

GROWTH AND MORPHOGENESIS OF SUN AND SHADE PLANTS

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

W. J. CORRÉ

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

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 as 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. Moreover, more recently, the great importance of plant size at the moment the competition starts has been pointed out (ELBERSE & DE KRUYF 1979, SPITTEERS 1982). 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 has 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 $6.0 \text{ me. l}^{-1} \text{ NO}_3^-$, $0.5 \text{ me. l}^{-1} \text{ H}_2\text{PO}_4^-$, $3.5 \text{ me. l}^{-1} \text{ SO}_4^{2-}$,

Table 1. Experimental design of the competition experiments.

Experiment no.	9	10	12	13
<i>a: experiments in glasshouse and experimental field</i>				
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	c. 200 W.m ⁻²	c. 175 W.m ⁻²	c. 75 W.m ⁻²	c. 200 W.m ⁻²
light source	natural light	natural light	natural light + Philips HPIT	natural light
red/far-red ratio	c. 1.1	c. 1.1	c. 1.5-3.5	c. 1.1
day length	natural	natural	16 hrs.	natural
max. day temperature	c. 30°C	c. 30°C	c. 25°C	c. 25°C
min. night temp.	c. 20°C	c. 20°C	c. 15°C	c. 10°C
min. air humidity	c. 30%	c. 25%	c. 40%	c. 30%
max. air humidity	c. 75%	c. 70%	c. 85%	c. 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.
Experiment no.	14	15	16	17
<i>b: experiments in climatic rooms</i>				
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	c. 2.5	c. 2.5	c. 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 c. 1.1; r/fr ratio HPIT c. 3.3).
- 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).

3.5 me. 1⁻¹ K⁺, 4.5 me. 1⁻¹ Ca⁺⁺, 2.0 me. 1⁻¹ 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 H₂O c. 6.0), solutions containing 16 me NO₃⁻, 1 me H₂PO₄⁻, 4.5 me SO₄⁻, 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.m²). 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 cm². In the other experiments 12 plants were placed per pot with an area of 625 cm². 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. 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:

$$RY = O/M \quad O: \text{yield in mixture, } M: \text{yield in monoculture}$$

$$RYT = RY_a + RY_b \quad RY_a: \text{RY species a, } RY_b: \text{RY species b}$$

$$k = \frac{RY_a^t}{RY_a^o} / \frac{RY_b^t}{RY_b^o} \text{ or } RY^o: \text{RY at start, } RY^t: \text{RY at harvest}$$

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

When the species are competing for the same growth factor (light in my experi-

ments) 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

$$M = \frac{\beta \cdot d}{1 + \beta \cdot d} \times \Omega.$$
 This formula implies a rectangular hyperbole, and that implies a linear relationship between $1/M$ and $1/d$, in accordance with the formula
$$\frac{1}{M} = \frac{1}{\Omega} + \frac{1}{\beta \cdot \Omega} \times \frac{1}{d}.$$
 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 ($k \gg 1$). 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.

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

expt. no.	sun species shade species	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	<i>Galinsoga parviflora</i> <i>Stachys sylvatica</i>	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	<i>Galinsoga parviflora</i> <i>Urtica dioica</i>	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	<i>Urtica urens</i> <i>Urtica dioica</i>	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	<i>Galinsoga parviflora</i> <i>Circaea lutetiana</i>	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
14	<i>Plantago major</i> <i>Geum urbanum</i>	3%	0.03	0.02	0.06	0.03	.65	.50	1.15	1.3	0.3
		60 W.m ⁻²	48.3	37.9	27.9	6.9	.78	.25	1.03	3.1	10
		30 W.m ⁻²	30.0	17.0	18.0	6.8	.57	.38	0.95	1.5	8
15	<i>Galinsoga parviflora</i> <i>Urtica dioica</i>	15 W.m ⁻²	9.3	5.9	9.3	3.9	.63	.42	1.05	1.5	4.5
		60 W.m ⁻²	51.4	36.4	54.2	15.6	.71	.29	1.00	2.4	18
		30 W.m ⁻²	39.0	22.9	31.7	15.0	.59	.47	1.06	1.3	17
16	<i>Galinsoga parviflora</i> <i>Impatiens parviflora</i>	15 W.m ⁻²	22.7	11.4	20.7	11.2	.50	.54	1.04	0.9	14
		60 W.m ⁻²	33.9	21.5	28.2	9.9	.63	.35	0.98	1.8	12
		22 W.m ⁻²	13.0	3.4	19.4	13.9	.26	.72	0.98	0.4	8
17	<i>Plantago major</i> <i>Geum urbanum</i>	8 W.m ⁻²	5.0	0.72	13.2	6.7	.14	.51	0.65	0.3	5
		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

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

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

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 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 competition, 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 harvests or during the growth period in experiment 14, 15 and 17 (table 3). 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.

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 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*

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

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

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).

light intensity	plant density	<i>Galinsoga parviflora</i>			<i>Impatiens parviflora</i>		
		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

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.

