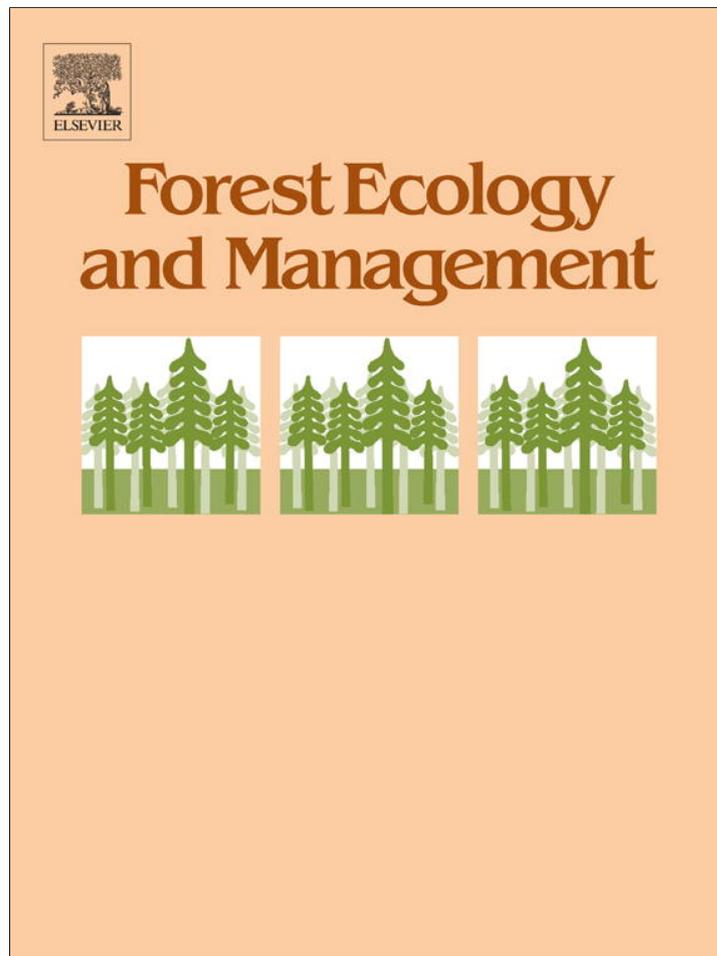


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Epiphytic lichen colonization in regenerating black spruce forest stands of clearcut origin

Catherine Boudreault^{a,*}, Yves Bergeron^a, Darwyn Coxson^b^a Centre d'Étude de la Forêt and the Natural Sciences and Engineering Research Council, UQAM-UQAT Industrial Chair in Sustainable Forest Management, Université du Québec à Montréal, C.P. 8888, Succursale Centre-Ville, Montréal, QC, Canada H3C 3P8^b University of Northern British Columbia, Ecosystem Science and Management Program, 3333 University Way, Prince George, BC, Canada V2N 4Z9

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ABSTRACT

Colonization of young forest stands by epiphytic lichens is an important phenomenon for the maintenance of viable populations of epiphytic lichens in forest landscapes affected by periodic severe disturbances. We examined colonization of epiphytic species in regenerating black spruce stands in boreal forests of western Québec. The number of thalli of each species were counted on branches sampled on young trees located in recently harvested stands, at different distances from adjacent mature forests (from 5 to 100 m). We sampled stands that were regenerated with two methods: stands that regenerated using advance regeneration that established in the understory before harvest and stands that were regenerated with post-harvest plantations. Lichens were also inventoried in two age classes: between 6 and 10 years and between 12 and 18 years after harvest. The results indicate that for the younger age class, the number of thalli on branches was superior in stands regenerated using advance regeneration for most epiphytic lichen species, whereas the difference between the two types of regeneration disappeared in the older age class. Distance from the adjacent stand had little influence on thalli number for most species, except for *Bryoria* spp. that disperse mainly through thallus fragments. These results suggest that most lichen species can colonize the microsites present in regenerating stands, independently from regeneration type. However, we underline that this result should be put in perspective because the forest matrix still contains a high proportion of virgin mature stands, and that diaspore sources (and colonization rates) could decline as these mature stands continue to be harvested and replaced by younger stands.

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1. Introduction

In landscapes that are fragmented by forest management activities, interruption of the connectivity between forest habitats can hamper species dispersal and colonization among forest remnants, and could also have repercussions on the recolonization of recently disturbed areas (Kupfer et al., 2006; Lindenmayer and Franklin, 2002). At the landscape scale, forest management causes a decrease of the proportion of old forests (Bergeron et al., 2002; Jetté et al., 2008; Kuuluvainen, 2009; Pennanen, 2002), and can result in vast expanses of regenerating forests. The few mature forest remnants that are left after clearcutting are often either unproductive (Bergeron et al., 2002), or very small in size. At the stand scale, few residual living trees that could act as reservoir of diaspores are generally left following clearcut.

In Canadian boreal forests where clearcutting is a major disturbance factor, it is important to obtain basic knowledge on recolonization patterns of vulnerable organisms with limited dispersal capabilities in landscapes that have been fragmented by recent disturbances. Epiphytic lichens are a sensitive group in this respect. Several studies suggest that many species associated with relatively old forest habitats are dispersal limited (Hilmo and Sæstad, 2001; Keon and Muir, 2002; Sillett et al., 2000). Other studies have shown that as distance from mature adjacent forests increases, lichen abundance on the branches of small regenerating trees (Dettki et al., 2000; Stevenson, 1988) and the number of thallus fragments that dispersed from neighboring trees (Dettki, 1998) tend to decrease. These dispersal limitations could partly explain the slow accumulation rates of epiphytic lichens in forest environments (Boudreault et al., 2009; Dettki and Esseen, 1998; Esseen et al., 1996; Hyvärinen et al., 1992).

Factors other than dispersal capabilities could also influence species colonization in recently disturbed environments. After the arrival of a diaspore in a new habitat, fixation to the substrate, diaspore germination, initial development of the juvenile thallus,

* Corresponding author. Tel.: +1 011 514 987 3000x7608.

E-mail addresses: boudreault.catherine@courrier.uqam.ca (C. Boudreault), yves.bergeron@uqat.ca (Y. Bergeron), darwyn@unbc.ca (D. Coxson).

juvenile and mature thallus growth and reproduction are essential life stages (Armstrong, 1988; Hilmo and Sastad, 2001; Larsson and Gauslaa, 2011). Depending on circumstances, most of these life stages could be limiting for the colonization process. For example, rapid development of the hyphae that fix the lichen to the tree or branch substrate is crucial for lichen establishment (Hilmo and Sastad, 2001). Substrate quality, substrate availability, and micro-climatic conditions can also influence diaspore fixation on the substrate, diaspore survival, and thallus growth (Armstrong, 1988). For instance, Hilmo et al. (2011) observed a decrease in establishment success of *Lobaria pulmonaria* and *Lobaria scrobiculata* on the most exposed branches in young *Picea abies* plantations.

Lichens reproduce sexually through spore production by the fungal associate, or asexually through the production of symbiotic propagules, containing at the same time the mycobiont and the phycobiont (soredia, isidia, thallus fragments, etc.). Some authors suggest that spores would be the best dispersal agents for long distance dispersal (Barkman, 1958; Hedenas et al., 2003). Soredia and isidia allow lichen colonization on intermediate distances, and thallus fragments facilitate colonization on short distances (Barkman, 1958). For the fruticose lichen species that are dominant in mature and old forests of western Quebec (Boudreault et al., 2009), thallus fragmentation plays an important role in epiphytic lichen dispersal (Stevenson, 1988) on short distances or at the stand scale (Gauslaa et al., 1997). Dispersal on longer distances for these species would be insured by spores or soredia (Gauslaa et al., 1997). Size of diaspores not only influences dispersal distance but also lichen establishment. Larger diaspores could have more resources for the establishment phase than smaller ones (Hilmo et al., 2011).

