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Interspecific interactions between bryophytes in a Dutch chalk grassland after pulse perturbation

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Abstract. In order to analyze the role of interspecific competition in the dense, but species-rich bryophyte layer of chalk grasslands, two dominant species (in cover and biomass) were severely reduced in cover. The direct response of all species in such manipulated plots of 12.5 x 12.5 cm was compared with their behaviour in control plots.

From the positively density-dependent growth response found in earlier studies, attributed to more favourable water conditions in dense bryophyte stands, perturbation was expected to lead to growth reduction. No such reduction was, however, observed. Instead, vigorous regrowth was observed in the first months after the perturbation.

The most vigorous response after the manipulation was shown by the reduced species themselves: within a year *Calliergonella cuspidata* and *Ctenidium molluscum* had largely refilled the open spaces in the plots from which they had been removed. The responses of each of the less abundant species were not significantly different from those in control plots, suggesting that these species were not competitively suppressed by the dominant species in the control plots. Apparently, *Calliergonella* and *Ctenidium* did not achieve dominance solely by competitive processes. Regrowth of the manipulated species took place all over the plots, and may be explained by the fact that inevitably many small fragments were left in the plots after reduction. Thus, many growing points were available for these species to grow out again. Moreover, since these fragments were appressed to the soil, where water conditions were more favourable than at higher levels around isolated shoots of the less abundant species, the growth rate of the manipulated species may have been higher than that of the other species.

1 Introduction

The impact of interspecific competition in a plant community is determined by local interactions between neighbouring individuals of different species. One way to approach interspecific competition in the field is to analyse neighbour interactions by experimental manipulations: the abundance of a possible competitor is decreased and the direct response of all species in the plot is measured (CONNELL 1983, BENDER et al. 1984). An increase in abundance of one or more other species in the manipulated plots in comparison to control plots is an indication that competition played an important role in structuring the vegetation.

In nearly all neighbour manipulation experiments that have been carried out, a significant increase in one or more other species was shown after removal or reduction of the most abundant species (ARMESTO & PICKETT 1986, BOBBINK et al. 1987, GUREVITCH & UNNASH

1989, AARSSEN & EPP 1990, HERBEN et al. 1997). These experiments always concerned phanerogams. However, the effect of a reduction of the most abundant species in a bryophyte community may be different. Earlier studies on chalk grassland bryophyte communities showed that competition for nutrients does not play a significant role (VAN TOOREN et al. 1990). Competition for light takes place but is mainly symmetrical and does not seem to play an important role in structuring the vegetation, although senescence of older stem parts at the bottom of a dense moss canopy is enhanced by the poor light conditions at this level (BATES 1979, VAN DER HOEVEN et al. 1993). Beside competitive interactions for light, mutualistic interactions for water take place between the shoots (PROCTOR 1980), and at natural shoot densities this facilitation may be even more important than interspecific competition (see also BATES 1988, ØKLAND & ØKLAND 1996). Destroying the vegetation structure and creating gaps may undo the facilitative interactions and may even cause mortality of the remaining shoots due to water stress. In this case, regrowth might take place from the intact moss layer surrounding the manipulated plots or from the diaspore bank (LLORET 1994, HEINKEN & ZIPPEL 2004).

Alternatively, if water sharing is not an essential factor for survival, regrowth will not only take place from the edges but also from within the plot. If interspecific competition and dominance determine the structure of the bryophyte layer and the species with the most vigorous growth in that particular microhabitat is able to overgrow other species, its reduction will result in more favourable (light) conditions for the subordinate species and thus to increased growth rates for at least a few of these species. Since earlier observations suggested that possible competitive interactions in bryophyte communities only take place between species with a similar growth form (TAMM 1953, DURING & LLORET 1996, BATES 1998), it is expected that the increased growth rates will be shown mainly by species with the same growth form as the reduced species, together with the regrowth of this species itself.

In the present study we analyse the influence of two dominant bryophyte species (by cover and biomass) with different stature on co-existing bryophyte species. We focus on three questions: 1. Does total bryophyte mass recover after a severe reduction of the dominant species, or does the decrease in density lead to deteriorated water conditions that keep bryophyte cover low? And if the bryophytes recover rapidly, 2. Which of the species in the plot respond with an increase in cover after the reduction? 3. Does regrowth take place from the remaining shoots within the plots or mainly from the margins, i. e., from the undisturbed moss layer surrounding the manipulated plots?

