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Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 5. Vertical dynamics of individual shoot segments

Rune Halvorsen Økland

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Demographic information was obtained for 12528 mature segments (for which dry weight was estimated and vertical position in the bryophyte carpet recorded) and 3109 regenerated growing points for the perennial clonal moss *Hylocomium splendens*, recorded in Norwegian boreal spruce forests during a 6-year period. Branching frequency varied with vertical position in the bryophyte carpet. Termination risk (probability of producing no offspring) was highest (44%) for buried segments, lowest (12%) for segments at intermediate vertical positions, and also high (26%) for emergent segments (due to increasing exposure to external mortality agents). Segment size increased from low levels in the bryophyte carpet to a maximum ca 2–10 mm below the top of the bryophyte carpet. This intermediate level was interpreted as the optimal compromise between incoming radiation (attenuating downwards) and microclimatic moisture conditions (improving downwards). Size-corrected fitness, the number of offspring emerging from a mature segment within one year after maturation after allowance for differences in size, was lower for buried and emergent segments than for segments at intermediate positions. Small emergent segments were apparently liable to suffer from vitality reductions due to desiccation. The vertical position of a daughter segment depended on that of its parent segment, but also showed considerable stochastic variation. Burial acted as a strong sink for small segments regardless of vertical position. No evidence was found for species-specific differences in the way pleurocarpous bryophytes interact, but reduced vertical mobility of *H. splendens* when growing among acrocarps indicated that growth-form is an important determinant of bryophyte interactions. Evidence was found for vertical layering of the bryophyte carpet according to dominant type of interactions among individuals: none (environmental stress) above and at top, facilitation [a (+, +) interaction] at intermediate levels because of favourable water relationships in closed stands, and amensalism [a (0, −) interaction] from higher-situated segments that deprive lower-situated segments access to light at lower relative levels. The intensity of amensalism increased downwards in the bryophyte carpet as indicated by a reinforced size hierarchy. The tendency for small *H. splendens* segments to become buried and lost from the population by amensalism is likely to represent a general mechanism for interactions between bryophyte species and succession in bryophyte-dominated stands. Population effects of climatic and local environmental factors (favourability vs stress), disturbance and apparently random events are discussed with reference to their impact on the relative sizes of subpopulations acting as sources (due to facilitation) and sinks (due to amensalism).

R. H. Økland, Botanical Garden and Museum, Univ. of Oslo, Trondheimsveien 23B, N-0562 Oslo, Norway (r.h.okland@toyen.uio.no).

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Bryophytes have a significant role in the functioning of the boreal forest. The large carpets covering the forest floor retard soil biological processes by thermal insulation (Sirén 1955, van Cleve et al. 1983) and affect nutrient circulation by retention and immobilization of nutrients (Oechel and van Cleve 1986, Chapin et al. 1987, Pastor et al. 1987, Paré et al. 1993). Moreover, they promote paludification of the forest floor by retention of water (Romell 1922, Sarvas 1938), and by denying germinating seeds access to water and mineral soil they strongly influence regeneration of trees and other vascular plants (Perttula 1941, Eriksson and Ehrlén 1992, Hörnberg et al. 1997).

Like other communities, bryophyte carpets are structured by physiological tolerance to the main environmental conditions at the site, which determines the available species pool (Eriksson 1993). At finer scales, species composition and the abundance of each species are determined by an interplay between inter- and intraspecific interactions, disturbance, climatic fluctuations, environmental stress and apparent randomness (cf. Grime 1979, Fowler 1990, R. Økland 1990). The relative importance of these factors is considered to vary among sites (R. Økland and Eilertsen 1993, R. Økland and T. Økland 1996, Rydin 1997), but all may be locally important (cf. R. Økland 1994, Frego and Carleton 1995a, Rydgren et al. 1998a).

The performance of bryophytes in boreal forests, like vascular plant assemblages (cf. Mithen et al. 1984) is controlled by mechanisms operating at the scale of individuals, and the dynamics of populations and communities result as the sum of individual fates (R. Økland 1995a, R. Økland and T. Økland 1996). However, bryology has not benefited from a prolific development of population biology during the last thirty years, as has been the case for vascular plants (R. Økland 1995a, Rydin 1995). A theoretical understanding of how boreal forest bryophyte carpets function has instead been built on observations and experiments performed at the community scale, on theoretical reasoning, and on ecophysiological facts (see reviews by During 1992, Rydin 1997, van der Hoeven and During 1997a, Bates 1998).

A majority of the dominant bryophytes in the boreal forest floor are ectohydric (Buch 1947) and poikilohydric (Hosokawa et al. 1964), changing water content with the ambient air (Stålfelt 1937). The growth of ectohydric bryophytes is mainly controlled by microclimate (Busby et al. 1978, Skre and Oechel 1981, Sonesson et al. 1992, R. Økland 1997). Periodic drought and insufficient radiation are considered the most import growth-restricting factors while nutrients are normally not in short supply (Clymo 1973, Bates 1987, van der Hoeven and During 1997a).

Hylocomium splendens is well suited for population studies (R. Økland 1995a). Its mainly sympodial growth pattern gives rise to distinct modules, segments, with determinate growth. When fully grown, these segments occupy a fixed horizontal and vertical position in the bryophyte carpet and are excellently suited to be taken as the basic unit, the individual, in demographic studies. The modular growth also provides innate markers to be used in monitoring of demographic transitions (R. Økland 1995a; also see Tamm 1953). Coloured plastic rings may therefore be used for non-destructive tagging of single shoot segments (R. Økland 1995a). Furthermore, *H. splendens* is large, it has a wide distribution with high local abundance (T. Økland 1996), and its ecophysiology has been thoroughly studied (cf. Busby et al. 1978, Callaghan et al. 1978, Sonesson et al. 1992). The use of *H. splendens* as a model species has opened for new insights into bryophyte population biology: size dependence of demographic processes and number of offspring (the number of offspring emerging from a mature segment within one year after maturation may be used as measure of fitness) in *H. splendens* was demonstrated by R. Økland (1995a); demographic variation over time in two areas was studied by R. Økland (1997); and dependence of branching patterns on total bryophyte cover was demonstrated empirically by R. Økland and T. Økland (1996) and experimentally by Rydgren et al. (1998b).

The aims of this study are:

(1) To provide an account of the vertical dynamics and the vertical variation in fitness components of *Hylocomium splendens*, using data on size, branching patterns and vertical dynamics of 15637 segments and growing points emerging by regeneration of *H. splendens*, over a six-year period in seven Norwegian boreal spruce forest areas.

(2) To use empirical evidence of the vertical dynamics of *Hylocomium splendens* to evaluate eight predictions from current hypotheses about the functioning of boreal bryophyte carpets: (i) that the tendency to produce extra offspring branches, which is assumed mainly to be regulated by incoming radiation (R. Økland and T. Økland 1996), decreases downwards in the bryophyte carpet in response to light attenuation (Hayward and Clymo 1983, Skre et al. 1983, van der Hoeven et al. 1993); (ii) that the risk of mortality due to external factors increases upwards in the carpet, with increasing exposure to mortality agents (cf. R. Økland 1995a); (iii) that the favourability for growth and survival (and thus fitness) increases from below and above the bryophyte carpet to an optimal position in the upper part of the carpet, because of a trade-off between radiation and moisture (cf. Tamm 1953); (iv) that shoot apices tend to hold their vertical position in the bryophyte carpet for many years (cf. Hayward and Clymo 1983); (v) that large shoots may grow out of the bryophyte carpet, but rapidly return to the main sward because of growth reductions brought about by the unfavourable moisture microclimate above a closed carpet (Clymo 1973, During 1990); (vi) that shoots with

retarded growth tend to become irrevocably immersed in the bryophyte carpet by a process driven by the increasingly unfavourable light conditions at greater depths (Tamm 1953, Hayward and Clymo 1983; but see Rydin 1995); (vii) that interactions for light in the bryophyte carpet are completely asymmetric (van der Hoeven and During 1997b, Rydin 1997), i.e. that a moss shoot affects all shoots underneath by denying them light (van der Hoeven and During 1997b), without itself being affected, creating a vertical competitive hierarchy (cf. Keddy and Shipley 1989, van der Hoeven and During 1997a) that reinforces the vertical size hierarchy as resulting from vertical variation in fitness; and (viii) that interactions may differ among growth forms (cf. Tamm 1953, Pakarinen and Rinne 1979, Rydin 1997) but are not species-specific for species with similar growth form (R. Økland and T. Økland 1996).

(3) To use the patterns of vertical dynamics and vertical variation in fitness components to provide a mechanistic understanding of the dynamics of bryophyte carpets. Notably, I intend to show how an increase in density under favourable conditions, as well as a density reduction due to fine-scale disturbance and environmental stress, brings about changes in bryophyte carpets by changing the vertical distribution of individual shoot segments.

Terminology, materials and methods

More detailed descriptions of the species, study areas, sampling procedures and demographic techniques are provided by R. Økland (1995a).

The species

Hylocomium splendens wefts are built up by reiteration of the architecture of whole branching systems (Harper 1985), with some repeats being produced after a time-delay (R. Økland 1995a). Normally, a *single* new *growing point* emerges from each main axis in spring (it is often visible as a small bud the previous autumn) by sympodial *ramification* (branching) of one-year-old tissue (R. Økland 1995a: Fig. 1). *Multiple* growing points are also occasionally found. In autumn the new growing point develops branches of first (and often also second) order. By the following August, at the age of ca 1.5 years, the bipinnately branched growing point has reached full size, and become a *mature segment*. Growing points may also develop from detached fragments and from older parts (age of axis two or more years) of intact segment chains (Knoop 1984) by *regeneration*. Modules remain connected in *segment chains* [clonal fragments in the terminology of Angevine and Handel (1986)], until decomposed from below or physically injured. The terms *source segment* and *offspring segment* are used for interconnected segments, irrespective of time of development. The terms *parent segment* and *daughter segment* are only used for segment chains with regular (annual) ramification.

Sporophytes are rarely produced by *Hylocomium splendens* on the Norwegian boreal forest floor (R. Økland 1995a, Rydgren et al. 1998b, cf. also Jonsson 1993). *H. splendens* is ectohydric and poikilohydric and depends mainly on aerial supply of water and nutrients (Tamm 1953, Busby et al. 1978, Callaghan et al. 1978; but see T. Økland et al. 1999).

Study areas

The study was carried out in Norway, in seven reference areas used for monitoring boreal forests (R. Økland 1995a: Table 1). Six were among the ten areas intensively investigated by the Norwegian Institute of Land Inventory (T. Økland 1996), the seventh was investigated by R. Økland and Eilertsen (1993). Only virtually unmanaged Norway spruce [*Picea abies* (L.) Karst.] forest vegetation dominated by *Vaccinium myrtillus* L. on poor to moderately rich submesic sites [terminology of R. Økland and Eilertsen (1993)] was included.

Sampling and annual census

Hylocomium splendens growing points were censused annually in one subplot of fixed size (ranging from 39 to 10000 cm^2, depending on the abundance of *H. splendens*), the *active area* (selected by a standard procedure; see R. Økland 1995a), within each of 131 permanent vegetation plots [1 m^2; restricted random positioning; see T. Økland (1996) and R. Økland and Eilertsen (1993) for details of sampling]. Data from annual censuses performed between 25 August and 10 October (i.e. after the new segments had reached maturity, but before the first snowfall) in each of the years 1992–1997 were used.

Percentage cover of all bryophytes (*BC*) and the cover of *H. splendens* (*BH*) was recorded for the active areas of all plots in all years.

At each census, all growing points present at the previous census as well as new growing points were carefully searched for, mapped and non-destructively tagged, using PVC rings according to procedures described by R. Økland (1995a).

This study is based upon mature segments ($n = 12528$) and regenerated growing points ($n = 3190$) recorded in the active areas of plots, 1992–1996, and the offspring recorded the subsequent year (1993–1997). Mature segment properties were always recorded the year a segment reached maturity. The number of daughter growing points was noted. Size (*DW*, dry weight) was estimated from measurements of segment

Table 1. Classification of *Hylocomium splendens* mature segments in Norwegian boreal coniferous forests 1992–1996 into seven categories according to branching pattern (number of offspring recorded one year after maturity). The total number of mature segments in each category recorded in the five-year period is given as percentages of N_t, the total number of mature segments ($N_t = 12\,528$). MS = mature segment, GP = growing point.