In boreal forests, young stands that were regenerated following planting could represent ideal conditions to retrospectively study and quantify colonization from adjacent unlogged stands, because it is known that these young trees were initially devoid of epiphytic lichens. Moreover, by comparing epiphytic lichen communities on young planted trees with those on young trees that regenerated naturally in the understory (advance regeneration), it is also possible to evaluate the influence of silvicultural practices used to restock former clearcuts on the development of lichen communities. This type of information could be very useful for the conservation of epiphytic lichen communities in managed forest mosaics.

The objectives of this study were (1) to compare epiphytic lichen colonization in clearcut-origin stands that were regenerated naturally with stands regenerated through plantation, (2) to evaluate the influence of the time-since-harvesting on species colonization in the regenerating stands, and (3) to determine if epiphytic lichen colonization decreases with increasing distance from adjacent unlogged forests. Our hypotheses are: (1) that the colonization (number of lichen thalli or cover of lichen thalli) will be higher in stands that regenerated naturally because natural advance regeneration had initial lichen loading, (2) that species colonization will increase with time since harvesting, and (3) that the colonization of species whose main mode of dispersion is through fragments of thalli will decrease with increasing distance to the edge.

2. Methods

2.1. Study area

The study was conducted in Quebec's closed-crown boreal forest, more precisely in the western part of the *Picea mariana*-feathermoss bioclimatic domain (Saucier and Robitaille, 1998). The sampling sites (49°00'–49°45' N, 76°00'–77°30' W) were

Table 1

Characteristics of the sampled stands and trees in naturally regenerated stands and in plantations in function of the time since harvesting (young and old).

	Naturally regenerated stands			Plantations			Differences between main factors
	n	Men	SE	n	Mean	SE	
<i>Number of regenerating trees (No./ha)</i>							
Young	44	1440.9a	104.9	31	2185.5a	299.9	y < o
Old	28	3025.0a	393.2	26	3065.4a	415.0	n = p
<i>Diameter at breast height (cm)</i>							
Young	43	1.6b	0.1	31	0.9c	0.1	y < o
Old	30	2.4ab	0.2	26	2.9a	0.2	n > p
<i>Tree height (cm)</i>							
Young	43	188.7bc	4.6	31	161.8c	7.4	y < o
Old	30	234.7ab	8.2	26	293.6a	16.5	n = p
<i>Branch age (year)</i>							
Young	44	13.3a	0.6	31	5.1c	0.1	y = o
Old	32	10.7ab	0.7	26	8.7b	0.3	n > p
<i>Branch diameter (cm)</i>							
Young	39	0.88a	0.02	31	0.63a	0.01	y = o
Old	23	0.85a	0.03	26	0.71a	0.02	n > p

Note: ANOVAs were used to compare means between different age classes. The last column showed significant differences for the main factors (y = young, o = old; n = naturally regenerated, p = plantation). Differences that were significant ($p \leq 0.05$) for the interaction between classes of regeneration type and time since harvesting according to least squares means Tukey's honestly significant difference tests are indicated by different letters for each variable.

Table 2

ANOVA summaries for the effects of regeneration type after harvesting (naturally regenerated stands and plantations) and time since harvesting (young and old) on stand, tree, and branch characteristics.

	dfn	dfd	F	p
<i>Number of regenerating trees (n = 129)</i>				
Regeneration type (R)	1	29	0.92	0.346
Time since harvesting (T)	1	29	8.55	0.007
R × T	1	29	0.56	0.462
Site (R × T)	29	96	26.62	<0.001
<i>Diameter at breast height of regenerating trees (n = 130)</i>				
Regeneration type (R)	1	30	4.29	0.047
Time since harvesting (T)	1	30	48.00	<0.001
R × T	1	30	15.29	0.001
Site (R × T)	30	96	7.49	<0.001
<i>Tree height of regenerating trees (n = 130)</i>				
Regeneration type (R)	1	30	1.91	0.178
Time since harvesting (T)	1	30	43.44	<0.001
R × T	1	30	11.62	0.002
Site (R × T)	30	96	6.21	<0.001
<i>Branch age (n = 133)</i>				
Regeneration type (R)	1	30	37.80	<0.001
Time since harvesting (T)	1	30	2.42	0.130
R × T	1	30	19.45	<0.001
Site (R × T)	30	99	8.01	<0.001
<i>Branch diameter (n = 119)</i>				
Regeneration type (R)	1	27	24.76	<0.001
Time since harvesting (T)	1	27	0.33	0.568
R × T	1	27	3.31	0.080
Site (R × T)	27	84	7.47	<0.001

Note: Significant effects ($p \leq 0.05$) are shown in boldface. The sampling site nested within the interaction of regeneration type and time since harvesting is a random factor. The random effects were used as error term when testing for differences between fixed effects. dfn refers to degrees of freedom numerator and dfd refers to degrees of freedom denominator.

located in the eastern part of the Abitibi region, around the localities of Lebel-sur-Quevillon and Matagami. The topography of this region is relatively flat. Surficial deposits in this region are

