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Microclimatic buffering by logging residues and forest edges reduces clear-cutting impacts on forest bryophytes

Dynesius, Mats* ; Åström, Marcus & Nilsson, Christer

Landscape Ecology Group, Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden;

*Corresponding author; E-mail mats.dynesius@emg.umu.se

Abstract

Question: The practice of extracting logging residues after clear-cutting for bioenergy purposes is spreading. Logging residues constitute a shelter in clear-cut areas and therefore concerns have been expressed that their removal could make the ground and its vegetation more exposed to extreme microclimatic conditions. We asked whether logging residues and forest edges can protect ground-dwelling forest bryophytes from fatal microclimate events following clear-cutting.

Location: Boreal forests of central Sweden.

Methods: Using transplants of eight forest floor bryophyte species we experimentally analysed the sheltering effect (less solar radiation and less wind) of logging residues and forest edges in seven clear-cut areas. Transplants were placed in two contrasting positions in each area; near a north-facing forest edge and in the centre of the clear-cut area. In each position, half of the transplants were covered by a layer of spruce branches and the other half was left uncovered. We estimated proportion of apparently living shoots (apparent vitality) and measured radial growth of transplants during one growing season.

Results: Position in the clear-cut area, but not cover of spruce branches, clearly influenced radial growth. Vitality scores were higher among transplants covered with branches and the lowest apparent vitality was observed in uncovered transplants in the middle of clear-cut areas. The change in area of apparently living shoots during the course of the experiment (growth minus mortality) was unaffected by branch cover close to the edge but positively affected in the centre of the clear-cut area. In general, the effect of branch cover on bryophytes was higher in the centre of clear-cut areas. Here, climatic measurements showed that branch cover buffers during periods of extreme microclimates.

Conclusions: Extraction of logging residues after clear-felling may reduce the survival of some ground-dwelling forest organisms. The additional sheltering provided by branches was unimportant close to forest edges. We suggest smaller clear-cut areas, green-tree retention and other ways to make logged areas shadier and less windy to mitigate the reduced shelter caused by harvest of logging residues.

Keywords: Disturbance; Edge effect; Habitat quality; Liverwort; Logging residue; *Picea abies*; Slash.

Nomenclature: Hallingbäck et al. (2006) for bryophytes and Krok & Almqvist (1994) for vascular plants.

Introduction

The ground is warmer during daytime and colder at night in a clear-cut area compared to a forest (Keenan & Kimmins 1993) and clear-cut areas generally experience higher wind velocity close to the ground (Chen et al. 1993). These factors affect physical and physiological processes that, in turn, influence species persistence and colonization. Forest mosses and liverworts (bryophytes) and other organisms that can neither seek shelter nor effectively control water uptake or loss are particularly vulnerable to the microclimatic changes caused by clear-cutting (Hylander et al. 2005). For bryophytes, microclimate is a key factor for growth, mortality and reproduction (Økland 1997; Rydgren & Økland 2002). Under a closed canopy, air moisture close to the ground may be high, fed by evapotranspiration from the ground and the understorey vegetation. The increased daytime temperature at ground level after canopy removal lowers air moisture, which is further depressed by increased wind speeds. The resulting longer periods in a dehydrated state may reduce bryophyte growth and increase shoot mortality, although lower night temperatures may reduce losses through respiration.

Forest bryophytes may persist in clear-cut areas in sheltered positions where the microclimate is more similar to pre-harvest conditions. For example, northern slope aspect or remnant canopies moderate the microclimate and its negative effects on forest bryophytes (Fenton & Frego 2005; Hylander et al. 2005; Heithecker & Halpern 2006; Åström et al. 2007). Shading by shrubs, logs and stumps improve survival and growth of plants typical of shady habitats in otherwise exposed settings (Busby et al. 1978; Minore 1986; Gray & Spies 1997).

Post-harvest extraction of logging residues (e.g. tree-tops, branches and twigs) is increasing to meet the rising demand for renewable energy (Proe et al. 1994; Doherty et al. 2002). This practice reduces shelter and heterogeneity following clear-cutting (Gunnarsson et al. 2004; Åström et al. 2005) and adversely affects many forest bryophytes (especially liverworts), whereas occasional

moss species in acrocarpous ground-living genera such as *Dicranum* and *Polytrichum* may increase (Nykqvist 1997; Åström et al. 2005). Several studies suggest that logging residues shelter forest plants (Olsson & Staaf 1995; Bråkenhielm & Liu 1998; Åström et al. 2005), but this has not been tested in controlled manipulative experiments and the spatial variation of the sheltering effect within a clear-cut area has not been established.

