

Edge effects on epiphytic lichens in managed black spruce forests of eastern North America

Héloïse Rheault, Pierre Drapeau, Yves Bergeron, and Per-Anders Esseen

Abstract: We studied the spatial and temporal response of three epiphytic lichens (*Bryoria* spp., *Evernia mesomorpha* Nyl., and *Usnea* spp.) to edge effects in conifer forests of northwestern Quebec. Lichen abundance and substrate variables were sampled at four distances (5, 25, 50, and 100 m) from the edge in 15 edge–interior transects in managed black spruce (*Picea mariana* (Mill.) BSP) forests. Responses to edge effects were assessed for short-term (1–3 years) and long-term (8 and 16–23 years) periods. We also assessed the effect of forest fragment size on lichen abundance in 27 forest fragments ranging in size from 0.03 ha to >4 ha. We found a significant effect of distance to edge on mass of *E. mesomorpha* and *Usnea* spp. Lichen mass was lower in the first 50 m of edge compared with the forest interior (100 m). Size of forest fragments had no significant effect in any of the three lichens. However, mass of *Usnea* spp. was low in the seven smallest (<0.5 ha) fragments. Our results suggest that the response of epiphytic lichens to edge conditions could be used by forest managers as an indicator in determining the size of remnant stands that should be left to increase the proportion of interior forest habitat in harvested forest landscapes.

Résumé : Nous avons étudié la réponse spatio-temporelle de trois groupes de lichens épiphytes (*Bryoria* spp., *Usnea* spp. et *Evernia mesomorpha* Nyl.) aux effets de lisière dans les forêts conifériennes du Nord-Ouest québécois. L'abondance des lichens et les variables du substrat ont été comparées à différentes distances de la bordure (5, 25, 50 et 100 m) le long de 15 transects s'étendant de la bordure de parterres de coupe à l'intérieur de pessières noires matures. Les réponses à court terme (1–3 ans) et à long terme (8 et 16–23 ans) sont comparées. Nous avons aussi évalué l'effet de la taille des fragments forestiers résiduels sur l'abondance des lichens dans 27 fragments variant de 0,03 ha à plus de 4 ha. Nos résultats montrent un effet de lisière significatif sur l'abondance d'*E. mesomorpha* et d'*Usnea* spp., leur biomasse étant plus faible dans les premiers 50 m de la bordure comparativement à l'intérieur de la forêt (100 m). La taille des fragments forestiers résiduels n'a pas eu d'effet significatif sur aucun des trois lichens. Cependant, la biomasse d'*Usnea* spp. s'est avérée faible dans les sept plus petits fragments forestiers (<0,5 ha). Nos résultats suggèrent que la réponse des lichens épiphytes aux conditions de lisière pourrait servir d'indicateur aux aménagistes forestiers pour déterminer la taille des fragments forestiers qui devraient être laissés en paysage aménagé afin que soit maintenue une plus grande proportion d'habitats d'intérieur.

Introduction

In Canada, timber harvesting is progressing quickly in the virgin boreal forest, and as a consequence, results in an increasingly fragmented landscape pattern. A large number of studies have demonstrated how ecological processes can be altered when continuous forest cover is converted into forest remnants scattered across the landscape (Harris 1984; Saunders et al. 1991; Harrison and Bruna 1999). In many cases, these forest remnants are not suitable to ensure persistence of some forest species. The increased amount of edge habitat within remnants has been viewed as a major factor

for changes in biodiversity. Edge influence is now a well-known mechanism involved in abiotic and biotic degradation of residual stands (Saunders et al. 1991; Camargo and Kapos 1995; Esseen and Renhorn 1998; Matlack and Litvaitis 1999).

Microclimatic conditions at forests edges adjoining clearcuts are different from those prevailing in the forest interior. These consist mainly of increased solar radiation, higher wind velocity, and lower air humidity (Chen et al. 1993; Matlack 1993; Renhorn et al. 1997). These modifications influence vegetation structure and composition and may also have negative consequences on organisms associated with stable forest interior conditions (Murcia 1995).

Several studies have described edge effects on different organisms and illustrated how the extent of edge effects can be used to predict the amount of unaltered habitat preserved in managed forests (Ranney et al. 1981; Laurance and Yensen 1991; Matlack and Litvaitis 1999). Esseen and Renhorn (1998) showed that epiphytic lichens are suitable as indicators of edge influence.

Lichens confined to old-growth forests are considered particularly sensitive to forest fragmentation. This originates from the incompatibility of their habitat requirements and forestry practices based on clear-felling. First, metabolic

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activity and growth of lichens are directly associated to microclimatic conditions (Coxson et al. 1983; Gauslaa and Solhaug 1996; Renhorn et al. 1997). Thus, lichens may respond rapidly to environmental stress caused by local changes in abiotic conditions (Nash et al. 1990). Second, most epiphytic lichens are preferentially found in mature to old-growth conifer forests (McCune 1993; Esseen et al. 1996; Boudreault et al. 2000). Logging has a direct impact on epiphytic lichens by eliminating their substrate and by creating sharp edges and a mosaic of contrasting environments. By imposing a harvest rotation generally shorter than natural disturbance cycles it also reduces the time available for establishment and development of epiphytic lichens. In northwestern Quebec where forests are naturally fragmented by wildfires, timber harvesting may increase fragmentation and the 100-year commercial rotation cycle leads to the elimination of overmature forests (Bergeron et al. 1999).

Recent studies have shown that dispersal limitation of lichen propagules is an important factor preventing the establishment of lichens in managed forests (Dettki et al. 2000; Hilmo and Sæstad 2001; Sillett et al. 2000). Inadequate dispersal may lead to extirpation of these species in managed forest, especially for lichen populations in landscapes where remnant patches are small and isolated with a high perimeter length/area ratio. Thus, the fate of forest remnants to act as sources of propagation is linked to isolation of remnants and their amount of core habitat which are more favourable for lichen persistence than edge habitat (Kruys and Jonsson 1997; Dettki et al. 2000; Harrison and Bruna 1999).