2 Methods

The experiment took place in chalk grasslands in South Limburg, The Netherlands. It was carried out simultaneously in two sites, one in the Gerendal (Laamhei) and one in Wylre. Both sites are on slopes with a north-west exposition, grazed each year for several weeks by sheep in August and mown afterwards.

The bryophyte layer in these grasslands is species-rich and locally very dense (up to 100 mg dry weight per m^2; VAN TOOREN et al. 1988). Pleurocarpous species are dominant (both by cover and in biomass). Sporophyte production in these pleurocarps very rarely takes place.

These species are almost absent from the diaspore bank in the soil (DURING & TER HORST 1983) and nearly only spread vegetatively: branches or small fragments break off and continue growth as separate individuals. The pleurocarpous shoots usually grow intermingled with each other in a fine-grained pattern, with a few acrocarps in between (DURING & LLORET 1996). However, patches where one species is dominant also occur.

The experiment started at the end of May 1992. 40 plots of 12.5 x 12.5 cm were selected in the field: 20 in each of the two chalk grassland sites. Ten plots per site were selected to have *Calliergonella cuspidata* (Hedw.) Loeske as the most abundant species, and ten plots to have *Ctenidium molluscum* (Hedw.) Mitt. as the most abundant species, both taking ca. 70-80% of the total bryophyte cover in their plots (corresponding to 47-58% of the ground area). The bryophyte layer in these plots ranged in cover from 62-88% of the available ground area. The remaining 20-30% of the bryophyte layer was covered with one to nine species per plot. In total 18 bryophyte species were found in the 40 plots: eleven pleurocarps, five acrocarps and two liverworts (Tab. 1).

Tab. 1: Bryophyte species found in the experimental plots.

Pleurocarps	**Acrocarps**
Calliergonella cuspidata (Hedw.) Loeske	*Plagiomnium undulatum* (Hedw.) T. Kop.
Ctenidium molluscum (Hedw.) Mitt.	*Fissidens* spp.
Pseudoscleropodium purum (Hedw.) Fleisch.	*Bryum* spp.
Rhytidiadelphus squarrosus (Hedw.) Warnst.	*Pottia* spp.
Eurhynchium hians (Hedw.) Lac.	*Barbula* spp.
Eurhynchium striatum (Hedw.) Schimp.	
Brachythecium rutabulum (Hedw.) Schimp.	
Brachythecium glareosum (Spruce) Schimp.	
Campylium chrysophyllum (Brid.) J. Lange	**Liverworts**
Thuidium tamariscinum (Hedw.) Schimp.	*Lophocolea bidentata* (L.) Dum.
Cirriphyllum piliferum (Hedw.) Grout	*Plagiochila porelloides* (Torrey ex Nees) Lindenb.

In five (randomly chosen) plots out of ten, the cover of the most abundant species (*Calliergonella* or *Ctenidium*) was severely reduced to ca 10-13% of its original cover (corresponding to 5-9% of the ground area) by carefully removing as many shoots as possible. Both green and brown shoot parts were removed with help of a pincer. Only small fragments of the reduced species (that could not be determined in the field) and shoot parts that could not be removed without damaging the rest of the vegetation were left. Disturbance of shoots of the other species in the plots was kept to a minimum. The remaining plots were left undisturbed, serving as controls.

The species mixture in every plot was recorded with help of a grid with 100 subplots of 1.25 x 1.25 cm. In each subplot, all bryophyte species present were recorded and their cover assessed using six classes (0-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%). Mean cover of each species in each plot was calculated by converting cover to the mean of each cover class.

All 40 plots were repeatedly surveyed for two years after manipulation. Recordings took place on six occasions: 1. In May 1992, at the start of the experiment, just before manipulation; 2. In June 1992, just after manipulation, to measure the magnitude of the reduction and the effect of disturbance on the other species; 3. In November 1992; 4. In March 1993; 5. In June 1993; 6. In May 1994 (at the end of a very wet spring). By use of twelve fixed iron markers in each plot, it was possible to place the grid in exactly the same position at every recording. The phanerogam layer in the plots was usually rather low (due to grazing and mowing at the end of the summer) and removal of phanerogams (by clipping) was only occasionally necessary, to be able to place the grid in the right position.