Mature segment category	Number of offspring		Population effect	Number	% of N_t
	MS	GP			
MRa2+ – multiple ramification	≥2	0	Increase	752	6.00
MRa1 – single ramification	1	0	None	8018	70.67
MRe1L – lateral regeneration with one year's delay (also classified to MRa2+ or Mra1)	≥1	≥1	Increase	835	6.67
MRe1T – terminated, but with terminal regeneration	0	≥1	None	464*	3.70
MTeGr – terminated by grazing	0	0	Decrease	128	1.02
MTeOt – terminated for other reasons and not regenerating terminally the first year)	0	0	Decrease	1687	13.47
MTeLo – lost	0	0	Decrease	644	5.14

* fraction of all terminations not due to grazing or loss; MRe1T/(MRe1T + MTeOt) = 21.08%.

length, number of branches and length of the longest branch (nonlinear regression model: $R^2 = 0.913$, $n = 328$; cf. R. Økland 1995a). For convenience, size is reported as base-2 logarithms of estimated dry weights ($\log_2 DW = a \Leftrightarrow DW = 2^a \cdot 10^{-4}$ g), as an increase by one unit then corresponds to doubling the size.

All mature segments were classified to seven M-classes according to *branching pattern*, i.e. number and type of offspring recorded one year after maturity (see Table 1 for definitions). *Ramifying* mature segments gave rise to new mature segments within one year, while *terminating* mature segments produced no mature daughter segment. Furthermore, mature segments are referred to as *regenerating* if they gave rise to new growing points with one (or more) year's delay relative to the normal developmental cycle. Segments classified to class MRe1L also belong to class MRa2+ or MRa1, depending on the number of offspring segments produced by ramification.

Regenerated growing points were classified to three G-classes: GRe1L (lateral regeneration with one year's delay, i.e. on a non-terminated source segment), GRe1T (terminal regeneration with one year's delay, i.e. on a terminated source segment; cf. R. Økland et al. 1997), and GRe2+ (regeneration with two or more years' delay, or from fragments of unknown age). Growing points arising by normal ramification were classified as GRa.

All mature segments were classified (at census, the year they reached maturity, by visual estimation of the percentage visible from above) to six V-classes according to vertical position in the bryophyte carpet: V0 (buried; less than 5% visible from above due to coverage by litter or by other bryophytes), V1 (low; 5–25% visible), V2 (intermediate; 25–75% visible), V3 (high; 75–95% visible), V4 (on top; 95–100% visible, but with contact with substratum or other bryophytes), V5 (emergent; 100% visible and without contact with substratum or other bryophytes). The cover of a segment's daughter growing points was disregarded when cover was assessed. Whenever possible, buried segments were classified to two subclasses according to burying agent: burials by litter, and burials by bryophytes. Burials brought about by shoots of one particular species were recorded and used to divide burials by bryophytes into burials by acrocarps (including *Sphagnum*) and burials by pleurocarps. Burials by *Hylocomium splendens* were recorded as a subgroup of the latter.

All mature segments were classified to seven S-classes by use of estimated dry weights: S2 ($\log_2 DW < 3$), S3 ($3 \le \log_2 DW < 4$), and so on till S8 ($\log_2 DW \ge 8$).

Data analyses

In order to find whether the vertical distribution of mature segments was related to the cover of the bryophyte carpet, linear regression was used to relate the V-class mean, calculated for all mature segments recorded in each of the 131 plots over the six-year (1992–1997) study period, to the mean percentage cover of bryophytes (*BC*).

The fitness of a single mature segment was defined as the sum of the numbers of daughter mature segments and regenerated growing points emerging from it within one year after it reached maturity. The fitness of a population of mature segments was calculated as

$$\text{Population fitness} = (N_t + (x-1) \cdot MRa2 + MRe1L - MTeGR - MTeOt - MTeLo)/N_t$$

where italicized letters denote the number of segments in each M-class (see Table 1 for explanation), x denotes the average number of daughter segments produced by multiple ramification and N_t is the number of mature segments present at the beginning of each one-year period (from census to census).

When size was recorded as $\log_2 DW$, variance distributions were sufficiently homogeneous for all of the analysed subsets (M-classes, V-classes, etc.) to allow the use of parametric statistical methods (ANOVA, T-tests) for all comparisons (see Sokal and Rohlf 1995). ANOVA was used to compare the size of V-classified mature segments and to compare relative sizes (differences in $\log_2 DW$) of V-classified parent and daughter segments. All of these tests were highly significant ($p < 0.001$). Thus only the results of pair-wise tests are reported. G-tests were used to test the deviation of observed from expected frequencies (Sokal and Rohlf 1995).

All 9634 MRa1 and MRa2+ segments were used to study the effect of vertical position on the relative size change (i.e. the difference in $\log_2 DW$) from one segment generation (year) to the next. For these analyses, $\log_2 DW$ of the summed, back-transformed $\log_2 DW$ for the individual daughter segments was used as the size of multiple daughters. Multiple daughter segments were V-classified according to the percentage of their total area being visible from above. Average segment size differs significantly between years (although the magnitude of between-year differences is not large) and between areas, among others due to climatic impact on growth (R. Økland 1997, unpubl.). The *relative size change corrected for area and year* was therefore obtained from the relative size change by subtracting the mean relative size change for all MRa2+ and MRa1 segments in the same area in the same one-year period.

The odds-ratio test (Sokal and Rohlf 1995) was used to assess if the probability for a *Hylocomium splendens* segment to become buried by other *H. splendens* segments reflected the species' average relative abundance on the forest floor. As reference value for the odds for self-burials (burials by *H. splendens*, as compared to all burials) was used the value 0.272, obtained as the weighted average of BH/BC (the average fraction of a plot's bryophyte cover contributed by *H. splendens*) over all years 1992–1996 and all plots, using the number of mature *H. splendens* segments in each plot as weights. The odds-ratio test was also used to assess if a transition to or from one V-class to burial was more likely to be brought about by pleurocarps than by acrocarps. In this case, the reference value 0.500 was used, obtained as the ratio of the total number of transitions involving burial by pleurocarps (over all plots and years) to the total number of recorded transitions involving burial by acrocarps or pleurocarps.

All of the 12528 recorded mature segments were used to study the effect of vertical position on branching pattern and fitness. For each V-class, the number of segments in each M-class was compared with the expected number, calculated as the product of the number of segments in the V-class and the frequency of the M-class (as given in Table 1) in the total material. Because most demographic processes in *Hylocomium splendens* depend on size (R. Økland 1995a), branching patterns and fitness may show a relationship with vertical position merely because of vertical variation in average segment size. In order to rule out this size effect, observed numbers of segments in each M-class were compared with *size-corrected expected numbers*, calculated as follows: First, the probability for a mature segment in a given S-class to be classified to a M-class was calculated, using all mature segments recorded (also see R. Økland 1995a: Table 3). For each V-class, the size-corrected expected number of segments in a given M-class was then obtained as the sum, over all S-classes, of the products of the number of mature segments in an S-class and the probability that a segment in this size class belonged to the M-class in question. Similarly, *size-corrected expected fitness* was calculated from the population fitness (number of offspring produced within one year after maturation; see above), determined for segments in each S-class by use of all recorded mature segments. The observed fitness for a given V-class was then compared with the size-corrected expected fitness.

Size characteristics of mature segments developing from each of the three classes of regenerated growing points (GRe-classes; GRe1L, GRe1T and GRe2+) were compared with size characteristics of the pooled 9634 offspring mature segments that arose by ramification (GRa), in order to assess the role played by vertical position for the lower mean size of mature segments produced by regeneration than by ramification (cf. R. Økland 1995a). First, the average segment size (in $\log_2 DW$ units) was calculated for all combinations of V-class and GRe-class. Next, VD was calculated for each combination of V- and G-class (GRe and GRa) as the difference between the average size of segments in this combination of V- and GRe-classes and the overall mean size of segments belonging to this GRe-class. For the three classes of segments that arose by regeneration, relative VD values (RVD) were calculated for each V-class as the difference between VD and VD of the corresponding V-class for offspring that arose by ramification. RVD was used as an indicator of the specific effect of regeneration on size, as compared to ramification. The overall contribution of differences in vertical distribution of segments to the difference in mean ($\log_2$-transformed) size between segments that arose by a particular type of regeneration (a GRe-class) and by ramification was assessed by calculating the *V-class-corrected size difference* as the weighted average of VD values, using the number of segments in each V-category as weights.

Results

Relationship between total bryophyte cover and mean vertical position of mature segments

The mean vertical position of mature segments (as assessed by the visibility from above at the time of

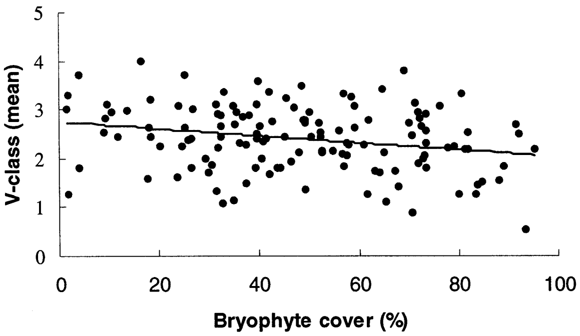

Fig. 1. Relationship between vertical position (*MV*; mean V-class) of *Hylocomium splendens* segments and density of the bryophyte carpet (*BC*, total cover, in %) in Norwegian boreal spruce forests. Regression equation: $MV = -0.0071 \cdot BC + 2.74$, $R = 0.244$, $n = 131$, $p = 0.0050$.

maturity) was significantly correlated with total bryophyte cover, although with considerable scatter (Fig. 1). The percentage of an average segments that was visible from above was, thus, on average, lower in dense than in open bryophyte carpets.

Relationships between size and vertical position of mature segments

Except for emergent segments (class V5: 9.9%), mature segments were relatively evenly distributed over the six V-classes (Fig. 2). The burying agent was recorded for 95.1% of the segments classified to V0, of which 64.7% were covered by litter and 35.3% were covered (buried) by bryophytes. In order of decreasing frequency, the recorded litter types were: coniferous litter (needles, twigs and cones; 48.0%), ericaceous leaf litter (21.2%), broad-leaf litter (20.8%) and herb litter (10.0%). For 345 segments buried by bryophytes, the burying species was recorded. Of these, 117 (33.9%, as compared with the expected value of 27.2%; *G*-test: $G_1 = 7.46$, $n = 345$, $p = 0.006$) were buried by *Hylocomium splendens*. Equal numbers of burials by a unique, recorded species (164) were brought about by acrocarpous (of which *H. splendens* accounted for 72% and *Rhytidiadelphus* spp. 19%) and by pleurocarpous mosses (of which *Dicranum majus* and *D. scoparium* accounted for a total of 54% and *Sphagnum* spp. for 45%).

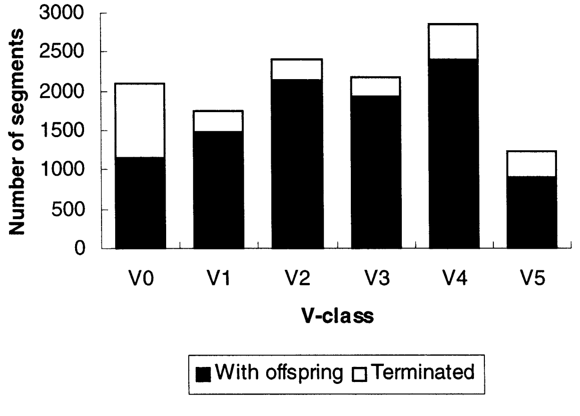

Fig. 2. Frequency distribution of mature *Hylocomium splendens* segments in Norwegian boreal spruce forests, classified into V-classes that reflect vertical position in the bryophyte carpet. Open and filled area of columns indicate relative frequency of terminated or lost segments vs ramifying segments.

Mean segment size differed significantly between all pairs of V-classes except V2 and V3 (intermediate and high positions in the moss carpet; see Fig. 3). Segments were largest in V3, closely followed by V2, then followed by V4 (on top), V1 (low), V5 (emergent) and V0 (buried). V0 segments had, on average, about half the size of V5 (back-transformed values, corresponding to 1 $\log_2 DW$ units), and about a quarter the size of V3 segments (2 $\log_2 DW$ units).

Relationships between vertical position of ramifying segments and their daughter segments

With few exceptions, daughter segments were most likely to enter the same V-class as their parent segment (Table 2). The largest fraction of daughter segments entering the same V-class as its parent (44%) was found for buried segments. Transitions to burial were also the most frequent transition from segments low (V1) in the bryophyte carpet. Transitions to burial from buried and low parent segments were relatively more frequently brought about by other bryophytes, while litter was the main cause of burial of segments whose mother was classified as V2–V5 (Fig. 4A). Mature segments immersed in the bryophyte carpet (classes V0–V2) rarely (in less than 5% of cases) produced emergent offspring, while as many as 8.5% of daughter segments of emergent parents became buried. Transitions from V0 to V2–V5 were significantly more frequent for segments buried in litter than for segments buried in the bryophyte carpet (Fig. 4B). A higher number of transitions were to lower than to higher relative positions in the bryophyte carpet (4113 vs 3386 segments giving rise to daughter segments in lower and higher V-classes, respectively; *G*-test: $G_1 = 110.73$, $n = 10\,321$, $p < 0.0001$).