Until recently, the few studies on edge effects on lichens were conducted in conifer forests in Fennoscandia (Renhorn et al. 1997; Esseen and Renhorn 1998; Hilmo and Holien 2002; Kivistö and Kuusinen 2000) or in the Pacific Northwest in North America (Sillett 1994). Little is known about edge influence on lichens in eastern North American boreal forests. Similarities between Canadian and Fennoscandian boreal forests may, however, provide new insights on how general the responses of epiphytes are to forest management at a circumpolar scale. In Sweden, large pendulous fruticose lichens such as *Alectoria sarmentosa* (Ach.) Ach. and *Usnea longissima* Ach., which are strongly associated with old Norway spruce (*Picea abies* (L.) Karst.) forests, are very sensitive to altered conditions at forest edges (Esseen et al. 1981; Esseen and Renhorn 1998). *Evernia divaricata* (L.) Ach., a species found in humid forests, is declining in isolated forests surrounded by clearcuts (Sjöberg and Ericson 1992). In black spruce (*Picea mariana* (Mill.) BSP) forests of eastern Canada, little is known on the sensitivity of epiphytic lichens to edge effects.

In this study, we document edge effects on three epiphytic lichens (*Bryoria* spp., *Evernia mesomorpha* Nyl., and *Usnea* spp.) commonly encountered in *Picea mariana* forests of northwestern Quebec. We addressed the following questions: (i) what is the magnitude and depth-of-edge influence on abundance of epiphytic lichens in remnant forest blocks, and (ii) does the magnitude of edge effects on lichens change over time when comparing recently induced and older edges? We hypothesized that pendulous lichens may be negatively affected at sharp edges because of direct exposure to strong winds and low levels of atmospheric humidity. These effects may lead to decreases in biomass as a direct result of

mechanical damage to the thallus as previously found for *Alectoria sarmentosa* (Esseen and Renhorn 1998). Changes in biomass distribution along edge-interior transects may be dynamic over time, and we hypothesized that the distance of edge influence may extend deeper with time. Indeed, in boreal *Picea mariana* ecosystems, regeneration of trees in clearcuts takes some time to reach a considerable height (Boily and Doucet 1993; Morin and Gagnon 1992) such that edge effects in the adjacent mature canopy may be long lived.

We then assessed lichen abundance in forest fragments of different size classes to determine how size of fragments influences these organisms, i.e., to what extent can remnant forest fragments support epiphytic lichens. We expected the size of forest fragments to influence lichen biomass in a manner consistent with the depth of edge influence determined at cutblock edges. Hence, we hypothesized that smaller remnants were less suitable for maintaining epiphytic lichens, because they may lack interior forest conditions.

Materials and methods

Study area

The study was conducted in black spruce – feathermoss forests in northwestern Québec (49°11'–49°42'N, 78°34'–79°19'W). This area belongs to the *Picea mariana* – moss bioclimatic domain (Saucier et al. 1998). The topography is dominated by a flat landscape with scattered low-elevation hills (400 m maximum elevation). Organic soils and clay are the most important surface deposits (Gauthier et al. 2000). The forest mosaic originates from wildfires with fire cycles averaging 139 years (Bergeron et al. 2001). Mean annual temperatures and precipitation average between 0 and –2.5°C and between 600 and 1000 mm, respectively. The vegetation is dominated by *Picea mariana* and jack pine (*Pinus banksiana* Lamb.) stands. Timber harvesting in this area started in the 1970s.

The study area is divided into two sectors representing two distinctive logging histories. Old clearcuts (1976–1985) are located 20 km north of the village of Val-Paradis, and recent clearcuts (since 1992) are located about 50 km further east. Studied forests were dominated by *Picea mariana* (72–100%) with up to 13 and 28% *Pinus banksiana* or *Abies balsamea* (L.) Mill., respectively, with sparsely distributed tree species such as *Larix laricina* (Du Roi) K. Koch and *Populus tremuloides* Michx. (aspen). Maximum tree height reached 7–14 m and canopy cover was between 50 and 80%. The forest floor was dominated by mosses including *Pleurozium schreberi* (Brid.) Mitt. and *Sphagnum* spp., and the understory was mainly composed of *Ledum groenlandicum* Oed. and *Kalmia angusifolia* L. Vegetation in the clearcuts was dominated by *Picea mariana* seedlings and saplings up to 2 m tall at the edge of older clearcuts (23 years). Some differences in regard to stand structure can be noted between the two harvested areas. Higher tree densities and mean basal area was observed in the younger forest stands (70 years since fire) adjoining the 1992 clearcuts (Table 1). The oldest forests had the lowest basal areas and were found next to the old harvested areas (1976–1985).

Table 1. Characteristics of study sites: area of mature forest, age of adjoining clearcuts, edge orientation, stand age, density, basal area, and tree composition for 15 transects in large forest blocks and 12 plots in forest fragments.

