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GROWTH AND MORPHOGENESIS OF SUN AND SHADE PLANTS III. THE COMBINED EFFECTS OF LIGHT INTENSITY AND NUTRIENT SUPPLY

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SUMMARY

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

1. INTRODUCTION

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

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

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

Studying these relationships between nutrients, light intensity and plant growth is complicated by the fact that the results greatly depend on the methods used. In most of the studies mentioned above, the nutrient supply per plant was the same in alle light intensities, and therefore the shortage of nutrients was felt more strongly under high light intensities, simply because of the faster growth of the plants (INGESTAD 1962). This is particularly true for mobile nutrients such as nitrate, and for nutrient solutions, but sometimes also for less mobile nutrients in soil (e.g. phosphate), when the soil volume is limited. For this reason, in my experiments I chose a method in which the problem of adjust-

ing the nutrient supply according to the size of the plants was avoided: the limiting nutrient was supplied in optimum concentration in a water culture for a limited constant period each day. The use of a water culture implies, however, free access of the nutrients to the surface of the roots. In soil this is more or less assured for nitrate, but not for phosphate. In the case of phosphate, one aspect of the influence of the light intensity on the root weight ratio was ignored. Plants with a lower root weight ratio (low light intensity plants) explore a relatively smaller volume of soil and so the effects of a low phosphate supply could be greater in these plants in the field than in my experiments.

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

2. MATERIALS AND METHODS

2.1. Plant materials

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

2.2. Light intensity and nutrient supply

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

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

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

2.3. Growth conditions and harvest procedures

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

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

experiments, the total nitrogen content of the plants of the final harvest was measured after wet ashing with sulphuric acid and salicylic acid, and the nitrate-nitrogen content was measured after extraction with demineralized water. The organic nitrogen content was calculated by subtracting the nitrate-nitrogen content from the total nitrogen content. In addition, in experiment 11 the phosphate content was measured after the wet ashing.

3. RESULTS

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

3.1. Control series (N24, P24)

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

3.2. Nitrate series (N1, N2, N3)

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

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

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

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

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

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

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

decreased under higher light intensities; in *Stachys sylvatica* it decreased under all light intensities.

3.3. Phosphate series (P0. 5)

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

4. DISCUSSION

4.1. Growth and morphogenesis

The well-known interaction between the effects of nitrate supply and light intensity, i.e. an increased effect of nitrate supply under high light intensity, was clearly supported in these experiments. Nitrate supply had major effects on morphogenesis (i.e. on dry matter distribution) and only minor effects on metabolism (i.e. on net assimilation rate). Yet HEWITT & SMITH (1975) and ROBSON & PARSONS (1978) found that a limited nitrate supply depressed the net assimilation rate appreciably under high light intensity but not under low light intensity. This disaccordance, however, might have resulted from the use of other methods of ensuring a low nitrate supply. If the nitrate supply is not adjusted to the size of the plant, but remains constant or even decreases over time (ROBSON & PARSONS treated their experimental plants for 25 days with a high nitrate supply and thereafter with a constant low supply of nitrate), the nitrogen status of the plant will decline (INGESTAD 1962). A declining nitrogen status during growth is known to produce a large decrease in the photosynthetic capacity (NATR 1975). The effects of this on the net assimilation rate were illustrated in an experiment done by WELBANK (1962). He found that the nitrogen content and the net assimilation rate of *Impatiens parviflora* declined rapidly after the start of the experiment when the plants had to compete with *Agropyron repens* for a small amount of nitrogen, supplied in one dose at the start of the experiment. Without competition the nitrogen content and the net assimilation rate did not decline until after several weeks. Under a low light intensity, light will

generally limit photosynthesis; thus the effect of a lower photosynthetic capacity will not be as important as it is under a high light intensity. It seems logical that plants growing under a low light intensity will require smaller adaptations to low nitrate supply, because slow-growing plants have a lower absorption rate on the basis of plant weight and thus they require a smaller root weight ratio to maintain normal levels of nutrients, provided that the absorption capacity on the basis of root weight is not affected. The actual absorption rate on the basis of root weight may be low under low light intensity (see, for example, RUFTY et al. 1981). The very high levels of free nitrate and the almost normal levels of organic nitrogen that I recorded in the low light intensity plants, suggest that this lower absorption rate is probably primarily the results of the lower growth rate and the concomitant fall in the demand for nitrogen, and not the result of a fall in absorption capacity, or of the absorption rate being limited by energy supply. Indeed, the absorption rates of nutrients have been found to be lower when the energy supply of the roots is limited (CRAPO & KETELLAPPER 1981, HÄNISCH TEN CATE & BRETELER 1981, KOSTER 1973), but in all those experiments it was always measured in high light intensity plants in which the energy supply of the roots was limited artificially, for example by moving the plants into shade. And since CRAPO & KETELLAPPER (1981) found that root growth was restricted much more than nutrient (potassium) absorption by low energy supply, it seems probable that these results do not apply unconditionally for plants adapted to a low energy supply. It can be concluded that plants react to low nitrate supply mainly by means of morphogenetic adaptations and they maintain a reasonable organic nitrogen content. When an appreciably lower photosynthetic rate or net assimilation rate is reported in the literature, it probably results from the fact that the method used to supply the nitrate has not been adjusted to the size of the plants.

