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RESEARCH ARTICLE

Initiating the transition from open-canopy lichen woodland to productive forest by transplanting moss, results from a 10-year experiment

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Abstract
Background and aims Low productivity open lichen (*Cladonia* spp.) woodlands have been rapidly expanding in the closed-crown feather moss (*Pleurozium schreberi* (Brid.) Mitt.) boreal forest of eastern Canada. While open-woodland areas are progressing, there is little information on the recoverability of open lichen woodlands back to closed-canopy forests.
Methods An experimental set-up using moss transplantation was installed on a poor jack pine (*Pinus banksiana* Lamb.) stand with a lichen ground cover in 2011. Treatments included: 1) lichen cover removed, 2) lichen cover removed and transplantation of a feather moss cover, 3) lichen control, and 4) a natural jack pine site with feather moss cover (moss control). We extracted tree stem increment cores and collected needles and soil samples for nutrient analysis.
Results The transplanted-moss treatment can counteract the adverse effects of lichen on jack pine growth. This treatment enhanced foliar nutrition and soil nutrients, especially ammonium (N-NH_4^+) and nitrate (N-NO_3^-). With this treatment, the soil conditions (e.g., soil nutrients, soil moisture) and foliar nutrition were closer to that of moss control. Surprisingly, lichen removal treatment did not improve growth and resulted in poorer jack pine growth and harsher soil conditions.
Conclusion Feather moss can establish, survive, and remain healthy in an environment previously occupied by lichen. The replacement of lichen by feather moss establishes soil conditions that appear conducive to better tree growth and have the potential of restoring the productivity of boreal forests in open-canopy lichen woodlands.

Keywords Feather moss · Lichen · Restoration · Recoverability · Jack pine · Boreal forests

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Introduction

With global change, the rate of natural disturbances is predicted to increase over large portions of the boreal region (Boulanger and Pascual Puigdevall 2021). Open lichen (*Cladonia* spp.) woodlands, through an increased frequency of fires and through compound disturbances (insect outbreaks and fires), have been rapidly expanding in closed-canopy boreal forests of eastern Canada (Girard et al. 2008; Pacé et al. 2020a). Open lichen woodlands were described as an alternative stable state for closed-canopy feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forests (Payette et al. 2000; Jasinski and Payette 2005). In eastern Canada, the structure of lichen woodlands is simple with two main strata: sparse trees (mainly black spruce and/or jack pine) several meters apart (generally 10–40% cover) and large expanses of fruticose lichens of the genus *Cladina* and *Cladonia* (Payette et al. 2000). Feather moss tends to survive in shaded conditions of closed-canopy forests, while lichen tends to dominate in well-drained and high light conditions (Bonan and Shugart 1989; Sedia and Ehrenfeld 2003; Haughian and Burton 2015). Furthermore, lichen and feather moss, as two types of common ground cover in boreal forests, could affect forest growth and regeneration by influencing the physical and biochemical condition of the soil (Sedia and Ehrenfeld 2006; DeLuca et al. 2013; Mallik and Kayes 2018; Pacé et al. 2020b). Therefore, a better understanding of the factors that contribute to the transition between the two alternative states is needed to better promote sustainable management of boreal forests.

Feather moss is a common ground cover in boreal forests. It affects forest ecosystem processes by controlling soil moisture and temperature (Zackrisson et al. 1997; Gornall et al. 2011; Mallik and Kayes 2018), regulating soil nutrient availability (Wheeler et al. 2011; Bastianelli et al. 2017; Ouimet et al. 2018), and influencing the activity of soil microbial communities (Sedia and Ehrenfeld 2003) and incidentally the accumulation and mineralization of organic matter (Sedia and Ehrenfeld 2005). Ground cover composition can therefore exert an important control over soil carbon and nitrogen cycles (Turetsky 2003; Smith et al. 2017). Furthermore, DeLuca et al. (2022) showed that N_2 fixated in feather moss mats is retained in moss tissue for extended periods and then slowly transferred to the Organic (O) layer of the forest soil as the moss tissue decomposes. These observations suggest that feather mosses are a source of nitrogen for forest ecosystems and likely contribute to the nitrogen supply of boreal forest ecosystems (DeLuca et al. 2002; Haughian and Burton 2015). Lichens also have different roles in forest ecosystems. For example, lichens can increase seedling biomass accumulation, increase needle nitrogen uptake, serve as fodder for reindeer and caribou (Stark et al. 2007; Kytöviita and Stark 2009), and are a source of energy for soil microorganisms (Stark and Hyvärinen 2003). In contrast, other previous studies have shown that lichen appears to be detrimental to the growth of trees (Hawkes and Menges 2003; Pacé et al. 2019). Lichen could reduce the availability of soil nutrients (Wheeler et al. 2011; Pacé et al. 2016; Bastianelli et al. 2017), inhibit microbial communities (Sedia and Ehrenfeld 2003), and maintain lower soil moisture (Mallik and Kayes 2018) and allelopathy (Pacé et al. 2020b). These studies give solid scientific evidence for an important role of lichen in maintaining open woodland conditions. However, to our knowledge, there is no research on the potential for forest mosses to invade lichen woodlands and to potentially break the resilience of stable open-canopy woodlands that could lead to more productive forests. Moreover, processes of natural succession, from lichen to mosses, as well as the success of man-made transplantation of forest mosses have not been evaluated.