This experiment was designed to test if logging residues buffer microclimate and thereby promote survival and growth of forest floor bryophytes when *Picea abies* stands are clear-felled and if this effect varies with proximity to north-facing forest edges. North-facing edges provide shade during the mid-day peak of solar radiation but also shelter from wind. We expected that cover by spruce branches would improve growth and vitality of forest bryophytes by buffering radiation and temperature and that this effect would be smaller close to forest edges.

Methods

Study area

Our study was conducted in the middle boreal zone (Ahti et al. 1968) in the southernmost part of the province of Ångermanland in central Sweden between 62°50' and 63°05' N. The growing season is ca. 150 days; mean monthly temperatures for May, June, July, August and September are 7, 13, 15, 14 and 9 °C, respectively. Mean monthly precipitation for these months are 35, 40, 60, 70 and 70 mm, respectively (Raab & Vedin 1995). Compared to the mean monthly temperatures, June 2003 (the year of the experiment) was 1 °C colder, July 4 °C warmer and August and September 1 °C warmer. The precipitation in June, July, August and September 2003 was 6 mm above, 43 mm below, 68 mm above and 34 mm below means, respectively. Weather data for 2003 are from Lännäs weather station (temperature) and from Lännäs and Kramfors weather stations (precipitation) located 21 km and 13 km, respectively, from the midpoint of the study area (courtesy of Swedish Meteorological and Hydrological Institute). The coniferous forests in the area have been intensively managed for wood production for the last 150 years. Selective cuttings totally dominated the early management, but clear-cutting has been the main mode of timber harvest for the last 50–60 years (Wastenson & Nilsson 1995).

Bryophyte species

We selected six pleurocarpous mosses and two leafy liverworts that are common components in the understorey in mesic–moist *Picea abies* forests in the study

area. We excluded vertically growing species (acrocarps) for methodological reasons. The species were chosen to represent a range of tolerance to open habitats. The mosses *Hylocomium splendens*, *Pleurozium schreberi* and *Rhytidiadelphus triquetrus* are assumed to be the least moisture demanding of the eight species and *Hylocomiastrum umbratum*, *Ptilium crista-castrensis* and the liverwort *Plagiochila asplenoides* are considered to be the most shade-tolerant (Ellenberg et al. 1992). The liverwort *Barbilophozia lycopodioides* and the moss *Rhytidiadelphus subpinnatus* are considered to be more moisture demanding than the first group of species and less shade-tolerant than the second group (Ellenberg et al. 1992). Another selection criterion was that the species should frequently grow in more or less mono-specific patches to facilitate the collection of transplants.

H. umbratum is encountered in shady and humid habitats and is relatively sensitive to edge effects (Hylander 2005). In the southern and middle parts of Sweden (including the study area) its presence is considered to indicate long forest continuity and constantly high air moisture (Nitare 2000). *H. splendens* is abundant and often dominates mesic ground. It is highly resilient to herbivory and small-scale disturbance (Økland 1995; Rydgren et al. 2001). *P. schreberi* is abundant in dry to mesic forests, but may also grow in relatively open habitats. *R. subpinnatus* occurs mostly in humid *Picea* forests and is considered indicative of species-rich habitats with high conservation value, particularly in the southern and middle parts of Sweden (Nitare 2000); whereas *R. triquetrus* is primarily encountered in drier microhabitats in herb-rich communities. *P. asplenoides* is restricted to shady and moist habitats, whereas *B. lycopodioides* may grow there but also occurs in exposed sites (Damsholt 2002).

Monospecific mats of each species were collected from the forest floor of mature forests within the study area to be used as transplants. Loose substrate attached to bryophytes was removed together with the mats, but the soil was not dug up. All species grew on litter and humus on the ground. When target species occurred near the clear-cut areas we collected transplants immediately before transplantation. In other cases we collected transplants in advance and stored them for a few days in a shady and moist *Picea* swamp forest until transplantation.