Site	Area (ha) ^a	Age of clearcut (years)	Edge orientation	Stand age (years) ^b	Density (stems/ha) ^c	Basal area (m ² /ha) ^c	Tree species composition (%) based on stem density ^c			
							<i>Picea mariana</i>	<i>Pinus banksiana</i>	<i>Abies balsamea</i>	Other
Edge-interior transects										
1	4	23	NW	100	2183	26	92	8	0	0
2	6	16	E	140	1408	15	95	0	0	5
3	15	15	E	140	1367	19	94	0	5	1
4	9	14	SE	200	1308	21	72	0	28	0
5	12	14	W	140	1225	14	99	0	1	0
6	24	8	W	70	2417	35	100	0	0	0
7	6	8	W	70	2842	39	100	0	0	0
8	9	8	W	70	2008	49	100	0	0	0
9	8	8	E	70	2792	59	86	11	0	3
10	4	8	E	70	2533	50	91	8	0	1
11	9	3	E	90	1608	38	98	0	1	1
12	18	3	SE	80	1167	25	95	0	1	4
13	4	2	NW	80	1400	31	99	0	0	1
14	16	1	W	100	1592	38	95	0	5	0
15	48	1	SW	80	3325	43	87	0	12	1
Fragments										
1	0.03	8	—	70	1433	37	91	0	2	7
2	0.03	8	—	70	2367	32	100	0	0	0
3	0.03	8	—	70	2367	28	80	20	0	0
4	0.09	15	—	120	2333	20	100	0	0	0
5	0.12	8	—	120	2533	45	100	0	0	0
6	0.25	16	—	120	1067	16	100	0	0	0
7	0.36	17	—	120	2367	27	100	0	0	0
8	1	8	—	120	2467	19	84	16	0	0
9	1.4	20	—	120	2400	33	100	0	0	0
10	2	8	—	70	4133	52	72	28	0	0
11	2	8	—	70	2167	27	98	2	0	0
12	2.8	24	—	120	2067	19	94	0	0	6

^aStand area of same forest cover type (tree species composition, crown closure, tree height, stand age) based on ecological maps.

^bTime since fire based on fire-history reconstruction (Bergeron et al. 2001).

^cMean of four 10 × 30 m plots per edge-interior transect.

Sampling design

Depth-of-edge influence on epiphytic lichen abundance was assessed in 15 residual forests adjacent to 1- to 23-year-old clearcuts that were sampled in the summers of 1999 and 2000 in mature and overmature *Picea mariana* forests (Table 1). The sampled forest stands were relatively homogeneous (same stand density, basal area, height, age, and composition), over 4 ha in size, and were adjacent, on only one side, to a clearcut of more than 4 ha; the other sides were generally facing either wetlands or *Pinus banksiana* stands. Forests edges were delimited by mature trees located at the extreme limit of the forest and the clearcut, and were straight over at least 200 m. At each site, a single 105 m long transect was established, oriented perpendicular to the edge. To minimize confounding effects, transects were established to avoid large gaps or wetlands and were at least 50 m from the cutblock corners. Data were collected from four 30 × 10 m plots (oriented with the long axis parallel to the forest edge) centred at 5, 25, 50, and 100 m from the edge.

The effect of size of remnant forest fragments on lichen abundance was measured in 12 smaller forest fragments ranging from 0.03 to 2.8 ha in size (Table 1). These fragments are representative of the original mature forest. They have been left out by the industry either to separate cutblocks or to create moose refuges. Considering their structural features, these stands are comparable with the studied forest blocks (Table 1). Fragments were isolated on clearcuts with at least 100 m to the nearest forest. Sampling was conducted from one plot (10 × 30 m) centred in the interior of each fragment. Time since isolation of fragments varied between 8 and 24 years.

Data collection

The field sampling was based on the methods of Esseen and Renhorn (1998). Within each 10 × 30 m plot, the number, diameter at breast height (DBH), species, and vitality (snags or live trees) of all mature trees (DBH >8 cm) were noted. All logs (DBH >8 cm) with their base in the plot were also counted. Canopy cover was determined using a

convex spherical densiometer. In each plot, 10 live trees were cored at breast height to estimate the age of lichen substrate, i.e., the length of time available for epiphytic lichens to establish on live bark substrates (we assumed that lichens did not establish on saplings). For these trees, we also counted the number of dead and live branches (≥ 1 m long) between 1 and 5 m above ground to estimate the quantity of long branches available for lichen establishment in the lower canopy. In *Picea mariana* forests, lichen loading is more likely to occur in the lower canopy since branches are longer and older, thus increasing the chances for lichen colonization. Twenty live mature *Picea mariana* trees were randomly selected for sampling. On each tree, one branch, at least 1 m long, was randomly collected with a pruning saw between 1 and 5 m above ground. Branches were generally short in the studied forests. Mean length of sampled branches was 1.3 m, and only 4% exceeded 2 m. We sampled branches up to 5 m to increase the chance of collecting long branches. We recorded the length, diameter, height of attachment, orientation, and vitality (dead or live) for each branch. All lichen sampling was done on the outermost 1 m section of the branches.

Studied lichens

Three groups of fruticose lichens were considered in this study: *Bryoria* spp., *Evernia mesomorpha*, and *Usnea* spp. (hereafter *Bryoria*, *Evernia*, and *Usnea*). These species, together with foliose lichens, such as *Hypogymnia physodes* (L.) Nyl. and *Tuckermanopsis americana* (Spreng.) Hale, and crustose lichens, such as *Mycoblastus sanguinari* (L.) Norman, account for a significant proportion of the epiphyte standing crop in boreal *Picea mariana* forests (Boudreault et al. 2002). *Bryoria* spp. and *Usnea* spp. have filamentous thalli with long narrow branches and are attached at their base to the substrate, principally on branches of trees. *Evernia mesomorpha* has a coarser thallus with angular branches. *Bryoria* spp. was treated collectively. It was almost completely dominated by *Bryoria furcellata* (Fr.) Brodo & D. Hawksw., a species with an erect shrubby growth form. Other species were *Bryoria nadvornikiana* (Gyelnik) Brodo & D. Hawksw. (erect-pendulous) and *Bryoria trichodes* (Michaux) Brodo & D. Hawksw. (pendulous). The taxonomy of *Usnea* spp. is too complex to be divided into species by field identification. However, the pendulous species *Usnea filipendula* Stirton was clearly the dominant species. Lichen thalli are exposed to different mechanical stress considering their position in the canopy and pendulous species have been shown to be particularly sensitive to edge effects (Esseen and Renhorn 1998). Asexual reproduction by soredia, isidia, and thallus fragments dominate in the studied species.