Our interest in investigating the potential conversion of lichen woodlands to closed-canopy moss forests was linked to the observation of an increase in the area covered by open-canopy lichen forests at the northern limit of the commercial boreal forest over the past decades (Girard et al. 2008). Additionally, ecosystem services provided by boreal forests, including biodiversity conservation and timber supply, could be negatively impacted by the expansion of lichen woodlands. The main goal of this research was to test the impact of changing the ground cover to enhance tree growth and improve soil conditions in slow-growing open-canopy lichen woodlands. The objectives of this study were (i) to determine the 10-year effects of ground cover manipulation (lichen, lichen removal, lichen removal with transplantation of feather moss) on the growth and foliar nutrient status of mature jack pine in boreal forests, (ii) to observe the response of soil properties to the manipulation of ground cover, and (iii) to gain information on the potential for a transition of lichen woodlands to more productive closed-canopy forests through the manipulation of ground cover. Based on previous studies, we hypothesized that feather moss transplantation would improve soil properties (soil nutrients and soil moisture) in open lichen woodlands. We also hypothesized that feather moss transplantation would result in better tree growth and foliar nutrition than lichen removal, and lichen, in that order.

Method

Study area

The study area location (49° 19′ 59” N; 79° 11′ 51” W) is in the spruce-feather moss bioclimatic domain of western Quebec, Canada (Saucier et al. 2011). The mean annual temperature and precipitation in the study area are 0 ± 2.9 °C and 909 mm, respectively (Pacé et al. 2020a). Our experiment was implemented on a 40-year-old jack pine (*Pinus banksiana* Lamb.) stand of 15 ha planted around 1980 (MFFP 2022). The stand lies over sandy to coarse-grained fluvioglacial and glaciolacustrine deposits (MFFP 2022). Ground cover is mainly composed of terricolous lichens including *Cladonia stellaris* (Opiz) Pouzar & Veda, *C. rangiferina* (L.) F.H. Wigg. and *C. mitis* Sandst (Pacé et al. 2020a). A sawfly outbreak was present near the study area during 2012–2014 (MFFP 2012). In June 2021, we selected a nearby naturally productive jack pine site, which had a continuous feather moss cover composed of *Pleurozium schrberi*. All soils are Humo-ferric Podzols or Dystric Brunisoils (Soil Classification Working Group 1998).

Experimental design and field sampling

The site that was selected in September 2011 for this study had homogeneous stand and site conditions. Thirty focal trees were selected at the center of plots. The selected trees were all the same age and size, and the spacing of the trees was regular with trees at least 15 m apart from each other. Each focal tree represented the center of a 160 m^2 circular plot (experimental units). We randomly applied treatments to each tree (10 replicated focal trees times 3 treatments). Three ground layer treatments (Fig. 1) were randomly and equally assigned to these plots: 1) complete lichen cover removal by hand ($n = 10$ plots), 2) complete lichen cover removal and feather moss (*P. schreberi*) transplantation ($n = 10$ plots), and 3) lichen control (no treatment, $n = 10$ plots). We obtained the moss transplants from a mature productive forest located less than 2 km away. Large sections of moss were cut out and transported in a trailer. Each experimental unit received several sections of intact mosses that were placed side by side with no spacing

Fig. 1 Appearance of forest and ground cover for the different treatments in 2013 and 2021

for infill. In addition, in June 2021, we selected 10 plots in a nearby naturally productive jack pine site, which had a continuous feather moss cover composed mostly of *Pleurozium schrberi*, to serve as a natural benchmark for this forest type and to compare with the transplanted moss treatment. For control moss sites, we considered a nearby closed-canopy jack pine stand with feather moss ground cover, flat topography, and sandy soil texture. We selected 10 plots (center trees), and like the lichen site, a distance of at least 15 m between selected trees was ensured. In total, there were 40 focal trees, 40 plots and 4 treatments: Lichen removal (No Lichen); transplanted moss (Moss Transplanted); control-lichen (No Treatment), and control-productive-moss (Moss Control). In all treatments, the understory was sparse and composed of only a few common species, including *Epigaea repens* (L.), *Vaccinium angustifolium* (Ait.), and *Kalmia angustifolia* (L.). We observed in the field that *Pleurozium* survived in all plots and expansion was not obvious. Additionally, composition of similar stands and vegetation were reported for the same region (Boudreault et al. 2002).

In 2021, tree stem increment cores were collected at breast height (1.3 m above ground). Needles were collected from each focal tree. All cores were prepared following standard dendrochronological procedures (Stokes 1996), and then scanned at 1200 dots per inch resolution to measure ring-width series using the program CooRecorder version 9.6 (Larsson 2020). We clipped branches from the crown of each focal tree to collect current and older year needles. Needle samples were oven-dried at 60 °C for 24 h and then ground for chemical analysis.

We extracted soil samples from each plot as follows. Within each plot, three locations were randomly sampled and pooled per layer. Both the forest floor (complete O layer; the depth of this layer varied from 2 to 8 cm) and the top 20 cm of the mineral soil were sampled at each of these locations. Moist samples were air-dried and sieved using 6-mm (forest floor) or 2-mm (mineral soil) meshes. Considering the low productivity of the sites, in situ available N was expected to be extremely low. Thus, we incubated the soil samples in the field prior to extraction to generate higher concentrations and obtain more reliable values. Specifically, as a relative index of N availability, we measured soluble N following an 8-week period using in situ buried bags for the forest floor and mineral soil separately (Hart et al. 1994; Kranabetter et al. 2021). We retrieved forest floors without decayed wood and placed them into polyethylene bags. Mineral soils were extracted to 20 cm and gently poured back into a polyethylene bag lining the sample hole. Forest floor samples were placed on top of the mineral soil bags and covered with lichen, moss or leaf litter. After 8 weeks, the bags were retrieved, and each sample ran through a 6-mm (forest floor) and 2-mm (mineral soil) sieve. One subsample was taken for moisture content, while a second subsample was kept frozen until extracted for NH_4^+-N, NO_3^--N, total dissolved nitrogen (TDN), and dissolved organic nitrogen (DON) determinations (Kranabetter et al. 2021). Soil temperature was recorded each hour from June to September 2021 using temperature data loggers (Spectrum®1000 Series) that were buried at a depth of 10 cm and at an approximate distance of 30 cm from focal trees. In each plot, soil moisture was measured with a portable TDR probe (Spectrum® TDR300) six times during the growing season (June–August) at two-week intervals.