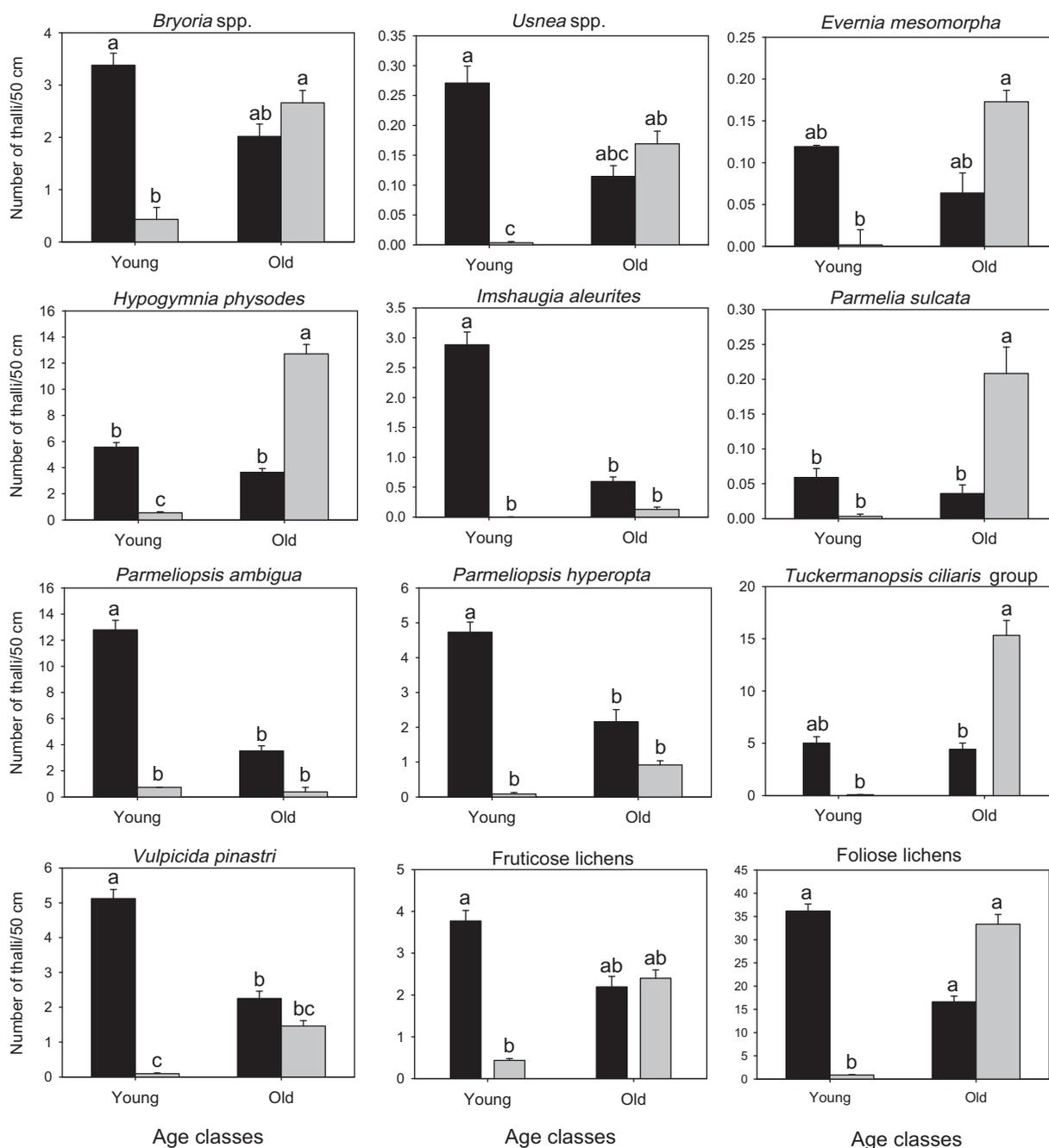


Fig. 1. Mean number of thalli and SE by regeneration type and by time since harvesting classes for each lichen species, and for the foliose and fruticose lichen groups ($n = 2569$ branches). ANOVA models were used to compare means. Black bars represent number of thalli on naturally regenerated trees, and gray bars represent number of thalli on planted trees. Differences that were significant ($p \leq 0.05$) according to least squares means Tukey's honestly significant difference tests are indicated by different letters.

co-dominated by glacial tills, interspersed with lacustrine deposits originating from the proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). Forest composition on both kinds of deposits is overwhelmingly dominated by black spruce stands (*P. mariana*) (Rowe, 1972). Ground cover in closed-crown black spruce stands is generally dominated by *Pleurozium schreberi*. Over time, successional paludification generally takes place, meaning that *P. schreberi* is replaced by *Sphagnum* species, and that tree stem density and tree size decrease (Simard et al., 2007). The closest weather station is located in Matagami (~100 km from our study sites). During the 1970–2000 period, the annual mean temperature recorded at this station was -0.7 °C, the mean annual precipitation

was 905 mm, the monthly maximum and minimum mean temperature were 16.1 and -20.0 °C, respectively and the monthly maximum and minimum mean precipitation were 110.2 and 34.1 mm, respectively (Environment Canada, 2004).

Forest management activities have been taking place in this region since the early 1970s, coinciding with the initial development of road access in this remote region. Clearcutting is by far the most common harvesting method. Since the mid-1980s, forestry standards in the province of Québec demand that any advance regeneration present in the understory must be protected in stands that are to be harvested, and tree-planting is generally used only if such regeneration is absent. Natural advance regeneration in these

Table 3
Frequency (%) of each species studied in each type of plots.

	Mature forest (%)	Naturally regenerated stand (%)		Plantation (%)	
	n = 237	Young n = 833	Old n = 611	Young n = 620	Old n = 509
<i>Bryoria</i> spp.	98.3	51.1	42.2	22.9	57.8
<i>Usnea</i> spp.	74.7	15.0	8.0	0.3	13.8
<i>Evernia mesomorpha</i>	48.9	7.7	4.4	0.2	12.0
<i>Hypogymnia physodes</i>	90.3	58.1	57.4	17.6	78.4
<i>Imshaugia aleurites</i>	86.9	55.9	31.4	2.1	26.3
<i>Parmelia sulcata</i>	21.5	3.6	2.1	0.2	8.3
<i>Parmeliopsis ambigua</i>	49.8	68.2	43.4	5.3	34.6
<i>Parmeliopsis hyperopta</i>	20.7	70.5	43.5	2.3	31.8
<i>Tuckermanopsis ciliaris</i> group	63.7	39.1	17.3	0.2	4.9
<i>Vulpicida pinastri</i>	7.2	34.9	28.0	2.4	54.8

stands is generally dominated by black spruce, and this species is also the one that is used the most often when planting is considered. Isolated mature veteran trees are sometimes left in naturally regenerated stands but generally not in plantations; they generally represent less than 5% of the original tree cover in a given stand, and in the context of this study were mostly represented by trees with diameter at breast-height <10 cm.

2.2. Sampling design

We studied epiphytic lichen colonization along 34 transects established across clearcuts that were done between 1985 and 1999. The sampling was stratified according to (1) the regeneration type after cutting: stands that regenerated naturally with advance regeneration (19 transects) and plantations (15 transects), and (2) time since harvesting: young clearcuts (6–10 years) or old clearcuts (12–18 years). All transects were placed perpendicular to unlogged forest edges. In addition to this stratification, the following factors were considered during site selection: the transect had to be located perpendicular to straight edges that were at least 200 m in length, topography had to be flat, the regenerated stands and adjacent stands had to be >4 ha in size, adjacent stands had to be mature or overmature (>90 years), the distance of the transects from the road had to be >100 m, adjacent stands had to be dominated by black spruce, advance regeneration had to be nearly absent from plantations (a mechanical site preparation was done in all plantations), and naturally regenerated stands and plantations had to be dominated by black spruce. Also, we made sure that the portion of the transect located farthest from the forest edge (100 m) was not located close to another edge located elsewhere around the clearcut area. Because the number of available stands that fulfilled all our criteria was limited, we did not control for edge orientation, although we recognize the importance of this factor for dispersal study.

We studied lichen colonization on black spruce branches collected in each transect in plots located at four distances from the forest edge: 5, 25, 50, and 100 m. The 10 regenerating black spruce trees that were located closest to the center of the plots were selected and the height and diameter at breast height (DBH) of each tree were measured. On each tree, two branches with length of at least 50 cm were selected. The branches were collected at random height (between 30 and 100 cm above ground) and orientation. The outermost 50 cm segment of each main branch axis was sampled and the branch diameter at the cutting point was measured.

At each distance, inside a circular 40 m² plot, we also counted the number of regenerating trees (DBH > 1 cm at height of 1.3 m). On the 2720 branches that were collected (136 plots × 20 branches per plot), 147 branches were damaged during storage, including all the branches coming from three plots. The analyses were performed on the 2573 branches remaining.

The number of thalli (>1 mm) of each lichen species was counted on the upper portion of the main axis of each branch. The proportion of the upper portion of the main axis covered by each species was also estimated on each branch. We used standard chemical tests in lichenology (spot tests; see Brodo et al., 2001) to identify small lichen thalli. On one out of two collected branches (outermost 50 cm segment), age was evaluated by counting the number of foliar scars or, for larger branches, the number of growth rings.

In order to compare species colonization on branches of regenerating stands with species colonization on branches of mature or old adjacent stands, we randomly selected half of the adjacent stands. A sample plot was established 100 m towards the interior of each of these stands, perpendicular to the forest edge. In each plot, we selected the 10 trees (DBH > 10 cm) that were located the closest from the center of the plot, and we collected two branches (length > 50 cm) per tree at random height (between 1.5 and 5 m). On each of these branches, we evaluated the cover (%) of the fruticose and the foliose lichen groups and recorded the presence of the most common lichen species (see Section 2.3.).

