

The effect of initial density on interactions between bryophytes at individual and community levels

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Summary

1 A glasshouse experiment was conducted with seven bryophyte species to determine the effects of competition. We tested whether competitive hierarchies varied with initial abundance (density and biomass) and between two different experimental approaches.

2 Relative competition intensities were calculated based on proportional growth (G) and relative biomass (R). The standards for comparison (i.e. no interactions) were species' performance in monocultures at one of two sowing abundances (the combined monocultures method; CM) and in a low-density mixture of equal proportions of all species (the community density series method; CDS).

3 Proportional growth decreased with increasing initial abundance for all species. Community effects (relative biomass of each species) were generally weaker and more variable than individual effects. R increased linearly with abundance for only one species, while three species showed a quadratic response (of which two were negative).

4 Competitive hierarchies derived by the CM method differed with abundance, and we argue that the CDS method is likely to provide a more reliable comparison.

5 With CDS, competitive hierarchies were similar along the community abundance gradient, implying that non-linear competitive effects are not likely to be a mechanism of coexistence in this community.

6 There were significant competitive effects on community composition, but not on diversity as measured by evenness. At the community level individual species tended to show either competitive or positive effects throughout the gradient of initial community abundance, with decreasing values for most species at high initial community abundance, as were the effects of interactions on community composition.

Key-words: bryophytes, community structure, competition, density, experimental null community, facilitation, growth, microcosm

Journal of Ecology (2000) **88**, 243–255

Introduction

There is abundant experimental evidence (Aarssen & Epp 1990; Goldberg & Barton 1992) for interactions between individual plants. However, the ways in which species composition and relative abundances of entire plant communities are affected by both negative (competitive) and positive interactions have been investigated directly much less (Bengtsson *et al.* 1994; Goldberg 1994).

Probably the most common type of experiment to investigate community structure in plants is to manipulate the abiotic environment of experimental plant communities or multispecies microcosms consisting either of vascular plants (Austin & Austin 1980; Austin *et al.* 1985; Campbell & Grime 1992; Ikeda & Okutomi 1992; Weiher & Keddy 1995; van Acker *et al.* 1997) or bryophytes (Li & Vitt 1994, 1995; Rydin 1997b). It is usually assumed that when different final communities result from same set of species placed in different environments, it is due to changes in competition or positive interactions (Campbell & Grime 1992; Weiher & Keddy 1995).

However, few microcosm experiments manipulate plant density and therefore cannot separate the degree to which different communities are due to changes in interactions rather than to direct effects of the environment on performance of the component species (for exceptions see Austin & Austin 1980; Austin *et al.* 1985; Campbell & Grime 1992).

A more direct approach to investigate the effect of species' interactions on plant community structure is to manipulate density in field experiments. While this has been done in a number of cases, it is almost always by removal of one dominant species and monitoring the effects on the remainder of the community (reviewed by Gurevitch & Unnasch 1989). Such experiments have two important limitations: first, they only investigate a subset of potential interactions within the community (the effect of a single dominant on other species); and secondly, they compare only two densities (presence at natural density vs. complete absence). The second limitation holds for most previous experiments on competition in plants, whether in the field (Goldberg & Barton 1992) or in a glasshouse (Gibson *et al.* 1999). If the per capita effects of neighbours on targets changes with density, then results from single-density experiments cannot be extrapolated to other densities. This greatly limits their usefulness (Firbank & Watkinson 1985) both for parameterizing models and for testing hypotheses about interactions. For example, competitive hierarchies may not be the same at different densities and that observed at a particular density cannot therefore be used to predict the influence of competition on community structure (Taylor & Aarssen 1989; Pantastico-Caldas & Venable 1993).

A third approach to investigate effects of competitive interactions on plant community structure is to determine hierarchies of competitive abilities from multiple pairwise experiments. It is generally accepted that competitive hierarchies will influence relative abundances in the field (Keddy 1989). However, both of the methods most frequently used for determining such hierarchies (pairwise substitutive experiments; Keddy & Shipley 1989; and the phytometer approach, Gaudet & Keddy 1988) have received severe criticism (Herben & Krahulec 1990; Silvertown & Dale 1991; and Bailey 1989; Firbank & Watkinson 1989; Silvertown 1989, respectively). The limitations of studying only pairs or a few species at a time and at only one density is also compounded by the use of species' performance in monoculture(s) for quantifying the effects of competition in interspecific mixtures (Gibson *et al.* 1999). This may introduce size biases in that the initially larger species of a pair is likely to appear to be a better competitor than the smaller species regardless of the actual interactions (Connolly 1986; Grace *et al.* 1992). Moreover, as the degree of interspecific competition affects the amount of intraspecific com-

petition (Miller 1996), it may be inappropriate to define interspecific competitive hierarchies by comparing each species' performance in monocultures and in mixtures (Connolly 1997).

Two recently developed methods allow the study of many species at once, as well as the quantification of community-level effects of species' interactions at a range of densities (Goldberg 1994; Goldberg *et al.* 1995). The 'combined monocultures' analytical approach of Goldberg (1994) is based on experiments by Campbell & Grime (1992) and is a simple extension of the methods used by Austin (1982). This approach uses species' performance in monocultures to standardize performance in mixtures, whereas the 'community density series' of Goldberg *et al.* (1995) uses the performance of species in low-density mixtures to standardize performance at higher mixture densities. Parallel use of the two approaches allows an experimental evaluation of the relative usefulness of defining competitive hierarchies by standards provided by monocultures (absence of interspecific interactions) rather than those in low-density mixtures, where it is assumed that plants are far enough apart to prevent any interactions (intra- or interspecific).

