

Effects of light and nitrogen on morphological plasticity of the moss *Calliergonella cuspidata*

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In a short-term experiment we studied the effects of increased light and nitrogen (N) availability on the moss *Calliergonella cuspidata* by cutting vascular plants and adding nitrogen in a calcareous fen in the mountainous region of central Switzerland.

Shoots of *Calliergonella* growing in plots with reduced vascular plant competition showed smaller increments in length of the main axis and produced shorter offshoots, but showed higher branching densities at the main axis, higher number of offshoots and higher dry mass per unit length.

Although the growth forms of pleurocarpous bryophytes are quite different from stolon- and ramet-producing clonal vascular plants, the overall morphological responses to changing light levels are very similar and, at least in part, comparable to the 'spacer and branching' strategy exhibited by some stolon-bearing vascular plants. The observed morphological plasticity of *Calliergonella* would in principle allow for foraging of heterogeneously distributed resources.

Nitrogen supply, on the other hand, had no effects on either dry mass or shoot morphology of *Calliergonella*. Moreover, interactions between the effects of removal of vascular plants and increased nutrient supply on biomass and shoot morphology of *Calliergonella* did not occur. This could be explained by the short duration of the experiment. However, since above-ground biomass of vascular plants was increased by the nutrient supply, it cannot be excluded that in the long run, increased N inputs will have serious secondary consequences on *Calliergonella*, e.g. due to heavy shading by vascular plants.

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Bryophytes and vascular plants often co-exist in the same habitats and, like all green plants, depend on the same essential resources, namely water, carbon dioxide, dissolved nutrients, and solar radiation. Since bryophytes are usually much smaller than vascular plants, it is often possible to distinguish between a bryophyte and a vascular plant layer in the field. Due to the larger stature of vascular plants, they deprive bryophytes of access to light (asymmetric competition, see Rydin 1997). Although bryophytes are known to have rather low light compensation values (Proctor 1982), light can become a limiting factor for bryophytes

growing beneath a dense cover of vascular plants, which is shown by a few experimental studies (Kooijman 1993, Bartsch 1994, Hogg et al. 1994). Within dense bryophyte stands, light extinction in the upper few centimetres is nearly complete (van der Hoeven et al. 1993) and browning of bryophyte shoots and leaves due to shortage of light occurs (van der Hoeven and During 1997).

Nutrient limitation of bryophyte growth has been shown for several bog-inhabiting *Sphagnum* species (Aerts et al. 1992, Lütke Twenhöven 1992, Svensson 1995). For pleurocarpous mosses of ecosystems richer

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in nutrients than bogs, growth seems only rarely to be limited by nutrients (Skre and Oechel 1979, Bates 1987, van Tooren et al. 1990). However, it is not yet possible to draw general conclusions about effects of nutrient supply on bryophyte growth, since experimental data are still very scarce. Kooijman (1993), for example, has shown that nutrient limitation of growth of *Calliergonella cuspidata* was dependent on moisture conditions, with additional nutrients stimulating growth only at relatively dry conditions.

Essential resources for plant growth such as light and nutrients are patchily distributed in space. Plasticity in vegetative growth, as exhibited by plants, allows plastic responses to resource-rich patches such as increased branching densities or shortening of plagiotropic growing axes (Slade and Hutchings 1987a, b, Schmid 1990, de Kroon and Hutchings 1995).

Branching patterns of bryophytes are strongly dependent on environmental conditions, and often species show highest branching frequencies at rather high light levels (Davy de Virville 1927–1928, van der Hoeven and During 1997). The morphological responses of bryophytes to low and high light levels are in accordance with those reported for some vascular plants (Schmid 1986, Hutchings and de Kroon 1994, Stoll and Schmid 1998), but this is not always the case. For instance, van der Hoeven et al. (1998) found no effects of high and low light levels on shoot elongation and branching frequency in *Rhytidiadelphus triquetrus* and *Calliergonella cuspidata*, and Scandrett and Gimingham (1989) found highest yields of two pleurocarpous moss species in the shade. However, radiation and moisture conditions experienced by the bryophytes are not independent, i.e. higher radiation may lead to faster desiccation of the bryophytes. By this, physiological activity and, thus, growth may be reduced.

