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Influence of Ground Substrate on Establishment of Reindeer Lichen after Artificial Dispersal

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Methods to improve the recovery of reindeer lichen after soil disturbance or overgrazing are being sought for areas where reindeer are herded. The effects of four substrates – mineral soil, moss, twigs and pine bark – on the establishment of lichen fragments after total removal of the vegetation were thus studied in a middle-aged pine stand and a clear-cut, both located in a lichen-rich pine-heath. *Cladina mitis* fragments of two sizes were manually dispersed in 1 m^2 quadrats and their movements from their respective dispersal points were registered after one year. The natural re-establishment of lichens in the quadrats was monitored over three years by using digital pictures. In the forest stand, no significant differences were detected in either the fragment movement or the lichen establishment between the different substrates, but the fragment size had positive effects on both parameters. In the clear-cut, the moss substrate was the most suitable not only for the artificially dispersed lichens to fasten to, but also for the natural settlement of lichens from the surrounding lichen mat. More lichen thalli fastened to the bark and twigs substrates than to the mineral soil, but the settlement of lichens from the surrounding was greater on bare mineral soil substrate. The results indicate that artificial dispersal of lichen thalli on an appropriate substrate could be a successful strategy for promoting lichen recovery.

Keywords bark, *Cladina mitis*, image analysis, lichen colonization, mineral soil, moss, thallus, twigs

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1 Introduction

In northern boreal forests, semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) herding and forestry exploit two different natural resources, often at the same location, and land use conflicts may thus arise (Bostedt et al. 2003). One of the main reasons for conflicts between reindeer herders and forest owners is the use of large-scale soil preparation techniques in forests after clear-felling, which affect reindeer winter ranges in several ways, most notably in this context in the abundance of epigeic reindeer lichens (*Cladina* spp.).

Soil scarification is intended to improve the site conditions for tree seeds and seedlings via its effects on soil temperature, nutrient mineralization, water and oxygen status, competing vegetation and damage by insects (see, e.g., Mattsson 2002). When conventional techniques like mechanical scarification are used, they can affect up to 35–69% of the vegetation cover (Lundmark 1986) and have very long-term consequences for the recovery of ground vegetation and, thus, reindeer pastures (Eriksson and Raunistola 1990).

The growth rate of reindeer lichens is generally low (Kärenlampi 1971, Helle et al. 1983, den Herder et al. 2003), as is their branching, which is assumed to be an annual event (Scotter 1963). The first natural colonizers of bare soil in boreal regions are crustose lichens and bryophyte species, followed by cup lichens (*Cladonia* spp.), then fruticose lichens like reindeer lichens eventually become dominant. *Cladina mitis* (Sandst.) is one of the first fruticose lichens to appear, then *C. arbuscula* (Wallr.), *C. rangiferina* (L.), and *C. stellaris* (Opiz) is usually the last (Kershaw 1977, Ahti and Oksanen 1990). Lichens can reproduce either sexually or asexually. Asexual reproduction is the most common mode in the genus *Cladina*, through the propagation of thallus fragments (Kiss 1985, Webb 1998). Fragments can grow in three different ways: by the growth/elongation of the apical part, by the formation of new branches at the internodes between existing branches and by new podetia from undifferentiated thalli spreading from points of contact between the lichen fragment and the organic substrate (Webb 1998).

Reindeer lichens grow mainly in oligotrophic habitats (Ahti and Oksanen 1990), such as dry sites dominated by Scots pine (*Pinus sylvestris* L.), where they compete successfully with other ground vegetation species because they can rely on water supplied through precipitation and atmospheric humidity. Thus, unlike vascular plants they are not limited to taking up water, or nitrogen and phosphorous, from the soil (Crittenden et al. 1994, Ellis et al. 2004). However, since lichens are poikilohydric organisms, their growth depends on their water status and the irradiance they receive when wet (Palmqvist and Sundberg 2000, Gaio-Oliveira et al. 2006).

During the winter, lichen constitutes 50 to 80% of the reindeer's diet (Bergerud and Nolan 1970, Danell et al. 1994, Kumpula 2001) because of their high content of readily digestible carbohydrates (Klein 1990), and lichen-rich pine-heaths constitute the most valuable foraging areas for reindeer husbandry, especially in late winter.

