NRC Research Press

ARTICLE

Ground-layer composition affects tree fine root biomass and soil nutrient availability in jack pine and black spruce forests under extreme drainage conditions

Marine Pacé, Nicole J. Fenton, David Paré, and Yves Bergeron

Abstract: In the boreal forest, long-lasting canopy gaps are associated with lichens on dry sites and with *Sphagnum* spp. on wet sites. We hypothesize that ground-layer composition plays a role in maintaining gaps through its effects on fine root biomass (diameter ≤ 2 mm) and soil nutrient availability. Along gradients of canopy openness in both jack pine (*Pinus banksiana* Lamb.) – lichen and black spruce (*Picea mariana* (Mill.) B.S.P.) – moss forests, the relationships between canopy closure, ground-layer composition, tree fine root biomass, and soil nutrients were analyzed and decomposed using path analysis. The effects of lichen and *Sphagnum* spp. removal on tree fine root biomass and soil nutrients were tested in situ. Although variations in pine fine root biomass were mainly explained by stand aboveground biomass, lichen removal locally increased fine root biomass by more than 50%, resin extractable soil potassium by 580%, and base cations by 180%. While *Sphagnum* cover was identified as a key driver of stand aboveground biomass reduction in paludified forest sites, its removal had no short-term effects on spruce fine root biomass and soil nutrients. Our results suggest that lichens, more than *Sphagnum* spp., affect tree growth via direct effects on soil nutrients. These two different patterns call for different silvicultural solutions to maintain productive stands.

Key words: lichen, moss, *Sphagnum* spp., fine root, forest regeneration.

Résumé : En forêt boréale, l'ouverture prolongée du couvert forestier favorise un couvert de lichens sur les stations xériques et un couvert de sphaignes sur les stations hydriques à subhydriques. Nous posons l'hypothèse que la composition de la strate des mousses et lichens joue un rôle dans le maintien de clairières ouvertes par ses effets sur la biomasse de racines fines (diamètre ≤ 2 mm) et la disponibilité des nutriments dans le sol. Nous avons analysé et décomposé les relations entre l'ouverture de la canopée, la composition de la strate de végétation basse, la biomasse de racines fines des arbres et les nutriments du sol à l'aide d'une analyse de pistes le long de gradients d'ouverture du couvert en pinède (*Pinus banksiana* Lamb.) à lichens et en pessière (*Picea mariana* (Mill.) B.S.P.) à mousses. Les effets de l'enlèvement des lichens et des sphaignes sur la biomasse de racines fines des arbres et les nutriments du sol ont été testés in situ. Quoique la variation de la biomasse de racines fines des pins ait été principalement expliquée par la biomasse aérienne du peuplement, l'enlèvement des lichens a localement augmenté la biomasse de racines fines de plus de 50 %, ainsi que la disponibilité en potassium et en cations basiques extraits de résine de respectivement 580 % et 180 %. Bien que le couvert de sphaignes ait été identifié comme un facteur clé de la réduction de la biomasse aérienne des peuplements établis sur les stations forestières paludifiées, son enlèvement n'a pas eu d'effet à court terme sur la biomasse de racines fines des épinettes ni sur le contenu en nutriments du sol. Nos résultats indiquent que les lichens, plus que les sphaignes, influencent la croissance des arbres en ayant des effets directs sur les nutriments du sol. Le maintien de peuplements forestiers productifs sur ces deux types de station nécessite des solutions sylvicoles différentes.

Mots-clés : lichens, mousses, sphaignes, racines fines, régénération forestière.

Introduction

The ground layer (i.e., bryophyte and lichen layer) is an important component of the boreal forest biome (Cornelissen et al. 2007), whose composition largely influences ecosystem processes, including the carbon cycle via differential rates of primary production (Turetsky 2003) and decomposition (Lang et al. 2009) and the nitrogen cycle via differential rates of atmospheric nitrogen fixation (DeLuca et al. 2002) or nitrogen immobilization (Augusto et al. 2015). It also influences soil processes through the modification of drivers such as pH, temperature, oxygenation, and moisture regime (Fenton et al. 2006). Moss and lichen species affect microbial and fungal community composition (Ohtonen and Väre 1998; Sedia and Ehrenfeld 2003), either indirectly through their effects on soil conditions (Nilsson and Wardle 2005) or directly through allelochemical emission (Molnár and Farkas 2010; Chiapusio et al. 2013), although this second pathway remains highly controversial (Kytöviita and Stark 2009).

The influence of the ground layer on ecosystem functions in the boreal forest may have visible consequences at the stand scale.

Received 16 August 2016. Accepted 1 December 2016.

M. Pacé. Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada; Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 10380, Stn Sainte-Foy, Québec, QC G1V 4C7, Canada.
N.J. Fenton and Y. Bergeron. Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada.
D. Paré. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S., P.O. Box 10380, Stn Sainte-Foy, Québec, QC G1V 4C7, Canada.
Corresponding author: Marine Pacé (email: marine.pace@uqat.ca).

Can. J. For. Res. **47**: 433–444 (2017) dx.doi.org/10.1139/cjfr-2016-0352

Under some conditions, a forest can move from a productive state to an alternative state that is commercially unproductive (i.e., lichen woodland or forested peatland). These conditions of openness are maintained by deficits in tree regeneration and (or) growth. They tend to occur on sites with extreme drainage conditions, i.e., either rapidly drained sites on coarse-grained deposits (Jasinski and Payette 2005) or poorly drained sites subject to paludification (Simard et al. 2007). In both cases, long-term forest stand opening is associated with a shift in the composition of the ground layer. Feather mosses are replaced by lichens on rapidly drained sites (Payette et al. 2000) and by *Sphagnum* spp. mosses on poorly drained sites (Bisbee et al. 2001) as the two are favoured by the increase in light availability. Because mosses and lichens have different effects on the physical, chemical, and biological conditions of the forest soil, ground-layer compositional changes may have consequences on tree regeneration and (or) growth. For example, it has been demonstrated that seedling growth is greater in feather mosses than in *Sphagnum* spp. (Lafleur et al. 2011) and that some secondary metabolites produced by lichens (e.g., usnic acid) may have allelopathic effects on microorganisms, fungi, and trees (Sedia and Ehrenfeld 2003; Molnár and Farkas 2010). As the ground layer may affect tree growth through its effects on roots, we used fine root biomass as an indicator of the impact of the ground layer on tree physiology.

While aboveground forest processes have been relatively well studied, belowground processes remain poorly understood (Augusto et al. 2015). Trees adapt to belowground conditions and resource availability by changes in biomass allocation between above- and below-ground organs (Brassard et al. 2009; Noguchi et al. 2012), root branching pattern and longevity (Persson and Ahlström 2002), and mycorrhizae colonization (Kalliokoski et al. 2010). Tree fine root biomass constitutes an easily measurable indicator of tree adaptation in contrasted environments. Indeed, fine roots are particularly important for nutrient and water uptake (Brassard et al. 2009) as they offer a maximized exchange area (Taskinen et al. 2003), in part through their association with symbiotic mycorrhizae (Hinsinger et al. 2009). Moreover, fine roots have a relatively short life-span and adapt quickly to changes in soil conditions or water supply (Persson and Ahlström 2002).

In this study, we focus on the effects of ground-layer composition on tree fine root biomass, as an indicator of tree physiology adjustment, and on the way that these effects interact with the shading effect of forest cover. This approach is innovative for several reasons: firstly, we consider two types of sites that are very different a priori but that are undergoing similar processes; secondly, we focus on the ground layer, whose role in forest ecosystem processes is poorly appreciated; and finally, we examine fine root biomass, while previous research on long-term canopy opening focused on aboveground tree growth (Gower et al. 1996; Fauria et al. 2008). We hypothesize that lichen and *Sphagnum* spp. covers, which are favored by the absence of shading effect from the forest cover, contribute to maintaining stand openness by inhibiting tree fine root development and maintaining a low soil nutrient availability. Based on both observational and experimental approaches, the objectives of this study are (*i*) to determine the relationships between ground-cover composition, tree fine root biomass, canopy closure, and soil nutrient availability in forests that include the two stable states, i.e., open- and closed-crown stands, and (*ii*) to determine the effects of lichen and *Sphagnum* spp. removal on tree fine root biomass and soil nutrient availability, as well as the way that these effects are modified by shade and fertilization in open-crown forests. The first approach allows us to establish general correlation patterns of tree fine root biomass at the stand scale, while the second provides experimental support and a better understanding of the drivers responsible for the correlation patterns that we observe.