Experimental setup

We used a database provided by the forest company SCA to select seven recently clear-cut *Picea*-dominated stands with an adjacent north-facing forest edge that was at least 15 m high and 30 m wide. In each clear-cut area we located two sites with similar vegetation and soil

moisture conditions. One site was positioned close to the north-facing edge (ca. 10 m from the edge) and the other in the centre of the clear-cut area (ca. 50-300 m from the north-facing edge, depending on the size of the clear-cut area). In each site we established two 0.7 m × 2.1 m experimental plots. We removed vegetation, roots and stones in the plots and mixed, levelled and gently compacted the soil to minimize internal heterogeneity. In each of the four plots we placed three circular transplants of each species at least 0.1 m from the plot periphery and 0.1 m apart. We ensured that the transplants were in close contact with the ground by planting them into shallow depressions, which were filled with water immediately before transplantation. The position of each transplant was randomly selected. Transplants varied in size (21-83 cm²) depending on species but we kept the 12 transplants of each species similar with respect to size and appearance within each site. Each transplant was equipped with three vertically inserted plastic pins as reference points. In transit, as well as during and directly after planting, the transplants were sprayed with water.

After transplantation we randomly selected and covered one of the two plots in each position with branches that we collected from living spruces and placed on a 0.7 m × 2.1 m wooden frame elevated 0.1 m above the plot surface. The frame enabled temporary removal of the branches during collection of bryophyte response data with minimal disturbance (needle loss etc.). The branches were placed in a single layer, with primary branches 15 cm apart but with over-lapping secondary branches. The branches, twigs and needles covered ca. 95% of the plot. In each clear-cut area all transplants and branches were put in place within a day. Altogether we planted 672 bryophyte transplants (7 clear-cut areas × 4 treatments × 8 species × 3 replicates) between May 29 and June 5, 2003. By the end of the growing season (September 15-20), 105-114 days after transplantation the experiment was terminated because transplants would have been disturbed (compressed) by snow making relevant further measurements impossible. On two occasions we removed colonizing vegetation within the plots. At the end of the experiment no transplants had grown to merge with adjacent transplants.

Simultaneously to our study, an experiment on wood-ash recycling was conducted, using the same transplantation method and the same species in seven nearby spruce stands (M. Dynesius, unpubl. data). The control plots of this experiment were analysed by us in a similar fashion as the clear-cut plots but they are not formally used as forest control plots, because the number of replicates was small. However, the data are presented in the Discussion and in App. 2 to give a general picture of growth conditions for this particular year and in closed forests compared to clear-cut areas.

Habitat properties

Clear-cutting was carried out 2-8 years before the experiment and the sites were located 151-239 m above sea level. Soil type was either a sandy-loamy till (six areas) or loamy sediment (one area). Vegetation type (according to Hägglund & Lundmark 1987) was either herb type (six areas) or broad-leaved grass type (one area). Site productivity ranged between 5.2-5.7 m³sk per ha and year, i.e. trunk volume above stump height potentially produced per ha and year, including the bark (data from SCA).

In the field we measured tree height and basal area of north-facing edges using a Suunto Clinometer and a relascope, respectively. Mean tree height ranged 15-23 m among sites. Mean basal area of *Picea*, *Pinus* and broad-leaved trees were 19, 3 and 5 m²/ha, respectively and basal area of all trees ranged between 21-33 m²/ha. Distances between plots and edges were determined using a measuring-tape or a laser range finder. The plots at the edges were located 10 m (range 7-13 m) from north-facing edges. Plots in the centre of clear-cut areas were located 113 m (range 49-280 m) from north-facing and 96 m (range 39-310 m) from south-facing edges.

Light intensity (W/m²) was measured at the plot surface at six random points and the plot mean was used for analysis. This measurement was done once in each stand 0-22 days (June) after transplantation during clear days and all readings were taken within a 30 min time span close to noon. Maximum daytime temperature (°C) inside the most central transplant of *H. umbratum* was automatically recorded between 0900 hrs and 1800 hrs simultaneously in all four plots in a site using pre-calibrated digital thermometers with 4 mm × 11 mm steel probes. This was done on clear days once in each stand 8 to 22 days after transplantation. Soil water content (% of volume) was measured using a TDR (Time Domain Reflectometer) on September 8 at ten systematically selected points in each plot and the mean was used as one observation in the analyses.

Bryophyte growth and vitality

We developed a rapid and simple field method to obtain non-destructive assessments of bryophyte growth. Directly after transplantation we drew the outline of the periphery of the vertical projection of each transplant and the position of the reference pins on a plastic film placed on a Plexiglas board situated 6 cm above the plot surface. At the end of the experiment we used the same plastic film and reference pins to draw a new peripheral projection and outlined patches of dead tissue. It was clearly observed from morphology that the expansion was a result of bryophyte growth and did not depend

on flattening of the transplant. By using peripheral projections and circle-approximation we calculated the initial and final mean radii of each transplant using the formula: $radius = \sqrt{area / \pi}$. Area which included both dead and living tissue was calculated using the software UTHSCSA Image Tool 3.0 (Wilcox et al. 1995-2002). Radial growth (mm) was expressed as change in radius rather than change in area to avoid variation in growth caused by variations in initial size of the transplants.

