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Biomass and shoot/root allocation of five species from a grassland succession series at different combinations of light and nutrient supply*

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Abstract. In recent literature the relative importance of interspecific differences in shoot/root allocation patterns and differences in growth rate have been discussed, especially with regard to the mechanisms of succession. We studied growth, leaf area and shoot/root ratio under controlled conditions at various combinations of light and nutrient supply of five species from a grassland successional series. This series was initiated by stopping the application of fertilizers to agricultural grassland but continuing hay-making. Species from the later successional stages (lower nutrient availability, higher level of light at the soil surface) had a higher shoot/root ratio at most treatments, contrary to the predictions of the resource ratio hypothesis. However, a three-way interaction was also found, and thus the combination of light and nutrient level determined whether or not a correspondence between successional position and the sequence of species in shoot/root ratio was found. Some possible explanations are discussed for these results with regard to the mechanisms of succession.
Key-words: Allocation, light, mineral nutrition, plant strategies, resource interaction, succession

Introduction

In recent debates on mechanisms which determine patterns of plant community structure and the course of succession, emphasis has been laid upon

the relative importance of different ecological factors (see Thompson 1987; Tilman 1987a,b; Thompson & Grime, 1988; Berendse & Elberse, 1989). Tilman (1988) hypothesized that the relative abundances of plant species change in response to changes in the ratio of limiting resources. Succession often proceeds by accumulation of nutrients in the soil, and when this results in a higher standing crop (such as in old-field succession), then a shift from nutrient limitation towards light limitation might be found. Therefore, during succession on a poor soil the early successional species would be characterized by a higher allocation of available resources to the roots, which should make them better competitors for nutrients. The later successional species would, however, allocate more resources to stems and leaves, which should make them better competitors for light. This opinion contrasts with Grime's (1979) view, who considered both a low-nutrient level and a low-light level as 'stress factors' which will select for similar life histories. This view was supported by Berendse & Elberse (1989), who found that species from relatively poor successional stages had a higher shoot/root ratio than species from richer stages, thus contradicting the expectations of the resource ratio hypothesis of Tilman (1988). The aforementioned theories have been based on a fixed allocation pattern of resources to the root and shoot, though it has long been known that this allocation pattern is very plastic, and especially dependent on light and nutrient levels (Brouwer, 1962a,b; Wilson, 1988). Tilman (1988) has argued that, on the basis of simulation results, such interspecific differences in plasticity would not alter his conclusions. However, until now this view is not supported by any experimental evidence. Berendse & Elberse (1989) determined the dependence of the shoot/root ratio on the nutrient level, but did not include the interaction effect with light. This interaction however seems crucial to the mechanisms proposed by Tilman (1985, 1988), since a resource-ratio effect can be experimentally translated into a resource-interaction effect (cf. Peace & Grubb,

1982; Van Baalen, 1982). When the statistical interaction effect between two resources is significant, this implies a significant effect of any shift in their ratio.

The aim of the present study was to determine the growth and shoot/root ratio allocation of species from a grassland successional series, grown individually at different combinations of light and nutrient supply, and to relate the (treatment-dependent) growth and allocation patterns to the successional position of the species. Five species from a grassland successional series were used. This series was initiated by stopping fertilizer application to agricultural hay-fields, as part of restoration management practices (Bakker, 1987, 1989). This change in management practice has led to a restoration of species-rich communities from swards which were formerly dominated by only a few species. The decrease in the availability of nutrients (Pegtel, 1987) was reflected by a substantial decrease in the above-ground standing crop, resulting in an increased light availability at the soil surface (Bakker, 1989). This implies that the direction of succession in this case is in reverse order, as described for old fields by Tilman (1988), viz. from a nutrient-rich, low-light to a nutrient-poor, high-light community. However, any theory about the mechanisms of succession should not depend on the direction of change.

The vegetation development of these hay-fields was recorded during a 16-year period. These data will be used to quantify the successional positions of these species, which will be related to their growth and allocation patterns at various combinations of light and nutrient supply.

Materials and methods

Species

Five species were selected for the present experiment (Table 1); selection was based on differences in ecological amplitude. *Succisa pratensis* Moench is a perennial rosette-forming species, while the remaining four species are perennial grasses. *Lolium perenne* L. is a characteristic species of fertilized meadows and pastures, while the other three grass species are found under more nutrient-poor conditions (Kruijne *et al.*, 1967). *S. pratensis* is only found under clearly nutrient-poor conditions (Pegtel, 1986).