2.3. Studied lichen species

This study focused on common species in the study area to avoid difficulties associated to juvenile thalli identification. Species belonging to the genera *Bryoria* and *Usnea*, which are common epiphytic species in this region, were not identified at the species level due to the difficulties associated with species-level identification of juvenile thalli. Knowing the dispersal mode of these main species or species groups is also important in order to interpret correctly the results of this study. The fruticose lichen species studied and their principal mode of dispersal were: *Bryoria* spp. (soredia, thalli fragments), *Evernia mesomorpha* (soredia), and *Usnea* spp. (soredia, thalli fragments). The foliose lichen species and their principal mode of dispersal were: *Hypogymnia tubulosa* (soredia; may include some thalli of *Hypogymnia tubulosa* that also disperse by soredia), *Imshaugia aleurites* (isidia), *Parmelia sulcata* (soredia), *Parmeliopsis ambigua* (soredia; may include some thalli of *Parmeliopsis capitata* that also disperse by soredia), *Parmeliopsis hyperopta* (soredia), *Tuckermanopsis ciliaris* group (spores), and *Vulpicida pinastri* (soredia).

2.4. Statistical analyses

Differences in number and DBH of regenerating trees, branch age, and branch diameter between regeneration types and time since harvesting classes were tested with mixed ANOVAs. Stand regeneration type (natural or plantation) and time since harvesting (young or old clearcuts) were considered fixed effects and sampling site nested within the interaction of regeneration type and time since harvesting was considered a random effect. The response variables were mean values of each variable calculated at the plot level. Data were log transformed to satisfy the normality and homoscedasticity of ANOVA. The number of plots used in each analysis varied (see Table 1 for the exact number of plots in each age class and treatment combination) because information about tree density, tree DBH, or branch diameter was missing in some plots. The number of thalli and the cover of each species or group of species (fruticose and foliose lichens) were analyzed using mixed ANOVA models. Regeneration type, time since harvesting, and distance from the edge were fixed factors, sampling site was a random factor nested within the interaction of regeneration type

Table 4

ANOVAs summaries for the effects of regeneration type after cutting (naturally regenerated stands and plantation), time since harvesting (young and old), and distance from the edge (5, 25, 50, and 100 m) on the number of thalli for each species and for foliose and fruticose lichen groups ($n = 2569$ branches).

	No. of thalli				No. of thalli		
	dfn	F	p		dfn	F	P
<i>Bryoria</i> spp.				<i>Evernia mesomorpha</i>			
Regeneration type (R)	1	1.78	0.193	Regeneration type (R)	1	0.01	0.933
Time since harvesting (T)	1	2.15	0.153	Time since harvesting (T)	1	2.55	0.121
Distance (D)	3	3.34	0.023	Distance (D)	3	1.22	0.309
D × T	3	1.11	0.348	D × T	3	1.07	0.365
R × T	1	14.36	0.001	R × T	1	8.25	0.007
R × D	3	2.02	0.117	R × D	3	0.10	0.958
R × D × T	3	1.18	0.323	R × D × T	3	0.36	0.780
Site (R × T)	30	5.74	<0.001	Site (R × T)	30	4.76	<0.001
Site × D (R × T)	87	2.81	<0.001	Site × D (R × T)	87	1.85	<0.001
<i>Usnea</i> spp.				Fruticose lichens			
Regeneration type (R)	1	2.50	0.125	Regeneration type (R)	1	5.24	0.029
Time since harvesting (T)	1	0.92	0.344	Time since harvesting (T)	1	0.53	0.470
Distance (D)	3	0.51	0.677	Distance (D)	3	0.69	0.558
D × T	3	0.56	0.643	D × T	3	1.31	0.275
R × T	1	11.17	0.002	R × T	1	9.98	0.004
R × D	3	0.84	0.478	R × D	3	1.13	0.343
R × D × T	3	0.48	0.699	R × D × T	3	1.28	0.285
Site (R × T)	30	3.55	<0.001	Site (R × T)	30	4.61	<0.001
Site × D (R × T)	87	2.20	<0.001	Site × D (R × T)	87	3.64	<0.001
<i>Hypogymnia physodes</i>				<i>Imshaugia aleurites</i>			
Regeneration type (R)	1	0.04	0.837	Regeneration type (R)	1	19.13	<0.001
Time since harvesting (T)	1	24.43	<0.001	Time since harvesting (T)	1	4.77	0.037
Distance (D)	3	0.26	0.855	Distance (D)	3	1.36	0.261
D × T	3	1.22	0.308	D × T	3	1.46	0.232
R × T	1	38.20	<0.001	R × T	1	7.32	0.011
R × D	3	1.10	0.355	R × D	3	1.25	0.297
R × D × T	3	0.34	0.794	R × D × T	3	1.57	0.202
Site (R × T)	30	4.89	<0.001	Site (R × T)	30	4.70	<0.001
Site × D (R × T)	87	3.50	<0.001	Site × D (R × T)	87	4.52	<0.001
<i>Parmelia sulcata</i>				<i>Parmeliopsis ambigua</i>			
Regeneration type (R)	1	1.59	0.218	Regeneration type (R)	1	19.19	<0.001
Time since harvesting (T)	1	8.69	0.006	Time since harvesting (T)	1	0.65	0.428
Distance (D)	3	2.00	0.121	Distance (D)	3	1.14	0.337
D × T	3	0.21	0.889	D × T	3	2.36	0.077
R × T	1	18.01	<0.001	R × T	1	13.41	0.001
R × D	3	0.02	0.995	R × D	3	0.11	0.953
R × D × T	3	0.82	0.485	R × D × T	3	1.92	0.133
Site (R × T)	30	1.71	0.029	Site (R × T)	30	7.99	<0.001
Site × D (R × T)	87	1.58	0.001	Site × D (R × T)	87	4.41	<0.001
<i>Parmeliopsis hyperopta</i>				<i>Tuckermanopsis ciliaris</i> group			
Regeneration type (R)	1	18.69	<0.001	Regeneration type (R)	1	0.18	0.671
Time since harvesting (T)	1	0.61	0.440	Time since harvesting (T)	1	10.95	0.002
Distance (D)	3	0.33	0.805	Distance (D)	3	1.59	0.198
D × T	3	2.32	0.081	D × T	3	2.61	0.057
R × T	1	10.20	0.003	R × T	1	14.09	<0.001
R × D	3	0.23	0.878	R × D	3	0.70	0.555
R × D × T	3	1.25	0.296	R × D × T	3	0.11	0.955
Site (R × T)	30	7.75	<0.001	Site (R × T)	30	9.47	<0.001
Site × D (R × T)	87	2.61	<0.001	Site × D (R × T)	87	2.96	<0.001
<i>Vulpicida pinastri</i>				Foliose lichens			
Regeneration type (R)	1	22.51	<0.001	Regeneration type (R)	1	11.58	0.002
Time since harvesting (T)	1	0.17	0.685	Time since harvesting (T)	1	7.97	0.008
Distance (D)	3	0.38	0.765	Distance (D)	3	0.11	0.952
D × T	3	3.35	0.023	D × T	3	2.43	0.071
R × T	1	12.72	0.001	R × T	1	35.47	<0.001
R × D	3	0.58	0.629	R × D	3	1.21	0.311
R × D × T	3	2.19	0.095	R × D × T	3	1.44	0.237
Site (R × T)	30	6.95	<0.001	Site (R × T)	30	7.79	<0.001
Site × D (R × T)	87	3.64	<0.001	Site × D (R × T)	87	4.95	<0.001

Note: Significant effects ($p \leq 0.05$) are shown in boldface. Sampling site nested within the interaction of regeneration type and time since harvesting and the interaction of sampling site with distance nested within the interaction of regeneration type after cutting and time since harvesting were considered as random factors. The random effects were used as error term when testing for differences between fixed effects.

and time since harvesting, and the interaction of sampling site and distance was nested within the interaction of regeneration type and time since harvesting. All interactions among the fixed effects were included in the model. Response variables were the number of thalli and the cover per branch for each lichen taxa. Data

were log transformed ($\log x + 1$) to satisfy the normality and homoscedasticity of ANOVA for all variables except for *Usnea* spp., *E. mesomorpha* and *P. sulcata* that were rank transformed.