Lichen biomass

Lichen abundance was estimated by measuring the length of the tallest thallus (to the nearest mm) on the 1-m branch sections directly in the field for each of the three lichen groups. Length measurements were only performed when the thalli were dry. Lichen mass was then calculated from the relationship between maximum thallus length of a lichen group and total mass of this lichen on 1-m branch sections (McCune 1990; Esseen and Renhorn 1998). These empirical

relationships were obtained using a subsample of 10 sites. We measured the maximum length and removed all thalli of the three lichen groups on a total of 800 branches. Lichen mass was measured after drying at 60°C for 24 h. After log transformation of the data, simple regression analyses were then conducted to assess the relationship between maximum thallus length and total mass on branch sections (Fig. 1). Maximum thallus length explained between 57% (*Bryoria* spp.) and 71% (*Usnea* spp.) of the variation in lichen mass. We assessed the habitat quality of the studied sites by estimating lichen biomass per hectare in the lower canopy (1–5 m). This was done by combining the mean lichen mass per 1-m branch section, the number of branches per tree, and the number of trees per hectare.

Statistical analysis

Nested analysis of covariance (ANCOVA) was used to compare lichen biomass distribution on branches along the 15 edge–interior transects adjacent to clearcuts of different age. The transects were divided into three edge age-classes: 1–3 years, 8 years, and 14–23 years, based on age of the clearcut (Table 1). We used general linear models general factorial procedures in SPSS (SPSS, Inc. 1999) and treated edge age and distance from edge as fixed factors and site location as a random factor nested within edge age. The response variable was the mean lichen biomass per branch calculated over the 20 sample branches per plot. Each plot was treated as one replicate. Lichen mass was square-root transformed ($x^{0.5} + (x + 1)^{0.5}$) to fulfill the requirements of parametric analysis. Because of variation in stand structure among sites, we included stem density and mean tree age at breast height as covariates. Pairwise comparisons (contrasts) of means were done using 100 m as reference category.

For the stand variables (density, basal area, mean tree age, percent logs, percent snags, etc.), we considered plots as independent replicates. Nested analysis of variance (ANOVA) was used to assess differences in stand variables among edge age, site location (nested within edge age) and distance from the edge. Number of logs was square-root transformed ($x^{0.5} + (x + 1)^{0.5}$), while percent snags, percent *Picea mariana* and canopy cover were arcsine transformed ($\arcsin x^{0.5}$) prior to analysis.

The forest fragments were divided into three size groups: (i) <0.5 ha fragments, (ii) 1–2.8 ha, and (iii) >4 ha. The 12 isolated fragments were compared with the interior (100 m) sample plots of each transect in 15 residual forests (>4 ha). A one-way ANOVA was used to assess the effect of fragment size on stand variables and lichen mass. Each fragment was treated as one replicate. Lichen mass was square-root transformed prior to analysis.

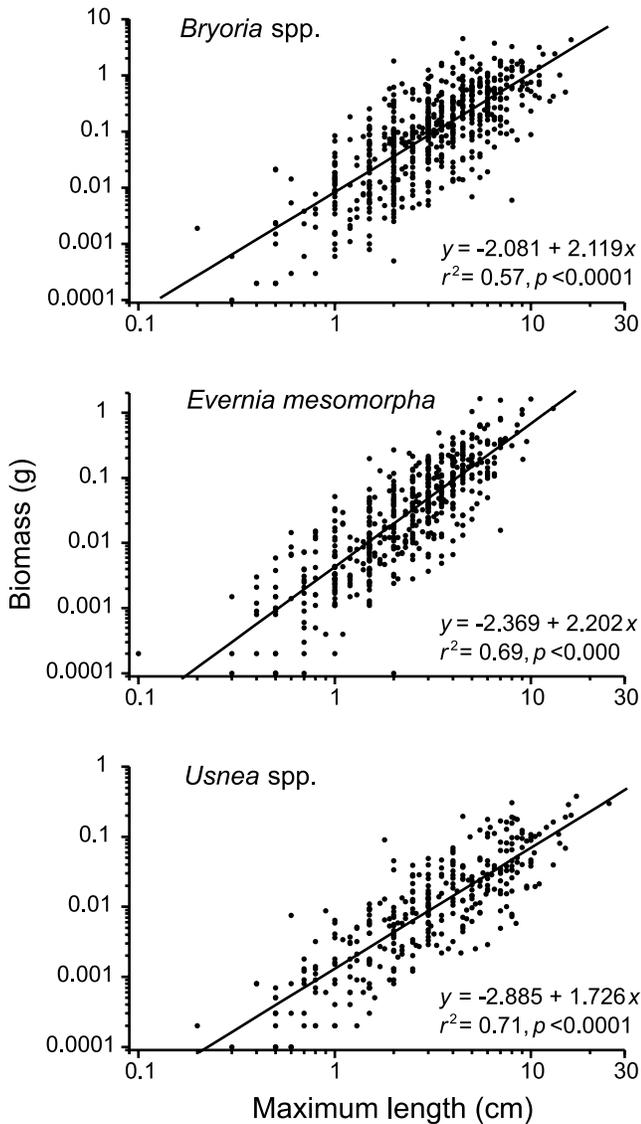
Results

Effect of distance to edge and edge age in residual forests

Stand characteristics

Stand structure showed much variability between sites and between edge age-classes (Table 2). Site had a significant effect on all stand variables (Table 2). This is not surprising considering the large distances between the study sites and given that older edges were concentrated in a landscape

Fig. 1. Relationships (\log_{10} scale) between maximum thallus length and mass (grams dry mass) of *Bryoria* spp. ($n = 645$), *Evernia mesomorpha* ($n = 544$), and *Usnea* spp. ($n = 342$) and on 1-m branch sections of *Picea mariana*.



dominated by old-growth forests (>140 years), which had an open canopy structure, whereas newly created edges where close to mature forests (100–120 years), which had a much more closed canopy (Harper et al. 2002). Nevertheless, some significant differences within the edge–interior transects also emerged from the analysis. Distance to edge had a significant effect on canopy cover, abundance of snags and logs, and availability of suitable branches for epiphytes (Table 2).