The mean cover of each species (in each plot) was compared between manipulated plots and control plots during the two years after the manipulation. This was done with an ANOVA procedure for repeated measurements using SAS (SAS 1988), after testing for the sphericity assumption (DIXON et al. 1992). The first recording in May 1992 was left out here. Polynomial contrasts were used to overcome the different length of the time intervals between the five subsequent recordings. All data were square root transformed because some of the subsets were not normally distributed.

Many of the 18 species found in the plots (Tab. 1) were too low in cover or absent in too many plots to allow a test of their response. The six species that could be tested (both in manipulated plots dominated by *Calliergonella* and *Ctenidium*) were the pleurocarps *Calliergonella cuspidata*, *Ctenidium molluscum*, *Pseudoscleropodium purum* (Hedw.) Fleisch. and *Rhytidiadelphus squarrosus* (Hedw.) Warnst. and the acrocarps *Plagiomnium undulatum* (Hedw.) T. Kop. (including some *Plagiomnium affine* (Bland.) T. Kop.) and *Fissidens dubius* P. Beauv. (including some *Fissidens taxifolius* Hedw.).

Regrowth in the manipulated plots two years after perturbation was also expressed as a percentage of the original cover, calculated plotwise for the total cover of bryophytes and for the cover of *Calliergonella* and *Ctenidium* after reduction (Tab. 3). In this calculation the change in cover over the period of the experiment was taken into account by applying the following formula:

$$R = 100 \cdot x_t / (x_0 (1+c)) \qquad \text{with } c = \Sigma ((y_t - y_0) / y_0) \ / 5$$

with: R = % regrowth in manipulated plot; x_t, x_0 = cover at time t and at start in manipulated plot; c = correction term for development in control plots (average of five plots); y_t, y_0 = cover in control plot at time t and at start.

Data at subplot scale were used to assess the source for regrowing shoots. In order to test if regrowth took place from the intact moss layer outside the plots or from remaining shoots within the plots, the plots were divided in two parts, a centre (consisting of the 36

centre subplots) and a margin (consisting of the 64 subplots in the two outer rows). For each manipulated species in each perturbed plot the mean change in cover per subplot from the moment of the perturbation to the next recording was calculated separately for the two plot-parts. The difference in growth (change in cover) between centre and margin was tested in a one-way ANOVA using SAS (SAS 1988).

Since the pattern of cover change with time occasionally differed between the two sites, the effect of the manipulation on the bryophyte cover was tested separately for the two sites.

Tab. 2: Percentage of the total bryophyte cover (as recorded before manipulation in May 1992) left just after the manipulation (June 1992) and two years after the manipulation (May 1994). Values are the mean of five replicate plots per species per site. Numbers in parentheses are standard deviations. All figures are adjusted, in terms of percentage, for the change in cover in control plots.

		Calliergonella	*Ctenidium*
Laamhei	June 1992	28.5 (6.4)	25.1 (5.1)
	May 1994	80.8 (20.2)	87.1 (35.3)
Wylre	June 1992	41.3 (6.1)	31.0 (5.8)
	May 1994	102.4 (25.2)	92.0 (18.0)

3 Results

The manipulation caused a significant decrease of the bryophyte cover in all cases ($p<0.05$; Tab. 2). Two years after the manipulation, the total bryophyte cover per plot had nearly or completely returned to the original level (Tab. 2). The development of bryophyte cover through time was significantly different between manipulated and control plots of *Calliergonella* in Laamhei ($p<0.01$) and between manipulated and control plots of *Ctenidium* in both sites ($p<0.01$). In *Calliergonella* plots in Wylre, where the reduction had been smallest, the difference in (re)growth between perturbed plots and controls after the manipulation was not significant ($p=0.13$).

