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Differential effects of feather and *Sphagnum* spp. mosses on black spruce germination and growth

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ABSTRACT

The composition of the bryophyte layer influences boreal forest regeneration and growth through its effect on soil conditions. Canopy openings in boreal spruce stands can favor the expansion of *Sphagnum* spp. in the understory at the expense of feather mosses. We use an experimental approach in both paludified field and greenhouse fully-randomized conditions to examine the differential effects of these two ground cover types on black spruce germination and growth, specifically the role of nutrient limitation in generating these effects. We also tested the impact of ground cover shading, simulating the effect of a closed forest canopy on the ground layer, with the assumption that the stress induced to mosses, especially to *Sphagnum* spp., would have a beneficial impact on tree growth. The two moss types had no differential effects on spruce germination and 0–6-month-old seedling growth in the greenhouse. However, the growth of 2-year-old seedlings in the greenhouse was lower in *Sphagnum* spp. than in feather mosses. This negative effect was removed by fertilization, suggesting that soil nutrient availability could explain the seedling growth difference between moss types. Greenhouse 2-year-old seedlings also allocated a greater proportion of biomass to roots in *Sphagnum* spp. than in feather mosses. In the field, feather and *Sphagnum* spp. mosses had no differential effects on 3-year-old seedling growth, and ground cover shading did not have any short-term positive impact on spruce growth. Although they were not validated in the field, the results we obtained in the greenhouse suggest that the replacement of feather mosses by *Sphagnum* spp. mosses do not only affect spruce growth through the build-up of an organic layer often associated with low soil temperature and excess water, but also through more direct effects on nutrient availability. Therefore, silvicultural treatments that would favor *Sphagnum* spp. expansion at the expense of feather mosses, such as partial or total harvesting with protection of regeneration and soils, may result in subsequent tree growth problems even in sites with moderate organic layer accumulation.

1. Introduction

There is an increasing awareness of the influence the bryophyte layer has on ecosystem function in different ecosystems, including boreal forests (Cornelissen et al., 2007; Turetsky et al., 2012). The composition of this layer can influence soil carbon as well as nutrient accumulation and cycling (Bond-Lamberty and Gower, 2007; Lang et al., 2009; Lindo and Gonzalez, 2010) with visible consequences on ecosystem processes and states (Pacé et al., 2017a). An example is the long-term decline in forest productivity associated with paludification that is directly driven by ground layer composition changes in the Clay Belt region of Quebec and Ontario (Lavoie et al., 2005; Simard et al., 2007). The functional traits of *Sphagnum* spp. mosses, which have a higher net primary productivity (Bisbee et al., 2001; Swanson and Flanagan, 2001; O'Connell et al., 2003) and a lower decomposition rate (Lang et al., 2009; Fenton et al., 2010) than feather mosses, favor long-term organic matter accumulation and water table rise (Fenton et al., 2005, 2006). This results in a decrease in soil oxygenation and temperature, which in turn reduces microbial activity and nutrient availability in the organic layer (Gower et al., 1996; Elliott-Fisk, 2000). Although these long-term effects of feather moss replacement by *Sphagnum* spp. mosses are relatively well known, information is still sparse on the short-term effects of this change on tree growth conditions, i.e. before the *Sphagnum* spp. cover is associated with the accumulation of a thick organic layer.

Black spruce (*Picea mariana* [Mill.] B.S.P.) is one of the most widespread and important commercial tree species in the North American boreal forest (Gagnon and Morin, 2001). Because it is tolerant to nutrient-poor conditions, this tree species is able to colonize a wide range of environments, from wet peatlands to highly-drained sandy

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soils. Several studies have reported deficits in black spruce growth after low-severity fires (Fenton et al., 2005; Lecomte et al., 2006; Simard et al., 2007) and careful logging (Fenton and Bergeron, 2007; Lafleur et al., 2010a,b). These regeneration problems have been attributed to the bryophyte layer and its effect on soil conditions.

The differential effects of *Sphagnum* spp. and feather mosses on black spruce germination and growth have mainly been investigated in paludified sites (Ohlson and Zackrisson, 1992; Groot and Adams, 1994; Hörnberg et al., 1997; Lavoie et al., 2007b; Lafleur et al., 2011), and thus the direct effects of living *Sphagnum* spp. mosses on black spruce have rarely been separated from their long-term effects *via* the gradual accumulation of fibric material in the forest soil. Moreover, few studies have tested the differential effects of intact living layers of *Sphagnum* spp. and feather mosses on tree growth in conditions of complete randomization of seedling location (Stuiver et al., 2014 for *Pinus sylvestris*). In other words, ground cover effects have rarely been investigated independently of the micro-environmental conditions that are closely related to ground cover composition in the field such as light, temperature, moisture or soil characteristics (Bisbee et al., 2001; Fenton and Bergeron, 2006). We propose to (1) determine the differential effects of living *Sphagnum* spp. and feather mosses on black spruce germination, survival and growth in both paludified field and greenhouse fully-randomized conditions, and (2) explore the drivers associated with these effects by investigating the role of nutrients and analyzing how these effects are impacted by ground cover shading.

We hypothesize that a ground layer of living *Sphagnum* spp. facilitates germination by providing and maintaining moist conditions (Ohlson and Zackrisson, 1992; Groot and Adams, 1994), but constitutes a less suitable substrate for spruce seedling growth than feather mosses, as it is associated with a lower soil nutrient availability. Light availability plays a crucial role in the competitive balance between *Sphagnum* spp. and feather mosses (Bisbee et al., 2001; Fenton and Bergeron, 2006). We make a second hypothesis that ground cover shading constitutes a stress for mosses, especially *Sphagnum* spp., resulting in an increase in moss tissue senescence. As moss senescing segments are likely to release more nutrients than green segments (Carleton and Read, 1991), the effect of shading on mosses, especially *Sphagnum* spp., is supposed to stimulate tree growth by increasing nutrient availability in the forest soil.