Comparison of means (Fig. 2) show that the proportions of snags and logs increased towards the edge, averaging a total of 20% of mature trees mortality (10.1% snags and 11.3% logs) at the edge (5 m). This represent twice the mortality found in interior forest plots (4.2% snags and 5.6% logs). The edge is also characterized by an opening of the canopy with a mean canopy cover of 50.6% compared with 67.2% in the interior. There is also a change in the number of branches (>1 m long) in the lower canopy with distance

into the forest. The quantity of branches gradually declined with proximity to edge and was 23% lower at the edge compared with the interior.

Lichens abundance on branches

Bryoria spp. was the most frequent and abundant group of epiphytic lichens; it was found on 87% of the sampled 1-m branch sections. Its mass was more than 0.1 g/branch in 45% of the cases, and the overall mean was 0.20 ± 0.01 g (mean \pm SE, $n = 1188$). The maximum mass per branch was 4.7 g. *Evernia mesomorpha* and *Usnea* spp. occurred on 65 and 36% of sampled branches, respectively. The overall means were 0.048 ± 0.003 g and 0.0076 ± 0.0006 g for *Evernia* and *Usnea*, respectively. Maximum mass per branch reached 1.2 g for *Evernia* and 0.3 g for *Usnea*.

The lichen mass was influenced by the vitality of the sampled branch, branch diameter, and DBH of the sampled tree. Branch vitality accounted for most of the variation in lichen mass. Dead branches supported 2.6 times (*Evernia* and *Usnea*) and 3.3 times (*Bryoria*) higher lichen mass than live ones. All three groups of lichens showed significant ($p \leq 0.02$) correlations (Spearman's coefficients) with branch diameter. *Bryoria* and *Usnea* were also correlated with tree diameter ($p < 0.001$).

All three groups of lichens were less abundant on branches in edge plots (5, 25, 50 m) than in the interior (100 m; Fig. 3). The edge/interior (5 m/100 m) ratios were 0.86, 0.55, and 0.49 for *Bryoria*, *Evernia*, and *Usnea*, respectively. After controlling for differences in stem density and tree age among plots, lichen mass on branches differed significantly among sites and with distance to edge for *Evernia* and *Usnea* (Table 3). *Bryoria* was not affected by distance, but there was an effect of edge age. The highest mass of *Bryoria* was found in edges of intermediate age (8 years). There was also a significant effect of edge age in *Usnea*. The highest means were found in residual forests from recently harvested areas (1–3 years), whereas the lowest means were found in residual forests adjoining 8-year-old clearcuts. Since the interaction between edge age and distance from the edge was not significant, we assumed that the influence of distance on the biomass of *Evernia* and *Usnea* was prevalent over time.

The estimated standing biomass of lichens in the lower canopy of the sites averaged 5596 ± 922 , 1214 ± 182 , and 143 ± 20 g/ha for *Bryoria*, *Evernia*, and *Usnea*, respectively. The corresponding edge/interior ratios were 0.63, 0.53, and 0.37, respectively.

Effect of fragment size

We found no significant effect of size of forest fragments on stand variables including stem density, basal area, tree mortality, and branch availability (ANOVA, $p > 0.05$, $df = 2, 26$), nor did we find a significant effect of fragment size on any of the three lichen groups; however, the mass of *Usnea* was notably lower in all seven small fragments (<0.5 ha; Fig. 4).

Discussion

Edge effects

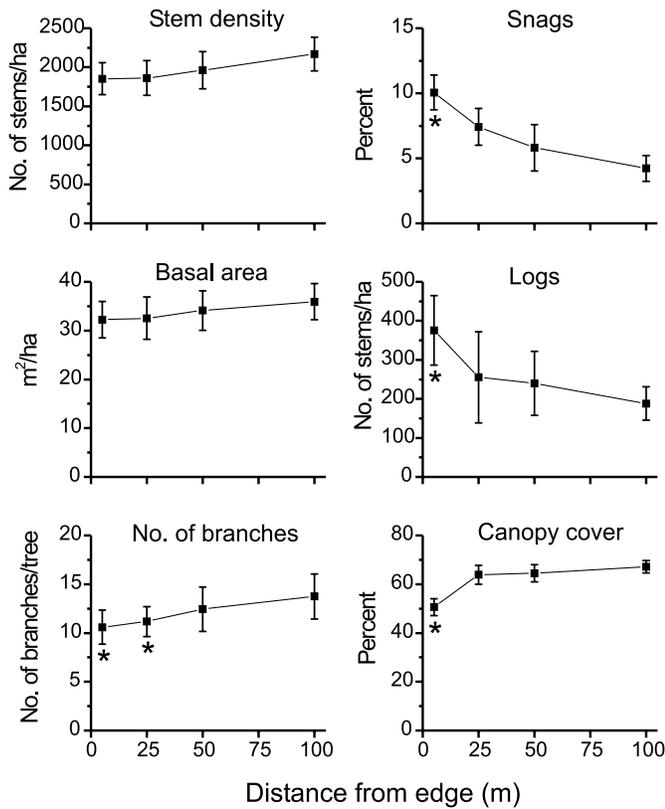
We found significant effects of distance to forest edge on

Table 2. Summary of nested analysis of variance tests for the effects of two fixed factors (distance to edge, edge age) and one random factor (site) on nine stand variables.

