

Effects of selection cutting on the abundance and fertility of indicator lichens *Lobaria pulmonaria* and *Lobaria quercizans*

Mattias Edman*, Anna-Maria Eriksson† and Marc-André Villard

Chaire de recherche du Canada en conservation des paysages, Département de biologie, Université de Moncton, Moncton, New Brunswick, Canada E1A 3E9

Summary

1. Although selection cutting is probably less harmful to forest ecosystems than clear cutting, its effects on biodiversity remain largely unexplored. We investigated the previously unstudied effects of selection cutting on the abundance and fertility of two dominating species of epiphytic lichens, *Lobaria pulmonaria* and *Lobaria quercizans*, in a northern hardwood forest of New Brunswick, Canada.

2. Twenty-eight forest stands were selected representing two contrasting silvicultural treatments: fairly recent selection cuts (5–9 years) and ‘uncut’ stands that had been subjected to low-intensity single-tree cutting at least 35 years ago. Within each stand, we quantified the abundance and fertility of lichens on 36 trees together with selected forest stand variables.

3. Although both species had survived harvesting, the abundance of *L. quercizans* and *L. pulmonaria* was four and five times higher, respectively, in uncut stands than in selection cuts. The most important predictive factors for lichen abundance at the stand level were total basal area and canopy closure, which were much lower in selection cuts. Furthermore, the abundance of both species at the tree level was significantly correlated with tree size.

4. Most interestingly, fertile *L. quercizans* and *L. pulmonaria* were, respectively, five and 26 times more frequent in uncut stands. In addition, for *L. pulmonaria* the fertility frequency was only 3% in selection cuts, compared with 37% in uncut stands. The fertility of both lichen species was strongly correlated with their abundance at the tree level.

5. *Synthesis and applications.* Our results indicate that selection cutting has a strong impact on the abundance and fertility of these two *Lobaria* species, and that studies ignoring fertility may underestimate the negative effects of forestry on lichens. To reduce the negative effects we have three recommendations. (i) Large trees from old seral stages should be retained during selection cuts. (ii) The cutting cycle should be extended and the basal area removed should be reduced. These actions would improve the microclimate, increase the amount of suitable habitat and prolong the time window for lichen colonization in selection cuts. (iii) Some mature deciduous forest stands should be protected at the regional scale. This would promote the long-term persistence of large, sexually reproductive lichen populations and concurrently benefit all species tightly linked with mature hardwood forests.

Key-words: *Acer saccharum*, Canada, forest management, *Lobaria quercizans*, northern hardwood forest, sexual reproduction, single-tree cutting

Introduction

Epiphytic lichens constitute a key functional component of forest ecosystems. As well as their contribution to nutrient cycling by nitrogen fixation and, eventually, release of litter, epiphytic lichens provide food, shelter and nest material for animals (Gearson & Seaward 1977; Pettersson *et al.* 1995).

*Correspondence and present address: Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden. E-mail mattias.edman@szoek.slu.se

†Present address: Department of Natural Sciences, Mid Sweden University, Sundsvall, Sweden.

However, the changes in stand structure and landscape composition that follow various forest management practices adversely affect many lichens. The availability of suitable substrates decreases (Hedenås & Ericson 2000), dispersal becomes limiting (Dettki & Esseen 1998; Sillet *et al.* 2000; Hilmo & Sástad 2001) and lichen growth rates are often reduced because of microenvironmental changes (Hedenås & Ericson 2000; Gauslaa *et al.* 2001). Consequently, there is usually a strong contrast between managed and old-growth stands in terms of the species composition and abundance of epiphytic lichens (Lesica *et al.* 1991; McCune 1993; Esseen, Renhorn & Pettersson 1996; Kuusinen 1996; Dettki & Esseen 1998). Clearly, the impact of forestry on epiphytic lichens depends on the silvicultural practices, forest type and lichen species involved. Thus there is a growing need for scientifically based knowledge that can be implemented in forestry practices. In New Brunswick, Canada, mature naturally regenerated forests are gradually being converted into clear cuts (usually followed by spruce plantation) or selection cuts. In deciduous stands, only selection cutting is allowed on public lands, according to provincial regulations. Although selection cutting is probably less harmful to these forest ecosystems than clear cutting, its effects on biodiversity remain largely unexplored (but see Bourque & Villard 2001; Jobes, Nol & Voigt 2004; Lindner, Burdsall & Stanosz 2006).

In addition to the decline in lichen abundance that often follows forest management, lichen sexual reproduction may be affected. Although there is a growing body of literature concerning the effects of forestry on epiphytic lichens, no previous study, to our knowledge, has addressed this question. Many lichens are able to reproduce both sexually and asexually. However, sex has metabolic costs and, if they are subjected to large microenvironmental changes, lichens might be predicted to favour vegetative/asexual reproduction (Seymour, Crittenden & Dyer 2005). In lichens, vegetative reproduction is carried out through the production of isidia and soredia, which are propagules containing both the fungal and photosynthetic partner. Vegetative dispersal is therefore advantageous in the short term, as both the myco- and photo-biont are dispersed simultaneously (Seymour, Crittenden & Dyer 2005). In the long term, however, sexual reproduction is vital because sexual propagules are believed to promote long-distance dispersal and to enhance genetic diversity within populations, thereby facilitating appropriate responses to environmental changes (Maynard Smith 1978; Walser *et al.* 2004).