Chemical analyses

Needle total carbon and nitrogen concentrations were measured by dry combustion using a Leco TruMac (Leco Corp., St-Joseph, MI, USA). Major and minor nutrients (P, K, Ca, Mg, Mn, Cu, Zn, Al, Fe, Mn, B, Sr, Na) were analyzed by inductively coupled plasma (ICP) using an optical emission spectrometer (Optima 7300 DV, PerkinElmer, Waltham, MA, USA) after ashing at 500 °C for 2 hours and recovery in 1 M HCl following Kalra (1997).

Soil pH was measured both in $CaCl_2$ and demineralized water solutions with a glass electrode and a pH meter (Orion 2 Star) (Carter and Gregorich 2007). Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), aluminum (Al), iron (Fe), sodium (Na) and strontium (Sr) were extracted with a Mehlich III extraction solution (Carter and Gregorich 2007) and analyzed by inductively coupled plasma (ICP) using an optical emission spectrometer (Optima 7300 DV, PerkinElmer, Waltham, MA, USA). The effective cation exchange capacity (CEC) was computed as the sum of exchangeable base cations (K, Ca, Mg, Mn, Al, Fe, Na). Total carbon (TC) and total nitrogen (TN) concentrations were measured by dry combustion using a Leco TruMac

CNS analyzer (Leco Corp., St-Joseph, MI, USA). Soil available N (NH_4^+, NO_3^- and TDN) was first extracted from incubated samples with a 1.0 M KCl solution (Carter and Gregorich 2007) and then analyzed by the FIA on a Lachat QuikChem® 8500 Series 2. Dissolved organic nitrogen (DON) was obtained by subtracting mineral nitrogen from total dissolved nitrogen after persulfate oxidation (Cabrera and Beare 1993).

Statistical analyses

The resulting ring-width series were statistically crossdated using the programs CDendro version 9.6 (Larsson 2020) and COFECHA (Holmes 1983). For each series, we estimated the distance to pith (Duncan 1989) by calculating basal area increments (BAI) using the R package "dplr" (Bunn 2008). We visually compared mean BAI values for series in each treatment and the control as follows. We focused our comparison of mean BAI on the nine years before (2002–2010) and nine years after (2012–2020) the treatment year, i.e., 2011. In one plot of the lichen cover with the transplantation of feather moss treatment, the branch of a focal tree was partially broken. We did not include the series for this focal tree in the analysis of mean BAI.

Differences in foliar nutrients and soil nutrients between ground cover treatments were analyzed by one-way ANOVA with Turkey post-hoc tests ($\alpha = 0.05$). Because TN, K, Ca, Mg and Mn concentrations in mineral soil were extremely low, the statistical results, even if significant, were not practically meaningful. Therefore, we did not include such nutrient information. In our data, extremely low values are those near or equal to the detection limit I (Mengel and Kirkby 2001). Control moss was not randomized as the other treatments; however, the stands were nearby and covered a similar area, thus we still considered this treatment. Data were transformed to meet the assumptions of normality and homogeneity of variance as necessary. All statistical analyses of ANOVA were performed in SPSS 26.0 (SPSS Inc., Chicago, USA). Principal component analysis (PCA) was conducted to visualize the soil properties and foliar nutrients of the four forest-ground treatments using the R software, version 4.2.2 (R Development Core Team 2022).

Results

Ten-years after transplantation, the moss had survived. However, we did not observe in the field an expansion of the planted moss outside of the area where it was transplanted, nor a colonization of lichen on the transplanted moss.

Effects of ground cover on soil properties

Ten years after ground cover treatments, there were clear differences in soil properties between ground cover treatments (Table 1; Figs. 2 and 3). Soil nutrients were mainly concentrated in the forest floor, and forest floor nutrients responded more strongly to ground cover treatments than the mineral soil (Table 1). Overall, soil properties of the transplanted-moss treatment were significantly different from those of the control lichen and lichen removal, but more similar to those of the control moss (Table 1; Fig. 3). On the forest floor, the transplanted-moss treatment and control moss had significantly higher TC and TN, followed by control lichen, while the lowest concentrations were found in the lichen removal treatment. No such effect was found for the C/N ratio. Moreover, the transplanted moss treatment had significantly higher available P and exchangeable Sr, K, Ca, Mg, Mn, Al, Fe, and CEC than control lichen and lichen removal treatments, while values were more similar to those of control moss. Both transplanted-moss treatment and control moss showed significantly higher TDN, N-NH_4^+, N-NO_3^- and DON concentrations than control lichen, whereas the lichen removal treatment showed the lowest values. In the mineral soil, except for exchangeable Sr, Fe, DON and soil pH, the element concentrations did not differ significantly between ground cover treatments. Mineral soil pH ($CaCl_2$) of control moss was more acidic and lower by 0.4 units compared to the lichen treatments, while that of transplanted moss was intermediate and not statistically different from other treatments.

Compared to other treatments, the lichen removal treatment showed significantly higher soil temperature and lower moisture content (Fig. 2). The transplanted moss treatment did not bring significant changes to these properties compared to the lichen control (Fig.2). However, PCA indicated that both moss treatments showed conditions tending to be wetter and cooler than lichen and lichen removal treatments (Fig. 3).