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

light intensity	<i>Galinsoga parviflora</i>			<i>Impatiens parviflora</i>		
	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 W.m ⁻²	1470	13.4	0.999	170	26.3	0.997
8 W.m ⁻²	(690)	(6.0)	0.783	145	18.5	0.998

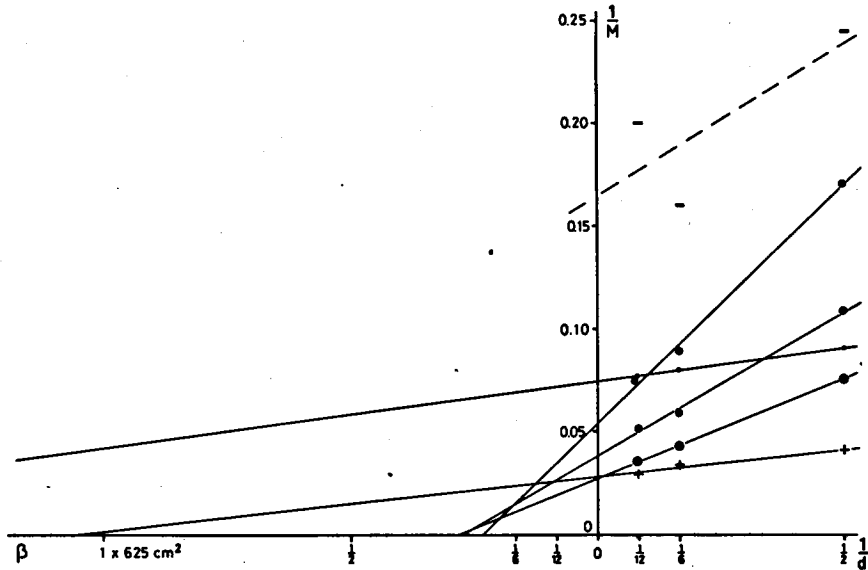


Fig. 1. The relation between $1/M$ and $1/d$ for two species in expt. 16. M : yield in g dry matter per pot, d : plant density in plants per pot, \oplus , \ominus : 60 W.m^{-2} , \odot , \ominus : 22 W.m^{-2} , $+$, \oplus , \ominus : 8 W.m^{-2} , $+$, \oplus , \ominus : *Galinsoga parviflora*, \oplus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

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 TRENATH (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.

ACKNOWLEDGMENTS

I am very grateful to Mrs. Martje Verf and to Mr. Kees Braak for their indispensable contribution to this study.

REFERENCES

- BAEUMER, K. & C. T. DE WIT (1968): Competitive interference of plant species in monocultures and mixed stands. *Neth. J. Agric. Sc.* **16**: 103–122.
- BERGH, J. P. VAN DEN (1968): An analysis of yields of grasses in mixed and pure stands. *Agric. Res. Rep.* **714**: 1–71.
- CORRÉ, W. J. (1983a): Growth and morphogenesis of sun and shade plants I. The influence of light intensity. *Acta Bot. Neerl.* **32**: 49–62.
- (1983b): — II. The influence of light quality. *Acta Bot. Neerl.* **32**: 185–202.
- (1983c): — III. The combined effects of light intensity and nutrient supply. *Acta Bot. Neerl.* **32**: 277–294.
- ELBERSE, W. TH. & N. DE KRUYF (1979): Competition between *Hordeum vulgare* L. and *Chenopodium album* L. with different dates of emergence of *Chenopodium album*. *Neth. J. Agric. Sc.* **27**: 13–26.
- GRIME, J. P. (1981): Plant strategies in shade. In: H. SMITH (ed.). *Plants and the daylight spectrum*. Academic Press, London, p. 159–186.
- MONTGOMERY, E. G. (1912): Competition in cereals. *Bull. Nebr. Agr. Exp. Sta.* **26**, art. 5, 22 p.
- RHODES, I. & W. R. STERN (1978): Competition for light. In: J. R. WILSON (ed.). *Plant relations in pastures*. CSIRO, East Melbourne, p. 111–127.
- SMITH, H. (1982): Light quality, photoperception and plant strategy. *Ann. Rev. Plant Physiol.* **33**: 481–518.
- SPITTERS, C. J. T. (1983): Effects of intergenotypic competition in the selection process. Proc. 10th Eucarpia Congr. (in press).
- TRENBATH, B. R. (1974): Biomass productivity of mixtures. *Advances in Agronomy* **26**: 177–210.
- WASSINK, E. C. & M. E. VAN DEN NOORT (1981): Effects of irradiance on growth and development of a more heliophilic plant species (*Calendula officinalis*) and a more ombrophilic plant species (*Impatiens parviflora*) grown separately and in 1:1 competition experiments. *Photosynthetica* **15**: 231–237.
- WIT, C. T. DE (1960): On competition. *Agric. Res. Rep.* **66**(8): 1–82.
- WONG, C. C. & J. R. WILSON (1980): Effects of shading on the growth and nitrogen content of green panic and siratro in pure and mixed swards defoliated at two frequencies. *Austr. J. Agric. Sc.* **31**: 269–285.