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Objekttyp: **Article**

Zeitschrift: **Bulletin of the Geobotanical Institute ETH**

Band (Jahr): **67 (2001)**

PDF erstellt am: **28.03.2024**

Persistenter Link: https://doi.org/10.5169/seals-377837

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Effects of light and nutrient supply on the growth and competitive ability of five Carex species

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Summary

1 Interspecific competition is known to be influenced by the availability of limiting resources. However, the relative influence of above- and below-ground resources on the outcome of competition is not well understood, due to a lack of experiments where these resources have been varied independently from each other. We therefore investigated the effects of nutrient supply and shading on the ability of five wetland *Carex* species to compete with tall forbs.

2 *Carex* plants (*C. davalliana, C. flacca, C. flava, C. elata* and *C. panicea*) were grown in pots, either alone or in competition with tall forbs (*Lythrum salicaria, Solidago serotina*), in an additive design. Treatments consisted in all possible combinations of four nutrient supplies (48, 16, 5.6 and 1.4 mg N plant^{-1} growing season^{-1}) and four light levels (100%, 20%, 10%, 4% of full daylight). Above-ground biomass was harvested after one growing season.

3 The biomass production of all plants in the study (measured as above-ground dry weight) was significantly affected by the availability of nutrients and light, although response patterns differed among species. Both resources interacted in that the growth response to increasing availability of one resource strongly depended on the availability of the other resource. Thus, depending on the treatment, one of the resources (or both together) limited plant growth in the experiment. Growth responses to light differed more clearly among species than growth responses to nutrients.

4 Competitive interactions between the *Carex* species and the forbs were significantly affected by the availability of nutrients and light, but in opposite directions. Competitive responses of the *Carex* (ratio of biomass with competition to biomass without competition) were maximal at high light availability, but minimal at high nutrient supply. In addition, relationships between competitive responses and resource supply were unimodal, with a minimum at intermediate light availability and a maximum at intermediate nutrient supply. These effects of light and nutrient supply on competitive responses were similar for the five *Carex* species.

5 It is proposed that resource supply affected the ability of the *Carex* species to compete against tall forbs in two ways: through an effect on the relative importance of light vs. nutrient limitation, and through an effect of competition intensity. The two effects probably acted in synergy along the nutrient gradient, but in opposite directions along the light gradient, which resulted in a unimodal relationship between light supply and the ability of *Carex* plants to compete against tall forbs. Further research will be carried out to explain the occurrence of unimodal relationships between nutrient supply and competitive responses as observed in this experiment.

Keywords: above-ground biomass; additive design; competitive response; competition; resource ratio, shade

Bulletin of the Geobotanical Institute ETH (2001), **67**, 41–55

Introduction

Competition for resources, mainly nutrients, light and water, is one of the most important factors determining the structure and diversity of herbaceous plant communities (e.g. Grime 1977; Tilman 1982, 1985; Connell 1983; Aerts *et al.* 1990). Many field and laboratory studies have shown that growth and competitive abilities of herbaceous plants are strongly influenced by the availability of above- and below-ground resources (e.g. Twolan-Strutt & Keddy 1996; Wetzel & van der Valk 1998; Weihe & Neely 1997, see Campbell *et al.* 1991 or Goldberg & Barton 1992 for reviews). However, there has been – and still is – much controversy about the role of the relative availabilities of above- and below-ground resources, i.e. whether and how competitive interactions differ between conditions poor in nutrients but rich in light and conditions rich in nutrients but poor in light (e.g. Grime 1977, 1979; Tilman 1982, 1986). Experimental evidence is scarce because most competition studies have only varied the supply of either above-ground or below-ground resources (mostly the latter, see Edelkraut *et al.* 2000). These studies yielded contrasting results on the main factors regulating competitive abilities due to differences in experimental design, treatments and plant species investigated (Goldberg 1990). Therefore the comparison of independent studies on the influence of either above-ground or below-ground resources on competition does not allow a reliable assessment of the relative roles of these resources.

The objective of our experiment was to investigate the relative importance and the interactions of above- and below-ground resources (nutrients and light) in their effects on competition between perennial wetland plants. For this purpose we varied both resources in a factorial design and measured the ability of five *Carex* species to compete against two tall forb species. In the field, stands of these *Carex* species become increasingly dominated by tall forbs when sites are eutrophicated (e.g. Klötzli 1986). This shift has been ascribed to the competitive effect (especially shading) of tall forbs on the shorter *Carex* plants, which are less nutrient-demanding but require more light (Güsewell & Edwards 1999). We therefore hypothesised that the forbs would respond to high nutrient supply more strongly than the *Carex*, and thus, that their competitive effect on the *Carex* would increase with increasing nutrient supply. Regarding the role of light, we hypothesised that low light availability would reduce the growth of the *Carex* species more than that of the forbs and therefore reduce the ability of the former to compete against the latter. Finally, we expected that the effect of nutrient supply on competitive interactions between *Carex* and forbs would depend on light supply, and vice-versa.