Many lichen species that have declined in Europe are still common in North America, probably because of its shorter history of forestry and fragmentation (Walser 2004). One example of such a species is the epiphytic lichen *Lobaria pulmonaria*, which was previously a dominating species in temperate forests of Europe but has decreased markedly in the last century and is now extinct or rare in large areas (Hallingbäck & Martinsson 1987; Rose 1988). In North America, it is still widespread and locally common but decreasing (Brodo, Duran Sharnoff & Sharnoff 2001). Based on their genetic structure, *L. pulmonaria* populations in central Europe appear to have lower frequencies of sexual reproduction than populations in

North America (Walser *et al.* 2005). Indeed, fertile *L. pulmonaria* is rare in Europe but it is believed to have been more common in the past (Wirth 1995; Gu *et al.* 2001; Öckinger, Niklasson & Nilsson 2005). The reasons for this change are unclear; higher levels of air pollution in Europe have been suggested as one possible explanation (Öckinger, Niklasson & Nilsson 2005). However, the decline in fertility may also be related to a severe reduction in the availability of suitable substrates and to adverse changes in site quality, resulting from the longer history of forestry in Europe. Thus there is a need for more knowledge about the effects of forestry on *L. pulmonaria* and other epiphytic lichen species in North America, as they may be at the beginning of a decline similar to the one that has already occurred in Europe.

This study examined the influence of selection cutting on two epiphytic *Lobaria* species, *Lobaria pulmonaria* (L) Hoffm. and *Lobaria quercizans* Mich., the dominating epiphytic lichen species in hardwood forests of New Brunswick. We addressed the following questions. (i) Are there any differences in species presence, abundance and fertility between uncut, mature stands and first-entry selection cuts? (ii) Which forest stand variables are the most important predictors of lichen occurrence at the stand level? (iii) Does tree size have any influence on lichen abundance at the tree level? (iv) Is there any relationship between the abundance of these lichen at the tree level and the presence of fertile thalli, as indicated by the presence of apothecia?

Methods

STUDY AREA

The study was conducted on industrial freehold land owned by Acadian Timber Income Fund, north-western New Brunswick, Canada (47°10' N, 67°13' W). The area is characterized by an undulating forest landscape, with shade-tolerant deciduous tree species dominating on hill tops, coniferous species in the valleys, and scattered mixed-wood stands on hillsides. The dominant tree species in the study area was sugar maple *Acer saccharum* Marsh., with American beech *Fagus grandifolia* Ehrh. and yellow birch *Betula alleghaniensis* Britt. as subdominants. Other tree species that occurred in lower proportions were white birch *Betula papyrifera* Marsh., red maple *Acer rubrum* L., balsam fir *Abies balsamea* (L.) Mill., black spruce *Picea mariana* (Mill.) (BSP), white spruce *Picea glauca* (Moench) Voss and red spruce *Picea rubens* Sarg. The shrub layer consisted mainly of seedlings and saplings of canopy trees.

The deciduous and mixed forest stands in the study area are subjected to selection cutting in which typically c. 30% of the basal area (c. 40 m³/ha) is removed every 20 years (Anonymous 1995). Management of these forests began in the late 1980s. Prior to that, only low-intensity 'high-grading' was performed, whereby the most valuable tree species and individuals were harvested opportunistically.

STUDY SPECIE

Lobaria pulmonaria and *L. quercizans* are large foliose lichens that grow on the bark of deciduous trees in North America, particularly maples. In suitable habitats they may grow to be very large, covering large parts of tree stems and, like all *Lobaria* species they are good

indicators of rich, unpolluted and often very old forests (Brodo, Duran Sharnoff & Sharnoff 2001). In addition, high abundance of *L. pulmonaria* has been shown to indicate a high diversity of macrolichens (Nilsson *et al.* 1995; Campbell & Fredeen 2004). The global distribution of *L. quercizans* is limited to eastern North America and South America, whereas *L. pulmonaria* is widespread throughout the northern hemisphere and in parts of the southern hemisphere (Yoshimura 1971). *Lobaria pulmonaria* is known to reproduce both sexually via ascospores produced in apothecia (fruiting bodies) and asexually via soredia and thallus fragments (Scheidegger 1995), while *L. quercizans*, as far as we know, only reproduces sexually (Brodo, Duran Sharnoff & Sharnoff 2001).

FIELD DATA COLLECTION

From July to August 2005 we surveyed *L. pulmonaria* and *L. quercizans* in 28 mature, deciduous stands dominated by sugar maple. All the stands were selected a priori from forest stand maps provided by Fraser Papers Inc. (Toronto, Canada). Fourteen stands were subjected to single-tree selection cutting during the period 1996–2000 and 14 stands were uncut. However, all stands labelled 'uncut' had been subjected to low-intensity single-tree cutting before the 1970s. The stands surveyed were at least 600 m apart, but most stands were separated by more than 1 km. Within each stand we quantified lichens along three 80-m transects orientated towards the north, south-east and south-west of a centre point, which was located at least 120 m from clearings, plantations and roads to reduce edge effects. In each transect, 12 maples of ≥ 15 cm diameter at breast height (d.b.h.) were sampled by selecting the nearest maple on each side of the transect every 10 m up to 60 m. By applying this procedure, we sampled trees representing the whole transect. Thus a total of 36 trees was sampled in each stand. For each tree, the d.b.h. was measured.