We estimated vitality of each transplant in June (23-29 days after transplantation) and in September when the experiment was ended. Vitality was rated in seven classes according to the appearance of the transplant. Only brown and yellow tissue was considered dead. This may underestimate mortality somewhat in some species making the measure of change conservative. The classes were: (1) entire transplant dead; (2) occasional leaves alive; (3) occasional shoots alive; (4) $< 1/2$ transplant alive; (5) $> 1/2$ transplant alive; (6) occasional shoots dead; (7) the whole transplant alive (adapted from Hylander et al. 2002). At the start of the experiment all transplants were considered fully vital (7). As a measure of the net change in area of living bryophyte (growth minus mortality) of each species we measured the area (using UTHSCSA Image Tool 3.0) of apparently living green bryophyte tissue at the start and at the end of the experiment and calculated the difference. Before assessing vitality and before drawing vertical projections the transplants were hydrated by spraying water to create similar conditions in all transplants and on all three occasions.

Statistical analyses

Normality and homogeneity of variances were tested using the Kolmogorov-Smirnov's and Levene's test, respectively. Radial growth of each species was analysed using two-way ANOVAs where branch cover (covered vs not covered) and position (edge vs centre) were considered fixed factors. One-way ANOVAs and *post-hoc* Tukey tests were used to locate differences among treatments in radial growth as well as net change in area of apparently living shoots for each species. For *Plagiochila asplenoides*, we used square root transformed radial growth data in all analyses to meet assumptions of homoscedasticity and normality.

One-way ANOVAs and *post-hoc* tests were also applied to locate differences among treatments in plot temperature (Tukey test), soil water content (Tukey test) and radiation. Radiation data were log-transformed to meet assumptions of normality but since homoscedasticity could not be achieved we used Dunnett's *C post-hoc* test. Reductions in radiation input and temperature caused by branch cover (i.e. pair-wise comparisons between covered and uncovered plots) were compared between

plots at edges and in centres of clear-cut areas using the non-parametric Mann-Whitney *U*-test due to non-normality of the distribution of the reductions.

Pearson correlations were used to analyse the relationships between radiation, temperature and pooled growth of all species (mean of all transplants within a plot) and to investigate the relationship between soil water content and the pooled growth in each of the four treatments. In analyses including apparent vitality we used non-parametric methods as the data were categorical on an ordinal scale. We applied the Kruskal-Wallis *H*-test to analyse differences in final vitality of each species among treatments. The Wilcoxon's signed rank test was used to analyse reductions in apparent vitality four and 15 weeks after transplantation. Spearman rank correlation was used to investigate the relationship between radiation, temperature and pooled apparent vitality.

In analyses of individual species we used plot mean values (from three transplants) as input data (apparent vitality, change in area of apparently living shoots and radial growth). Due to animal (mainly moose) disturbance 5% of the transplants were excluded. In such cases we instead used the means of the remaining undisturbed transplants in the plot. Since disturbance was sporadic and evenly distributed between plots and stands we obtained data for all species and plots, i.e. $N = 7$ throughout the study. SPSS for Windows Version 13.0.1 was used for all statistical analyses (Anon. 1989-2004).

Results

Across all treatments, light intensity at noon and maximum daily temperature were positively correlated (Pearson's $r = 0.71$, $P < 0.0001$, $n = 28$) and differed among the four types of plots (One-way ANOVA: $P < 0.0001$, $df = 3$ for both variables). Both branch cover and proximity to forest edge reduced light intensity. Uncovered plots in the centre of the clear-cut area received ca. 20 times more radiation at noon than branch-covered plots at the edge (Fig. 1A). Branch cover reduced light intensity more in central parts of clear-cut areas than close to edges (mean reduction 648 vs. 242 W/m²; Mann-Whitney *U*-test: $P = 0.002$, $n = 7$; Fig. 1A), but reduced maximum daily temperature in transplants to a similar extent (ca. 10 °C) in both positions (Mann-Whitney *U*-test: $P = 0.902$, $n = 7$; Fig. 1B). Position close to the edge reduced maximum temperature by 5 °C regardless of branch-cover (Fig. 1B). There were no differences in soil water content among treatments (One-way ANOVA: $P = 0.893$, $df = 3$; Fig. 1C).

