.39	0.28	0.20
LAR $cm^2.mg^{-1}$	0.89	0.93	0.89	0.58	0.66	0.71	0.29	0.37	0.42	0.77	0.83	0.83	0.52	0.58	0.63	0.27	0.32	0.37
NAR $mg.cm^{-2}.day^{-1}$	(100%) 0.12	(104%) 0.12	0.13	(82%) 0.38	(93%) 0.35	0.35	(69%) 0.87	(88%) 0.78	0.81	(93%) 0.12	(100%) 0.12	0.12	(83%) 0.30	(92%) 0.29	0.31	(73%) 0.66	(86%) 0.62	0.66
RGR $mg.mg^{-1}.day^{-1}$	(92%) 0.106	(92%) 0.112	0.116	(109%) 0.222	(100%) 0.231	0.246	(107%) 0.251	(96%) 0.288	0.339	(100%) 0.094	(100%) 0.100	0.103	(97%) 0.156	(94%) 0.167	0.198	(100%) 0.177	(94%) 0.198	0.245
total N $mg.mg^{-1}$	(91%) 0.029	(97%) 0.040	0.041	(90%) 0.021	(94%) 0.024	0.042	(74%) 0.015	(85%) 0.023	0.026	(91%) 0.019	(97%) 0.028	0.038	(79%) 0.014	(84%) 0.017	0.037	(72%) 0.016	(81%) 0.018	0.038
NO_3-N $mg.mg^{-1}$	0.002	0.008	0.022	0.000	0.002	0.022	0.000	0.001	0.008	0.000	0.001	0.012	0.000	0.000	0.013	0.000	0.000	0.011
organic N $mg.mg^{-1}$	0.027	0.032	0.019	0.021	0.022	0.020	0.015	0.022	0.018	0.019	0.027	0.026	0.014	0.017	0.024	0.016	0.018	0.027
USR $mg.mg^{-1}.day^{-1}$	0.123	0.126	0.126	0.322	0.296	0.283	0.440	0.417	0.435	0.109	0.111	0.113	0.208	0.206	0.225	0.290	0.275	0.306
SAR $mg.mg^{-1}.day^{-1}$	0.022	0.041	0.059	0.015	0.025	0.079	0.009	0.021	0.040	0.013	0.028	0.043	0.009	0.015	0.061	0.007	0.011	0.046
experiment 10	Galinsoga parviflora									Urtica dioica								
SLA $cm^2.mg^{-1}$	1.56	1.65	1.62	1.14	1.26	1.29	0.56	0.62	0.80	1.29	1.31	1.23	0.96	1.02	0.96	0.58	0.59	0.59
LWR $mg.mg^{-1}$	0.52	0.52	0.52	0.50	0.51	0.53	0.45	0.47	0.54	0.65	0.64	0.66	0.60	0.64	0.68	0.57	0.59	0.68
SWR $mg.mg^{-1}$	0.37	0.39	0.41	0.21	0.25	0.37	0.17	0.20	0.29	0.23	0.24	0.26	0.15	0.16	0.19	0.10	0.13	0.17
RWR $mg.mg^{-1}$	0.11	0.09	0.07	0.29	0.24	0.10	0.38	0.33	0.17	0.12	0.12	0.09	0.25	0.20	0.13	0.33	0.28	0.15
LAR $cm^2.mg^{-1}$	0.81	0.86	0.84	0.57	0.64	0.68	0.25	0.29	0.43	0.84	0.84	0.81	0.58	0.65	0.65	0.30	0.35	0.40
NAR $mg.cm^{-2}.day^{-1}$	(97%) 0.13	(102%) 0.13	0.14	(84%) 0.34	(94%) 0.34	0.37	(58%) 1.00	(65%) 0.96	0.82	(104%) 0.11	(104%) 0.12	0.13	(89%) 0.27	(100%) 0.27	0.31	(75%) 0.62	(88%) 0.66	0.70
RGR $mg.mg^{-1}.day^{-1}$	(93%) 0.106	(93%) 0.110	0.116	(92%) 0.195	(92%) 0.216	0.249	(122%) 0.250	(117%) 0.277	0.353	(85%) 0.090	(92%) 0.099	0.106	(87%) 0.159	(87%) 0.174	0.200	(89%) 0.186	(94%) 0.230	0.280
total N $mg.mg^{-1}$	(91%) 0.023	(95%) 0.034	0.046	(78%) 0.016	(87%) 0.019	0.034	(71%) 0.009	(79%) 0.018	0.025	(82%) 0.031	(93%) 0.034	0.043	(80%) 0.021	(87%) 0.025	0.039	(70%) 0.018	(82%) 0.023	0.038
NO_3-N $mg.mg^{-1}$	0.001	0.011	0.027	0.000	0.001	0.021	0.000	0.001	0.008	0.002	0.002	0.018	0.000	0.001	0.016	0.000	0.000	0.011
organic N $mg.mg^{-1}$	0.022	0.023	0.019	0.016	0.018	0.013	0.009	0.017	0.017	0.029	0.032	0.025	0.021	0.024	0.023	0.018	0.023	0.027
USR $mg.mg^{-1}.day^{-1}$	0.119	0.121	0.125	0.275	0.284	0.277	0.403	0.413	0.425	0.102	0.113	0.116	0.212	0.218	0.230	0.278	0.319	0.329
SAR $mg.mg^{-1}.day^{-1}$	0.022	0.042	0.076	0.011	0.017	0.085	0.006	0.015	0.052	0.023	0.028	0.051	0.013	0.022	0.060	0.010	0.019	0.071

Table 2. Data on growth analysis and chemical composition of plants from experiment 11.

	Galinsoga parviflora						Urtica dioica					
	L1		L2		L3		L1		L2		L3	
N series	N2	N24	N2	N24	N2	N24	N2	N24	N2	24	N2	N24
SLA $cm^2.mg^{-1}$	1.69	1.60	1.27	1.26	0.75	0.69	1.31	1.30	0.96	0.96	0.55	0.53
LWR $mg.mg^{-1}$	0.56	0.58	0.49	0.59	0.41	0.56	0.62	0.63	0.52	0.63	0.46	0.61
SWR $mg.mg^{-1}$	0.30	0.34	0.18	0.26	0.16	0.26	0.22	0.25	0.19	0.22	0.20	0.20
RWR $mg.mg^{-1}$	0.14	0.08	0.33	0.15	0.43	0.18	0.16	0.12	0.29	0.15	0.34	0.19
LAR $cm^2.mg^{-1}$	0.94	0.93	0.62	0.74	0.31	0.38	0.81	0.82	0.50	0.60	0.25	0.32
NAR $mg.cm^{-2}.day^{-1}$	(101%) 0.11	0.12	(84%) 0.25	0.27	(82%) 0.63	0.68	(99%) 0.08	0.10	(83%) 0.26	0.29	(78%) 0.60	0.73
RGR $mg.mg^{-1}.day^{-1}$	(92%) 0.100	0.109	(93%) 0.158	0.199	(93%) 0.194	0.259	(80%) 0.066	0.082	(90%) 0.128	0.172	82%) 0.151	0.235
total N $mg.mg^{-1}$	(92%) 0.044	0.062	(79%) 0.033	0.061	(75%) 0.027	0.064	(84%) 0.047	0.061	(74%) 0.030	0.055	(64%) 0.033	*0.054*
NO_3–N $mg.mg^{-1}$	0.012	0.031	0.001	0.024	0.000	0.019	0.007	0.022	0.001	0.020	0.000	0.020
organic N $mg.mg^{-1}$	0.032	0.031	0.032	0.037	0.027	0.045	0.040	0.039	0.029	0.035	0.033	*0.034*
USR $mg.mg^{-1}.day^{-1}$	0.116	0.118	0.234	0.234	0.340	0.316	0.079	0.093	0.180	0.202	0.229	0.290
SAR $mg.mg^{-1}.day^{-1}$	0.035	0.084	0.016	0.081	0.012	0.091	0.019	0.041	0.014	0.063	0.015	*0.067*
P series	P0.5	P24	P0.5	P24	P0.5	P24	P0.5	P24	P0.5	P24	P0.5	P24
SLA $cm^2.mg^{-1}$	1.64	1.60	1.23	1.26	0.70	0.69	1.30	1.30	0.94	0.96	0.52	0.53
LWR $mg.mg^{-1}$	0.58	0.58	0.56	0.59	0.48	0.56	0.64	0.63	0.59	0.63	0.50	0.53
SWR $mg.mg^{-1}$	0.31	0.34	0.24	0.26	0.19	0.26	0.23	0.25	0.21	0.22	0.19	0.20
RWR $mg.mg^{-1}$	0.11	0.08	0.20	0.15	0.33	0.18	0.13	0.12	0.20	0.15	0.31	0.19
LAR $cm^2.mg^{-1}$	0.95	0.93	0.69	0.74	0.34	0.38	0.85	0.82	0.55	0.60	0.26	0.32
NAR $mg.cm^{-2}.day^{-1}$	(102%) 0.11	0.12	(93%) 0.26	0.27	(89%) 0.69	0.68	(104%) 0.08	0.10	(92%) 0.27	0.29	(81%) 0.74	0.73
RGR $mg.mg^{-1}.day^{-1}$	(92%) 0.101	0.109	(96%) 0.182	0.199	(101%) 0.236	0.259	(80%) 0.069	0.082	(93%) 0.147	0.172	(101%) 0.194	0.235
PO_4 $mg.mg^{-1}$	(93%) 0.016	0.033	(91%) 0.024	0.032	(91%) 0.017	0.025	(84%) 0.021	0.030	(85%) 0.012	0.041	(83%) 0.011	0.024
USR $mg.mg^{-1}.day^{-1}$	0.113	0.118	0.228	0.234	0.352	0.316	0.079	0.093	0.184	0.202	0.281	0.290
SAR $mg.mg^{-1}.day^{-1}$	0.015	0.047	0.022	0.043	0.012	0.041	0.011	0.020	0.006	0.047	0.007	0.030

Changes in the dry matter distribution were responsible for this. Specific leaf area and net assimilation rate did not react to low supply of nitrate or reacted independently of the light intensity. The growth of the various species reacted very similarly to a low supply of nitrate, but in experiment 11 *Urtica dioica* showed a greater decrease in relative growth rate than did *Galinsoga parviflora.*

Total nitrogen content was, of course, lower when the nitrate supply was limited. The free nitrate content became particularly low, although *Galinsoga parviflora* still contained an appreciable amount of free nitrate when subjected to a limited supply of nitrate under the lowest light intensity (except for the N1 treatment). In *G. parviflora* and *Urtica dioica* the content of organic nitrogen decreased under higher light intensities; in *Stachys sylvatica* it decreased under all light intensities.

3.3. Phosphate series (P0. 5)

When little phosphate was supplied, the relative growth rate in both species fell by exactly the same proportion under all light intensities, which suggests that light does not affect the effects of phosphate supply. *Urtica dioica* was more sensitive to phosphate than *Galinsoga parviflora*. However, the data on leaf area ratio and net assimilation rate in both species showed that there was an interaction between the effects of light intensity and phosphate supply. When the supply of phosphate was low the leaf area ratio only decreased under high light intensities, but the net assimilation rate decreased only under low light intensities. The reaction of the leaf area ratio was similar to that induced by a low supply of nitrate and was also caused by changes in the dry matter distribution. The way the net assimilation rate reacted cannot be explained by the total phosphate content, which was not lower under the lowest light intensity than under the highest light intensity, where the net assimilation rate remained unchanged. The phosphate content was lower with low phosphate supply, but it did not show a clear relation with light intensity.

4. DISCUSSION

4.1. Growth and morphogenesis

The well-known interaction between the effects of nitrate supply and light intensity, i.e. an increased effect of nitrate supply under high light intensity, was clearly supported in these experiments. Nitrate supply had major effects on morphogenesis (i.e. on dry matter distribution) and only minor effects on metabolism (i.e. on net assimilation rate). Yet HEWITT & SMITH (1975) and ROBSON & PARSONS (1978) found that a limited nitrate supply depressed the net assimilation rate appreciably under high light intensity but not under low light intensity. This disaccordance, however, might have resulted from the use of other methods of ensuring a low nitrate supply. If the nitrate supply is not adjusted to the size of the plant, but remains constant or even decreases over time (ROBSON & PARSONS treated their experimental plants for 25 days with a high nitrate supply and thereafter with a constant low supply of nitrate), the nitrogen status of the plant will decline (INGESTAD 1962). A declining nitrogen status during growth is known to produce a large decrease in the photosynthetic capacity (NATR 1975). The effects of this on the net assimilation rate were illustrated in an experiment done by WELBANK (1962). He found that the nitrogen content and the net assimilation rate of *Impatiens parviflora* declined rapidly after the start of the experiment when the plants had to compete with *Agropyron repens* for a small amount of nitrogen, supplied in one dose at the start of the experiment. Without competition the nitrogen content and the net assimilation rate did not decline until after several weeks. Under a low light intensity, light will generally limit photosynthesis; thus the effect of a lower photosynthetic capacity will not be as important as it is under a high light intensity. It seems logical that plants growing under a low light intensity will require smaller adaptations to low nitrate supply, because slow-growing plants have a lower absorption rate on the basis of plant weight and thus they require a smaller root weight ratio to maintain normal levels of nutrients, provided that the absorption capacity on the basis of root weight is not affected. The actual absorption rate on the basis of root weight may be low under low light intensity (see, for example, RUFTY et al. 1981). The very high levels of free nitrate and the almost normal levels of organic nitrogen that I recorded in the low light intensity plants, suggest that this lower absorption rate is probably primarily the results of the lower growth rate and the concomitant fall in the demand for nitrogen, and not the result of a fall in absorption capacity, or of the absorption rate being limited by energy supply. Indeed, the absorption rates of nutrients have been found to be lower when the energy supply of the roots is limited (CRAPO & KETELLAPPER 1981, HÄNISCH TEN CATE & BRETELER 1981, KOSTER 1973), but in all those experiments it was always measured in high light intensity plants in which the energy supply of the roots was limited artificially, for example by moving the plants into shade. And since CRAPO & KETELLAPPER (1981) found that root growth was restricted much more than nutrient (potassium) absorption by low energy supply, it seems probable that these results do not apply unconditionally for plants adapted to a low energy supply. It can be concluded that plants react to low nitrate supply mainly by means of morphogenetic adaptations and they maintain a reasonable organic nitrogen content. When an appreciably lower photosynthetic rate or net assimilation rate is reported in the literature, it probably results from the fact that the method used to supply the nitrate has not been adjusted to the size of the plants.