Experimental studies exploring changes in branching patterns of pleurocarpous bryophytes as a response to increased nutrient supply are very scarce and often failed to find any effect (Bates 1987). Vascular plants with plagiotropic growth often exhibit higher branching frequencies under high nutrient conditions, but response of internode length is quite variable (Hutchings and de Kroon 1994, Stoll et al. 1998).

In this study, we explored the effects of increased light and nitrogen (N) availability on bryophytes by manipulating the vascular plant layer and adding nitrogen in a field experiment. We conducted the study in a calcareous wet meadow (fen) in the mountainous region of Switzerland. As our target species we chose the pleurocarpous moss *Calliergonella cuspidata* (Hedw.) Loeske (hereafter called *Calliergonella*).

We hypothesized that growth and shoot morphology of *Calliergonella* would respond to enhanced light and N availability. Since our study was conducted in a fen, enhanced light levels should not necessarily lead to much faster desiccation of the bryophytes. Thus, we

expected responses consistent with those reported for some plagiotropic vascular plants, such as reduced growth of the main axis, increased branching density, production of shorter branches, and increased mass per unit length (see Hutchings and de Kroon 1994). Furthermore, we expected vascular plant biomass to increase due to enhanced N supply, which would lead to intensified shading of the bryophyte layer. Therefore, we hypothesized that effects of increased N availability on *Calliergonella* would only occur if vascular plants were removed. Thus, we expected significant interactions between the effects of removal of vascular plants and increased nutrient supply on biomass and shoot morphology of *Calliergonella*.

Material and methods

Study species

Calliergonella cuspidata (Amblystegiaceae) is a tall, moderately robust pleurocarpous moss growing in single-species patches or intermingled with other bryophytes. *Calliergonella* is distributed world-wide in most temperate regions (Eon 1967, Düll 1992). It occurs predominantly in moist or wet habitats, but also at drier places (Eon 1967). In montane, calcareous fens in Switzerland it is the most frequent bryophyte species (Bergamini et al. 2001a).

Shoots of *Calliergonella* are more or less pinnately branched and often flattened. Rhizoids are missing. There are two branch types: branches with finite growth ('branches'), and branches with potentially infinite growth ('offshoots', Fig. 1). Offshoots are morphologically and functionally identical to the main axis of the plants and after disintegration they become main axes themselves. Local population maintenance is mainly by offshoot production, i.e. by clonal growth, since the production of spores is rather rare and safe sites for protonemal development are presumably very scarce. The production frequency of both branches and offshoots is, at least in part, controlled by the light environment (Davy de Virville 1927–1928).

Study site

The study was conducted in a calcareous fen in the mountainous region of central Switzerland (canton of Schwyz, Alpthal, 'Rund Blätz', approx. 1200 m a.s.l., Swiss grid co-ordinates: 696.9/210.9). Calcareous fens are nutrient-poor, low-productive ecosystems, but they are threatened by nutrient influx from adjacent farmland and by atmospheric deposition. Bulk N deposition at the study site is 12.3 kg N ha⁻¹ yr⁻¹, which is comparatively low (Schleppi et al. 1998). In some areas of Switzerland bulk N deposition is already as high as