While all plots showed strong seasonal fluctuations, the difference between perturbed plots and controls gradually disappeared over the two-year observation period. Fig. 1 and 2 show that the return of bryophyte cover to original values was mainly the result of the regrowth of the reduced species themselves. The change in cover of *Ctenidium* through time was significantly different in plots in which it was manipulated as compared to the control plots in both sites ($p<0.05$). For *Calliergonella*, the difference was significant in Laamhei ($p<0.01$) and marginally significant in Wylre ($p=0.0512$). The regrowth of either of the reduced species after perturbation was monotonous in all cases (taking the seasonal fluctuations in the control plots into account). Two years after the reduction, the reduced species were back at 62-75% of their original cover (Tab. 3).

Tab. 3: Percentage of the cover of the manipulated species (as recorded before manipulation in May 1992) left just after the manipulation (June 1992) and two years after the manipulation (May 1994). Values are the mean of five replicate plots per species per site. Numbers in parentheses are standard deviations. All figures are adjusted, in terms of percentage, for the change in cover in control plots.

		Calliergonella	*Ctenidium*
Laamhei	June 1992:	10.6 (7.6)	13.4 (8.8)
	May 1994:	62.1 (11.4)	72.4 (29.2)
Wylre	June 1992:	11.7 (11.7)	13.3 (6.5)
	May 1994:	62.7 (42.6)	65.5 (13.7)

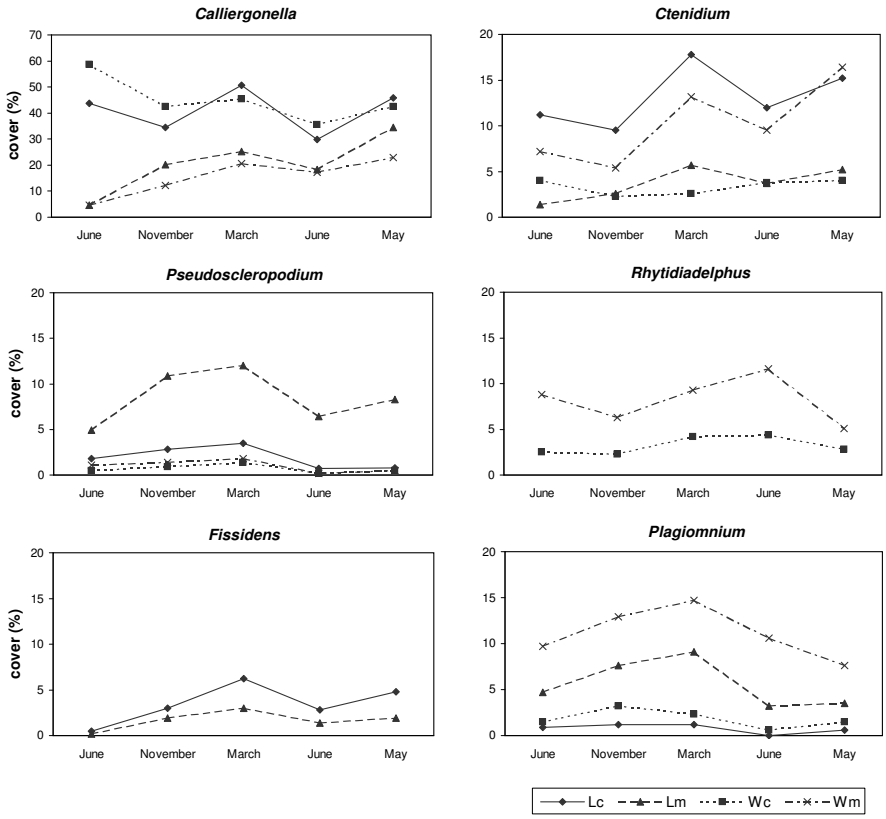

Fig. 1: The response of several bryophyte species to a severe reduction of *Calliergonella cuspidata* in plots (12.5 x 12.5 cm) that used to be dominated by this species. The graphs show the change in cover (in % of the total bryophyte cover) through time in manipulated plots and in control plots in two chalk grassland sites. Values are averages of at least three and maximally five replicate plots. Species with low cover and/or frequency are not shown. Lc = control plots Laamhei; Lm = manipulated plots Laamhei; Wc = control plots Wylre; Wm = manipulated plots Wylre.