The fact that smaller morphogenetic adaptations are required under low light intensity also holds true when the phosphate supply is limited, provided that the phosphate has free access to the surface of the roots, as in experiment 11. Thus it is not surprising that when the phosphate supply was restricted, the leaf area ratio decreased more under high light intensity than under low light intensity. It is, however, remarkable that with a low supply of phosphate, the net assimilation rate decreased under low light intensity. No reason could be found for this; the phosphate contents gave no clues for an explanation. That no interaction was found between the effects of light intensity and phosphate supply on the relative growth rate does not exclude the possible existence of any interaction (for example, if the phosphate supply is limited more drastically). The clear interactions between the effects of light intensity and phosphate supply on the leaf area ratio and the net assimilation rate give credence to this hypothesis. Whether this interaction implies a larger decrease in the relative growth rate under high light intensity or under low light intensity is difficult to assess. Because smaller morphogenetic adaptations are necessary under low light intensity (provided that the phosphate has free access to the surface of the roots), it is probable that the relative growth rate would decrease relatively more under high

Table 3. Relative growth rate and dry matter production at two light levels and two phosphate levels in experiment 11.

	Galinsoga parviflora				Urtica dioica			
	RGR $g.g^{-1}.day^{-1}$		dry weight g		RGR $g.g^{-1}.day^{-1}$		dry weight g	
	P0.5	P24	P0.5	P24	P0.5	P24	P0.5	P24
L1	0.101	0.109	0.050	0.060	0.069	0.082	0.036	0.049
	(93%)		(83%)		(84%)		(77%)	
L3	0.236	0.259	1.27	2.20	0.194	0.234	0.73	1.94
	(91%)		(58%)		(83%)		(38%)	

light intensity, but the effects on the assimilation rate remain unpredictable.

Although my data on relative growth rate show that light intensity and phosphate supply act independently on relative growth rate, the data on dry weight suggest that there is an interaction between the effects of these two factors. Because the relative growth rate is an exponential term in the relation between initial weight, final weight and time, $W_2 = W_1 \cdot e^{RGR(t_2 - t_1)}$, the same percentage decrease in the relative growth rate causes a larger relative decrease in the final weight in faster growing (high light intensity) plants. This is illustrated in *table 3*. This also means that when a larger relative decrease in the final weight is found under high light intensity, as is often cited in the literature (e.g. PIGOTT 1971, PIGOTT & TAYLOR 1964), a concomitantly larger relative decrease in the relative growth rate should not be inferred. For the same reason, interactions mentioned in the literature should be regarded with caution. It can be concluded that the possible interactions between the effects of light intensity and phosphate supply are not yet clear and that experiments with lower supplies of phosphate will be necessary. Also, interactions between the effects of light intensity and other nutrients are not easy to predict. An important factor in determining the interaction is the effect of the nutrient involved on the root/shoot ratio, and this effect is very different for the various nutriens, depending on their functions in the plant (CURTIS & CLARK 1950). This, and the fact that the nutrients have different mobilities in the soil, makes it probable that the interactions are nutrient-specific.

The fact that the growth of *Urtica dioica* was hampered more by a limited supply of phosphate than that of *Galinsoga parviflora* agrees with the results obtained by RORISON (1968) (who found that *U. dioica* grew very poorly on nutrient solutions with a low phosphate concentration) and by PIGOTT & TAYLOR (1964) (who found that *U. dioica* was especially restricted in its distribution by its need for a high phosphate supply).

4.2. The functional equilibrium between roots and shoots

The adaptions in the dry matter distribution of the experimental plants to light intensity and nutrient supply are expressions of a functional relationship between root and shoot systems (see, for example, TROUGHTON 1960), a relationship known as the functional equilibrium (BROUWER 1963). On empirical grounds, DAVIDSON (1969) found that the equilibrium could be expressed by the equation:

$$\text{root mass} \times \text{rate}_{(\text{absorption})} \propto \text{leaf mass} \times \text{rate}_{(\text{photosynthesis})} \qquad (1)$$

This means that the root/shoot ratio reacts to changes in the activity rates that result from changes in the functioning of the plant (e.g. caused by ageing) or in the environment, in order to maintain a constant level of a given nutrient. Later, THORNLEY (1972) described a theoretical quantitative model for root/shoot ratios in which the content of the nutrient (nitrogen) or, more precisely, the utilization rate of nitrogen to carbon was also considered to be constant, but in which pools of nitrogen and carbon were also involved. These pools were not considered to be constant, but to depend on the rates of absorption and photosynthesis. As these pools are relatively small compared with the total amounts of structural carbon and nitrogen, Thornley believed that the equation

$$\begin{aligned}&\text{specific root activity} \times \text{root weight ratio} = \\ &\text{N/C ratio} \times \text{specific shoot activity} \times \text{shoot weight ratio}\end{aligned} \qquad (2)$$

was a justified approximation. This equation is essentially the same as equation (1). HUNT & BURNETT (1973) introduced another approximation of equation (1):

$$\text{root mass/shoot mass} \propto 1/(\text{specific absorption rate/ unit shoot rate}) \qquad (3)$$

THORNLEY (1975) contends that this is not an approximation but is also essentially the same equation; thus equations (1), (2) and (3) express the same relationship. After plotting the data, however, Hunt & Burnett concluded that equation (3) was not sufficient, and that the root/shoot equilibrium could be described more satisfactorily by the equation:

$$\text{mass ratio} = a + b \times 1/\text{activity ratio} \qquad (4)$$

In the Hunt & Burnett's experiment the model

$$\text{mass ratio} = -0.001 + 45.0 \times 1/\text{activity ratio}$$

was found. In that model, a was insignificantly small and thus the nutrient (potassium) content was constant. THORNLEY'S (1975) criticism that (4) is an undesirable complication of (3) therefore seems to be justified. The potassium limitation in that experiment, however, was not severe enough to decrease the growth rate of the experimental plants, and a constant potassium content was only to be expected. In other experiments with a more severe stress of various nutriens

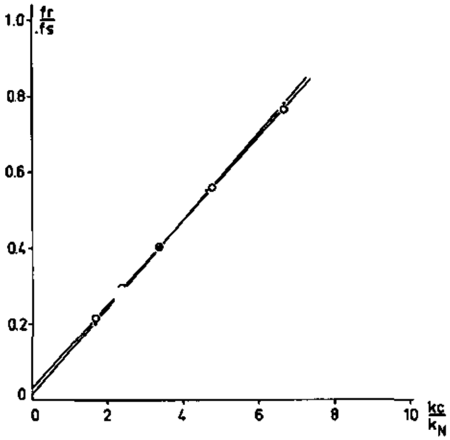

Fig. 1. Relationship between root/shoot mass ratio and shoot/root activity ratio, data from THORNLEY (1972).

●: data from Thornley, table 1. $\frac{fr}{fs} = 0.017 + 0.115 \frac{k_C}{k_N}$ r = 0.9999

○: data from Thornley, table 2. $\frac{fr}{fs} = 0.035 + 0.110 \frac{k_C}{k_N}$ r = 0.9999.

(K, N, P), however, *a* was positive and significant (HUNT 1975, HUNT et al. 1975, HUNT 1976). A positive *a* means that the content of the nutrient is not constant, but that it decreases as the root/shoot ratio increases; this seems more feasible.

It would be very interesting to see what relationship would emerge if in Thornley's model (equation 2) not only the structural nitrogen and carbon, but also the pools of non-structural nitrogen and carbon were taken into account. Because the nitrogen pool is thought to be smaller when the nitrogen absorption rate is lower or when the carbon assimilation rate is higher, the total nitrogen content will be lower as the root/shoot ratio increases, as in Hunt & Burnett's model. In this case, equation (2) (which is Thornley's equation (43)) must not be used, but instead his equation (42), of which (43) is an approximation. This equation (42):

$$k_N \times fr - \mu \times \overline{N} = \lambda(k_C \times fs - \mu \times \overline{C}) \qquad (5)$$

can be converted (after Thornley's equations (40) and (41)) to:

$$k_N \times fr - k_N \times fr \times \frac{1}{\overline{N} + \frac{\lambda}{\Theta Y_G}} \times \overline{N} = \lambda(k_C \times fs - k_C \times fs \times \frac{1}{\overline{C} + \frac{1}{\Theta Y_G}} \times \overline{C})$$

and further to:

$$\frac{fr}{fs} = \lambda \times \frac{k_C}{k_N} \times \frac{\left(1 - \dfrac{\bar{C}}{\bar{C} + \dfrac{1}{\Theta Y_G}}\right)}{\left(1 - \dfrac{\bar{N}}{\bar{N} + \dfrac{\lambda}{\Theta Y_G}}\right)} \qquad (6)$$

Equation (5), and thus also equation (6), do apply for Thornley's model plant (THORNLEY 1972, tables 1 and 2). In my *fig. 1*, fr/fs for this model plant was plotted against k_C/k_N, using Thornley's data (fr/fs was recalculated after equation (6), in order to minimize rounding errors). Using the data of Thornley's table 1, where k_C was varied, the model

$fr/fs = 0.017 + 0.115\, k_C/k_N$ ($r = 0.9999$; 0.017 is 99% significantly higher than 0)

was obtained, while the data from Thornley's table 2, where k_N was varied, gave the model

$fr/fs = 0.035 + 0.110\, k_C/k_N$ ($r = 0.9999$; 0.035 is 99% significantly higher than 0.017).

Both models are exactly the same type as equation (4) and this adds credence to Hunt & Burnett's model. On the other hand, it does not seem to be justified to suppose that the behaviour of the root/shoot ratio in an experiment can be described by a single model, particularly when, for example, a high k_C/k_N ratio can be caused by a high k_C or by a low k_N, as in Hunt & Burnett's work. That the model has a larger *a* when k_N is varied than when k_C is varied means that the nitrogen content of the plant, or the N/C ratio, changes more with a changing k_C/k_N ratio when k_N is varied, which seems quite reasonable. Concomitant with a larger *a* a varying k_N causes a smaller *b*. This means that variations in the k_C/k_N ratio, resulting from changes in k_N cause smaller changes in the fr/fs ratio than equal variations in the k_C/k_N ratio, as a result of changes in k_C. This is logical, because if a changing k_N causes a greater change in the nitrogen content, a smaller change will be needed in the fr/fs ratio to achieve this nitrogen content.

The validity of these assertions was tested using data from experiments 9, 10 and 11, in which both light intensity (k_C) and nitrogen supply (k_N) were varied. Because the values of k_C and of k_N were not measured, the root/shoot ratio was plotted against the USR/SAR ratio, which could be calculated from the harvest data (*fig. 2*). According to THORNLEY (1975) the use of the USR/SAR ratio is justifiable. In *fig. 2* the data are from plants that received either a varying light intensity or a varying nitrogen supply. The validity of the model

$fr/fs = a + b \times USR/SAR$

seemed to be good, r was mostly 0.999 and never below 0.998. In experiments 9 and 10, when light intensity was varied and the variation in USR was much larger than the variation in SAR, *a* varied beteen 0.054 and 0.060, and was 99% significantly higher than zero in all cases. When the nitrogen supply was varied and the SAR varied greatly, but the USR remained fairly constant, *a* varied