ANOVA analyses were performed with the MIXED procedure in SAS (SAS Institute, 2002). The random effects were used as error

term when testing for differences between fixed effects. Significant differences ($p \leq 0.05$) between classes in all ANOVAs analyses were detected with LS means Tukey HSD tests.

Linear regressions were used to detect significant relationships between tree and branch characteristics (independent variables), and the number and the cover of fruticose and foliose lichens (dependent variables) for each regeneration type. The independent variables selected were number of regenerating trees, DBH of regenerating trees, branch age, and branch diameter. Regressions were based on mean values calculated at the plot level (>11 branches/plot).

Because few differences were observed between analyses based on the number of thalli or on lichen cover, only the results of the analyses performed on the number of thalli will be presented in the following sections. The results of the analyses performed on lichen cover are presented in the Appendices.

3. Results

3.1. Stand, tree, and branch characteristics

DBH of regenerating trees, branch diameter, and branch age of regenerating trees were significantly higher in stands that regenerated naturally compared with plantations (Tables 1 and 2). Number, DBH, and height of regenerating trees were also significantly higher in old clearcuts than young clearcuts (Tables 1 and 2). A significant interaction between the type of regeneration and time since harvesting for tree DBH, tree height, and branch age indicate that trees were smaller and shorter and that branches were younger in young plantations (Tables 1 and 2).

3.2. Overall lichen colonization in regenerating stands

Among fruticose lichen species, the *Bryoria* species group was the most abundant, both in naturally regenerated stands and in plantations (Fig. 1). Among foliose lichen species, *P. ambigua* was the most abundant species in naturally regenerated stands, whereas *H. physodes* and *T. ciliaris* group were the most abundant species in plantations (Fig. 1). The number of foliose lichens was higher than the number of fruticose lichens, both in naturally regenerated stands and in plantations.

By contrast with what was observed in regenerating stands, fruticose lichen cover per branch in adjacent forests was two times more important on average (33.6%) than foliose lichen cover (15.4%). Common fruticose lichen species in forests >90 years such as *Usnea* spp. and *E. mesomorpha* were uncommon in regenerating stands (Table 3). Most foliose lichen species that are typical of mature or old neighboring stands were found in regenerating stands (Table 3), but some were considerably more frequent in regenerating stands (e.g., *V. pinastri* and *P. hyperopta*) while others were more frequent in >90 years old forests (e.g., *P. sulcata* and *T. ciliaris* group).

3.3. Effects of regeneration type, time since harvesting, and distance from the remnant stand on the number of lichens in regenerating stands

The number of thalli differed significantly between regeneration types for *I. aleurites*, *P. ambigua*, *P. hyperopta*, *V. pinastri*, fruticose lichens, and foliose lichens (Table 4), and was higher in naturally regenerated stands compared to plantations. For instance, foliose and fruticose lichens were 1.8 times and 2.3 times more numerous respectively in naturally regenerated stands compared to plantations. Time since harvesting had a significant effect, as a higher number of thalli was encountered in old clearcuts for *T. ciliaris* group, *H. physodes*, *P. sulcata*, and foliose lichens, whereas a higher number was encountered in young clearcuts for *I.*

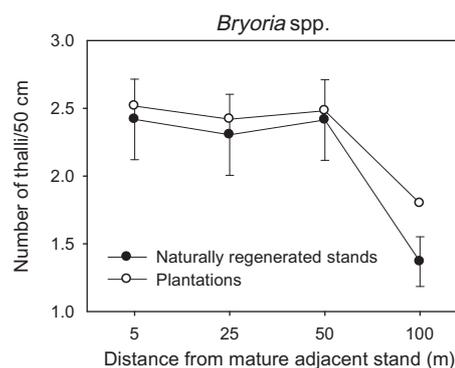


Fig. 2. Changes of number of thalli in regenerating stands with increasing distance from adjacent mature stands. Data represent mean number of thalli and SE by distance ($n = 2569$ branches).

aleurites. The effect of distance from adjacent forests was significant only for *Bryoria* spp.: the number of thalli was 1.5 times higher at 5 m comparatively to 100 m, but did not differ significantly from values observed at 25 and 50 m (Fig. 2). A significant interaction between regeneration type and time since harvesting was identified for all species and for foliose and fruticose lichens (Table 4 and Fig. 1), indicating that the effect of time since harvesting was inconsistent between regeneration types. Within naturally regenerated stands, significant differences between time since harvesting categories were observed for many species (*I. aleurites*, *P. ambigua*, *P. hyperopta*, and *V. pinastri*), all of which were more numerous in young clearcuts (Fig. 1). Conversely, when plantations are analyzed separately, significant differences were observed between time since harvesting categories for several species and species groups (*Bryoria* spp., *E. mesomorpha*, *H. physodes*, *P. sulcata*, *Usnea*, *T. ciliaris* group, and foliose lichens), the number of thalli being higher in old plantations (Fig. 1). In general, branches of regenerating trees in older plantations had similar numbers of lichen thalli compared with older naturally regenerated stands, and some species were even more numerous in old plantations (*H. physodes*, *P. sulcata*, and *T. ciliaris* group) (Fig. 1).

3.4. Influence of branch, tree, and stand characteristics on the number of lichens in regenerating stands

The number of foliose and fruticose thalli increased significantly with branch age (Fig. 3a) and branch diameter (Fig. 3b) in both types of regeneration. Fig. 3c shows an increase in number of fruticose and foliose lichens with DBH of regenerating trees in plantations. Tree DBH was positively correlated with branch age in plantations ($r_{\text{Spearman}} = 0.650$, $p < 0.001$). No relationship between tree DBH and branch age was observed in naturally regenerated stands ($r_{\text{Spearman}} = 0.107$, $p = 0.366$). The number of thalli of foliose and fruticose species decreased significantly with the number of regenerating trees in naturally regenerated stands, but r^2 values are low, indicating relatively weak relationships (Fig. 3d). The number of foliose lichens increased significantly with the number of regenerating trees in plantations (Fig. 3d).