In this paper we report results from experiments using both approaches, with communities of seven alvar grassland bryophytes. Although bryophytes provide excellent systems for the study of the role of interactions (they are seldom grazed and, for those species that lack rhizoids, below-ground competition is absent; Rydin 1997a), they have been the subject of relatively few experiments (reviewed by Rydin 1997a) compared with numerous glasshouse and field competition experiments with vascular plants. However, density is likely to play an important role for bryophytes, which are poikilohydric, i.e. they quickly absorb water over the entire surface and lose it in the same way (Proctor 1982). In habitats where water is only intermittently available, isolated shoots will be prone to drought, and high density should favour shoot growth because evapotranspiration is then reduced (Proctor 1982). This suggests that facilitative rather than competitive effects will predominate, although both positive and negative effects of density on bryophyte growth have been found for *Sphagnum* species by Rydin (1995) and for grassland bryophytes by van der Hoeven & During (1997). Nevertheless, only a few experimental studies have examined the outcome of interspecific competition in bryophytes over a range of densities (Marino 1991; Rydin 1995).

Bryophytes regenerate easily from shoot fragments, and this is the most common mode of reproduction for many grassland species (During 1990). The initial biomass of moss fragments therefore often replaces initial density when describing competition experiments (Scandrett & Gimingham 1989; McAlister 1995). Accordingly, we manipulated

initial community biomass to manipulate competition intensity, but to avoid confusion with a gradient in productivity (the normal corollary of a gradient in standing biomass) we refer to initial conditions as reflecting a gradient of community abundance.

We explored how both individual performance and community structure were influenced by interactions, and evaluated the use of different types of standards for species' performance. Specifically, we asked:

- 1 For each species in the community, does increasing abundance positively or negatively influence its individual growth rate and/or relative biomass?
- 2 Do competitive effects measured by individual-level parameters show trends similar to community-level measurements?
- 3 Do competitive hierarchies change with initial abundance or is one species consistently the best competitor regardless of initial abundance of competing individuals?
- 4 Does standardizing by monocultures give the same results as standardizing to the absence of any interactions?
- 5 Does increasing abundance change the overall species composition and diversity of the community?

Materials and methods

EXPERIMENTAL SPECIES AND COMMUNITY

Alvar grasslands are situated on limestone bedrock and relatively shallow soil and are characterized by locally high cover of bryophytes and lichens. Earlier work found that in the *Avenetum* alvar grassland on the Baltic Island of Öland these plants form small (20–80 cm) multispecies patches, which suggests that interactions between species may play a role at the community level (Zamfir *et al.* 1999).

Seven of the abundant bryophyte species in these grasslands were chosen for the experiments: two acrocarps, *Dicranum scoparium* Hedw. and *Racomitrium canescens* (Hedw.) Brid., and five pleurocarps, *Homalothecium lutescens* (Hedw.), *Hypnum cupressiforme* Hedw. var. *lacunosum* Brid., *Hylocomium splendens* (Hedw.) Br. Eur., *Rhytidiadelphus triquetrus* (Hedw.) Warnst and *Rhytidium rugosum* (Hedw.) Kindb. In bryophytes, growth form characteristics determine their strategy for occupying space and thus their competitive ability. In most acrocarps, the stems grow erect from the substrate and often have determinate growth, whereas the stems of pleurocarps, which can be differentiated into principal and lateral shoots, have mostly indeterminate growth and grow relatively close to the substrate. Thus pleurocarpous bryophytes may quickly monopolize the available space

or grow over the acrocarps, and are therefore considered to be the better competitors (Lloret 1991; McAlister 1995).

EXPERIMENTAL NULL COMMUNITIES

In the combined monocultures approach (Goldberg 1994), the null community is derived by combining the behaviour of each of the species as determined in low-density monocultures. This generates an expected species composition that can be compared with the observed community formed by the corresponding additive mixture of the same species. Differences either in individual species' performances or in community parameters are considered to be the result of interspecific interactions. In the community density series method (Goldberg *et al.* 1995), the null community is defined by the performance of species in an initially low-density mixture of species, under the assumption that few or no interactions between individuals occur at low total density and thus neither intra- nor interspecific competition is present. The plant species are sown in constant initial proportions at a range of initial total densities to give a gradient in initial community density ranging from low (null community) to densities above those observed in nature. Deviations of individual performance or community parameters from the values in the null community are assumed to be due to both interspecific and intraspecific interactions.

EXPERIMENTAL DESIGN AND PROCEDURE

Samples of the moss species were collected in the field and kept at 4 °C until use. The green part was cut with a pair of scissors into small fragments, the size of which varied (0.5–1.5 cm) because of variability in the green parts of the mosses used. Fragments were similar in size to those that colonize gaps in the field (M. Zamfir, personal observation). The fragments were air dried for 48 h and weighed. Two monocultures of each species (7 and 20 mg) and eight mixtures of equal proportions [1, 3, 5, 7, 10, 12, 14 and 20 mg per species, for total initial community abundances (ICA) of 7, 21, 35, 49, 70, 84, 98 and 140 mg] of the seven species were prepared. Each treatment was replicated five times.