Successional position

The experimental species occur in fields which are situated in the Nature Reserve 'Stroomdalland-schap Drentsche A' (53°N, 6°40'E). The management changed from cutting twice a year and fertilizing (100–200 kg N ha^{-1} year^{-1}) to cutting once a year (July) without the application of fertilizers. The vegetation composition thereafter changed from a *Poo-Lolietum* via a *Lolio-Cynosuretum* to a *Festuco-Cynosuretum*. Standing crop changed from 1000 to 300 gm^{-2} (see Bakker, 1989 for further details). The temporal change in the abundance of species over a 16-year period was compared to a time-sequence of fields for which fertilizing was stopped for different time intervals. This comparison made it possible to separate non-successional fluctuations in cover percentage (caused by e.g. extreme weather conditions) from directional (successional) changes. Five fields were compared, for which the duration of the management practices (hay-making without fertilizer application) varied from 16 to 42 years. The cover percentage of all species present was determined each year in June from 1972 until 1988 in several permanent plots in each field. In this analysis only the moist parts of each field were used, since the experimental species were frequently found in this habitat (Bakker, 1989).

The combined data of the changes over the study period and the spatial variation of fields which were no longer fertilized for different time intervals, were used to draw smooth curves of the changes in the first 42 years after the cessation of fertilizer application. However, an increase or decrease over the experimental period was only drawn in Fig. 1 if this change was significantly different from zero. This significance of change

Table 1. Seed sources of the experimental species.

Species	Abbreviation	Population	Location
Anthoxanthum odoratum	AO	Burgvallen	53°N 6° 40'E
Cynosurus cristatus	CC	Burgvallen	53°N 6° 40'E
Holcus lanatus	HL	Burgvallen	53°N 6° 40'E
Lolium perenne	LP	Gasteren	53°N 6° 40'E
Succisa pratensis	SP	Appelbergen	53°N 6° 37'E

195

*Allocation of
plant species
from a
grassland
succession
series*
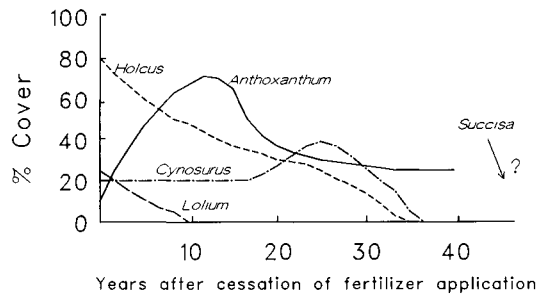
Fig. 1. Changes in coverage of five species from a grassland successional series after the cessation of fertilizer application. Smoothed curves were drawn for each species by comparing observed temporal changes during a 16-year study period between fields which were not fertilized for different time intervals (see text). The oldest field was not fertilized since 1946.

over the 16-year study period was not tested in a simple regression model, since the differences in absolute coverage between species could result in scaling errors. These scaling errors could be enlarged by single-year deviations (caused by fluctuations in weather) from successional trends (cf. Fresco *et al.*, 1989). In order to test the significance of successional trends the relative cumulative cover was computed and the significance of change was tested as the second order regression coefficient in a stepwise regression analysis with the linear coefficient already in the model. All permanent plots in which the summed coverage of a species over the study period was lower than 5% were excluded from the analysis.

Climate chamber experiment: growth conditions

The seeds of each species were cold stratified for 3 months on wet filter paper at 5 °C and subsequently germinated at 25/15 °C. The seedlings were transferred to pots, one seedling per pot, each containing 800 g of silver sand containing 1% (v/v) potting soil, 1% perlite and 1% peat. Three different nutrient supply rates were created by adding different dilutions of a nutrient solution twice a week, as described by Biere (1990). The nutrient supply rates corresponded to total additions of 10, 40 and 160 mg N per pot, respectively. Previous experiments (A. Biere, personal communication) justified the expectation that the biomass accumulation of these species would be a linear function of N-supply rate, expressed on a double-logarithmic scale.

Ten replicates per species per treatment combination were grown in climate chambers at 23/17 °C. Light was supplied by fluorescent tubes.