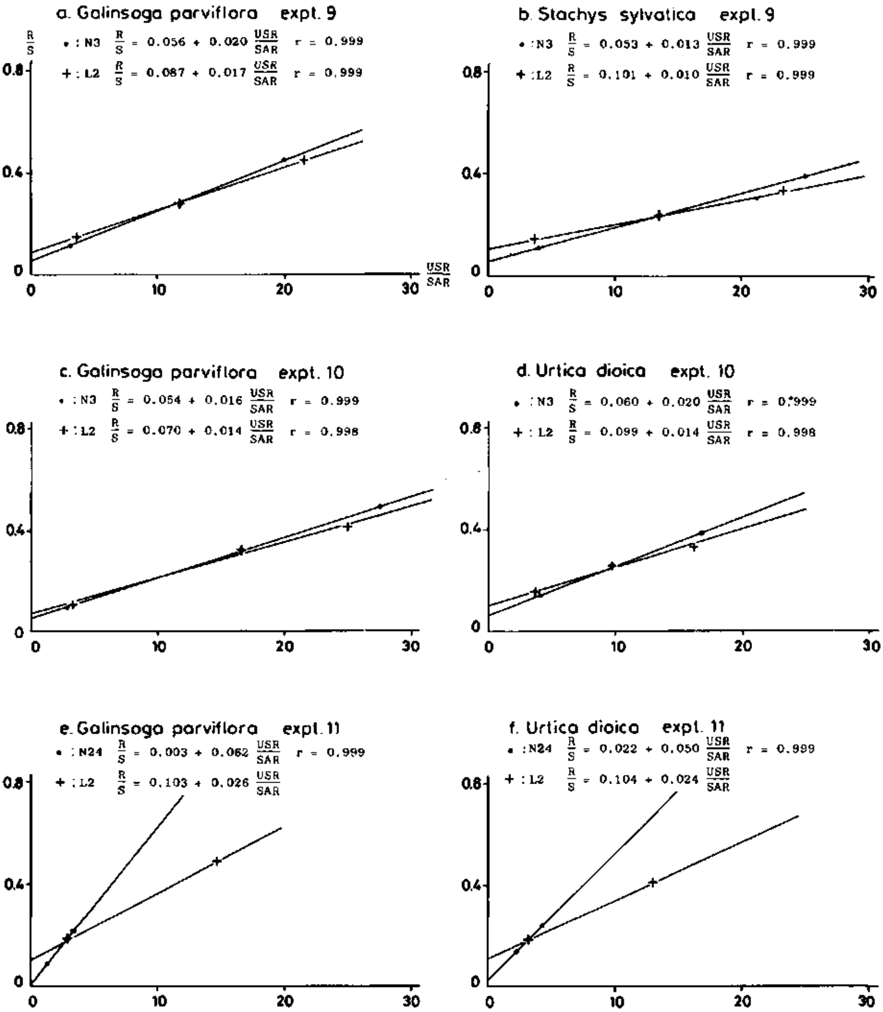

Fig. 2. Relationship between root/shoot mass ratio and shoot/root activity ratio for different light levels and for different nitrate levels in experiments 9, 10 and 11.

between 0.070 and 0.101. this range of values for *a* was clearly higher than that when light intensity was varied (99% significant in experiment 9 (for both species), but not significant in experiment 10). In experiment 11, when light intensity was varied, a lower *a* was found: 0.003 to 0.022, only 0.022 being significantly higher than zero (99%). But the nitrogen supply to the plants whose data I used was higher, and this might have influenced the model. When the nitrogen supply was varied, *a* was similar to the values for *a* found in experiments 9 and 10 (0.103 to 0.104). Thus in experiment 11 too, *a* was definitely higher when the nitrogen supply varied than when the light intensity varied, although this was not mathematically significant because with varying nitrogen supply the regression was based on only two data.

It can be concluded that in agreement with Thornley's model, the nitrogen content changes more when nitrogen supply is changed than when light intensity is changed, although these changes have the same effects on the USR/SAR ratio. My experimental data fitted Thornley's model very well, but the approximations made by Thornley himself and by Hunt & Burnett are simplifications that are not justified. The fact that the model fitted my experimental data well also means that the prerequisites THORNLEY (1972) stipulated, i.e. a steady state exponential growth with a constant dry matter distribution, net assimilation rate and specific absorption rate, were met in my experiments. Thus, my decision to supply the optimum amount of the nutrient for a limited period each day, appeared to be correct and very useful. The failure of other researchers to acknowledge that the exact model gives much better results than the approximations probably results from the widespread use of methods of nutrient supply in which the supply is not adjusted to the size of the plants, but is constant (e.g. x mg per plant per day) or even decreases with time (e.g. one single dose in soil at the start of the experiment); this disturbs the steady-state exponential growth. It can also be concluded that Thornley's assumption that in a broad range of light intensities and nutrient supplies the N/C ratio of the structural dry matter of the plant remains constant and the differences in the nitrogen content are mainly caused by changes in the nitrogen content of the non-structural dry matter, is justifiable.

5. CONCLUSIONS

The effects of light intensity and nitrate supply on growth did interact in all species tested. The interaction was apparent in the morphogenesis. With a low supply of nitrate the leaf weight ratio decreased much more under high light intensity than under low light intensity, while the effect on the net assimilation rate was small and did not depend on light intensity.

No interaction was found between the effects of light intensity and phosphate supply on the growth of both species, because the interactions between these effects on morphogenesis (LAR) and on productivity (NAR) cancelled each other out. With a low supply of phosphate, the leaf area ratio only decreased under high light intensity, but the net assimilation rate only decreased under low light intensity.

The different species reacted very similarly to light intensity and to nitrate supply; the reaction to phosphate supply was stronger in *Urtica dioica* than in *Galinsoga parviflora*.

The interactions between the effects of light intensity and nutrient supply did not differ between species. Thus it is unlikely that the shade tolerance of *Stachys sylvatica* and *Urtica dioica* is partly or wholly based on a lower sensitivity to low nutrient supply under low light intensity.

The method used for limiting the nutrient supply, an optimum supply during a limited period each day, enabled the nutrient supply to be adjusted to the size of the plants and this allowed the results to be accurately evaluated.

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ABBREVIATIONS

The abbreviations and formulas for growth analysis used conform with HUNT (1978).

Abbreviations used in chapter 4.2.

R	root mass	mg	(1)
S	shoot mass	mg	(1)
USR	unit shoot rate	$mg.mg^{-1}.day^{-1}$	(1)
SAR	specific absorption rate	$mg.mg^{-1}.day^{-1}$	(1)
k_C	specific shoot activity	$kgmol.m^{-3}s^{-1}$	(2)
$\bar{C}$	mean carbon substrate concentration	$kgmol.m^{-3}$	(2)
k_N	specific root activity	$kgmol.m^{-3}.s^{-1}$	(2)
$\bar{N}$	mean nitrogen substrate concentration	$kgmol.m^{-3}$	(2)
Y_G	conversion efficiency of carbon substrate into plant dry matter		(2)
fr	root weight ratio		(2)
fs	shoot weight ratio		(2)

Θ	dry matter to volume conversion factor	$m^3.kgmol^{-1}$	(2)
λ	atomic ratio of nitrogen atoms to carbon atoms in the plants		(2)
μ	specific growth rate	$m^3.m^{-3}.s^{-1}$	(2)

(1) cf. HUNT & BURNETT (1973), (2) cf. THORNLEY (1972)

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CHAPTER IV

GROWTH AND MORPHOGENESIS OF SUN AND SHADE PLANTS
IV. COMPETITION BETWEEN SUN AND SHADE PLANTS IN DIFFERENT LIGHT ENVIRONMENTS

SUMMARY

In eight experiments the competition between sun and shade plants was studied in different light environments. In higher light intensities the competitive ability of sun species was definitely greater. In lower light intensities, competitive ability did not differ basically between sun and shade species, but seemed mainly to depend on the weight of the plant at the start of the experiment. It is concluded that the competitive ability of sun and shade plants does indeed correlate positively with the light intensity of their natural habitats. The effect of the red/far-red ratio on competitive ability cannot be predicted from the experiments, but it is probable that when competing, sun species will be disadvantaged by a low red/far-red ratio.

1. INTRODUCTION

In previous papers (Corré 1983a, 1983b) it was concluded that the morphogenetic adaptations to low light intensity that occur in the juvenile phase are very similar in sun and shade species. The decrease in the relative growth rate in low light intensity was also found to be very similar. Only in a very low light intensity did some sun species grow very poorly, while others still showed the same adaptations as the shade species did. Thus, the growth response of free growing plants in the juvenile phase to low light intensity could not explain why the sun and shade species studied occur in different habitats. Nevertheless, some effect of the light intensity cannot be excluded. Since exponential growth only occurs in free spaced plants and only for a limited period, the relative growth rate is of limited value for predicting the productivity of a species at higher plant densities and in competition with other species. In addition, it is well known that a high productivity in a monoculture is no guarantee for a high competitive ability in mixtures. This is known the 'Montgomery effect', after Montgomery (1912), who discovered that higher yielding varieties of cereals were often crowded out in competition with lower yielding varieties, see also de Wit (1960) and van den Bergh (1968). It is even generally assumed nowadays (e.g. Trenbath 1974, Rhodes & Stern 1978) that plant characteristics that encourage a high growth rate in monoculture (especially the ability to use light efficiently) are more likely to reduce the competitive ability of a species. Hence, competition experiments could add useful information to this subject.

Grime (1981) and Smith (1982) have suggested that sun species have a more competitive strategy of avoiding shade, and that shade species have a less competitive strategy of tolerating shade. According to this we might expect sun species to have a greater ability to compete, especially when high growth rates are possible i.e. in high light intensity. In shaded conditions in a low light intensity, but especially in a low red/far-red ratio, it seems possible that competitive ability is less important and that the better shade tolerance of the shade species is crucial. But, more recently, the great importance of plant size at the moment the competition starts has been pointed out (Elberse & de Kruyf 1979, Spitters 1983). This plant size is partly determined by the relative growth rate of the free spaced plants in the early stages of an experiment, but the size of the seedlings (which depends on the time of emergence and on the weight and leaf area ratio of the seedlings) seems to be more important. Since the seedlings that were used in the present experiments were raised in a controlled environment, it will be clear that the starting positions in the experiments have no relation to the possible starting positions under field conditions. For example, any differences between species in temperature requirements for spring emergence and growth might appreciably influence the mutual starting positions in the field. Therefore we must be very cautious when applying the actual results of the competition experiments to field situations.

At the start of this study no experiments on the competition between sun and shade plants were known to have been published. In some experiments (e.g. Wong & Wilson 1980) it had been shown that the competitive ability of legumes *vis-à-vis* grasses was lower in lower light intensities, but species known to prefer naturally shaded habitats had not been studied. In 1981 a relevant paper was published (Wassink & van den Noort 1981). In that paper, the competitive ability of a sun species (*Calendula officinalis*) *vis-à-vis* a shade species (*Impatiens parviflora*) seemed to be clearly lower in lower light intensities, although it was not evaluated quantitatively.

In the present paper the results of eight experiments (nos. 9, 10 and 12 to 17) on the competition between sun and shade species will be discussed. In all experiments the effects of light intensity on competition were studied; in experiment 17 in addition to this the effects of the red/far-red ratio were investigated. Experiments 1 to 8 and 11 and the aspect of nutrient supply of experiments 9 and 10 have been discussed in earlier papers (Corré 1983a, 1983b and 1983c).

2. MATERIALS AND METHODS

2.1. Experimental design

Most data on the materials and methods in the competition experiments are listed in table 1. Except for experiment 13, all plants were grown on a nutrient solution containing 6.0 $me.l^{-1}$ NO_3^-, 0.5 $me.l^{-1}$ $H_2PO_4^-$, 3.5 $me.l^{-1}$ SO_4^{--}, 3.5 $me.l^{-1}$ K^+, 4.5 $me.l^{-1}$ Ca^{++}, 2.0 $me.l^{-1}$ Mg^{++} and the trace elements 2.0 ppm Fe, 0.5 ppm B, 0.7 ppm Mn, 0.05 ppm Mo, 0.1 ppm Zn and 0.02 ppm Cu. The solution had a pH of 6.5, was aerated constantly and was changed weekly. In experiment 13 the plants were grown in soil. To each pot containing circa 1100 g (air dried) rather poor sandy soil (pH H_2O ca. 6.0), solutions containing 16 me NO_3^-, 1 me $H_2PO_4^-$, 4.5 me SO_4^{--}, 6 me K^+, 11 me Ca^{++}, 4.5 me Mg^{++}, 11 mg Fe, 3.5 mg Mn, 2.5 mg B, 0.25 mg Mo, 0.6 mg Zn and 0.1 mg Cu were added partly before planting and partly during the growth period. When necessary, the plants were watered daily with tap water.

Seeds collected from plants growing in their natural habitats were germinated in a climatic room at 20° C under fluorescent light (40 $W.m^2$). Most of the experiments were started two weeks after germination, but the experiments with *Urtica* species started after circa three weeks. For *Impatiens parviflora* (expt. 16) seedlings were collected in the field.

2.2. Harvest procedures

In all experiments the species were grown in monoculture and in a 1:1 mixture. In experiment 13, 4 plants were planted per pot with an area of 120 cm^2. In the other experiments 12 plants were placed per pot with an area of 625 cm^2. In experiment 16, monocultures of 6 and of 2 plants per pot were also used. In experiment 13, 3 pots of each monoculture and 6 pots of the mixture were harvested at each harvest. In experiments 9, 10, 12, 14 and 15, at each harvest 1 pot of each monoculture and 2 pots of the mixture were harvested. In experiments 16 and 17, respectively 4 and 3 pots of each monoculture and 8 and 6 pots of the mixture were harvested simultaneously at the end of the growth period. The length of this period varied depending on the different light intensities.

Only in experiment 13 were enough space and seedlings available to allow a row of extra pots to be placed around the experimental plots; in all the other experiments side effects of varying importance will have occurred. In all experiments, leaf area and fresh and dry weights of leaf blades, of stems with petioles and of roots were recorded per pot, and per species for the mixtures.