The moss fragments were cultivated in 10 × 12-cm plastic pots filled with equal volumes of vermiculite and sand, with dry sterilized (80 °C for 24 h) soil from the *Avenetum* community on the top. The pots were saturated with distilled water and the bryophyte fragments were mixed, evenly spread on the surface and sprayed with distilled water. At the two highest ICA the entire pot surface was covered and the moss fragments overlapped. The pots were covered (not sealed) with transparent plastic lids and placed in a glasshouse, in a complete randomized

design. Daylight was supplemented so that average light intensity at the moss surface, as measured with a PAR Special Sensor (SKP 210; Skye Instruments Ltd, UK), which records quantum flux density of photosynthetically active radiation, was $120 \mu\text{mol m}^{-1} \text{s}^{-1}$. The temperature was 18°C during daytime (12 h) and 10°C at night (12 h). The plants were sprayed with distilled water every second day in the first month to promote establishment. Thereafter the plants were sprayed weekly. The lids were open at one corner and the plants were allowed to dry between watering. A weak (2.5 ml l^{-1}) commercial complete nutrient solution (which contained N 2.0, P 0.5, K 1.6 mg l^{-1} and traces of Ca, S and Mg) was added three times during the experiment. The pots were rearranged randomly every week, to account for variation of light and temperature in the glasshouse.

Some pots became contaminated with non-experimental 'weedy' moss species, mostly with *Funaria* sp. and *Bryum* spp. but also with *Weissia* spp. These probably developed from the diaspore bank, or from spores attached to the moss fragments, and were removed with forceps during the first 3 months but not removed thereafter. The experiment lasted 5 months (August 1997 to January 1998) before harvest.

The plants were collected, separated by species when in mixture, washed free of soil particles in a sieve, dried for 24 h at 40°C , and weighed. The cover of weedy mosses was noted for each pot.

DATA ANALYSIS

For the community density series (Goldberg *et al.* 1995) the multispecies mixture with the lowest initial community abundance (7 mg) was taken to be the null community to which all higher mixture abundances were compared. For the combined monocultures (Goldberg 1994), a null community, defined as the sum of the performances of species in monocultures of 7 mg, was compared with the additive mixtures of 49 mg. Comparisons with both types of null communities were also possible for 140 mg ICA, as data for a combined monocultures approach at 20 mg were available.

Response variables

Two response variables were calculated for each species at each initial abundance. (i) Proportional growth, G :

$$G_j = B_{j\text{harvest}}/B_{j\text{initial}}$$

(where B_j is the biomass of species j). G represents the output at the end of the growth period per unit input (Connolly *et al.* 1990), or the per unit increase

in biomass, and is a measure of relative growth rate that does not assume exponential growth over the growth interval or the abundance gradient, respectively.

(ii) Relative biomass, R :

$$R_{j\text{ICA}i} = B_{j\text{harvestICA}i}/\Sigma B_{\text{harvestICA}i}$$

where $\text{ICA}i$ is community abundance i . R is therefore the proportion of the total biomass of all species in that community abundance treatment that is represented by a particular species. The biomass proportion of a species in monoculture relative to the combined biomass of all species in monocultures is calculated in the same way:

$$R_{j\text{harvestmon}} = B_{j\text{harvestmon}}/\Sigma B_{\text{harvestmon}}$$

$R_{j\text{harvestmon}}$ represents the expected relative biomass of species j in the absence of interspecific interactions (Goldberg 1994).

G and R were computed for each species in each replicate. G measures the individual growth rate regardless of the performance of other species in the community, while R describes the relative contribution of each species to the entire community and depends additionally on biomass of all the other species in the community.

Calculation of competitive effects

We compared competition intensities over the community abundance gradient with the community density series experiments by expressing each response variable as a proportional change from the value in the null community. This will remove effects due to differences among species in growth rate or relative biomass that occur in the absence of interactions (Grace 1995).

$$RCI_j = (P_{j\text{null}} - P_{j\text{ICA}i})/(P_{j\text{null}})$$

where RCI_j is the relative competition intensity on species j , $P_{j\text{null}}$ is either growth (G) or relative biomass (R) of species j in the null community and $P_{j\text{ICA}i}$ is the performance of species j in initial community abundance treatment i . Due to large variation among replicates in G and R , especially at low abundance, RCI for each species in each replicate of the non-null community treatments was computed using the mean of the corresponding null community values.

For the combined monocultures approach, quantifying competitive effects on individual growth rate only needs the single corresponding monoculture (i.e. the standard comparison from an additive experiment), while quantifying effects on relative biomass requires combined monocultures.

Calculation of community effects

We also calculated the effects of interspecific interactions on composition and diversity of the bryophyte communities following Goldberg (1994). An index of effects on change in community composition (D) was obtained by summing the absolute values (both increase and decrease) of the deviation of the relative biomass of each of the species from its biomass in the null community:

$$D_i = \sum |R_{j\text{null}} - R_{j\text{ICA}_i}|$$

The proportional index of change (PD) was obtained by summing the absolute values of RCI (proportional deviation) from the null community of all species in an initial community abundance treatment:

$$PD_i = \sum |RCI_j|$$

Change in diversity can be measured in the same way. However, species richness was the same along the abundance gradient (no species was competitively excluded in any treatment) and diversity indices are not sensitive to small changes in relative proportions. Therefore, evenness was preferred as a measure for diversity. The evenness index, E , based on the Shannon diversity index which is sensitive to the variation of minor species (Smith & Wilson 1996), was used. The change in E is:

$$DE = E_{\text{null}} - E_{\text{ICA}_i}$$

where

$$E = 1/\sum(R_j)^2/S$$

and S is the number of species in the sample; E_{null} is the evenness index for the null community and E_{ICA_i} is the evenness index for the i th initial community abundance.

Statistical analysis

To describe the relationship between final total biomass and initial community abundance, linear and non-linear regressions were fitted to the data. Exponential and hyperbolic functions that have been shown to describe the relations between final yield and density quite well (Mead *et al.* 1993) were chosen for non-linear analyses.