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

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

	Galinsoga parviflora				Urtica dioica			
	RGR $g.g^{-1}.day^{-1}$		dry weight g		RGR $g.g^{-1}.day^{-1}$		dry weight g	
	P0.5	P24	P0.5	P24	P0.5	P24	P0.5	P24
L1	0.101 (93%)	0.109	0.050 (83%)	0.060	0.069 (84%)	0.082	0.36 (77%)	0.049
L3	0.236 (91%)	0.259	1.27 (58%)	2.20	0.194 (83%)	0.234	0.73 (38%)	1.94

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

Although my data on relative growth rate show that light intensity and phosphate supply act independently on relative growth rate, the data on dry weight suggest that there is an interaction between the effects of these two factors. Because the relative growth rate is an exponential term in the relation between initial weight, final weight and time, $W_2 = W_1 \cdot e^{RGR(t2-t1)}$, the same percentage decrease in the relative growth rate causes a larger relative decrease in the final weight in faster growing (high light intensity) plants. This is illustrated in *table 3*. This also means that when a larger relative decrease in the final weight is found under high light intensity, as is often cited in the literature (e.g. PIGOTT 1971, PIGOTT & TAYLOR 1964), a concomitantly larger relative decrease in the relative growth rate should not be inferred. For the same reason, interactions mentioned in the literature should be regarded with caution. It can be concluded that the possible interactions between the effects of light intensity and phosphate supply are not yet clear and that experiments with lower supplies of phosphate will be necessary. Also, interactions between the effects of light intensity and other nutrients are not easy to predict. An important factor in determining the interaction is the effect of the nutrient involved on the root/shoot ratio, and this effect is very different for the various nutriens, depending on their functions in the plant (CURTIS & CLARK 1950). This, and the fact that the nutrients have different mobilities in the soil, makes it probable that the interactions are nutrient-specific.

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

4.2. The functional equilibrium between roots and shoots

The adaptions in the dry matter distribution of the experimental plants to light intensity and nutrient supply are expressions of a functional relationship be-

tween root and shoot systems (see, for example, TROUGHTON 1960), a relationship known as the functional equilibrium (BROUWER 1963). On empirical grounds, DAVIDSON (1969) found that the equilibrium could be expressed by the equation:

$$\text{root mass} \times \text{rate}_{(\text{absorption})} \alpha \, \text{leaf mass} \times \text{rate}_{(\text{photosynthesis})} \quad (1)$$

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

$$\text{specific root activity} \times \text{root weight ratio} = \text{N/C ratio} \times \text{specific shoot activity} \times \text{shoot weight ratio} \quad (2)$$

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

$$\text{root mass/shoot mass} \, \alpha \, 1/(\text{specific absorption rate/ unit shoot rate}) \quad (3)$$

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

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

In the Hunt & Burnett's experiment the model

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

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

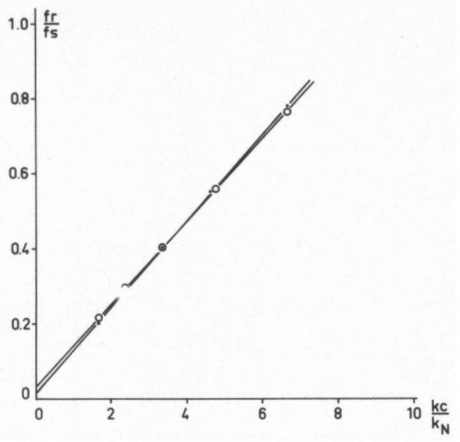

Fig. 1. Relationship between root/shoot mass ratio and shoot/root activity ratio, data from THORNLEY (1972).