Methods

PLANT MATERIAL

The target species in the experiment were *Carex davalliana, C. flacca, C. flava, C. elata* and *C. panicea,* all of which typically occur in

base-rich, mesotrophic to moderately eutrophic wetlands and represent a range of requirements for light and nutrients (see Edelkraut *et al.* 2000). Cuttings of the five species were gathered from field sites on the Northern Swiss Plateau in summer 1998 or 1999 and cultivated in the garden of the Geobotanical Institute until the beginning of the experiment. In February 2000, plants were split into individual shoots (128 individuals per species). The shoots were grown for six weeks in the greenhouse to obtain individuals of approximately the same size. As competitors two forbs which are often invasive in wetlands, *Lythrum salicaria* and *Solidago serotina,* were grown from seed. Seeds were sown end of February in garden mould and kept in climate chambers at a 16/8 h day/night cycle at 20 °/5 °C until germination. Seedlings were transplanted in the greenhouse until they were included into the experiment.

EXPERIMENTAL DESIGN

Plants were grown in 3-l pots (19 cm diameter) filled with quartz sand. An additive design was used, with a control treatment (a single *Carex* plant per pot) and a competition treatment (a central *Carex* plant surrounded by four competitors, i.e. two plants of each forb species). As further treatments, four light and four nutrient levels were applied in a split-plot design. Each light level (= main-plot factor) was replicated four times, and the resulting 16 shading cages (main plots) were arranged in four blocks. Each cage contained 40 pots (= subplots), i.e. one pot for each combination of four nutrient levels, five *Carex* species, and the two competition treatments, giving a total of 640 pots for the whole experiment.

The four light levels were created through cages covered with green shading cloth (ST30, HORTIMA, Hausen, Switzerland), using no shading material (full light, L4), one layer (20% daylight, L3), one layer with additional stripes (10% daylight, L2), and two layers (4% daylight, L1; light measured with a Decagon Sunfleck Ceptometer from Delta-T Devices LTD, Pullmann, WA, USA). The four nutrient levels were created using a commercial liquid fertilizer (WUXAL, Maag Agro, Dielsdorf, Switzerland) that had been supplemented with KNO_3 to obtain a N:P-ratio of 10:1 and diluted to four different concentrations so that plants received 48 (N4), 16 (N3), 5.6 (N2) and 1.4 (N1) mg N $plant^{-1}$ $growing\ season^{-1}$. To disperse the nutrients in the pots as uniformly as possible, the sand was water-saturated before fertilizing, and nutrients (2 ml per plant) were given with a pipette close to each plant within the pot. Pots were watered daily to prevent water stress. Treatments lasted 15 weeks from May until August 2000.

HARVEST

At the end of August 2000, the above-ground biomass of all plants was harvested 2 cm above soil surface. We collected the biomass separately for *Carex* plants and competitors, but pooled the four competitors per pot. Plant material was dried for 48 h at 70 °C and weighed.

DATA ANALYSIS

The effects of experimental treatments and species on the above-ground biomass of the *Carex* plants were analysed with split-plot-ANOVA with the main-plot factors "light" and "block" and the subplot factors "nutrients", "competition" and "species". Since this ANOVA showed that the effects of light level, nutrient supply and competition all differed significantly among species, treatment effects were subsequently analysed for each *Carex* species separately (split-plot ANOVA with-

Table 1. *Results of split-plot ANOVA testing the effects of light, nutrients, competition and* Carex *species on the log-transformed biomass of* Carex *plants and the competitors. F-values with significance levels are given (*** = P ≤ 0.001; ** = P ≤ 0.01; * = P ≤ 0.05; ns = P > 0.05).*

Factor		Biomass *Carex*		Biomass competitors	
	df	*F*	*P*	*F*	*P*
Block	3	1.32	ns	3.47	ns
Light	3	113.11	***	12.77	***
Nutrients	3	112.60	***	151.60	***
Nutrients*Light	9	15.01	***	9.75	***
Species	4	93.09	***	5.76	***
Species*Light	12	3.84	***	1.21	ns
Competition	1	113.61	***		
Comp*Light	3	25.86	***		
Nutrients*Species	12	1.88	*	1.00	ns
Nutrients*Species*Light	36	1.35	ns	0.69	ns
Nutrients*Comp	12	29.02	***		
Nutrients*Comp*Light	36	1.69	ns		
Species*Comp	4	3.72	*		
Species*Comp*Light	12	0.96	ns		
Nutrients*Species*Comp	12	1.63	ns		
Nutrients*Species*Comp*Light	36	1.12	ns		

out the factor "species"). A similar ANOVA was also carried out to test the effects of treatments and *Carex* species on the above-ground biomass of the competitors. The design of all ANOVAs followed Zar (1996, App. 9), i.e. main plots were treated as subjects and subplot factors as within-subject factors. Data were log-transformed to obtain normally distributed residuals. Calculations were carried out with the statistical package JMP version 3.2.2. (SAS Institute Inc. 1989–97).