To test whether individual growth or relative biomass was influenced by abundance, the G and R for each species were fitted with linear and quadratic regressions over the gradient in ICA. Because variances were not homogeneous (more variation at low abundance than at high abundance) and transformations (i.e. \log_{10} , square root, arcsine, arcsine square root, $1/x$, $1/y$) did not improve heterogeneity, statistical inferences from these regressions must be

viewed with caution. However, they are nevertheless useful for visualizing the relationships.

All other analyses used non-parametric methods on untransformed data. To test whether competitive hierarchies changed with abundance over the abundance gradient, we calculated Kendall's coefficient of concordance when seven categories were compared, and Spearman rank correlation coefficient when only two abundances were compared (Siegel & Castellan 1988). To test whether the change in community composition (indices of change in D and PD) and evenness (index of change DE) was significantly different from 0, the one-sample Wilcoxon sign rank test for the median was used. Spearman rank correlation between RCI and initial community abundance was used in order to see how competition intensity based on G and R varied with community abundance. Spearman rank correlation of the indices of community change (D , PD and DE) with ICA was used to see how the community indices varied with increasing potential competition intensity.

Results

The biomass of each species between replicates contaminated by low vs. high cover of weedy mosses did not differ significantly (Kruskal–Wallis test, $P > 0.05$). It seemed thus that the weedy mosses did not affect the outcome of the experiment.

COMMUNITY DENSITY SERIES APPROACH

Final biomass of the entire community varied relatively little among the replicates of each initial community abundance treatment (Fig. 1). Even though the linear relationship between total final biomass

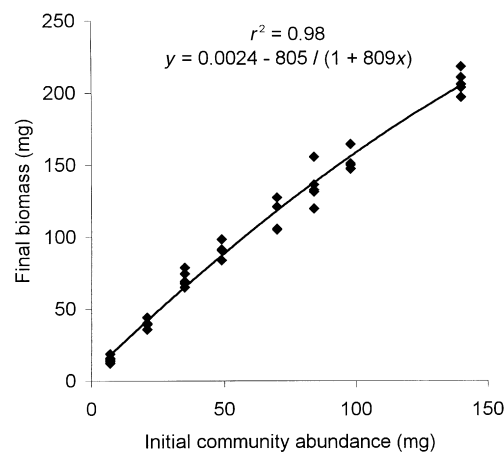


Fig. 1 Final total biomass of seven moss species for five replicates of each of eight initial community abundances ($n=40$). Statistics are given for the best-fit (hyperbolic) function.

and initial community abundance was highly significant ($r^2=0.98$; $P < 0.01$; d.f. = 39), the residuals were not randomly distributed. The best-fit model was a rectangular hyperbola ($r^2=0.98$; $P < 0.001$; d.f. = 39).

Does increasing abundance influence proportional growth and relative biomass?

The biomass for each species was variable among replicates, with the greatest variance usually at the lowest community abundance and decreasing variation with increasing ICA (Fig. 2). Averaged across the entire community abundance gradient, *Hypnum* had the highest proportional growth rate and relative biomass and *Racomitrium* the lowest (Fig. 2). For all seven species, effects of initial community abundance on individual growth rate were clearly competitive: increasing community abundance led to a decline in proportional growth (Fig. 2).

Effects of initial community abundance on relative biomass were much weaker. Only *Dicranum* showed significant linear and quadratic relationships (increasing in relative biomass with initial community abundance). Three other species showed weak but significant quadratic relationships (Fig. 2): of these *Hylocomium* and *Rhytidium* had minimum relative biomass at intermediate ICA, while *Hypnum* had maximum relative biomass at intermediate ICA. Thus, despite strong and consistently competitive effects on individual growth for all species, effects on relative biomass contribution were less consistent, with some species increasing and some decreasing with increasing total abundance.

Competitive effects

Competition intensities based on G (RCI_G) were largely positive, especially at high initial community abundances (confirming the suggested competitive effects in Fig. 2). Values also increased with initial community abundance (Spearman rank correlation, $P < 0.05$) for all species, with the exception of *Racomitrium* (Fig. 3a).

The results for RCI based on R showed a different pattern. Although some species consistently declined in relative biomass relative to the null community (positive RCI_R at all values of ICA) while others increased, the magnitude of the positive or negative effect was largely independent of initial community abundance. Competitive effects were significantly (positively) correlated (Spearman rank correlation, $P < 0.01$) with increasing community abundance only for *Homalothecium* and *Hypnum*.

Competitive hierarchies

Species differed in overall competitive ability when assessed by either RCI_G or RCI_R (Kruskal–Wallis

tests, $P < 0.01$; d.f. = 6). In addition, the competitive hierarchies based on RCI_G and RCI_R were similar to each other (Fig. 3) and varied little over the gradient in community abundance ($W=0.943$; $P < 0.01$). The competitive hierarchy was *Hypnum* > *Dicranum* > *Homalothecium* > *Hylocomium* > *Rhytidiadelphus* > *Rhytidium* > *Racomitrium* (Fig. 3). The only consistent change from this hierarchy was seen at the two highest ICA, when *Dicranum* replaced *Hypnum* as the strongest competitor (Fig. 3).

Community level effects of interactions

Averaged over all community abundances, competition caused a significant change in species composition relative to the null community (D and PD significantly different than 0; Wilcoxon median test, $P < 0.05$). D and PD significantly declined with ICA (Spearman rank correlation coefficient, $P < 0.01$; $n=35$; Fig. 4), indicating that, somewhat surprisingly, the magnitude of change in species composition due to competition declined at higher initial community abundance. On the other hand, the index of change in evenness of final relative biomass (DE) did not differ from 0, i.e. interactions did not have an effect on this measure of community diversity, and DE was not correlated with initial community abundance.