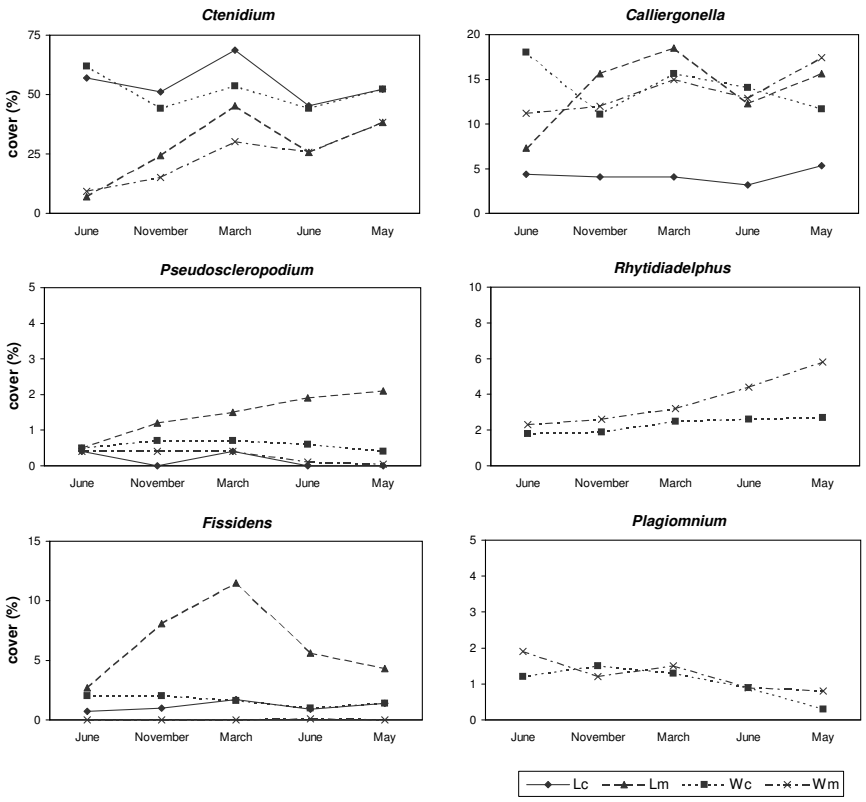

Fig. 2: The response of several bryophyte species to a severe reduction of *Ctenidium molluscum* in plots (12.5 x 12.5 cm) that used to be dominated by this species. The graphs show the change in cover (in % of the total bryophyte cover) through time in manipulated plots and in control plots in two chalk grassland sites. Values are averages of at least three and maximally five replicate plots. Species with low cover and/or frequency are not shown. Lc = control plots Laamhei; Lm = manipulated plots Laamhei; Wc = control plots Wylre; Wm = manipulated plots Wylre.

In nearly all cases, the cover of each of the six species for which regrowth could be tested, did not differ significantly between manipulated and control plots at the start of the experiment (May 1992). Only in *Calliergonella*-dominated plots in Laamhei, the cover of *Plagiomnium undulatum* happened to be significantly higher ($p<0.05$) in manipulated plots than in control plots. There is no reason to assume that this had a significant impact on the results.

A moderate response was observed for some of the less abundant species in some of the manipulated plots after reduction of *Calliergonella* or *Ctenidium*. However, the magnitude of the response differed considerably between the replicate plots and the mean response was not significant for any of the species (Fig. 1 & 2).

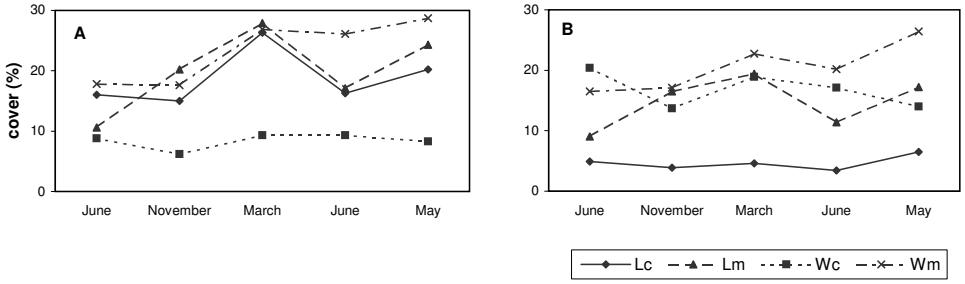

Fig. 3: The response of all less abundant pleurocarpous bryophyte species in plots (12.5 x 12.5 cm) that used to be dominated by A. *Calliergonella cuspidata* or B. *Ctenidium molluscum*, to a severe reduction of the dominant. The graphs show the change in cover (in % of the total bryophyte cover) through time in manipulated plots and in control plots in two chalk grassland sites. Values are averages of five replicate plots. None of the differences in change in cover between control plots and manipulated plots were significant. Lc = control plots Laamhei; Lm = manipulated plots Laamhei; Wc = control plots Wylre; Wm = manipulated plots Wylre.