The ability of the five *Carex* species to withstand competition by forbs (their "competitive response", CR) was assessed as $CR = \log (Y_C/Y_A) = \log Y_C - \log Y_A$ where YC = above-ground biomass of the *Carex* plant grown with competition and Y_A = above-ground biomass of the *Carex* plant grown alone. CR was calculated for each pair of plants of the same *Carex* species that had received the same nutrient-light treatment within the same block. The effects of light level, nutrient supply and species on CR were analysed with split-plot-ANOVA with the main-plot factors "light" and "block" and the subplot factors "nutrients" and "species". The effects of nutrients and light were analysed further with polynomial contrasts. Linear contrasts (coefficients -0.75, -0.25, 0.25 and 0.75 for levels 1 through 4, respectively) were used to test whether there was an increasing or decreasing trend in CR across the four nutrient or light levels. Quadratic contrasts (coefficients 0.5, -0.5, -0.5 and 0.5) were used to test for a unimodal dependence of CR on nutrient or light levels.

Results

BIOMASS PRODUCTION

Above-ground biomass production of all plants was significantly affected by nutrient and light availability. The two resources interacted considerably, so that their effects need

Table 2. *Effects of light, nutrients and competition on the log-transformed biomass of* Carex *plants (cf. Table 1), tested separately for each of five* Carex *species.* F*-values with significance levels are given (*** = P ≤ 0.001; ** = P ≤ 0.01; * = P ≤ 0.05; ns = P > 0.05).*

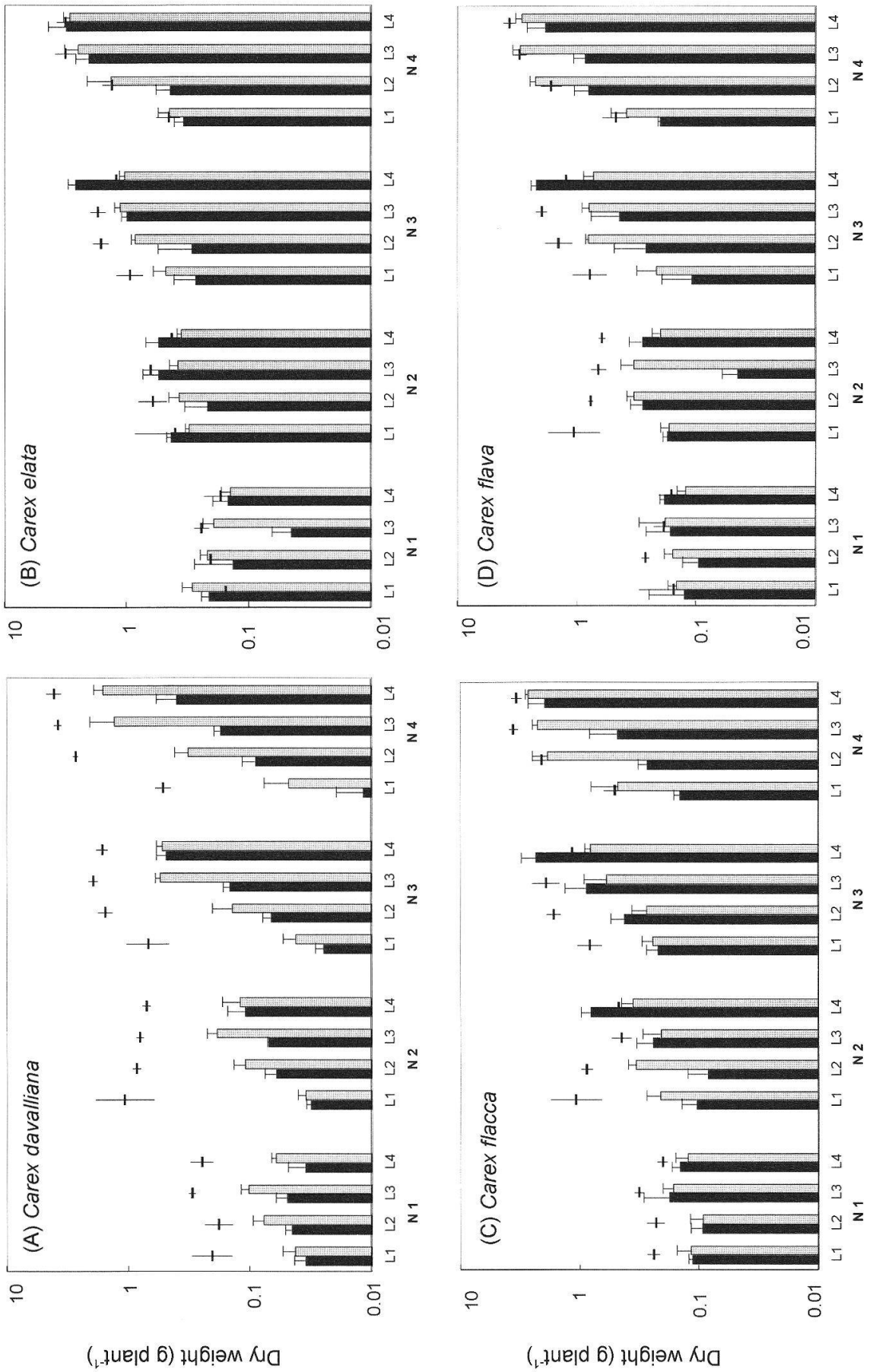
Factor		*C. davalliana*		*C. elata*		*C. flacca*		*C. flava*		*C. panicea*	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Block	3	1.1	ns	0.6	ns	0.7	ns	0.7	ns	0.7	ns
Light	3	102.6	***	15.3	***	30.3	***	11.4	**	53.1	***
Nutrients	3	42.2	***	59.2	***	35.6	***	19.9	***	29.2	***
Nutrients*Light	9	16.0	***	6.2	*	2.9	*	3.3	**	5.3	***
Competition	4	92.0	***	1.8	ns	6.5	*	26.5	***	8.4	*
Comp * Light	12	3.8	*	4.3	*	2.8	ns	5.5	*	4.4	*
Nutrients*Comp	12	10.3	***	2.0	ns	8.7	***	1.2	ns	9.4	***
Nutrients*Comp*Light	36	0.4	ns	0.6	ns	1.3	ns	1.4	ns	1.5	ns