Material and methods

Study area

The study area is located in the spruce–moss forest of western Quebec (Table 1). Forest composition is dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) with variable abundance of jack pines (*Pinus banksiana* Lamb.), depending on soil conditions. The natural regeneration of these two tree species particularly depends on the occurrence of fires, which constitute the main natural disturbance in the study area (Bergeron et al. 2004). Average annual temperature is 0 ± 2.9 °C and average annual precipitation is 909.1 mm (Joutel, Quebec; Environment Canada 2016). The territory is relatively flat and covered by organic or well-sorted mineral deposits. Two forest types were selected for this study: (*i*) pure jack pine – lichen stands located on fluvioglacial coarse-grained deposits and (*ii*) essentially pure black spruce – moss stands situated on lacustrine clay deposited by the proglacial lake Ojibway (Blouin and Berger 2005). Common understory plant species are *Epigaea repens* L., *Kalmia angustifolia* L., *Linnaea borealis* L., and *Vaccinium angustifolium* Ait. in pine–lichen stands and *Chamaedaphne calyculata* (L.) Moench, *Cornus canadensis* L., *Gaultheria hispidula* (L.) Muhl. ex Bigelow, *Rhododendron groenlandicum* (Oeder) Kron & Judd, and *Vaccinium angustifolium* Ait. in spruce–moss stands. *Pleurozium schreberi* (Brid.) Mitt., *Dicranum polysetum* Swartz, *Dicranum undulatum* Schrad. ex Brid., *Polytrichum strictum* Brid., *Sphagnum capillifolium* (Ehrh.) Edw., *Sphagnum angustifolium* (C. Jens. ex Russ.) C. Jens., and *Sphagnum fuscum* (Schimp.) Klinggr. were the most frequent bryophyte species. Terricolous lichens were mainly represented by *Cladonia stellaris* (Opiz) Pouzar & Vězda, *Cladonia rangiferina* (L.) F.H. Wigg., and *Cladonia mitis* Sandst.

Sampling design

In 2014, we sampled 25- to 38-year-old stands of each forest type with variable post-fire or post-logging density (Table 1). Each forest type was replicated four times using four geographically separate sites (2 to 12 km apart for the pine–lichen stands and 1.5 to 6 km apart for the spruce–moss stands), each containing four to six randomly distributed circular 100 m² plots (located at least 200 m apart) with different degrees of forest canopy closure, for a total of 20 plots per forest type. Within each forest type, variations in canopy closure among plots were not related to variations in soil conditions (Table 2).

Aboveground characteristics of the plots were sampled in August 2014. In each 100 m² plot, we surveyed species composition and cover of the ground layer in a central circular 5 m² subplot. Given the moderate speed of moss and lichen growth (Turetsky 2003; Kytöviita and Crittenden 2007), ground-cover composition was assumed to be relatively constant through the growing season. Canopy closure was measured using photos taken with a fisheye lens from the centre of the subplot. The photos were analyzed in terms of percentage of pixels attributable to trees (including trunk, branches, and foliage) using Adobe Photoshop Elements software (Adobe Systems, San José, California). For six plots per forest type, temperature and air humidity close to the ground layer were recorded from June to September 2014 (Table 1) using HOBO® data loggers (HOBO® U23 PRO V2, Onset Data Loggers, Bourne, Massachusetts). All living trees were recorded within the 100 m² circular plots surrounding each subplot. Trees measuring less than 1.5 m were classified into three different height classes (less than 0.5 m, between 0.5 and 1 m, and between 1 and 1.5 m). Diameter at breast height (DBH) was recorded on trees > 1.5 m tall. Stand age was estimated based on the time since the last disturbance determined from local archives (Y. Bergeron, personal communication) and was verified for each site by selecting 12 to 18 dominant trees and counting tree rings based on nondestructive cores (Table 1). Aboveground tree biomass was calculated from DBH using species-specific biomass equations (Ung et al. 2008).

Table 1. Characteristics of the two sampled areas and experimental sites (mean and range).

Forest type	Pine–lichen	Spruce–moss
Sampled areas (20 plots nested in four sites for each forest type)		
Longitude		
Northern limit	49°25′N	49°45′N
Southern limit	49°19′N	49°42′N
Latitude		
Western limit	79°15′W	79°18′W
Eastern limit	79°11′W	79°16′W
Drainage	Rapid	Poor
Area covered by the study	2400 ha	1200 ha
Dominant tree species	*Pinus banksiana* Lamb.	*Picea mariana* (Mill.) B.S.P.
Percentage of dominant species' stems (%)	97 (77–100)	99 (92–100)
Last disturbance type	Clearcut	Fire
Year of the last disturbance	1980 and 1989	1976
Regeneration	Sowing or plantation	Natural
Dominant tree age estimated from tree rings (years)	26.8 (17–37)	22.3 (18–35)
Stand density (trees·ha^{-1}, all sizes)	3310 (1200–5500)	8800 (1600–17000)
Stand aboveground biomass (t·ha^{-1})[a]	66.0 (27.2–104.0)	15.4 (1.2–45.9)
Stand canopy closure (%)	61.0 (37.0–72.7)	51.5 (11.0–86.2)
Microenvironmental conditions of the understory from June to September 2014		
Temperature (°C)	16.1 (–3.2–44.5)	16.0 (–3.2–43.6)
Air humidity (%)	87.1 (12.1–100)	86.8 (12.3–100.0)
Ericaceae aboveground biomass (t·ha^{-1})	1.65 (0.56–3.55)	2.75 (0.44–6.72)
Ground cover composition (%)		
Feather mosses	45 (1–90)	45 (10–90)
Lichens	45 (1–90)	15 (0–25)
Sphagnum spp.	—	40 (0–90)
Ground living biomass (t·ha^{-1})[b]	11.0 (4.4–18.1)	8.1 (0.5–28.4)
Tree fine root biomass (kg·ha^{-1})	1380 (660–2060)	2810 (310–4440)
Experimental sites		
Longitude	49° 23′N	49° 43′N
Latitude	79° 14′W	79° 17′W
Drainage	Rapid	Poor
Area of the experimental site	2 ha	4 ha
Dominant tree species	*Pinus banksiana* Lamb.	*Picea mariana* (Mill.) B.S.P.
Percentage of dominant species' stems	99%	92%
Last disturbance type	Clearcut	Fire
Year of the last disturbance	1980	1976
Regeneration	Plantation	Natural
Dominant tree age estimated from tree rings (years)	26 (24–28)	27 (23–30)
Stand density (trees·ha^{-1}, all sizes)	2570	17000
Stand aboveground biomass (t·ha^{-1})[a]	69.0	45.9
Stand canopy closure (%, one measure per plot)	60.2 (53.4–66.0)	80.54 (78.6–82.0)
Microenvironmental conditions of the understory from June to September 2014		
Temperature (°C)	16.3 (–1.0–40.6)	14.3 (–1.0–45.4)
Air humidity (%)	83.3 (11.0–100)	96.9 (34.4–100.0)
Initial tree fine root biomass (kg·ha^{-1})	1070 (520–2110)	1010 (300–2760)

[a] Stand aboveground biomass was estimated from the sum of individual-tree biomasses. Individual-tree biomasses were estimated based on species-specific biomass equations developed for tree species of Canada (Ung et al. 2008). Model calibration is based on trees ranging from 1.6 to 38.4 cm in diameter at breast height (DBH) for black spruce and from 2.5 to 48.9 cm in DBH for pine.

[b] Ground living biomass corresponds to the living biomass of the moss and (or) lichen layer. The whole cryptogam part that did not present leaf and (or) stem blackening or traces of decomposition was considered as living. In the case of *Sphagnum* spp., which can accumulate a thick layer of undecomposed fibric material, the white parts (unpigmented stems) that were more than 30 cm deep were not considered.

Because tree fine roots are mainly located in the top 20 cm of soil (Kalliokoski et al. 2010), especially in jack pine and black spruce stands (Noguchi et al. 2012), tree fine root abundance was estimated by extracting three cores randomly located within the central circular 5 m² subplots of each plot. These cores, which were 5 cm in diameter and 20 cm deep from the bottom base of the living ground layer, were extracted using an auger in the beginning of September 2014. This date corresponds to the early end of the growing season, i.e., shortly before the seasonal peak of fine root decomposition (Brassard et al. 2009). We assumed that all of the roots that we found in the cores at this date had been produced under the influence of the ground layer sampled in August 2014. Soil cores were transported to the laboratory in a cooler and kept frozen at −20 °C until analysis. Each core was examined to discriminate tree roots from roots of other species (mainly Ericaceae) and to separate fine roots (≤2 mm diameter) from the larger roots (>2 mm diameter) that were not considered in this study. We harvested one to three root samples of the most common species from the study sites, i.e., jack pine, black spruce, *Kalmia* spp., *Vaccinium* spp., and *Rhododendron* spp., and used them to develop recognition criteria based on morphological characteristics. Humidified pine fine roots were beige to slightly reddish,

Table 2. Soil characteristics (mean ± standard error (SE)) of the two sampled areas and links between these characteristics and the degree of canopy closure (Pearson correlation coefficient).

Soil characteristics	Mean (±SE)	r^a
Pine–lichen stands		
Mineral soil texture (20 cm deep)		
Proportion of sand (%)	87 (±5)	0.37
Proportion of silt (%)	8 (±6)	0.24
Proportion of clay (%)	5 (±2)	0.36
Organic layer depth (m)	0.12 (±0.03)	0.14
Mineral soil		
Dissolved inorganic nitrogen (mg·kg^{-1})	0.86 (±0.20)	0.17
Phosphorus (mg·kg^{-1})	0.67 (±0.29)	0.20
Spruce–moss stands		
Organic layer depth (m)	0.72 (±0.30)	0.10
Water table depth (m)	0.21 (±0.06)	0.00
Deep organic matter (1 m deep)		
Dissolved inorganic nitrogen (mg·kg^{-1})	11.66 (±16.23)	0.00
Phosphorus (mg·kg^{-1})	1.90 (±1.91)	0.20

[a] No relationships were significant (p value > 0.1).

and their root tips mostly presented a characteristic "Y" shape when mycorrhized. Spruce roots were reddish brown, darker in colour than pine. Ericaceae roots tended to be darker, thinner, and less curved than those of the two tree species. Tree fine roots were rinsed with water, sorted (alive vs. dead) following the criteria established (Brassard et al. 2011), dried at 65 °C, and weighed. Fine root biomass was expressed in kilograms per unit area (kg·ha^{-1}).