Transitions from V1–V5 to V0 by *Hylocomium splendens* occurred more often than expected from the relative cover of *H. splendens* (40.1% of transitions to burial with recorded burying species; *G*-test: $G_1 = 20.73$, $n = 246$, $p < 0.0001$). Escape from burial by *H. splendens* also occurred more often than expected (transitions from V0 to V1–V5, 38.8% of total; *G*-test: $G_1 = 6.12$, $n = 98$, $p = 0.013$). The probability of transitions to burial from burial by *H. splendens* did not differ from the expected value (24.6% of total number of segments buried by *H. splendens*; $G_1 = 0.43$, $n = 122$,

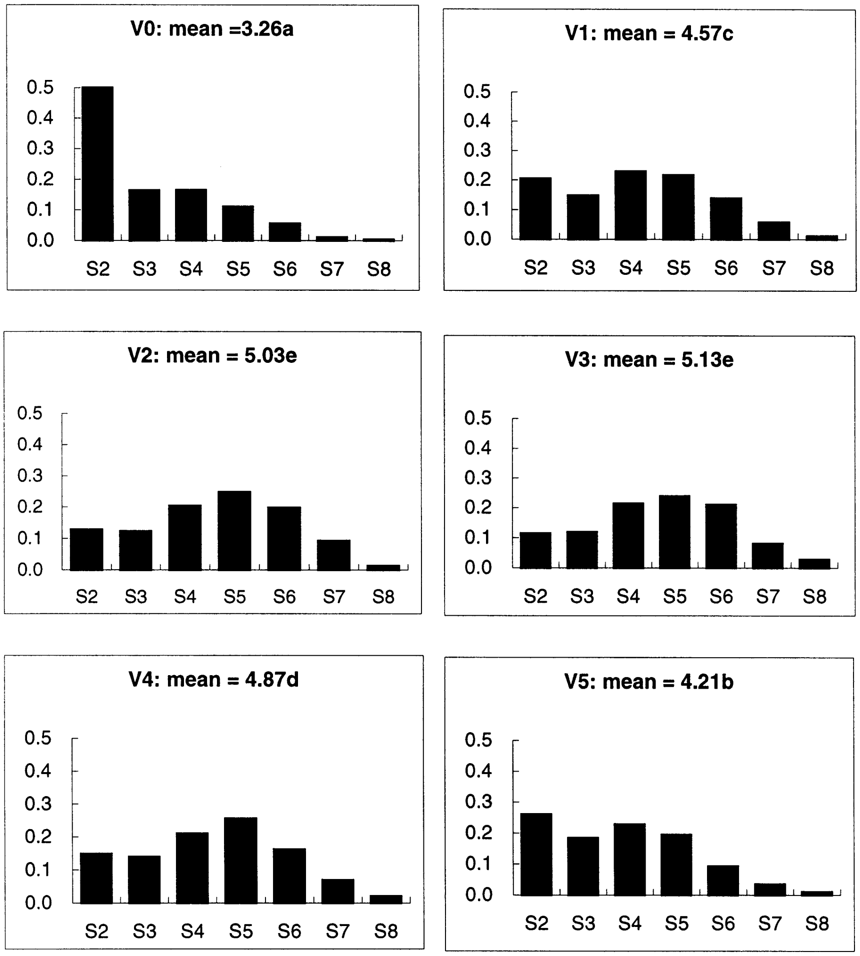

Fig. 3. Size distributions of V-classified mature *Hylocomium splendens* segments in Norwegian boreal spruce forests: proportion of segments in each size class. Mean sizes (given in $\log_2 DW$ units) followed by identical letters are not significantly different (two-tailed T-test; $p < 0.01$).

$p = 0.512$). Pleurocarps were involved in significantly more transitions from V1–V5 to burial by bryophytes and escapes from burial by bryophytes than were acrocarps, while acrocarps accounted for a larger fraction of persistent burials (V0-to-V0 transitions) by bryophytes (Fig. 5).

The V-class distributions of offspring were significantly different between all pairs of parent-segment V-classes, as well as between subclasses of buried segments (pair-wise G-tests; df $= 5$; $p < 0.0001$).

Transitions to V-classes V3 and V4 were invariably associated with an increase in mean relative segment size difference (difference between $\log_2 DW$ of daughter and parent segments) corrected for area and year (Table 3), and no significant relative difference was found between these two classes in this respect. The rank order of the other V-classes by (increasing) relative size reduction upon transition to the same class was: V2, V1, V5 and V0. Burial implied a mean size reduction of 21–44% (0.34–0.83 $\log_2 DW$ units; see Table 3). Emergent daughter segments (transition to V5) were also significantly smaller than their parent segments, except for transitions from buried segments. Transitions to the same V-class as the parent segment implied size reduction for buried and emergent segments, indicating that shoots could not survive in the long run if remaining in these vertical positions. Buried or low segments gave rise to daughter segments that were significantly smaller than their parents ($p < 0.05$) if burial was brought about by litter than when brought about by other bryophytes (Table 4). The magnitude of size reduction for transitions from V0Bry to V0 did, however, not differ among pleurocarps and acrocarps (23% and 18%, respectively; T-test: $T = 0.35$, $n = 118$, $p = 0.726$). A significantly lower relative size reduction was observed for transitions to burial from buried and low parent segments than for parent segments in V3–V5. Transitions to V1–V4 implied a more favourable size development the lower the parent segments were situated. Transitions to burial from buried parent segments implied lower relative size reduction when parent segments were buried by bryophytes (Table 4). The size differences associated with transitions from buried and emergent parent segments, respectively, to segments in classes V2–V4 differed considerably: while daughters of buried segments were on average ca 50% larger than their parents, daughters of emergent segments were not significantly larger than their parent segment for any V-class (Table 3).

Relationships between branching patterns and size and vertical position of segments

The frequencies of multiple ramification, regeneration and termination were significantly related to vertical position of mature segments (Table 5). The frequency of lateral regeneration with one year's delay (MRe1L) was more than ten times higher for segments classified to V-class V4 (at the top of the bryophyte carpet) than for buried segments. After size differences had been accounted for, the frequency of MRe1L regeneration declined in steps from V5 to V0. V4 and V5 had significantly higher frequencies than V2 and V3, which in turn had significantly higher frequencies than V0 and V1. The tendency for terminated segments to regenerate (MRe1T) after one year's delay showed a similar relationship to the vertical position of source segments and was also significantly higher for terminated segments buried in litter than for terminated segments buried by bryophytes (9.42% vs 1.95%; *G*-test: $G_2 = 10.25$, $n =$ 635 and 205, $p < 0.0001$).

The pattern of variation in frequency of multiple ramifications differed from that of regeneration in being highest for segments in intermediate (V2) and high (V3) positions and declining both towards buried and towards emergent segments (Table 5). This trend remained after differences in size had been accounted for, except that the highest surplus of ramifications over expected values was found for V1 and V2 and the lowest values were found for V5.

Buried segments had the highest, and segments in V1–V3 the lowest risk of termination (also see Fig. 2). The probability of termination increased significantly from V1–V3 to V4, from V4 to V5, and from V5 to V0. This pattern was not altered by correcting for differences in size. Segments buried in litter had a significantly higher risk of termination than segments buried by bryophytes (44.9% vs 28.6%; *G*-test: $G_2 = 56.95$, $n = 1288$ and 704, $p < 0.0001$). The risks of termination after burial by acrocarps and after burial by pleurocarps did not differ (Fig. 5). The probabilities of loss and grazing were not significantly related to vertical position of the parent segment.

Fitness was significantly lower for buried segments than for an average segment (regardless of vertical position), even after size had been accounted for (Fig. 6). Emergent segments also had lower than average fitness, but not significantly so. Segments in V-classes V2–V4 had significantly higher than average fitness, also significantly higher than that of V5 (Fig. 6A). Differences in fitness between V5 and V2–V4 were significant at the $p < 0.01$ level even after differences in size had been accounted for (Fig. 6B).

Small segments within all V-classes had high termination risk (Table 6). The rank order of non-ramifying mature segments according to mean size was the same for all V-classes: MTeOt < MRe1T < MTeLo < MTeGr. Ramifying segments that gave rise to buried offspring had lower mean size than segments in the same V-class that gave rise to non-buried offspring. No significant size difference was found between segments buried in litter and segments buried in the bryophyte carpet (mean size of ramifying segments: 3.74 and 3.80 $\log_2 DW$ units; *T*-test: $T = -0.58$, $n = 590$ and 434, $p = 0.560$; mean size of non-ramifying segments: 2.69 $\log_2 DW$ units for both; *T*-test: $T = -0.02$, $n =$ 698 and 270, $p = 0.988$). For V4 parent segments, however, the mean size of V0 offspring was only weakly significantly different from that of V1 ($p = 0.016$), and for V5 parent segments, significant differences were only found between V0 and V2 ($p < 0.01$), and between V0 and V3 and V5 daughter segments ($p < 0.05$). For all except emergent mature segments, segments that gave rise to V3 offspring had higher mean size than segments giving rise to offspring in other vertical categories (see Table 6).

Table 2. Annual transition matrix for ramifying mature, V-classified *Hylocomium splendens* segments in Norwegian boreal spruce forests 1992–1997. The V-classes indicate vertical position, from V0 (buried; fully shaded) to V5 (emergent from the bryophyte carpet). The highest probability for transition from each class is given in bold. *n*, number of parent segments in each category.

Daughter segment V-class	Transition probabilities, from parent segment in V-class					
	V0	V1	V2	V3	V4	V5
V0	**0.444**	**0.250**	0.177	0.126	0.091	0.085
V1	0.166	0.185	0.167	0.133	0.090	0.047
V2	0.151	0.218	**0.238**	**0.228**	0.177	0.095
V3	0.105	0.166	0.189	0.221	0.201	0.155
V4	0.106	0.139	0.182	0.219	**0.314**	0.301
V5	0.027	0.042	0.047	0.072	0.127	**0.318**
n	1131	1581	2297	2041	2446	825

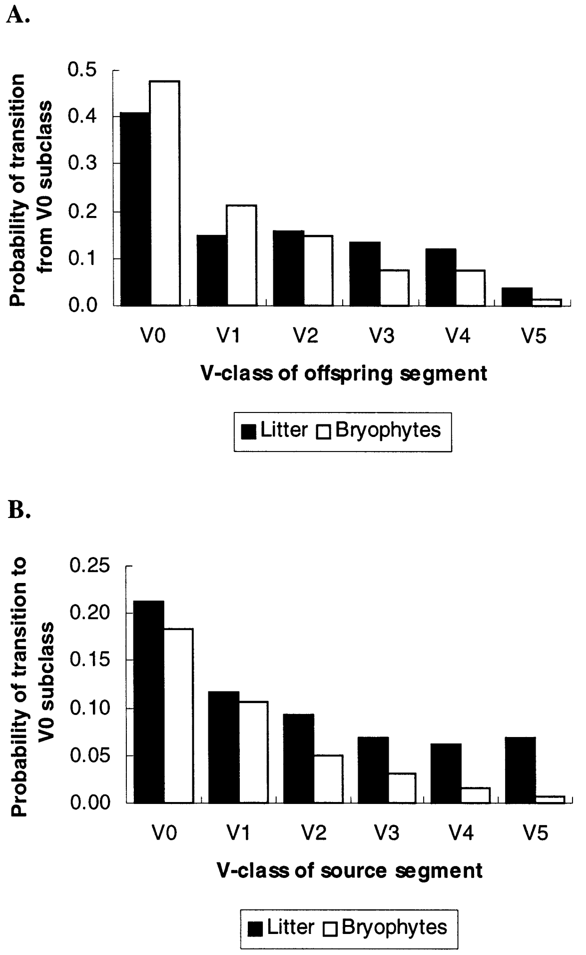

Fig. 4. Probability of transitions from (A), and to (B) buried mature *Hylocomium splendens* segments in Norwegian boreal spruce forests classified to subclass according to burial agent (burial in litter and burial in the bryophyte carpet). The V-classes indicate vertical position, from V0 (buried; fully shaded) to V5 (emergent from the bryophyte carpet). Transition probabilities from V0 subclasses in (A) calculated from total number of ramifying segments in subclass; to V0 subclasses in (B) from total number of ramifying segments in offspring V-class.

For small segments (in size class S2), both buried and emergent segments had significantly lower fitness ($p <$ 0.05) than segments in the intermediate V-classes V1–V4 (Table 7). For all other S-classes, the fitness of emergent segments was close to that of V2–V4 while buried segments' fitness was always lower than average for the S-class (Table 7). Fitness maximum, compared among vertical positions for segments in the same S-class, shifted with increasing segment size from lower to higher relative positions in the bryophyte carpet: for S2–S4 highest in V2–V3, for S5 highest in V4, and for S6–S7 highest in V5. This indicated that emergence was unfavourable for medium-sized and small segments only.