Table 3. *Results of split-plot ANOVA testing the effects of light, nutrients and species on the ability of* Carex *plants to compete against tall forbs (competitive responses, see Fig. 3).* F*-ratios with significance levels are given for all factors in the model. In addition,* t*-values and significance levels of linear and quadratic contrasts are given for the effects of nutrients and light (*** = P ≤ 0.001; ** = P ≤ 0.01; * = P ≤ 0.05; ns = P > 0.05).*

Factor		Whole model		Polynomial contrasts			
	df	*F*	*P*	Linear		Quadratic	
Block	3	1.5	ns				
Light	3	21.2	***	4.1	**	6.1	***
Nutrients	3	28.7	***	-7.1	***	-6.3	***
Nutrients*Light	9	1.7	ns				
Species	4	4.2	**				
Species * Light	12	1.2	ns				
Nutrients*Species	12	1.6	ns				
Nutrients*Species*Light	36	1.3	ns				

to be considered in combination (Table 1; Fig. 1, 2). At high nutrient supply (N3 and N4) all species produced an increasing amount of biomass with increasing light availability up to the third level of light (L3, 20%). The biomass of all *Carex* species grown in the presence of competitors was also higher at 100% light supply (L4) than at 20% (L3), but the biomass of tall forbs and of *Carex* grown alone generally did not differ between the two highest light levels. At lower nutrient supply (N2), increasing light availability tended to increase the biomass production of *C. davalliana, C. flacca* and *C. panicea,* whereas this was not the case for *C. elata, C. flava* and the forbs. At the lowest nutrient supply (N1), biomass production was either independent of light or actually decreased with higher light availability (Fig. 1).

These interactions between the effects of nutrients and of light on biomass are illustrated for all species together in Fig. 2. The growth of all species was more strongly enhanced by high nutrient supply (comparing N4 to N1) at the highest light level (L4) than at the lowest light level (L1; Fig. 2A). Likewise, plant growth was more enhanced by high light availability (L4 vs. L1) at the highest nutrient supply (N4) than at the lowest nutri-


(A) Carex davalliana
(B) Carex elata
(C) Carex flacca
(D) Carex flava
Dry weight (g plant-1)
10
1
0.1
0.01
L1 L2 L3 L4
N 1
N 2
N 3
N 4