Fig. 3 shows the cumulative response of all less common pleurocarps, i.e., of all species with a similar growth form as the manipulated species. In all cases the increase in cover after the manipulation was slightly larger in manipulated plots than in control plots, but the results were not significant.

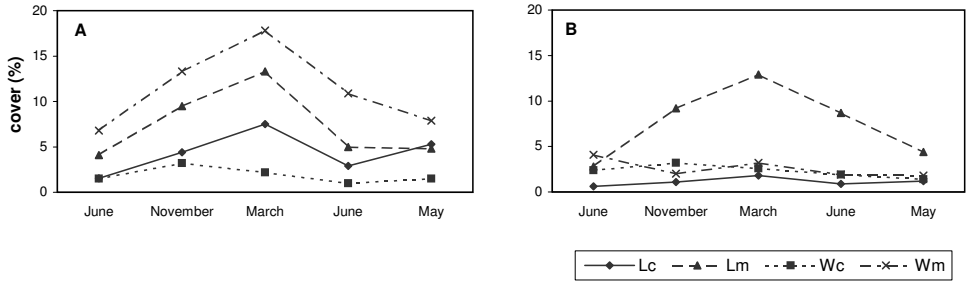

Fig. 4: The response of all acrocarpous bryophyte species in plots (12.5 x 12.5 cm) that used to be dominated by A. *Calliergonella cuspidata* or B. *Ctenidium molluscum*, to a severe reduction of the dominant. The graphs show the change in cover (in % of the total bryophyte cover) through time in manipulated plots and in control plots in two chalk grassland sites. Values are averages of five replicate plots. The cover in manipulated plots increased significantly compared to control plots in Wylre after the reduction of *Calliergonella* ($p<0.05$), and in Laamhei after the reduction of *Ctenidium* ($p<0.05$). The other differences in change in cover between control plots and manipulated plots were not significant. Lc = control plots Laamhei; Lm = manipulated plots Laamhei; Wc = control plots Wylre; Wm = manipulated plots Wylre.

Fig. 4 shows the cumulative response of all acrocarpous species. Only in some cases did the acrocarps increase after the reduction in cover of the abundant pleurocarp. In Wylre, reduction of *Calliergonella* was followed by an increase in cover of acrocarps during the next growing season ($p<0.05$), whereas differences between manipulated plots and control plots in Laamhei were not significant. Reduction of *Ctenidium* was followed by a significant increase ($p<0.05$) of acrocarps during the next growing season only in Laamhei.

Regrowth was not restricted to the margins of the plots but took place also in the centre of the plots (Tab. 4). Although the increase in cover of the manipulated species from manipulation to the next recording (five months later) was slightly higher in the margins of the plots, the differences from the centre were not significant.

Tab. 4: Regrowth (range of increase in % cover) of *Calliergonella* and *Ctenidium* from June 1992 (just after manipulation) to November 1992 in the centre of the plots and at the margins of the plots. Data represent the mean cover (%) per subplot (36 central subplots and 64 marginal subplots in five replicate square plots of 10 x 10 subplots of 1.25 x 1.25 cm each). Values are given separately for the two sites (Laamhei and Wylre). No significant differences were found between centre and margin ($p<0.05$).

species	position	Laamhei	Wylre
Calliergonella cuspidata	centre	9% - 19%	-4% - 12%
	margin	4% - 28%	0% - 29%
Ctenidium molluscum	centre	-3% - 23%	1% - 10%
	margin	-2% - 29%	-14% - 14%

4 Discussion

The results show that cover did not remain low for a long time after bryophyte density was severely reduced; regrowth was vigorous from the beginning. In November, only five months after reducing the bryophyte cover to ca 33% of the original level, the bryophyte cover in manipulated plots originally dominated by *Calliergonella* had reached 77.5% of the original value, and in plots originally dominated by *Ctenidium*, 63.0% (compensated, in terms of percentage, for the change in cover in the control plots during the same period).