Relationships between fate, size and vertical position of regenerated segments and the vertical position of the source segment

Mature segments that arose by GRe2 + regeneration were, on average, situated deeper in the bryophyte carpet than segments that arose by GRe1L regeneration or by ramification, while segments that arose by terminal regeneration (GRe1T) were situated higher in the bryophyte carpet than those that arose by ramification (Fig. 7). Pairwise *G*-tests for similarity of V-class distributions between segments that arose by regeneration and segments that arose by ramification of parent segments in a given V-class (as given in Table 2) demonstrated that: the vertical distribution of segments that arose from GRe2 + regeneration came closest to that of offspring from V1 parent segments, that of GRe1L came closest to that of V3, and that of GRe1T came closest to those of V3 and V4.

Mature segments that arose by GRe2 + regeneration were, on average, significantly smaller than GRe1T offspring, which were in turn significantly smaller than GRe1L offspring, which in turn were significantly smaller than daughter segments that arose by ramification (Table 8). GRe2 + offspring were less than half as large (back-transformed values) as GRe1L offspring and only ca 30% the size of offspring that arose by ramification. Offspring that arose by terminal regeneration was less than half the size of offspring produced by ramification. For all the four categories of offspring, V3 segments had highest mean size, followed by V2 or V4, V1 or V5, and V0 (Table 8). V3 and V4 segments that arose by GRe1L and GRe2 + regeneration were proportionally larger than segments in the corresponding V-class that arose by ramification while the converse

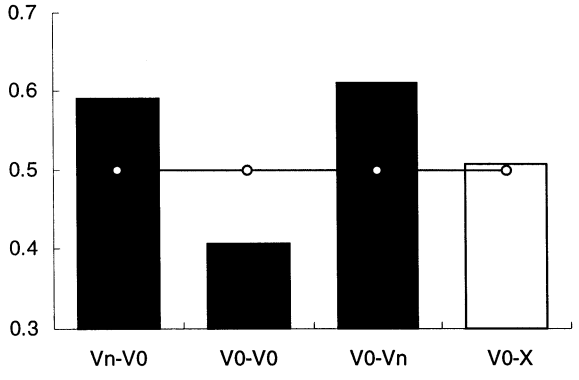

Fig. 5. Ratio of transitions from or to burial in the bryophyte carpet attributed to pleurocarps to total number of burials attributed either to acrocarps or pleurocarps. Filled columns indicate ratio significantly different from the expected value of 0.500 [ratio of burials due to pleurocarps to sum of burials due to acrocarps and pleurocarps ($n = 328$); indicated by line with dots] at $p < 0.05$ (*G*-test, df = 1). The V0-X transition refers to non-ramifying segments (terminated and not regenerating terminally within one year, or lost).

Table 3. Mean relative size difference (difference between $\log_2$-transformed dry weights) between V-classified, mature *Hylocomium splendens* daughter segments and their (normally ramifying) parent segments in Norwegian boreal spruce forests 1992–1997, corrected for differences in mean $\log_2 DW$ between one-year periods in each area (see Materials and methods). The V-classes indicate vertical position, from V0 (buried; fully shaded) to V5 (emergent from the bryophyte carpet). Negative mean relative differences indicate lower size of daughter than of parent segments. Entries significantly different from zero (two-tailed T-test; $p<0.01$) are given in bold. Entries in the same row sharing a capital letter, and entries in the same column sharing a lower-case letter, are not significantly different at the $p<0.01$ level (two-tailed T-test).

Daughter segment V-class	Mean relative size difference corrected for area and year, from parent segment in V-cass																	
	V0			V1			V2			V3			V4			V5		
V0	**−0.43**	a	AB	**−0.34**	a	A	**−0.56**	a	ABC	**−0.74**	a	C	**−0.71**	a	BC	**−0.83**	a	BC
V1	**0.31**	b	A	0.18	b	AB	0.02	b	B	**−0.27**	b	C	−0.24	b	C	−0.20	bc	ABC
V2	**0.57**	b	A	**0.48**	c	A	**0.22**	bc	B	**0.16**	c	B	−0.11	bc	C	−0.06	bc	BC
V3	**0.68**	b	A	**0.52**	c	AB	**0.31**	c	BC	0.04	c	D	0.13	d	CD	0.11	bc	CD
V4	**0.68**	b	A	**0.49**	c	AB	**0.31**	c	BC	0.09	c	CD	0.01	cd	D	0.17	c	CD
V5	0.22	ab	A	−0.31	a	AB	**−0.35**	a	AB	**−0.36**	a	AB	**−0.49**	a	B	**−0.27**	b	AB

was true for V5 segments. This indicated that the vertical position in the bryophyte carpet exerted a stronger impact on the development of segments that arose by regeneration than of segments that arose by ramification.

The contributions of V-class distributions of offspring to the difference in mean size between regenerated offspring and offspring that arose by ramification were $+0.01 \log_2 DW$ units for GRe1L (T-test of difference from 0: $T=0.26$, $n=990$, $p=0.795$), 0.00 units for GRe1T ($T=0.01$, $n=443$, $p=0.990$), and -0.12 units for GRe2+ ($T=-3.13$, $n=1757$, $p=0.002$). Thus, only for GRe2+ regenerated offspring was the small size partly accounted for by unfavourable vertical position.

Size differences between segments that arose by GRe1 regeneration and their source segments were only weakly related to V-class of source segment (ANOVA; GRe1L: $F_{5,620}=2.246$, $n=626$, $p=0.048$; GRe1T: $F_{5,311}=2.913$, $n=317$, $p=0.014$). Systematic differences between pairs of source segment V-categories were not observed, indicating that the relative size of regenerated offspring was not dependent on vertical position of source segment. The vertical position of offspring segments was, however, both for GRe1L and GRe1T, related to vertical position of source segments much the same way as for ramified segments; source segments situated low in the bryophyte carpet giving rise to lower-situated offspring than higher-situated source segments.

Discussion

Dependence of fitness components on vertical position

Branching patterns

The strong size dependence of branching patterns (ramification as well as regeneration) in *Hylocomium splendens* (cf. R. Økland 1995a) is confirmed by the results. Size dependence is particularly strong for multiple ramification, which is suppressed by apical dominance as it takes place closer to the growing apex of the shoot chain. Multiple ramification is restricted to large segments within which normal internal hormone transport distances can be exceeded (R. Økland 1995a). Regeneration with one year's delay is also demonstrated to be strongly dependent on vertical position in the bryophyte carpet (decreasing downwards) while the tendency to produce multiple ramifications appears less strongly related to vertical position. However, this difference may, at least partly, result from the recording of vertical positions for all mature segments the autumn they reach maturity. For ramifying segments this is the year ramification took place, but for segments arising by lateral regeneration with one year's time delay this is one year before the offset of regeneration. Assuming that one generation of mature segments on average will be bogged two V-classes further down into the bryophyte carpet in one year [which is not unreasonable, according to R. Økland (pers. obs.); also see Tamm (1953)], the results are in agreement with the hypothesis that production of additional offspring, by lateral regeneration or ramification, depends on radiation above a minimum threshold level below which branching frequency rapidly declines. The higher vertical position of current than of one-year-old mature segments indicates that ramification is inhibited by low radiation less often than regeneration. If the negative relationship between total cover and mean vertical position of segments is taken into account, this accords with observations made in previous studies: low dependence of ramification rates and high dependence of regeneration rates on total cover (R. Økland and T. Økland 1996), and low residual variation in ramification rates between years after size differences are accounted for (R. Økland 1997).

The strong decrease in regeneration frequency from middle via low to buried source segments also accords with light attenuation profiles for carpets of pleurocarpous bryophytes (Skre et al. 1983, van der Hoeven et al. 1993). The regeneration mechanism in *Hylocomium splendens* (and other moss species) involves breaking of dormancy in resting buds (Knoop 1984), a process promoted by light (Davy de Virville 1927–28, Berthier et al. 1976, Bopp 1983). More specifically, bud induction in bryophytes is influenced by red and far-red treatment (see Berthier et al. 1976 and Bopp 1983 for reviews; also see Hoddinott and Bain 1979), indicating that a phytochrome system, perhaps similar to the mechanism for regulation of tillering (shoot initiation) in vascular plants by radiation quantity and/or quality (downward decrease in the red:far red ratio; Casal et al. 1985, Deregibus et al. 1985, Solangaarachchi and Harper 1987, de Kroon and Kwant 1991), is involved (R. Økland and T. Økland 1996, Bates 1998).

The significantly higher ramification frequency of segments within (V-classes V1–V3), than of segments on top of, or emergent from, the bryophyte carpet, indicates that branching, like growth of ectohydric bryophytes in general, is influenced by the microclimate around each segment. This also accords with the high importance of moisture for branching of bryophytes as demonstrated experimentally, e.g., by Clymo and Duckett (1986) and Myrmæl (1993).

Because of the gradual loss of a tissue's production potential with age (Bates 1979, R. Økland 1995a), regenerated growing points are more strongly dependent, than offspring by ramification, on their own ability to produce assimilates. This explains why the size of regenerated offspring is more strongly dependent on vertical position than offspring by ramification (being relatively larger if they enter the upper part of a bryophyte carpet and relatively smaller if emergent). The role of internal translocation of resources over short distances within a moss chain for regeneration remains poorly known (van der Hoeven and During 1997a).

Termination and loss

Strong negative size dependence of termination, the tendency for a mature *Hylocomium splendens* segment not to ramify (R. Økland 1995a), is confirmed by this study. Furthermore, it is shown that termination also depends on vertical position, even after effects of size have been taken into account.

Terminations may be caused by burial in the bryophyte carpet, burial by litter, exposure to other external factors, and other, not readily apparent (e.g. shoot-internal), causes. As there is no a priori reason to expect vertical variation in mortality risk due to shoot-internal factors (which is likely to be low throughout), the upward increase in size-corrected termination risk, particularly strong near the top of the carpet, is interpreted as a response to a gradient in exposure to external factors that may bring about termination. The most important recognized causes of damage (all confirmed by R. Økland, pers. obs., also see R. Økland 1995a) include: the action of frost and ice during winter (Hancock and Brassard 1974, Collins 1976, R. Økland

Table 4. Mean relative size difference (difference between $\log_2$-transformed dry weights) between V-classified, mature *Hylocomium splendens* daughter segments and their (normally ramifying) parent segments in Norwegian boreal spruce forests 1992–1997, corrected for differences in mean $\log_2 DW$ between one-year periods in each area (see Terminology, materials and methods). Transitions from, and to, buried segments are divided into two subclasses according to burial agent: burial in litter, and burial in the bryophyte carpet. The V-classes indicate vertical position, from V0 (buried; fully shaded) to V5 (emergent from the bryophyte carpet). Negative differences indicate lower size of daughter than of parent segments. V0 subclasses with mean relative size differences significantly different at the $p < 0.05$ level are given in bold.

Transitions	V0 subclass	Mean relative size difference corrected for area and year, from parent segment in V-class					
		V0	V1	V2	V3	V4	V5
From	Litter	**−0.53**	**0.08**	0.41	0.61	0.57	**−0.15**
V0	Bryophytes	**−0.26**	**0.49**	0.75	1.05	1.02	**1.67**
To	Litter	**−0.53**	**−0.58**	−0.51	−0.77	−0.74	−0.89
V0	Bryophytes	**−0.26**	**−0.16**	−0.66	−0.71	−0.66	−0.26

Table 5. Dependence of branching pattern (number and type of offspring segments the next year; M-classification as explained in Table 1) on vertical position of mature *Hylocomium splendens* segments in Norwegian boreal spruce forests 1992–1997. The V-classes indicate vertical position, from V0 (buried; fully shaded) to V5 (emergent from the bryophyte carpet). The overall frequencies refer to Table 1. Ratios between observed and expected numbers are calculated for each M-class and V-class and each of: the total number of mature segments (in all V-classes), and the size-corrected number (as explained in Terminology, materials and methods). Deviations from the expected value of unity are tested by *G*-tests ($p<0.01$ indicated in bold). Entries in the same row sharing a letter are not significantly different at the $p<0.01$ level (two-sample *G*-test).