Table 1. Experimental design of the competition experiments

a: experiments in glasshouse and experimental field

experiment no.	9	10	12	13
site	glasshouse	glasshouse	glasshouse	field
date	18-6/22-7-1980	5-8/9-9-1980	28-1/3-3-1980	4-8/19-9-1980
sun species	Galinsoga parviflora	Galinsoga parviflora	Urtica urens	Galinsoga parviflora
shade species	Stachys sylvatica	Urtica dioica	Urtica dioica	Circaea lutetiana
light levels	100%, 30%, 12%	100%, 30%, 12%	100%, 35%, 15%	100%, 30%, 10%, 3%
max. light intensity	ca. 200 W.m^{-2}	ca. 175 W.m^{-2}	ca. 75 W.m^{-2}	ca. 200 W.m^{-2}
light source	natural light	natural light	natural light + Philips HPIT	natural light
red/far-red ratio	ca. 1.1	ca. 1.1	ca. 1.5-3.5	ca. 1.1
day length	natural	natural	16 hrs.	natural
max. day temperature	ca. 30° C	ca. 30° C	ca. 25° C	ca. 25° C
min. night temp.	ca. 20° C	ca. 20° C	ca. 15° C	ca. 10° C
min. air humidity	ca. 30%	ca. 25%	ca. 40%	ca. 30%
max. air humidity	ca. 75%	ca. 70%	ca. 85%	ca. 90%
growth period	2, 3, 4, 5 wks.	2, 3, 4, 5 wks.	2, 3, 4 wks. or 2, 3, 4, 5 wks. (15%)	3, 5, 7 wks.

b: experiments in climatic rooms

experiment no.	14	15	16	17
sun species	Plantago major	Galinsoga parviflora	Galinsoga parviflora	Plantago major
shade species	Geum urbanum	Urtica dioica	Impatiens parviflora	Geum urbanum
light levels	60, 30, 15 W.m^{-2}	60, 30, 15 W.m^{-2}	60, 22, 8 W.m^{-2}	18, 7 W.m^{-2}
light source	fluorescent (Philips tl 33) + incandescent light (all expts.)			
red/far-red ratio	ca. 2.5	ca. 2.5	ca. 2.5	1.40 (18, 7 W.m^{-2}) 0.25 (7 W.m^{-2})
day length	16 hrs.	16 hrs.	16 hrs.	16 hrs.
day temperature	20° C	20° C	20° C	20° C
night temperature	15° C	15° C	15° C	20° C
air humidity	65%	65%	65%	65%
growth period	2, 3, 4, 5 wks.	2, 3, 4, 5 wks.	5 wks. (60 W.m^{-2}) 6 wks. (22 W.m^{-2}) 8 wks. (8 W.m^{-2})	8 wks. (18 W.m^{-2}) 11 wks. (7 W.m^{-2})

- in experiment 12 the red/far-red ratio depended on the relative quantity of natural light and was the same for all light levels (r/fr ratio natural light ca. 1.1; r/fr ratio HPIT ca. 3.5).
- in the shaded compartments of the glasshouse and the experimental field the temperature was mostly 1° or 2° higher and the air humidity was mostly 10 - 20% higher than the ambient values.
- the low red/far-red ratio in experiment 17 was established as described in Corré (1983b).

In experiments 9, 10, 13, 15 and 16, stem length was also measured.

2.3. Analysis of competition

The analysis of competition was done in accordance with the well-known model of de Wit (de Wit 1960, van den Bergh 1968). In this model the behaviour of two species in competition is described by their relative yield (RY), the relative yield total (RYT) and the crowding coefficient (k). In formula:

$RY = O/M$ O: yield in mixture, M: yield in monoculture

$RYT = RY_a + RY_b$ RY_a : RY species a, RY_b : RY species b

RY^o : RY at start, RY^t : RY at harvest

$k = \frac{RY_a^t}{RY_a^o} / \frac{RY_b^t}{RY_b^o}$ or $k = RY_a^t / RY_b^t$ (since RY_a^o and RY_b^o both are 0.50 in all expts.)

When the species are competing for the same growth factor (light in my experiments) the relative yield total is expected to be 1. Trenbath (1974) reviewed a number of mechanisms that might lead to a relative yield total differing from 1, such as differing growth rhythms or differing rooting depths, all of which are unlikely to occur in my controlled small-scale experiments. The crowding coefficient k was always calculated as the crowding coefficient of the sun species *vis-à-vis* the shade species, i.e. when k exceeded 1, the sun species was the stronger competitor and when k was lower than 1, the shade species was more successful in competition.

The analysis of the effects of plant density was also done according to de Wit (1960, see also Baeumer & de Wit 1968). This model is based on the assumption of a relationship between M (yield per pot in monoculture) and d (plant density in plants per pot), in accordance with the formula $M = \frac{\beta . d}{1 + \beta . d} \times \Omega$. This formula implies a rectangular hyperbole, and that implies a linear relationship between 1/M and 1/d, in accordance with the formula $\frac{1}{M} = \frac{1}{\Omega} + \frac{1}{\beta . \Omega} \times \frac{1}{d}$. In these formulas Ω is the theoretical yield at infinite plant density and β is the maximum area that can be occupied by a single free spaced plant under the given conditions and during the given growth period.

3. RESULTS

3.1. Competition

The results of the competition in all experiments are summarized in table 2. Beside the yields, the relative yields and the crowding coefficient, the leaf area index of the mixtures is listed. This latter value is important for the interpretation of k, because it quantifies the severity of the competition and it indicates the duration of the period during which competition occurred in an experiment. In the highest light intensity of all experiments, except for expt. 17, where no real high light intensity was used, the leaf area index indicated severe competition and the sun species was clearly the stronger competitor ($k>>1$). In the medium light intensities of experiments 9, 10 and 13, competition also clearly occurred, but was less severe, and the sun species was also the stronger competitor, but the k values were lower than in the highest light intensity. This is defined as a relatively smaller competitive ability, probably resulting from the fact that the competition lasted for a shorter period (as indicated by the lower leaf area index). In the lowest light intensity of these experiments, however, the leaf area index was very low, indicating that competition did not occur, and therefore k necessarily had to be circa 1. In the medium light intensity of experiments 12, 14 and 15 the same results were found, the competition was less severe and the sun species was the stronger competitor. In the low light intensity, however, the results were different. The values of the leaf area index indicated that competition did indeed occur. In experiment 14 the sun species was also the stronger competitor in this light intensity, but in experiments 12 and 15 the k value was circa 1, indicating a rough equilibrium between the sun and the shade species. In experiment 16 the shade species finally proved to be a stronger competitor in both the medium and the low light intensities, while the sun species was stronger in the high light intensity, as in all experiments. In the higher light intensity of experiment 17, which was only slightly higher than the lowest light intensity of experiment 14, in which the same species (*Plantago major* and *Geum urbanum*) were grown, the shade species was the stronger, while in experiment 14 the sun species was still the stronger competitor. In the lower light intensity of experiment 17 the shade species appeared to be a much stronger competitor under both the normal and the low red/far-red ratios, despite the lower leaf area index of the mixture in this light intensity.

Since the success of a species in the competition for light is assumed to be

Table 2. Dry matter yields (in g per pot), relative yields and crowding coefficients in competition experiments

expt. no.	sun species shade sp.	light intensity	d.m. prod. sun species		d.m. prod. shade species		RY sun sp.	RY shade sp.	RYT	k	leaf area index of mixture
			monoc.	mixt.	monoc.	mixt.					
9	Galinsoga parviflora Stachys sylvatica	100%	33.1	22.0	15.1	4.2	.63	.28	0.91	2.3	12
		30%	6.0	3.4	4.6	1.5	.57	.33	0.90	1.7	3.5
		12%	0.29	0.17	0.71	0.33	.59	.46	1.05	1.3	0.6
10	Galinsoga parviflora Urtica dioica	100%	50.8	38.2	18.4	3.4	.75	.18	0.93	4.2	15
		30%	9.6	6.5	4.3	1.3	.68	.30	0.98	2.3	5
		12%	0.78	0.38	0.42	0.18	.49	.43	0.92	1.1	0.6
12	Urtica urens Urtica dioica	100%	31.0	20.7	23.8	7.9	.67	.33	1.00	2.0	8
		35%	9.5	5.2	5.0	2.1	.55	.42	0.97	1.4	4
		15%	8.0	3.5	2.0	0.9	.44	.45	0.89	1.0	2.5
13	Galinsoga parviflora Circaea lutetiana	100%	8.6	4.7	1.3	0.2	.54	.16	0.70	3.4	9
		30%	3.5	2.5	1.1	0.2	.70	.16	0.86	4.4	7
		10%	0.50	0.35	0.31	0.11	.70	.35	1.05	2.0	2
		3%	0.03	0.02	0.06	0.03	.65	.50	1.15	1.3	0.3
14	Plantago major Geum urbanum	60 W.m^{-2}	48.3	37.9	27.9	6.9	.78	.25	1.03	3.1	10
		30 "	30.0	17.0	18.0	6.8	.57	.38	0.95	1.5	8
		15 "	9.3	5.9	9.3	3.9	.63	.42	1.05	1.5	4.5
15	Galinsoga parviflora Urtica dioica	60 W.m^{-2}	51.4	36.4	54.2	15.6	.71	.29	1.00	2.4	18
		30 "	39.0	22.9	31.7	15.0	.59	.47	1.06	1.3	17
		15 "	22.7	11.4	20.7	11.2	.50	.54	1.04	0.9	14
16	Galinsoga parviflora Impatiens parviflora	60 W.m^{-2}	33.9	21.5	28.2	9.9	.63	.35	0.98	1.8	12
		22 "	13.0	3.4	19.4	13.9	.26	.72	0.98	0.4	8
		8 "	5.0	0.72	13.2	6.7	.14	.51	0.65	0.3	5
17	Plantago major Geum urbanum	18 W.m^{-2}	23.6	7.2	26.9	17.2	.31	.64	0.95	0.5	10
		7 (r/fr:1.40)	3.4	0.26	8.4	7.6	.08	.90	0.98	0.1	5
		7 (r/fr:0.25)	2.3	0.22	8.0	7.0	.10	.88	0.98	0.1	4.5

primarily based on its ability to overtop its competitors, it seems probable that the cover value of a species in a mixture is a good indicator of its chances in competiton, not so much for its actual success, (for which k has proved to be a sufficient parameter) but especially for its chances in the future, i.e. if the experiments were continued. Baeumer & de Wit (1968) used the height growth of species in monoculture to predict the competitive abilities of those species in mixtures. The height growth seemed to give a reliable indication of the relative light interception of the species in a mixture. This is also likely to apply for the relative cover values, especially in experiments in climatic rooms, where only little light is measured under low angles of inclination. In my experiments, cover value is possibly even better than height growth as an indicator of competitive ability, because differences in height growth between the competing species were mostly small. The relative cover values of the two competing species were estimated from photographs taken at the final harvest or during the growth period in experiment 14, 15 and 17 (table 3).

Table 3. Relative cover values of a sun species and a shade species in mixtures

				relative cover values	
expt. no.	light intensity	growth period	k	sun species	shade species
				Plantago major	Geum urbanum
14	60 $W.m^{-2}$	5 wks.	3.1	90%	10%
	30 "	5 "	1.5	77%	23%
	15 "	5 "	1.5	55%	45%
17	18 "	5 "	-	31%	69%
	18 "	8 "	0.5	23%	77%
	7 "	8 "	-	0%	100%
				Galinsoga parviflora	Urtica dioica
15	60 $W.m^{-2}$	5 wks.	2.4	58%	42%
	30 "	5 "	1.3	52%	48%
	15 "	5 "	0.9	31%	69%

In all cases where k was higher than 1 the relative cover value of the sun species appeared to exceed 50%, indicating that it is a reliable estimation of success in competition. It is, however, remarkable that in experiment 14 the relative cover value of *Plantago major* in the lowest light intensity was lower than in the medium light intensity, while the k values were the same (1.5). This suggests that if the experiment had been continued, the relative k value in the lowest light intensity might have fallen. The same may hold for experiment 15, where the relative cover value of *Galinsoga parviflora* in the lowest light intensity was only 30%, suggesting that the insignificant advantage of *Urtica dioica* (k = 0.9) might have increased appreciably with continuing growth.

As was expected in these experiments, the relative yield total approximated 1.0 in all experiments, but two very significant exceptions were found. In both cases the weaker competitor had a very small relative yield, and the stronger competitor (this was the sun species in the highest light intensity of experiment 13 and the shade species in the lowest light intensity of experiment 16) had a relative yield just over 0.5. No explanation could be found for these unexpected results.

3.2. Growth in monocultures

Total dry matter production per pot (12 plants, but 4 plants in expt. 13) at the start and at the end of the growth period and mean stem length at the end of the growth period are given in table 4. Evidently, the dry matter production of the monocultures depended primarily on the light intensity. Stem elongation is stimulated by a lower light intensity, but is retarded by a lower supply of assimilates in low light intensities, and this is why the longest stems were mostly found in the highest light intensity and sometimes in the second highest light intensity. The effects of the light intensity on dry matter production and on stem length did not seem to differ between sun and shade species. In higher light intensities the sun species usually had a higher dry matter production, irrespective of the starting weight of the species. In lower light intensities, however, the dry matter production depended much more on the starting weight. In some experiments the sun species produced a higher yield, in others the shade species did. Generally, the higher producing species in an experiment also had longer stems than the lower producing one.