As discussed by various authors (e.g. Eriksson et al. 1987, Sandström et al. 2003), the co-existence of reindeer husbandry and forestry is a key socio-economic feature of the boreal forest, and numerous initiatives have been undertaken to avoid land use conflicts arising between them. For instance, more environmentally friendly, milder soil scarification techniques have been developed (Roturier and Bergsten 2006), but since reindeer lichens can grow directly from undifferentiated thallus fragments, it would also be advantageous to accelerate and improve their re-establishment by artificial dispersal, as suggested by results in Heinken (1999), and already practiced for endangered epiphytic lichens (Lidén et al. 2004).

Since reindeer lichens lack below-ground anchoring systems, their establishment and early growth presumably depends on the soil surface characteristics and the ability of thalli to fasten to the substrate. An important, related variable could be the size of the fragments that are spread. Therefore, a field experiment was laid out in boreal Sweden in autumn 2002 to evaluate the establishment of reindeer lichen on various substrates based on materials that are readily available in boreal forests. The objectives of the experiment were to quantify the ability of reindeer lichen fragments, of different sizes, to fasten and establish on different substrates, in order to identify the most suitable substrate for promoting the re-establishment of reindeer lichen in areas disturbed by forestry machines or over-grazing.

2 Material and Methods

2.1 Design and Experimental Area

In October 2002 lichen fragments of two sizes (1 cm and 3 cm-long thalli) were manually dispersed at two sites, a former clear-cut and a middle-aged pine forest 400 m away, in quadrats (1 × 1 m) on four different substrates. The tested substrates were: mineral soil, moss, twigs and bark. The quadrats were spaced one meter apart, and the substrates were randomly placed within each site. The experiment was laid out in a generalised randomised block design, with two blocks (sites), four levels for the factor substrate, two levels for the factor fragment size and four replications of each combination. Thus, 64 quadrats were laid out in total, in each of which the bases of 30 thalli fragments were vertically placed in the substrate, regularly spaced in a 0.25 m^2 square in the middle of each quadrat (Fig. 1), and their initial places were marked by plastic sticks, giving 1920 thalli fragments. For the twigs and bark substrates, two subclasses (fine and coarse) were also created to test different templates, so the quadrats with these substrates were each divided into two, 0.5 × 1 m, patches.

The experiment was established in a pine-heath on a flat glacial delta 175 m above sea level in Vindeln Experimental Forests, northern Sweden (64°14'N, 19°47'E). Both sites are typical of lichen-rich boreal forest environments. The experimental areas were fenced to avoid disturbance from reindeers between January and March. The climate at the experimental sites is of the cold temperate humid type, according to the Köppen climate classification system, with an annual mean temperature of +1.0 °C (average 1970–1996) and annual precipitation close to 600 mm (1981–1997). The soil was classified as a Regosol and the soil texture was sandy loam (70% sand, 28% silt, 2% clay) according to the American soil textural classification system (Soil Taxonomy 1975). The vegetation in the clear-cut was dominated by epigeic lichens (*Cladonia* spp. and *Cladina* spp.), heather (*Calluna vulgaris* L.), cowberry (*Vaccinium vitis-ideae* L.) and some pine seedlings/saplings. The pine forest was a 40–50 years old unthinned stand of Scots pine with a density of 1800 stems per ha, in which the bottom layer was dominated by mosses (*Pleurozium schreberi* Bridd. and *Hylocomium splendens* Hedw.) with only sparse reindeer lichen colonies, and the field layer by cowberry.

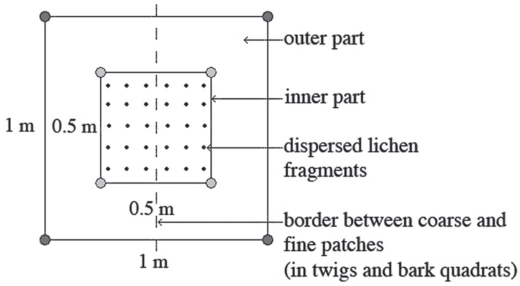

Fig. 1. Arrangement of the experimental quadrats for the artificial dispersal of lichen fragments.

2.2 Substrate and Lichen Fragment Preparation

Fluorescent paint was applied to a 10 cm buffer zone around each of the quadrats. The ground vegetation, including roots, within each quadrat was manually removed to expose bare mineral soil. Substrate materials were then spread to create a 2 cm-thick layer. The mineral soil was from the respective quadrats. Moss (consisting mainly of *Pleurozium schreberi* and *Hylocomium splendens*) was collected from the surrounding area, rinsed and a compost mill was used to obtain a homogenous substrate composed of ca. 3 cm-long moss fragments. The twigs substrates were made by milling cowberry and heather twigs in the compost mill at two milling levels in order to obtain a fine substrate composed of ca. 1 cm-long pieces and a coarse substrate with ca. 5 cm-long pieces. Finally, a horticultural pine-bark substrate was used as the fourth substrate type, after separation into two size ranges, designated fine and coarse, using a 12 × 12 mm sieve.