Regrowth did not only take place from the intact bryophyte layer surrounding the manipulated plots (Tab. 4), but also took place from within the plots, from bryophyte shoots left in the plots and/or from the diaspore bank (acrocarps). This indicates that the mutualistic interactions taking place in an undisturbed dense moss layer are not essential for (re)growth. Apparently, growth can take place when space is made available such as after opening of the moss layer.

While in the control plots bryophyte cover decreased in the months following the perturbation (from June to November), apparently because senescence occurred at higher rates than new growth, cover increased in the perturbed plots. Thus, while the increase in cover in the manipulated plots relative to the change in the control plots may be partly explained by a delayed senescence of older green stem parts of the remaining shoots due to the enhanced light conditions, there was also an actual increase in cover, which was mainly due to the growing out of many new, young shoots of the manipulated species.

The fact that the largest response to the perturbation was shown by the perturbed species themselves was somewhat surprising. The response of the other species in the plots was not consistent, although in some plots some species showed a moderate increase in cover. In theory, this return to dominance of the perturbed species might be due to this particular microsite, being most suitable for this species. This is, however, rather unlikely since the patches with one dominant species were small (a few dm^2), more or less randomly distributed over the sites, and not visibly correlated with any observable characteristic (such as vascular species composition, soil surface) of the environment.

An alternative explanation is that this pattern is due to regrowth from the margins of the plot, where the dominant species was still the most abundant one. Analysis of the fine-scale pattern of regrowth shows, however, that regrowth took place from within the plots and that another factor is likely to play an important role: the reduction of *Calliergonella* and *Ctenidium* left a fair number of very small fragments at soil surface in the open spaces in the plots. Removal of these fragments was not attempted, since this would have caused too much damage to the other species. These fragments could grow out again as is common in mosses (CORRENS 1899, KNOOP 1984). This means that there was a large number of remnant growing points of *Calliergonella* and *Ctenidium* in the plots from which they had been taken out. The larger, undisturbed shoots of the other species grew mainly from the top of the main axis, and the number of growing points was restricted (possibly through apical dominance; KNOOP 1984, CLYMO & DUCKETT 1986, ØKLAND 1995).

Moreover, the negative effect of environmental stress after the destruction of the interwoven structure of the moss layer and the severe decrease of the shoot density after the manipulation, is likely to have been stronger for the large remaining shoots of the less common species that were left isolated from their neighbours, than for the tiny fragments of the reduced species that were left appressed to the soil. Air humidity was probably relatively favourable at soil level compared to the situation around the larger isolated shoots. This means that small fragments of the dominant species remained moist and photosynthesized for a longer time, and that the accumulated period of growth over the time between successive measurements was longer compared to the shoots of the other species (growth rate is independent of the size of the bryophyte shoot, RINCON 1988). With a higher number of faster growing individuals, the reduced species had an advantage during regrowth.

Reducing the most abundant pleurocarp did not lead to a larger response of less abundant pleurocarps than of acrocarps. Apparently, similarity in growth-form with the reduced species did not determine the magnitude of the response to manipulation. On the con-

trary, only the response of the acrocarps was significant in some of the cases. Increased light levels probably enhanced germination of acrocarpous diaspores during the first growing season after the perturbation (JONSSON 1993, DURING 1997, RYDGREN & HESTMARK 1997, HEINKEN & ZIPPEL 2004).

In conclusion, the removal of the dominant species in dense bryophyte patches in chalk grassland resulted in restoration of the high cover by rapid regrowth of the removed species, presumably due to the high number of meristems (small detached fragments falling to the ground) available after the removal. The other species present hardly increased in cover; we hypothesize that the positive effect of the increased light intensity was offset by negative effects of the increased canopy openness on the water availability to their shoots. To what extent delayed senescence of old parts due to the improved light conditions in the disturbed plots contributed to this increase in cover relative to the situation in the control plots, remains to be investigated.

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