40 kg ha⁻¹ yr⁻¹ (Bundi et al. 1993). The study site is mown once a year at the beginning of September. The vegetation of the site belongs mainly to the Caricion davallianae (vegetation classification after Ellenberg 1996). Vascular plant vegetation is dominated by graminoids such as *Molinia caerulea* (L.) Moench, *Carex davalliana* Sm., *C. panicea* L. and various other sedges as well as by characteristic forbs such as *Primula farinosa* L., *Parnassia palustris* L., *Succisa pratensis* Moench, and *Tofieldia calyculata* L. The bryophyte layer is well developed and bare ground is only occasionally visible at disturbed places due to animal activity and mowing. Various pleurocarpous mosses such as *Calliergonella cuspidata*, *Brachythecium mildeanum* Jur., *Campylium stellatum* (Hedw.) J. Lange & C. Jens, *Climacium dendroides* (Hedw.) Web. & Mohr, and *Hypnum lindbergii* Mitt. dominate the bryophyte vegetation. Occasionally, acrocarpous mosses such as *Fissidens adianthoides* Hedw. and *Atrichum undulatum* (Hedw.) P. Beauv. are dominant. Liverworts are very scarce and only *Chiloscyphus polyanthos* (L.) Corda and *Pellia endiviifolia* (Dicks.) Dum. can be found regularly, although with low abundance.

Study design

In order to study the effects of increased N and light availability on bryophytes as well as interactions be-

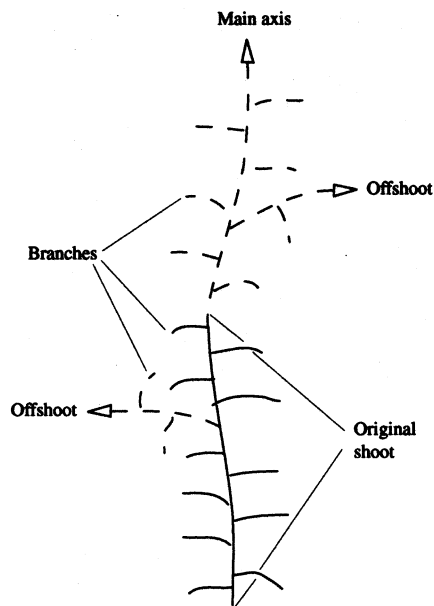


Fig. 1. Scheme of a shoot of *Calliergonella cuspidata*. Solid lines: original shoot of 3 cm length before implantation in experimental subplots; dashed lines: new-grown parts during the course of the experiment (3 months).

tween factors, we used a full-factorial block design. We established five blocks (each 1 × 6 m) at the study site. Blocks were located in areas of relatively homogeneous vegetation and microtopography. *Calliergonella* occurred naturally in all blocks. Each block contained 3 plots (1 × 2 m) which contained four randomly arranged subplots each (0.3 × 0.3 m). Between adjacent subplots, we kept buffer stripes of at least 0.2 m. Each of the studied factors had two levels (nitrogen: control, +N; light: control, removal of vascular plants), leading to four treatment combinations. In total, there were 5 × 3 = 15 replicates for each treatment.

On 22 May 1998, we planted four shoots of *Calliergonella* in the central 0.2 × 0.2 m part of each subplot, leading to a total of 240 planted shoots. These shoots had been sampled two days previously at the study site. In the laboratory, they were then cut to 3 cm in length and tagged (nylon threads of about 5 cm length, tied to plastic labels). Before and after this procedure, shoots were stored in plastic bags to prevent desiccation. To control, at least in part, for the variation among shoots, we only used shoots which had at least ten lateral branches and no offshoots.

To assure high N levels during the course of the experiment, N was applied four times during the growing season (23 May, 15 June, 6 July, and 8 August 1998). Nitrogen was solved in demineralized water and applied as top dressing (0.2 l per subplot) using spraying bottles. Control plots received the same amount of demineralized water. Total nutrient supply for N subplots corresponded to 50 kg per ha which were applied as follows: May 25 kg; June, July, and August 8.33 kg each. Nitrogen was applied as NH₄NO₃. The pH of the N dressings (pH ≈ 6.1) was slightly lower than that of the water added to controls (pH ≈ 6.8). Soil pH of the study site was approximately 6.1.

Before every N application, we removed all above-ground vascular plant biomass in half of the subplots by cutting vascular plants just above the bryophyte layer. Vascular plant biomass was sampled and weighed after drying for 48 h at 70°C.