M-class	Overall frequency	Observed/expected numbers, for mature segment in V-class					
		V0 ($n=2095$)	V1 ($n=1741$)	V2 ($n=2414$)	V3 ($n=2180$)	V4 ($n=2857$)	V5 ($n=1241$)
Not corrected for size							
MRa2+	0.0600	**0.397** a	1.137 bc	**1.433** c	**1.328** c	0.932 b	**0.548** a
MRe1L	0.0667	**0.157** a	**0.447** b	0.979 c	**1.243** c	**1.553** d	**1.300** cd
MRe1T*	0.2108	**0.384** a	0.877 b	1.114 bc	1.322 bc	**1.602** c	**1.578** c
MTeOt	0.1347	**2.843** d	**0.505** a	**0.438** a	**0.497** a	**0.698** b	**1.507** c
MTeLo	0.0514	1.196 ab	1.226 b	0.877 ab	0.802 a	0.986 ab	0.953 ab
MTeGr	0.0102	0.510 a	1.353 a	1.294 a	0.990 a	1.029 a	0.706 a
Size-corrected							
MRa2+		0.816 ab	1.194 bc	**1.193** c	1.014 abc	**0.815** a	0.697 a
MRe1L		**0.285** a	**0.468** a	0.842 b	1.028 b	**1.509** c	**1.607** c
MRe1T*		**0.418** a	0.794 b	0.936 b	1.244 b	**1.577** c	**1.870** c
MTeOt		**1.686** d	**0.518** a	**0.602** a	**0.649** a	0.887 b	**1.356** c
MTeLo		1.159 a	1.239 a	0.885 a	0.819 a	1.001 a	0.962 a
MTeGr		0.693 a	1.351 a	1.172 a	0.897 a	0.968 a	0.772 a

* expressed as fraction of (MRe1T + MTeOt), the fraction of all terminations not due to grazing or loss.

1995a), long-lasting summer drought (Kimmel 1962, Vallin 1974, R. Økland 1997), trampling (Ericson 1977) and urination by mammals (Frisvoll and Flatberg 1990), collecting of nest material by birds (Henze 1962), decomposing fungal fruit-bodies (Vallin 1974, Ingelög and Nohrstedt 1993) and exposure to airborne acidifying pollutants (Frisvoll 1989, R. Økland et al. 1997). Death by exposure to full sunlight, as observed in clearcut forests (Busby et al. 1978, Nykvist 1997), rarely occurs in northern old-growth spruce forests where a low solar angle makes even distantly spaced trees produce sufficient shade (cf. Canham et al. 1990).

Risks of loss and grazing damage are unrelated to vertical position, in accordance with the low density dependence of these processes (R. Økland and T. Økland 1996). Most likely, this pattern is the result of two groups of factors with contrasting vertical distributions: physical removal by trampling or uprooting by rodents (Tamm 1953, Hancock and Brassard 1974, Ericson 1977, During and ter Horst 1987) and the actions of heavy rain (Watson 1960) and minor snow- or earthslides (van Tooren and During 1988) which are likely to become more important upwards with decreasing contact with, and attachment to, the surrounding mosses; and burial which becomes more important downwards. Low number may be the main reason why no relationship with vertical position was found for grazed segments.

Unimodal variation in fitness within bryophyte carpets

The patterns of vertical variation in mean segment size and fitness coincide almost perfectly with modes (maxima) for V-class V3, i.e. ca 2–10 mm below the top of the bryophyte carpet. I interpret this as a strong indication that accumulated time in a photosynthetically active state is the most important single factor restricting growth of ectohydric bryophytes on the scale of individual shoots just as has been demonstrated for entire bryophyte carpets (cf. Tamm 1953, Busby et al. 1978, Callaghan et al. 1978, Bates 1988, R. Økland and T. Økland 1996, R. Økland 1997). The existence of an optimum level high in the bryophyte carpet accords with model calculations (Hayward and Clymo 1983), showing this level to be the optimal compromise between radiation and moisture conditions. The nearly 50% decrease in mean size (after back-transformation) from segments at the optimum level to emergent segments indicates a strong deterioration of growth conditions from a sheltered position near the top but just within a closed bryophyte carpet, to an exposed position in the free air immediately above it (cf. Clymo 1973, Proctor 1980, Hayward and Clymo 1983).

Several lines of evidence indicate that emergence causes not only a reduction in size but also additional loss of vitality: the less favourable size development associated with transitions from emergent than from buried and low segments (which are, on average, smaller and larger than emergent ones, respectively); the lower (than expected) size of emergent offspring produced by regeneration (from source segments of reduced vitality); and the much lower fitness of small emergent segments compared to other small segments while no difference was found for larger segments (i.e. that for the largest segments, maximal fitness is associated with emergence while for successively smaller segments the vertical level of maximum fitness is displaced downwards in the bryophyte carpet). Particularly high sensitivity of small segments, with lower resilience to damage of all kinds (cf. R. Økland 1995a, 1997), makes a strong case for recurrent desiccation as the important factor (Dilks and Proctor 1974; cf. also Vallin 1974, Hearnshaw and Proctor 1982, R. Økland 1997). This hypothesis also accords with the very strong dependence of mean thallus size on the time in a hydrated state, and thus on time available for assimilation, demonstrated for the foliose lichen *Degelia plumbea* (Gauslaa and Solhaug 1998). Most likely, a stronger proportional advantage of larger over smaller segments near the top of the bryophyte carpet is brought about by two factors: relatively better moisture-capturing and moisture-retaining capacities of larger shoots, which are thus able to remain photosynthetically active for a longer time, and higher resilience of larger shoots to desiccation damage.

The results suggest that segments that arose by regeneration are small because of low supply of resources from the source segment, due to depletion by previous daughter ramets and further loss of production potential with time (R. Økland 1995a). Only for segments regenerated with two or more years' delay does unfavourable vertical position contribute significantly to decrease in size.

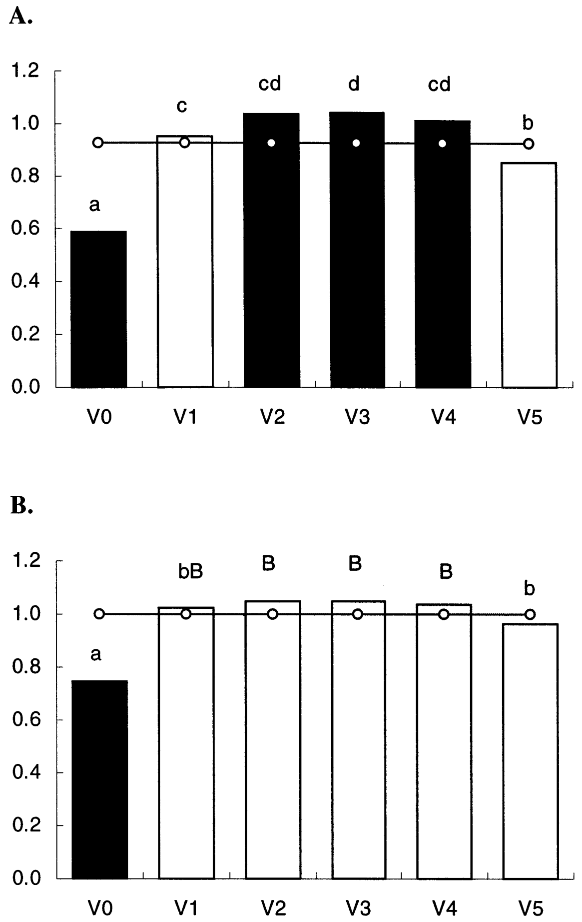

Fig. 6. Dependence of fitness (vertical axes) of mature *Hylocomium splendens* segments in Norwegian boreal spruce forests on vertical position (V-class). Fitness is defined as the number of offspring emerging from a mature segment within one year after maturation. (A) Fitness not corrected for size differences among V-classes. Filled columns indicate fitness significantly different from overall mean (0.927; indicated by line with dots) at $p < 0.01$ (test: comparison of means for Poisson-distributed counts). V-classes sharing letters not significantly different at $p < 0.01$ (test as above). (B) Fitness corrected for size differences (see Terminology, materials and methods for explanation). Filled columns indicate fitness significantly different from the expected value of 1.000 (as indicated by line with dots) at $p < 0.01$ (test as above). V-classes sharing capital letters are not significantly different at $p < 0.01$; V-classes sharing lower-case letters are not significantly different at $p < 0.05$ (test as above).

Vertical dynamics and causes of vertical stochasticity

The vertical position of apical segments on *Hylocomium splendens* shoot chains varies strongly from year to year: less than 30% of daughter segments end up in the same V-class as their parent segment and ca 35% do not even end up in the adjacent V-class. This contrasts with model predictions for *Sphagnum* growth (Hayward and Clymo 1983) but is in accordance with assumptions of Tamm (1953), During (1990) and Rydin (1997).

The prediction that emergence arises when large vigorous segments produce large daughter segments at vertical growth rates unmatched by other bryophytes is not supported by the results: the size of parent segments in V-classes V0–V4 that give rise to emergent daughter segment is invariably lower than that of segments which remain within the bryophyte carpet. On the contrary, the results indicate that large parent segments are more likely to give rise to daughters that enter the optimal upper part of the bryophyte layer.

The prediction that the current apical mature segment of shoot chains with retarded growth will be left behind at a successively higher rate until eventually dying from lack of light is confirmed. At all vertical levels more than 8% of the segments are buried every year and buried daughter segments are smaller than non-buried daughter segments that arise from parent segments at the same vertical level. Burial is thus an important sink for segments in *Hylocomium splendens* populations, directly due to the high termination risk of buried segments, as well as indirectly due to the ca 26% lower (back-transformed) size of buried daughters of buried parent segments.

Vertical stochasticity is a result partly of the mode of growth of *Hylocomium splendens*; growth gradually passes from being directed upwards when growing points are young to become more horizontal at later developmental stages. During this process the shoot

Table 6. Dependence of branching pattern (M-class; see Table 1 for explanations; M-class MRa = MRa1 and MRa2+) of offspring segments (for daughter segments of normally ramifying parent segments also vertical position) on the vertical position and mean size of source *Hylocomium splendens* segments in Norwegian boreal spruce forests, 1992–1997. Size is given as $\log_2 DW$ units. Entries in the same column sharing a letter are not significantly different at the $p<0.01$ level (two-tailed T-test).

Classification of offspring		Mean size of mature source segment in V-class					
M-class	V-class	V0 ($n=2095$)	V1 ($n=1741$)	V2 ($n=2414$)	V3 ($n=2180$)	V4 ($n=2857$)	V5 ($n=1241$)
MRa	V0	3.37 cd	4.09 bc	4.55 bc	4.51 bc	4.37 bc	4.37 de
MRa	V1	4.09 fg	4.92 d	5.17 e	5.24 d	4.75 cd	4.43 cdef
MRa	V2	4.05 fg	5.02 d	5.42 ef	5.28 d	5.21 ef	5.04 f
MRa	V3	4.46 g	5.14 d	5.45 f	5.61 e	5.29 f	4.89 ef
MRa	V4	3.88 ef	4.79 d	5.19 ef	5.26 d	5.15 ef	4.70 ef
MRa	V5	4.04 defg	4.61 cd	5.09 def	5.13 cd	4.95 de	5.14 ef
MRe1T		2.95 abc	3.15 a	4.00 ab	4.53 bc	4.27 b	3.63 b
MTeOt		2.55 a	3.05 a	3.36 a	3.85 a	3.41 a	2.92 a
MTeLo		3.40 cde	4.14 bc	4.53 bcd	4.88 bcd	5.02 def	4.06 bcd
MTeGr		4.76 fg	4.90 cd	5.10 cdef	5.76 cde	5.49 def	4.41 bcdef

enters new environments where new neighbours are encountered and intermingled with (also see Tamm 1953). At high vertical levels litterfall is the dominant burial agent (the annual probability of becoming covered by litter never falls below 6%), contributing strongly to vertical stochasticity. Coverage by litter exerts a stronger negative effect on affected segments than burial in the bryophyte carpet: the risk of termination is higher, the decrease in relative size from parent to daughter segment is greater, and the relative size increase after escape from litter coverage is lower than after escape from shading by bryophytes. Most probably, this is due to the lower incoming radiation and the more unfavourable moisture conditions under litter than deep within the bryophyte carpet (Tamm 1953). However, in the long run these disadvantages are partly outweighed by the much higher probability for segments buried in litter to escape burial and re-enter higher vertical levels in the bryophyte carpet. Such escapes may result from etiolated growth (cf. Kujala 1926, Tamm 1953, Bates 1988, Kosiba and Sarosiek 1993, van der Hoeven and During 1997a) or because the litter is blown away or decomposes (R. Økland pers. obs.).

Daughters of mature segments tend to be displaced downwards in the bryophyte carpet year by year, with burial-induced termination acting as a strong sink for mature segments. This sink may be compensated for by the addition of extra offspring by multiple ramification and, notably, by regeneration. The dependence of branching on light ensures that input of new segments occurs where the risk of burial is lowest. Just like in a tree canopy, the behaviour of each bud is determined, precisely and locally, by the conditions in which it finds itself (Harper 1985). But because of their small size, regenerated segments are always at great risk of rapidly becoming eliminated by burial. Low long-term contribution by regeneration to the population growth rate accords with empirical results (elasticities associated with regeneration) for natural populations of *Hylocomium splendens* (R. Økland 1995a). However, immediately after the bryophyte carpet opens up, e.g. by fine-scale disturbance, regeneration plays an important role (Rydgren et al. 1998b).