Source of variation	df	Stem density	Basal area	No. of branches/tree	Snags ^a	Logs ^b	Canopy cover ^a	% <i>Picea</i> ^a	Tree age	Maximum tree height
Distance (D)	3	0.708	0.771	0.007	0.003	0.005	<0.001	0.568	0.826	0.101
Edge age (A)	2	0.042	0.000	0.001	0.498	0.380	0.131	0.525	0.032	0.262
Site(A)	12	0.001	0.003	<0.001	0.005	<0.001	<0.001	0.003	<0.001	<0.001
D × A	6	0.772	0.392	0.040	0.081	0.781	0.850	0.124	0.729	0.586
Error	35									

Note: Values are probabilities.
^aArcsine transformed.
^bSquare-root transformed ($x^{0.5} + (x + 1)^{0.5}$).

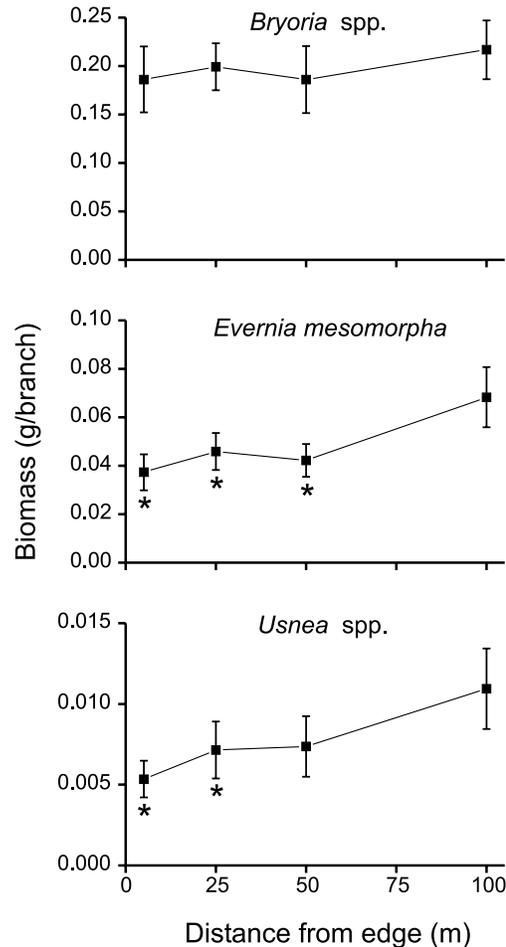
Fig. 2. Change in stand characteristics (mean ± 1 SE) in edge to interior transects in *Picea mariana* forests (N = 15 plots per distance). Distances with asterisks are significantly different (p < 0.05) from 100 m based on nested ANOVA (cf. Table 2).



abundance of epiphytic lichens in *Picea mariana* forests. The abundance of *E. mesomorpha* and *Usnea* spp. at the edge represented about half of that found in the forest interior. Our results indicate that edge influence may extend about 50 m into the forest for *E. mesomorpha* and *Usnea* spp. This is consistent with results found for *Alectoria sarmentosa* in *Picea abies* forests in Sweden (Esseen and Renhorn 1998).

Substrate quality and quantity are important to consider when studying edge effects on epiphytic lichens. First, it has been reported that abundance of fruticose species is correlated with mass, diameter, length, state of defoliation, and

Fig. 3. Change in mass (mean ± 1 SE) of *Bryoria* spp., *Evernia mesomorpha*, and *Usnea* spp. per branch with distance into the forest in 15 edge–interior transects. Distances with asterisks are significantly different (p < 0.05) from 100 m based on nested ANOVA (cf. Table 3).



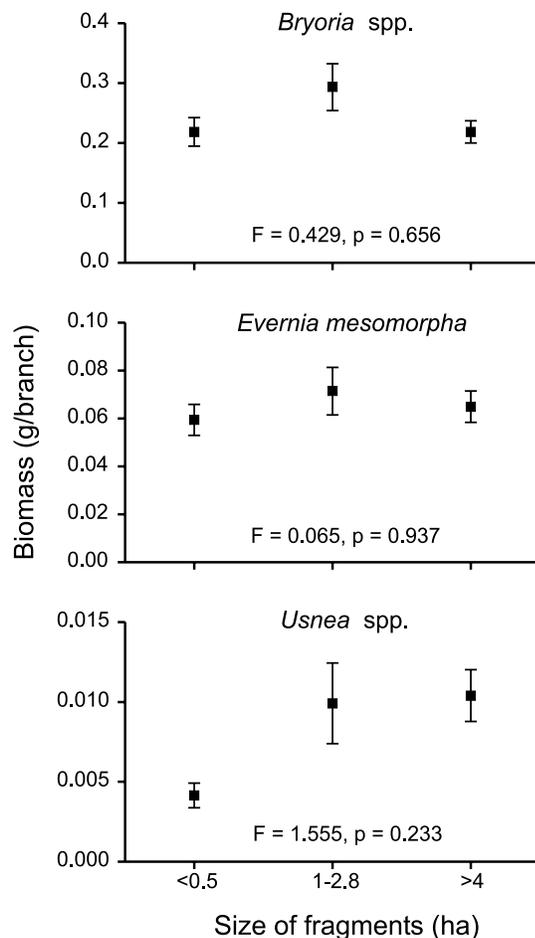
age of branches as well as DBH, height, and tree age (Arseneau et al. 1998; Esseen et al. 1996; Gauslaa et al. 1998; Boudreault et al. 2002). In our study, in conjunction with the effects of edges, DBH of the sampled tree, branch diameter, and vitality influenced the abundance of the studied species. The highest lichen mass was found on dead

Table 3. Summary of three nested analysis of covariance tests for the effects of distance to edge, edge age, site location, stem density, and tree age on biomass of three groups of epiphytic lichens on 1-m branch sections.