Table 4. Growth in monocultures (growth period in weeks, weight in g dry matter per pot, mean stem length in cm)

				sun species			shade species		
expt. no.	sun species shade sp.	light intensity	growth period	starting weight	final weight	stem length	starting weight	final weight	stem length
9	Galinsoga parviflora	100%	5	0.006	33.1	65	0.016	15.1	32
	Stachys sylvatica	30%	5	"	6.0	46	"	4.6	24
		12%	5	"	0.29	14	"	0.71	10
10	Galinsoga parviflora	100%	5	0.016	51	80	0.010	18	42
	Urtica dioica	30%	5	"	9.6	64	"	4.3	28
		12%	5	"	0.8	26	"	0.4	9
12	Urtica urens	100%	4	0.029	31.0		0.008	23.8	
	Urtica dioica	35%	4	"	9.5		"	5.0	
		15%	5	"	8.0		"	2.0	
13	Galinsoga parviflora	100%	7	0.006	8.6	53	0.013	1.3	6
	Circaea lutetiana	30%	7	"	3.5	61	"	1.1	10
		10%	7	"	0.5	28	"	0.3	7
		3%	7	"	0.03	9	"	0.06	7
14	Plantago major	60 W.m^{-2}	5	0.023	48.3		0.030	27.9	
	Geum urbanum	30 "	5	"	30.0		"	18.0	
		15 "	5	"	9.3		"	9.3	
15	Galinsoga parviflora	60 W.m^{-2}	5	0.010	51.4	55	0.015	54.2	65
	Urtica dioica	30 "	5	"	39.0	60	"	31.7	60
		15 "	5	"	22.7	50	"	20.7	60
16	Galinsoga parviflora	60 W.m^{-2}	5	0.010	33.9	76	0.086	28.2	61
	Impatiens parviflora	22 "	6	"	13.1	71	"	19.4	84
		8 "	8	"	5.0	53	"	13.2	76
17	Plantago major	18 W.m^{-2}	8	0.020	23.6		0.035	26.9	
	Geum urbanum	7 (r/fr:1.40)	11	"	3.4		"	8.4	
		7 (r/fr:0.25)	11	"	2.3		"	8.0	

3.3. Growth in different plant densities

Table 5 shows the effects of plant density on dry matter production and stem length for the species in experiment 16 and table 6 shows the corresponding values of β and Ω (see also fig. 1). The effect of plant density on dry matter production

Table 5. Growth of two species in monoculture at different plant densities in expt. 16 (weight in g dry matter per pot, mean stem length in cm)

		Galinsoga parviflora			*Impatiens parviflora*		
light intensity	plant density	starting weight	final weight	stem length	starting weight	final weight	stem length
60 $W.m^{-2}$	2	0.002	23.4	71	0.014	13.3	45
	6	0.005	29.9	75	0.043	23.6	59
	12	0.010	33.9	76	0.086	28.2	61
22 $W.m^{-2}$	2	0.002	11.1	73	0.014	9.2	68
	6	0.005	12.5	73	0.043	16.9	86
	12	0.010	13.0	71	0.086	19.4	84
8 $W.m^{-2}$	2	0.002	4.1	61	0.014	5.9	75
	6	0.005	6.2	68	0.043	11.2	83
	12	0.010	5.0	53	0.086	13.2	76

Table 6. Values of β and Ω and the correlation coefficient of the relation $1/M = 1/\Omega + 1/\beta.\Omega \times 1/d$ for two species in expt. 16

	Galinsoga parviflora			*Impatiens parviflora*		
light intensity	β (cm^2/plant)	Ω (g/pot)	r	β (cm^2/plant)	Ω (g/pot)	r
60 $W.m^{-2}$	660	35.5	0.988	175	37.2	0.999
22 "	1470	13.4	0.999	170	26.3	0.997
8 "	(690)	(6.0)	0.783	145	18.5	0.998

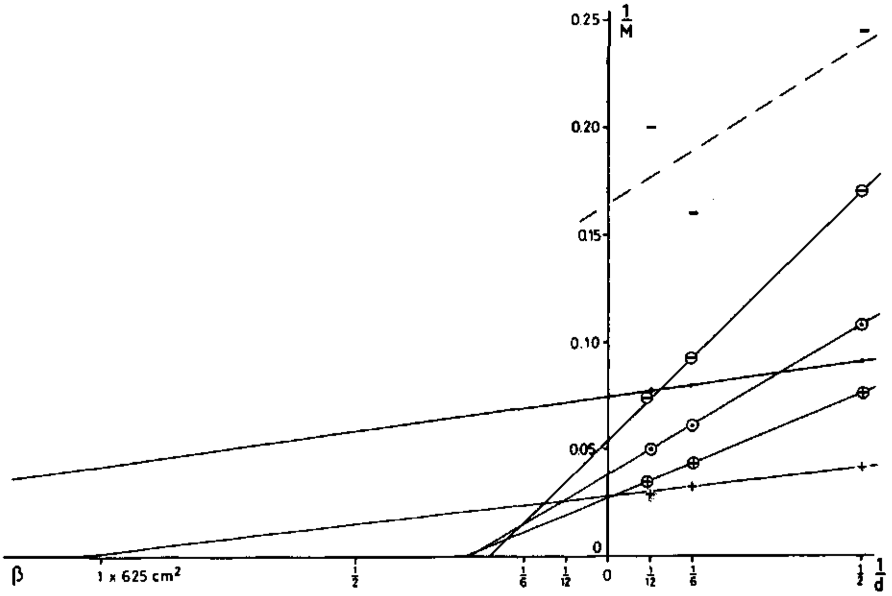

Fig. 1. The relation between 1/M and 1/d for two species in expt. 16. M: yield in g dry matter per pot, d: plant density in plants per pot. +, ⊕: 60 $W.m^{-2}$, ·, ⊙: 22 $W.m^{-2}$, −, ⊖: 8 $W.m^{-2}$.
+, ·, −: Galinsoga parviflora, ⊕, ⊙, ⊖: Impatiens parviflora.

was clearly greater in *Impatiens parviflora* than in *Galinsoga parviflora*. This is reflected in a much higher β for *G. parviflora*, indicating that this species has a more spreading growth. On the other hand, the values of Ω indicate that *Impatiens parviflora* can produce more dry matter at higher plant densities, especially in lower light intensities. It is remarkable that the density of 12 plants per pot already seemed to be excessive for dry matter production for *Galinsoga parviflora* in the low light intensity. This was probably because too weak stems were formed, which made it impossible to maintain an efficient producing canopy of planotrophic leaf blades. Stems should be longer when plant density is higher. In the lower light intensity, however, the greatest mean stem length was found in a lower plant density. This was caused by the presence of a few very short stems in the highest plant density: the maximum stem length was indeed longer in the highest plant density in all light intensities.

4. DISCUSSION

4.1. Competition in higher light intensities

In the higher light intensities of all experiments (i.e. 30% or more of the maximum light intensity in glasshouse or experimental field and 30 $W.m^{-2}$ or more in climatic room) the sun species was always clearly the stronger competitor. In the monocultures in these light intensities the sun species also produced more dry matter and formed longer stems, irrespective of whether its starting weight was higher or lower than that of the shade species. Only in the highest light intensity of experiment 15 did the shade species (*Urtica dioica*) have a somewhat higher dry matter production and clearly longer stems in monoculture than the sun species (*Galinsoga parviflora*), but here too the sun species was clearly stronger in competition (k = 2.4); this recalls the 'Montgomery effect' and the observation of Trenbath (1974) that the efficient utilization of light can reduce competitive ability.

To sum up, the chances of shade species in competition in higher light intensities seem pretty small. Firstly, they generally produced less dry matter and secondly, their competitive ability was also clearly less, even when their productivity was not lower.

4.2. Competition in lower light intensities

The results of competition in lower light intensities (the lowest light intensity of experiments 9, 10, 12, 14 and 15, the two lowest light intensities of experiments 13 and 16 and both light intensities of experiment 17) are not uniform. In some experiments the sun species was stronger and in others the shade species was the better competitor, while in a third group of experiments the productivity was too low to ensure competition. Therefore the results will be discussed for the experiments separately.

In experiments 9 and 10 and in the lowest light intensity of experiment 13, productivity was too low to ensure competition. In the second lowest light intensity of experiment 13, however, competition was still apparent, although not severe, with the sun species as the stronger competitor and the more productive and longer species in monoculture. In experiment 12 with *Urtica urens* and *U. dioica*, the competitors seemed to be in equilibrium (k = 1.0), while in monoculture the sun species reached a higher production (8 g per pot vs. 2 g per pot). This suggests the shade species had a greater competitive ability in that light intensity.

In experiment 14, with *Plantago major* and *Geum urbanum*, productivity was the same in both species and when competing the sun species was found to have a slight advantage (k = 1.5), although the relative cover values of the two species implied very little advantage for the sun species with continuing competition. In experiment 17, with the same two species as experiment 14, the shade species was already clearly the stronger competitor in a light intensity in which the sun species was still stronger in experiment 14. The shade species also had a clearly higher relative cover value and a slightly higher dry matter production. The discrepancy between these two experiments might have been caused by the relative starting weights, which tended to favour the shade species in experiment 17. Another difference that might have favoured the shade species in experiment 17 was the red/far-red ratio; 2.5 in experiment 14 and 1.40 in experiment 17. The longer growth period in experiment 17 was probably less important: five weeks after the start of the experiments the relative cover value of the shade species was already clearly higher in experiment 17. In the lowest light intensity of experiment 17 the productivity of the sun species was very low and it was totally overgrown by the leaves of the shade species.

In experiment 15, with *Galinsoga parviflora* and *Urtica dioica*, the shade species had a slightly lower dry matter production, but it had clearly longer stems and a small advantage in competition (k = 0.9). The relative cover values, however, implied an appreciable advantage with continuing competition. In experiment 16 the shade species had a higher dry matter production and longer stems and was clearly the stronger competitor in the two lower light intensities.

To sum up: success in competition in lower light intensities, without a concomitant lower red/far-red ratio, does not seem to depend on whether a plant is shade tolerant. The strongest competitor was generally the species with the highest dry matter production (or the longest stems) in monoculture, and this was generally the species with the heavier starting weight. Thus, in lower light intensities the starting weight of the species appeared to predetermine the results of the competition experiments (cf. Elberse & de Kruyf 1979, Spitters 1983), and whether the species was a sun or a shade species was less important.

4.3. Possible effects of the red/far-red ratio on competition

In the lowest light intensity of experiment 17 the competitive ability of the shade species (*Geum urbanum*) was so much greater than the competitive ability of the sun species (*Plantago major*) (which disappeared under a cover of leaves of the shade species) that a different red/far-red ratio was no longer likely to have any influence on the results of competition. On the other hand, in the low red/far-red ratio, the dry matter production of the monoculture fell by circa 30% for the sun species and by only circa 5% for the shade species. And, since the competitive ability of a species in lower light intensities seemed to depend largely on its dry matter production, it seems probable that the competitive ability of a sun species will be depressed in a low red/far-red ratio. In Corré (1983b) it was concluded that the decrease in the growth rate of sun species under a low red/far-red ratio was principally caused by an enhanced stem elongation, at the expense of the leaf weight ratio. *Plantago major* shows never stem elongation, but in this species a low red/far-red ratio causes an appreciable redistribution of dry matter, from leaf-blades to petioles.

A main effect of a low red/far-red ratio is an enhanced stem elongation, especially in sun species. In theory, an enhanced stem elongation could lead to overtopping and could therefore be advantageous in competition. However, the results of experiment 16, where the sun species (*Galinsoga parviflora*) had already formed stems too weak for optimal growth under a red/far-red ratio of 2.5, suggest that in practice this response could prove to be a further disadvantage for the sun species.

In an earlier paper (Corré 1983b) it was suggested that the habit of shade species to maintain a compact growth pattern under a low red/far-red ratio could be an important factor enhancing survival under a tree canopy. Differences between sun and shade species in this respect did not seem to be absolute, but merely gradual. When competition occurs, however, it is possible that relatively small differences might influence the mutual competitive abilities to an appreciable extent, and thus be very important for survival in the long term.

To sum up: the effects of a low red/far-red ratio on the competitive abilities of sun and shade species cannot be predicted from the results of these experiments, but it seems probable that these effects will be disadvantageous for the sun species.

4.4. Competition and plant strategies

Since sun species are supposed to have a more competitive strategy than shade species (Grime 1981, Smith 1982), they were expected to have a greater competitive ability in the experiments. In higher light intensities their competitive ability was indeed definitely greater, but in lower light intensities, having one strategy or another did not seem to influence the competitive ability of a species very much. Also, when competition was still relatively severe in a low light intensity (e.g. expt. 15), the competitive strategy did not succeed. Furthermore, a low red/far-red ratio would probably cause the competitive ability of sun species to decrease even more.

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GENERAL DISCUSSION

MORPHOGENESIS

In the experiments described in chapter I similar morphogenetic responses to light intensity were observed in sun and shade species. When plants in the same stage of development were compared, the area of the individual leaves and the internode length (fig. 7) appeared to be independent of the light intensity, but root development, leaf thickness (fig. 1) and stem thickness were clearly less in a low light intensity. With respect to the dry matter distribution, in a lower light intensity a lower root weight ratio and a higher stem weight ratio were found, whereas the leaf weight ratio was hardly affected (fig. 3, 4). The general opinion (Björkman 1981), however, is that the leaf weight ratio increases in a low light intensity. It seems probable that this opinion is the result of the usual comparison of plants of similar ages. With such a comparison an increase in the leaf weight ratio was indeed found in experiment 3 in *Stachys sylvatica* (ch. I, fig. 3). When, however, plants of similar dry weights were compared, the leaf weight ratio appeared to be completely independent of the light intensity and to decrease with increasing plant weight (ch. I, fig. 4). A decrease in the leaf weight ratio with increasing plant weight seems to be a general ontogenetic phenomenon, at least in larger plants (Evans 1972), and therefore the conclusion that the leaf weight ratio is not affected by the light intensity seems to be justified. This conclusion does not apply to very low light intensities (below ca. 10 $W.m^{-2}$), as here a decrease in the leaf weight ratio was found in both sun and shade species (ch. I, fig. 3d, ch. II, tab. 2).

Stem extension, measured as the final length of the individual internodes, was found to be hardly affected by the light intensity (ch. I, fig. 7), except for very low light intensities where it was generally stimulated (ch. II, tab. 2) The degree of this stimulation varied appreciably with species, but was not systematically different for sun and shade species. This confirms Smith's (1982) conclusion that reduced light levels cause increased stem extension in some, but by no means in all species. Grime & Jeffrey (1965) found an increased stem extension in a low light intensity in seedlings of many species, but the degree of increase seemed to depend primarily on the seed reserves of the species, and not on their shade tolerance. This again confirms the conclusion of chapter I that the morphogenetic adaptations to light intensity are caused by the different energy supply, and not directly by the light intensity. This conclusion is also supported by the finding of Hughes & Evans (1963) that in experiments with different daylengths the specific leaf area of *Impatiens parviflora* was much more closely related to the net assimilation rate than to the light intensity. Newton (1963) found that the growth rate of *Cucumus sativus* was also influenced far more by the total amount of radiation per day than by either light intensity or daylength.

