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. (1), *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$_2$PO$_4^-$, 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
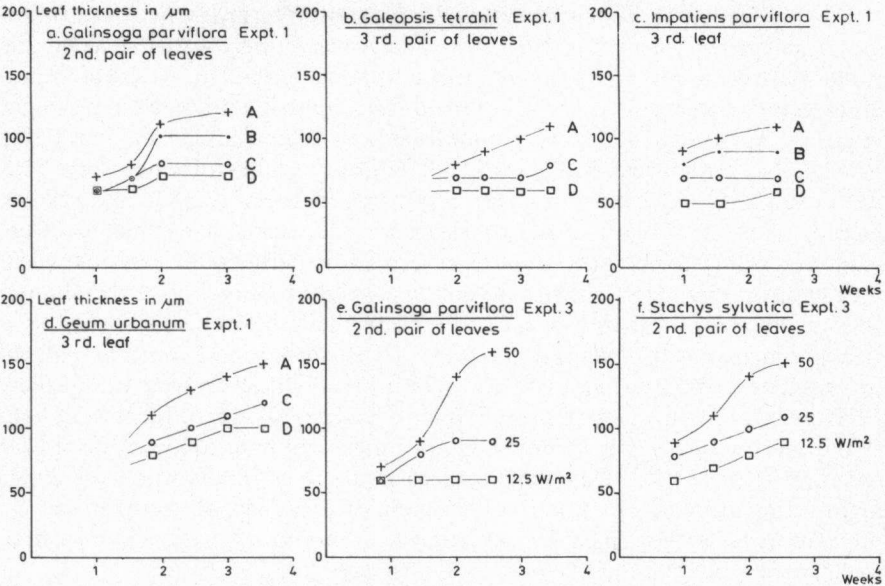
Fig. 1. Development of leaf thickness with time in different light intensities in expts. 1 and 3. Light level A = 100%; B = 80%; C = 60%; D = 40%.

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
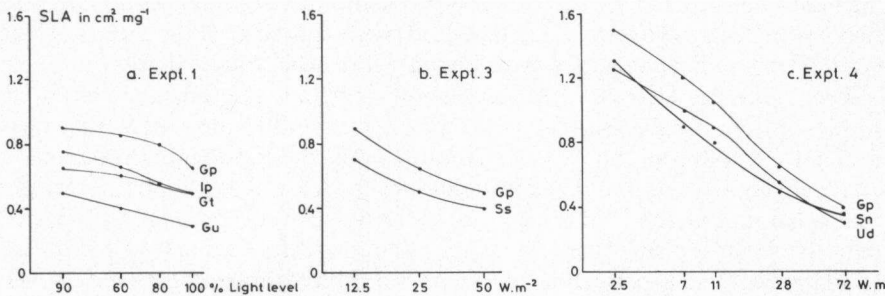

Fig. 2. Specific leaf area of plants of final harvest in expts. 1, 3 and 4. Species cf. *fig. 3.*
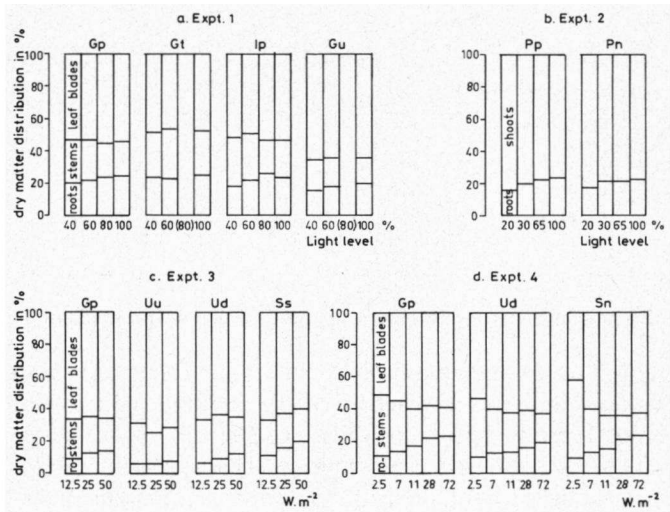
Fig. 3. Dry matter distribution of plants of final harvest in expts. 1, 2, 3 and 4. Species: Gp: *Galinsoga parviflora*, Gt: *Galeopsis tetrahit*, Gu: *Geum urbanum*, Ip: *Impatiens parviflora*, Pn: *Poa nemoralis*, Pp: *Poa pratensis*, Sn: *Scrophularia nodosa*, Ss: *Stachys sylvatica*, Ud: *Urtica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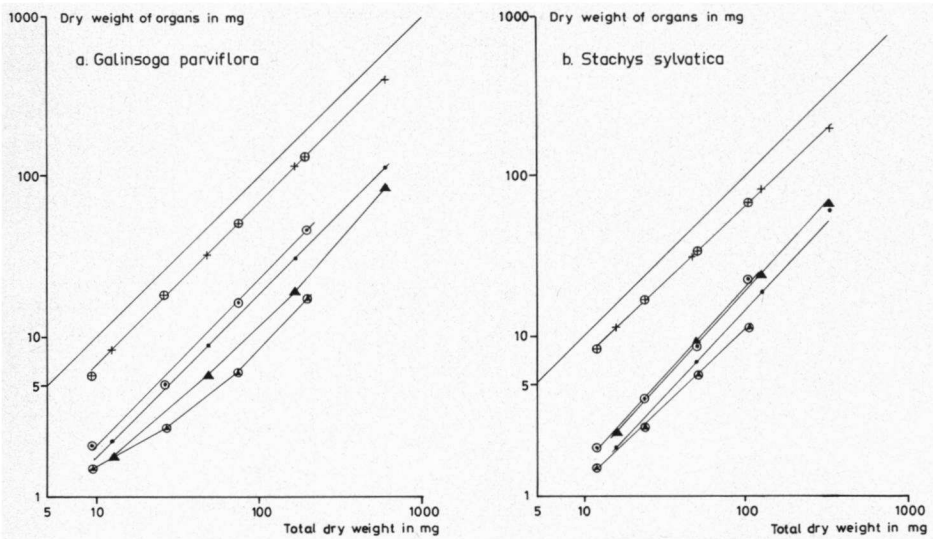