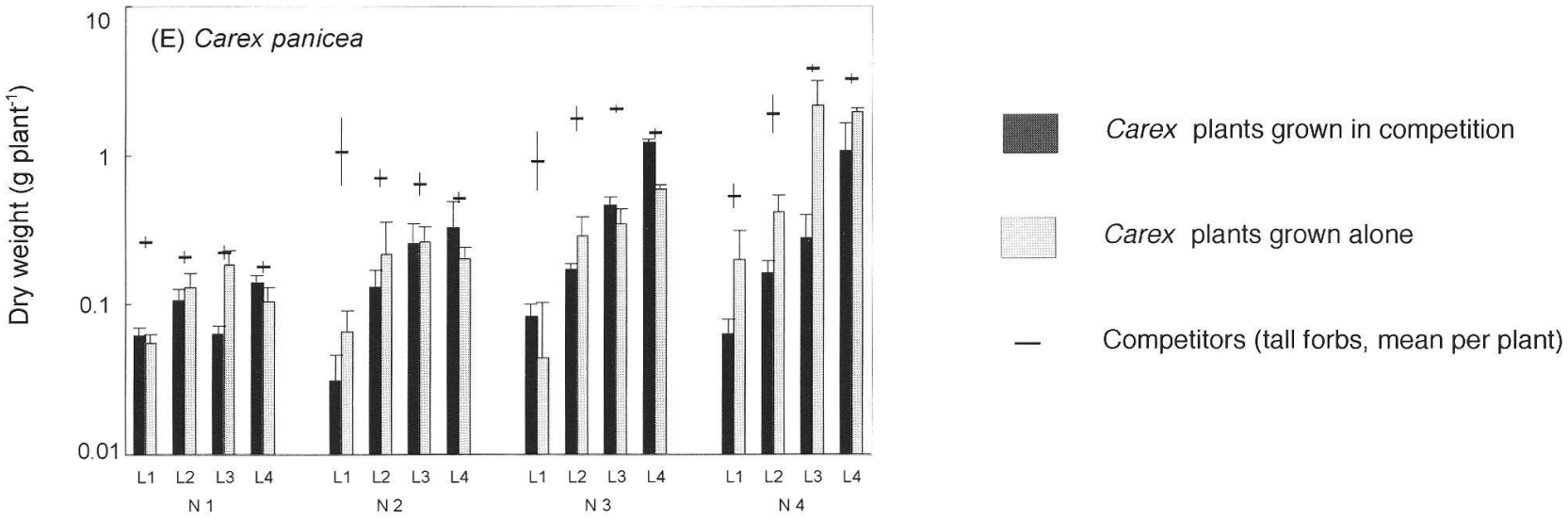


Fig. 1. *Above-ground biomass (mean + SE, logarithmic scale) of* Carex *plants grown in pots either alone or in competition (surrounded by four tall forbs) under 16 experimental treatments given by all possible combinations of four nutrient levels (N1–N4) and four light levels (L1–L4; 1 = low supply, 4 = high supply). The difference in height between light and dark bars for a given treatment indicates whether (and how strongly)* Carex *plants were suppressed by competition. The above-ground biomass of competitors is shown by horizontal lines; values are given per plant (i.e. 1/4 of total competitor biomass per pot). The difference in height between bars and horizontal lines indicates the difference in biomass between* Carex *plants and competitors. This difference varied considerably among* Carex *species and treatments.*

ent supply (N1; Fig. 2B). Overall, plant biomass differed more between the highest and the lowest nutrient level than between the highest and the lowest light level. Nevertheless, consistent interspecific differences were only apparent in the effects of light: The biomass of *C. panicea* and *C. davalliana* differed more between L1 and L4 than the biomass of the other species, including the forbs, and the biomass of *C. elata* differed least.

Averaged over all treatments, the five *Carex* species could be ranked according to their above-ground biomass as follows: *C. elata* > *C. flacca* ≈ *C. flava* > *C. panicea* > *C. davalliana* (Tukey HSD test, $P < 0.05$). The above-ground biomass of the competitors (tall forbs) was in most cases higher than the biomass of the *Carex* plants, but still depended on the *Carex* species with which the forbs had been competing (Table 1; Fig. 1).

COMPETITIVE ABILITY

Competition significantly reduced the biomass production of four *Carex* species when averaged over the 16 treatments; only for *C. elata* the effect of competition was not significant (Fig. 1, Table 2). The effect of competition on biomass depended significantly on the light level for all species except *C. flacca,* and depended on nutrient supply for *C. davalliana, flacca* and *panicea* (significant interactions, cf. Table 2). Three-way interactions (Competition*Light*Nutrients) were not significant for any *Carex* species.

The competitive responses (CR) of the five *Carex* species, which measured their ability to compete against the forbs, significantly depended on light availability, nutrient supply and species (Table 3). Linear and quadratic contrasts among resource supply levels were significant for both nutrients and light, but with opposite signs (Table 3), indicating that the ability of *Carex* plants to compete against forbs was related to above- and below-ground resources in opposite ways. This is shown by Fig. 3: Regardless of nutrient supply, CR was highest at light level L4 (100%), intermediate at level L1 (6%), and lowest at levels L2 and L3. In contrast, CR was always lowest at high nutrient supply (N4). Rankings of the three other