Lichen, consisting of *Cladina mitis* (Sandst.), was collected from the surrounding area, rinsed and cut into 1 or 3 cm-long fragments from the top, preserving the upper part of the thalli, where the photobiont density is highest (Nash et al. 1980). The lichen fragments were each marked by tying a thin red cotton thread to the base to allow them to be distinguished from fragments that may have been moved into the quadrats, e.g. by wind.

2.3 Inventory and Measurements

A first inventory was carried out in August 2003 in which ≤ 3 cm and ≤ 5 cm movements of the lichen fragments from their initial dispersal points were recorded. In addition, the numbers of fragments left in the whole quadrat were counted. The cotton thread and fluorescent paint covering lichen fragments from outside the quadrat allowed the artificially dispersed fragments to be easily identified.

A photographic inventory was also undertaken to follow the natural re-establishment of the ground surface by the lichen, including artificially dispersed and naturally colonizing fragments. For this purpose, photographs were taken of all the quadrats, from vertically above, using a Nikon Coolpix 4500 digital camera mounted on a tripod at 2272 × 1704 resolution, with high quality definition, on overcast days to avoid shadows, under natural lighting conditions but using a flash to homogenize light intensity differences. Three series of such photographs were taken: just after the establishment of the quadrats in November 2002, a year after establishment in October 2003 and three years after establishment in November 2005.

Since it proved impossible to analyse the images obtained automatically in a satisfactory manner with the available equipment, the photographs were manually processed; an approach that yields satisfactory results for unsaturated vegetation according to Dietz and Steinlein (1996) and Vanha-Majamaa et al. (2000). Digital pictures were analysed using ImageJ 1.34s software (Abramoff et al. 2004) for Macintosh. The scale was set in the *scale* function using a ruler laid on the ground. Colour pictures were first split into three channels – red, green and blue – and the information in the blue channel was used in the analyses, because it provided the best contrast. Then a threshold level was set in the grey scale to maximise the visibility of the lichen fragments. Each individual lichen fragment was selected manually with the *magic wand* tool and the selected area was measured in cm^2 using the measurement function, thus including possible empty spaces between the branches. However, since there were very large numbers of very small lichen fragments on the mineral soil in the clear-cut stand, their area was measured using the *Analyse Particle* function over a selected threshold.

2.4 Statistics

To determine the effects of the different factors on the displacement of the fragments and the re-establishment of the lichen, a variance analysis (ANOVA) was performed using the general linear model (GLM) procedure in Minitab 14.1 (Minitab Inc. 2003). Site, fragment size and substrate were considered as fixed factors. The dependent variables were the percentage of fragments remaining within a 3- or 5-cm radius of their respective dispersal points for the displacement of the fragments, and the area covered by lichen in the quadrats as measured by image analysis for the re-establishment of the lichen. Differences were considered significant if $p \leq 0.05$. When significant effects were found, Tukey *post-hoc* tests were applied to compare the effects of the sites, substrates and fragment sizes on the early displacement of the fragments. The same procedure was applied to assess the re-establishment of the lichens. Paired *t*-tests were used to evaluate the differences between coarse and fine patches for the bark and twigs substrates.

3 Results

3.1 Displacement of Thallus Fragments after Manual Dispersal

The data on the displacement of fragments from their points of establishment show that 70% and 94% of the artificially dispersed fragments

Table 1. Percentage of remaining fragments within 3-cm and 5-cm radii from their establishment points and within all quadrats for the different sites and substrates one year after establishment (Mean ± SD). Different letter within columns indicate significant between-substrate differences (Tukey's test: $p \leq 0.05$).

Site Substrate	Percentage of remaining fragments within: 3-cm radius	 5-cm radius	 1 m^2 quadrat
CLEAR-CUT			
moss	76^a	92^a	92^a
twigs	70^a	83^a	87^a
pine bark	27^b	40^b	55^b
mineral soil	7^c	15^c	47^b
Mean	45 (±5.5)	58 (±5.9)	70 (±4.1)
PINE FOREST			
moss	78	95	97
twigs	74	94	95
pine bark	64	88	89
mineral soil	66	93	96
Mean	70 (±2.7)	93 (±1.5)	94 (±1.4)

Table 2. Pairwise T-test comparisons of the percentages of 1-cm and 3-cm lichen fragments remaining after one year in quadrats with coarse and fine bark substrates in the clear-cut. Results marked with different letters are significantly different (T-test: $p \leq 0.05$).