Fig. 4. Dry weight of plant organs plotted against total dry weight for two species and two light intensities in expt. 3 on logarithmic scale. + ⊕ : leaf blades, · ⊙ : stems and petioles, ▲ Ⓐ: roots; ⊕ ⊙ Ⓐ 12.5 $W.m^{-2}$, + · ▲ : 50 $W.m^{-2}$.
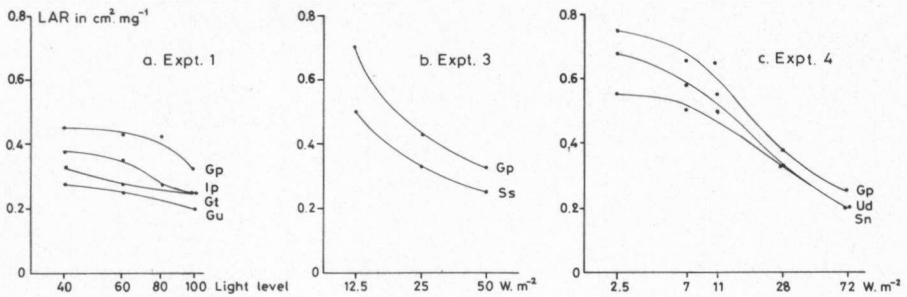
Fig. 5. Leaf area ratio of plants of final harvest in expts. 1, 3 and 4. Species cf. *fig. 3.*

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
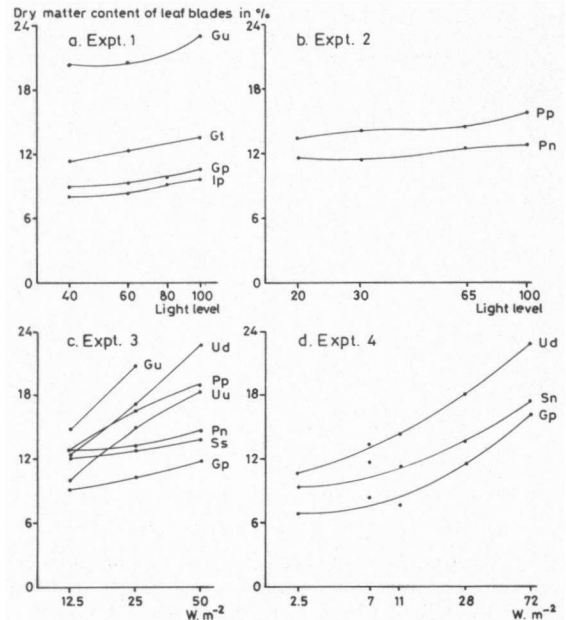