Repeated removal of vascular plants reduced their biomass considerably. At the final harvest, the vascular plant biomass in the cut plots was about 90% smaller than in the controls. Removal of vascular plants led to very large differences for photon flux density (16.3 without removal vs 138 μmol s⁻¹ m⁻²).

The final harvest was on 26 August 1998, i.e. 3 months after the beginning of the experiment. On this day we sampled vascular plant biomass in all subplots and searched for the tagged *Calliergonella* shoots. We found 205 shoots (ca 85%) of the originally planted 240 shoots. At least two shoots were found in every subplot.

Table 1. Measured features to assess the effects of nitrogen supply and the removal of vascular plants on shoot morphology of *Calliergonella*. *: data \log_{10} -transformed for ANOVAs.

| Feature | Calculation | Unit |
|--|--|--------------------------------------|
| 1. Length increment of main axis of offshoots* | total length incr. of offshoots/no. of offshoots | cm cm |
| 2. Branching density at main axis at offshoots | no. of branches at new-grown part of main axis/length incr. of main axis no. of branches at offshoots/total length incr. of offshoots | cm^{-1} cm^{-1} |
| 3. Number of offshoots | | – |
| 4. Dry mass total* | sum of old and new parts | mg |
| per unit length* | total dry mass/(original length + total length increment) | mg cm^{-1} |

Response variables

The effects of N supply and removal of vascular plants on *Calliergonella* were examined with measurements of (1) length increment, (2) branching density, (3) number of offshoots, and (4) dry mass (see Table 1). Total dry mass was assessed after drying the shoots for 48 h at 70°C.

We used vascular plant above-ground biomass from the final harvest to test for effects of increased N supply on the vascular plant layer.

Statistical analysis

For all statistical analyses we used means of the retrieved shoots within subplots for all the measured variables. Effects of the factorial treatments were tested using nested analysis of variance (ANOVA). Block effects were tested against the variation among plots within blocks, differences among plots within blocks against the residual variation. Effects of nutrient supply and removal of vascular plants on *Calliergonella* were analysed at subplot level. To get normally distributed residuals, several variables were \log_{10} -transformed (see Table 1).

The number of replicates for the ANOVAs was normally 60. However, in some of the analyses total n was reduced because it was obviously not possible to count the number of lateral branches or calculate their density at the main axis and at offshoots if there was no growth of the main axis or if no offshoots were produced.

Since the removal of vascular plants was one of the treatments, we analysed above-ground biomass of vascular plants only for the effect of N supply. We used the same ANOVA model as mentioned above, but we omitted all subplots where vascular plants had been removed, leading to the total of $n = 30$.

All statistical analyses were carried out with the GENSTAT 5.0 program, release 3.2 (Payne et al. 1993).

Results

Vascular plant biomass

There was a significant block effect on vascular plant biomass ($F_{4,10} = 5.21$, $p < 0.025$), indicating spatial variation of productivity within the study site. The increased supply of N caused a 13% increase of above-ground biomass production of vascular plants ($F_{1,14} = 4.59$, $p < 0.05$), indicating that productivity of vascular plant vegetation was limited by N.

Shoot morphology and dry mass of *Calliergonella cuspidata*

There were no significant block effects on any of the measured moss variables, and, with the exception of effects on length increment of offshoots, no effects of plots within blocks occurred. This indicates that there was only negligible environmental heterogeneity between and within blocks with respect to the growth of *Calliergonella*, which was also largely independent of vascular plant productivity.

The complete removal of vascular plants, however, had pronounced effects on shoot morphology and dry mass per unit length of *Calliergonella*, but not on total dry mass (Tables 2, 3, Figs 2, 3). Length increment of the main axis (–43%) and length increment of offshoots (–41%) were distinctly reduced by the removal of vascular plants, whereas the number of offshoots was significantly increased (+79%, Fig. 2).