Mechanisms of interactions between bryophytes in the boreal forest floor

Facilitation, amensalism and the vertical size hierarchy

The recorded frequency of self-burials (burial by *Hylocomium splendens*) is higher than predicted from this species' share of the total bryophyte cover. Bryophyte species are, however, patchily distributed on the boreal forest floor (cf. Maslov 1989, R. Økland 1994, Frego and Carleton 1995b) and the frequency of self-burials is no higher than expected if the aggregation of conspecific shoots is taken into account. This lends some support to the view that interactions among boreal forest floor bryophytes are asymmetric, nonspecific (cf. R. Økland and T. Økland 1996) and short-lasting (R. Økland 1995a).

From the vertical level of maximum average fitness, fitness gradually decreases both upwards and downwards in the bryophyte carpet. Positive interactions thus appear to prevail around the maximum fitness level, where segments benefit from the favourable water relations in closed stands as well as the absence of light deficit (light stress). The inverse vertical size hierarchy towards the top of the bryophyte carpet demonstrates that environmental stress (cf. Grime 1979, R. Økland 1990) together with increasing exposure to disturbance gradually takes over as the most important processes as the modules emerge from the boundary layer, desiccate faster and thus are photosynthetically active for shorter periods (cf. During 1990, van der Hoeven 1999; see Fig. 8). The vertical size hierarchy below the maximum fitness level indicates increasing prevalence of negative interactions downwards in the bryophyte carpet (Fig. 8).

The positive interactions are bilateral and accord with the definition of facilitation [of a (+, +) type; Goldberg 1990]: as all shoots contribute to, and benefit from, the better water relationships of closely spaced shoots (Filzer 1933, Mägdefrau and Wutz 1951, Callaghan et al. 1978). The negative interactions, on the other hand, are unilateral: neither empirical data nor theoretical reasoning give reasons to assume that a segment (negatively) influences segments above it. Although unilateral (0, −) interactions are fundamentally different from (−, −) interactions (cf. Connell 1990), both are usually referred to as "competition" [asymmetric and symmetric competition, respectively, see Connell (1990)]. In my opinion, the term asymmetric competition is inadequate for the (0, −) interactions for two reasons: (1) that most (−, −) interactions are also asymmetric; asymmetry merely implies that the interacting plants do not exert the same effect on each other, and (2) that competition gives associations to an active struggle, e.g. for resources in short supply, while the (0, −) interactions mostly take place by a more or less passive process [resource competition is assumed in general to be of little importance in bryophyte communities (Li et al. 1992, Rydin 1997)]. I therefore suggest that the precise term amensalism (Burkholder 1952, Connell 1990) is revived to be used for (0, −) interactions of the kind described here.

The vertical size hierarchy below the maximum fitness level is an amensalism hierarchy in which segments negatively affect segments beneath them. The much lower size of buried than other segments indicates that amensalism is a strong structuring force in the lower parts of a bryophyte carpet while at intermediate levels the size hierarchy is not much stronger than would be expected to develop within one year from a population of equal-sized segments. This is due to randomly occurring transitions among V-classes V1–V3, only weakly related to size and vertical position of the source segment.

Importance of growth-form

Hylocomium splendens segments have a higher probability of transitions to, and escapes from, burial in pleurocarp-dominated than in acrocarp-dominated communities. The more vertical orientation of acrocarpous moss shoots probably makes them act as physical barriers that restrict the horizontal movement of pleurocarps and impose on them a more erect mode of growth (R. Økland pers. obs.). The lower vertical dynamics of *H. splendens* in such communities gives support to predictions of a more fixed vertical structure in acrocarp-dominated carpets. The converse is likely to be true when acrocarpous species take on a more horizontal mode of growth, e.g. during gap colonization (Frego 1996, Rydgren et al. 1998a), lateral expansion (Noble et al. 1984, Rydin 1995, 1997) and in very wet environments (Boatman 1983).

Penetration of light deeper into carpets of vertically orientated shoots (Davey and Ellis-Evans 1996) may

Table 7. Dependence of fitness of mature *Hylocomium splendens* segments in Norwegian boreal spruce forests 1992–1997 (i.e. the number of offspring emerging from a mature segment within one year after maturation) on vertical position [V-class; from V0 (buried; fully shaded) to V5 (emergent from the bryophyte carpet)] of mature segments, given separately for each size class (S-class; see Terminology, materials and methods) with ≥ 25 segments. Overall fitness is the mean fitness of segments in the size class, regardless of vertical position. Fitness significantly different from overall fitness within an S-class at $p < 0.01$ (test: comparison of means for Poisson-distributed counts) are given in bold. Entries in the same row sharing a letter are not significantly different at $p < 0.05$ (test as above).

S-class	Overall fitness	Fitness for mature segments in V-class											
		V0		V1		V2		V3		V4		V5	
S2	0.586	**0.415**	a	**0.755**	b	**0.762**	b	**0.802**	b	0.697	b	0.472	a
S3	0.827	**0.653**	a	0.875	b	0.895	b	0.872	B	0.864	b	0.833	b
S4	0.930	**0.736**	a	0.942	b	0.967	b	0.985	B	0.967	b	0.911	b
S5	1.014	0.846	a	0.992	ab	1.029	b	1.033	B	1.051	b	1.021	ab
S6	1.137	0.841	a	1.071	b	1.139	b	1.167	B	1.196	b	1.209	b
S7	1.324	..		1.347	a	1.364	a	1.371	A	1.269	a	1.419	a

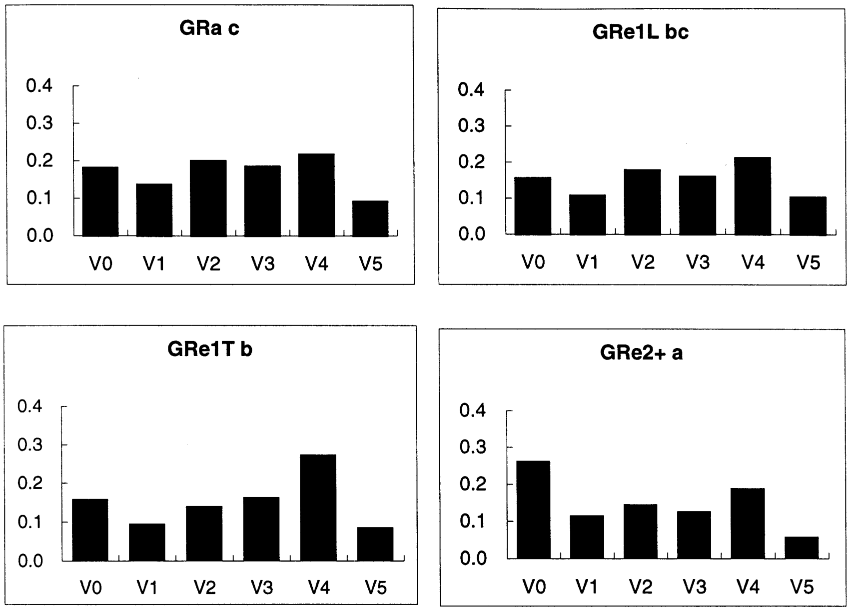

Fig. 7. Distribution of mature *Hylocomium splendens* segments in Norwegian boreal spruce forests, having arisen from four categories of growing points (G-classes), on V-classes. The G-classes are: GRa – by ramification ($n = 10321$); GRe1L – by lateral regeneration after one year's delay ($n = 990$); GRe1T – by terminal regeneration after one year's delay ($n = 443$); GRe2 + – by regeneration after two or more years' delay ($n = 1\ 757$). Proportion of segments in each class is indicated on the vertical axes. Offspring that was lost or grazed before maturity was not included. Distributions sharing a letter are not significantly different at the $p < 0.01$ level (G-test; df = 5).

partly alleviate the negative effects of reduced horizontal mobility, thus explaining why the annual decrease in size from buried ramifying parent segments to their daughter segments and the termination risk do not differ for *Hylocomium splendens* between acrocarp- and pleurocarp-dominated communities. Nevertheless, the results suggest that growth-form is an important determinant of mechanisms of interactions between bryophytes (cf. Tamm 1953, Barkman 1958, Pakarinen and Rinne 1979, Bates 1998).

Interactions between species and species replacements

If, as suggested by R. Økland (1995a), fitness of bryophytes is size dependent also across species, just as species persistence is positively size dependent (R. Økland 1995b), larger-sized species will tend to suppress smaller-sized species by the same amensalism mechanism that causes downward displacement of small *Hylocomium splendens* segments. Smaller species will then be in danger of becoming locally extinct after extended periods where they are unable to keep up with the vertical growth rates of the larger species overtopping them. Reported successional patterns among bryophytes in the forest floor follow this pattern: exposed mineral soil is colonized by hepatics and small acrocarps ["pocket species" of R. Økland and Bendiksen (1985); fugitives and colonists in During's terminology (During 1992)] that emerge from a subterranean diaspore bank (Jonsson 1993, Rydgren and Hestmark 1997). Later on, these may become overtopped by pleurocarps and/or large acrocarps (Foster 1985, van Tooren and During 1988, Jonsson and Esseen 1990, 1998, Lloret 1991, Rydgren et al. 1998a). This pattern corresponds to succession by the tolerance model of Connell and Slatyer (1977): species replacements are driven by more rapid establishment of earlier-successional species rather than by the later-successional species benefitting from changes of site conditions during the initial phase (cf. Rydin 1997).

In the long run, small and slow-growing species will survive only on sites that are unsuitable for the larger species, e.g. on unstable soil, high slopes and/or sites with low incoming radiation (cf. van Tooren and During 1988, R. Økland 1994, 1995a, 1997), and on sites where interactions are frequently interrupted by fine-scale disturbance (e.g. Jonsson and Esseen 1990, van der Hoeven and During 1997a, Rydgren et al. 1998a). Two different processes may therefore give rise to a gradient in species composition in the forest floor from dominance by smaller to dominance by larger species, as described by R. Økland (1994) and T. Økland et al. (unpubl.): species replacing each other in space along a gradient in one or more environmental stress factors, and species replacing each other in time along a successional gradient after disturbance.

Predicting impacts of some ecological processes on bryophyte populations by means of effects on the vertical distribution of shoots

Because of the strong vertical variation in fitness components and the vertical variation in the importance of environmental stress, positive and negative interactions (cf. Fig. 8), effects of important ecological processes on bryophyte populations may be predicted from the changes they cause in the vertical distribution of modules.

Favourable environmental and climatic conditions

In periods with favourable growth conditions, the density of bryophyte carpets increases due to the positive density dependence of size and fitness (R. Økland and T. Økland 1996). In the initial phase, when a closed bryophyte carpet develops by coalescence of patches, the population is expected to benefit from increased importance of facilitation and reduced impact of environmental stress. This study shows that after a continuous bryophyte carpet has developed, further density increase is inevitably followed by increase of the subpopulation that suffers from amensalism and thus acts as a sink for segments, while the subpopulation that benefits from facilitation and thus acts as a source is reduced. By this simple model, density is expected to stabilize when a dynamic balance between source and sink is reached. Furthermore, the density at which this balance is achieved will depend on bryophyte growth rates, as determined by local environmental and climatic conditions.

Periods with density increase due to high growth rates are likely to act as bottlenecks for small individuals, and for species with low maximum size. How often such bottlenecks occur, e.g. in boreal forests under natural conditions, is not known. The synchronous increase or decrease observed for a majority of species in a S Norwegian spruce forest 1988–1993 (R. Økland 1995c, R. Økland and Eilertsen 1996), i.e. that small species also increased in abundance when the abundance of larger species increased, may indicate that such periods are rare and/or of short duration (cf. R. Økland and T. Økland 1996). The frequent occurrence of species-poor stands on the forest floor (R. Økland 1994) suggests that bottleneck events may be important for local species richness patterns even if they are rare, in time as well as in space.

Environmental and climatic stress

Unfavourable climatic (e.g. arid; cf. Potter et al. 1995, R. Økland 1997) or local environmental (e.g. underneath large spruce trees; cf. R. Økland and Eilertsen 1993) conditions (stress sensu Grime 1979) may reduce growth rates and hence mean segment sizes by a mechanism opposite to the one operating under favourable conditions: after an initial decrease in size, further reduction in size and density (total cover) may lead to disintegration of a closed carpet structure and an increase in the subpopulation that suffers from environmental stress due to unfavourable vertical position. In the long run, such populations are at risk of extinction.