LICHEN SAMPLING

The abundance of the lichens was estimated on the lowest 3 m of the trunk of each tree, including the basal portion. Absolute values in cm² were estimated using a measuring tape. We also determined their presence or absence on the whole trunk using binoculars. In addition, to assess the fertility of the lichen thalli, the lowest 3 m of the trunk were investigated for the presence-absence of vital apothecia.

VEGETATION SAMPLING

Forest structure was quantified along the three 80-m transects in each stand. Species and d.b.h. were recorded for all trees within a 2-m band on either side of the transects. At the centre point and every 20 m along the transect (10 plots stand⁻¹), we quantified canopy closure and sapling (> 2 m high, ≤ 8 cm d.b.h.) density within a 2-m radius and determined basal area with a prism. Canopy closure was estimated by counting the squares with canopy foliage through a 5 × 5 transparent grid made of Plexiglass, held overhead. The density of saplings higher than 2 m was counted because they could potentially influence the microclimate around the lower parts of the tree trunks.

STATISTICAL ANALYSE

We analysed the data at two spatial scales: stand level and single-tree level. To compare differences in forest stand characteristics between uncut stands and selection cuts, we used a two-sample independent *t*-test. Differences in the frequencies of lichen-hosting trees, lichen

abundance and the abundance of trees with fertile lichen between uncut stands and selection cuts were examined using Mann–Whitney's *U*-test. To account for the effects of variation in tree size when analysing lichen abundance, cover values were divided by the total stem surface area. Stem surface area was calculated approximately by multiplying d.b.h. with pi and height (lowest 3 m of the stem). The influence of the measured forest stand variables (i.e. basal area of different tree species, canopy closure, sapling density and d.b.h.) on the frequency of lichen-hosting trees at the stand level was examined separately for uncut stands and selection cuts using multiple stepwise regressions. Although there were some correlations among forest stand variables (see Appendix S1 in the supplementary material), tolerances were high except for the basal area of *Acer saccharum*, which showed high collinearity with total basal area. The basal area of *A. saccharum* was therefore omitted from regression models. Lichen abundance data were log-transformed and frequency data were arcsin square-root transformed prior to analyses, to homogenize variances. The residuals of the regression models were checked for independence and normality.

At the tree level, the influence of d.b.h. and stand type on lichen abundance was analysed with generalized mixed-effect models with Poisson errors, using a penalized quasi-likelihood in the MASS package within the statistical packages (R Development Core Team 2006). Stand type was treated as a fixed, categorical factor and d.b.h. as a fixed, continuous covariate. The influence of lichen abundance on the presence of fertile thalli at the tree level was analysed with analyses of covariance (ANCOVA), including only trees on which the respective lichen species were present. Locality was treated as a random factor and fertility as a categorical covariate; d.b.h. was not included as a covariate because it showed collinearity with fertility. The residuals were checked for independence and normality. The analyses were performed using SPSS 15.0 (SPSS 2006).

Results

STAND LEVEL

Selection cuts and uncut stands differed significantly for all measured forest structure characteristics, except for the basal area of *F. grandifolia*. The mean d.b.h. was 12.6% higher, total basal area 40.8% higher, canopy closure 24.9% higher and sapling density 69.2% lower in uncut stands compared with selection cuts (see Appendix S2 in the supplementary material). The frequencies of maple trees hosting *L. quercizans* and *L. pulmonaria* were significantly lower in selection cuts than in uncut stands (Mann–Whitney *U*-test, $P < 0.001$; Fig. 1). In addition, the abundance of *L. quercizans* and *L. pulmonaria* (measured on the lowest 3 m of the stems) was more than four and five times higher, respectively, in uncut stands than in selection cuts (Mann–Whitney *U*-test, $P = 0.001$; Fig. 1). Even when the larger total stem surface in uncut stands was accounted for, lichen abundances were still higher than in selection cuts (Mann–Whitney *U*-test, $P < 0.01$).

Lichen fertility also differed significantly between stand types. The average numbers of maple trees hosting fertile *L. pulmonaria* were 10.4 in uncut stands and 0.4 in selection cuts, implying that it was 26 times more frequent in uncut stands (Mann–Whitney *U*-test, $P < 0.001$; Fig. 1). The same pattern, although not as strong, was found for *L. quercizans*. On average