Table 1 Effects of ground cover treatment on soil nutrients (forest floor and mineral soil)

		Control-L ($n=10$)	Lichen– ($n=10$)	Moss+ ($n=10$)	Control-M ($n=10$)	*df*	*P* value
Forest floor							
TC	%	5.79(0.85)b	1.35(0.12)c	13.07(1.30)a	13.82(1.32)a	4	**<0.001**
TN	%	0.11(0.02)b	0.03(0.00)c	0.30(0.03)a	0.27(0.02)a	4	**<0.001**
C/N		51.72(0.66)	56.11(6.56)	43.80(1.05)	52.14(1.61)	4	0.099
pH	H_2O	3.74(0.09)b	4.15(0.09)a	3.91(0.04)ab	3.78(0.04)b	4	**0.001**
pH	$CaCl_2$	3.00(0.09)b	3.59(0.10)a	3.22(0.05)b	3.07(0.04)b	4	**<0.001**
P	mg kg^{-1}	16.54(2.05)b	12.68(2.10)b	39.27(3.15)a	29.66(2.83)a	4	**<0.001**
Sr	mg kg^{-1}	1.61(0.40)b	0.68(0.09)b	4.17(0.33)a	3.82(0.34)a	4	**<0.001**
K	*cmol*(+) kg^{-1}	0.22(0.03)b	0.08(0.01)b	0.56(0.05)a	0.56(0.06)a	4	**<0.001**
Ca	*cmol*(+) kg^{-1}	0.48(0.11)c	0.17(0.03)c	4.45(0.41)a	2.36(0.36)b	4	**<0.001**
Mg	*cmol*(+) kg^{-1}	0.16(0.03)b	0.06(0.01)b	0.80(0.09)a	0.95(0.09)a	4	**<0.001**
Mn	*cmol*(+) kg^{-1}	0.03(0.01)b	0.01(0.00)b	0.26(0.04)a	0.05(0.01)b	4	**<0.001**
Al	*cmol*(+) kg^{-1}	9.35(0.53)b	12.09(2.10)ab	14.12(0.84)a	10.17(0.84)ab	4	**0.045**
Fe	*cmol*(+) kg^{-1}	1.88(0.12)ab	1.53(0.12)b	2.07(0.10)a	1.95(0.08)a	4	**0.008**
Na	*cmol*(+) kg^{-1}	0.02(0.00)bc	0.01(0.00)c	0.05(0.00)b	0.15(0.02)a	4	**<0.001**
CEC	*cmol*(+) kg^{-1}	12.14(0.65)b	13.94(2.03)b	22.30(1.18)a	16.18(1.20)b	4	**<0.001**
TDN	mg kg^{-1}	13.99(1.54)b	7.12(1.00)b	45.95(6.69)a	36.22(5.42)a	4	**<0.001**
N-NH_4^+	mg kg^{-1}	4.31(1.07)b	2.16(0.82)b	25.14(4.54)a	21.04(4.06)a	4	**<0.001**
DON	mg kg^{-1}	9.79(1.26)bc	5.16(0.38)c	20.79(2.62)a	15.17(2.30)ab	4	**<0.001**
N-NO_3^-	mg kg^{-1}	0.25(0.01)b	0.25(0.00)b	0.29(0.01)a	0.27(0.01)ab	4	**0.005**
Mineral layer							
TC	%	0.46(0.03)	0.35(0.04)	0.51(0.06)	0.43(0.05)	4	0.118
pH	H_2O	5.1(0.01)a	5.1(0.02)a	5.0(0.02)a	4.9(0.05)b	4	**0.006**
pH	$CaCl_2$	5.0(0.02)a	5.0(0.05)a	4.8(0.05)ab	4.6(0.1)b	4	**0.003**
P	mg kg^{-1}	14.60(1.51)	16.35(2.54)	16.80(2.07)	15.26(2.38)	4	0.844
Sr	mg kg^{-1}	0.10(0.00)b	0.11(0.01)b	0.19(0.01)a	0.17(0.02)a	4	**<0.001**
Al	*cmol*(+) kg^{-1}	28.46(0.33)	28.12(0.34)	28.50(0.48)	26.92(0.82)	4	0.140
Fe	*cmol*(+) kg^{-1}	0.30(0.02)b	0.27(0.03)b	0.39(0.02)b	0.68(0.09)a	4	**<0.001**
CEC	*cmol*(+) kg^{-1}	28.81(0.34)	28.44(0.33)	28.98(0.49)	27.69(0.79)	4	0.317
TDN	mg kg^{-1}	1.32(0.14)	1.23(0.51)	1.71(0.30)	3.48(1.13)	4	0.063
N-NO_3^-	mg kg^{-1}	0.17(0.01)	0.21(0.03)	0.17(0.00)	0.20(0.01)	4	0.178
DON	mg kg^{-1}	1.14(0.23)ab	0.50(0.21)b	1.57(0.25)ab	2.45(0.80)a	4	**0.031**
N-NH_4^+	mg kg^{-1}	0.15(0.05)	0.72(0.40)	0.39(0.12)	1.29(0.48)	4	0.086

Significant differences between ground-cover treatments are represented by different letters. Standard error values are in parentheses

Control-L is control lichen; Lichen- is lichen removal; Moss+ is moss transplantation; Control-M is control moss. Significant *P* values are shown in bold

Foliar nutrients

The foliar nutrient composition of jack pine trees showed significant differences between ground cover treatments (Table 2). The current-year foliage and the one-year-old foliage showed similar variability in composition between ground cover treatments (Table 2; Fig. 4; Fig. S1). For current-year as well as one-year-old foliage, there were no significant differences between ground cover treatments in foliar N, P, C/N and C/P concentrations. However, the transplanted-moss treatment had significantly higher foliar Ca, Mg, Mn, Zn and Na concentrations than control lichen and lichen removal treatments. The transplanted-moss treatment showed foliar concentration values that were comparable to those