Source of variation	df	<i>Bryoria</i>		<i>Evernia</i>		<i>Usnea</i>	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Distance (D)	3	0.485	0.695	4.571	0.01	4.393	0.01
Edge age (A)	2	6.491	0.004	1.365	0.281	4.659	0.025
Site	12	0.683	0.755	2.557	0.016	3.228	0.004
D × A	6	0.400	0.874	1.392	0.247	0.410	0.867
Stem density	1	0.137	0.713	9.330	0.004	8.756	0.006
Tree age	1	4.011	0.053	0.000	0.983	5.288	0.028
Error	33						

Note: Tree age and stem density were treated as covariates. The biomass data were square-root transformed ($x^{0.5} + (x + 1)^{0.5}$).

Fig. 4. Comparisons of mass per branch (mean \pm 1 SE) of *Bryoria* spp., *Evernia mesomorpha*, and *Usnea* spp. among three size classes of forest fragments ($N = 7$ (<0.5 ha), $N = 5$ (1–2.8 ha), and $N = 15$ (> 4 ha)). Results from one-way ANOVA ($df = 2, 26$) are shown for each species. The lichen mass data were square-root transformed ($x^{0.5} + (x + 1)^{0.5}$) prior to analysis.



branches still covered with bark, which is essential for their attachment. The lower abundance at the edge may possibly be due to lower substrate quality because of a high proportion of dry and exposed branches. Moreover, thallus penetra-

tion depends also on physical and chemical characteristics of bark (Van Haluwyn and Lerond 1993) that may have been altered at the edge.

Second, assessing substrate availability provides information on the potential of a site to support epiphytes. A lichen thallus may be resistant to microclimatic edge effects but not to the loss of their substrate. Higher tree mortality and damage levels were an indication of the unfavourable microclimatic conditions prevailing at edges. There was an increasing proportion of logs and snags and a decreasing number of branches on living trees with proximity to the edge. Studies that considered external microclimate and structural variables revealed that edge effects such as higher temperature, higher wind speeds, and lower humidity extended from 30 to 240 m in tall Douglas-fir forests (Chen et al. 1992) and led to higher rates of treefall that prevailed at distances up to 60 m into Amazonian forests (Laurance et al. 1998). Young and Mitchell (1994) suggest that such microclimatic and structural changes extended approximately 50 m in a podocarp–broadleaf forest in New Zealand. The same result was observed in an oak–chestnut forest in the eastern United States (Matlack 1993). Depth of edge influence on microclimate is strongly related to the height of the canopy (Matlack and Livaitis 1999). The trees in the studied boreal *Picea mariana* forests are much shorter (mean height of 12 m) thus explaining why the depth-of-edge influence on the structural features (opening of the canopy, quantity of snags, logs and long tree branches) is shorter for this vegetation type. However, the response of epiphytes revealed that sensitivity to edge effects extended to distances beyond the limit of detectable structural changes in forest canopy.

Temporal pattern

The expression of edge effects may change with time since edge creation (Matlack 1993; Esseen and Renhorn 1998). High tree mortality generally occurs in the initial phase of isolation of forest fragments (Williams-Linera 1990) followed by high regeneration due to increased understory irradiance. The edge functions as a screen for penetration of open conditions into the forest (Wales 1972; Ranney et al. 1981; Palik and Murphy 1990; Williams-Linera 1990; Brothers 1993; Didham and Lawton 1999). In our study area, regeneration at the edge was not high enough

to reduce edge effects at the canopy level, even in sites adjoining 23-year-old clearcuts. As a consequence, edge effects may affect residual *Picea mariana* forests for a long time before a buffer zone develops. The extent of edge influence was constant over time for both *Evernia* and *Usnea* as well as for stand characteristics such as the proportion of snags, logs, and loss of branches. As already observed in the mixedwood boreal forest in Alberta (Canada) (Harper and McDonald 2001) structural parameters at stand edges respond rapidly to the clear-cut logging of adjacent stands. Thus maximum damage occurs during the first years of exposure, killing most the vulnerable individuals. In the present study, the 8- to 23-year-old edges still showed evidence of this initial edge influence.

Remnant forests

In theory, the size of an isolated forest fragment determines its potential to support viable populations because with decreasing size, greater will be the influence of external factors (Saunders et al. 1991). In our study, we found no significant effect of fragment size on epiphyte abundance. However, the mean mass of *Usnea* on branches in small fragments (<0.5 ha) was very low compared with that found in some interior forests of uncut blocks (larger than 4 ha). This is consistent with our results on *Usnea*'s response to edge influence. Overall, this group of epiphytic lichens seems to be sensitive to habitat fragmentation either through edge effects or by size reduction of remnant patches. In such small fragments, if the depth-of-edge-influence truly averaged 25 m, interior forest conditions disappeared. In a study of the richness and composition of calicioid lichens in forest islands, Krusys and Jonsson (1997) suggested that edge effects were responsible for changes in habitat quality restricting the presence of sensitive species to the interior environment of large islands (>3 ha) whereas these species were absent from smaller ones (<1 ha). Esseen (1994) reported severe tree damage in isolated forests and mortality in forest fragments ranging in size from ~0.06 to 1 ha. Even though our sample was small, our results for *Usnea* are consistent with the general trend observed by Esseen (1994).