The three nutrient supply rates were combined with two irradiances of 130 and 65 W m^{-2} respectively, over an 18-h photoperiod, in a factorial design. All plants were harvested after 2 months. The total leaf area of each shoot was determined using a Li-Cor photoelectric leaf area meter. The shoot and root dry weight were determined after drying at 80 °C for 48 h.

Analyses of variance

The significance of the effects of light, nutrients and their interaction was first computed in a full factorial design. The relative contribution of each effect in this design was assessed as its relative contribution (%) to the explained variance in the dependent variable (Winer, 1971). All variables except the shoot/root ratio were log transformed prior to analysis, to reduce inhomogeneity of variances.

It was investigated whether or not the (treatment-dependent) sequence of responses of the species in the climate chamber experiment corresponded to their position in the successional series. This was tested by specifying polynominal contrasts between the species. The 4 degrees of freedom of the factor-species were subdivided into two terms, where the first effect (1 d.f.) represented the linear relationship between the species responses and their successional positions. The second term (3 d.f.) represented the pooled effect of all higher-order polynomials. The parameter estimate of the linear polynomial coefficient was computed for each treatment combination by nesting the linear polynomial effect within the interaction term Light × Nutrients (Winer, 1971).

Results

Successional position

A good correspondence was found between the spatial variation in mean coverage of the species in plots with a different duration of succession (up to 42 years) and the changes with time computed from data of monitoring over a period of 16 years. Smooth curves could, therefore, be drawn of the changes in the cover percentage of each species over a 42-year time period (Fig. 1). At the moment of cessation of fertilizer application, *Holcus lanatus* L. was the most abundant species. During the following 10 years, *L. perenne* disappeared from the vegetation, while *Anthoxanthum odoratum* L. reached its maximum coverage after these 10 years. *H. lanatus* decreased during the whole time

interval of 41 years. *Cynosurus cristatus* L. reached its maximum after 30 years. *S. pratensis* did not occur in the studied permanent plots, but was, however, locally abundant in the oldest field. This species is therefore assumed to be the last species in this successional sequence. The relative successional position of these five species was determined from Fig. 1 by combining the data on the maximum and magnitude of change. This resulted in the following sequence: *L. perenne* > *H. lanatus* > *A. odoratum* > *C. cristatus* > *S. pratensis*. This sequence will be used in the following analysis of the relationship between successional position and allocation parameters.

Factorial ANOVA

The results of the factorial analyses of variance for assessing the effect of irradiance and nutrient supply rate on the shoot dry weight, root dry weight, shoot/root ratio and leaf area of the five species are listed in Table 2. The treatment means for each species are presented in Fig. 2. The main effects were significant for all characteristics, but the magnitude of the effects was different. The species effect was very large for all traits, except for the shoot/root ratio. The shoot dry weight increased with the nutrient supply rate (Fig. 2) which explained 40% of the total variance (Table 2). The increase in shoot dry weight, caused by a higher level of irradiance (Fig. 2) was much less pronounced (1% explained, Table 2). For the root dry weight, the irradiance effect and the nutrient effect explained an equal portion of total variance (17 and 13%, respectively). Since the relative impact of nutrients and irradiance was different for the root and the shoot, both factors had a large impact on the shoot/root ratio (Table 2). The

shoot/root ratio increased with the nutrient supply rate and decreased with the level of irradiance (Fig. 2). Like the shoot dry weight, the leaf area mainly increased with the nutrient supply rate (55% explained, Table 2, Fig. 2).

The interaction Species × Irradiance was significant for the root dry weight, shoot/root ratio and for the leaf area, with the largest effect on the shoot/root ratio. The Species × Nutrient interaction was significant for the shoot/root ratio and for leaf area. The interaction Species × Nutrient × Irradiance was only significant for the shoot/root ratio (Table 2).

*Treatment-dependent species – differences in relation to the successional sequence*

The aforementioned Species × Treatment interactions might be interpreted as the dependence of species differences on the treatment combination. As described in the introduction, we are particularly interested in a special kind of species differences, namely whether the sequence of response of the species is related to their sequence in the successional series. To investigate the statistical significance of this relationship, the effect of the factor Species was partitioned into two polynomial effects. The first effect (Spe[1]) represents the linear polynomial correlation between the response in the dependent variable and the successional order (Table 3). The parameter estimate of this effect was computed for each treatment combination and is given in Fig. 2.