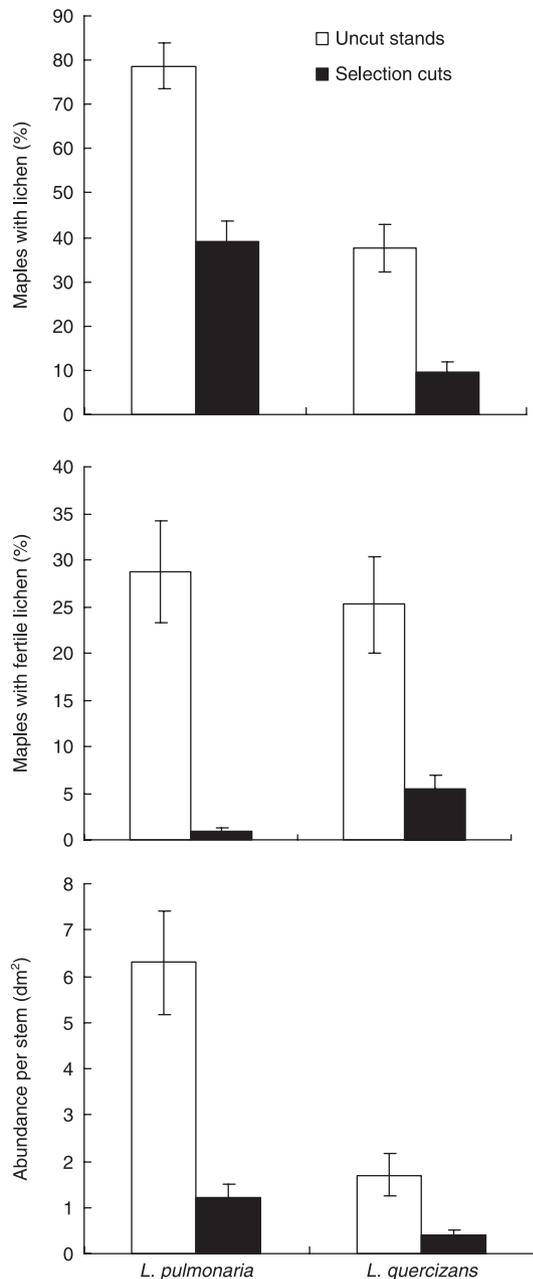


Fig. 1. The frequency of lichen trees, the frequency of maples hosting fertile lichens and lichen abundance per stem (\pm SE) of *L. pulmonaria* and *L. quercizans* in uncut stands ($n = 14$) and selection cuts ($n = 14$). Thirty-six maples were sampled in each stand. All maples, even those without lichen presence, are included.

9.1 maples with fertile lichens were found in uncut stands, compared with 1.8 in selection cuts. Thus fertile *L. quercizans* was five times more frequent in uncut stands (Mann–Whitney U -test, $P < 0.001$; Fig. 1). Furthermore, the fertility frequency, i.e. the frequency of trees hosting fertile *L. pulmonaria*, was much higher in uncut stands (Fig. 2). Pooled data showed that fertile *L. pulmonaria* was present on 36.9% of the trees hosting it in the uncut stands, compared with only 2.6% in the selection cuts (Fig. 2). In contrast, there was no difference in the fertility frequency of *L. quercizans* between uncut stands and selection cuts (69.8% and 66.7%, respectively; Fig. 2).

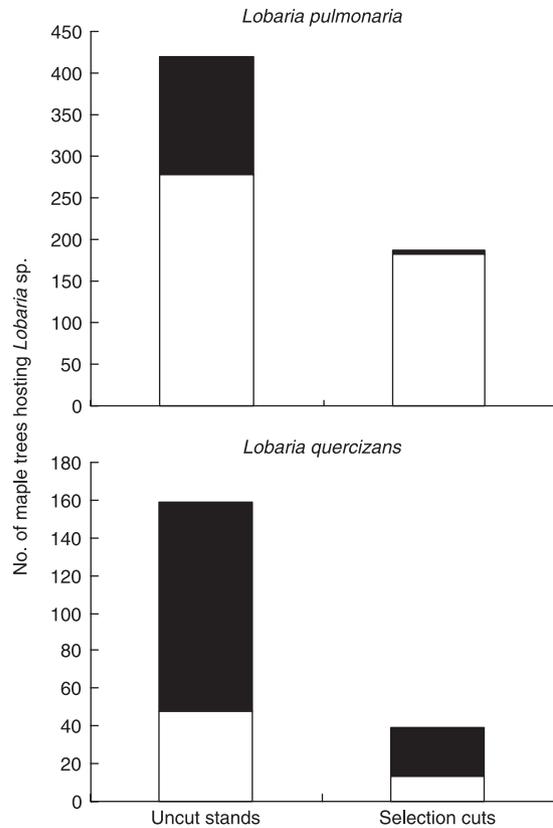


Fig. 2. Pooled data only for trees hosting *L. pulmonaria* and trees hosting *L. quercizans*, showing the total number of lichen trees with the respective lichen present on the lowest 3 m of the stem in uncut stands ($n = 14$) and selection cuts ($n = 14$). The proportion of lichen-hosting trees that displayed fertile thalli (i.e. fertility frequency) is shown in black.

Multiple regression analysis with selected forest stand variables yielded significant models, with total basal area as the single predictive variable for the frequencies of maples hosting *L. quercizans* in both uncut stands (Adj $R^2 = 0.25$, $P = 0.039$) and selection cuts (Adj $R^2 = 0.25$, $P = 0.039$) and *L. pulmonaria* trees in uncut stands (Adj $R^2 = 0.35$, $P = 0.026$). For *L. pulmonaria* trees in selection cuts, canopy closure was the single predictive variable (Adj $R^2 = 0.38$, $P = 0.011$).

TREE LEVEL

The generalized linear models of *L. pulmonaria* abundance showed a significant interaction effect between d.b.h. and stand type (Table 1). For *L. quercizans*, both d.b.h. and stand type showed a strong effect on lichen abundance, but no significant interaction (Table 1).