Soil content in dissolved inorganic nitrogen (DIN) was measured in each 5 m^2 subplot. The organic layer (O or FH) was sampled in both forest types. In spruce–moss stands, the organic layer was separated into surface and deep (1 m deep) layers. Mineral soil was sampled only in the pine–lichen stands (top 20 cm). Mineral samples were air-dried and sieved at 2 mm. Organic samples were first sieved at 6 mm to remove large roots and debris, dried at 60 °C, and then ground and sieved at 2 mm. NH_4-N and NO_3-N were extracted with a 2 mol·L^{-1} KCl solution and analyzed by spectrophotometry (QuikChem R8500 Series 2, Lachat Instruments, Milwaukee, Wisconsin).

Experimental design

One site per forest type, including a pine–lichen stand and a spruce–*Sphagnum* spp. stand, was selected in each study area for the experiment (Table 1). For each forest type, 38 1 m^2 circular plots were randomly distributed within the 2 to 4 ha sites so that they contained a homogeneous cover of lichen or *Sphagnum* spp. The aboveground portion of the ericaceous plants was clipped off at the soil surface. Ericaceae roots were not removed to avoid ground-cover disturbance. Initial tree fine root biomass (expressed in kg·ha^{-1}) was estimated by extracting two cores (5 cm diameter and 20 cm deep from the bottom base of the living ground layer) per plot at the beginning of the experiment (June 2014) using an auger. Lichens or *Sphagnum* spp. were then removed on 19 plots, while the other 19 plots were used as controls. Among the 19 plots of each modality, seven were covered with a 50% shade cloth (perforated net positioned 20 cm above the ground surface and covering the whole 1 m^2 plot) and five were fertilized with 5 g of controlled-release fertilizer (20% nitrogen, 7% phosphorus, and 10% potassium; Plant-Prod Smartcote®, Master Plant-Prod Inc., Brampton, Ontario). Because trees can produce fine roots within a radius of 5 m around the trunk (Taskinen et al. 2003), all trees located within a radius of 5 m around the 1 m^2 plots were counted and their DBH were measured. Two other cores per plot were extracted at the end of the experiment (September 2014) to estimate final tree fine root biomass per unit area. June and September cores were stored and analyzed as previously described. For each plot, soil nutrient availability was measured for the duration of the experiment using ion-exchange resins buried 10 cm deep in the soil from June to September 2014. Ion-exchange resin bags (see McCavour et al. 2014) were made using 20 g of mixed-bed ion-exchange resin (J.T. Baker®, Avantor Performance Materials, Central Valley, Pennsylvania) contained in beige nylon bags (made of standard stockings) and regenerated with 1 mol·L^{-1} HCl. Resins were delicately removed from the soil, kept separately in sealed plastic bags, transported to the laboratory in a cooler, and stored at 4 °C until analysis. NO_3-N and NH_4-N were extracted using a 2 mol·L^{-1} KCl solution and analyzed by spectrophotometry (QuickChem R8500 Series 2, Lachat Instruments) to estimate soil DIN. Phosphorus, potassium, magnesium, calcium, and sodium were extracted using a 2 mol·L^{-1} HCl solution and analyzed by inductively coupled plasma (ICP) using an optical emission spectrometer (OES) (Optima 7300 DV, Perkin Elmer, Waltham, Massachusetts). Soil base cations were estimated by summing the concentrations of the major base cations contained in the resins (K, Ca, Mg, and Na).

Statistical analyses

We considered each forest type separately for statistical analyses. We first used a correlation analysis to examine the relationships between ground-cover composition (lichen–*Sphagnum* spp. cover, %), tree fine root biomass (kg·ha^{-1}), canopy closure (%), tree aboveground biomass (tonnes (t)·ha^{-1}) and DIN (mg·kg^{-1}). A path analysis was then used to discriminate partial correlations between stand aboveground biomass, canopy closure, lichen–*Sphagnum* spp. cover, and tree fine root biomass (Shipley 2002). The use of four variables in the path analysis allowed us to respect the recommendation advising a limit of eight free parameters for 20 observations for an acceptable performance of the general least squares χ^2 statistic (Shipley 2002). Path coefficients between these variables made possible the discrimination of direct, nondirect, and noncausal correlations. Because our sample was small and may slightly deviate from normality, we used a Yuan–Bentler scaled test statistic (Bentler and Yuan 1999) for the directional-separation (d-sep) test (Shipley 2002) to determine the likelihood that an a priori structure was correct. Kurtoses were verified for the different variables used in the path analyses (Shipley 2002).

The relationships between initial tree fine root biomass and stand aboveground biomass in the two experimental sites were first tested to verify if this parameter should be included in the models. The effects of ground-cover removal (lichen or *Sphagnum* spp., according to the forest type) and secondary treatments (shade and fertilization) were then tested on final tree fine root biomass (kg·ha^{-1}) and soil nutrient availability (measured from the ion-exchange resins). Linear models were used to decompose the effects of the second factor (secondary treatments), i.e., to analyze the effects of fertilization vs. control in a first phase and shade vs. control in a second phase. When necessary, the dependent variables of the linear models were transformed to respect normality (log-transformations). When errors were heteroscedastic for one factor (especially for the secondary treatments because variance was higher in fertilized plots than in control and shaded plots), degrees of freedom were sacrificed to estimate the variance associated with each level of factor. All analyses were performed on R-3 software (R Core Team 2014).

Results

Relationships between stand aboveground biomass, canopy closure, ground-cover composition, tree fine root biomass, and soil nutrient availability in the sampled area

Pine–lichen stands

In the pine–lichen stands, variation in stand aboveground biomass was partly related to stand age (Fig. 1*a*). Feather mosses and lichens varied with canopy closure as expected, with greater lichen cover under open canopies (Fig. 1*a*; Table 3). Pine fine root biomass, which was 1380 kg·ha^{-1} on average (range: 660 to

Fig. 1. Scores of the 20 plots along axes 1 and 2 of the principal component analysis (PCA) based on six target variables: (*a*) pine–lichen stands; (*b*) spruce–moss stands. Each plot (20 per forest type) is represented by the letter of the matching site (A, B, C, or D); see figure legend for stand age of sites. For each variable, the direction of variation is indicated by an arrow.

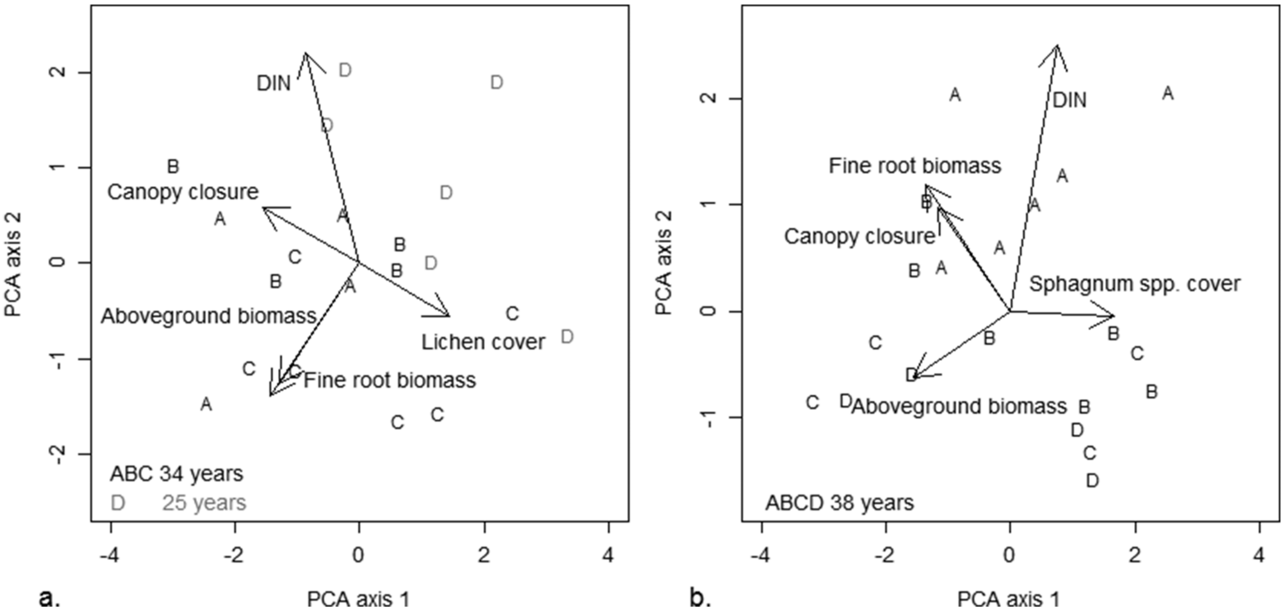


Table 3. Pearson correlation coefficients between canopy closure, lichen–*Sphagnum* spp. cover, fine root biomass, stand aboveground biomass, and dissolved inorganic nitrogen (DIN) for the two forest types.