In a low red/far-red ratio marked differences between responses of sun and shade species were observed. The sun species showed a greatly increased stem extension and concomitantly a markedly higher stem weight ratio and a lower leaf weight ratio. Shade species responded in the same way, but to a much lesser degree. This confirms the results obtained by Morgan & Smith (1979), who also found a quantitatively systematic difference between responses of sun and shade species, but not an absence of response in the shade species. Also, Whitelam & Johnson (1982) found an appreciable stem extension in the shade-tolerant *Impatiens parviflora* in a low red/far-red ratio. Since I inferred that the higher stem weight ratio was a result of the extra demand for assimilates by the rapidly extending stem, and that changes in the dry matter distribution were the result of changes in the mutual competitive abilities of the plant parts for energy and other growth essentials, and therefore I expected not only the leaf weight ratio, but also the root weight ratio to decrease and the specific leaf area to increase in a low red/far-red ratio. This was not found in my experiments (ch. II, tab. 2, fig. 3). However, it seems very possible that in the low light intensities used in my experiments the root weight ratio and the specific leaf area were already at the end of the range of possible adaptation, and that the expected responses would have occurred if the light intensity had been higher. For the root weight ratio this was confirmed by McLaren & Smith (1978), who indeed found a lower root weight ratio in *Rumex obtusifolius* in a low red/far-red ratio in a higher light intensity (ca. 13 $W.m^{-2}$), and no effect in a lower light intensity (ca. 5 $W.m^{-2}$). Kasperbauer & Peasly (1973) found a higher specific leaf area in tobacco with a far-red 'end-of-day' light treatment than with a red 'end-of-day' light treatment, but Holmes & Smith (1975) found a much lower specific leaf area in *Chenopodium album* in a continuous light treatment with a low red/far-red ratio. This may be explained in the following way. In experiment 8 it was found that the dry matter content of the leaf blades was appreciably higher in the low red/far-red ratio (ch. II, fig. 5). It is known that a higher dry matter content results in a lower specific leaf area. This higher dry matter content was thought to be a possible result of a higher leaf temperature, although no measurements were available.

Later, in experiment 17, with similar light treatments, the leaf temperatures of *Plantago major* and *Geum urbanum* were measured with an infrared thermometer. In both species the leaf temperature appeared to be higher in a low red/far-red ratio: 21-25° C vs. 19-20° C in a normal red/far-red ratio, the ambient air temperature being 20° C in both treatments. This difference in temperature, however, is unlikely to cause a systematically higher dry matter content (e.g. van Dobben et al. 1984). A more probable reason could be a difference in leaf structure. McLaren & Smith (1978) found that the cells of the leaves of *Rumex obtusifolius* were much smaller in a low red/far-red ratio. This implies the presence of more cell walls, with a higher dry matter content as a result.

In chapter III it was shown that plants did not experience problems in adapting morphogenetically to a combination of a low light intensity and a low nutrient supply. In a low light intensity, the root weight ratio appeared to be less increased by a low nutrient supply than in a high light intensity. With a low nutrient supply, the nutrient contents and the specific absorption rates were not lower in a lower light intensity than they were in a high light intensity (ch. III, tab. 1, 2). In a low light intensity the increase in the root weight ratio led to a lower stem weight ratio, whereas the leaf weight ratio remained almost unaffected. In a high light intensity, however, not only the stem weight ratio was lower, but also the leaf weight ratio, and therefore the leaf area ratio too.

These results were found for nutrient solutions where the nutrients had free access to the surface of the roots, and it therefore seemed probable that different responses might be found under field conditions, depending on the mobility of the appropriate nutrient in soil (ch. III, introduction). For nutrients with a low mobility in soil (e.g. phosphate), the amount available for absorption will be determined by the rooted soil volume. This volume may be smaller in a low light intensity (lower root weight ratio) and thus a greater adaptation to the low nutrient supply can be expected in a low light intensity.

The adaptations engendered by limiting water supply will differ from those engendered by nutrient supply, because the need for water is not primarily determined by the growth rate, but by the size of the plant, i.e. by the leaf area. The decrease in plant water potential depends on the actual transpiration, which is much lower in the shade than in a high light intensity, and on the ratio of leaf area to root weight, which is much higher in a low light intensity. Thus, it is difficult to predict whether the effects of water availability on the morphogenesis of a plant will be greater in higher or in lower light intensities. Since most references on this subject only deal with the effects on growth, this problem will be discussed further in a later paragraph.

GROWTH

In chapter I it was confirmed that over a wide range of decreasing light intensities the lower net assimilation rate was compensated for by a higher leaf area ratio and that this resulted in a relative growth rate independent of the light intensity. In lower light intensities, below circa 60 $W.m^{-2}$ in my experiments, the increase in the leaf area ratio could no longer keep pace with the decrease in the net assimilation rate, and a lower relative growth rate resulted. It was argued that where the relative growth rate was independent of the light intensity, growth was not limited by energy supply, but by another factor. This was supported by the results of van Dobben et al. (1981), who observed that the relative growth rate of *Phaseolus vulgaris* at a high light intensity became constant from the second day after germination on, although at that time the leaf area ratio was no more than 60% of it final value. This means that the net assimilation rate decreased with time, although there was no reason to assume that the photosynthetic capacity decreased too. In *Populus euramericana* Pieters (1974, 1983) also observed that the relative growth rates of the leaf length and width and of the stem length were independent of the light intensity. He postulated that in this case leaf and stem growth were limited by processes on a sub-cellular level. This agrees with Kemp's (1981) observation that it is most likely that the concentration of protein in the growing region of a leaf determines its relative growth rate when light is not limiting. Therefore it seems probable that the rate of protein synthesis limits growth.

In the range of light intensities over which the relative growth rate is independent of the light intensity, the value of the relative growth rate is temperature dependent. Moreover, at higher temperatures the critical light intensity of this range is clearly higher (Hunt & Halligan 1981, van Dobben et al. 1984). According to Hunt & Halligan the net assimilation rate in higher light intensities is also temperature dependent, much more so than photosynthesis. This means that the photosynthetic capacity is not fully used for dry matter production. This could be caused by a decrease in the photosynthetic rate, resulting from a low utilization of assimilates (e.g. King et al. 1967), but the respiration might also play a part in this. Both maintainance respiration (Penning de Vries 1975) and cyanide-resistant 'waste' respiration (Lambers 1979) could be involved.

As mentioned earlier, in lower light intensities the increase in the leaf area ratio cannot fully compensate for the decrease in the net assimilation rate, and therefore the relative growth rate falls. No differences between light intensity dependence in sun and shade species were found in the experiments reported in chapter I. Grime's conclusion (1965) that sun species generally have higher maximum relative growth rates was not confirmed. Possibly Grime's conclusion applies to a group of strong competitors, to which *Galinsoga parviflora* could belong, but not for sun species in general. Furthermore the relative growth rates of the shade species used in my experiments were also higher than those obtained by Grime & Hunt (1975), and more extreme shade species, such as *Oxalis acetosella*, and shade-tolerant species from poor soils, such as *Deschampsi* *flexuosa*, probably have lower maximum relative growth rates.

In a very low light intensity, two of the three sun species showed a very low relative growth rate, clearly lower than the shade species and than the third sun species (*Galinsoga parviflora*). In *Polygonum lapathifolium* this low relative growth rate was caused by a low net assimilation rate and in *Urtica urens* by a low leaf area ratio. This again indicates that some difference in response to a low light intensity, especially to a very low light intensity, can be found, but that this response does not differ systematically for sun and shade species.

In a low red/far-red ratio the net assimilation rate seemed to be generally a little lower than in a normal red/far-red ratio. This effect seemed to be the same for the sun and shade species in experiment 5, but somewhat greater for the sun species in experiment 7 (ch. II, fig. 6). A somewhat greater decrease in the sun species was to be expected; the lower leaf area ratio in sun species implies the presence of more respiring tissue per unit leaf area, and also the respiratio rate itself seemed to be enhanced to a greater extent in sun species grown in a low red/far-red ratio (ch. II, tab. 3). The combined effect of a lower leaf area ratio and a lower net assimilation rate resulted in a lower relative growth rate for sun species in a low red/far-red ratio. This finding may help explain why sun species are absent from shaded habitats.

COMPETITION

In contrast to free spaced plants, in higher plant densities the growth rate does not depend on plant size and relative growth rate only, but also on the efficiency of the interception and utilization of the light. The direct effects of plant density on growth were only studied in two species, but the results were very interesting (ch. IV, tab. 5). In a low plant density the period with exponential growth is relatively long. The relative growth rate of *Galinsoga parviflora* is much higher than that of *Impatiens parviflora* (ch. I, fig. 9), and for this reason *G. parviflora* could make up for its initial arrears in weight. The arrears were made up completely in the highest light intensity but only partly in the lower light intensities. At a higher plant density the period of exponential growth is short and the dry matter production depends much more on the efficiency of the interception and utilization of the light. From the yields in different plant densities it is possible to calculate a theoretical yield for infinite plant density; this is the yield that would have been reached if all the available light had been intercepted from the start of the experiment (de Wit 1960). This theoretical yield, Ω (see ch. IV, tab. 6), was similar for the two species in the high light intensity, indicating that the efficiency of the interception and utilization of high light intensities was the same for these two species. In a lower light intensity, however, Ω was much smaller in *G. parviflora*, indicating that this species is not capable of using low light intensities efficiently. A reason for this could be seen in the lowest light intensity, where the yield in the highest plant density was even less than the yield at half that density, because the stems became too weak to support the leaves and collapsed. In this way it became impossible to maintain a canopy of planotrophic leaves, which is necessary for an efficient interception of a low light intensity. This weakening of stems in a low light intensity must be the result of an enhanced stem extension caused by mutual shading. This was probably not the only reason, because in the medium light intensity *G. parviflora* also had a smaller Ω than *I. parviflora*, whereas the stems were still sufficiently strong to support the leaves. This difference in efficiency of the interception and utilization of low light intensities between a sun and shade species might be important for explaining the absence of sun species from shaded habitats, but the underlying reasons for the difference remain obscure. That the weakening of the stems is important becomes even more probable given the lower red/far-red ratio of the natural shade, because this will enhance stem extension even more, resulting in even weaker stems in the sun species. Although the direct effects of plant density were not studied, no such weakening of the stems was apparent in the other experiments where the same high plant density and sometimes even the same sun species was used. This lack of weak stems could have been caused by the low dry matter yield, with the subsequent absence of mutual shading (expts. 9, 10, 13), or by the higher light intensity, which produced firmer stems (expts. 12, 15), or by the sun species being a rosette plant (expts. 14, 17). Probably for the same reasons no conclusions on differences between sun and shade species in efficiency of interception and utilization of lower light intensities can be drawn from the values of the yields in monocultures (see ch. IV, tab. 4). Differences in yield seemed to depend primarily on the starting weights of the species. In higher light intensities the sun species mostly had higher yields in the monocultures. A large difference in yield suggests a difference in the efficiency of the interception or utilization of the light, but since the yields of *Galinsoga parviflora* and *Urtica dioica* were similar in experiment 15 and very different in experiment 10, no further conclusions can be drawn for high light intensities either.

Lowering the red/far-red ratio (expt. 17) hardly affected the yield of the shade species *Geum urbanum*, but the yield of the sun species *Plantago major* was much lower. This lower yield was assumed to be the result of a lower relative growth rate at the beginning of the experiment and of a lower efficiency of the utilization of the light, due to an enhanced respiration rate (cf. ch. II, tab. 3). In sun species with ascending stems the red/far-red ratio might affect growth even more, because the stem extension will be enhanced by a low red/far-re ratio, with even weaker stems and a more probable collapse as a consequence.

The competitive ability of a species depends on its seedling size and its relative growth rate at the beginning of the experiment, as these determine the space that is occupied by the species at the moment that the competition starts. There after its efficiency of interception and utilization of the light and its ability to overtop its competitors are decisive. In the higher light intensities of all experiments the sun species was clearly the stronger competitor. This is at least partly based on a better ability to overtop, since the sun species was also the stronger competitor when its dry matter production in monoculture was lower than that of the opposing shade species (expt. 15). A better overtopping ability was to be expected in the sun species, because of the stem extension in a low red/far-red ratio was enhanced more, which in these experiments was caused by mutual shading.

In a low light intensity the competitive ability of the species seemed to correlate best with their starting weights, but as suggested in the context of growth in higher plant densities, this was not the only important factor. In experiment 16 it was observed that *Galinsoga parviflora* collapsed in the lowest light intensity. This would also have happened with plants with a higher startin weight, and probably also in other experiments with a similar low light intensity, if these experiments had been prolonged. Experiment 16 was carried out in a red/far-red ratio of 2.5. A low red/far-red ratio, occurring under a tree canopy, would have caused still greater stem extension, with an earlier collapse as a result. For sun species another disadvantage of a low red/far-red ratio is a marked decline in the relative growth rate (cf. ch. II, fig. 7). This will result in smaller plants when the competition starts, with little chance of overtopping the competing shade species.