Branching density at the main axis was markedly enhanced by the removal of vascular plants (+35%), whereas branching density at offshoots was distinctly lowered (–67%, Fig. 2). This was most likely due to the much shorter offshoots in subplots without vascular plants.

Since total dry mass did not differ between treatments but length increments of the main axis and of offshoots were reduced by the removal of vascular plants, dry mass per unit length was higher without vascular plants (+23%, Fig. 3, Table 3).

The increased supply of N had no influence either on dry mass or on shoot morphology or on dry mass per unit length of *Calliergonella* (Tables 2, 3, Figs 2, 3). Furthermore, the hypothesized interaction between the removal of vascular plants and increased N supply could not be confirmed (Tables 2, 3).

Discussion

Removal of vascular plants

Our experiment clearly demonstrated that the overall shoot morphology of *Calliergonella* was greatly affected by the removal of vascular plants. *Calliergonella* growing without vascular plants showed smaller increments in length of the main axis and produced shorter offshoots with less dense branches, but showed higher branching densities at the main axis, higher number of offshoots and higher dry mass per unit length. Total dry mass, however, was unaffected.

In contrast to our study, van der Hoeven et al. (1998) found no effects of different light levels on the number of new branches of *Calliergonella*, possibly because of confounding effects of light intensity and moisture relations. However, experimental thinning of dense stands of *Calliergonella* in the field increased the productivity of new shoots from dormant buds on brown shoot parts (van der Hoeven and During 1997), confirming the dependence of branching density and offshoot production on light levels (see also Rydgren et al. 1998). This was also demonstrated by Davy de Virville (1927–1928), who found reduced branching of *Calliergonella* and several other bryophytes at experimentally lowered light levels. Similar responses were observed by Rincon and Grime (1989) for four pleurocarpous mosses in an experiment where effects of spatial patchiness of irradiance on morphological plasticity were studied. By producing elevated and attenuated shoots in the shade treatments, the four mosses were effective colonists of local light patches (Rincon and Grime 1989).

Table 2. ANOVA for the effects of removal of vascular plants and nitrogen supply on A: length increment, B: branching density, and C: number of offshoots of *Calliergonella*. When differing from the usual, residual degrees of freedom are given in parenthesis. *: $p \leq 0.05$, ***: $p \leq 0.001$.

| A | | Length increment | | | |
|---------------------|------|------------------|----------|--------------|----------|
| | | of main axis | | of offshoots | |
| | d.f. | SS | F-ratio | SS | F-ratio |
| Blocks | 4 | 2.17 | 0.91 | 0.1181 | 0.49 |
| Plots within blocks | 10 | 5.96 | 1.07 | 0.6019 | 2.56* |
| Removal (R) | 1 | 7.53 | 13.48*** | 0.5024 | 21.34*** |
| Nitrogen (N) | 1 | 0.33 | 0.59 | 0.0206 | 0.87 |
| R × N | 1 | 0.07 | 0.13 | 0.0006 | 0.02 |
| Residuals | 42 | 23.47 | | 0.8474 (36) | |

| B | | Branching density | | | |
|---------------------|------|-------------------|---------|--------------|---------|
| | | at main axis | | at offshoots | |
| | d.f. | SS | F-ratio | SS | F-ratio |
| Blocks | 4 | 11.36 | 1.50 | 10.50 | 2.18 |
| Plots within blocks | 10 | 18.87 | 0.81 | 12.05 | 0.68 |
| Removal (R) | 1 | 14.55 | 6.26* | 9.70 | 5.46* |
| Nitrogen (N) | 1 | 0.85 | 0.36 | 2.63 | 1.48 |
| R × N | 1 | 0.00 | 0.00 | 1.14 | 0.64 |
| Residuals | 42 | 92.25 (41) | | 63.92 (36) | |

| C | | Number of offshoots | |
|---------------------|------|---------------------|---------|
| | d.f. | SS | F-ratio |
| Blocks | 4 | 0.385 | 0.13 |
| Plots within blocks | 10 | 7.267 | 0.96 |
| Removal (R) | 1 | 5.098 | 6.74* |
| Nitrogen (N) | 1 | 0.002 | 0.00 |
| RN | 1 | 0.023 | 0.03 |
| Residuals | 42 | 31.77 | |