Site	Fragment size	Radius	Course bark	Fine bark
Clear-cut	1-cm	3-cm	47^a	20^b
	1-cm	5-cm	56^a	25^b
	3-cm	3-cm	27^a	13^a
	3-cm	5-cm	52^a	28^a

remained in the 1 m^2 quadrats in the clear-cut and forest stand, respectively, a year after their dispersal. In the latter, no significant differences were observed between the different substrates; 70% of the lichen fragments, on average, remained within a 3-cm radius of their dispersal points and 93% within a 5-cm radius (Table 1). In contrast, in the clear-cut only 45% of the fragments remained within a 3-cm radius and 58% within a 5-cm radius, and there were significant differences between substrates. The rates of lichen fragment movement were highest on the mineral soil substrate, where only 7% of fragments remained within a 3-cm radius of their dispersal points and 15% within a 5-cm radius. On the moss and twigs substrates 70 and 76%, respectively, of the artificially dispersed fragments remained within a 3-cm radius, and 83 and 92% within a 5-cm radius of their initial positions, and the differences between these two substrates were not significant. The corresponding values for the bark substrate were intermediate; 27% of fragments remained within a 3-cm radius and 40% within a 5-cm radius. In the clear-cut, significant differences in the establishment of lichen fragments were also found between the coarse and fine bark patches, but not in the forest stand and not between the two twigs substrates. On the coarse bark, the lichen fragments had a clear tendency to stay closer to their dispersal point than on the fine bark, and the tendency was significant for the 1-cm long fragments within 3- and 5-cm radii (Table 2).

The size of the lichen fragments also significantly affected the total number of artificially dispersed fragments remaining in the quadrats; 77% and 87% of the 1-cm and 3-cm fragments remaining within them, respectively.

3.2 Estimates of Lichen Cover by Photographic Analysis

In November 2002, at the time of dispersal, the area covered by lichen fragments in the inner parts of the quadrats, corresponding to the total area at this time, was on average 55 cm^2 (±10.5) for the 3-cm fragments and 16.5 cm^2 (±4.1) for the 1-cm fragments (Fig. 2).

In autumn 2003, lichen cover in the clear-cut was significantly higher than in the pine forest (116 cm^2 and 31 cm^2, respectively), and the difference was greater in autumn 2005 (425 cm^2 in the clear-cut and 46 cm^2 in the forest) (Table 3). The fragments' size did not have any significant effect on lichen cover in the clear-cut (Table 3), where the mean values for the 1-cm and 3-cm fragments were very similar (Fig. 3). However, in the forest differences between the two sizes of fragments were significant (Table 3); the cover being greater in quadrats with 3-cm fragments than in quadrats with 1-cm fragments in both 2003 and 2005 (Fig. 4). The ratio between the lichen cover in the inner-part and the total lichen cover in the quadrats differed between the two

Table 3. Effects of site, substrate and fragment size on the lichen cover in the quadrats (in cm^2) according to the ANOVA.

Trait	Source of variation	df	Adj MS	*F*	*p*
Total cover in 2003	Site	1	117279	43.68	<.001
	Substrate	3	12319	4.59	0.006
	Fragment size	1	1414	0.53	0.471
	Error	58	2685		
Total cover in 2003 (Clear-cut)	Substrate	3	28482	8.04	0.001
	Fragment size	1	845	0.24	0.629
	Error	27	3544		
Total cover in 2003 (Pine forest)	Substrate	3	216.6	1.24	0.313
	Fragment size	1	6766.3	38.89	<.001
	Error	27	174		
Total cover in 2005	Site	1	2297741	114.15	<.001
	Substrate	3	132250	6.57	0.001
	Fragment size	1	1235	0.06	0.805
	Error	58	20130		
Total cover in 2005 (Clear-cut)	Substrate	3	259605	9.34	<.001
	Fragment size	1	410	0.01	0.904
	Error	27	27788		
Total cover in 2005 (Pine forest)	Substrate	3	1566.5	1.60	0.212
	Fragment size	1	4893.8	5.01	0.034
	Error	27	977.3		