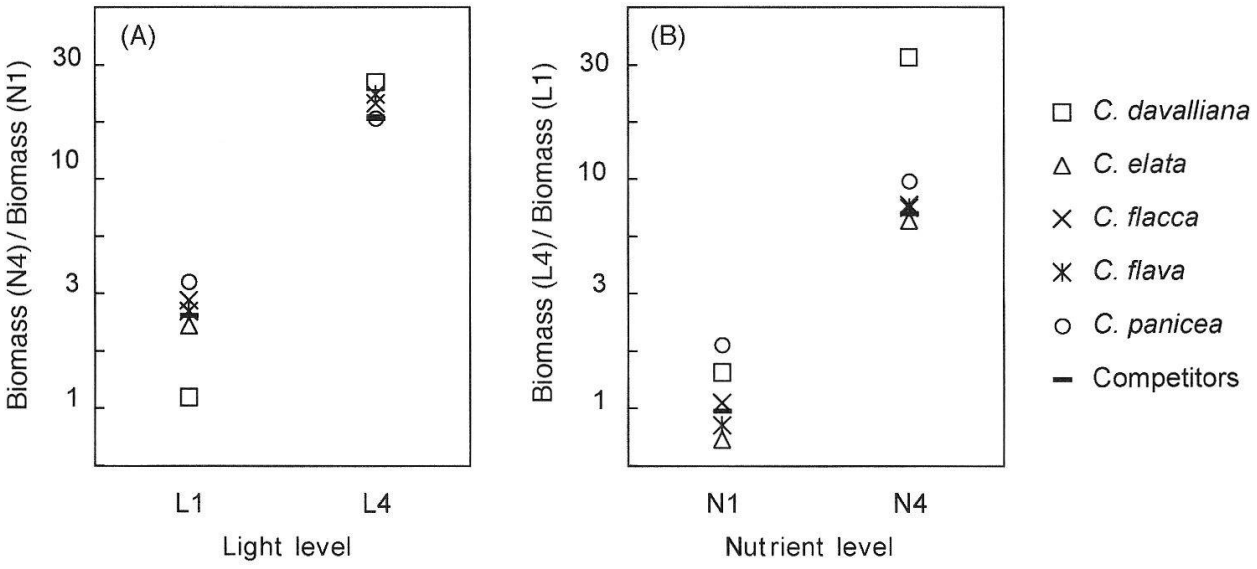


Fig. 2. *Growth responses of the five* Carex *species and of the tall forbs acting as competitors (A) to nutrient supply and (B) to light availability, as the ratio of mean biomass at highest resource level to mean biomass at lowest resource level, on a logarithmic scale. Growth responses were calculated for the highest and for the lowest level of the other resource, respectively, using data from plants grown without competition (except for the forbs).*

nutrient treatments appeared to depend on light level (despite the non-significant Nutrient*Light interaction, cf. Table 3): CR decreased monotonically with increasing nutrient supply at the two lower light levels, whereas at the two higher light levels CR was maximal at intermediate nutrient supply (N3). Mean CR of the five *Carex* species, averaged over all treatments, decreased in the order *C. elata* ≈ *C. flacca* > *C. panicea* ≈ *C. flava* > *C. davalliana* (Tukey HSD test, $P < 0.05$). These interspecific differences in CR did not depend significantly on light availability or nutrient supply (interactions not significant in Table 3)

Discussion

Experimental design and consequences for competitive interactions

An additive (target-neighbour) design was used in this study to examine the effects of nutrient and light availability on the growth and competitive ability of five *Carex* species. This design has been criticised by some authors for being artificial and arbitrary, arguing that the use of a single plant without competitors as reference does not reflect natural conditions, and that the intensity of competition depends on initial plant densities (Cousens 1991; Gibson *et al.* 1999). The advantage of an additive design is that the competitive effect of neighbours can be measured directly as the amount of growth reduction of the target plants. This contrasts with substitutive designs, where the effects of inter- and intraspecific competition are compared and no absolute measure of competition intensity is provided. The additive design is therefore more appropriate to investigate how the intensity of competition depends on resource supply (Connell 1983; Connolly *et al.* 2001).

In fact, the design of our experiment was not strictly additive in that a fivefold amount of nutrients was supplied to the pots with *Carex* and competitors (five plants) compared to those containing only the *Carex* (one plant). This unequal nutrient addition was chosen for two reasons. First, giving a fixed amount of nutrient per pot would have resulted in

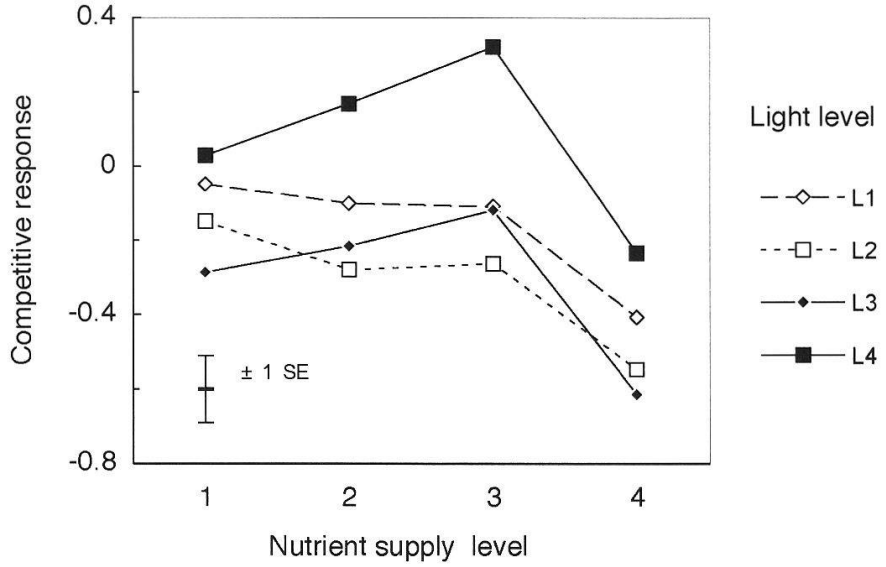


Fig. 3. Interaction plot showing the effects of light level and nutrient supply on the ability of five Carex *species to compete against tall forbs (competitive response, difference between log-transformed biomass with competition and log-transformed biomass without competition). Symbols are means for the five* Carex *species; standard errors for comparisons between two nutrient-light treatments are shown as separate error bars.*