The Spe(1) effect explained a significant part of the variance in all traits (Table 3). For the shoot dry weight, this effect represented a negative correlation between the sequence of response and the sequence in succession, in all treatment combinations (Fig. 2). However, this was clearly caused by

Table 2. Factorial analysis of variance of the effect of the level of irradiance and nutrients on various weight and allocation parameters of five grassland species.

Effect	d.f.	Shoot dry weight		Root dry weight		Shoot/root ratio		Leaf area	
		F	% Var.	F	% Var.	F	% Var.	F	% Var.
Nutrients	2	684·3***	39·9	166·3***	12·6	170·0***	30·2	1122·5***	55·0
Irradiance	1	12·9***	1·0	152·7***	17·3	138·3***	36·8	37·2***	2·7
Species	4	376·1***	54·8	336·3***	63·9	10·8***	4·4	302·7***	36·9
Nutrient × Irradiance	2	20·1***	3·4	24·0***	5·2	27·0***	12·4	5·9**	0·8
Species × Irradiance	4	2·4^NS	0·3	3·5**	0·9	5·3***	3·8	3·5**	0·7
Species × Nutrients	8	3·0^NS	0·6	1·6^NS	0·1	8·0***	6·3	14·8***	0·7
Species × Irradiance × Nutrients	8	1·0^NS	0	1·0^NS	0	3·3**	6·1	1·9^NS	0·7
Error		(0·02)		(0·02)		(0·35)		(0·02)	

F-values are given, with their level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant. The percentage of the total variance explained was computed for each effect. The within-cells error mean square is given for each effect. All variables except the shoot/root ratio were log-transformed prior to the analyses.
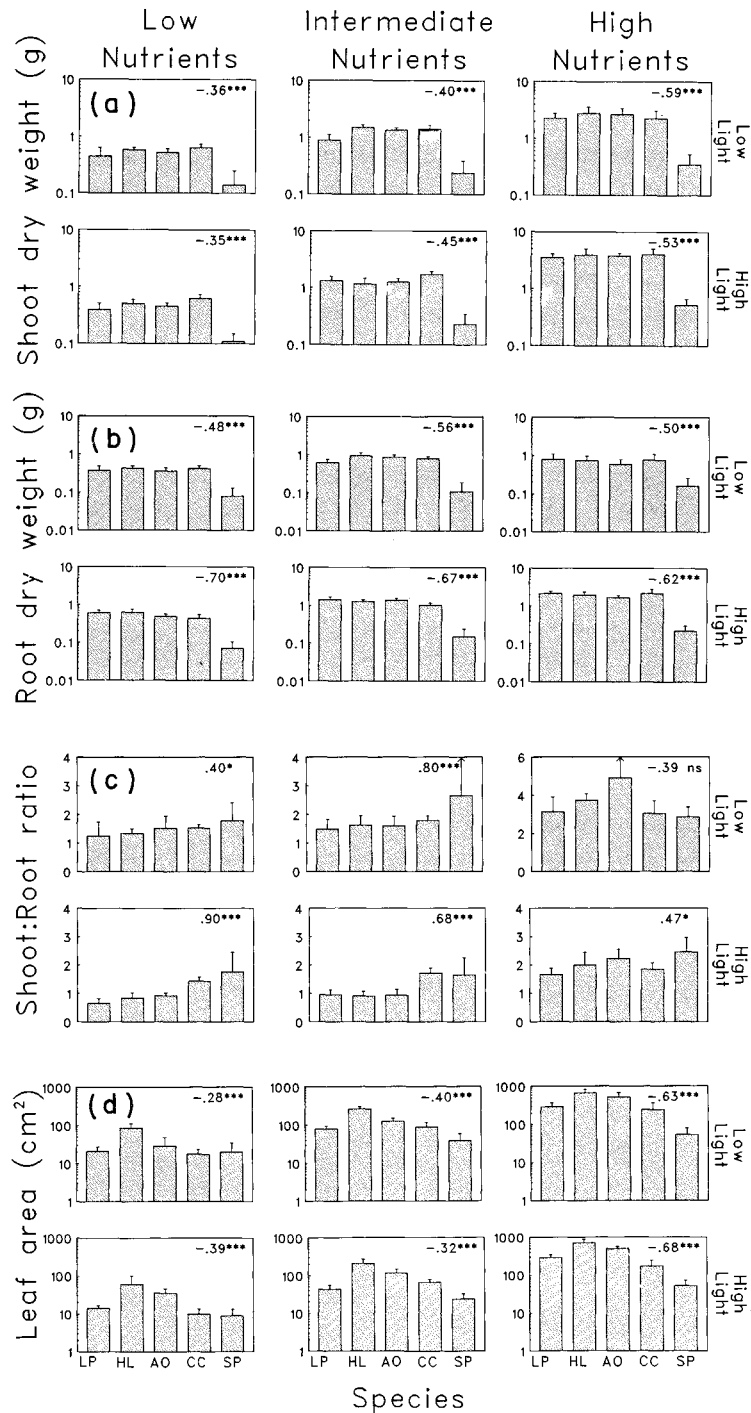
Fig. 2. Shoot dry weight (a), root dry weight (b), shoot/root ratio (c) and leaf area (d) of five species from a grassland successional series at various combinations of irradiance and nutrient supply rate. For each treatment combination, the linear polynomial coefficient (with level of significance) is presented as a test for the correspondence between order of response and order in the successional sequence (see text). The species are ordered from early to late according to their occurrence after the cessation of fertilizer application (see Fig. 1). Levels of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Species abbreviations: LP, *Lolium perenne*; HL, *Holcus lanatus*; AO, *Anthoxanthum odoratum*; CC, *Cynosurus cristatus*; SP, *Succissa pratensis*.