The presence of fruiting bodies in uncut stands co-varied significantly with the abundance of lichen at the tree level for both *L. pulmonaria* and *L. quercizans* (Table 2). There was also an effect of locality on the lichen abundance in uncut stands (Table 2). In selection cuts, fertile lichens were too rare to be analysed.

Table 1. Generalized mixed-effect models under quasi-Poisson distribution, with lichen abundance of *L. pulmonaria* (Lp) and *L. quercizans* (Lq) at tree level as the dependent variable

Source	Estimate		SE		<i>t</i> -value		<i>P</i>	
	Lp	Lq	Lp	Lq	Lp	Lq	Lp	Lq
Intercept	1.16	-0.52	0.13	0.29	8.68	-1.84	< 0.001	0.065
d.b.h.	0.02	0.03	0.00	0.01	5.99	4.58	< 0.001	< 0.001
Stand type	-2.95	-2.24	0.36	0.69	-8.28	-3.22	< 0.001	0.001
d.b.h. × stand type	0.04	0.03	0.01	0.02	4.27	1.52	< 0.001	0.127

Table 2. ANCOVA of lichen abundance at the tree level as dependent on locality and fertility, including only trees on which the respective lichen species were present

	Variable	Type ^{III} SS	d.f.	Mean square	<i>F</i> -value	<i>P</i>
<i>L. pulmonaria</i>	Intercept	66.4	1	66.4	303.9	< 0.001
	Fertility	25.5	1	25.5	253.8	< 0.001
	Locality	3.8	13	0.3	2.9	< 0.001
	Error	37.0	369			
<i>L. quercizans</i>	Intercept	2.6	1	2.6	19.1	< 0.001
	Fertility	4.5	1	4.5	50.5	< 0.001
	Locality	5.0	13	0.4	4.3	< 0.001
	Error	12.8	144			

Discussion

Our data indicate that first-entry selection cutting strongly affects the abundance, frequency and fertility of the studied *Lobaria* species. The average abundance of *L. quercizans* and *L. pulmonaria* per tree was four and five times higher in uncut stands than in selection cuts, respectively. Similarly, the frequency of sugar maples hosting these lichen species was four and two times higher, respectively, in uncut stands.

Although we found strong effects on lichen abundance, selection cutting does not always affect epiphytic lichens negatively. The effect may differ depending on species, forest type, study area and cutting intensity (Coxson, Stevenson & Campbell 2003; Hedenäs & Ericson 2003; Coxson & Stevenson 2005). The results of our study are probably because of several contributing factors. An important factor is that trees were larger in the uncut stands than in selection cuts. For both lichen species, there was a strong relationship between tree size and the abundance of lichens, indicating the importance of large trees. In addition, for *L. pulmonaria* we found an interaction between d.b.h. and stand type, reflecting the fact that the correlation between d.b.h. and lichen abundance was less pronounced in selection cuts because of a smaller diameter range in those stands. The importance of large trees to some epiphytic lichens has previously been documented by several authors (Gu *et al.* 2001; Johansson & Ehrlén 2003; Öckinger, Niklasson & Nilsson 2005). However, whether it is the tree size *per se* or tree age that is the most important factor remains to be clarified, as these variables are usually strongly correlated. Tree age is important because it increases the time window for colonization, while tree size, which is usually correlated with coarse bark, probably facilitates successful

establishment of lichen propagules (Gu *et al.* 2001; Riiali, Penttinen & Kuusinen 2001). Furthermore, the bark chemistry of large, old trees often differs from that of younger, smaller trees in ways that may make them more suitable for lichen establishment (Gustafsson & Eriksson 1995).

Not surprisingly, basal area was on average 41% higher and canopy closure 25% higher in uncut stands than in selection cuts. These somewhat correlated variables were significant predictors of lichen abundance. Thus it is likely that the reduced basal area and the opened canopy in selection cuts have adversely affected the studied lichens, probably (at least in part) because such structural changes increase the exposure of lichen thalli to intensive light, which in *L. pulmonaria* has been shown to cause permanent damage, particularly in dry thalli (Gauslaa & Solhaug 1996, 1999; Gauslaa *et al.* 2001, 2006). The magnitude of lichen responses to changes in microclimate appears to depend on its spatial orientation on the stem, with thalli growing on the north side having higher vitality and survival rates than those growing on the south side (Hazell & Gustafsson 1999; Gauslaa *et al.* 2001). Indeed, we noticed bleached, dying and dead thalli of both species on the southern side of the stems in some of the selection cuts.

Sexual reproduction is important, because it enhances the genotypic variation within populations and increases the chances of survival in a competitive and/or changing environment (Maynard Smith 1978; Walser *et al.* 2004). It is therefore alarming that there was a strong contrast between uncut stands and selection cuts in lichen fertility. To our knowledge, such effects of forestry on lichen reproduction have not been documented previously. The low abundance of trees with fertile *Lobaria* species observed in selection cuts is not surprising, as the overall abundance of lichen-hosting trees was lower there

than in uncut stands. However, in addition to an overall decrease in the abundance of trees with fertile lichen, our results indicate that selection cutting affects the fertility frequency of *L. pulmonaria*. A possible explanation for the low fertility frequency in selection cuts may simply be that sex becomes too costly for the lichen when the microenvironment is suboptimal, and that it instead favours vegetative/asexual dispersal. Alternatively, environmental conditions just do not suit sexual reproduction. Walser *et al.* (2004) found large variations in the frequency of apothecia among populations in British Columbia and suggested that it depended on exogenous factors such as oceanity. In the present study there was a strong positive relationship between the amount of lichen per stem and the presence of fruiting bodies, indicating that fruiting bodies may only be produced when growth conditions are favourable. However, the presence of small, unfertile thalli may merely reflect recent colonization of the tree by lichen that is not yet sufficiently mature to produce fruiting bodies. In fact, Dennison (2003) has shown that apothecia in *L. pulmonaria* develop in late life stages.