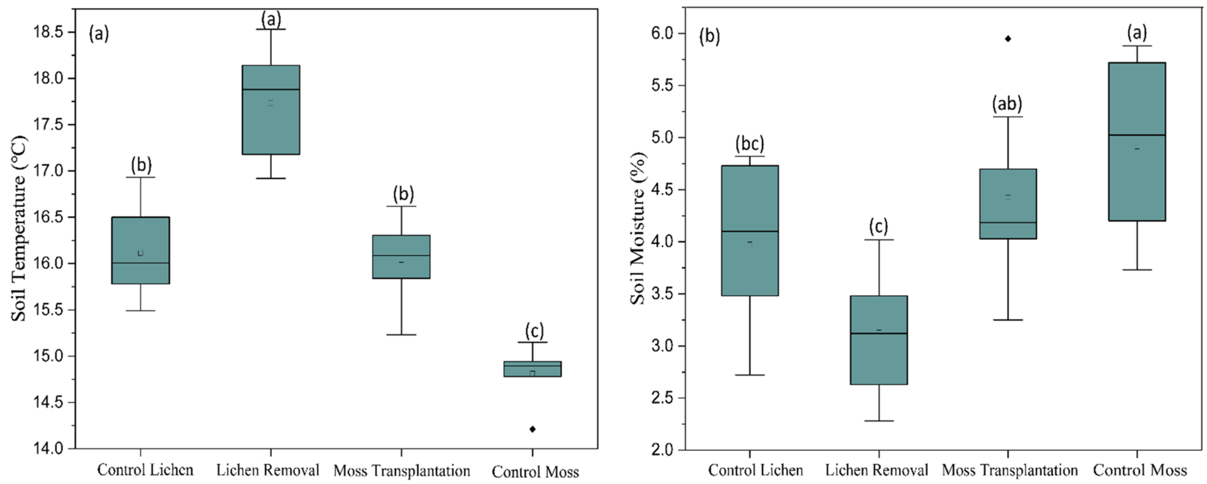


Fig. 2 The response of soil temperature (**a**) and soil moisture (**b**) to ground cover treatments. Sampling took place between June and September 2021. The soil temperature and moisture data for each treatment is an average of the period. Significant differences between ground-cover treatments are represented by different letters

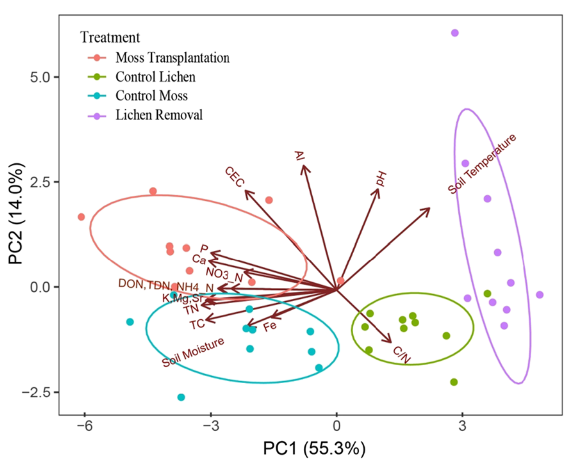


Fig. 3 Principal component analysis (PCA) biplot of individuals (i.e., treatment plots, $n = 40$) and explanatory variables (i.e., forest floor soil properties, $n = 18$). The biplot shows PCA scores of explanatory variables as vectors (dark-red arrows) and individuals of each forest-ground treatment (circles), of the first (x-axis) and second (y-axis) principal components (PCs). Individuals on the same side as a given explanatory variable should be interpreted as having a high contribution on it

of the control moss treatment, particularly for Ca, Mg, Zn and Na (Table 2; Fig. 4). These values were significantly higher than those of the control lichen and lichen removal treatments ($P < 0.001$). The foliar K concentration in the control moss treatment was significantly higher than with other treatments ($P < 0.05$), whereas foliar nutrient concentrations of lichen removal were similar to values found in control lichen, with low foliar nutrient concentrations.

Tree growth

We measured radial growth of jack pine over 2002–2020. Overall, there was a similar trend in jack pine growth (basal area increment, BAI) between ground cover treatments until 2011, the treatment year. After 2011, jack pine growth showed distinct trends (Fig. 5). The growth of jack pine with a lichen ground cover (control lichen) declined over time but revealed sharper decline between 2012 and 2014. The lichen removal treatment showed sharp decline after the disturbance in 2011 and then remained with a low growth rate. In comparison, the transplanted-moss treatment initially declined after disturbance, and then recovered from 2014 and maintained higher growth until the end of the observation period. Overall, all three treatments showed a similar declining trend in the first three years after 2011 (the treatment year).

Discussion

To our knowledge, this study represents the first experimental study reporting on the effects of transplanting moss in an open-canopy lichen woodland.

Table 2 Effects of ground cover treatment on jack pine foliar nutrients (current year and old years)