Disturbance

Fine-scale disturbance that physically disrupts the bryophyte carpet, e.g. rodent activity (Ericson 1977), instantaneously brings about transition of a smaller or larger fraction of individuals to higher relative vertical levels. In most cases, this causes a regeneration burst and, to a lesser extent, increased ramification (Rydgren et al. 1998b). Small gaps are then rapidly filled by clonal growth (Frego 1996, van der Hoeven and During 1997b, Rydgren et al. 1998b) while larger gaps undergo succession (see above).

Acting as a fine-scale disturbance agent for forest-floor bryophytes (R. Økland 1995a), deciduous litter instantaneously brings about transitions to burial, and, later on, causes emergence of non-buried segments, as the litter is overgrown. Buried and emergent segments are both likely to act as sinks, among others because the size of segments remaining in each of these categories gradually decreases. In sites with extensive litterfall, notably of large-sized deciduous litter resistant to decomposition, bryophyte populations are likely not to maintain positive growth rates over longer periods,

Table 8. Dependence of size of V-classified mature *Hylocomium splendens* segments in Norwegian boreal spruce forests 1992–1997 on origin [G-class; by ramification (GRa) or regeneration (GRe1L – arising by lateral regeneration after one year's delay, GRe1T – arising by terminal regeneration after one year's delay or GRe2+ – regenerating after two or more years' delay)]. Size is given as $\log_2 DW$ units. Entries in the same column sharing a letter are not significantly different at the $p < 0.01$ level (two-tailed, two-sample T-test). The difference between mean size for a V-class and the overall mean size for the GRe-class is compared with the corresponding difference for offspring that arose by ramification by the RVD index (see Terminology, materials and methods). RVD values significantly different from 0 ($p < 0.05$), as tested by two-tailed, one-sample T-tests (and given in bold if larger than expected or italics if smaller than expected), indicate that the regeneration process itself has a specific effect on the size of offspring segments in this V-class. Overall mean sizes were significantly different at the $p < 0.001$ level (two-tailed, two-sample T-test).

Offspring V-class	Mean size of mature offspring segments arising from growing points in G-class			
	GRa ($n = 9634$)	GRe1L ($n = 990$)	GRe1T ($n = 443$)	GRe2+ ($n = 1757$)
V0	4.08 a	3.30 a	2.67 a	2.33 a
V1	4.89 b	4.14 b	3.69 bc	3.06 b
V2	5.15 c	4.85 c	4.01 bcd	3.44 c
V3	5.30 d	**5.12** c	4.51 d	**3.92** d
V4	5.03 bc	**4.74** c	4.10 cd	**3.62** cd
V5	5.00 bc	*3.76* ab	*3.28* ab	*2.94* b
Mean	4.92	4.40	3.79	3.14

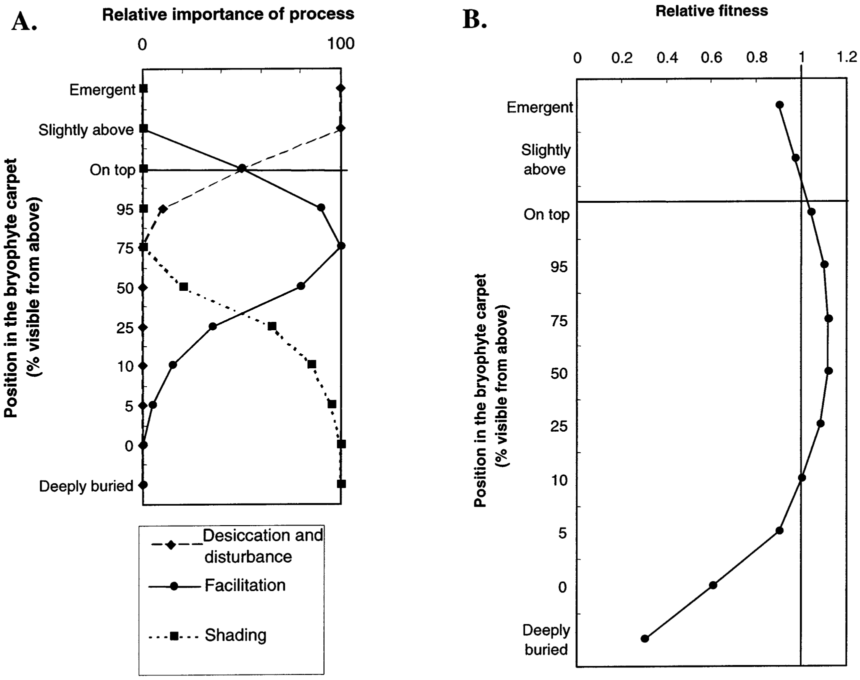

Fig. 8. A conceptual model of vertical variation in the relative importance of main ecological processes for *Hylocomium splendens* in a bryophyte carpet in the boreal forest floor (A). In B, performance is expressed as fitness on a relative scale, indicating the long-term average number of offspring segments produced per segment. Position in the bryophyte carpet is given as percentage of mature segment visible from above. The surface of the bryophyte carpet is indicated in B by solid line.

except perhaps in sites with locally very favourable microclimatic (moisture) conditions and over stones, etc., from which the litter easily blows off (cf. Kujala 1926, Tamm 1953).

Apparent randomness

The results demonstrate that stochastic vertical shifts in the relative positions of growing shoot apices may be one of the strongest causes of unpredictability – "disorderliness" (Fowler 1990), "disorder" (Rydin 1997) or apparent randomness (R. Økland 1990) – in the boreal forest floor. Random events of dispersal into, and emergence from, a diaspore bank (giving rise to "preemptive competition" or "competition for empty space"; Chesson and Case 1986) also add to self-dissimilarity of ecologically similar stands.

Conclusions

The considerable spatiotemporal variation observed in demographic studies of vascular plants (e.g. Nault and Gagnon 1993, Horvitz and Schemske 1995, Oostermeijer et al. 1996, Valverde and Silvertown 1998) as well as in *Hylocomium splendens* (R. Økland 1997) demonstrates that both climatic and local environmental factors are highly important for variation in plant performance at the population level. In this study, I demonstrate strong variation in forest bryophyte carpets also with respect to the performance of individual shoot segments, due to strong vertical gradients in the relative importance of different regulation mechanisms (environmental stress, exposure to fine-scale disturbance, and positive and negative interactions). I suggest this is a fundamental characteristic of bryophyte carpets and predict that the nature and magnitude of effects of climatic and local environmental factors on co-occurring bryophyte shoots will depend on their vertical position in the bryophyte carpet. External factors will then influence bryophyte population growth rates via effects on the vertical distribution of bryophyte shoots. My results also indicate that the growth forms of co-occurring species are important for the nature and outcome of interactions (cf. also Bates 1998), because growth-form affects the vertical dynamics of individual shoots. Experimental studies and long-term monitoring of individual bryophyte shoots in permanent plots are needed for further improving our understanding of interactions in bryophyte carpets.

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References

Angevine, M. W. and Handel, S. N. 1986. Invasion of forest floor space, clonal architecture, and population growth in the perennial herb *Clintonia borealis*. – J. Ecol. 74: 547–560.

Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. – van Gorcum, Assen.

Bates, J. W. 1979. The relationship between physiological vitality and age in shoot segments of *Pleurozium schreberi* (Brid.) Mitt. – J. Bryol. 10: 339–351.

Bates, J. W. 1987. Nutrient retenion by *Pseudoscleropodium purum* and its relation to growth. – J. Bryol. 14: 565–580.

Bates, J. W. 1988. The effect of shoot spacing on the growth and branch development of the moss *Rhytidiadelphus triquetrus*. – New Phytol. 109: 499–504.

Bates, J. W. 1998. Is 'life-form' a useful concept in bryophyte ecology? – Oikos 82: 223–237.

Berthier, J., Larpent, J. P. and Larpent-Gourgaud, M. 1976. Light action on vegetative propagation in bryophytes. – J. Hattori Bot. Lab. 41: 193–203.

Boatman, D. J. 1983. The Silver Flowe national reserve, Galloway, Scotland. – J. Biogeogr. 10: 163–274.

Bopp, M. 1983. Developmental physiology of bryophytes. – In: Schuster, R. M. (ed.), New manual of bryology, Vol. 1. Hattori Botanical Laboratory, Tokyo, pp. 276–324.

Buch, H. 1947. ber die Wasser- und Mineralstoffversorgung der Moose. II. – Soc. Sci. Fenn. Comm. Biol. 20 (16): 1–49.

Burkholder, P. R. 1952. Cooperation and conflict among primitive organisms. – Am. Sci. 40: 601–631.

Busby, J. R., Bliss, L. C. and Hamilton, C. D. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. – Ecol. Monogr. 48: 95–110.

Callaghan, T. V., Collins, N. J. and Callaghan, C. H. 1978. Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. – Oikos 31: 73–88.

Canham, C., Denslow, J. S., Platt, W. J. et al. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. – Can. J. For. Res. 20: 620–631.

Casal, J. J., Deregibus, V. A. and Sanchez, R. A. 1985. Variations in tiller dynamics and morphology in *Lolium multiflorum* Lam. vegetative and reproductive plants as affected by difference in red/far-red irradiation. – Ann. Bot. 56: 553–559.

Chapin, F. S. I., Bloom, A. J., Field, C. B. and Warning, R. H. 1987. Plant responses to multiple environmental factors. – Bioscience 37: 49–57.

Chesson, P. L. and Case, T. J. 1986. Overview: nonequlibrium theories: chance, variability, history, and coexistence. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper & Row, New York, pp. 229–239.

Clymo, R. S. 1973. The growth of *Sphagnum*: some effects of environment. – J. Ecol. 61: 849–870.

Clymo, R. S. and Duckett, J. G. 1986. Regeneration of *Sphagnum*. – New Phytol. 102: 589–614.

Collins, N. J. 1976. Growth and population dynamics of the moss *Polytrichum alpestre* in the maritime Antarctic. – Oikos 27: 389–401.

Connell, J. H. 1990. Apparent versus "real" competition in plants. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, San Diego, CA, pp. 9–26.

Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. – Am. Nat. 111: 1119–1144.

Davey, M. C. and Ellis-Evans, J. C. 1996. The influence of water content on the light climate within Antarctic mosses characterized using an optical microprobe. – J. Bryol. 19: 235–242.

Davy de Virville, A. 1927–28. L'action du milieu sur les mousses. – Rev. Gen. Bot. 39–40: 364–383, 449–457, 515–522, 560–586, 638–662, 711–726, 767–783; 30–44, 95–110, 156–171.

de Kroon, H. and Kwant, R. 1991. Density-dependent growth responses in two clonal herbs. I. Regulation of shoot density. – Oecologia 86: 298–304.

Deregibus, V. A., Sanchez, R. A., Casal, J. J. and Trlica, M. J. 1985. Tillering responses to enrichment of red light beneath the canopy in a humid natural grassland. – J. Appl. Ecol. 22: 199–206.

Dilks, T. J. K. and Proctor, M. C. F. 1974. The pattern of recovery of bryophytes after desiccation. – J. Bryol. 8: 97–115.

During, H. J. 1990. Clonal growth patterns among bryophytes. – In: van Groenendael, J. and de Kroon, H. (eds), Clonal growth in plants: regulation and function. SPB Acad. Publ., The Hague, pp. 153–176.

During, H. J. 1992. Ecological classifications of bryophytes and lichens. – In: Bates, J. W. and Farmer, A. M. (eds), Bryophytes and lichens in a changing environment. Clarendon Press, Oxford, pp. 1–31.

During, H. J. and ter Horst, B. 1987. Diversity and dynamics in bryophyte communities on earth banks in a Dutch forest. – Symp. Biol. Hung. 35: 447–455.

Ericson, L. 1977. The influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. – Wahlenbergia 4: 1–114.

Eriksson, O. 1993. The species-pool hypothesis and plant community diversity. – Oikos 68: 371–374.

Eriksson, O. and Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. – Oecologia 91: 360–364.

Filzer, P. 1933. Experimentelle Beiträge zur Synökologie der Pflanzen. – Jahrb. Wiss. Bot. 79: 9–130.

Foster, D. R. 1985. Vegetation development following fire in *Picea mariana* (black spruce) – *Pleurozium* forests of south-eastern Labrador, Canada. – J. Ecol. 73: 517–534.

Fowler, N. L. 1990. Disorderliness in plant communities: comparisons, causes, and consequences. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, San Diego, CA, pp. 291–306.

Frego, K. 1996. Regeneration of four boreal bryophytes: colonization of experimental gaps by naturally occurring propagules. – Can. J. Bot. 74: 1937–1942.

Frego, K. and Carleton, T. J. 1995a. Microsite tolerance of four bryophytes in a mature black spruce stand: reciprocal transplants. – Bryologist 98: 452–458.