4. Discussion

The colonization of lichen thalli on regenerating trees will depend mostly on (1) post-disturbance dispersal of diaspores which is function of the distance from adjacent forests and the dispersal capabilities of each lichen species, on (2) pre-disturbance colonization, which is function of initial lichen loading on regenerating trees and survival of pre-established individuals, and (3) branch age, which is mainly a function of time since

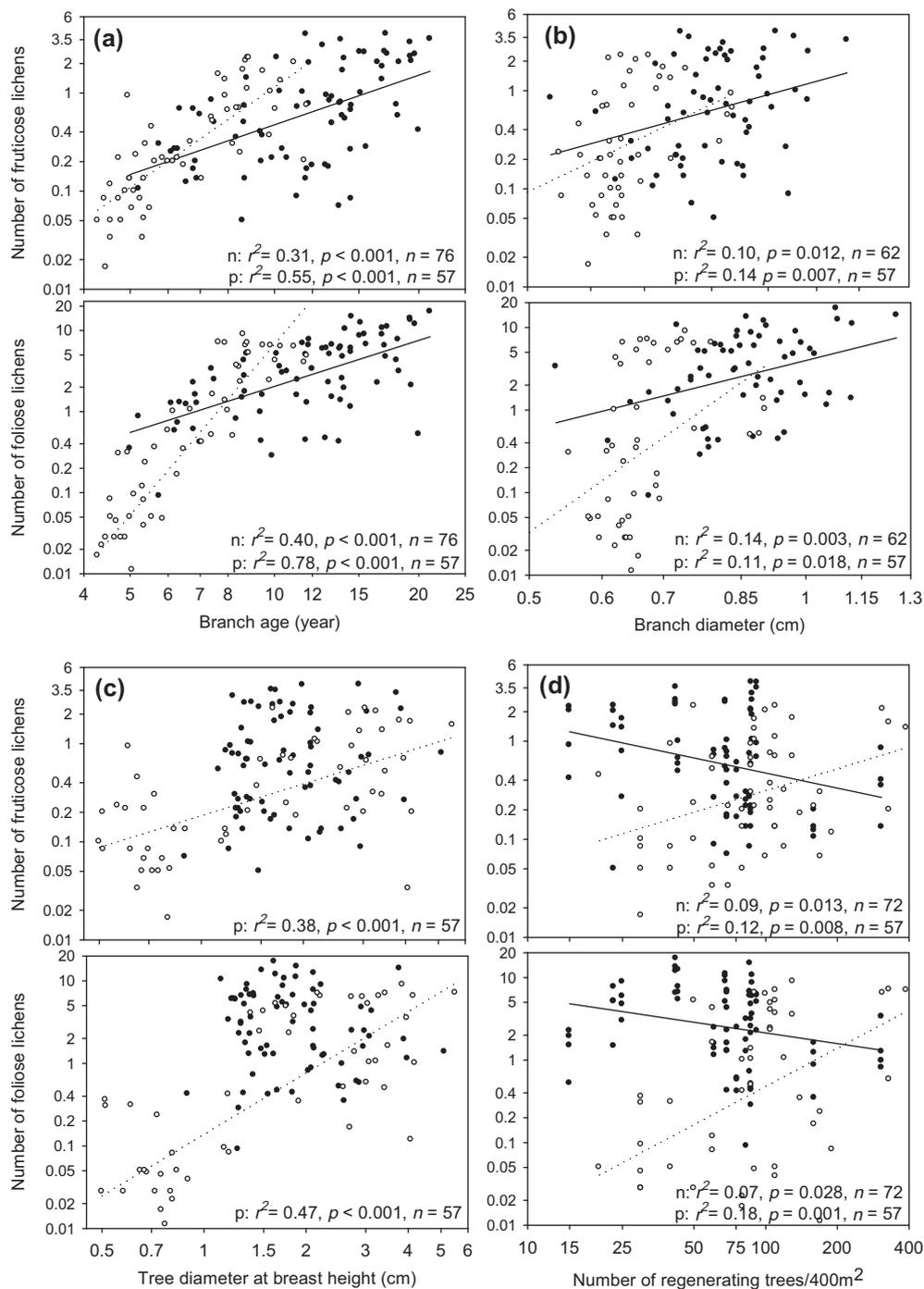


Fig. 3. Linear regressions (log₁₀ scale) of the number of lichen thalli against (a) branch age ($n = 133$), (b) branch diameter ($n = 119$), (c), mean regeneration diameter at breast height ($n = 130$), and (d) number of regenerating trees ($n = 129$) for the two regeneration types (natural regeneration: filled circles, a black regression line and an equation preceded by the letter 'n'; plantation: empty circles, dotted regression line and an equation preceded by the letter 'p'). Regression lines are only shown for significant relationships ($p \leq 0.05$).

harvesting. These different processes will be discussed in the following sub-sections.

4.1. Post-disturbance dispersal

Overall, our results show that distance from adjacent forests had little influence on lichen abundance in regenerating areas for many species that disperse by isidia (e.g., *I. aleurites*), spores (e.g., *T. ciliaris* group) and soredia (*E. mesomorpha*, *H. physodes*, *P. sulcata*, *P. ambigua*, *P. hyperopta*, *Usnea* spp., and *V. pinastri*). For those

species, 100 m probably does not represent a significant dispersal distance in the actual forest context where harvest history is relatively recent. However, dispersal limitation was found for the *Bryoria* species group whose dispersal is mainly insured by fragments of thalli and soredia, both in artificially and naturally regenerated areas (see Fig. 2). Other studies showed a decline of *Bryoria* with distance from residual forests. For instance, Dettki et al. (2000) and Stevenson (1988) show a reduction of about 50% in colonization rates of *Bryoria* at 100 m compared with sites immediately adjacent with residual forests, and Stevenson and

Coxson (2003) show a dramatic decline in the dispersal of *Bryoria* fragments at distance greater than 10 m from the forest edge. We believed that dispersal limitation for some *Bryoria* species could have been higher in our study if distinction between species dispersed by soredia and those dispersed by fragments of thalli had been done. For instance, it is likely that bushy species such as *Bryoria furcellata* or *Bryoria simplicior* which produce numerous soredia and are associated with young stands (Boudreault et al., 2002) have more efficient dispersal capabilities than long filamentous species whose dispersal is mainly insured by fragments and are associated with relatively old stands such as *Bryoria trichodes* ssp. *trichodes* and *Bryoria lanestris*.

In our study, we observed more foliose lichens with reproductive structures in naturally regenerated stands than in plantations, but their number increased with time since harvesting in plantations (Boudreault, personal observation). Therefore, some foliose lichen thalli may have originated from already established lichens in regenerating stands, meaning that the importance of adjacent forest proximity as a source of diaspores for colonization may decline with time since harvesting. However, as very few reproducing thalli of fruticose lichens were observed in both types of regenerating stands, it is likely that their colonization is still mainly dependant on diaspores present in the surrounding forests.

4.2. Pre-disturbance colonization

Results from our study indicate that young black spruce stands originating from advance regeneration contain a higher number of lichen thalli of epiphytic lichen species compared with young black spruce plantations. In stands dominated by natural regeneration, the young trees probably established mostly from seed or layering before harvest (confirmed by the age of the sampled branches, see Table 1), an advance regeneration mechanism is commonly observed in coniferous stands in this region (Doucet, 1988). These young trees probably benefited from nearby epiphytic lichen diaspore sources, such as the dominant canopy trees that were subsequently harvested (Peck and McCune, 1997; Sillett and Goslin, 1999). Consequently, compared with planted trees that were initially devoid of lichens, advance regeneration in naturally regenerated stands had initial lichen loading prior the stand harvesting.