the very low shoot dry weight at all treatments of *S. pratensis*; the other species did not show a negative trend. The same result was found for the root dry weight (Fig. 2).

For the shoot/root ratio, the interaction Species × Nutrients × Irradiance (Table 2) could be explained by the interaction Spe(1) × Nutrients × Irradiance (Table 3). This suggests that the magnitude of the correspondence between the order of response and successional position depended on the treatment combination. The shoot/root ratio was for all but one of the combinations positively related to the successional position. Only at the combination (low irradiance – high nutrients) was the polynomial coefficient not significant (Fig. 2). In the case of positive correlations, all species showed a trend towards a higher shoot/root ratio for later successional species.

The significant Spe(1) effect for the factor leaf area (Table 3) could be interpreted as a negative relationship between the order of response and successional position (Fig. 2). *L. perenne* was an exception to this pattern; this species had a smaller leaf area than *H. lanatus* at all treatment combinations (Fig. 2). The other four species showed a distinct trend, which was not caused by just one species. The interaction Species × Nutrients and Species × Irradiance were both significant in their effect on the leaf area (Table 2). These interactions could be partially explained by the corresponding interaction effects of the linear polynomial effect (Table 3). This suggests that the Spe(1) effect depended on both individual factors, but not on their combination. The magnitude of the correlation between the order of response and successional position increased both with the level of

irradiance and the nutrient supply rate; the differences between species became more pronounced. Overviewing the results it can be concluded that in general later successional species had a higher shoot/root ratio, except at the treatment high nutrients/low light. Later successional species had in general a lower total leaf area.

Discussion

The direction of the relationship between shoot/root ratio allocation and successional position shown in most treatments of our experiment is the same as reported by Berendse & Elberse (1989), who also found a higher shoot/root ratio in species from poorer successional stages. In our field study area, Bakker (1989) also found an overall increase in the ratio above-ground/below-ground production of the vegetation after cessation of fertilizer application. However, the interaction Species × Nutrients × Irradiance was significant in our experiment, and this interaction was reflected by a deviance from the general pattern in the treatment high nutrients/low irradiance. In this treatment no clear relationship was found between shoot/root ratio allocation and successional position. The abiotic conditions in the successional series which started after the cessation of fertilizer application in the grassland communities in the Drentsche A valley, probably changed from high to lower availability of nutrients (Bakker, 1987) and from low- to high-light conditions on the soil surface (Bakker, 1989). The early stages might, therefore, be compared with the treatment high nutrients/low light and the later stages with the treatment low nutrients/high light. Since no relationship

Table 3. Analysis of variance of the effect of the level of irradiance and the nutrient supply rate on various weight and allocation parameters of five grassland species. The effect of the factor Species (d.f. = 4) was partitioned into two polynomial terms, in which the first term (Species 1) represents the linear relationship between order of response and successional position (see text).