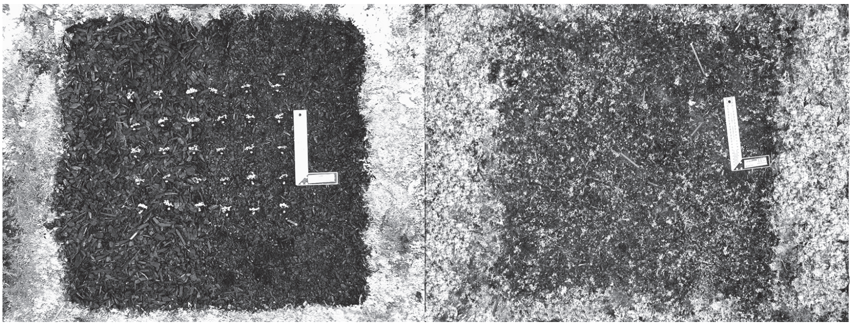

Fig. 2. Colonization of the quadrats by the lichen fragments between November 2002 (left panel) and November 2005 (right panel).

sites and was significantly larger in the forest stand than in the clear-cut (Fig. 3 and 4).

In the clear-cut, the area covered by lichen in the quadrats differed significantly between the substrates (Table 3). The lichen cover was significantly higher on the moss and bare mineral soil substrates than on the twigs and bark substrates in both 2003 and 2005, except for the 3-cm fragments in 2003, where the differences were not significant (Fig. 3). In all cases, lichen cover in the outer-part of the quadrats was higher on the mineral soil than on the other substrates, except in 2003 for 1-cm fragments, and the cover in the inner-part of the quadrats was higher on the moss substrate than on the other substrates. The ratio between inner-part cover and total cover also revealed significant differences between substrates in 2005, since the ratios were significantly higher for the moss and twigs substrates than for the mineral soil and bark substrates.

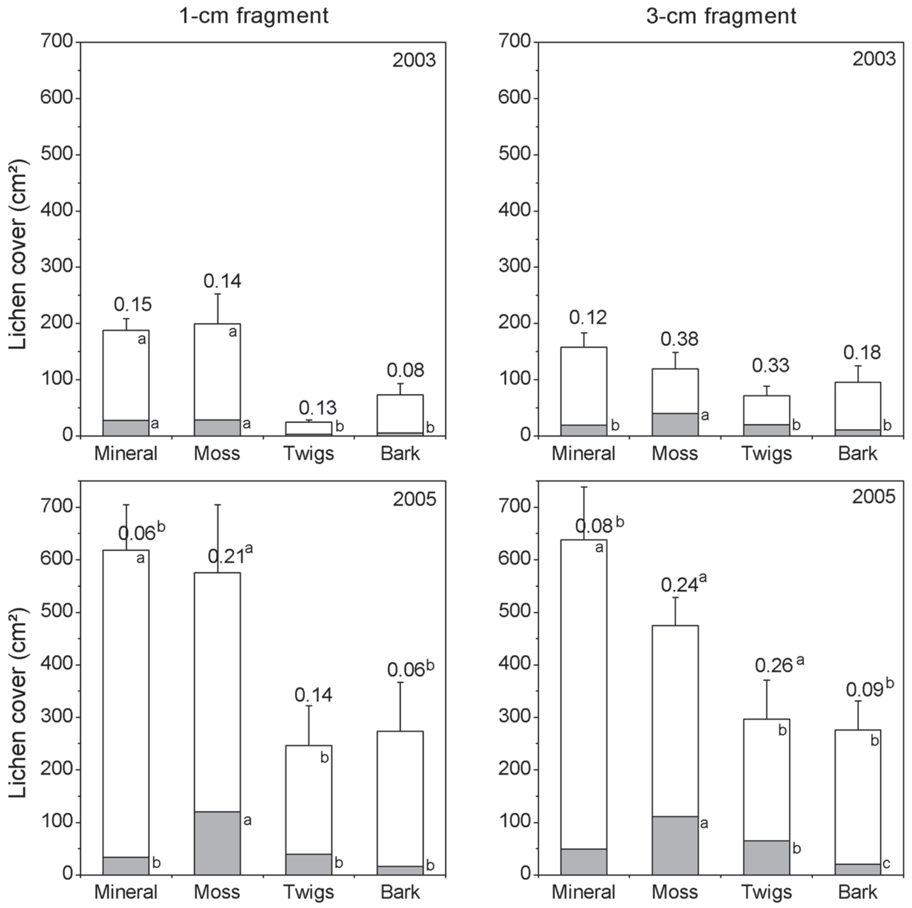

Fig. 3. Mean lichen cover (in cm^2) in the years 2003 and 2005, in the quadrats (grey, in the inner-part; white, in the outer-part) established in the clear-cut, after artificial dispersal of 1-cm and 3-cm fragments on mineral soil, moss, twigs and bark substrates. Figures above the column refer to the ratio between inner-part cover and total cover. Different letter within columns indicate significant between-substrate differences (Tukey's test: $p \leq 0.05$). Error bars = SD.