		Control-L ($n = 10$)	Lichen- ($n = 10$)	Moss+ ($n = 10$)	Control-M ($n = 10$)	*df*	*P* value
Foliage (old years)							
N	%	1.00(0.03)	1.01(0.02)	0.98(0.03)	0.95(0.02)	4	0.432
P	g kg^{-1}	0.88(0.02)	0.92(0.04)	0.90(0.02)	0.85(0.02)	4	0.349
C/N		54(1.19)	54(1.03)	55(1.82)	56(1.23)	4	0.726
N/P		11.35(0.88)	11.11(0.98)	10.92(1.12)	11.18(0.74)	4	0.781
K	g kg^{-1}	2.50(0.17)ab	2.33(0.15)b	2.34(0.10)b	2.91(0.11)a	4	**0.014**
Ca	g kg^{-1}	2.44(0.20)b	2.47(0.16)b	4.62(0.27)a	4.44(0.34)a	4	**<0.001**
Mg	g kg^{-1}	0.37(0.03)c	0.44(0.04)c	0.62(0.03)b	0.80(0.07)a	4	**<0.001**
Mn	g kg^{-1}	0.25(0.02)b	0.37(0.04)b	0.52(0.05)a	0.29(0.02)b	4	**<0.001**
Zn	mg kg^{-1}	25.57(1.99)c	43.25(4.11)b	68.82(4.33)a	70.85(5.18)a	4	**<0.001**
Al	g kg^{-1}	0.38(0.03)ab	0.49(0.03)a	0.33(0.03)b	0.35(0.03)b	4	**0.003**
Fe	mg kg^{-1}	67.62(5.85)a	65.41(5.02)ab	74.46(5.88)a	47.58(3.18)b	4	**0.005**
B	mg kg^{-1}	9.52(0.46)	9.29(0.57)	8.32(0.84)	8.96(0.83)	4	0.642
Sr	mg kg^{-1}	5.77(0.65)b	8.98(1.28)a	7.42(0.54)ab	5.46(0.56)b	4	**0.015**
Na	mg kg^{-1}	6.37(1.14)b	11.13(1.51)b	13.07(1.36)ab	21.90(4.05)a	4	**<0.001**
Foliage (current)							
N	%	0.92(0.02)	1.00(0.04)	0.95(0.03)	1.00(0.02)	4	0.189
P	g kg^{-1}	0.94(0.02)	0.96(0.04)	0.99(0.02)	0.96(0.02)	4	0.534
C/N		57.08(1.35)	53.08(1.80)	54.77(1.56)	52.24(1.23)	4	0.127
N/P		9.85(0.58)ab	10.40(0.51)a	9.61(0.65)b	10.36(0.61)a	4	**0.011**
K	g kg^{-1}	2.64(0.19)b	2.57(0.16)b	2.80(0.06)b	3.63(0.16)a	4	**<0.001**
Ca	g kg^{-1}	1.37(0.11)c	1.47(0.11)bc	2.34(0.16)a	1.95(0.12)ab	4	**<0.001**
Mg	g kg^{-1}	0.49(0.03)c	0.59(0.03)bc	0.68(0.03)ab	0.75(0.03)a	4	**<0.001**
Mn	g kg^{-1}	0.17(0.02)b	0.25(0.03)ab	0.31(0.03)a	0.17(0.01)b	4	**<0.001**
Zn	mg kg^{-1}	27.80(1.16)c	34.96(2.24)c	42.93(2.01)b	52.02(2.03)a	4	**<0.001**
Al	g kg^{-1}	0.24(0.02)b	0.32(0.02)a	0.21(0.02)b	0.25(0.01)ab	4	**0.003**
Fe	mg kg^{-1}	33.32(2.40)a	27.29(0.67)ab	29.81(2.26)ab	25.31(1.57)b	4	**0.026**
B	mg kg^{-1}	9.85(0.48)	9.49(0.45)	8.82(0.77)	9.82(0.96)	4	0.705
Sr	mg kg^{-1}	3.16(0.37)ab	4.75(0.65)a	3.46(0.31)ab	2.55(0.25)b	4	**0.007**
Na	mg kg^{-1}	12.95(1.92)b	12.77(1.58)b	17.70(3.29)b	28.50(3.40)a	4	**<0.001**

Significant differences between ground-cover treatments are represented by different letters. Standard error values are in parentheses. Control-L is control lichen; Lichen- is lichen removal; Moss+ is moss transplantation; Control-M is control moss. The significant *P* values are shown in bold

The treatments had effects on the soil, tree growth, and foliar nutrition.

Ground cover and soil conditions

The transplanted moss treatment generated soil conditions that were similar to those of moss control and enhanced soil nutrients with respect to lichen control. These effects were mostly observed on the forest floor only. Exchangeable cations, extractable P, and all N availability indices (total N, total dissolved N, nitrate, ammonium, and DON) were significantly higher in the forest floor of the transplanted moss treatment compared to the lichen control. Previous research has shown that feather moss mats have a high potential for nitrogen fixation thanks to associated cyanobacteria (DeLuca et al. 2002; DeLuca et al. 2008; Bay et al. 2013; Rousk et al. 2013; Jean et al. 2021; Renaudin et al. 2022). We also observed that the transplanted-moss soil had a slightly higher nitrogen concentration