The results of the competition experiments were evaluated according to the theory put forward by de Wit (1960), but for some experiments an evaluation was also made on the basis of the relative cover values, which were estimated from photographs (ch. IV, tab. 3). The relative cover value of a species seems to be a good estimate of its light interception, especially in experiments in climatic rooms, where only little light is measured under low angles of inclination. The light interception is the factor that will primarily determine the success of a species in the competition for light. This gives the relative cover values some predicting value, which makes them very useful in situations where the competition has only lasted for a short time and not much difference in competitive abilities between species can be observed using de Wit's methods. In this way some useful additional information can be obtained by a simple, non-destructive method.

COMBINED EFFECTS OF LIGHT INTENSITY AND NUTRIENT SUPPLY

When different combinations of light intensity and nutrient supply are established, it is difficult to establish a limiting nutrient supply in such a way that this limitation is not influenced by the light intensity, or more precisely, by the size of the plants, which depends on light intensity. The usual methods, which involve applying similar amounts of nutrients per plant, are not suitable, because they naturally cause a greater limitation in larger plants, i.e. in a higher light intensity. A further problem is how to establish a limitation that is constant during the growth period. The usual methods also usually involve the nutrient supply deminishing with time.

Three methods are thought to be suitable for ensuring a constant nutrient limitation during plant growth, with exponential growth as a result. The first method has been described by Ingestad (1962) and by Ingestad & Lund (1979), and involves applying an exponentially increasing amount of nutrients each day. This method indeed provides exponential growth, but it has the disadvantage that the relative growth rate is determined by the researcher and is not influenced by the responses of the plants to the low nutrient supply. This implies that the method is not suitable for investigating the effects that a limiting nutrient supply could have on the relative growth rates of different species or in different light intensities. The second method has been described by e.g. Clement et al. (1974) and Edwards & Asher (1974). It implies growth on a nutrien solution with a very low, but constant nutrient concentration. This method does not have the disadvantage of Ingestad's method, but to keep the nutrient concentration constant, much equipment and very large volumes of nutrient solutions are required. Moreover, when the nutrient concentration is properly kept constant, even an extremely low concentration (e.g. 1 μM $NO_3^-.l^{-1}$) can be found to cause hardly any reduction in growth (Clement et al. 1974). Ingestad (1982) opined that the limitation of the growth produced by this method will mostly be caused by a disturbance of the steady-states of the plant, because of e.g. temporary depletions of the solution, and not by the low nutrient concentra itself. The third method implies an intermittent nutrient supply and has been described by Clement et al. (1979) for low nutrient concentrations in a flowing nutrient solution. The same vast amount of equipment was used as before (Clement et al. 1974), but the principle of intermittent nutrient supply seemed attractiv for the experiments I proposed to carry out. To minimize the equipment needed I simplified the method. Instead of one solution, to which nutrients were added intermittently, two solutions were used; one standard solution and one solution from which one nutrient was omitted. The plants were placed on the standard solution each day for a short time, and then after the roots had been rinsed with demineralized water, they were placed on the incomplete solution for the rest of the day. To avoid a premature depletion of the limiting nutrient, a high concentration was used, as is normal for non-flowing standard solutions, and the solutions were refreshed regularly. With this method the nutrient supply is also independent of the plant size, and growth was found to be exponential in all combinations of light intensity and nutrient supply, both with limiting levels of nitrate and of phosphate. With intermittent nitrate supply, Jackson et al. (1972) found a lower nitrate absorption during the first hours of renewed supply to depleted plants. This did not occur in my experiments, with 21 to 23 hours of depletion, nor in the experiments of Clement et al. (1979), with 48 hours of depletion. This might be explained by the results obtained by Doddema et al. (1978), who observed a lag phase in the absorption of nitrate after two days of depletion, but only in plants in which all free nitrate had been reduced during those two days. They assumed that after all the free nitrate had been reduced the nitrate uptake system had to be re-activated by the presence of nitrate.

It was found that the relative growth rate was lower with a lower supply of nitrate, mainly because of a lower leaf area ratio, but the net assimilation rate was only slightly lower. As a consequence of the lower leaf area ratio the relative growth rate declined more at high light intensities than at low light intensities. The results were found to satisfy Thornley's (1972) quantitative balanced model for root/shoot partitioning very well. This suggests that in the experiments the conditions for the validity of the model, i.e. exponential growth with a constant net assimilation rate and specific absorption rate, were fulfilled. On the other hand these experiments gave one of the first empirical corroborations for this theoretical model, which again confirms that the choice of the experimental methods is critical and that the chosen method of intermittent nutrient supply with high nutrient concentrations is very suitable for the establishment of similar limiting nutrient supplies for plants with different relative growth rates. The model also implies that the N/C ratio in the structural dry matter of the plant is similar whether nitrate supply is high or low; this agrees with the observation that the net assimilation rate is hardly affected by the nitrate supply.

It was found that in both higher and lower light intensities the relative growth rate was decreased to the same extent by a low phosphate supply; the cause of the decrease, however, was different. The effects on the morphology (leaf area ratio) were larger in a higher light intensity, but this was exactly compensated for by larger effects on the metabolism (net assimilation rate) in a lower light intensity.

As argued before (page 92), under field conditions the combined effects of light intensity and nutrient supply will be influenced by the mobility of the limiting nutrient in soil. For nitrate, which is fairly mobile, at least under moist conditions, effects similar to those found with nutrient solutions can be expected. For phosphate, however, it was inferred that a limiting supply in soil would probably cause a larger decrease in the leaf area ratio in a low light intensity than in a high light intensity. In combination with the larger decrease in the net assimilation rate, a low phosphate supply will probably also cause a larger decrease in the relative growth rate in a low light intensity under field conditions.

In my experiments the lower light intensities were established by artificial shading, with an unchanged red/far-red ratio. A lower red/far-red ratio, as found in natural shade, would have caused a decrease in the leaf area ratio of the sun species in low light intensity. Since in a low light intensity the leaf area ratio was hardly affected by the nutrient supply, there is no reason to expect that a low nutrient supply would have different effects on plants growing in a low or a high red/far-red ratio; furthermore, the interaction of the effects of light intensity and nutrient supply would probably also be similar. Since this interaction was the same for sun and shade species in the artificial shade, the same phenomenon can be expected in a natural shade.

COMBINED EFFECTS OF LIGHT INTENSITY AND WATER SUPPLY

A decrease in the water potential is known to limit leaf growth much earlier, i.e. at much lower water deficits, than photosynthesis (e.g. Hsiao et al. 1976). Thus, it is to be expected that a decrease in the relative growth rate, caused by a low availability of water will mainly be caused by a lower leaf area ratio and that the net assimilation rate will be much less affected. In the literature references have been made to low water supply having a larger effect on dry matter production in higher light intensities and also in lower light intensities Thus, Kulasegaram & Kathiravetpillai (1976) found that a low water supply had a larger effect on tea in a higher light intensity than in a lower light intensity, whereas in perennial ryegrass Deinum (1966) and Luxmoore & Millington (1971) found that a low water supply had a larger effect in a lower light intensity than in a higher light intensity. Since my results showed that a similar relative decrease in the relative growth rate caused a larger relative decrease in the dry matter production in a higher light intensity (see also ch. III, tab. 3), a larger relative decrease in the dry matter production in a low light intensity must surely be the result of a larger relative decrease in the relative growth rate in this light intensity. On the other hand, Kulasegaram & Kathiravetpillai found a much larger relative decrease in the relative growth rate in a higher light intensity. The contradictory findings of these researchers make it impossible to predict or even to postulate a universally valid interactio of the effects of light intensity and water availability. Neither is it possible to predict different interactions in sun and shade species.

According to the concept of the 'strategies' of 'shade avoidance' and 'shade tolerance' (Grime 1979), sun species are supposed to show enhanced stem extension in the shade and to have higher relative growth rates, higher respiration rates and higher turn-over rates in general. In chapter II this was roughly confirmed, but only when the low light intensity coincided with a low red/far-red ratio. In a low red/far-red ratio, stem extension and dark respiration were enhanced much more in sun species than in shade species, whereas the relative growth rate was decreased more in sun species. In chapter I, however, where only the light intensity was varied and the red/far-red ratio remained unchanged, no systematic differences were found between sun and shade species. Still, the concept of the strategies was framed long before the importance of the low red/far-red ratio in shade was known.

Insofar that the concept was based on evidence from field situations, this unintentional disregard of the red/far-red ratio is no problem: natural shade does include a low red/far-red ratio. Grime's experimental evidence, however, was based on experiments with variation in light intensity only, and this evidence was not supported by the results presented in chapter I. With regard to stem extension, the conclusion that sun species show more stem extension in a low light intensity was mainly based on the experiments of Grime & Jeffrey (1966). As already argued (page 90), the extent of increase in the stem extension they observed seemed to be based primarily on the seed reserves, and not on shade tolerance. More experimental evidence was available on the supposition that shade-tolerant species show lower relative growth rates, lower respiration rates and lower turn-over rates, compared with sun species (Björkman & Holmgren 1963, 1966, Loach 1967, Mahmoud & Grime 1974). The comparisons, however, were always made with sun species from productive habitats, and when these species are compared with sun species from unproductive habitats (habitats with nutrient stress), these stress tolerators also appear to have lower relative growth rates, lower respiration rates and lower turn-over rates (Chapin 1980). Thus, it seems that this type of low activity applies to stress tolerators in general, and not only to shade tolerators. It seems that the original experimental evidence was not sufficient to support a universally valid concept, but nevertheless the recognition that stem extension and respiration rate are the key-processes in shade tolerance was perfectly justified given the evidence on the effects of a low red/far-red ratio on sun and shade species.

Theoretically, the strategies of shade avoidance and shade tolerance seem to be only functional in the extremes, an intermediate strategy seems to make no sense. In a herbaceous vegetation, the plant would be overtopped by 'full shade avoiders' and under a tree canopy the plant would be weaker than 'full shade tolerators'. Anyhow, Grime (1979) considered the two strategies to be a continuum and Ellenberg (1979) also distinguished all possible intermediate forms between 'full sun species' and 'full shade species'. In chapter II it was shown that the responses of sun and shade species to a low red/far-red ratio were not totally different, but that differences were merely gradual.

To explain the purpose of the existence of intermediate strategies, the experiments of chapter IV provided important results. Shade-avoiding species did indeed appear to have a clearly greater competitive ability in higher light intensities, but in lower light intensities the competitive abilities of shade-avoiding and shade-tolerating species did not seem to be principally different. Moreover, it was shown that in a low light intensity a sun species (*Galinsoga parviflora* in expt. 16) formed stems too weak for optimal growth. It seems reasonable to suppose that in situations where the tree canopy is not dense and the herbaceous vegetation can grow fast enough to ensure competition for light, an intermediate strategy would be the most successful. The 'full shade avoiders' will form stems too weak for a good growth and the 'full shade tolerators' will still be crowded out in competition. An intermediate strategy could also be useful in deciduous woodlands. Before the leaf expansion of the trees in late spring the light intensity on the forest floor is high, and a more competitive strategy will be advantageous. After leaf expansion, however, shade tolerance is required to survive in the low light intensity period in summer. The herbaceous plants must ensure that the energy, collected in spring, is not used for the excessive stem extension, typical for full sun species. Probably in this situation full shade species would die in summer as a result of the excessive stem extension. Moreover, a more competitive strategy seems to be necessary to be able to compete with 'shade avoiders in time', such as *Ranunculus ficaria*, in spring. These species do not need any shade tolerance, because they simply become inactive in late spring and escape from the shade in that way.

Another example that no absolute, but only small differences in response to shade can be decisive for survival is shown by Pons (1983). He found no conclusiv differences in response to shading in the field between seedlings of the sun species *Cirsium palustre* and the shade-tolerant *Geum urbanum*, but *C. palustre* showed much higher mortality rates. Possibly a higher respiration could be involved; this is supposed to lead to a higher susceptibility to pathogens (Grime 1965).

CONCLUSIONS

In the research reported in this thesis, the responses of free spaced plants of sun and shade species in the vegetative phase to a low red/far-red ratio, such as prevails under leaf canopies, differed systematically. This difference is the basis of shade tolerance and intolerance in the vegetative phase and can explain why sun species fail in shaded habitats. This was confirmed in experiments with higher plant densities, where in a low light intensity the production of sun species was lower than that of shade species. This also applies for a low light intensity with a high red/far-red ratio, but in such situations the red/far-red ratio plays a part too, because of mutual shading.

The responses of free spaced plants of sun and shade species in the vegetative phase to a low light intensity, without a lower red/far-red ratio, did not generally differ. In direct competition with shade species in higher light intensities, sun species always had a greater competitive ability, even when their production in monocultures was lower. This greater competitive ability is also based on the responses to a lower red/far-red ratio, caused by mutual shading, i.e. an enhanced stem extension, which can lead to overtopping in these situations. This finding is an important contribution to explaining the absence of shade species in exposed habitats.

The responses of sun and shade species to various combinations of light intensity and nutrient supply did not differ.

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SUMMARY

he herbaceous vegetations of exposed and shaded habitats largely differ and his enables sun species to be distinguished from shade species. Nevertheless, ost sun species show large morphogenetic adaptations to the light intensity, n a similar or even more pronounced way than shade species. To improve our nderstanding of their specific habitat preferences, a number of herbaceous un and shade species were grown in the vegetative phase under various nvironmental conditions. Responses of growth and morphogenesis were recorded. ree-spaced plants were grown in different light intensities (quantum flux ensities), different light qualities (red/far-red ratios) and different ombinations of light intensity and nutrient supply. Sun and shade species were lso grown at various plant densities and in direct interspecific competition in ifferent light intensities and qualities. In one experiment the plants were rown in soil in an experimental field, in sixteen other experiments the plants ere grown on nutrient solutions in a glasshouse or in climatic rooms.