strongly differing nutrient supplies between *Carex* plants growing alone and those growing in competition, so that toxic levels might have been reached for single plants while nutrient supply was still limiting for *Carex* with competitors. Second, the amount of light that could be intercepted by five plants was higher than the amount intercepted by a single plant, especially at the beginning of the experiment, given the small initial size of plants and the relatively large size of the pots. If, under these conditions, a fixed amount of nutrient had been given per pot, competition by forbs would have reduced the amount of nutrient available to the *Carex* more than the amount of light, so that competition for nutrients would have been decisive, as is often the case in this type of experiments (Aerts *et al.* 1991). By adapting the nutrient supply to the number of plants per pot, we increased the importance of competition for light. In this way we attempted to make the roles of competition for light and of competition for nutrients as similar as possible.

A consequence of our design was that, under some of the treatments, four of the *Carex* species produced more biomass in competition than alone; only *C. davalliana* was always reduced in the presence of competitors. Enhanced growth in the presence of competitors did not necessarily imply that the *Carex* took up part of "their neighbour's share" of nutrients; they may also simply have benefited from higher nutrient concentration in the pots. This would have been particularly likely in the initial phase of the experiment, when root systems were still too small to forage in the whole pot, so that part of the nutrients supplied to the *Carex* plants growing alone would have been inaccessible to them due to limited diffusion towards roots (Aerts & Chapin 2000). Alternatively, the lower nutrient concentration in pots without competitors may have forced the *Carex* plants to allocate more biomass to roots (Aerts *et al.* 1992; Olff 1992; van der Werf *et al.* 1993; but see Perez-Corona & Verhoeven 1999), so that less biomass could be allocated to leaves. Since specific leaf area does not change or decreases in response to low nutrient supply (Aerts *et al.* 1992; Perez-Corona & Verhoeven 1999; Poorter & Nagel 200), reduced allocation to leaves would imply that leaf area (i.e. photosynthetic capacity) developed less rapidly during the initial phase in the pots without competitors.

Thus, the net "effect of competition" as observed at the end of the growing season was in fact the difference between an initial positive effect of higher nutrient concentration and a subsequent negative effect of resource competition, and both effects need to be considered in the interpretation of results.

EFFECTS OF NUTRIENTS AND LIGHT ON PLANT GROWTH

Both nutrient and light supply significantly affected the biomass production of plants in this study, but effects differed among species and resource levels. The ranking of the five *Carex* species according to their above-ground biomass (*C. elata* > *C. flacca* ≈ *C. flava* > *C. panicea* > *C. davalliana*) was similar across treatments. It corresponds to the ranking of their ecological indicator values for nutrients or light (Edelkraut *et al.* 2000; Landolt 2001). This is consistent with the common finding that in short-term growth experiments, species from fertile sites grow faster than species from infertile sites regardless of resource supply (Aerts *et al.* 1992; McGraw & Chapin III 1989; Elberse & Berendse 1993; Ryser *et al.* 1997; but see Bollens 2000).

Growth responses of the *Carex* species and the forbs to either higher light or nutrient supply showed that both resources operated in-

teractively: the relative increase in biomass production in response to either light or nutrient availability was for all plants much stronger at the highest level than at the lowest level of the other resource. This indicates that both nutrients and light strongly limited plant growth in this experiment, contrary to other experiments where one resource was much more limiting than the other (Olff *et al.* 1990; Olff 1992). Nevertheless, growth responses to enhanced nutrient availability were generally stronger than those to enhanced light supply. A possible explanation is that nutrient supply differed relatively more (34 times higher at N4 than at N1) than light intensity (25 times higher at L4 than at L1). It must also be considered that 1% more light does not necessarily have the same effect on plant growth as 1% more nutrient. In addition, species respond differently (cf. Garnier 1998). This makes it difficult, if not impossible, to reach exactly the same degree of limitation by nutrients and by light in an experiment such as ours.

EFFECTS OF NUTRIENTS AND LIGHT ON COMPETITION

Based on species distribution in the field, where *Carex* species are replaced by tall forbs when sites are eutrophicated (Klötzli 1986; Egloff 1986; Zelesny 1994), we had hypothesised that competitive responses of the *Carex* would be negatively related to nutrient availability and positively related to light availability. However, the results only partly confirmed this hypothesis.