	Lichen–*Sphagnum* spp. cover	Fine root biomass	Stand aboveground biomass	DIN
Pine–lichen stands				
Canopy closure	**–0.66***	0.47	0.55	0.49
Lichen cover	—	–0.33	–0.56	–0.40
Fine root biomass	—	—	**0.69***	0.15
Stand aboveground biomass	—	—	—	0.01
Spruce–moss stands				
Canopy closure	**–0.68***	0.39	**0.62***	0.00
Sphagnum spp. cover	—	**–0.63***	**–0.70****	0.32
Fine root biomass	—	—	0.32	–0.04
Stand aboveground biomass	—	—	—	0.32

Note: Significant relationships (after Bonferroni correction) are given in bold. *, *p* value < 0.005; **, *p* value < 0.001.

2060 kg·ha^{-1}, respectively), was positively associated with stand aboveground biomass and poorly related to lichen cover (Fig. 1*a*; Table 3). Interestingly, pine roots tended to be thinner under lichen than under feather moss (personal observation). Lichen cover tended to be slightly associated with low soil DIN, although the trend was not significant ($R = -0.40$, $p = 0.0808$). The structure determined by path analysis for the pine–lichen stands (Fig. 2*a*) was not rejected by d-sep analysis ($\chi = 2.89$, df = 2, p value = 0.23), showing that the data were consistent with the proposed causal structure (Shipley 2002). It indicated that the direct effect of stand aboveground biomass on fine root biomass in the study area was much more important than its indirect effect via canopy closure and lichen cover and that the slight correlation between lichens and fine root biomass fell more under a noncausal relationship between the two rather than under a direct effect (Fig. 2*a*; Table 4).

Spruce–moss stands

The proportion of *Sphagnum* spp. in the ground layer significantly decreased with the degree of canopy closure in spruce–moss stands (Fig. 1*b*; Table 3). Tree fine root biomass was higher in spruce–moss stands than in pine–lichen stands with an average of 2810 kg of spruce fine roots per hectare (range: 310 to 4440 kg·ha^{-1}). Spruce fine root biomass was negatively associated with *Sphagnum* spp. cover and poorly related to stand aboveground biomass (Fig. 1*b*; Table 3). Moreover, ground-cover composition was closely related to stand aboveground biomass, which decreased significantly with *Sphagnum* spp. cover (Table 3). *Sphagnum* spp. cover was not linked to soil DIN. Considering the close relationship between *Sphagnum* spp. cover and stand aboveground biomass, we proposed two causal structures for the path analysis in spruce–moss stands. The first (Fig. 2*b*), which is the same as the one proposed for the pine–lichen stands, considers that the *Sphagnum* spp. cover results from the stand aboveground biomass effect on canopy closure. The second considers that *Sphagnum* spp. cover does not depend on canopy closure, but directly influences stand aboveground biomass, which in turn affects canopy closure. Contrary to the first structure determined by path analysis (Fig. 2*b*) that was rejected by d-sep analysis ($\chi = 11.48$,

Fig. 2. Schematic representation of three different hypothesized causal structures including stand aboveground biomass, canopy closure, ground-cover composition, and tree fine root biomass: (*a*) pine–lichen stands (χ = 2.91, df = 2, p value = 0.23, scaling correction factor for the Yuan–Bentler correction = 0.80); (*b*) spruce–moss stands, model 1 (χ = 11.48, df = 2, p value < 0.01, scaling correction factor for the Yuan–Bentler correction = 0.65); (*c*) spruce–moss stands, model 2 (χ = 2.59, df = 1, p value = 0.11, scaling correction factor for the Yuan–Bentler correction = 0.87). Significant correlations are indicated in bold (**, p value < 0.01; ***, p value < 0.001). As recommended by Shipley (2002) for small size samples, possible edges characterized by a significant level lower than 0.2 (†) are also represented as solid lines.

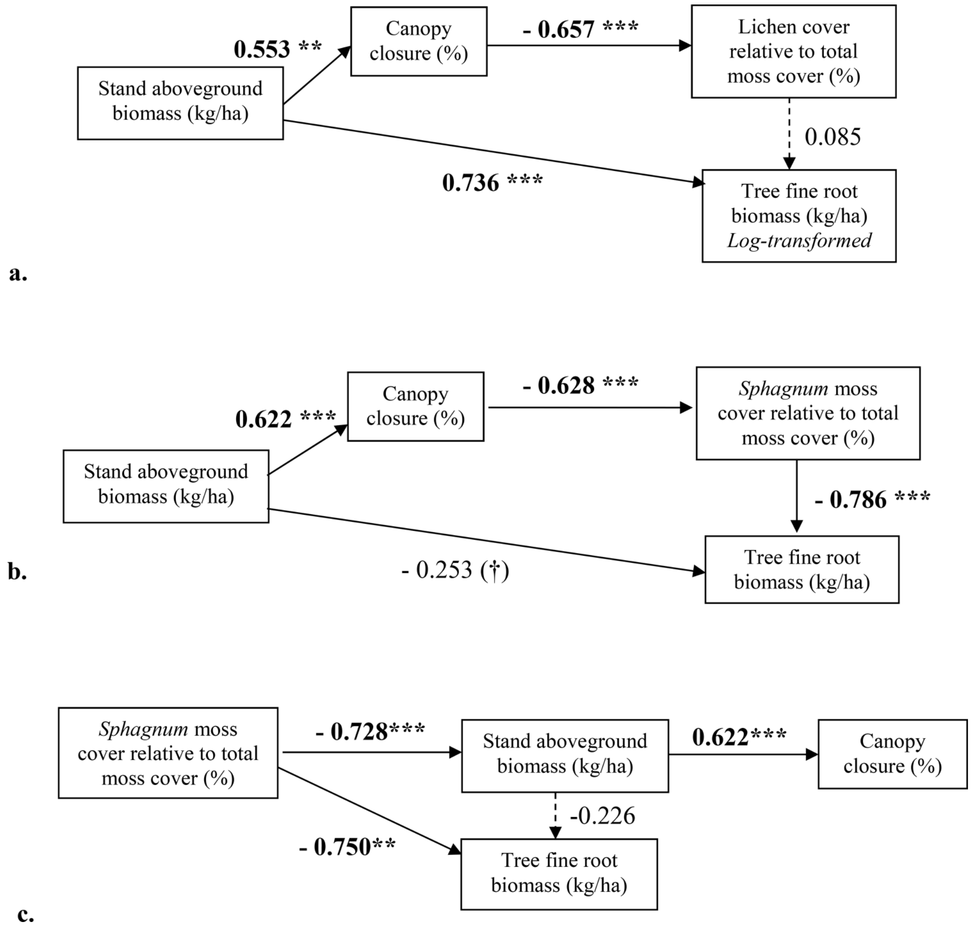


Table 4. Direct effect, indirect effect, noncausal variation, and total correlation for path analysis of tree fine root biomass per unit area based on the different hypothesized causal structures.

Variable	Direct effect (SE)	Indirect effect	Noncausal variation	Total correlation[a]
Pine–lichen forest				
Tree fine root biomass (log-transformed)				
Stand aboveground biomass	**0.736 (0.173)*****	–0.031	0	0.688
Lichen cover	0.085 (0.173)	0	–0.267	–0.327
Canopy closure	0	–0.056	0.407	0.469
Spruce–moss forest				
Tree fine root biomass (model 1)				
Stand aboveground biomass	–0.253 (0.189)	0.307	0	0.319
Sphagnum spp. moss cover	**–0.786 (0.189)*****	0	0.099	–0.602
Canopy closure	0	0.494	–0.157	0.390
Tree fine root biomass (model 2)				
Stand aboveground biomass	–0.226 (0.254)	0	0.546	0.319
Sphagnum spp. moss cover	**–0.750 (0.253)****	0.165	0	–0.633
Canopy closure	0	0	0.258	0.390

Note: Significant relationships are given in bold. **, p value < 0.01; ***, p value < 0.001.

[a] Total value represents the Pearson correlation coefficient (r).

df = 2, p value < 0.01), the second structure (Fig. 2*c*) was plausible considering the data (χ = 2.77, df = 2, p value = 0.11). Hence, it suggests that the second causal structure that we proposed was a better fit than the first, showing that *Sphagnum* spp. cover was less a consequence of canopy opening than the main factor explaining low stand aboveground biomass in the sampled area. The two path analyses indicate that tree fine root biomass was more closely related to *Sphagnum* spp. cover than to stand aboveground biomass (Table 4).

Table 5. Treatment effect on tree fine root biomass and soil characteristics for the two forest types.

