

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

W.J. CORRÉ

Vakgroep Vegetatiekunde, Plantenoeecologie en Onkruidkunde, Landbouwhogeschool. De Dreijen
11, 6703 BC Wageningen

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 NO₃⁻, 0.5 me.l⁻¹ H₂PO₄⁻, 3.5 me.l⁻¹ SO₄⁻, 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	—	—
C ¹	—	—	—	—	—	—	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 CO₂ contents of incoming (330 ppm) and outgoing 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

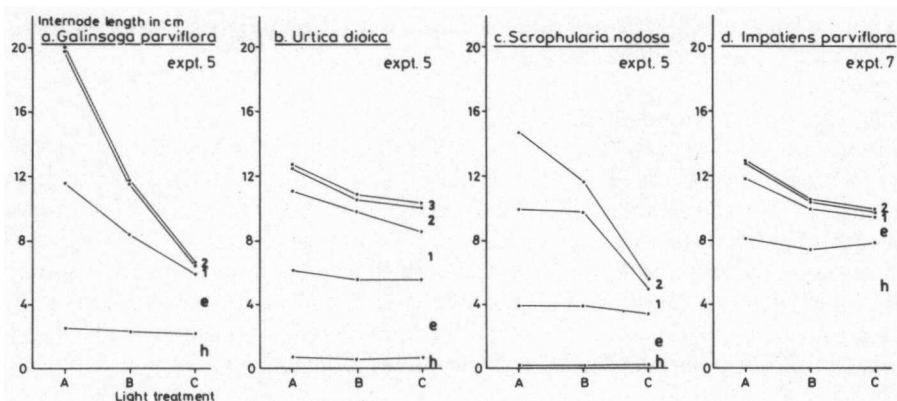


Fig. 1. Stem length of 4 species from experiments 5 and 7, divided into internodes. h = hypocotyl, e = epicotyl, 1, 2, .. = successive internodes.

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

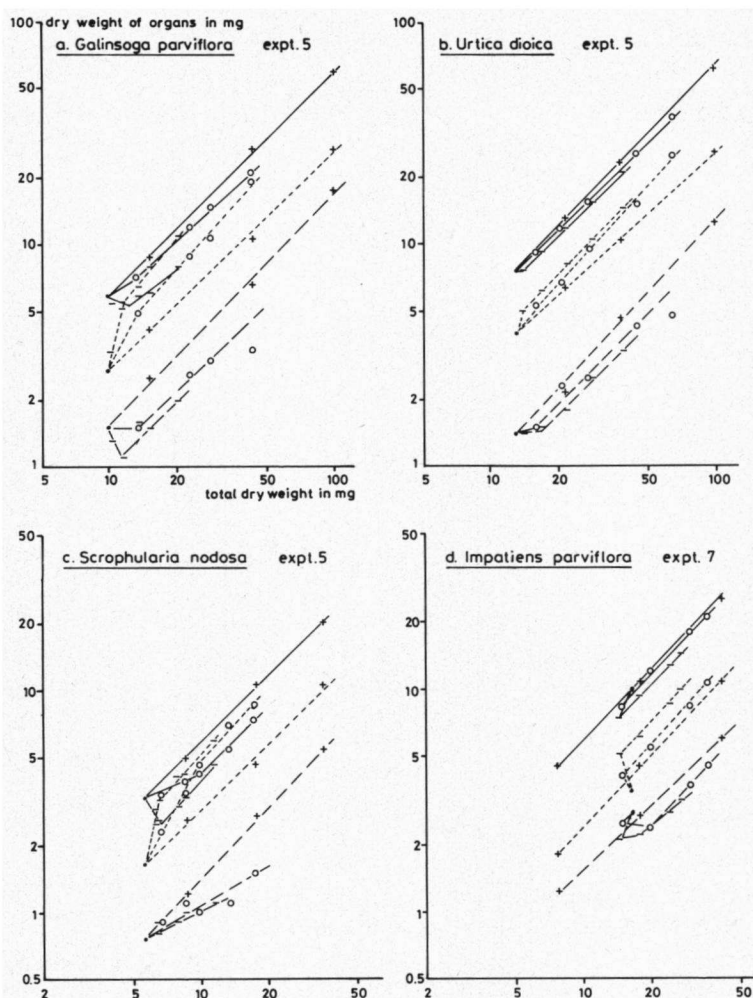


Fig. 2. Dry weight of plant organs plotted against total dry weight for 4 species from experiments 5 and 7, on a logarithmic scale. Light treatment: —: A, o: B, + C; —: leaf blades, ---- stems and petioles — —: roots.