Fig. 6. Dry matter content of leaf blades of plants of final harvest in expts. 1, 2, 3 and 4. Species cf. *fig. 3.*
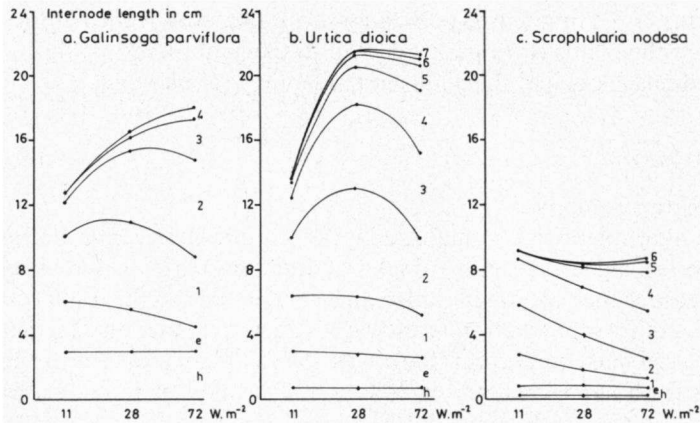
Fig. 7. Length of successive internodes of plants of final harvest in three light intensities in expt. 4. h = hypocotyl, e = epicotyl, 1, 2, ... = successive internodes.

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-
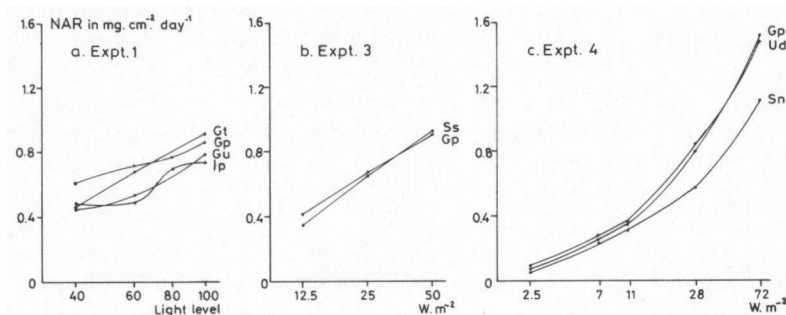

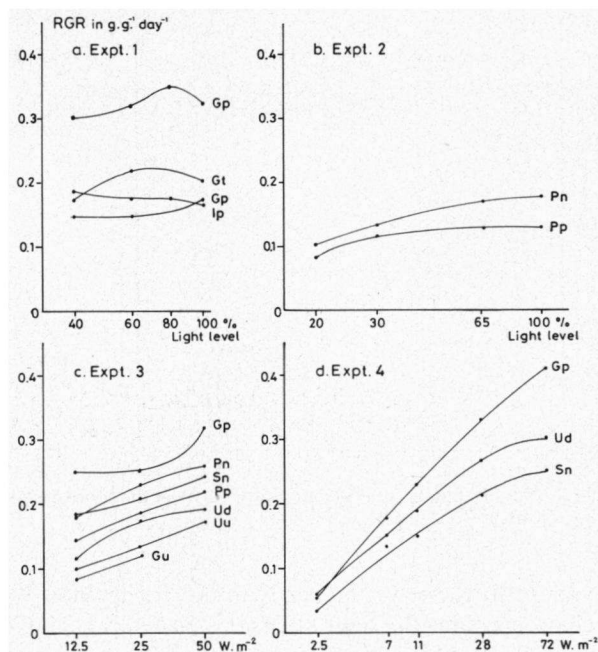Fig. 8, Net assimilation rate of plants in expts. 1, 3 and 4. Species cf. *fig. 3.*

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/m², 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
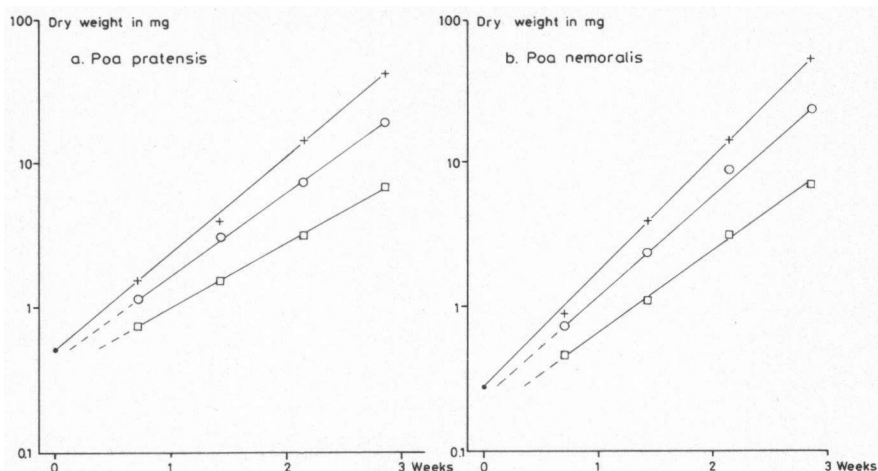
Fig. 10. Logarithmic total weight plotted against time for two species in expt. 3. □ : 12.5 W.m^{-2}, ○ : 25 W.m^{-2}, + : 50 W.m^{-2}.

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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