	Pine–lichen			Spruce–moss		
	t	*p* value	R^2	*t*	*p* value	R^2
Final tree fine root biomass (kg·ha^{-1})						
Lichen–*Sphagnum* spp. removal (1)	2.05	**0.0483**	0.04	0.15	0.8816	0.06
Fertilization (2)	1.29	0.2049		1.99	0.0550	
Shade (3)	0.35	0.7315		−0.21	0.8356	
Interaction 1 × 2	−1.53	0.1368		—	—	
Interaction 1 × 3	−0.41	0.6829		—	—	
Dissolved Inorganic Nitrogen (mg·kg^{-1})						
Lichen–*Sphagnum* spp. removal (1)	0.12	0.9065	0.58	−0.85	0.4044	0.66
Fertilization (2)	4.47	**0.0001**		3.57	**0.0011**	
Shade (3)	−1.26	0.2165		−0.77	0.4496	
Interaction 1 × 2	−2.16	**0.0383**		2.49	**0.0183**	
Interaction 1 × 3	1.75	0.0898		1.91	0.0651	
Phosphorus (mg·kg^{-1})						
Lichen–*Sphagnum* spp. removal	−1.09	0.2830	0.04	0.72	0.4746	0.30
Fertilization	1.26	0.2170		4.22	**0.0002**	
Shade	−0.50	0.6230		1.32	0.1972	
Potassium (cmol·kg^{-1})						
Lichen–*Sphagnum* spp. removal (1)	2.51	**0.0178**	0.26	−0.18	0.8560	0.19
Fertilization (2)	2.50	**0.0180**		2.87	**0.0071**	
Shade (3)	1.81	0.0803		−0.32	0.7486	
Interaction 1 × 2	−3.65	**0.0010**		—	—	
Interaction 1 × 3	−3.12	**0.0040**		—	—	
Sum of major base cations (cmol·kg^{-1})						
Lichen–*Sphagnum* spp. removal (1)	2.45	**0.0204**	0.24	−0.34	0.7335	0.13
Fertilization (2)	2.47	**0.0193**		−0.10	0.9204	
Shade (3)	1.07	0.2914		−0.77	0.4498	
Interaction 1 × 2	−3.47	**0.0016**		1.41	0.1690	
Interaction 1 × 3	−2.29	**0.0290**		2.03	0.0511	

Note: Significant *p* values are given in bold.

Effects of ground-cover removal, fertilization, and shade on tree fine root biomass and soil properties

Pine–lichen forest

Initially, there was on average 1070 kg of pine fine roots per hectare in the pine–lichen plots used for the experimental study (Table 1). Initial pine fine root biomass was poorly associated with stand aboveground biomass in the experimental site (Pearson's $R = 0.14$, *t*-test statistic = 0.87, p value > 0.1); thus, we did not consider this covariable in the ensuing models. Three months after treatment application, lichen removal on the 1 m² plots locally increased pine fine root biomass by more than 50% (Table 5), rising from 1099 kg·ha^{-1} on average for control plots to 1902 kg·ha^{-1} for plots where ground cover had been removed (Fig. 3). Fertilization and shade did not significantly affect pine fine root biomass (Fig. 3; Table 5).

Lichen removal had no effect on DIN and phosphorus, but it positively affected potassium and soil base cations (×6.8 and ×2.8, respectively), including magnesium (×2.3) and sodium (×3.6). Phosphorus, potassium, and DIN tended to be higher after fertilization (×3.1, ×8.8, and ×190, respectively; Fig. 4), although the trend was not significant for phosphorus (Table 5). Soil base cations were also significantly increased by fertilization (more than 3× higher in fertilized plots compared with control plots). With the exception of phosphorus, the positive effects of fertilization on nutrient availability and base cations were lower in the case of lichen removal (significant negative effect of the interaction between the two treatments; Table 5). Shade reduced the positive effects of lichen removal on potassium and base cations, although it did tend to increase the positive effect of lichen removal on DIN (marginal positive effect of the interaction).

Spruce–moss forest

Average initial tree fine root biomass in the plots of the spruce–moss experimental site was 1010 kg of spruce fine roots per hectare (Table 1). As for the pine–lichen site, stand aboveground biomass was poorly associated with the initial spruce fine root biomass in the experimental site (Pearson's $R = 0.12$, *t*-test statistic = 0.71, p value > 0.1) and was not considered in the ensuing models. Spruce fine root biomass was not affected by *Sphagnum* spp. removal and shade after 3 months; however, it was marginally increased by fertilization (+42% on average) (Fig. 3; Table 5).

Sphagnum spp. removal and shade did not affect any of the measured soil nutrient concentrations (Fig. 5; Table 5). However, fertilization strongly affected soil DIN, phosphorus, and potassium availability (×58, ×9.4, and ×3.8, respectively), although it had no effect on base cations. *Sphagnum* spp. removal increased the positive effect of fertilization on soil DIN, but not on phosphorus and potassium.

Discussion

Our results, along with those of previous studies (Fenton and Bergeron 2006; Boudreault et al. 2013; Haughian and Burton 2015), indicate that lichens and *Sphagnum* spp. are more abundant under open canopies than closed ones. The correlation and path analyses indicate that the patterns of variations in tree fine root biomass differ between the two forest types, suggesting that these two ground-cover types differ in their influence on soil and tree growth conditions. Because lichens and *Sphagnum* spp. mosses are mainly associated with open canopies, the close relationship between tree aboveground and fine root biomasses observed in the pine–lichen stands makes the assessment of the direct effect of ground-cover composition on fine roots difficult based only on observational data. The experimental manipulation of ground

Fig. 3. Treatment effect on tree fine root biomass for the two forest types: (*a*) pine–lichen stands; (*b*) spruce–moss stands. CC, control × control; CF, control × fertilization; CS, control × shade; RC, removal × control; RF, removal × fertilization; RS, removal × shade. Significant differences between ground-cover treatments are represented by different letters. Vertical bars represent standard deviations.

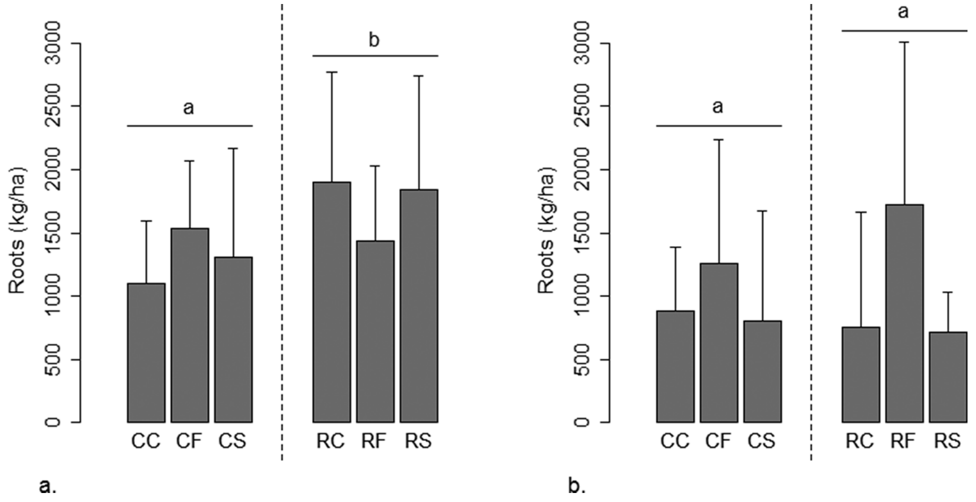


Fig. 4. Treatment effect on soil characteristics in the pine–lichen forest: (*a*) dissolved inorganic nitrogen (DIN); (*b*) phosphorus (P); (*c*) potassium (K); (*d*) base cations. CC, control × control; CF, control × fertilization; CS, control × shade; RC, removal × control; RF, removal × fertilization; RS, removal × shade. Significant differences between ground-cover treatments are represented by different letters. Vertical bars represent standard deviations.