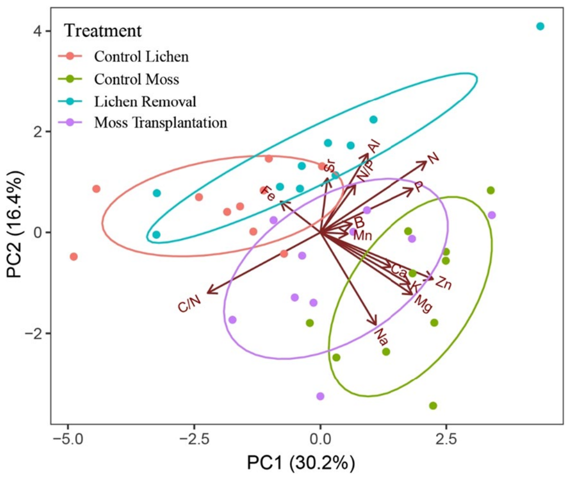


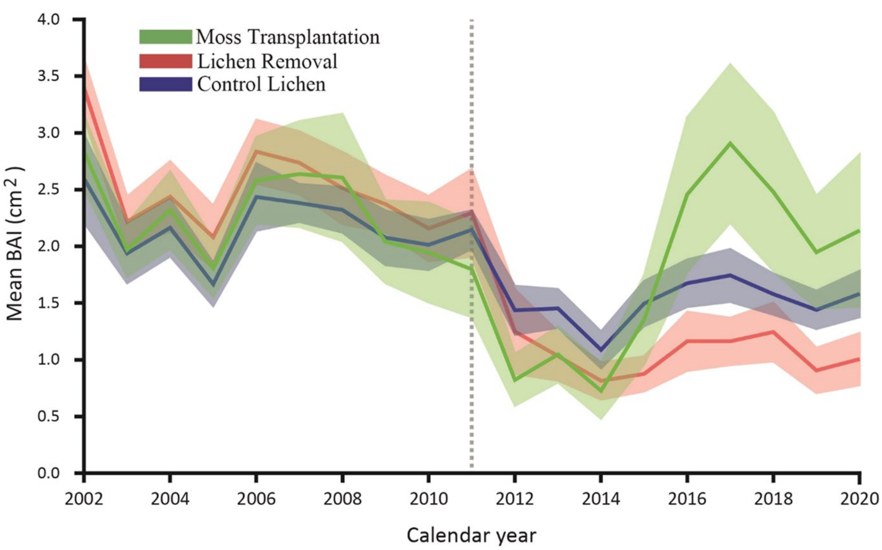
Fig. 4 Principal component analysis (PCA) biplot of individuals (i.e., treatment plots, $n = 40$) and explanatory variables (i.e., current foliar nutrients, $n = 14$). The biplot shows the PCA scores of the explanatory variables as vectors (dark-red arrows) and individuals of each forest-ground treatment (circles), of the first (x-axis) and second (y-axis) principal components (PCs). Individuals on the same side as a given explanatory variable should be interpreted as having a high contribution on it. For the PCA analysis of the nutrition of older-year foliar nutrients, see Supplementary Material Fig. S1

than the control moss in the forest floor, even though this difference was not statistically significant. A possible explanation is that the transplanted-moss treatment was in open lichen woodlands where sunlight is more available and conditions are warmer than forests with greater canopy closure (Gundale et al. 2012). However, direct measurement of N fixation activity would be needed to evaluate the source of available soil N and distinguish N provided by imports in the transplanted moss versus the amount that was fixed since the onset of the transplantation if this were the case.

Our results showed that the soil temperatures of the transplanted-moss treatment were significantly higher than that of control moss, and control moss and transplanted-moss were associated with higher soil moisture than the other treatments. Some studies have shown that soil moisture availability is an important factor regulating soil mineral weathering rates (Gordon 2005; Egli et al. 2006; Brady et al. 2008). Similarly, the leaching of organic acid can favor mineral weathering. While we did not assess the flux of dissolved organic carbon, it is presumably higher in moss treatments that contain much more organic carbon. Pacé et al. (2019) showed that feather mosses host a greater diversity of ectomycorrhizal fungi than lichens. In summary, more favorable physical, chemical, and biological conditions of the moss layer may explain our results; namely, a higher availability of base cations, and some trace elements, in the soil and foliage under moss control and transplanted moss treatment.

Soil nutrient concentrations were somewhat lower in both control lichen and lichen removal, and soil nutrients were slightly lower overall in the lichen removal than in the control lichen. A similar finding by Sedia and Ehrenfeld (2005, 2006) indicates that lichen creates low nutrient microhabitats, possibly due to the slower decomposition of litter under lichen

Fig. 5 Jack pine mean basal area increment (BAI) during 2002–2020 (Control Lichen/Lichen Removal, $n = 10$; Moss Transplantation, $n = 9$). The legend is as follows: Green line, transplanted moss; Blue line: no treatment, control lichen; Red line: lichen removal. Shaded areas represent the standard error of the mean (for a visualization including the control moss group, see Supplementary Material Fig. S2)



than under moss. Additionally, Pacé et al. (2020b) indicated a potential allelopathic effect of local lichens on jack pine seedlings.

Foliar nutrients and soil properties

The effect of ground cover on jack pine was reflected in foliar nutrient concentrations, and the variation in foliar nutrient concentrations between ground covers were similar in older and current year needles. In Canadian boreal forests, nitrogen and phosphorus are the most common limiting nutrients (Paquin et al. 1998; Maynard et al. 2014). Our study showed no significant differences in foliar N, P, C/N and N/P concentrations among the ground covers, except for foliar N/P in the current year. The foliar C/N ratio ranged from 52.24 (±1.23) to 57.08 (±1.35) and the foliar N/P ratio ranged from 9.61 (±0.65) to 11.35 (±0.88). Our N/P ratio results were similar to Vallicrosa et al. (2022), who reported a value of 12.35 ($SD = 1.73$) in boreal forests. However, we found that transplanted moss treatment significantly increased foliar Ca, Mg, Mn, Zn, Na in comparison to lichen control and yielded foliar concentrations that were similar to control moss. Foliar concentrations were generally lower and much more similar between control lichen and lichen removal.

Results from the soil and foliage were not fully coherent. While all cations as well as available P and N in the forest floor were higher in the moss transplant treatment than under other treatments, only the cations showed a positive foliar response. This was surprising because jack pine stands in particular have shown an almost ubiquitous positive response to N and to P fertilization in Canadian boreal forests (Maynard et al. 2014). The absence of a significant foliar N and P difference may be due to dilution (Imo and Timmer 1998), namely more N and P were taken up by the trees that produce more abundant foliage without modifying their foliar nutrient concentrations. Our result showed that the specific needle weight (dry mass current year needle par 100 needles) was not different between treatments (Supplementary Material, Table S1), indicating that if such an effect occurred following the onset of the treatments, it is not present today and perhaps the trees are producing a more extended canopy with stable N and P concentrations. The enhanced cation concentration in the foliage could indicate that trees are less water limited. Mass flow is the main process by which plants take up Ca and Mg (McGonigle and Grant 2015), so that a greater uptake may reflect a greater water flow through tree stems. These latter results were coherent with the greater soil water content observed in treatments with a moss cover. The drier conditions in the lichen removal treatment may have contributed to a lower tree nutrient uptake (Houle et al. 2016).