In the pine forest, the lichen cover did not significantly differ between the four substrates, except in the inner parts of the quadrats spread with 1-cm fragments, where the cover was significantly greater on the twigs substrate (Fig. 4), and a significant difference between coarse bark (1.3 cm^2) and fine bark (2.7 cm^2) patches was observed (results not presented). The ratio between inner-part cover and total cover within the quadrats on the different substrates were similar, indicating that levels of establishment of the lichen fragments on all of the substrates were similar in the forest.

4 Discussion

4.1 Lichen Establishment after Artificial Dispersal

The displacement inventory revealed significant differences between the two sites, i.e., the substrate effect differed between the two environments (Table 1). Climatic factors, especially the wind, combined with the composition of the surrounding vegetation, may account for these differences. Although not measured, the wind is likely to have had stronger effects in the clear-cut than

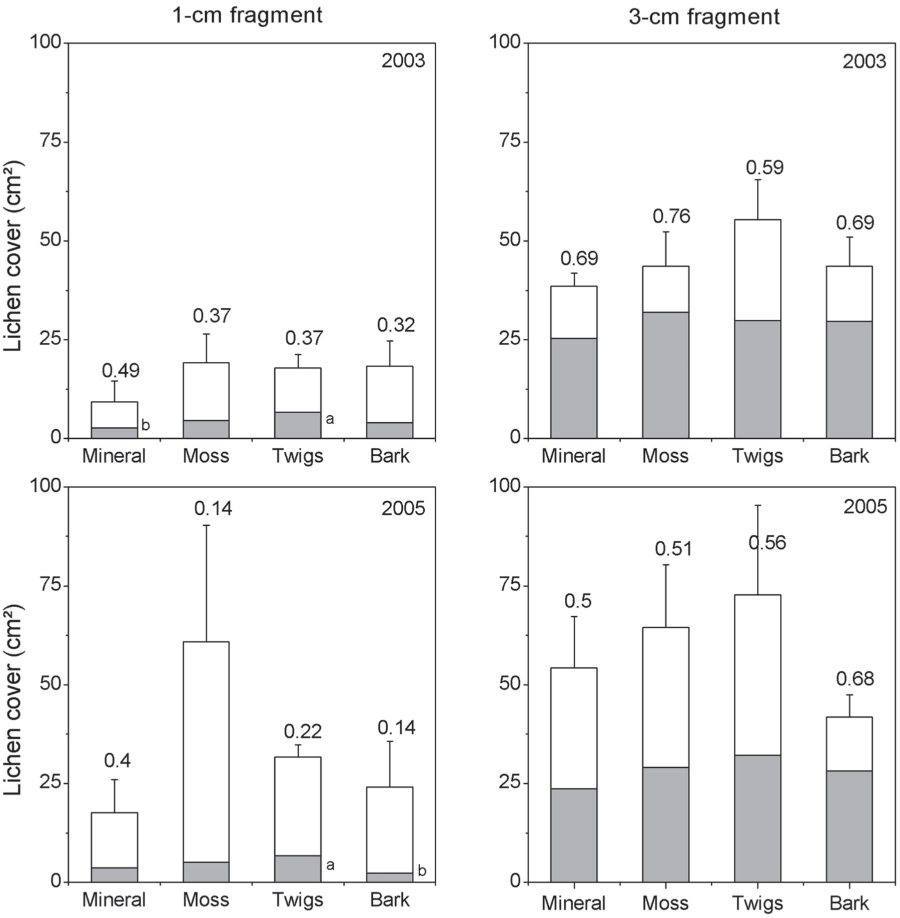

Fig. 4. Mean lichen cover (in cm^2) in the years 2003 and 2005, in the quadrats (grey, in the inner-part; white, in the outer-part) established in the forest, after artificial dispersal of 1-cm and 3-cm fragments on mineral soil, moss, twigs and bark substrates. Figures above the column refer to the ratio between inner-part cover and total cover. Different letter within columns indicate significant between-substrate differences (Tukey's test: $p \leq 0.05$). Error bars = SD.