COMBINED MONOCULTURES APPROACH

Species differed significantly in their growth rates in monocultures at both initial abundances (7 mg and 20 mg species⁻¹; Kruskal–Wallis tests, $P < 0.05$; d.f. = 6). *Racomitrium* had the lowest growth rate at both monoculture abundances, while *Hypnum* had the highest growth rate (Fig. 5), as was also found when values for mixtures were averaged over all values of ICA. Thus, the rankings of growth rate of the species did not seem to change with different degrees of intraspecific competition.

Competitive hierarchies

Competitive hierarchies at a given abundance were identical between RCI_G and RCI_R (Fig. 6), but the rankings of RCI using either of these were not concordant between the low and high abundance mixtures (Spearman rank correlations, $P > 0.05$). The competitive hierarchy at ICA 49 was *Racomitrium* > *Dicranum* > *Hylocomium* > *Homalothecium* > *Hypnum* > *Rhytidiadelphus* > *Rhytidium*, compared with *Dicranum* > *Racomitrium* > *Rhytidium* > *Rhytidiadelphus* > *Hylocomium* > *Hypnum* > *Homalothecium* at ICA 140 (Fig. 6). Furthermore neither of the competitive hierarchies from the combined monoculture approach was concordant with those for similar mixture densities derived from the

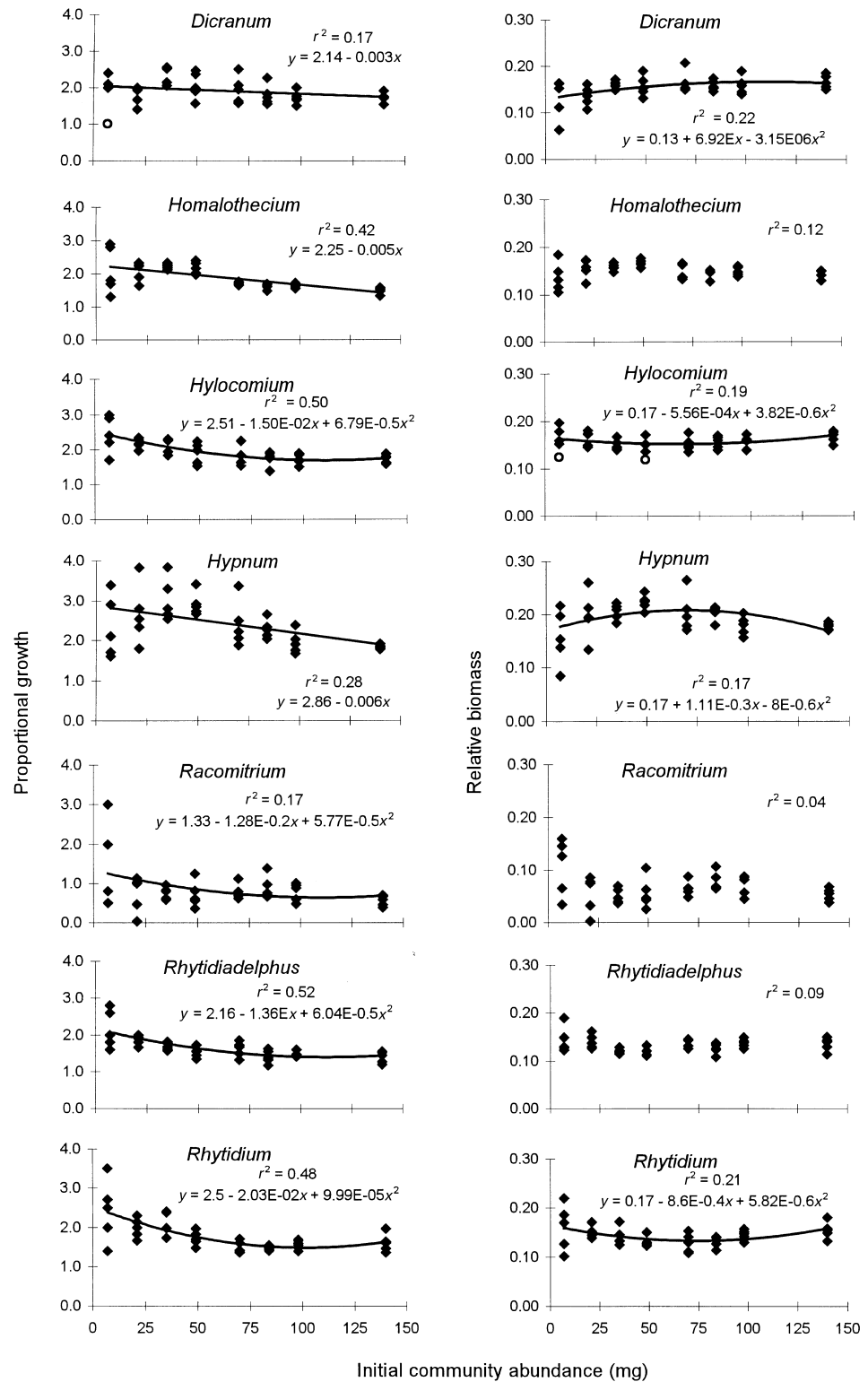


Fig. 2 Proportional growth and relative biomass for seven species grown at eight initial community abundances, $n = 40$. Open circles indicate outliers. Lines and equations are shown only for significant ($P < 0.05$) linear or quadratic relationships.