Effect	d.f.	Shoot dry weight	Root dry weight	Shoot/root ratio	Leaf area
Nutrients	2	684·3***	166·3***	170·0***	1122·5***
Irradiance	1	12·9***	152·7***	138·3***	37·2***
Species(1)	1	598·1***	732·9***	36·5***	493·8***
Species(2)	3	315·2***	216·0***	2·3^{NS}	246·2***
Nutrients × Irradiance	2	20·1***	24·0***	24·0***	5·9***
Species(1) × Irradiance	1	0·5^{NS}	11·8**	6·8*	0·5^{NS}
Species(2) × Irradiance	3	3·1*	0·8^{NS}	4·8**	4·5**
Species(1) × Nutrients	2	9·2***	0·6^{NS}	7·7**	25·0***
Species(2) × Nutrients	6	0·8^{NS}	1·9^{NS}	8·2***	11·6***
Species(1) × Irradiance × Nutrients	2	0·6^{NS}	0·5^{NS}	3·2*	1·8^{NS}
Species(2) × Irradiance × Nutrients	6	1·1^{NS}	1·2^{NS}	3·4**	1·9^{NS}
Error		(0·02)	(0·02)	(0·35)	(0·02)

F-values are given, with their level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

between allocation pattern and successional sequence was found in the former treatment, and a negative relationship was found in the latter treatment, these results suggest an increasing importance of differences in allocation patterns with successional age. This was also found by Tilman (1988) who reported that during old field succession on an intermediately nutrient-rich soil, the competitive relationships during the first successional stages are mainly determined by differences in maximum growth rate among the species already present (transient dynamics). The faster growing species were better competitors, because they could overtop slower growing species. In later successional stages resource ratio- and allocation-dependent competition increased in importance. Tilman has argued that the duration of the period during which these growth differences determine the successional sequence depends on the initial nutrient status of the soil. On very rich soil the full successional sequence is probably determined by these transient dynamics (Tilman, 1988). Berendse & Elberse (1989) also stressed the importance of growth differences between species, but from another point of view. They argued that the growth rate of grassland species is directly related to their loss rate, a relation which becomes increasingly important with decreasing nutrient availability. In the present study no clear relationship between bio-mass and successional position was found, but it should be kept in mind that relative growth rates have not been measured, and that the light intensities in our climate chambers were probably lower than under field conditions.

The higher shoot/root ratio of species from the poorer successional stages is contrary to the expectations of Tilman (1985, 1988), but the smaller leaf area of the species from the stages with a more open vegetation structure does correspond to his theories. Tilman (1988) explains the smaller leaf area of the species from poor habitats from a higher allocation of carbon and nutrients to their roots, which they could afford because of little need for competitive ability for light. However, this is not the case in our study; the species from the poorer stages showed in general a higher shoot/root ratio. The larger leaf area of the species from the richer stages could possibly be regarded as an adaptation to the low-light conditions (Givnish, 1988), since it was found in all treatments. The smaller leaf area of the species from the high-light habitat is, according to our experiment, not coupled to a higher relative investment in the roots. Then what is the advantage of a higher shoot/root ratio of

species in the poorer successional stages? From the viewpoint of acquisition of nutrients it is not advantageous, and the plastic response of the species in this experiment is also towards a higher shoot/root ratio at lower light and a lower shoot/root ratio at lower nutrient supply rates (see also Brouwer 1962a,b; Wilson, 1988). One possibility is that the higher shoot/root ratios of the species from poor habitats are compensated for by a higher specific root length, as was found by Berendse & Elberse (1989). There might be an allocation trade-off within the root system, rather than between root and shoot. Another possibility is that the carbon allocation patterns do not reflect the nutrient allocation patterns (Abrahamson & Caswell, 1982; Reekie & Bazzaz, 1987). Further experiments should test these hypotheses, as well as investigate the importance of these character-istics under competitive conditions, at different combinations of nutrient and light availability. Since climate chambers are highly artificial the importance of growth and allocation patterns in competitive displacement should also be studied under field conditions.

Acknowledgments

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