Low fertility in *L. pulmonaria* may also arise from low genetic variability within a population. Zoller, Lutzoni & Scheidegger (1999) found that populations in Switzerland with higher genetic variation were more likely to reproduce sexually than less variable populations (although see Wagner *et al.* 2006). They suggested that *L. pulmonaria* is heterothallic (self-sterile) and thus unable to reproduce sexually in populations with only one mating type. In *L. pulmonaria*, apothecia are formed when conidiospores of a compatible mating type hit another thallus. Conidiospores are formed in pycnidia, which are flask-like structures embedded in the thallus of the lichen. They are therefore not likely to be wind dispersed but splash dispersed, and thus in heterothallic lichens fertilization is most likely to occur within a few metres. Consequently, mature stands that are tens or hundreds of metres away will not contribute conidiospores, and it is possible that the low fertility in the selection cuts is a result of low genetic variability (i.e. lack of a compatible mating type). In fact, Werth *et al.* (2006) found that the genetic diversity of *L. pulmonaria* may be affected by large-scale disturbances. They concluded that the low genetic diversity was a result of a few founders that subsequently spread clonally (Wagner *et al.* 2006; Werth *et al.* 2006).

Although the abundance of trees with fertile *L. quercizans* was lower in selection cuts, there was no difference between uncut stands and selection cuts in fertility frequency. This may reflect the fact that *L. quercizans*, which to our knowledge only reproduces sexually, continues to produce fruiting bodies even when the microenvironment is suboptimal, because it has no alternative means of reproduction. Another possibility is that *L. quercizans* is a homothallic (self-fertile) species while *L. pulmonaria* is heterothallic. This would explain why *L. quercizans* is fertile in small populations and *L. pulmonaria* is not. Irrespective of the underlying mechanisms, our data show that selection cutting has a strong impact on the fertility of the studied lichens. Thus it is possible that studies ignoring fertility underestimate the negative effects of forestry.

SYNTHESIS AND APPLICATIONS

In this study we only surveyed two lichen species. However, because of their high abundance and thallus size they are two of the most dominant epiphytic lichen species in deciduous forests of New Brunswick and neighbouring areas in Canada, suggesting that they are also important in the northern hardwoods and Acadian forests as a whole. At the stand level, both species seem to persist after selection cutting, although their abundance is still strongly reduced 9 years after cutting. Similarly, Hazell & Gustafsson (1999) recorded high survival rates in transplanted thalli of *L. pulmonaria* on retained trees in Scandinavia 2 years after clear cutting. However, we have no data on whether some recovery of *L. pulmonaria* and *L. quercizans* has occurred after cutting, or how much these lichens will recover before the next cutting cycle. Kalwij, Wagner & Scheidegger (2005) found that *L. pulmonaria* populations in Switzerland did not show a negative association with stand-level disturbances resulting from intensive logging in the late 18th century. This indicates that *L. pulmonaria* may recover within 100–150 years after large disturbances. Although it is difficult to evaluate the long-term effect of the selection cutting in our study area, the repeated harvesting every 20 years will probably result in strongly reduced population sizes. Combined with the dramatically reduced fertility observed in the selection cuts, it has alarming implications for the long-term persistence of viable populations at a larger scale (Pykälä 2004). Management of hardwood forests in New Brunswick began recently (in the late 1980s). Prior to that, only low-intensity high-grading had taken place, whereby the most valuable tree species and individuals were harvested opportunistically. Now the remaining, relatively unbroken, mature hardwood and mixed forests are rapidly being replaced by selection cuts. Old stands with closed canopies and large trees are becoming increasingly rare, but they are essential for sustaining large, sexually reproductive populations of *Lobaria* species. These old stands may serve as source habitats from which lichens can disperse into the selection cuts, thereby increasing the chances of lichens persisting in the managed forest landscape. As second-entry selection cuts are starting to take place, the negative effects reported here can only increase. Thus there is an urgent need for conservation measures to be taken in this region to safeguard the last mature, closed-canopy deciduous forests.

Within the selection cuts there are still some large remnant trees that probably serve as microrefuges for some lichen and bryophyte species. It is likely that they also function as local dispersal sources that facilitate new lichen colonizations and population resilience after cutting. Furthermore, *Lobaria* species are often abundant on large, remnant trees, which increases the probability of fertile thalli. However, these large, old trees are at risk of being cut during the next harvest entry. To reduce the negative effects of selection cutting on the *Lobaria* species studied, we suggest that forest owners undertake the following actions. (i) Retain large trees from older seral stages in the selection cuts. (ii) Reduce the basal area removed during selection cutting. Although c. 30% of the basal area is typically removed every 20 years according to the forest owners

(Anonymous 1995), the studied uncut stands had 41% higher basal area than the selection cuts, indicating higher harvest intensity. Reducing the harvest intensity would improve the microclimate and create a forest structure more similar to that of natural forests, which are governed by small-scale gap dynamics (Frelich & Lorimer 1991). (iii) Extend the cutting cycle. By this action it would be possible to increase the amount of suitable habitats and prolong the time window for lichen colonization. However, it is unclear whether these recommendations will be enough to stop the decline of *Lobaria* species. To promote the long-term persistence of large, sexually reproductive populations it is also important to protect some mature deciduous forest stands at the regional scale. This would not only be beneficial to lichen populations but also to lichen-dependent species and all other species closely associated with mature hardwood forests.