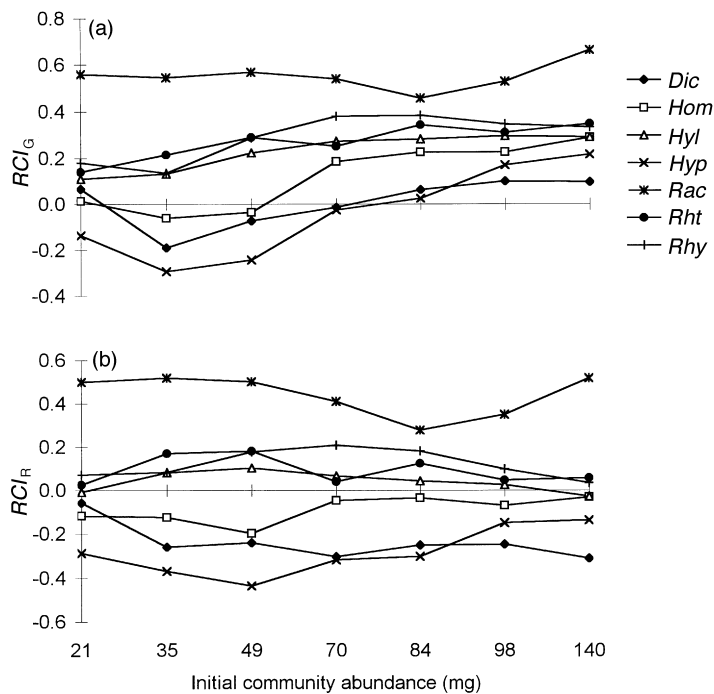


Fig. 3 Relative competition intensity based on proportional growth (RCI_G) (a) and relative biomass (RCI_R) (b) along a gradient in initial community abundance. Species: *Dic*, *Dicranum scoparium*; *Hom*, *Homalothecium lutescens*; *Hyl*, *Hylocomium splendens*; *Hyp*, *Hypnum cupressiforme*; *Rac*, *Racomitrium canescens*; *Rhy*, *Rhytidiadelphus triquetrus*; *Rht*, *Rhytidium rugosum*.

community density series method (Spearman rank correlations, $P > 0.05$).

Discussion

None of the seven species used in this experiment produce sporophytes regularly in the *Avenetum* grasslands (M. Zamfir, personal observation) and their local dispersal therefore relies on fragments created by disturbances. Mechanical disturbance (e.g. trampling, grazing) may create both propagules (moss fragments) and small gaps favourable for their recruitment in the established plant community. Due to establishment differences between bryophyte species and random factors, it has been suggested that events during colonization may be more important for structuring bryophyte communities than competition between established plants (Li & Vitt 1995; Rydin 1997b). Thus, the results from this study, which was based on interactions among bryophytes originating from fragments, should be directly relevant to field patterns.

COMPARISON BETWEEN METHODS

The two methods employed, community density series (CDS, standardization of response variables by low community abundance) and combined monocultures (CM, standardization by monocultures or

combined monocultures), gave conflicting results. With the CDS approach, the competitive hierarchies were concordant between communities starting with different initial total abundances. The ranking was a good reflection of differences in G and R between species, both in mixtures (Fig. 2) and monocultures (Fig. 5), with *Hypnum* having the highest values of G , R and competitive ability and *Racomitrium* the lowest. In contrast, the CM approach indicated that competitive hierarchies depended on initial abundances but neither corresponded with the observed values of G and R (Fig. 6).

Differences between results of competition experiments based on comparisons of species' performances in mixtures relative to monocultures and results obtained by analysing mixture dynamics have been reported by several authors (Connolly *et al.* 1990; Grace *et al.* 1992; Connolly 1997). The value of competition indices calculated relative to monocultures is reduced because interspecific interactions may change the intraspecific biomass and could therefore change intraspecific interactions (Miller 1996). Indeed, the different competitive hierarchies defined in this study by CM may be due to differences in the amount of such intraspecific competition between the two abundances. Miller (1996) suggested that the best standard would be in the absence of any interactions, and our results provide experimental support for this opinion. At the lowest

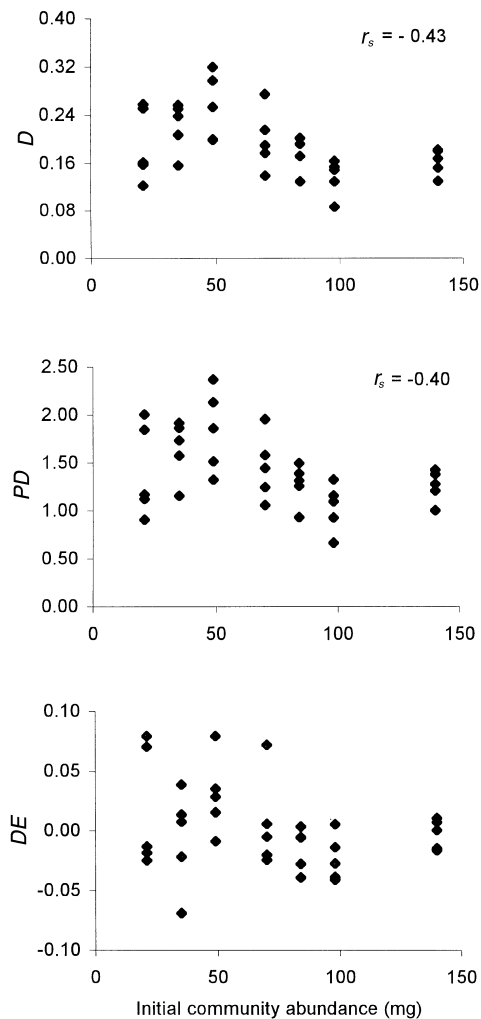


Fig. 4 Effects of interactions on absolute (D) and proportional (PD) change in community composition and effects on evenness (DE) along a gradient in initial community abundance. r_s is the Spearman rank correlation coefficient and is shown for significant correlations ($P < 0.05$), $n = 35$.

community abundance (our null community) the moss fragments did not touch each other at the end of the experiment (suggesting minimal interactions) and the results from CDS were less contradictory than those from CM. We therefore consider that the results obtained by the CDS approach are more valid and these form the focus for the rest of the discussion.