All species examined responded to light intensity strongly, and in very much he same way. The area of the individual leaves and the internode length ppeared to be independent of the light intensity. Root development, leaf hickness and stem thickness clearly decreased in a low light intensity. This esulted in a lower root weight ratio and a higher stem weight ratio, whereas he leaf weight ratio was hardly affected. At higher light intensities (above a. 60 $W.m^{-2}$) the relative growth rate was independent of the light intensity. t lower light intensities the relative growth rate decreased with light ntensity. In a very low light intensity (below ca. 5 $W.m^{-2}$) some sun species rew very poorly, but others showed morphogenetic adaptations and relative growth ates similar to those of the shade species. It was concluded that the habitat references as such cannot be explained by differences in response to light ntensity as such.

Sun species generally responded differently to a low red/far-red ratio than hade species: their stem extension increased markedly. This resulted in a igher stem weight ratio and a markedly lower leaf weight ratio, leaf area ratio nd relative growth rate. Also their dark respiration was found to have increased, ut the photosynthetic efficiency at non-saturating light intensities seemed to e unaffected. The shade species generally responded to a low red/far-red ratio n the same way, but to a lesser degree. These differences in response are resumed to be the underlying reasons for shade tolerance and shade intolerance

in plants in the vegetative phase. Under a tree canopy, stem extension only le to a weakening of the plant. In a herbaceous vegetation, however, it may lead a better light interception and is therefore functional.

The plants were provided with low nutrient supplies, using the principle of intermittent nutrient supply. This seemed the most suitable and simple method ensuring that plants of different sizes and with different growth rates receiv a similar limitation of the nutrient supply. The plants were placed on a standa nutrient solution for a short period each day and for the rest of the day on a solution with one nutrient (nitrate or phosphate) missing. The responses of su and shade species to various combinations of light intensity and nutrient supp (limiting nitrate or limiting phosphate) were studied. In all combinations of light intensity and nutrient supply, growth was exponential. For nitrate and phosphate supply interaction was observed between the effects of light intensi and nutrient supply, but differences between sun and shade species were not apparent.

When the nitrate or phosphate supply was limiting, the root weight ratio increased. In a low light intensity this increase was small and was achieved solely at the expense of the stem weight ratio. In a high light intensity, however, this increase was clearly larger and resulted in a lower stem weight ratio and a lower leaf weight ratio. This gave rise to a markedly smaller leaf area ratio in a high light intensity; in a low light intensity the leaf area ratio remained nearly unaffected. A low nitrate supply generally caused a slig fall in the net assimilation rate in all light intensities. As a result, the response of the relative growth rate was largely determined by the response of the leaf area ratio, i.e. a clearly greater decrease in a higher light intensi With a low phosphate supply the net assimilation rate remained unchanged in a high light intensity, but fell in a low light intensity. Because the leaf area ratio responded to a low phosphate supply in high and low light intensities in exactly the opposite way than the net assimilation rate responded, when the phosphate supply was low the relative growth rate decreased by exactly the sam extent in all light intensities. The data from the experiments on nitrate supply were compared with Thornley's balanced quantitative model for root/shoo partioning. The results were very satisfactory; this gave important experiment corroboration for this theoretical model.

In an experiment with different plant densities, a sun species (*Galinsoga parviflora*) was found to form stems too weak for optimum growth in a low light intensity. The efficiency of the interception and utilization of the light was uch lower than it was in the compared shade species (*Impatiens parviflora*).

When competing with shade species, sun species had definitely greater ompetitive abilities in higher light intensities. They usually produced more ry matter and had longer stems in monocultures too, but even when dry matter roduction and stem length were greater in the shade species in monocultures, the un species were still the stronger competitors. In lower light intensities, with high red/far-red ratio, the competitive abilities of the species seemed to orrelate best with their weight at the start of the experiment. The fact that *alinsoga parviflora* formed very weak stems, however, suggests a more general isadvantage for sun species when competing in a low light intensity. In an xperiment where the low light intensity had a concomitant low red/far-red ratio, he dry matter production of a monoculture of a sun species (*Plantago major*) was arkedly lower, whereas the dry matter production of a shade species (*Geum rbanum*) was hardly affected. This reinforces the hypothesis that sun species re at a disadvantage when competing in a low light intensity.

It can be concluded that the responses to the red/far-red ratio are crucial n explaining the habitat preferences of sun and shade species. Responses to the ight intensity might play a supplementary role, but systematic differences etween sun and shade species in this respect were not observed.

SAMENVATTING

De kruidachtige vegetatie van open en beschaduwde biotopen is zeer verschillend en dit maakt het onderscheiden van licht- en schaduwplanten mogelijk. Toch vertonen de meeste lichtplanten in experimenten vergelijkbare of zelfs meer uitgesproken morfogenetische aanpassingen aan het lichtniveau dan schaduwplanten. Met het doel meer inzicht te verkrijgen in de specifieke eigenschappen die hun voorkomen in verschillende biotopen kunnen verklaren, werd een aantal verschillende kruidachtige licht- en schaduwplanten onder verschillende omstandigheden opgekweekt en werden de reacties van groei en morfogenese geïnventariseerd. Vrijstaande planten werden opgekweekt bij gevarieerd lichtniveau, gevarieerde lichtkwaliteit (rood/ver-rood verhouding) en verschillende combinaties van lic niveau en nutrientenvoorziening. Licht- en schaduwplanten werden ook opgekweekt in verschillende dichtheden en in directe concurrentie bij verschillende lichtniveaus en lichtkwaliteiten. In één experiment werden de planten opgekweekt in grond in de proeftuin, zestien andere experimenten werden uitgevoerd in de kas of in klimaatkamers met planten op voedingsoplossingen.

Alle onderzochte soorten reageerden sterk en op vergelijkbare wijze op verschillen in lichtniveau. Bij vergelijking van planten in een gelijk ontwikkeli stadium bleek het oppervlak van de individuele bladeren en de lengte van de internodiën weinig door het lichtniveau beinvloed te worden. De groei van de wortels, bladdikte en stengeldikte werd duidelijk minder bij een lager lichtniveau. Hierdoor werd het wortelaandeel in het plantgewicht kleiner en het stengelaandeel groter, het bladaandeel werd nauwelijks beinvloed. Bij hogere lichtniveaus (boven ± 60 $W.m^{-2}$) was de relatieve groeisnelheid onafhankelijk van het lichtniveau. Bij lagere lichtniveaus daalde de relatieve groeisnelheid met het lichtniveau. Bij een zeer laag lichtniveau (onder ± 5 $W.m^{-2}$) groeide een aantal lichtplanten slecht, maar andere toonden nog dezelfde aanpassingen en vergelijkbare relatieve groeisnelheden als de schaduwplanten. De conclusie werd getrokken dat het voorkomen van licht- en schaduwplanten in verschillende biotopen niet kan worden verklaard door hun reacties op het lichtniveau alleen

De reacties van licht- en schaduwplanten op een lage rood/ver-rood verhoudi waren systematisch verschillend. Bij de lichtplanten werd een duidelijk versterkte stengelstrekking gevonden. Dit resulteerde in een groter stengelaandee en een kleiner bladaandeel in het plantgewicht, een kleiner relatief bladoppervlak en een lagere relatieve groeisnelheid. Ook de donker-respiratie blee hoger te zijn, maar de efficiency van de niet-lichtverzadigde fotosynthese lee niet te worden beinvloed. De schaduwsoorten reageerden in het algemeen op dezelfde wijze op een lage rood/ver-rood verhouding, maar in veel mindere mate. Deze verschillen in reactie worden verondersteld de basis te vormen van schaduwtolerantie en -intolerantie in planten in de vegetatieve groeifase. Het reageren op beschaduwing met strekking van de stengel leidt in een bos slechts tot verzwakking van de plant. In een kruidenvegetatie kan deze strekking echter leiden tot het opvangen van meer licht, en kan daarom in dergelijke vegetaties als een functionele aanpassing gelden.

Een lage nutrientenvoorziening werd gerealiseerd volgens het principe van de intermitterende nutriententoediening. Dit leek de beste methode te zijn om op een eenvoudige wijze een gelijke beperking te garanderen voor planten van ongelijke grootte en met ongelijke relatieve groeisnelheden. De planten werden dagelijks gedurende een korte tijd op een volledige voedingsoplossing geplaatst, de rest van de dag stonden ze op een oplossing waaraan één nutrient ontbrak. De reacties van licht- en schaduwplanten op een combinatie van gevarieerd lichtniveau en gevarieerde nitraat- en fosfaatvoorziening werden geinventariseerd. Bij alle combinaties was de groei exponentieel. Voor beide nutrienten werd een interactie tussen de effecten van lichtniveau en nutrientenvoorziening gevonden, maar verschillen tussen licht- en schaduwplanten werden niet gevonden.

Bij een beperkende nitraat- of fosfaatvoorziening was het wortelaandeel in het plantgewicht hoger. Bij een laag lichtniveau was deze verhoging klein en kon zij gerealiseerd worden door een verlaging van alleen het stengelaandeel. Bij een hoog lichtniveau was de verhoging duidelijk groter en werden stengel- en bladaandeel beide kleiner. Dit had een verlaging van het relatief bladoppervlak tot gevolg bij een hoog lichtniveau, terwijl dit nauwelijks veranderde bij een laag lichtniveau. Bij een lage nitraatvoorziening was de netto productiviteit van het bladoppervlak in het algemeen iets lager bij alle lichtniveaus. Aldus werd de reactie van de relatieve groeisnelheid op de nitraatvoorziening voornamelijk bepaald door de reactie van het relatieve bladoppervlak, met als gevolg een grotere daling van de relatieve groeisnelheid bij een hoog lichtniveau. Een lage fosfaatvoorziening had geen negatieve invloed op de netto productiviteit van het bladoppervlak bij een hoog lichtniveau, maar wel bij een laag lichtniveau. Het resultaat van de tegengestelde reactiepatronen van relatief bladoppervlak en netto productiviteit op een beperkende fosfaatvoorziening was een in precies dezelfde mate verlaagde relatieve groeisnelheid bij alle lichtniveaus. De gegevens van de experimenten met gevarieerde nitraatvoorziening werden getoetst aan het model van Thornley voor de verdeling van droge stof over spruit en wortel.

Het resultaat van de toetsing was zeer bevredigend en dat vormt een belangrijke experimentele ondersteuning voor dit theoretische model.

In een experiment met verschillende plantdichtheden vormde de lichtplant (*Galinsoga parviflora*) bij een laag lichtniveau te zwakke stengels voor een optimale groei. Het licht werd veel minder efficient opgevangen en benut dan bij de vergeleken schaduwplant (*Impatiens parviflora*).

In directe concurrentie met schaduwplanten hadden de lichtplanten bij hogere lichtniveaus duidelijk een grotere concurrentiekracht. In de meeste gevallen produceerden zij ook meer droge stof en langere stengels in de monocultures, maar zelfs wanneer de droge stof productie en de stengellengte in monocultuur achterbleef, was de lichtplant nog sterker in de concurrentie. Bij lagere lichtniveaus leek de concurrentiekracht van de verschillende soorten in de eerste plaats bepaald te worden door hun uitgangsgewichten in de experimenten. De genoemde vorming van zeer zwakke stengels door *Galinsoga parviflora* bij een laag lichtniveau suggereert echter een mogelijk meer algemeen nadeel voor lichtplanten in de concurrentie bij een laag lichtniveau. In een experiment waar het licht bij een laag lichtniveau tevens een lage rood/ver-rood verhouding had, zoals dat in een natuurlijke schaduw ook het geval is, was de productie van de lichtplant (*Plantago major*) duidelijk lager dan in hetzelfde lichtniveau en een hoge rood/ver-rood verhouding. De productie van de schaduwplant (*Geum urbanum*) was echter nauwelijks lager. Dit suggereert nog een bijkomend nadeel voor de lichtplanten in de concurrentie bij lage lichtniveaus in het veld.

Er werd geconcludeerd dat de reacties op de rood/ver-rood verhouding van het licht de basis vormen van de verklaring van het voorkomen van licht- en schaduwplanten in verschillende biotopen. Reacties op het lichtniveau kunnen een bijkomende rol spelen, maar systematische verschillen tussen licht- en schaduwplanten op dit punt zijn niet waargenomen.

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CURRICULUM VITAE

Wim Corré werd geboren op 27 januari 1951 te Oostkapelle.

Aan de Rijks Hogere Burger School te Middelburg werd in 1968 het eindexamen HBS-b afgelegd en in datzelfde jaar werd de studie aan de Landbouwhogeschool te Wageningen aangevangen. In september 1972 werd het kandidaatsexamen in de richting Landbouwplantenteelt, met als specialisatie de graslandoecologie, afgelegd. In januari 1976 volgde het doctoraalexamen met als hoofdvakken de Graslandcultuur en het Natuurbehoud en -beheer en als bijvak de Regionale Bodemkunde.

Na het vervullen van de dienstplicht werd van juni 1977 tot januari 1978 meegewerkt aan een onderzoekproject van de vakgroep Vegetatiekunde en Plantenoecologie van de Landbouwhogeschool middels het uitvoeren van groeiproeven met enkele Carex soorten.

Van januari 1978 tot januari 1979 werd gewerkt in een TAP-project van de vakgroep Bodemkunde en Bemestingsleer van de Landbouwhogeschool aan een onderzoek naar nitraat- en nitrietgehalten van groenten.

Van maart 1979 tot maart 1982 werd gewerkt als promotieassistent bij de vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde van de Landbouwhogeschool aan het onderzoek waarvan de resultaten zijn vastgelegd in dit proefschrift.