Acknowledgements

This project was supported by grants from the Kempe Foundation (to M. Edman) and the Natural Sciences and Engineering Research Council of Canada (to M.-A. Villard). We sincerely thank the former owners of the studied forests, Fraser Paper Inc., for giving us access to their private lands. We also thank J. Olofsson for statistical advice, and H. Hedenäs and three anonymous referees for valuable comments on the manuscript.

References

- Anonymous (1995) *New Brunswick Timberlands 1995–1999 Forest Resources Management Plan*. Fraser Papers Inc., Toronto, Canada.
- Bourque, J. & Villard, M.-A. (2001) Effects of selection cutting and landscape-scale harvesting on reproductive success of two neotropical migrant bird species. *Conservation Biology*, **15**, 184–195.
- Brodo, I.M., Duran Sharnoff, S. & Sharnoff, S. (2001) *Lichens of North America*. Yale University Press, London.
- Campbell, J. & Fredeen, A.L. (2004) *Lobaria pulmonaria* abundance as an indicator of macrolichen diversity in interior cedar–hemlock forests of east-central British Columbia. *Canadian Journal of Botany*, **82**, 970–982.
- Coxson, D. & Stevenson, K. (2005) Retention of canopy lichens after partial-cut harvesting in wet-belt interior cedar–hemlock forests, British Columbia, Canada. *Forest Ecology and Management*, **204**, 97–112.
- Coxson, D., Stevenson, S. & Campbell, J. (2003) Short-term impacts of partial cutting on lichen retention and canopy microclimate in an Engelmann spruce–subalpine fir forest in north-central British Columbia. *Canadian Journal of Forest Research*, **33**, 830–841.
- Dennison, W.C. (2003) Apothecia and ascospores of *Lobaria oregana* and *Lobaria pulmonaria* investigated. *Mycologia*, **95**, 513–518.
- Dettki, H. & Esseen, P.-A. (1998) Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. *Ecography*, **21**, 613–624.
- Esseen, P.-A., Renhorn, K.-E. & Pettersson, R.B. (1996) Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecological Applications*, **6**, 228–238.
- Frelich, L.E. & Lorimer, C.G. (1991) Natural disturbance regimes in hemlock hardwood forests of the Upper Great-Lakes region. *Ecological Monographs*, **61**, 145–164.
- Gauslaa, Y. & Solhaug, K.A. (1996) Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forests. *Functional Ecology*, **10**, 344–354.
- Gauslaa, Y. & Solhaug, K.A. (1999) High-light damage in air-dry thalli of the old forest lichen *Lobaria pulmonaria*: interactions of irradiance, exposure duration and high temperature. *Journal of Experimental Botany*, **50**, 697–705.
- Gauslaa, Y., Lie, M., Solhaug, K.A. & Ohlson, M. (2006) Growth and eco-physiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light regimes. *Oecologia*, **147**, 406–416.
- Gauslaa, Y., Ohlson, M., Solhaug, K.A., Bilger, W. & Nybakken, L. (2001) Aspect-dependent high-irradiance damage in two transplanted foliose forest lichens, *Lobaria pulmonaria* and *Parmelia sulcata*. *Canadian Journal of Forest Research*, **31**, 1639–1649.
- Gearson, U. & Seaward, M.R.D. (1977) Lichen–invertebrate associations. *Lichen Ecology* (ed. M. R. D. Seaward), pp. 69–119. Academic Press, London.
- Gu, W.-D., Kuusinen, M., Kontinen, T. & Hanski, I. (2001) Spatial pattern in the occurrence of the lichen *Lobaria pulmonaria* in managed and virgin boreal forests. *Ecography*, **24**, 139–150.
- Gustafsson, L. & Eriksson, I. (1995) Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *Journal of Applied Ecology*, **32**, 412–424.
- Hallingbäck, T. & Martinsson, P.O. (1987) The retreat of two lichens, *Lobaria pulmonaria* and *L. scrobiculata*, in the district of Gäsene (SW Sweden). *Windalia*, **17**, 27–32.
- Hazell, P. & Gustafsson, L. (1999) Retention of trees at final harvest: evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. *Biological Conservation*, **90**, 133–142.
- Hedenäs, H. & Ericson, L. (2000) Epiphytic macrolichens as conservation indicators: successional sequence in *Populus tremula* stands. *Biological Conservation*, **93**, 43–53.
- Hedenäs, H. & Ericsson, L. (2003) Response of epiphytic lichens on *Populus tremula* in a selective cutting experiment. *Ecological Applications*, **13**, 1124–1134.
- Hilmo, O. & Sästad, S.M. (2001) Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. *Biological Conservation*, **102**, 251–259.
- Jobes, A.P., Nol, E. & Voigt, D.R. (2004) Effects of selection cutting on bird communities in contiguous eastern hardwood forests. *Journal of Wildlife Management*, **68**, 51–60.
- Johansson, P. & Ehrlén, J. (2003) Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. *Journal of Ecology*, **91**, 213–221.
- Kalwij, J.M., Wagner, H.H. & Scheidegger, C. (2005) Effects of stand-level disturbances on the spatial distribution of a lichen indicator. *Ecological Applications*, **15**, 2015–2024.
- Kuusinen, M. (1996) Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. *Biological Conservation*, **75**, 43–49.
- Lesica, P.B., McCune, B., Cooper, S.V. & Hong, W.S. (1991) Differences in lichen and bryophyte communities between old-growth and managed second growth forests in Swan Valley, Montana. *Canadian Journal of Botany*, **69**, 1745–1755.
- Lindner, D.L., Burdsall, H.H. & Stanosz, G.R. (2006) Species diversity of polyporoid and corticoid fungi in northern hardwood forests with differing management histories. *Mycologia*, **98**, 195–217.
- McCune, B. (1993) Gradients in epiphyte biomass in three *Pseudotsuga*–*Tsuga* forests of different ages in western Oregon and Washington. *Bryologist*, **96**, 405–411.
- Maynard Smith, J. (1978) *The Evolution of Sex*. Cambridge University Press, Cambridge, UK.
- Nilsson, S.G., Arup, U., Baranowski, R. & Ekman, S. (1995) Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology*, **9**, 1208–1215.
- Öckinger, E., Niklasson, M. & Nilsson, S.G. (2005) Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capacity or habitat quality? *Biodiversity and Conservation*, **14**, 759–773.
- Pettersson, R.B., Ball, J.P., Renhorn, K.-E., Esseen, P.-A. & Sjöberg, K. (1995) Invertebrate communities in boreal forest canopies influenced by forestry and lichens with implications for passerine birds. *Biological Conservation*, **74**, 57–63.
- Pykälä, J. (2004) Effects of new forestry practices on rare epiphytic macrolichens. *Conservation Biology*, **18**, 831–838.
- R Development Core Team (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Riiala, A., Penttinen, A. & Kuusinen, M. (2001) Bayesian mapping of lichens growing on trees. *Biometrical Journal*, **43**, 717–736.
- Rose, F. (1988) Phytogeographical and geographical aspects of *Lobaria* communities in Europe. *Botanical Journal of the Linnean Society*, **96**, 69–79.
- Scheidegger, C. (1995) Early development of transplanted isidioid soredia of *Lobaria pulmonaria* in an endangered population. *Lichenologist*, **27**, 361–374.
- Seymour, F.A., Crittenden, P.D. & Dyer, P.S. (2005) Sex in the extremes: lichen-forming fungi. *Mycologist*, **19**, 51–58.
- Sillet, S.C., McCune, B., Peck, J.E., Rambo, T.R. & Ruchty, A. (2000) Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications*, **10**, 789–799.
- SPSS (2006) *SPSS for Windows, Release 15.0*. SPSS, Chicago, IL.