HOW DOES INCREASING ABUNDANCE INFLUENCE INDIVIDUAL GROWTH AND RELATIVE BIOMASS?

While positive interactions are well documented in vascular plants (Bertness & Callaway 1994), they appear to be much less common than negative interactions (Goldberg & Barton 1992; Goldberg *et al.* 1999). For ectohydric bryophytes, several authors have argued that the improved moisture regime

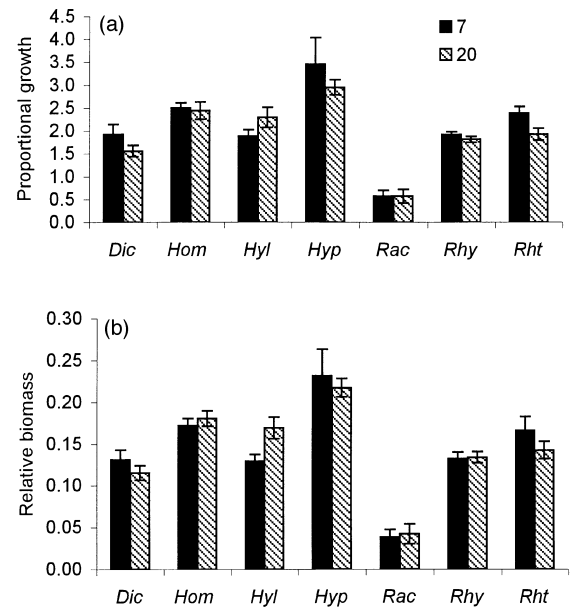


Fig. 5 Average (\pm 1 SE) of proportional growth and relative biomass in monocultures of 7 mg and 20 mg.

should lead to positive density-dependence even in multispecies stands (During 1990). Positive effects on shoot growth at high densities have been reported by Bates (1988) for *Rhythidiadelphus triquetrus* in a glasshouse experiment, by Økland & Økland (1996) for *Hylocomium splendens* in boreal forest floors, and by Kosiba & Sarosiek (1993) for four other moss species growing in a natural environment. However, Rydin (1995) found that proportional growth of *Sphagnum* mosses within experimental plots decreased with density, while van der Hoeven & During (1997) found that at increasing density shoots will compete for light. In our study, proportional growth, an individual-level measure, was significantly negatively related with initial community abundance (density) for all seven species (Fig. 2). Because we measured the averaged proportional growth per pot, this effect on proportional growth could have been due to increased shoot mortality as a result of crowding as well as to decreased growth of individual shoots when light availability became limiting. Our results confirm the recent suggestion (Rydin 1997a) that positive intra- or inter-specific effects of density are not as widespread in bryophytes as previously thought, but are more in line with the situation in vascular plants.

ARE COMPETITIVE EFFECTS BASED ON INDIVIDUAL AND RELATIVE MEASURES SHOWING THE SAME TRENDS?

The magnitude of competitive effects on growth increased with increasing initial community abundance for all species. In contrast, 'competitive'

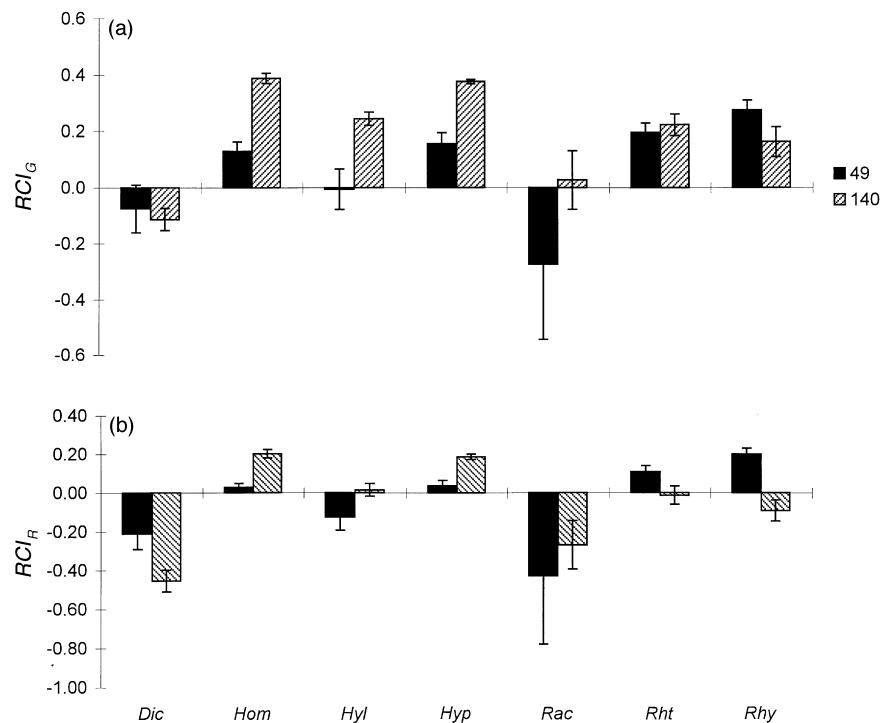


Fig. 6 Relative competition intensity based on proportional growth (RCI_G) and relative biomass (RCI_R) by the combined monocultures approach.