Treatment effect on tree growth

Compared to control lichen and lichen removal, the transplanted-moss treatment had a different effect on jack pine growth after 2011 than before this date. In the first three years after treatment installation, growth of jack pine decreased in all treatments. After this period, growth recovered and declined again until 2014. After 2014, the growth of trees in the transplanted moss treatment increased and recovered to the pre-experimental period, while that of the lichen and the lichen removal treatments remained lower than that of the transplanted moss treatment. The delay in a positive response in the transplanted moss treatment is probably due to the direct effects of the disturbance, potentially including root damage induced by the treatment, as well as to the slow acclimatation of the root system. Another potential explanation is that the supply of N fixed by cyanobacteria living in feather moss mats is preserved in the moss tissue for a long time before being transferred to the forest floor during the decomposition of the moss tissue (DeLuca et al. 2022). A potential explanation for the decline in growth for all treatments between 2011 and 2014 is that all trees may have been influenced by a combination of harsher climate (such as drought) and jack pine sawfly damage (*Neodiprion swainei* Middleton). A sawfly outbreak was present near the study area during this period, but we lack confirmation of an occurrence in our plots (MFFP 2012).

Enhanced tree growth in the transplanted moss treatment for the latest portion of the experiment (post 2011, and more specifically post 2014) was consistent with findings by Wheeler et al. (2011) and Pacé et al. (2020b) who showed that feather moss facilitates the establishment and growth of tree seedlings. Several factors can be responsible for enhanced tree growth in the transplanted moss treatment. A greater soil water availability was measured in the transplanted moss treatment. This is not surprising because the moss layer has a strong capacity to retain water and this may greatly change the amount of soil available water following a rainfall event (Ilek et al. 2015). In the coarse sandy soils of our study area, water availability may be critical even if the climate is not considered arid. Another factor that may influence growth is nutrient availability. Jack pine is responsive to nitrogen and phosphorus fertilization (Newton and Amponsah 2006; Maynard et al. 2014). Here, we found enhanced N and P availability in the soil but not in foliar nutrient concentrations. As discussed previously, a potential explanation is a dilution effect with homeostatic nutrient concentration in the foliage but a greater overall foliage mass, although this would need to be validated. Lastly, another potential cause for enhanced growth with mosses is a chemical inhibition of the plants or mycorrhizae from lichen. Mallik and Kayes (2018) showed that lichen seedbeds inhibit black spruce seedling regeneration, potentially through the presence of usnic acid, a common germination inhibiting allelochemical.

Our study also showed that lichen removal not only does not improve growth but appears to result in poorer jack pine growth. This is somewhat surprising because removal of lichen probably would reduce a source of allelochemicals, such as the usnic acid. Pacé et al. (2016) show that lichen removal increases fine root biomass of pine trees, whereas Fauria et al. (2008) indicate that lichen removal by grazing can enhance adult pine growth. Our results may be due to reduced accumulation of organic matter on the ground following lichen removal and direct exposure of the mineral soil, resulting in lower soil moisture and greater diurnal temperature fluctuation (Hawkes and Menges 2003; Lavoie et al. 2006; Houle et al. 2016) (Also, see our results Fig. 2). In addition, understory vegetation plays an important role in soil nutrient availability, tree production, and soil-plant interrelationships (Landuyt et al. 2019; Zhou et al. 2022). Therefore, the removal of the understory may adversely affect soil nutrients, soil water content, and microbial activity (Zhang et al. 2022).

Our findings suggested that feather moss has a key role in promoting and maintaining mature jack pine growth. Moreover, our results also suggested that the role of feather mosses in water regulation and litter decomposition rates may be a mechanism to promote tree growth in poor lichen woodlands. To our knowledge, our study is the first to suggest that controlling the ground layer could initiate a transition from open-lichen woodland conditions to those of a more productive closed-canopy moss forest. Although we recognize that the lichen woodland is a unique habitat playing an important role for the preservation of biodiversity, maintaining a mosaic of ecosystems of various composition and productivity contributes to ecological function diversity and thus enhances resilience to disturbance and environmental changes (Thompson et al. 2009).

Conclusion

Feather mosses are an important component in boreal forests, contributing to boreal forest growth and improving soil properties. Mansuy et al. (2013) suggested that afforestation of open lichen woodlands in boreal forests can be a means of increasing forest productivity. However, without appropriate soil conditions, productive closed-canopy forest conditions may not be achieved. Furthermore, to our knowledge, there are no studies documenting the recoverability of lichen woodlands to closed-canopy forests in Canada. Our 10-year results indicated that it is possible to replace a lichen cover with a feather moss cover and that feather moss can establish, survive, and remain healthy in an environment previously occupied by lichen. The replacement of lichen by feather moss establishes soil conditions that appear conducive to better tree growth and has the potential of restoring the productivity of boreal forests in open-canopy lichen woodlands. The mechanisms involved are not fully elucidated and could be related to a greater availability of water and nutrients thanks to inputs from cyanobacteria associated with *Pleurozium* moss mats and to a greater level of weathering of soil minerals. However, the importance of such mechanisms needs to be evaluated. Also, our results of no moss expansion after 10 years suggested that the effect may be local, at least in the short term. Therefore, the feasibility of transplanting mosses over large areas and the long-term survival of mosses need to be evaluated. Removing lichens as an alternative to increase productivity does not seem to be a good approach, as lichen removal conversely had an adverse effect on tree growth in our experiments. Moreover, considering the sensitivity of feather mosses to high light conditions, as well as the potential damage to the source forest caused by the transplantation process, transplantation may not be needed. Instead, productive forest conditions can be maintained by promoting low light conditions in the understory that are favorable to feather mosses rather than to lichens. Dense plantations or restocking natural stands could be possible solutions. Finally, forest managers could give preference to sites already dominated by feather moss that may be beneficial for tree growth when reforestation occurs.

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Declarations

Conflict of interest Authors declare that they have no conflicts of interest.

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