The lack of response of epiphytic lichens to fragment size, in particular *Evernia* and *Bryoria*, may indicate that these groups show a higher tolerance to habitat disruption than what was reported for lichens in Fennoscandia (Krusys and Jonsson 1997; Esseen and Renhorn 1998). Our results must be interpreted with caution, since our sample set was small. Additional research on the effect of remnant size in cutover blocks and their contribution to the maintenance of epiphytic lichens is necessary to assess these relationships with more statistical power.

Response mechanisms

In the present study, *Usnea* spp. was the most sensitive to edge influence, while *Bryoria* spp. was the least affected. *Evernia mesomorpha*, although more prone to mechanical damage than *Bryoria*, showed a more complex response to edges. Several factors may influence the sensitivity of lichens to forest edges. Thallus morphology (attachment to the substrate and thallus length) may contribute to explain the respective vulnerability of our studied lichens to edge effects. Attachment to the substrate varies among species and

may affect resistance to mechanical stress considerably. In our study, *Bryoria* spp. was dominated by *B. furcellata*, a tufted species that grows rolled up around branches thus having a better hold on the substrate. *Evernia mesomorpha* is fixed to its substrate along its entire base. This growth pattern allows thalli to have better contact with the substrate. In contrast, *Usnea* spp., predominantly pendulous in the study area, with only one point of attachment, can be rapidly dislodged. The thalli hang freely down from the substrate and are more prone to fragmentation. Hence, the studied lichen groups cover a range of sensitivity to substrate removal that is partly reflected in their response to edge effects.

The reduction in mass for our lichen groups was not as pronounced as documented for the pendulous lichen *Alectoria sarmentosa* in Fennoscandian *Picea abies* forests (Esseen et al. 1981; Esseen and Renhorn 1998). One possible explanation is that the studied lichen groups were potentially less prone to mechanical damage given that *Alectoria sarmentosa* was much longer. However, significant relationships with distance to edge were obtained for mass of both *Evernia mesomorpha* and *Usnea*, suggesting that epiphytic lichens are indeed suitable indicators for assessing edge effects. Finally, the erect and shrubby physiognomy of most lichens in the low *Picea mariana* forests may also explain the differences in lichen response compared with large pendulous lichens in the taller *Picea abies* forests in Fennoscandia.

The studied lichens also have different habitat preferences that contribute to their respective adaptability to disturbance. In general, epiphytic lichens are more frequent in older natural forests than in younger managed serial stages (Adams and Risser 1971; Lesica et al. 1991; Tibell 1992; Goward 1994; Dettki and Esseen 1998; Boudreault et al. 2002). Structural diversity (gaps, snags, veteran trees) and more stable climatic conditions in older forests are thought to favour development of sensitive lichens. In northwestern Quebec *Usnea* spp. is most abundant in forests older than about 160 years, whereas *B. furcellata* is a widespread generalist that is more abundant in mature forests (80–120 years old) (Boudreault et al. 2002). *Bryoria* spp. is also known to colonize the upper canopy where wind and dryness are the predominant conditions (Arseneau et al. 1998). Thus it is not surprising that this group didn't respond to edge effects considering the preference of *B. furcellata* for exposed habitats. *Evernia mesomorpha* is considered endangered in Sweden and used as an old-growth indicator species (Tibell 1992). In Quebec, however, it is common in different forest cover types and becomes particularly abundant on trunks of dead trees in humid open areas such as beaver swamps (I. Brodo, personal communication). Thus, this species shows a more complex response to edge effects. Habitat requirements of three groups of lichens thus demonstrate distinctive levels of adaptability to forest edge environments.

Conclusion

This study demonstrates that epiphytic lichens are potentially fine filter indicators for the evaluation of edge effects in Canadian *Picea mariana* forests. The results thus support those of Esseen and Renhorn (1998) from Scandinavia and

suggest that epiphytic lichens may respond to edge influence throughout the boreal forest. What remains to be evaluated is how far different edge effects on epiphytic lichens extend into managed forests compared with edge effects in natural forests. Monitoring the abundance of epiphytic lichens may be a valuable tool for comparisons of natural and man-altered systems and can guide sustainable forest management focused on emulating natural patterns and processes of forest ecosystems. More work should be conducted within such a comparative framework at the landscape scale.

Assessing edge effects and depth of edge influence in remnant forests may help to determine the proportion of forest that is dominated by “interior forest conditions”. The abundance of *Usnea* seems to be a potentially useful tool to forest managers in determining the size of remnant stands that should be left in timber harvested forest landscapes to ensure sufficient interior habitat for the long-term persistence of epiphytic lichens in *Picea mariana* forests. However, additional studies are required to fully explore the potential of epiphytic lichens as indicators of edge effects.

Depth of edge influence on epiphytic lichens may also provide baseline data for planning the shape of remnant forests. The width of linear remnant forests such as riparian buffer strips and upland strips between cutblocks is indeed often less than the depth of edge influence (50 m) confirmed for epiphytic lichens in this study. Hence, such remnant habitats may be devoid of interior forest conditions and epiphytic lichen populations may be more prone to edge effects, reducing the dispersal and subsequent recovery of these organisms in cutover areas.

Finally, while patch characteristics of remnant forests are important, their spatial arrangement within cutblocks is of critical importance for dispersal and, hence, long-term persistence of epiphytic lichens in managed landscapes. Sillett et al. (2000), Dettki et al. (2000), and Hilmo and S astad (2001) provide strong support for the hypothesis that dispersal limitation is an important cause for the low abundance of epiphytic lichens in young forests. At the landscape scale, fires are more likely to leave unburned patches (Kafka et al. 2001) and create sinuous and structurally complex edges that may reduce the dispersal distance between unburned and burned areas compared with the distinct and linear boundaries originating from timber harvesting. Thus, leaving peninsulas and large islands of old forest tracts in cutblocks may greatly enhance epiphyte colonization and accumulation of second-growth forest stands.

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