Table 3. ANOVA for the effects of removal of vascular plants and nitrogen supply on total dry mass and dry mass per unit length of *Calliergonella*. ***: $p \leq 0.001$.

| | d.f. | Total dry mass | | Dry mass per unit length | |
|---------------------|------|----------------|---------|--------------------------|----------|
| | | SS | F-ratio | SS | F-ratio |
| Blocks | 4 | 0.070 | 1.38 | 0.049 | 1.42 |
| Plots within blocks | 10 | 0.126 | 1.08 | 0.086 | 1.00 |
| Removal (R) | 1 | 0.017 | 1.47 | 0.119 | 13.82*** |
| Nitrogen (N) | 1 | 0.020 | 1.70 | 0.007 | 0.77 |
| R × N | 1 | 0.003 | 0.28 | 0.001 | 0.17 |
| Residuals | 42 | 0.491 | | 0.362 | |

By removing the vascular plants, we manipulated both light quantity and light quality. It has been shown that bud formation, breaking of dormancy of buds, and, thus, branching frequency of bryophyte protonemata is strongly light dependent, and it was presumed that the phytochrome system is involved (reviewed by Bopp 1983). If this would also apply to gametophytic shoots, a decreased red/far-red ratio as it is found beneath a vascular plant canopy should lower branching frequency. However, van der Hoeven et al. (1998), manipulating the red/far-red ratio experimentally, found no responses in shoot morphology of *Calliergonella cuspidata* and *Rhytidiadelphus squarrosus*, and, contrary to expectations, Hoddinott and Bain (1979) found higher branching frequencies of the acrocarpous moss *Ceratodon purpureus* at an experimentally lowered red/far-red ratio.

While most of the observed responses of *Calliergonella* can be explained by the changed light environment in the plots without vascular plants, the decreased branching density at the offshoots can not. Since the offshoots were relatively short in these plots (cf. Fig. 2), it seems that offshoots do not produce any branches below a certain threshold length.

By manipulating the light environment experienced by the bryophytes, humidity conditions are also changed. Although the experiment was conducted in a fen, unfavourable effects of the removal of vascular plants on moisture conditions (e.g. longer desiccation periods) cannot be excluded. However, they seem not to be very severe since *Calliergonella* produced the same amount of biomass in both environments. With respect to branching density at the main axis and to offshoot production, the removal of vascular plants ameliorated the microclimate (higher branching density and more offshoots without vascular plants).

Although the growth forms of pleurocarpous bryophytes are quite different from stolon- and ramet-producing clonal vascular plants such as *Glechoma hederacea* (see Hutchings 1988), the overall morphological responses to changing light levels are very similar and, at least in part, comparable to foraging tactics exhibited by some stolon-bearing vascular plants (e.g.

the 'spacer and branching' strategy, see Oborny and Cain 1997). The distinct changes of overall shoot morphology to the removal of vascular plants revealed that *Calliergonella* in principle could effectively occupy favourable microhabitats. The adaptive significance of the morphological plasticity exhibited by *Calliergonella*, however, is not known, since we conducted our experiment in two distinctly homogeneous environments, but foraging critically depends on the spatio-temporal distribution of the resources (Oborny and Cain 1997).

Nutrient supply

Addition of N had no effects on either dry mass or shoot morphology of *Calliergonella*. The absence of any reaction of *Calliergonella* to increased N supply is consistent with results of earlier studies by van Tooren et al. (1990) and Kooijman and Bakker (1995). In both studies, *Calliergonella* showed no increased growth after supply of additional nutrients. The lack of response to enhanced nutrient supply stands in contrast to studies conducted with bryophytes of more oligotrophic habitats such as bogs, where higher N levels often stimulate growth (Aerts et al. 1992, Svensson 1995).