in the pine forest, and the cowberry cover in the forest stand is likely to have provided a screen around the experimental quadrats, decreasing the potential effects of wind on the dispersed fragments. In the clear-cut, the wind almost certainly increased the importance of the substrates as a determinant factor for the thalli attachment, while substrates' effects were minor in the forest stand and the differences between them less important. In addition, the litter layer, consisting mainly of needles that gradually covered the quadrats in the forest stand, probably increased the likelihood that the fragments would remain, even on the bare mineral soil, after a certain, relatively short, period of time.

In this study, establishment was measured in terms of the area of lichen cover, estimated by digital picture analysis. The measured coverages were still small after three years, but this is consistent with the results of a similar experiment by Kallio, reported in Crittenden (2000), in which it took 20 years for a "luxurious lichen mat" to develop after 200 g of crushed thalli was spread in 1 m × 1 m quadrats. However, the increments between 2003 and 2005 provide indications that lichen fragments did establish, although it was not possible to confirm this with any certainty. Possible shrinkage of the thalli caused by drying (Scotter 1963) on some measurement occasions was not taken into account, and this could have influenced the cover estimates, but only weakly since the inventories were carried out at the same period of the year, and under similar climatic conditions, i.e. on overcast days, on every occasion.

The openness of the clear-cut and the luxurious lichen mat surrounding the quadrats in it, compared to the weaker winds and low lichen cover in the forest stand, probably explain the large differences in the lichen cover increments at the two sites. Heinken (1999) observed a rapid dispersal of thalli fragments over short distances and suggested that the wind was largely responsible. Dispersal by animals (birds and hares or other rodents) is difficult to evaluate, but also probably occurred, and is likely to have been more extensive in the clear-cut than in the forest stand. Moreover, the advance of the intact lichen mat surrounding the borders of the mineral soil and moss quadrats observed in the clear-cut increased the areas measured in their outer parts (Fig. 3), whereas the cover in the outer parts of the quadrats in the forest stand was very low (Fig. 4). The low ratios between the cover in the inner parts of the quadrats and total cover, in the clear-cut, also indicate that most colonisation had occurred along the sides of the quadrats, while colonisation was more equally divided between the inner and outer parts of the quadrats in the forest (Fig. 3 and 4). Relatively poorly ventilated sites, such as those in forest stands compared to those in clear-cuts, are more favourable for moss growth than lichen growth (Tamm 1964, Goward 1998).

The light level, which was clearly higher in the clear-cut than in the forest stand, also affects thalli establishment (Sulyma and Coxson 2001). When lichens are wet, there is a strong correlation between their growth and intercepted irradiance (Palmqvist and Sundberg 2000, Coxson and Wilson 2004). For instance Webb (1998) observed that light influences lichen's growth orientation and thus their ability to attach to substrates. Although they may have provided possible anchoring sites for the thalli in the forest, falling needles may also have obstructed the lichens' access to light simply by covering them, as suggested by Sulyma and Coxson (2001), levelling out the differences between the different substrates.

The light availability and the falling litter could explain the significant effect of thallus size on lichen cover, which was significantly greater in the quadrats with 3-cm fragments than in the quadrats with 1-cm fragments (Fig. 4), probably due to the longer fragments having greater photoreceptivity (see Hammer 1997) and the greater water-holding capacity of larger thalli (Gauslaa and Solhaug 1998).

4.2 Influence of Substrates on Thalli Establishment

In the clear-cut, the substrate seemed to have the strongest influence on thalli displacement and lichen establishment. The moss and mineral soil substrates appeared to be more appropriate for lichen colonisation and growth than the twigs and bark substrates. The poor lichen cover in the outer parts of the twigs and bark quadrats (Fig. 3), and the pronounced border observed between these substrates and their surroundings, illustrate the difficulties new fragments face in colonizing and establishing on such substrates. Despite the lichen cover on the mineral soil and moss substrates being quite similar (Fig. 3), it was significantly larger in the inner parts of the quadrats with the moss substrate. According to several authors, high densities and thicknesses of mat-forming lichens may help them avoid desiccation (Kershaw and Field 1975, Gauslaa and Solhaug 1998) and although the results of Gaio-Oliveira et al. (2006) indicate that the density effect may be weaker than previously thought, the moss is likely to have provided more humidity than bare mineral soil. If the large ratios between inner-part cover and total cover (Fig. 3), and the low movement of artificially dispersed thalli (Table 1), observed in the moss quadrats are also taken into account, moss clearly appeared to be the most appropriate substrate for effective lichen establishment three years after dispersal. The mineral soil also had some advantages, since intact surrounding lichen mat apparently readily colonised it, at least in areas close to it, although this substrate did not promote attachment and establishment of the artificially dispersed thalli.