As expected, the growth of all *Carex* species was severely reduced by competition at high nutrient availability (N4), while this was less so or even not the case in the low-nutrient treatments. This result was consistent with numerous other studies: Wetzel & van der Valk (1998) compared high and moderately productive species and found that under high nutrient availability the less productive *Carex* species was outcompeted by the other species in the experiment. Aerts *et al.* (1991) observed no competitive interactions between *Molinia caerulea* and dwarf shrubs at low nutrient availability, whereas competition occurred at high nutrient availability. Increasing intensity of competition along gradients of productivity were also found in riverine wetlands by Twolan-Strutt *et al.* (1996). Keddy *et al.* (1997) showed that competitive asymmetry (relative advantage of stronger competitors over weaker ones) increases with increasing productivity.

An unexpected result was that competitive responses did not always decrease monotonically with increasing nutrient supply; at high light levels responses were maximal at the third level of nutrient supply. This surprising pattern could not readily be explained. It might be that the initial phase of the experiment played a role here; possibly the *Carex* could take up and store nutrients that were available in excess of the need of forbs when the latter were still small (first weeks after planting). Fast uptake and storage of nutrients in periods of excessive supply have been considered a characteristic adaptation of plants from relatively infertile sites (Chapin 1980; Kielland & Chapin 1994). When moderate nutrient supply was combined with moderate to high light supply, shading by the forbs was not so strong that this initial advantage would have disappeared in the second part of the growing season.

The relationship between light availability and competitive response was unimodal at all levels of nutrient supply; competitive responses were not only highest in full light, but they were also higher in strong shade than in slight shade. A possible interpretation is that full light increased the competitive ability of the *Carex* relative to the forbs, whereas strong

shade reduced the overall intensity and asymmetry of competition. Since the *Carex* species were generally weaker competitors than the forbs, they would benefit from lower competition intensity and asymmetry under strong shade even if their competitive ability relative to that of the forbs is simultaneously decreased. The positive CR found at L4 indicates that photosynthesis (or other physiological processes) were inhibited by excessive light intensity, so that the *Carex* plants benefited from being shaded by competitors. A direct comparison of our results with published studies is not possible because competition experiments in which light has been varied independently of nutrient supply are rare (Edelkraut *et al.* 2000). However, some support for our interpretation is provided: Weihe & Neely (1997) found that strong shade reduced the intensity of competition and delayed the deplacement of the inferior competitor by the superior one, which is consistent with our results for strong shade. Eek & Zobel (1997) suggested that additional illumination could partly compensate the effects of fertilisation on interspecific interactions in a chalk grassland, which would be consistent with our results for full light.

Competitive responses differed among the five *Carex* species, and the rank order of the species corresponded approximately to their rank order of above-ground biomass production. This concurs with results of more extensive comparative studies of wetland plants, where plant biomass and height were found to be the most important determinants of competitive ability (Gaudet & Keddy 1988; Hirose & Werger 1995; Hills & Murphy 1996). A clear limitation of our study was that we only considered results from a single harvest after one growing season. Competitive interactions are known to be time-dependent, both within the first growing season (Connolly *et al.* 1990) and between the first and subsequent years (Weiher *et al.* 1996; Mal *et al.* 1997). In the initial phase of our experiment, no competition for light occurred since plants were too small to shade each other. In this phase, competitive success of either the *Carex* or the forbs must have been related to their ability to forage below ground, which would mostly depend on the length of their root systems (Ryser 1998). However, fast above- and below-ground growth generally correlate with each other in interspecific comparisons (Crick & Grime 1987; Ryser 1995). Thus, the competitive rankings observed after one growing season had probably already started to develop during the first phase of the experiment. Different rankings might be expected in the long term, especially at low nutrient supply, when interspecific differences in nutrient storage and nutrient losses become decisive (Berendse & Elberse 1990; Aerts & van der Peijl 1993). In a comparative study by Keddy *et al.* (2000), competitive rankings of 26 wetland plants differed more between the first and the second year at low than at high nutrient supply. Also, competitive rankings depended more on nutrient supply in the second than in the first year. We will take such possible differences into account by running the experiment for a second year.

In conclusion, the growth of experimental plants as well as their competitive ability were affected by both nutrient and light supply. These two resources had different effects on the biomass production of the five *Carex* species, but similar effects on their competitive ability. Resource supply probably affected the ability of the *Carex* plants to compete against tall forbs in two ways: through an effect on the relative importance of light vs. nutrient limitation, and through an effect on competition intensity. The two effects probably acted in synergy along the nutrient gradient, but in op-

posite directions along the light gradient; this resulted in a unimodal relationship between light supply and the ability of *Carex* plants to compete against tall forbs. Further research, including measurements of nutrient concentrations, biomass allocation and biomass turnover, will be performed with the same *Carex* species to investigate the causes of unimodal relationships between nutrient supply and competitive responses as observed in this experiment.

Acknowledgements

We are grateful to R. Aerts, P.J. Edwards and J. Liira for helpful comments on the manuscript. T. Fotsch, R. Graf, R. Koch and C. Theato kindly and efficiently assisted in establishing and maintaining the experiment. The research was funded through a grant from the Swiss Federal Institute of Technology.

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Received 6 May 2001
Revised version accepted 18 June 2001
Editor: P.J. Edwards