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

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

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

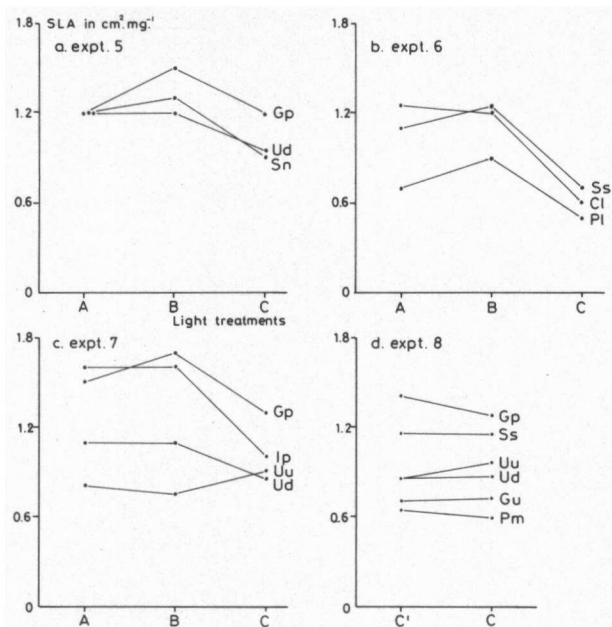


Fig. 3. Specific leaf area of plants in experiments 5, 6, 7 and 8. Species: Cl: *Circaea lutetiana*, Gp: *Galinsoga parviflora*, Gu: *Geum urbanum*, Ip: *Impatiens parviflora*, Pl: *Polygonum lapathifolium*, Pm: *Plantago major*, Sn: *Scrophularia nodosa*, Ss: *Stachys sylvatica*, Ud: *Urtica dioica*,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

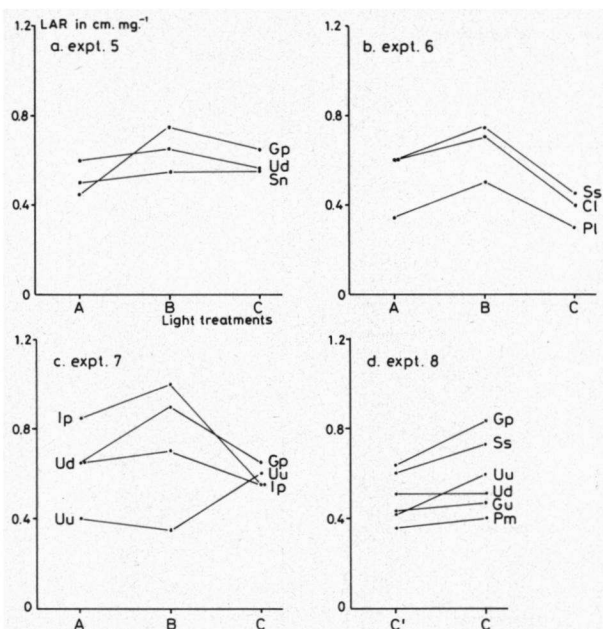


Fig. 4. Leaf area ratio of plants in experiments 5, 6, 7 and 8. For species, see fig. 3.

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

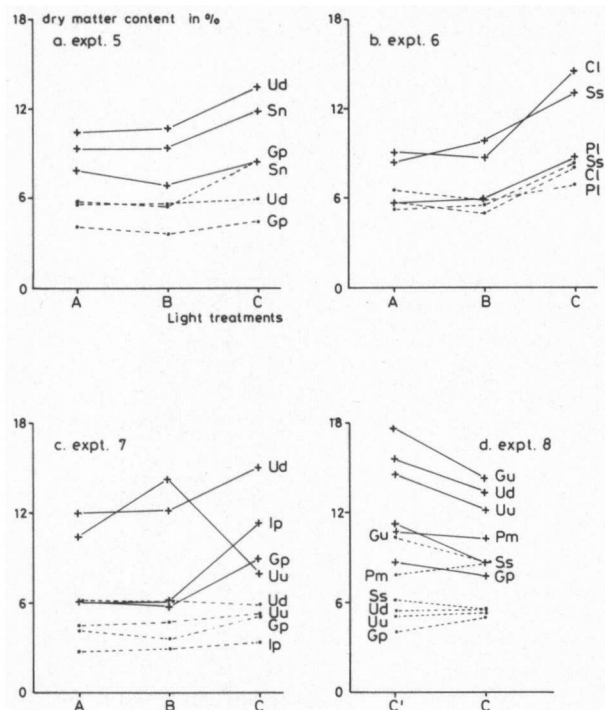


Fig. 5. Dry matter content of leaf blades and of stems and petioles of plants in experiments 5, 6, 7 and 8. +: leaf blades, •: stems and petioles. For species, see fig. 3.