The lichen cover on the twigs and bark substrates was somewhat lower than expected from the thalli movement results. But the ratios between the cover in the inner parts of the quadrats and total cover in the twigs quadrats were more favourable, indicating that the lichen may have established well in the inner parts, as seen in the moss quadrats, albeit to a lower degree. In addition, as observed by Webb (1998), podetia may form at points of contact between reindeer lichen fragments and organic substrates, such as bark or twigs, in some years. However, the fairly strong establishment of lichen on bare mineral soil that we detected is not supported by Webb (1998), who did not observe any reindeer lichen colonizing mineral soil. Our results were surprising in this respect, considering the small proportion of artificially dispersed thalli remaining in the quadrats after a year (Table 1), but taking into account the extension of the surrounding lichen mat, another possible explanation is that since the mineral soil surface facilitated displacement of the thalli, a large amount of small fragments could pass through the quadrats without establishing, but increasing the lichen cover measured. However, the ratio between inner-part and total covers moderated the efficiency of mineral soil as a substrate, and tended to limit colonisation at the borders of the quadrats.

The different templates of the bark and twigs substrates did not seem to influence the establishment or attachment of the lichen. There were some significant differences between the coarse and fine patches in these respects, but no clear trends.

4.3 Possibilities for Reindeer Lichen Re-establishment

The general increase in lichen cover during the study period revealed that it should be possible to promote the re-establishment of lichen by dispersing thallus fragments, even after total removal of the vegetation, and doing so could help reduce the long time required for a disturbed stand to recover fully without such assistance (Kershaw 1977, Morneau and Payette 1989).

The results of this study show that different strategies for artificial dispersal should be applied, depending on the site conditions. In the pine forest, the limiting factor seemed to be access to light and larger sizes of fragments could thus be favourable for artificial dispersal. Gaare and Wilmann (1998) concluded that fragments larger than 2 mm continue to grow, and Hammer (2000) confirmed that this is generally true, if their meristematic tissues are still alive. However, our results also indicate that artificial dispersal with fragments smaller than 1 cm would probably be hazardous, since the results obtained with the 1-cm fragments were poorer than those with the 3-cm fragments, at least in the forest. Nevertheless, this study like those of Heinken (1999) and Sulyma and Coxson (2001), reveals the difficulty of establishing lichen in a pine forest, even a middle-aged forest such as the one used in this study. In the clear-cut, the effect of the artificial dispersal was masked by the evident colonization of the quadrats by fragments from the surroundings, and control quadrats would have been required to quantify the true extent of colonization. However, natural colonization could be enhanced by using substrates that not only enable lichen fragments to fasten, but also help isolated thalli to avoid drying, and consequent reductions in their metabolic activity (cf. Helle et al. 1983, Hyvärinen et al. 2002). Moss seems to be a suitable substrate, since it generates relatively high humidity and thus should help to conserve thallus fragments. Although fragment size did not have a significant effect in the clear-cut, we suggest that use of relatively large fragments, which have a more ramified shape, could facilitate attachment of the lichen to the substrates. A further advantage of relatively heavy fragments, particularly under wet conditions, is that they should be less sensitive to wind than light fragments (Heinken 1999).

4.4 Concluding Remarks

It seems possible to spread a substrate composed of moss prior to dispersal of reindeer lichen in areas disturbed by scarification to favour lichen re-establishment. However, further studies are needed before applying such a practice on a large scale to restore reindeer lichen availability. The cost-effectiveness of lichen collection also requires further attention. In addition, it is important to evaluate fencing effects to quantify the disturbance of reindeer themselves on artificially dispersed lichens, cf. Gaare and Wilmann (1998) and Crittenden (2000). Eriksson et al. (1987), Sulyma and Coxson (2001) and other authors have stressed the importance of the effects of forest management practices on the availability of lichen resources. We agree that they are important, but we also see scope for using forest management practices as tools to meet the needs of the reindeer herders as well as the forest owners or companies.

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