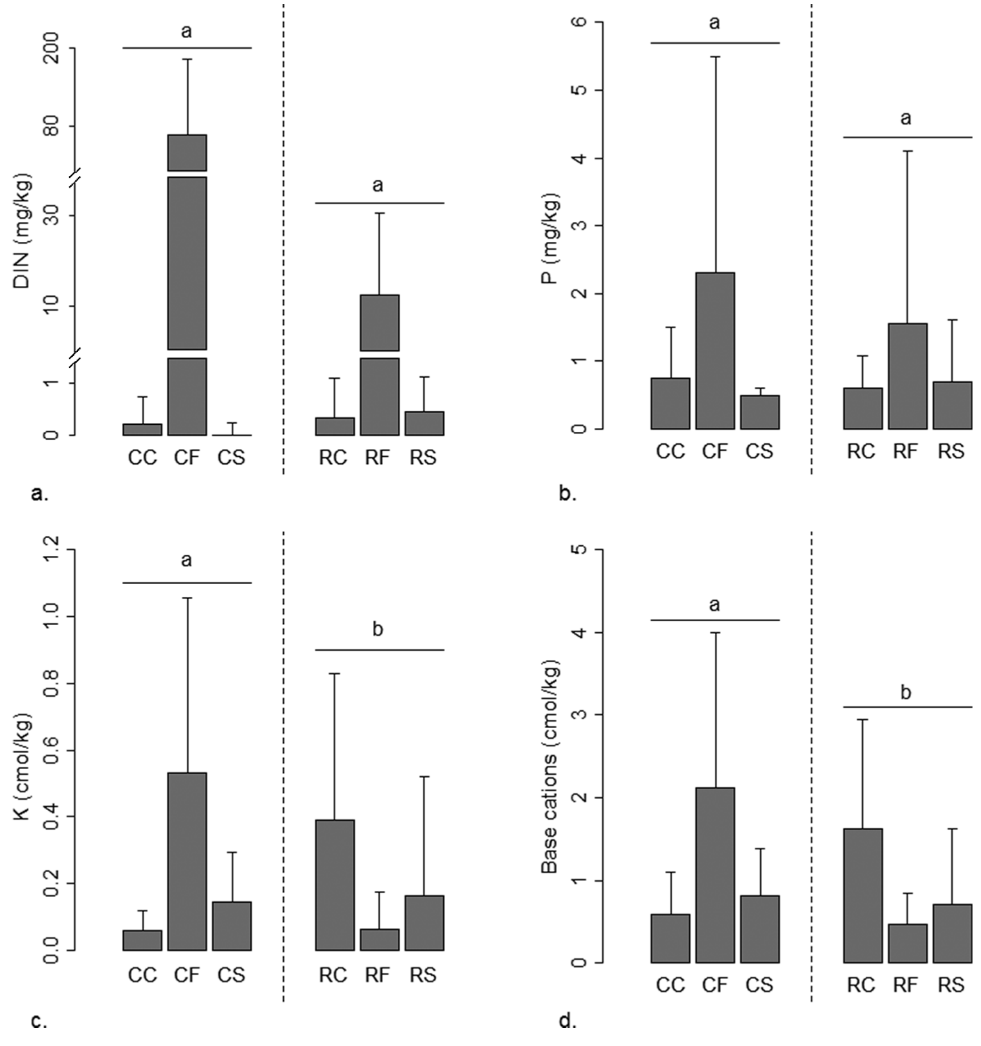
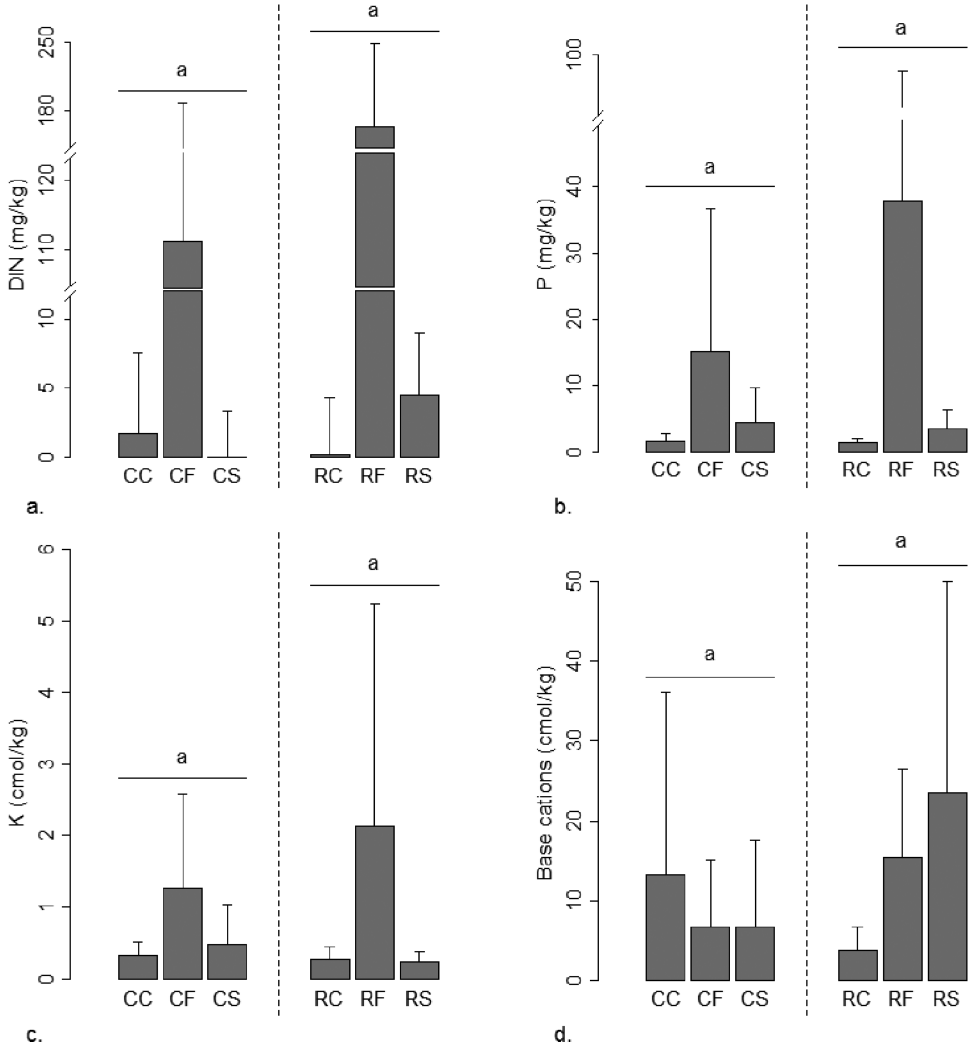


Fig. 5. Treatment effect on soil characteristics in the spruce–moss forest: (*a*) dissolved inorganic nitrogen (DIN); (*b*) phosphorus (P); (*c*) potassium (K); (*d*) base cations. CC, control × control; CF, control × fertilization; CS, control × shade; RC, removal × control; RF, removal × fertilization; RS, removal × shade. Significant differences between ground-cover treatments are represented by different letters. Vertical bars represent standard deviations.



cover in the second part of this study alleviates this problem by neutralizing the confounding effect of tree aboveground characteristics on tree fine root biomass through randomization of experimental plot location. Given the contrasting patterns observed in the two forest types, lichen and *Sphagnum* spp. effects on fine roots and soil properties are discussed separately.

Lichen effect on pine fine roots and soil properties

Our estimation of pine fine root biomass was lower than the average values reported by Finér et al. (2007) for Scots pine in the European boreal forest (2290 ± 1020 kg·ha^{-1}) and by Yuan and Chen (2010) for pine in the North American and Eurasian boreal forests (2520 ± 130 kg·ha^{-1}). By comparing plots with various degrees of canopy closure, we showed that pine fine root biomass per hectare was more closely linked to stand aboveground biomass than it was to lichen cover (Figs. 1 and 2; Tables 3 and 4). The positive relationship between fine root biomass and stand aboveground biomass in pine–lichen stands of the sampled area suggests that more abundant and (or) bigger pines produce more fine roots in the surface soil. This result seems logical as higher aboveground productivity means greater resource needs and, consequently, a larger fine root network to maximize tree resource acquisition. The absence of correlation between initial tree fine root biomass and stand aboveground biomass in the experimental even-aged stand probably results from the higher homogeneity of age and aboveground biomass of the 2 ha experimental site compared with the much larger sampled area.

Although the path analysis suggests that there was no direct relationship between lichen cover and pine fine root biomass in the sampled area, this link may have been concealed by the close relationship between tree fine root biomass and stand aboveground characteristics. If we refer to the experimental part of this study, we showed that lichen removal locally increases pine fine root biomass as observed by Fauria et al. (2008), who asserted that lichen grazing positively affects Scots pine growth. This result suggests a negative effect of lichens on tree fine root development as it indicates that pine fine root production may have been stimulated in the short term by a reduced influence of lichens. We also observed that jack pine roots tend to be thinner under lichens, thus indicating that either pines adapt to the local environment by modifying their fine root structure (Zadworny et al. 2016) or that lichens reduce the quantity of enlarged pine root tips through their negative effects on mycorrhization (Sedia and Ehrenfeld 2003).

It has been proposed that lichens modify soil hydric conditions (Bonan and Shugart 1989), as their hydrophobic properties (Shirtcliffe et al. 2006) might contribute to favour dry soils, surface runoff, and heterogeneous horizontal infiltration. Fine root growth can be largely affected by soil moisture (Yuan and Chen 2010) and dry conditions may favour denser tree root networks that optimize prospection and water absorption. Water deficit may also affect soil nutrient transport and diffusion from the soil to root absorbing surfaces and, in this way, affect tree access to nutritional resources (Barber et al. 1963). Because it was limited to 1 m^2 in our experiment, ground-layer removal might have favoured water infiltration and locally stimulated root densification. Therefore, the higher nutrient absorption by the resins when lichens were removed may have been favoured by a greater water flow, while shade cover may have partially mimicked the effects of a lichen mat that limits rain water supply at the surface and thus reduces nutrient transport to the resins.

Lichens have been shown to be associated with lower soil nitrogen availability than feather mosses (Ohtonen and Väre 1998). Haughian and Burton (2015) also found a strong negative correlation between lichen cover and phosphorus availability in the forest soil. Lichen removal did not affect DIN and phosphorus concentration in our experimental plots. One possible explanation is that lichen effects on soil nitrogen and phosphorus content are long-lasting and persisted for 3 months after ground-layer removal. However, we can point out that lichen removal significantly increased soil potassium and base cations (including calcium, sodium, and magnesium), which confirms that lichens also had short-term effects on soil chemical properties. Nutrient availability may be influenced by lichens not only by their low rate of litter accumulation (Sedia and Ehrenfeld 2005), but also through their impact on soil temperature and decomposer activity, as they are highly reflective and have low thermal conductivity (Bonan and Shugart 1989). Lichens might also produce antimicrobial and antifungal substances that have negative effects on the activity of soil microbial communities (Sedia and Ehrenfeld 2005) and fungi, including mycorrhizae (Sedia and Ehrenfeld 2003; Molnár and Farkas 2010). Nitrogen mineralization, which should have been stimulated by the positive effect of lichen removal, probably was limited in our experiment by the low availability of decomposable litter in the bare soil plots.