It seems very unlikely that the supplied amount of N was too low to cause a growth reaction, since vascular plant biomass did increase in the experimental plots. Moreover, it has been shown that growth is inhibited by high N concentrations (Rudolph and Voigt 1986, Lütke Twenhöven 1992, Gunnarsson and Rydin 2000). Gunnarsson and Rydin (2000) estimated an N influx of $< 1 \text{ g m}^{-2} \text{ yr}^{-1}$ to be optimal for *Sphagnum* growth. This may indicate that the $5 \text{ g N m}^{-2} \text{ yr}^{-1}$ applied in our experiment could have been too high to stimulate growth.

The short duration of our experiment (3 months) may be critical to detect any responses, although we do not know of any study reporting delayed responses of bryophytes to increased N. For *Sphagnum* species it has been shown that the outcome of short-term N addition experiments must not coincide with those of long-term

experiments (Gunnarsson and Rydin 2000, Aerts et al. 2001). These studies show that N addition had positive effects on growth in the first year but not in the following years, possibly due to growth-inhibiting effects of accumulated N in the bryophyte tissue (Gunnarsson and Rydin 2000, Aerts et al. 2001).

Contrary to our expectations, there were no interactions between the effects of removal of vascular plants and the increased N supply, although vascular plant

biomass increased due to N addition. However, it seems likely that such interactions would emerge if the experiment would be conducted over a longer period of time, since bryophyte biomass is negatively related to vascular plant biomass in calcareous fens (Bergamini et al. 2001b, Bergamini and Pauli in press). A future enrichment of the study site by nitrogen due to enhanced atmospheric N deposition might therefore increase above-ground biomass of vascular plants (Pauli 1998)