Across all treatments, radial growth decreased with increasing light intensity and maximum temperature (all species pooled; Pearson's $r = -0.40$, $P = 0.035$, $n = 28$;

Fig. 1. Light intensity at noon (radiation), maximum daily temperature and soil water content in the four types of plots. Treatment refers to position (close to a forest edge vs in the centre of a clear-cut area) and branch cover (uncovered vs covered with *Picea* branches). Differences were analysed with one-way ANOVA ($df = 3$) and the *post-hoc* tests Dunnett's C (radiation, $n = 7$ for all treatments) or Tukey (temperature and moisture, $n = 7$ for all treatments). For tests involving radiation log transformed data were used. ANOVAs for radiation and maximum temperature were significant ($P < 0.00001$), whereas the ANOVA for soil moisture was not ($P = 0.893$). Different letters denote significant ($P < 0.005$) differences between treatments according to *post-hoc* tests. Data are means ± 1 SE.

and $r = -0.48$, $P = 0.009$, $n = 28$, respectively). In the uncovered plots at the edge, growth increased with soil water content (all species pooled: Pearson's $r = 0.82$, $P = 0.024$, $n = 7$) but there were no such relationships in the remaining three treatments (Pearson's $r < 0.46$, $P > 0.136$, $n = 7$). Plot position in the clear-cut area significantly influenced growth of all species (App. 1) and growth was higher in edge plots (Fig. 2). Only *P. asplenioides* was significantly influenced by branch cover (App. 1) and it tended to grow better in covered plots irrespective of position in the clear-cut area (Fig. 2). Branch cover tended to reduce growth at edges but increase it in central parts of clear-cut areas for all the seven other species (Fig. 2).

For six species apparent vitality was significantly reduced in the uncovered plots in the middle of the clear-cut areas by four weeks after transplantation (Fig. 3d). There were large differences in vitality change among treatments and species. Across all treatments and at the end of the experiment, the vitality of all species pooled was negatively

Fig. 2. Radial growth (mm) during the course of the experiment (15 weeks). Treatments refer to position (close to a north-facing forest edge vs in the centre of a clear-cut area) and branch cover (uncovered vs covered with *Picea* branches). (M) and (L) denote mosses and liverworts. Differences were tested with one-way ANOVA ($df = 3$) and the Tukey test ($n = 7$ for all treatments). For *P. asplenioides* square root transformed data were used in the analyses. All ANOVAs were statistically significant ($P = 0.00002$ – 0.044). Different letters denote significant ($P < 0.05$) differences between treatments according to Tukey tests. Data are means ± 1 SE.

correlated with light intensity (Spearman rank correlation: $r = -0.78$, $P < 0.0001$, $n = 28$) and temperature ($r = -0.74$, $P < 0.0001$, $n = 28$). All individual species differed in apparent vitality among the four treatments (Kruskal-Wallis test: $P < 0.004$, $df = 3$; Fig. 3). Species located in plots covered by *Picea* branches at the edge appeared unaffected (Fig. 3a) and all eight species increased in area of apparently living shoots (Fig. 4). Although transplants in uncovered plots at edges and in plots covered by *Picea* branches in the central parts of clear-cut areas showed lower apparent vitalities, all species except *P. asplenioides* increased in areas of apparently living shoots (Fig. 4). In contrast, all species located in uncovered plots in central parts of clear-cut areas had deteriorated (Fig. 3). Here, the area of apparently living shoots was reduced for all species except *P. schreberi* and the response typically differed significantly from the other treatments, particularly in relation to edge plots (Fig. 4). The change in area

Fig. 3. Reduction in apparent vitality of transplants 4 (open bars) and 15 (shaded bars) weeks after transplantation in (a) branch-covered edge; (b) uncovered edge; (c) branch-covered centre and (d) uncovered centre. Differences in relation to initial apparent vitality (7) were tested using the Wilcoxon's signed rank test (* denote significant changes, $P < 0.05$). Vitality ratings are (1) entire transplant dead; (2) occasional leaves alive; (3) occasional shoots alive; (4) $< 1/2$ transplant alive; (5) $> 1/2$ transplant alive; (6) only occasional shoots negatively affected; and (7) the entire transplant alive and fresh. $n = 7$ for all treatments. Data are means ± 1 SE.