The direction of the correlation between fine root biomass and nutrient availability has been shown to be species-specific (Finér et al. 2007), and relationships in both directions have been found (Persson and Ahlström 2002; Kalliokoski et al. 2010). In the present study, although pine fine root biomass response to fertilization was highly variable and not significant, lichen removal stimulated pine fine root biomass at the same time as it increased soil potassium and base cations. These observations suggest that pines locally produce more fine roots in nutrient-rich spots in a globally low-nutrient forest site. Hence, pines are able to adapt quickly to heterogeneous environments via local stimulation of fine root production in places that are more favourable.

Sphagnum spp. effect on spruce fine roots and soil properties

Spruce fine root biomass was lower in our study sites than the average values reported by Finér et al. (2007) for Norway spruce in the European boreal forest (3300 ± 1570 kg·ha^{-1}) and very close to the average value reported by Yuan and Chen (2010) for spruce in the North American and Eurasian boreal forests (2780 ± 130 kg·ha^{-1}).

The key biological drivers of forest ecosystem processes can vary with time (forest succession) and space (disturbance history; Nilsson and Wardle 2005). The first structure that we proposed for the spruce–moss stands corresponds to a middle-aged forest in which canopy closure is the main biological ecosystem driver. In this theoretical model, stand aboveground biomass affects understorey vegetation through variation in canopy closure. The second considers *Sphagnum* spp. as the cause instead of the consequence of the variation in stand aboveground biomass. This pattern is more suited to paludified forests where *Sphagnum* spp. cover and ground-layer thickness constitute the most influent ecosystem drivers, more so than forest cover and stand aboveground biomass. Because this second structure best fitted our data, we can deduce that our sites were already quite advanced in the paludification process. The spruce–moss stands that we selected for the first part of this study were relatively young and originated from the same fire (1976). Hence, the paludification that we observe today on these sites has probably been favoured by a surface fire that burnt aboveground tree parts without completely removing the organic layer.

Spruce fine root growth was not stimulated by *Sphagnum* spp. removal, but it was stimulated by local fertilization. Hence, we can deduce that the absence of a *Sphagnum* spp. removal effect on spruce fine root biomass did not result from the lack of spruce reactivity to local environmental changes. Instead, it seems more likely that *Sphagnum* spp. removal did not sufficiently improve local root growth conditions to have visible consequences on spruce fine root biomass: either *Sphagnum* spp. effect on soil is long-lasting and continues long after removal, or *Sphagnum* spp. cover has limited effect on soil properties, at least in the case of a moderately thick moss layer. Another possibility is that the treated surfaces were too small to have a significant effect on root growing conditions, given that *Sphagnum* spp. cover disruption at the stand level has been shown to positively influence soil properties and tree growth (Lafleur et al. 2010). *Sphagnum* spp. cover was not related to soil DIN, and its removal had no effect on soil nutrients. However, *Sphagnum* spp. removal seemed to increase the positive effect of fertilization on spruce fine root biomass and significantly increased the fertilization effect on the accumulation of DIN in the forest soil. This suggests that *Sphagnum* spp. may have immobilized part of the DIN released from fertilizers or that the presence of a ground cover limited nutrient liberation from fertilizer pellets.

Management implications

Open pine–lichen and spruce–*Sphagnum* spp. woodlands occur naturally in the boreal forest. Hence, the restoration of forest productivity should not to be systematic and should only be encouraged in managed forests, especially on sites that have been modified by human interventions such as partial or total harvest. Three months of ground-layer shading were not sufficient to significantly modify tree fine root biomass and soil properties in both lichen and *Sphagnum* spp. covers, which confirms that the shading effect of forest cover mainly consists in an indirect long-term influence on soil through change in ground-layer composition. The contrasting effects of lichen and *Sphagnum* spp. cover on soil properties and tree fine root development indicate that the restoration of forest productivity in pine–lichen and spruce–moss woodlands may require different silvicultural approaches.

Lichen cover affects both pine fine root growth and soil nutrients, suggesting that nutrient management may be critical to restore forest productivity in excessively drained sites. Even if lichen removal locally stimulated pine fine root production in our experiment, the effect of lichen disturbance on tree regeneration at a larger scale may differ according to site conditions. Indeed, while Hébert et al. (2006) showed a positive effect of lichen disruption on jack pine growth on sites with good to moderate drainage, other studies suggested that lichen cover favours moisture retention in the surface soil in dry open woodlands and offers more appropriate conditions for jack pine germination and growth than bare soil or feather mosses (Bonan and Shugart 1989; Steijlen et al. 1995). Hence, favouring rapid reforestation that promotes rapid colonization of the understory by feather mosses would be more adapted than ground-cover disruption in open dry forests to restore forest productivity in excessively drained sites.

Under poor drainage conditions, partial or total harvesting, similarly to low-intensity wildfires and contrary to severe fire disturbances, opens the forest canopy without seriously disturbing the ground layer. In this way, harvesting may favour *Sphagnum* spp. at the expense of feather mosses. According to our results, *Sphagnum* spp. removal did not modify fine root development and soil properties. However, path analysis showed that *Sphagnum* spp. can be the main driver of stand aboveground biomass reduction in paludified forest, indicating that *Sphagnum* spp. cover becomes very influential late in the paludification process. Indeed, low temperature, low oxygenation, and excessive moisture, which are associated with *Sphagnum* spp. litter accumulation and may not induce particular root adaptations but rather a proportional reduction in both above- and below-ground biomass, may be the most important factors limiting forest productivity (Gower et al. 1996; Fenton et al. 2006). Hence, controlling *Sphagnum* spp. moss development may be the only key to a successful management of these ecosystems (Thiffault et al. 2013).

Conclusion

In this study, we showed that lichen and *Sphagnum* spp. covers, which are favoured by conditions of canopy openness, contribute to maintaining stand openness by affecting tree growth conditions in different ways. Lichens affect pine growth conditions by reducing fine root biomass and modifying soil nutrients and major base cations. *Sphagnum* spp. cover, which was found to be a key driver of spruce biomass reduction on paludified sites, affects black spruce growth through the long-term impact of the accumulation of a thick organic layer on soil physical conditions. The application of a shading cover, as a simulation of forest cover recovery, had no short-term influence on the effects of lichen and *Sphagnum* spp. on tree fine root growth. In both cases, it appears that managing forest regeneration to accelerate canopy closure and favour feather mosses instead of lichens or *Sphagnum* spp. mosses may be crucial to restoring forest productivity in sites characterized by extreme conditions of drainage.

Acknowledgements

This work was financially supported by the Natural Sciences and Engineering Research Council of Canada, by the Fonds de recherche — Nature et technologie du Québec, and by the Chair in Sustainable Forest Management (NSERC–UQAT–UQAM). We are also grateful to Hugues Massicotte and Sylvie Gauthier for their advice and support, Benjamin Gadet, Florence Auger, Samuel Laflèche, Pauline Suffice, Lili Perreault and Raynald Julien for their help and advice in the field, Marion Barbé for her support in bryophyte identification, Serge Rousseau for soil analysis, Julien Beguin for his support in statistical analyses, Marie-Hélène Longpré and Danielle Charron for their administrative support, and Isabelle Lamarre for her linguistic corrections.

References

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., and Ranger, J. 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. Biol. Rev. **90**: 444–466. doi:10.1111/brv.12119. PMID:24916992.

Barber, S.A., Walker, J., and Vasey, E.H. 1963. Mechanisms for movement of plant nutrients from soil and fertilizer to plant root. J. Agric. Food Chem. **11**: 204–207. doi:10.1021/jf60127a017.

Bentler, P.M., and Yuan, K.H. 1999. Structural equation modeling with small samples: test statistics. Multivar. Behav. Res. **34**: 181–197. doi:10.1207/S15327906Mb340203.

Bergeron, Y., Gauthier, S., Flannigan, M., and Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Québec. Ecology, **85**(7): 1916–1932. doi:10.1890/02-0716.

Bisbee, K.E., Gower, S.T., Norman, J.M., and Nordheim, E.V. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia, **129**: 261–270. doi:10.1007/s004420100719.

Blouin, J., and Berger, J.P. 2005. Guide de reconnaissance des types écologiques de la région écologique 6a – Plaine du lac Matagami et 6b – Plaine de la baie de Rupert. Ministère des Ressources Naturelles et de la Faune du Québec, Direction des inventaires forestiers, Division de la classification écologique et productivité des stations. Québec, Qué.

Bonan, G.B., and Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Annu. Rev. Ecol. Syst. **20**: 1–28. doi:10.1146/annurev.es.20.110189.000245.

Boudreault, C., Zouaoui, S., Drapeau, P., Bergeron, Y., and Stevenson, S. 2013. Canopy openings created by partial cutting increase growth rates and maintain the cover of three *Cladonia* species in the Canadian boreal forest. For. Ecol. Manage. **304**: 473–481. doi:10.1016/j.foreco.2013.05.043.

Brassard, B.W., Chen, H.Y.H., and Bergeron, Y. 2009. Influence of environmental variability on root dynamics in northern forests. Crit. Rev. Plant Sci. **28**(3): 179–197. doi:10.1080/07352680902776572.