For the older regenerating stands of natural or plantation origin, we observed that the advantages conferred by an inoculation prior to stand harvesting are no longer significant. A first explanation could be that planted trees could have more available microsites for lichen colonization than naturally regenerated trees, which could have favoured a faster increase in number of individuals, as observed by Romagni and Gries, 2000. Indeed, these authors observed a similar phenomenon when they compared lichen cover in sites that were severely and less severely burned: lichens located in severely burned habitats established faster due to lower competition levels. A second explanation could be that young stands present a hostile environment for thalli that remained on advance regeneration after harvesting. Thus the initially greater loading on naturally regenerated trees may largely be lost due to wind- and snow-scouring of branches, or from die-back beneath snow cover in the first decade after harvesting. Coxson and Coyle (2003) found that mechanical processes, especially wind scouring of thalli, were dominant in determining biomass accumulation of *Bryoria* in mature sub-boreal spruce forests, and were more important than establishment and growth rates in structuring community gradients. This could also explain why, as opposed to our initial expectations, a higher number of thalli were often observed in young naturally regenerated clearcuts compared with old naturally regenerated clearcuts. A third

potential explanation is related to branch age and will be discussed in the following subsection.

4.3. Branch age

Our results indicate that the abundance of most lichen species generally respond positively to an increase in time available for branch colonization (branch age) (Fig. 3a). Our results also suggest that branch age was more important than the substrate area/availability (branch diameter) to catch diaspores (see Fig. 3). In boreal forests, epiphytic lichen colonization or development rates are generally relatively low. For example, a relatively long period of dormancy is observed after the initial attachment of the diaspores on a tree branch substrate (Hilmo and Ott, 2002), and the appearance of the first lobules will take a relatively long time for many lichen species, for example 12, 21, and 24 months for *L. pulmonaria* (Scheidegger, 1995), *L. scrobiculata*, and *Platismatia glauca* (Hilmo and Ott, 2002), respectively. Following this period, several years must elapse before the appearance of a mature thallus (Hilmo and Ott, 2002) and before many species can produce diaspores, thus delaying the possibility of colonizing new habitats (Kalwij et al., 2005; Scheidegger, 1995). Larsson and Gauslaa (2011) estimated to 9–22 years the time necessary for development of reproductive structures in lichen species associated to old forests. Consequently, older branches provide longer period for diaspores arrival, germination and establishment as well as for thallus development and growth. Environmental factors such as low light availability, low temperatures, and the snow that covers the diaspores during winter also have for effect to shorten the duration of the growth period in boreal forests, and could also explain the long period of time needed for thallus development (Hilmo and Ott, 2002). In this study, small trees in naturally regenerated stands have branches that are generally older and larger than those on trees located in plantations.

The absence of significant differences in branch age between the two age classes of naturally regenerated stands might in part explain why, contrarily to what was expected, we did not observe a significant difference in lichen number between the young and old naturally regenerating stands. This result was probably influenced by the sampling protocol. Because we only studied lichen colonization on the outer part of branches (outer 50 cm), it is likely that a larger proportion of branch segments sampled in young regenerating stands were present before the logging took place, whereas in the older age class most branch segments had developed after logging (see Table 1).

5. Conclusion

As expected, we found that species mainly dispersed by fragments are more dispersal limited than species with other modes of dispersal. This study also showed that colonization by epiphytic lichens on regenerating trees is initially higher in stands that regenerated naturally compared with stands with artificial regeneration (plantations). However, in regenerating stands that are about 10 years older, no significant difference is found, and stands that are artificially regenerated exhibit relatively similar epiphytic communities compared with naturally regenerated stands. Consequently, using artificial reforestation measures when advance regeneration is deficient can provide adequate conditions for lichen colonization in stands that have been recently clearcut. However, it is noteworthy that in our study area, relatively large patches of virgin forest that could serve as sources of diaspores were relatively abundant in the surrounding forest matrix. Therefore, it is likely that the colonization rates observed in this study

do not reflect the colonization rates that could be observed in future fragmented landscape where the connectivity between residual stands is interrupted, and when source habitats are located far apart from one another (see Johansson and Ehrlén, 2003; Öckinger et al., 2004).

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Appendix A

ANOVAs summaries for the effects of regeneration type after cutting (naturally regenerated stands and plantation), time since harvesting (young and old), and distance from the edge (5, 25, 50, and 100 m) on cover of each species and for foliose and fruticose lichen groups ($n = 2569$ branches).

	Cover (%)				Cover (%)		
	df	F	p		df	F	p
<i>Bryoria</i> spp.				<i>Evernia mesomorpha</i>			
Regeneration type (R)	1	2.08	0.160	Regeneration type (R)	1	0.02	0.899
Time since harvesting (T)	1	0.13	0.720	Time since harvesting (T)	1	2.33	0.137
Distance (D)	3	6.00	0.001	Distance (D)	3	1.46	0.233
$D \times T$	3	0.40	0.756	$D \times T$	3	0.99	0.404
$R \times T$	1	7.31	0.011	$R \times T$	1	6.55	0.016
$R \times D$	3	0.97	0.410	$R \times D$	3	0.03	0.992
$R \times D \times T$	3	0.63	0.598	$R \times D \times T$	3	0.26	0.857
Site ($R \times T$)	30	5.72	<0.001	Site ($R \times T$)	30	4.41	<0.001
Site \times D ($R \times T$)	85	2.41	<0.001	Site \times D ($R \times T$)	85	2.13	<0.001
<i>Usnea</i> spp.				Fruticose lichens			
Regeneration type (R)	1	2.33	0.137	Regeneration type (R)	1	2.32	0.138
Time since harvesting (T)	1	0.98	0.331	Time since harvesting (T)	1	0.44	0.514
Distance (D)	3	0.57	0.633	Distance (D)	3	4.01	0.010
$D \times T$	3	0.34	0.796	$D \times T$	3	0.42	0.742
$R \times T$	1	10.81	0.003	$R \times T$	1	9.70	0.004
$R \times D$	3	0.56	0.642	$R \times D$	3	0.72	0.541
$R \times D \times T$	3	0.26	0.857	$R \times D \times T$	3	0.62	0.606
Site ($R \times T$)	30	3.27	<0.001	Site ($R \times T$)	30	5.19	<0.001
Site \times D ($R \times T$)	85	2.43	<0.001	Site \times D ($R \times T$)	85	2.72	<0.001
<i>Hypogymnia physodes</i>				<i>Imshaugia aleurites</i>			
Regeneration type (R)	1	3.93	0.057	Regeneration type (R)	1	22.52	<0.001
Time since harvesting (T)	1	18.73	<0.001	Time since harvesting (T)	1	4.53	0.042
Distance (D)	3	0.24	0.867	Distance (D)	3	0.98	0.407
$D \times T$	3	0.71	0.551	$D \times T$	3	0.72	0.541
$R \times T$	1	38.70	<0.001	$R \times T$	1	6.62	0.015
$R \times D$	3	2.07	0.111	$R \times D$	3	1.07	0.368
$R \times D \times T$	3	0.45	0.715	$R \times D \times T$	3	0.68	0.567
Site ($R \times T$)	30	2.79	<0.001	Site ($R \times T$)	30	3.60	<0.001
Site \times D ($R \times T$)	85	2.51	<0.001	Site \times D ($R \times T$)	85	3.83	<0.001
<i>Parmelia sulcata</i>				<i>Parmeliopsis ambigua</i>			
Regeneration type (R)	1	1.17	0.289	Regeneration type (R)	1	23.27	<0.001
Time since harvesting (T)	1	6.80	0.014	Time since harvesting (T)	1	0.88	0.357
Distance (D)	3	1.35	0.262	Distance (D)	3	2.04	0.114
$D \times T$	3	0.20	0.895	$D \times T$	3	2.00	0.120
$R \times T$	1	17.11	<0.001	$R \times T$	1	12.07	0.002
$R \times D$	3	0.40	0.755	$R \times D$	3	0.25	0.859

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(continued)