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 CO₂), 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,

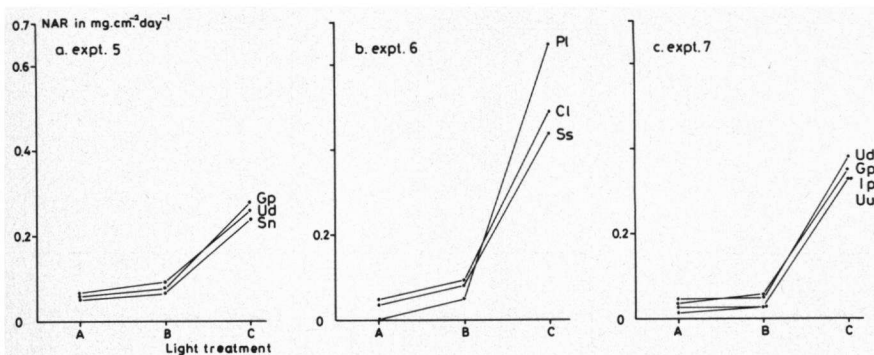


Fig. 6. Net assimilation rate of plants in experiments 5, 6 and 7. For species, see fig. 3.

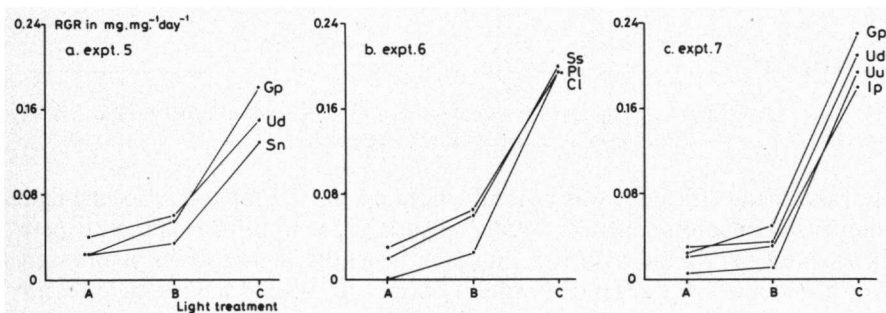


Fig. 7. Relative growth rate of plants in experiments 5, 6 and 7. For species, see fig. 3.

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

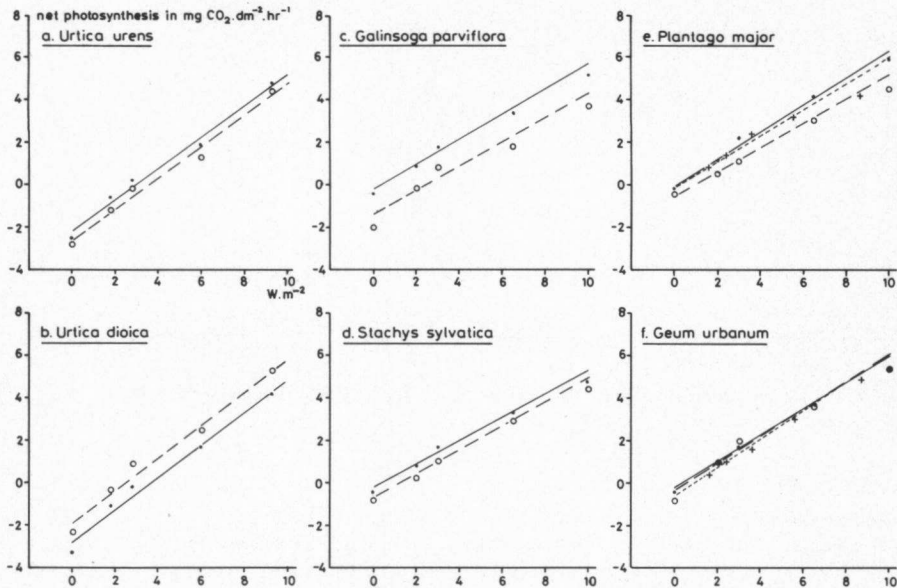


Fig. 8. Net photosynthesis/light intensity curves of plants in experiment 8. —○—: high r/fr ratio, ---○---: low r/fr ratio, ---+--- low r/fr ratio, measured at growing place.

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 reproducible 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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