Brassard, B.W., Chen, H.Y.H., Bergeron, Y., and Paré, D. 2011. Differences in fine root productivity between mixed- and single-species stands. Funct. Ecol. **25**(1): 238–246. doi:10.1111/j.1365-2435.2010.01769.x.

Chiapusio, G., Jassey, V.E.J., Hussain, M.I., and Binet, P. 2013. Evidences of bryophyte allelochemical interactions: the case of *Sphagnum*. *In* Allelopathy. *Edited by* Z.A. Cheema, M. Farooq, and A. Wahid. Springer-Verlag, Berlin. pp. 39–54. doi:10.1007/978-3-642-30595-5_3.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A., and During, H.J. 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Ann. Bot. **99**(5): 987–1001. doi:10.1093/aob/mcm030. PMID:17353205.

DeLuca, T.H., Zackrisson, O., Nilsson, M.C., and Sellstedt, A. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature, **419**(6910): 917–920. doi:10.1038/nature01051. PMID:12410308.

Environment Canada. 2016. Canada Climate Normals 1981–2010. Available at http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html [accessed 7 February 2017].

Fauria, M.M., Helle, T., Niva, A., Posio, H., and Timonen, M. 2008. Removal of the lichen mat by reindeer enhances tree growth in a northern Scots pine forest. Can. J. For. Res. **38**(12): 2981–2993. doi:10.1139/X08-135.

Fenton, N.J., and Bergeron, Y. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. J. Veg. Sci. **17**(1): 65–76. doi:10.1111/j.1654-1103.2006.tb02424.x.

Fenton, N.J., Légaré, S., Bergeron, Y., and Paré, D. 2006. Soil oxygen within boreal forests across an age gradient. Can. J. Soil Sci. **86**: 1–9. doi:10.4141/S05-004.

Finér, L., Helmisaari, H.S., Lohmus, K., Majdi, H., Brunner, I., Børja, I., Eldhuset, T., Godbold, D., Grebenc, T., Konôpka, B., Kraigher, H., Möttönen, M.-R., Ohashi, M., Oleksyn, J., Ostonen, I., Uri, V., and Vanguelova, E. 2007. Variation in fine root biomass of three European tree species: beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.). Plant Biosyst. **141**(3): 394–405. doi:10.1080/11263500701625897.

Gower, S.T., McMurtrie, R.E., and Murty, D. 1996. Aboveground net primary production decline with stand age: potential causes. Trends Ecol. Evol. **11**(9): 378–382. doi:10.1016/0169-5347(96)10042-2. PMID:21237883.

Haughian, S.R., and Burton, P.J. 2015. Microhabitat associations of lichens, feathermosses, and vascular plants in a caribou winter range, and their implications for understory development. Botany, **93**(4): 221–231. doi:10.1139/cjb-2014-0238.

Hébert, F., Boucher, J.-F., Bernier, P.Y., and Lord, D. 2006. Growth response and water relations of 3-year-old planted black spruce and jack pine seedlings in site prepared lichen woodlands. For. Ecol. Manage. **223**: 226–236. doi:10.1016/j.foreco.2005.11.005.

Hinsinger, P., Bengough, A.G., Vetterlein, D., and Young, I.M. 2009. Rhizosphere: biophysics, biogeochemistry and ecological relevance. Plant Soil, **321**(1–2): 117–152. doi:10.1007/s11104-008-9885-9.

Jasinski, J.P.P., and Payette, S. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecol. Monogr. **75**(4): 561–583. doi:10.1890/04-1621.

Kalliokoski, T., Pennanen, T., Nygren, P., Sievänen, R., and Helmisaari, H. 2010. Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. Plant Soil, **330**: 73–89. doi:10.1007/s11104-009-0177-9.

Kytöviita, M.M., and Crittenden, P.D. 2007. Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*. Ann. Bot. **100**: 1537–1545. doi:10.1093/aob/mcm249. PMID:17951586.

Kytöviita, M.M., and Stark, S. 2009. No allelopathic effect of the dominant forest-floor lichen *Cladonia stellaris* on pine seedlings. Funct. Ecol. **23**(2): 435–441. doi:10.1111/j.1365-2435.2008.01508.x.

Lafleur, B., Paré, D., Fenton, N.J., and Bergeron, Y. 2010. Do harvest methods and soil type impact the regeneration and growth of black spruce stands in Northwestern Quebec? Can. J. For. Res. **40**: 1843–1851. doi:10.1139/X10-128.

Lafleur, B., Paré, D., Fenton, N.J., and Bergeron, Y. 2011. Growth and nutrition of black spruce seedlings in response to disruption of *Pleurozium* and *Sphagnum* moss carpets in boreal forested peatlands. Plant Soil, **345**: 141–153. doi:10.1007/s11104-011-0767-1.

Lang, S.I., Cornelissen, J.H.C., Klahn, T., Van Logtestijn, R.S.P., Broekman, R., Schweikert, W., and Aerts, R. 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. J. Ecol. **97**(5): 886–900. doi:10.1111/j.1365-2745.2009.01538.x.

McCavour, M.J., Paré, D., Messier, C., Thiffault, N., and Thiffault, E. 2014. The role of aggregated forest harvest residue in soil fertility, plant growth, and pollination services. Soil Sci. Soc. Am. J. **78**: S196–S207. doi:10.2136/sssaj2013.08.0373nafsc.

Molnár, K., and Farkas, E. 2010. Current results on biological activities of lichen secondary metabolites: a review. Z. Naturforsch., C: J. Biosci. **65**: 157–173. doi:10.1515/znc-2010-3-401.

Nilsson, M.C., and Wardle, D.A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Front. Ecol. Environ. **3**(8): 421–428. doi:10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2.

Noguchi, K., Dannoura, M., Jomura, M., Awazuhara-Noguchi, M., and Matsuura, Y. 2012. High belowground biomass allocation in an upland black spruce (*Picea mariana*) stand in interior Alaska. Polar Sci. **6**: 133–141. doi:10.1016/j.polar.2011.12.002.

Ohtonen, R., and Väre, H. 1998. Vegetation composition determines microbial activities in a boreal forest soil. Microb. Ecol. **36**: 328–335. doi:10.1007/s002489900119. PMID:9852512.

Payette, S., Bhiry, N., Delwaide, A., and Simard, M. 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce–moss forest. Can. J. For. Res. **30**(2): 288–305. doi:10.1139/x99-207.

Persson, H., and Ahlström, K. 2002. Fine-root response to nitrogen supply in nitrogen manipulated Norway spruce catchment areas. For. Ecol. Manage. **168**: 29–41. doi:10.1016/S0378-1127(01)00726-5.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sedia, E.G., and Ehrenfeld, J.G. 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos, **100**: 447–458. doi:10.1034/j.1600-0706.2003.12058.x.

Sedia, E.G., and Ehrenfeld, J.G. 2005. Differential effects of lichens, mosses and grasses on respiration and nitrogen mineralization in soils of the New Jersey Pinelands. Oecologia, **144**: 137–147. doi:10.1007/s00442-005-0037-0. PMID:15791426.

Shipley, B. 2002. Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference. Cambridge University Press, Cambridge, UK.

Shirtcliffe, N.J., Pyatt, F.B., Newton, M.I., and McHale, G. 2006. A lichen protected by a super-hydrophobic and breathable structure. J. Plant Physiol. **163**: 1193–1197. doi:10.1016/j.jplph.2005.11.007. PMID:16434121.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., and Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. **17**(6): 1619–1637. doi:10.1890/06-1795.1. PMID:17913128.

Steijlen, I., Nilsson, M.C., and Zackrisson, O. 1995. Seed regeneration of Scots pine in boreal forest stands dominated by lichen and feather moss. Can. J. For. Res. **25**: 713–723. doi:10.1139/x95-079.

Taskinen, O., Ilvesniemi, H., Kuuluvainen, T., and Leinonen, K. 2003. Response of fine roots to an experimental gap in a boreal *Picea abies* forest. Plant Soil, **255**(2): 503–512. doi:10.1023/A:1026077830097.

Thiffault, N., Fenton, N.J., Munson, A.D., Hébert, F., Fournier, R.A., Valeria, O., Bradley, R.L., Bergeron, Y., Grondin, P., Paré, D., and Joanisse, G. 2013. Managing understory vegetation for maintaining productivity in black spruce forests: a synthesis within a multi-scale research model. Forests, **4**: 613–631. doi:10.3390/f4030613.

Turetsky, M.R. 2003. The role of bryophytes in carbon and nitrogen cycling. Bryologist, **106**(3): 395–409. doi:10.1639/05.

Ung, C.H., Bernier, P., and Guo, X.J. 2008. Canadian national biomass equations: new parameter estimates that include British Columbia data. Can. J. For. Res. **38**: 1123–1132. doi:10.1139/X07-224.

Yuan, Z.Y., and Chen, H.Y.H. 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. Crit. Rev. Plant Sci. **29**(4): 204–221. doi:10.1080/07352689.2010.483579.

Zadworny, M., McCormack, M.L., Mucha, J., Reich, P.B., and Oleksyn, J. 2016. Scots pine fine roots adjust along a 2000-km latitudinal climatic gradient. New Phytol. **212**(2): 389–399. doi:10.1111/nph.14048. PMID:27301778.