Fig. 4. Change in area of apparently living shoots (growth minus apparent mortality) of the eight bryophyte species during the course of the experiment (15 weeks). Treatment refers to position (close to a north-facing forest edge vs in the centre of the clear-cut area) and branch cover (plots covered with *Picea* branches vs uncovered). (M) and (L) denote mosses and liverworts. Differences were tested with one-way ANOVA ($df = 3$) and the Tukey test ($n = 7$ for all treatments). All ANOVAs were significant ($P = 0.00001 - 0.018$). Different letters denote significant differences between treatments according to Tukey tests. Data are means ± 1 SE.

of apparently living shoots in the other three treatments was generally similar although the increase tended to be smaller in the branch-covered plots in the centres of the clear-cut areas (Fig. 4).

Discussion

Position close to a north-facing forest edge enhanced growth and apparent vitality of ground-living forest bryophytes after clear-cutting. For some species, cover by *Picea* branches also increased vitality (Fig. 3) and net growth (Fig. 4) in the centre of clear-cut areas whereas the effect was smaller close to forest edges. The most probable explanation for this is that position and cover modified the microclimate (Fig. 1A, B) in turn affecting bryophyte growth and shoot mortality. It is well known that there are steep microclimatic gradients through forest edges (Chen et al. 1993) and adjacent north-facing forest edges and that microstructures such as logs and stumps moderate the radiation balance in clear-cuts (Keenan & Kimmins 1993; Burton 2002). Our results also corroborate the observation that extraction of logging residues after clear-cutting causes more extreme temperature shifts and higher daytime surface temperatures in clear-cut areas (Mahendrapa & Kingston 1994; Proe et al. 1994, 2001). Microstructures such as stumps and branches also reduce wind velocities (Proe et al. 1994, 2001), and wind speeds were certainly lower in plots covered by *Picea* branches (M. Åström, pers. obs.). High wind velocities, particularly in combination with low air humidity, increase transpiration rates, the risk of water stress (Van Gardingen & Grace 1991) and hence influence growth and vitality of bryophytes. However, as buffering effects of logging residues on wind are more important at high than at low wind velocities (Proe et al. 2001), this effect was probably more important in the centre than at the edge where wind speeds generally are lower (Chen et al. 1993).

Bryophyte growth

Wind and temperature affect ambient moisture conditions (Chen et al. 1993). Bryophytes are only metabolically active when wet and, therefore, dehydration during day-time negatively influences growth rates (Busby et al. 1978; Proctor 1990; Vitt 1990). The negative correlation between radiation and radial growth, the generally higher growth at the edges (Fig. 2) and the effect of branch cover on *P. asplenoides* (App. 1) show that edges and logging residues affect growth conditions. Branch cover had no significant effect on growth of other species but the tendency was always towards a negative effect at the edge but a positive effect in the centre of the clear-cut

area (Fig. 2). This interaction was nearly significant for several species (App. 1) and may at least partly explain the lack of significant effect of branch cover for most species.

Although litter input may affect bryophyte growth in both directions (Busby et al. 1978; Frego & Carleton 1995), the main effect of *Picea* branch cover, in our case, probably relates to light and moisture conditions. At the edge, the slightly lower growth in branch covered plots suggests that the cumulative effect of shading by adjacent trees and by *Picea* branches produced suboptimal growth conditions (Sveinbjörnsson & Oechel 1992) and light saturation was probably seldom reached. At the edge, evaporative stress was also low in the uncovered plots. In central parts of clear-cut areas, however, shading by *Picea* branches reduced evaporative stress while radiation was still high enough to support bryophyte growth.

Bryophyte vitality

Bryophyte vitality may be rapidly affected by reduced shelter (Busby et al. 1978; Hylander et al. 2002). We also found significant reductions in apparent vitality for most species by four weeks after initial exposure (Fig. 3). Many forest bryophyte species are sensitive to high light intensities, high temperatures, extensive droughts and fluctuating microclimates (Proctor 1990; Marschall & Proctor 2004). For example, temperatures exceeding 30 °C may be lethal to bryophyte tissue (Furness & Grime 1982) and the fact that such temperatures were frequently recorded in the uncovered plots helps explain the generally higher apparent vitality in branch covered plots (Fig. 3).