	Cover (%)				Cover (%)		
	df	F	p		df	F	p
$R \times D \times T$	3	1.21	0.310	$R \times D \times T$	3	1.09	0.360
Site ($R \times T$)	30	2.07	0.005	Site ($R \times T$)	30	7.93	<0.001
Site \times D ($R \times T$)	85	1.27	0.054	Site \times D ($R \times T$)	85	2.83	<0.001
<i>Parmeliopsis hyperopta</i>				<i>Tuckermanopsis ciliaris</i> group			
Regeneration type (R)	1	23.27	<0.001	Regeneration type (R)	1	0.02	0.891
Time since harvesting (T)	1	0.88	0.357	Time since harvesting (T)	1	10.47	0.003
Distance (D)	3	2.04	0.114	Distance (D)	3	0.97	0.413
$D \times T$	3	2.00	0.120	$D \times T$	3	1.42	0.243
$R \times T$	1	12.07	0.002	$R \times T$	1	13.46	<0.001
$R \times D$	3	0.25	0.859	$R \times D$	3	0.19	0.902
$R \times D \times T$	3	1.09	0.360	$R \times D \times T$	3	0.10	0.962
Site ($R \times T$)	30	8.34	<0.001	Site ($R \times T$)	30	5.53	<0.001
Site \times D ($R \times T$)	85	1.70	<0.001	Site \times D ($R \times T$)	85	3.15	<0.001
<i>Vulpicida pinastri</i>				Foliose lichens			
Regeneration type (R)	1	22.23	<0.001	Regeneration type (R)	1	23.22	<0.001
Time since harvesting (T)	1	0.08	0.776	Time since harvesting (T)	1	2.67	0.113
Distance (D)	3	1.59	0.198	Distance (D)	3	0.49	0.693
$D \times T$	3	6.72	<0.001	$D \times T$	3	2.16	0.099
$R \times T$	1	11.92	0.002	$R \times T$	1	28.44	<0.001
$R \times D$	3	0.51	0.676	$R \times D$	3	0.89	0.451
$R \times D \times T$	3	2.51	0.064	$R \times D \times T$	3	0.85	0.469
Site ($R \times T$)	30	9.36	<0.001	Site ($R \times T$)	30	7.19	<0.001
Site \times D ($R \times T$)	85	1.83	<0.001	Site \times D ($R \times T$)	85	4.09	<0.001

Note: Significant effects ($p \leq 0.05$) are shown in boldface. Sampling site nested within the interaction of regeneration type and time since harvesting and the interaction of sampling site with distance nested within the interaction of regeneration type after cutting and time since harvesting were considered as random factors. The random effects were used as error term when testing for differences between fixed effects.

Appendix B

See Fig. B1.

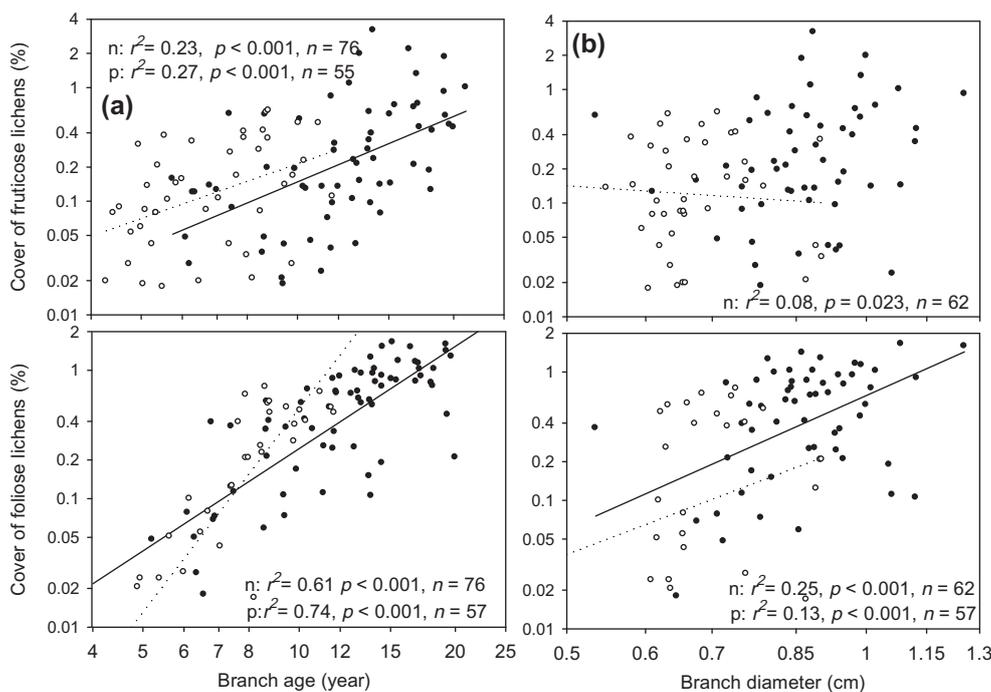


Fig. B1. Linear regressions (log₁₀ scale) of the lichen cover against (a) branch age ($n = 133$), (b) branch diameter ($n = 119$), (c) mean regeneration diameter at breast height ($n = 130$), and (d) number of regenerating trees ($n = 129$) for the two regeneration types (natural regeneration: filled circles, a black regression line and an equation preceded by the letter 'n'; plantation: empty circles, dotted regression line and an equation preceded by the letter 'p'). Regression lines are only shown for significant relationships ($p \leq 0.05$).

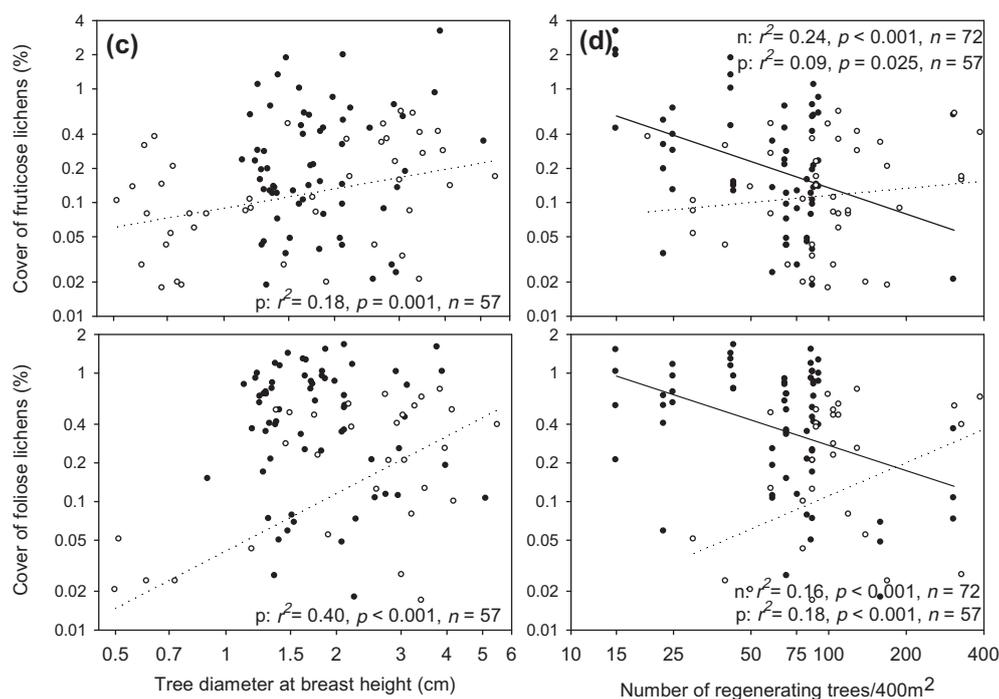


Fig. B1 (continued)

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