effects on relative biomass showed the full range of possible behaviours, with some species increasing in relative abundance as initial community abundance increased, others decreasing, and others not changing. The relative biomass contribution of each species was calculated based on the total biomass of all species, and so, if some species decrease due to increased competition at higher initial community abundance, than one or more other species must increase in relative biomass. The variation in results among species and initial abundances is apparently because some species were already suffering from competition at low initial abundance (positive values in Fig. 3a) whereas others were facilitated at low to medium abundance. Strong competitive effects at relatively low initial abundance may be a result of species' differences in establishment and in the drought tolerance of isolated fragments, which, together with random events, may play an important role in structuring bryophyte communities in nature (Rydin 1997b).

What is the best way to characterize the effects of competition? If the goal is to study the effects of competition on community composition, then the use of relative abundance measures is more appropriate. If the emphasis is on the absolute effects on competition of individual species, then the use of individual species measures is suitable. Both approaches are appropriate for the study of competitive hierarchies (see below).

ARE COMPETITIVE HIERARCHIES CONCORDANT ALONG THE GRADIENT IN COMMUNITY ABUNDANCE?

The seven bryophytes studied, which co-occur in the field layer of the *Avenetum* community, can be ranked in a competitive hierarchy. The existence of competitive hierarchies in bryophytes has been demonstrated in some cases (Scandrett & Gimingham 1989; Marino 1991; Kooijman & Bakker 1995) while in other cases all the investigated species had similar competitive abilities (McAlister 1995; Rydin 1997b; van der Hoeven 1999).

The rankings of competitive abilities among species were highly concordant along the community abundance gradient. Our results are consistent with those of Marino (1991), who found that competitive hierarchies among four coprophilous mosses were consistent for three initial densities of spores (10^3 , 10^4 , 10^5 spores 10 cm^{-2}).

Based on our results, changes in competitive hierarchies with abundance are not a likely mechanism promoting coexistence of bryophyte species in alvar grasslands. Nevertheless, spatial pattern may still determine competitive ability in vascular plants (van Andel & Nelissen 1981) and even more in bryophytes, because the colony acts as a unit (Proctor 1982) and competition at the boundaries of mono-specific clumps may well have a different outcome from competition between evenly mixed moss fragments.

The species' rankings found in this multispecies microcosm study generally agree with the abundance patterns observed in the field. *Dicranum scoparium*, *Hypnum cupressiforme* and *Homalothecium lutescens*, the three best competitors, are abundant in *Avenetum* alvar grasslands, whereas the other species used in the experiment are found with lower abundance (Zamfir 1999).

Growth form characteristics may determine species' competitive ability. Lloret (1991) and McAlister (1995) found that acrocarps were out-competed by pleurocarps, but one of the acrocarps in our study, *Dicranum*, was a good competitor although the other, *Racomitrium*, was the weakest competitor. Thus, growth form does not always correlate with position in competitive hierarchies.

The position of species in the competitive hierarchy might differ in other experimental conditions (Marino 1991; Kooijman & Bakker 1995) or if the experiment was run for a longer time (Connolly *et al.* 1990; Rydin 1993).

Competitive hierarchies based on results from competition experiments carried out between species pairs (Keddy & Shipley 1989) or on the effect of many species on a phytometer (Gaudet & Keddy 1995) have, besides the limitation of using only a single density, the potential limitation that the effects of competition might be different in the presence of additional species (Fowler 1981). Our experiment incorporated such indirect effects due to multiple competing species and still allowed the assessment of the competitive hierarchies. Thus, it is more likely to be relevant to field conditions than the more conventional approach of conducting a matrix of pairwise competition experiments.

COMMUNITY LEVEL EFFECTS OF SPECIES' INTERACTIONS

Most competition studies focus on the effects on individual species, and this study is one of the few that specifically test the effects of competition in structuring plant communities (Goldberg *et al.* 1995). A number of other studies address the question indirectly, by comparing the effects of competition with the effects of other factors such as herbivory, disturbance and fire (Ikeda & Okutomi 1992; Wardle & Barker 1997; Fraser & Grime 1999). We found that, at least in some circumstances, competition does play a role in structuring plant communities.

Although species composition was strongly affected by interactions, the total effects on diversity as measured by the difference in evenness (*DE*) were not significant, in line with the study of Wardle & Barker (1997). Interactions will increase with increasing density, but competition should lead to a decrease and positive interactions to an increase in diversity (Hacker & Gaines 1997). The community

response to interactions is a sum of individual-level responses, reflected in the shape of the responses of individual species (Fig. 3b). In this study, no species was driven to exclusion and, depending on species, the competitive or positive effects based on relative biomass remained relatively constant over the community abundance gradient. The balance between the two processes was reflected by the *DE*.

The present study with a simple artificial bryophyte community has the limitations of all experiments done in a glasshouse. Nevertheless, understanding interactions in a simple controlled community is a step in understanding complex processes as they occur in nature.

Acknowledgements

We are grateful to Håkan Rydin, Hugo Sjörs, Eddy van der Maarel, Roy Turkington and an anonymous referee for helpful comments on earlier drafts of the manuscript, and to Lindsay Haddon for her outstanding editorial help.

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Received 21 January 1999;
revision accepted 9 September 1999