- Wagner, H.H., Werth, S., Kalwij, J.M., Bolli, J.C. & Scheidegger, C. (2006) Modeling forest recolonization by an epiphytic lichen using a landscape genetic approach. *Landscape Ecology*, **21**, 849–865.
- Walsler, J.-C. (2004) Molecular evidence for limited dispersal of vegetative propagules in the epiphytic lichen *Lobaria pulmonaria*. *American Journal of Botany*, **91**, 1273–1276.
- Walsler, J.-C., Gugerli, F., Holderegger, R., Kuonen, D. & Scheidegger, C. (2004) Recombination and clonal propagation in different populations of the lichen *Lobaria pulmonaria*. *Heredity*, **93**, 322–329.
- Walsler, J.-C., Holderegger, R., Gugerli, F., Hoebee, S.E. & Scheidegger, C. (2005) Microsatellites reveal regional population differentiation and isolation in *Lobaria pulmonaria*, an epiphytic lichen. *Molecular Ecology*, **14**, 457–467.
- Werth, S., Wagner, H.H., Holderegger, R., Kalwij, J.M. & Scheidegger, C. (2006) Effect of disturbances on the genetic diversity of an old-forest associated lichen. *Molecular Ecology*, **15**, 911–921.
- Wirth, V. (1995) *Die Flechten Baden-Württembergs*. Eugen Ulmer, Stuttgart, Germany [in German].
- Yoshimura, I. (1971) The genus *Lobaria* of Eastern Asia. *Journal of Hattori Botanical Laboratory*, **34**, 231–364.
- Zoller, S., Lutzoni, F. & Scheidegger, C. (1999) Genetic variation within and among populations of the threatened lichen *Lobaria pulmonaria* in Switzerland and implications for its conservation. *Molecular Ecology*, **8**, 2049–2059.

Received 24 January 2007; final copy received 9 May 2007

Handling Editor: Phil Hulme

Supplementary material

The following supplementary material is available for this article.

Appendix S1. Pearson correlation coefficients between environmental variables in the forest stands

Appendix S2. Characteristics of uncut stands and selection cuts

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01354.x>.

(This link will take you to the article abstract.)

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.