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

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

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

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

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

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

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

and further to:

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

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

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

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

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

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

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

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

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

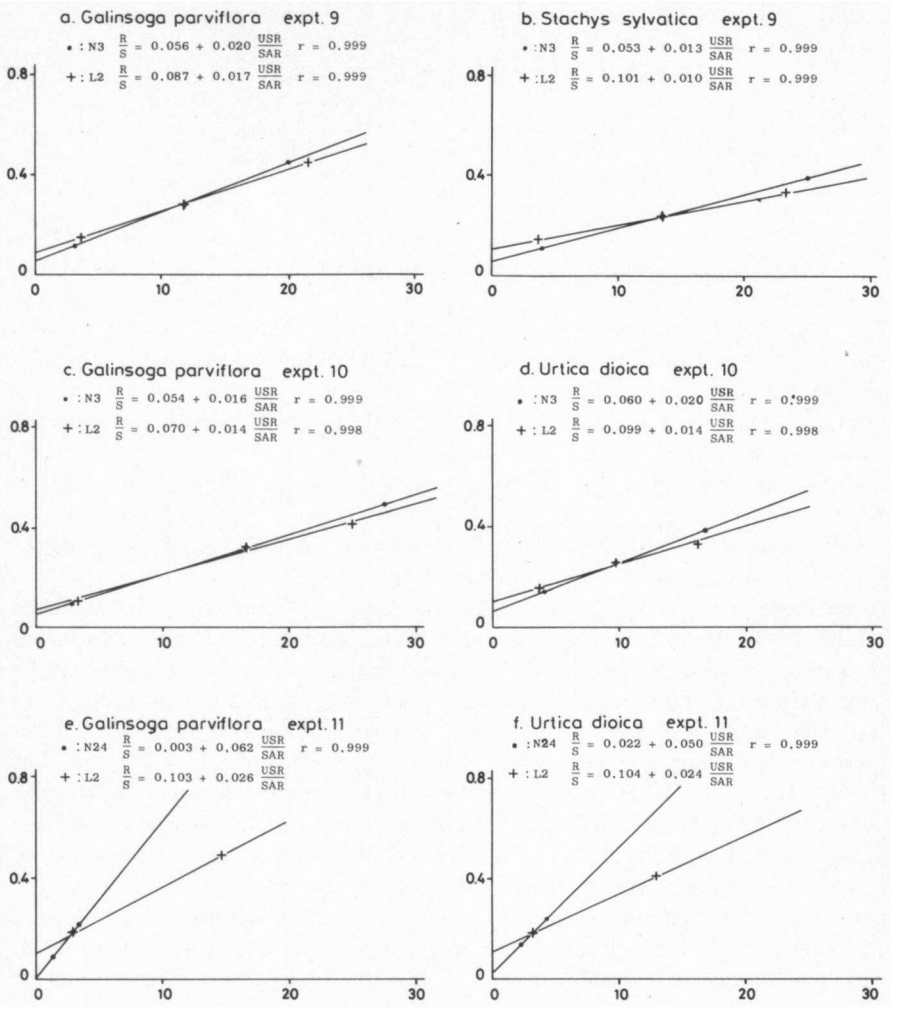

Fig. 2. Relationship between root/shoot mass ratio and shoot/root activity ratio for different light levels and for different nitrate levels in experiments 9, 10 and 11.

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

nitrogen supply varied than when the light intensity varied, although this was not mathematically significant because with varying nitrogen supply the regression was based on only two data.

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

5. CONCLUSIONS

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

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

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

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

The method used for limiting the nutrient supply, an optimum supply during

a limited period each day, enabled the nutrient supply to be adjusted to the size of the plants and this allowed the results to be accurately evaluated.

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ABBREVIATIONS

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

Abbreviations used in chapter 4.2.

R	root mass	mg	(1)
S	shoot mass	mg	(1)
USR	unit shoot rate	$mg.mg^{-1}.day^{-1}$	(1)
SAR	specific absorption rate	$mg.mg^{-1}.day^{-1}$	(1)
k_C	specific shoot activity	$kgmol.m^{-3}s^{-1}$	(2)
$\overline{C}$	mean carbon substrate concentration	$kgmol.m^{-3}$	(2)
k_N	specific root activity	$kgmol.m^{-3}.s^{-1}$	(2)
$\overline{N}$	mean nitrogen substrate concentration	$kgmol.m^{-3}$	(2)
Y_G	conversion efficiency of carbon substrate into plant dry matter		(2)
fr	root weight ratio		(2)
fs	shoot weight ratio		(2)
Θ	dry matter to volume conversion factor	$m^3.kgmol^{-1}$	(2)
λ	atomic ratio of nitrogen atoms to carbon atoms in the plants		(2)
μ	specific growth rate	$m^3.m^{-3}.s^{-1}$	(2)

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

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