Frego, K. and Carleton, T. J. 1995b. Microsite conditions and spatial pattern in a boreal bryophyte community. – Can. J. Bot. 73: 544–551.

Frisvoll, A. A. 1989. Moseskader i skog i S¢r-Norge. – Nor. Inst. Naturforsk. Oppdragsmeld. 18: 1–41.

Frisvoll, A. A. and Flatberg, K. I. 1990. Moseskader i S¢r-Varanger. – Nor. Inst. Naturforsk. Oppdragsmeld. 55: 1–25.

Gauslaa, Y. and Solhaug, K. A. 1998. The significance of thallus size for the water economy of the cyanobacterial old-forest lichen *Degelia plumbea*. – Oecologia 116: 76–84.

Goldberg, D. E. 1990. Components of resource competition in plant communities. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, San Diego, CA, pp. 27–49.

Grime, J. P. 1979. Plant strategies and vegetation processes. – Wiley, Chichester.

Hancock, J. A. and Brassard, G. R. 1974. Phenology, sporophyte production, and life history of *Buxbaumia aphylla* in Newfoundland, Canada. – Bryologist 77: 501–513.

Harper, J. L. 1985. Modules, branches, and the capture of resources. – In: Jackson, J. B. C., Buss, L. W. and Cook, R. E (eds), Population biology and evolution of clonal organisms. Yale Univ. Press, New Haven, CT, pp. 1–34.

Hayward, P. M. and Clymo, R. S. 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water table depht. – J. Ecol. 71: 845–863.

Hearnshaw, G. F. and Proctor, M. C. F. 1982. The effect of temperature on the survival of dry bryophytes. – New Phytol. 90: 221–228.

Henze, O. 1962. Nestbauweise und Nistmaterial der höhlenbrütenden Kleinvögel. – Angew. Ornithol. 1: 64–73.

Hoddinott, J. and Bain, J. 1979. The influence of simulated canopy light on the growth of six acrocarpus moss species. – Can. J. Bot. 57: 1236–1242.

Hörnberg, G., Ohlson, M. and Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. – Can. J. For. Res. 27: 1015–1023.

Horvitz, C. C. and Schemske, D. W. 1995. Spatiotemporal variation in demographic transitions of a tropical understorey herb: projection matrix analysis. – Ecol. Monogr. 65: 155–192.

Hosokawa, T., Odani, N. and Tagawa, H. 1964. Causality of the distribution of corticolous species in forests with special reference to the physio-ecological approach. – Bryologist 67: 396–411.

Ingelög, T. and Nohrstedt, H. Ö. 1993. Ammonia and soil pH increase caused by decomposing fruitbodies of macrofungi. – Oecologia 93: 449–451.

Jonsson, B. G. 1993. The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. – J. Veg. Sci. 4: 819–826.

Jonsson, B. G. and Esseen, P. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. – J. Ecol. 78: 924–936.

Jonsson, B. G. and Esseen, P. A. 1998. Plant colonization in small forest-floor patches: importance of plant group and disturbance traits. – Ecography 21: 518–526.

Keddy, P. A. and Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. – Oikos 54: 234–241.

Kimmel, U. 1962. Entwicklung einiger Moose und Flechten auf Dauer-Untersuchungsflächen. – Ber. Oberhessischen Ges. Nat.-Heilkd. Giessen. Naturw. Abt. N. F. 32: 151–160.

Knoop, B. 1984. Development in bryophytes. – In: Dyer, A. F. and Duckett, J. G. (eds), The experimental biology of bryophytes. Academic Press, London, pp. 143–176.

Kosiba, P. and Sarosiek, J. 1993. Growth as a function of density in populations of some selected species of mosses. – Crypt. Bot. 3: 103–117.

Kujala, V. 1926. Untersuchungen über die Waldvegetation in Süd- und Mittelfinnland. I. Zur Kenntnis des ökologisch-biologischen Charakters der Waldplanzenarten unter spezieller Berücksichtigung der Bildung von Planzenvereinen. B. Laubmoose. – Commun. Inst. Quaest. For. Finl. 10 (2): 1–59.

Li, Y., Glime, J. M. and Liao, C. 1992. Responses of to interacting *Sphagnum* species to water lavel. – J. Bryol. 17: 59–70.

Lloret, F. 1991. Population dynamics of the coprophilous moss *Tayloria tenuis* in a Pyrenean forest. – Holarct. Ecol. 14: 1–8.

Mägdefrau, K. and Wutz, A. 1951. Die Wasserkapazität der Moose- und Flechtendecke des Waldes. – Forstwiss. Centralbl. 70: 103–117.

Maslov, A. A. 1989. Small-scale patterns of forest plants and environmental heterogeneity. – Vegetatio 84: 1–7.

Mithen, R., Harper, J. L. and Weiner, J. 1984. Growth form and mortality of individual plants as a function of'available area'. – Oecologia 62: 57–60.

Myrmæl, A. 1993. Regeneration studies of five spruce, *Picea abies*, forest bryophytes. – Lindbergia 18: 7–18.

Nault, A. and Gagnon, D. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. – J. Ecol. 81: 101–119.

Noble, M. G., Lawrence, D. B. and Streveler, G. P. 1984. *Sphagnum* invasion beneath an evergreen canopy in southeastern Alaska. – Bryologist 87: 119–127.

Nykvist, N. 1997. Changes in species occurrence and phytomass after clearfelling, prescribed burning and slash removal in two Swedish spruce forests. – Stud. For. Suec. 201: 1–33.

Oechel, W. C. and van Cleve, K. 1986. The role of bryophytes in nutrient cycling in the taiga. – Ecol. Stud. 57: 121–137.

Økland, R. H. 1990. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. – Sommerfeltia Suppl. 1: 1–233.

Økland, R. H. 1994. Patterns of bryophyte associations at different scales in a Norwegian boreal spruce forest. – J. Veg. Sci. 5: 127–138.

Økland, R. H. 1995a. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. I. Demography. – J. Ecol. 83: 697–712.

Økland, R. H. 1995b. [1994]. Bryophyte and lichen persistence patterns in a Norwegian boreal coniferous forest. – Lindbergia 19: 50–62.

Økland, R. H. 1995c. Changes in the occurrence and abundance of plant species in a Norwegian boreal coniferous forest, 1988–1993. – Nord. J. Bot. 15: 415–438.

Økland, R. H. 1997. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. III. Six-year demographic variation in two areas. – Lindbergia 22: 49–68.

Økland, R. H. and Bendiksen, E. 1985. The vegetation of the forest-alpine transition in the Grunningsdalen area, Telemark, SE Norway. – Sommerfeltia 2: 1–224.

Økland, R. H. and Eilertsen, O. 1993. Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. – Sommerfeltia 16: 1–254.

Økland, R. H. and Eilertsen, O. 1996. Dynamics of understory vegetation in an old-growth boreal coniferous forest, 1988–1993. – J. Veg. Sci. 7: 747–762.

Økland, R. H. and Økland, T. 1996. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. II. Effects of density. – J. Ecol. 84: 63–69.

Økland, R. H., Steinnes, E. and Økland, T. 1997. Element concentrations in the boreal forest moss, *Hylocomium splendens*: variation due to segment size, branching patterns and pigmentation. – J. Bryol. 19: 671–684.

Økland, T. 1996. Vegetation-environment relationships of boreal spruce forest in ten monitoring reference areas in Norway. – Sommerfeltia 22: 1–349.

Økland, T., Økland, R. H. and Steinnes, E. 1999. Element concentrations in the boreal forest moss *Hylocomium splendens*: variation related to gradients in vegetation and local environmental factors. – Plant Soil 209: 71–83.

Oostermeijer, J. G. B., Brugman, M. L., de Boer, E. R. and den Nijs, H. C. M. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. – J. Ecol. 84: 153–166.

Pakarinen, P. and Rinne, R. J. K. 1979. Growth rates and heavy metal concentrations of five moss species in paludified spruce forests. – Lindbergia 5: 77–83.

Paré, D., Bergeron, Y. and Camiré, C. 1993. Changes in the forest floor of boreal forest after disturbance. – J. Veg. Sci. 4: 811–818.

Pastor, J., Gardner, R. H., Dale, V. H. and Post, W. M. 1987. Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North America. – Can. J. For. Res. 17: 1394–1400.

Perttula, U. 1941. Untersuchungen über die generative und vegetative Vermehrung der Blütenpflanzen in der Wald-, Hainwiesen- und Hainfelsenvegetation. – Ann. Acad. Sci. Fenn. Ser. A 558 (1): 1–388.

Potter, J. A., Press, M. C., Callaghan, T. V. and Lee, J. A. 1995. Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-arctic. – New Phytol. 131: 533–541.

Proctor, M. C. F. 1980. Estimates from hemispherical photographs of the radiation climates of some bryophytes habitats in the British isles. – J. Bryol. 11: 351–366.

Romell, L. G. 1922. Luftväxlingen i marken som ekologisk faktor [Deutsches Res.: Die Bodenventilation als ökologischer Faktor]. – Medd. Statens Skogsförs. Anst. 19: 125–359.

Rydgren, K. and Hestmark, G. 1997. The soil propagule bank in a boreal old-growth spruce forest: changes with depth and relationship to aboveground vegetation. – Can. J. Bot. 75: 121–128.

Rydgren, K., Hestmark, G. and Økland, R. H. 1998a. Revegetation following experimental disturbance in a boreal old-growth *Picea abies* forest. – J. Veg. Sci. 9: 763–776.

Rydgren, K., Økland, R. H. and Økland, T. 1998b. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. IV. Effects of experimental fine-scale disturbance. – Oikos 82: 5–19.

Rydin, H. 1995. Effects of density and water level on recruitment, mortality and shoot size in *Sphagnum* populations. – J. Bryol. 18: 439–453.

Rydin, H. 1997. Competition among bryophytes. – Adv. Bryol. 6: 135–168.

Sarvas, R. 1938. [1937]. Kuloalojen luontaisesta metsittymisestä. Pohjois-Suomen kuivilla lankailla suoritettu metsäbiologinen tutkielma [Deutsches Ref.: Über die natürliche Bewaldung der Brandflächen. Eine waldbiologische Untersuchung auf den trockenen Heideböden Nord-Finnlands]. – Acta For. Fenn. 46: 1–147.

Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. – Acta For. Fenn. 62: 1–408.

Skre, O. and Oechel, W. C. 1981. Moss functioning in different taiga ecosystems in interior Alaska. I. Seasonal, phenotypic, and drought effects on photosynthesis and response patterns. – Oecologia 48: 50–59.

Skre, O., Oechel, W. C. and Miller, P. M. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. – Can. J. For. Res. 13: 860–868.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry, 3rd ed. – Freeman, New York.

Solangaarachchi, S. M. and Harper, J. L. 1987. The effect of canopy filtered light on the growth of white clover *Trifolium repens*. – Oecologia 72: 372–376.

Sonesson, M., Gehrke, C. and Tjus, M. 1992. CO_2 environment, microclimate and photosynthetic characteristics of the moss *Hylocomium splendens* in a subarctic habitat. – Oecologia 92: 23–29.

Stålfelt, M. G. 1937. Die bedeutung der Vegetation im Wasserhaushalt des Bodens. – Sven. Skogsvårdsfören. Tidskr. 35: 161–195.

Tamm, C. O. 1953. Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). – Medd. Statens Skogsforskningsinst. 43 (1): 1–140.

Vallin, H. 1974. Vegetation changes in a moss cushion during 50 years. – Sven. Bot. Tidskr. 68: 169–191.

Valverde, T. and Silvertown, J. 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. – J. Ecol. 86: 545–562.

van Cleve, K., Oliver, L., Schlentner, R. et al. 1983. Productivity and nutrient cycling in taiga forest ecosystems. – Can. J. For. Res. 13: 747–766.

van der Hoeven, E. C. 1999. Reciprocal transplantations of three chalk grassland bryophytes in the field. – Lindbergia (in press).

van der Hoeven and During, H. J. 1997a. Positive and negative interactions in bryophyte populations. – In: de Kroon, H. and van Groenendael, J. (eds), The ecology and evolution of clonal plants. Backhuys, Leiden, pp. 291–310.

van der Hoeven and During, H. J. 1997b. The effects of density on size frequency distributions in chalk grassland bryophyte populations. – Oikos 80: 533–539.

van der Hoeven, Huynen, C. I. J. and During, H. J. 1993. Vertical profiles of biomass, light intercepting area and light intensity in chalk grassland mosses. – J. Hattori Bot. Lab. 74: 261–270.

van Tooren, B. F. and During, H. J. 1988. Early succession of bryophyte communities on dutch forest earth banks. – Lindbergia 14: 40–46.

Watson, E. V. 1960. Further observations on the bryophyte flora of the Isle of May. II. Rate of succession in selected communities involving bryophytes. – Trans. Proc. Bot. Soc. Edinb. 39: 85–106.