Drought sensitivity and temperature optima vary considerably among bryophyte species (Furness & Grime 1982). In our case the two liverworts (*B. lycopodioides* and *P. asplenoides*) were among the three species showing lowest apparent vitality in the uncovered plots in the centre of the clear-cut areas (Fig. 3d). This is not surprising since most liverworts are more sensitive to exposure than are most mosses (Marschall & Proctor 2004), although there is large variation in tolerance within groups. For example, the relatively closely related *H. splendens* and *H. umbratum* differ considerably in tolerance (Hylander 2005; Fig. 3d).

Net change in area of apparently living shoots

It may seem contradictory that most species had slightly higher growth in uncovered than in covered plots at the edge (Fig. 2) although their apparent vitality was generally lower (Fig. 3). However, irrespective of treatment, shoot mortality mostly occurred in the transplant centre, probably because these shoots had less

ground contact and, thus, were more often dehydrated (M. Åström pers. obs.). Økland (2000) also found high mortality in projecting shoots of *H. splendens*. Shoots located in the periphery of the transplant were less damaged and these peripheral shoots produced the radial growth. The general increase in area of apparently living shoots of transplants sheltered by *Picea* branches or adjacent trees (Fig. 4) indicates that these species may survive and increase their cover in these settings, although they may be initially damaged by the abrupt change in microclimate.

Soil moisture

Bryophyte responses to clear-cutting are also influenced by environmental factors other than sheltering structures. For example, ground moisture may stimulate bryophyte growth (Hylander et al. 2002). However, mean soil moisture did not differ between treatments (Fig. 1C). In uncovered plots at the edge (where growth was highest for most species; Fig. 2) growth increased with soil water content. No such relationship was found in the other three treatments probably because lack of light (edge, branch covered) or intense light and high temperature prevented bryophytes response to variations in soil water content.

Effects of transplantation

The transplants in the forest plots from the parallel ash recycling experiment (see Methods) showed no reduction in apparent vitality. This suggests small, if any, effects of the transplantation procedure. However, there may be interactions between treatments (position and branch cover) and effects of transplantation, as suggested by the described higher shoot mortality in the centre of the transplants. Radial growth in forest transplants was similar to growth at the edge (except for *P. asplenioides* which grew 2-3 times faster in forests) but much higher than in the uncovered plot in central parts of clear-cut areas. At the uncovered edge growth ranged 31% - 112% (among the eight species) of the growth in forests and in the uncovered centre 1 - 43% (App. 2).

Implications for harvest of logging residues

In a previous study we found lower bryophyte cover and lower richness of liverworts, forest bryophytes, and bryophytes associated with dead wood in clear-cut areas where logging residues had been harvested (Åström et al. 2005). Factors such as loss of woody substrate, mechanical damage during transport of slash and increased competition from vascular plants (mostly grasses) contributed to this change. Our

present study suggests, however, that the microclimatic buffering by logging residue may also play a role, particularly in open settings. This capacity may also benefit other organisms intolerant to the microclimate following clear-cutting. We designed the experiment to isolate the effect on microclimate, eliminating other effects of logging residue. For example, since we removed all spontaneously establishing plants from the plots, we did not include the potentially positive influence of branch cover on bryophytes caused by reduced competition from vascular plants (Åström et al. 2005). On the other hand, a developed understorey of vascular plants also provides shelter for bryophytes intolerant to exposure (Bergamini et al. 2001). Furthermore, we included neither the function of logging residues as bryophyte substrate (Åström et al. 2005) nor the negative smothering effect of thick covers of logging residues (Jalonen & Vanha-Majamaa 2001). The transplants were covered by a simple layer of branches on a wooden frame and no substantial negative effects of heavy shade (Fig. 2, branch-covered vs uncovered plots at the edge), smothering or litter-fall were apparent. The bryophyte shoots were able to penetrate the thin layer of litter produced by the dehiscing needles (M. Åström pers. obs.). The shading effect of cover by *Picea* branches diminishes successively as the needles dehisce. However, many bryophytes adapt to changing environmental conditions when these are moderate or occur slowly such as during canopy closure in spring (Kershaw & Webber 1986). A successive increase in light when needles dehisce would at least expand their opportunity to adapt to a new environment until a new understorey develops and provides further shelter (Bergamini et al. 2001).