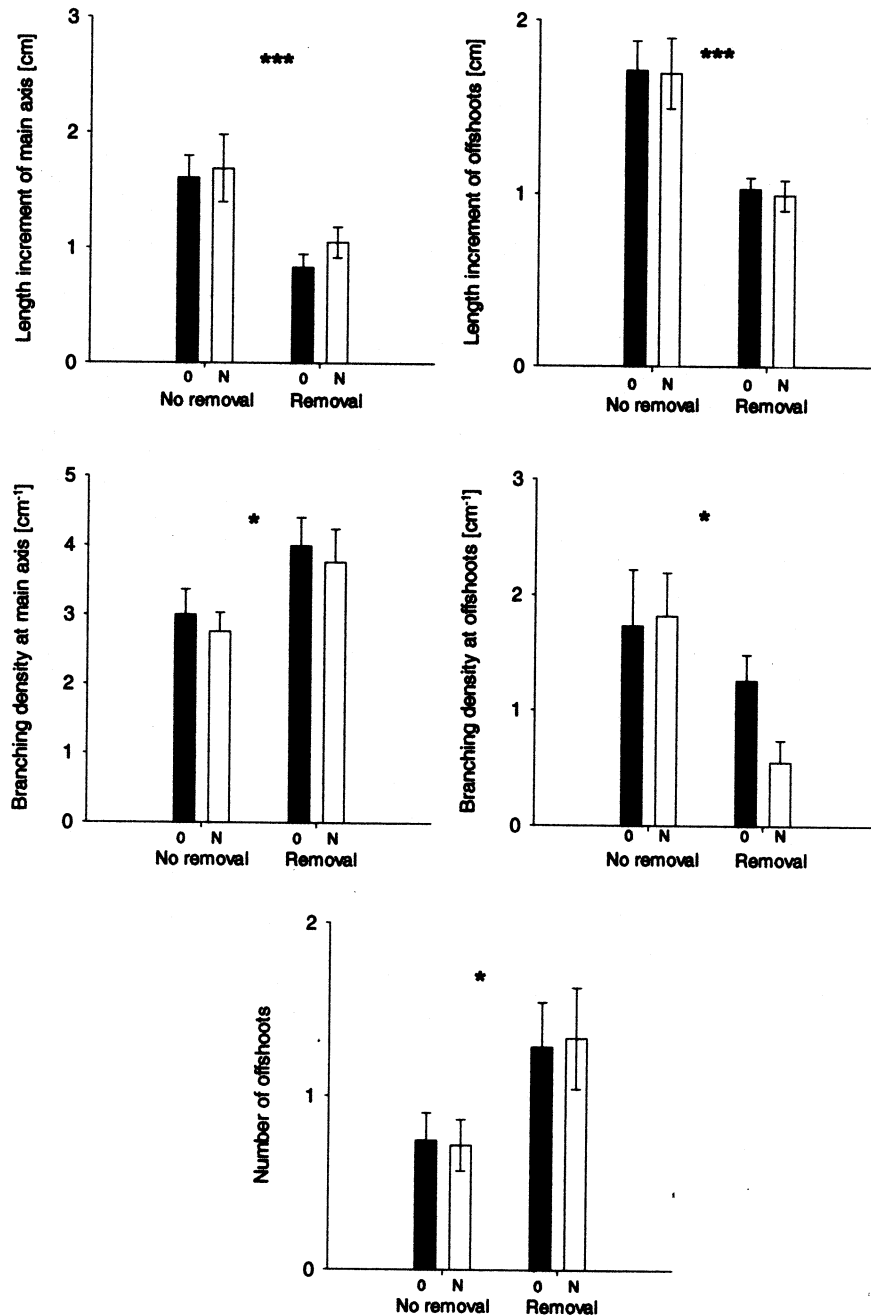


Fig. 2. Effects of nitrogen supply and removal of vascular plants on shoot morphology of *Calliergonella*. For explanations of variables see Table 1. Means and standard errors are given (calculated from untransformed values). No removal: vascular plants not removed, Removal: vascular plants removed, 0: no additional nitrogen, N: addition of nitrogen. Significant effects of removal of vascular plants indicated as follows: *: $p \leq 0.05$, ***: $p \leq 0.001$ (see Table 2).

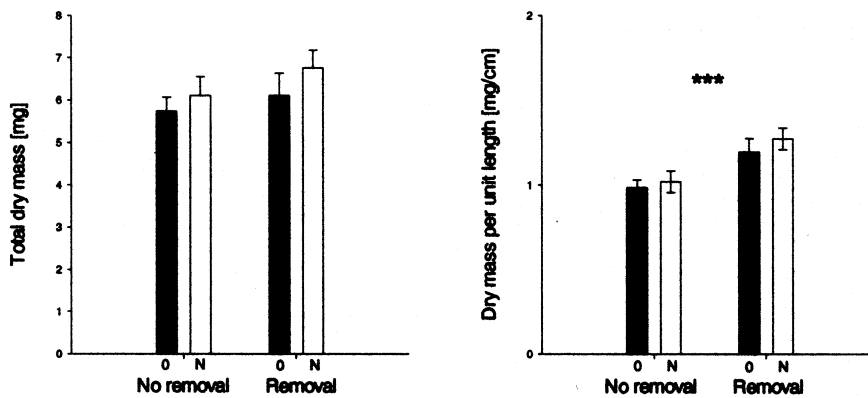


Fig. 3. Effects of nitrogen supply and removal of vascular plant on total dry mass and dry mass per unit length of *Calliergonella*. Means and standard errors are given (calculated from untransformed values). No removal: vascular plants not removed, Removal: vascular plants removed, 0: no additional nitrogen, N: addition of nitrogen. ***: significant effect ($p \leq 0.001$) of removal of vascular plants (see Table 3).

and, thus, indirectly negatively affect performance of *Calliergonella* by enhanced shading (van Tooren et al. 1990, Kooijman 1993).

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