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

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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.

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 Såstad, 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,

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juvenile and mature thallus growth and reproduction are essential life stages (Armstrong, 1988; Hilmo and Såstad, 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 Såstad, 2001). Substrate quality, substrate availability, and microclimatic 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; Hedenås 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 Québec (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.

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	
Number of regenerating trees (No./ha)							
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
Diameter at breast height (cm)							
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
Tree height (cm)							
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
Branch age (year)							
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
Branch diameter (cm)							
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 ($p \leqslant 0.05$) 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*
Number of regenerating trees (n = 129)				
Regeneration type (R)	1	29	0.92	0.346
Time since harvesting (T)	1	29	8.55	**0.007**
$R \times T$	1	29	0.56	0.462
Site ($R \times T$)	29	96	26.62	**<0.001**
Diameter at breast height of regenerating trees (n = 130)				
Regeneration type (R)	1	30	4.29	**0.047**
Time since harvesting (T)	1	30	48.00	**<0.001**
$R \times T$	1	30	15.29	**0.001**
Site ($R \times T$)	30	96	7.49	**<0.001**
Tree height of regenerating trees (n = 130)				
Regeneration type (R)	1	30	1.91	0.178
Time since harvesting (T)	1	30	43.44	**<0.001**
$R \times T$	1	30	11.62	**0.002**
Site ($R \times T$)	30	96	6.21	**<0.001**
Branch age (n = 133)				
Regeneration type (R)	1	30	37.80	**<0.001**
Time since harvesting (T)	1	30	2.42	0.130
$R \times T$	1	30	19.45	**<0.001**
Site ($R \times T$)	30	99	8.01	**<0.001**
Branch diameter (n = 119)				
Regeneration type (R)	1	27	24.76	**<0.001**
Time since harvesting (T)	1	27	0.33	0.568
$R \times T$	1	27	3.31	0.080
Site ($R \times T$)	27	84	7.47	**<0.001**

Note: Significant effects ($p \leqslant 0.05$) 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.

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