The buffering effects of branch cover are less pronounced in the more moderate microclimates on clear-cut areas close to north-facing edges (Figs. 1A, 2 and 4). Therefore, some of the negative effects of logging residue extraction would be mitigated by making clear-cut areas shadier and less windy. This could be obtained by smaller clear-cut areas (larger proportion of clear-cut area affected by edge-effects from surrounding forests) and some green-tree retention, practices that would also favour other organisms negatively affected by clear-cutting. This should, however, not be general practice since there are many species in the boreal region that have specialized requirements related to fire disturbance and therefore need, for example, coarse woody debris exposed to sunlight. A complementary and effective approach to secure the landscape level survival of forest species intolerant to open environments is to set aside forest patches of varying sizes such as forest reserves, key biotopes and buffer strips along small streams (e.g.

Dynesius & Hylander 2007), practices that are already being implemented in some boreal areas.

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*For App. 1 & 2, see below (online version)
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App. 1. Results from a two-way ANOVA for the effect of position (close to a north-facing forest edge vs in the centre of a clear-cut area) and branch cover (covered vs not covered with *Picea* branches) on radial growth (mm) of the eight transplanted bryophyte species. (M) and (L) represent mosses and liverworts. $n = 7$ for all species and treatments. Position and branch cover are considered fixed factors.

Species	Source of variation	df	Mean square	<i>F</i>	<i>P</i>
<i>Hylocomium splendens</i> (M)	Position	1	157.94	9.25	0.006
	Cover	1	0.30	0.02	0.896
	Position × cover	1	2.12	0.12	0.728
	Error	24	17.07		
<i>Hylocomiastrum umbratum</i> (M)	Position	1	257.43	21.54	0.000
	Cover	1	2.34	0.20	0.662
	Position × cover	1	26.23	2.19	0.152
	Error	24	11.95		
<i>Pleurozium schreberi</i> (M)	Position	1	281.62	26.75	0.000
	Cover	1	0.21	0.02	0.890
	Position × cover	1	32.57	3.09	0.091
	Error	24	10.53		
<i>Ptilium crista-castrensis</i> (M)	Position	1	172.01	15.56	0.001
	Cover	1	3.57	0.32	0.575
	Position × cover	1	39.84	3.60	0.070
	Error	24	11.06		
<i>Rhytidiadelphus subpinnatus</i> (M)	Position	1	517.72	40.25	0.000
	Cover	1	6.61	0.51	0.481
	Position × cover	1	6.41	0.50	0.487
	Error	24	12.86		
<i>Rhytidiadelphus triquetrus</i> (M)	Position	1	207.92	28.36	0.000
	Cover	1	0.72	0.10	0.756
	Position × cover	1	17.44	2.38	0.136
	Error	24	7.33		
<i>Barbilophozia lycopodioides</i> (L)	Position	1	145.83	24.04	0.000
	Cover	1	0.04	0.01	0.933
	Position × cover	1	13.58	2.24	0.148
	Error	24	6.07		
<i>Plagiochila asplenioides</i> (L)	Position	1	7.03	16.22	0.000
	Cover	1	2.12	4.88	0.037
	Position × cover	1	0.02	0.05	0.824
	Error	24	0.43		

App. 2. Mean radial growth (mm) of transplants collected from forest control plots in an ash-application experiment conducted in the same area and at the same time (Mats Dynesius unpubl.). Data from the four treatments on clear-cut areas in the present study are presented for comparison. The radial growth of transplants in clear-cut areas is expressed both as mean radial growth (mm) and as proportion (%) of the growth of transplants in forests.

Species	Forest Mean	Branch-covered edge Mean % of forest	Uncovered edge Mean % of forest	Branch-covered centre Mean % of forest	Uncovered centre Mean %
Mosses					
<i>Hylocomium splendens</i>	13.1	9.8 75	10.5 80	5.6 43	5.2 40
<i>Hylocomiastrum umbratum</i>	14.2	8.6 61	9.9 70	4.4 31	1.9 13
<i>Pleurozium schreberi</i>	12.3	11.4 93	13.8 112	7.2 59	5.3 43
<i>Ptilium crista-castrensis</i>	12.6	9 71	10.7 85	6.5 52	3.4 27
<i>Rhytidiadelphus subpinnatus</i>	18.1	13.6 75	13.6 75	6 33	4 22
<i>Rhytidiadelphus triquetrus</i>	10.2	9.8 96	11.1 109	6 59	4.1 40
Liverworts					
<i>Barbilophozia lycopodioides</i>	9.5	6.1 64	7.5 79	2.9 31	1.6 17
<i>Plagiochila asplenoides</i>	7.0	3.3 47	2.2 31	1.2 17	0.1 1
All species	13.9	10.2 74	11.3 82	5.7 41	3.7 26