2. Material and methods

2.1. Living material and substrate

The *Picea mariana* [Mill.] B.S.P. seeds and 2-year-old seedlings used in this study originated from provincial nurseries of the *Ministère des Forêts, de la Faune et des Parcs du Québec*. Seeds (germination success = 99%; germinative value = 46) were produced at the forest seed center of Berthier (Sainte-Geneviève de Berthier, Quebec, Canada). Seedlings came from the provincial nurseries of Guyenne and Trécesson (Abitibi, Quebec, Canada), where they had grown in greenhouses for 2 years. Spruce seedling growth in nurseries was stimulated by the application of fertilizers. Living material (feather and *Sphagnum* spp. mosses) and substrate were harvested in May 2015 in the boreal forest of western Quebec (spruce-moss bioclimatic domain; Bergeron et al., 1999). The substrate was 1-m-deep humic peat collected in a highly paludified black spruce-moss stand (organic layer > 1 m; 49°44′N, 79°17′W). The decomposition stage of the humic peat was 6–7 on the von Post scale (Stanek and Silc, 1977).

Moss layers (living moss and dead material) were harvested in a non-paludified forest characterized by alternating feather and *Sphagnum* spp. moss patches (49°44′N, 79°17′W). Dead material origin did not systematically correspond to the moss type above, e.g. a *Sphagnum* moss layer could include feather moss dead material. The two sampling sites were located on lacustrine clay deposited by the proglacial Lake Ojibway (Blouin and Berger, 2005). Common understory plant species were *Rhododendron groenlandicum* (Oeder) Kron & Judd, *Kalmia angustifolia* L., and *Vaccinium angustifolium* Ait. Ground covers were harvested with their associated poorly to well-decomposed dead organic matter and Ericaceae (above- and below-ground parts) were entirely removed from the moss layer. Harvested *Sphagnum* spp. mosses were mainly *Sphagnum capillifolium* (Ehrh.) Edw., *S. angustifolium* (C. Jens. ex Russ.) C. Jens., and *S. fuscum* (Schimp.) Klinggr., with few occurrences of *S. magellanicum* Brid. Feather moss covers were dominated by *Pleurozium schreberii* (Brid.) Mitt., with few occurrences of *Polytrichum strictum* Brid., *Dicranum polysetum* Swartz, and *Ptilidium ciliare* (L.) Hampe.

2.2. Greenhouse experiment 1: black spruce germination and early seedling growth

Sixty square pots (size: 12 × 12 × 14 cm) were used to test the effects of three different ground cover types on spruce germination in a greenhouse experiment: (1) 20 pots were filled with peat harvested in the field, referred to as controls; (2) 20 were filled with peat from the field (6–8 cm) and covered by feather moss (6–8 cm, including living mosses and organic matter); (3) 20 pots were filled with peat and covered by *Sphagnum* spp. (including living *Sphagnum* spp. and organic matter). Spatial distribution of the pots assigned to these three treatments was randomly determined. In May 2015, five seeds were sown on the surface of each pot. Pots were watered twice a day with 10 mL of demineralized water and checked for germination every day for 4 weeks.

Four weeks after spruce seed germination, three seedlings originating from the germination experiment were selected per pot. Extra germinated seeds were removed and attributed to low-germination success pots characterized by the same ground cover type. Spatial distribution of the seedling pots was randomized once a month for the duration of the seedling experiment, i.e. five times from June to November 2015. Water-diluted fertilizer (0.05 g; 20% nitrogen, 7% phosphorus and 10% potassium, Plant-prod Smartcote®) was applied to 10 seedling pots per ground cover type in July 2015. Pots were watered with demineralized water twice a day (10 mL per pot) throughout summer 2015 to spare seedlings from water stress. Watering was progressively reduced to 10 mL once a day in September 2015 and to 10 mL three times a week in October and November 2015. Spruce 6-month-old seedlings were harvested in November 2015. Below- and aboveground parts of the seedlings were dried (60 °C) and weighed separately.

2.3. Greenhouse experiment 2: two-year-old black spruce growth

The three same ground cover treatments as previously described were applied to 60 2-year-old spruce seedlings in a greenhouse: (1) 20 round pots (23 cm in diameter, 24 cm deep) were filled with peat from the field (control pots) while the other 40 pots were filled with peat (16–18 cm) and covered with (2) a living layer of feather mosses or (3) a living layer of *Sphagnum* spp. mosses (6–8 cm, including living and dead organic matter). Seedling roots were washed with demineralized water to remove nursery soil. Each tree was measured and weighed before planting. Ten spruces were used to calculate fresh to dry weight conversion factors. Controlled-release fertilizer (2 g; 20% nitrogen, 7% phosphorus and 10% potassium, granulated form, Plant-prod Smartcote®) was administered to 10 seedlings per ground cover type at the beginning of the experiment. Spruce placement in the greenhouse was randomized once a month from May to November 2015. Pots were watered twice a day with demineralized water at a rate of 60 mL per pot per day from May to August 2015 to spare seedlings from water stress. Watering was reduced to 30 mL per day in September 2015 and to 30 mL three times a week in October and November 2015. In November 2015, the 2-year-old spruce seedlings were harvested and their roots were washed with water to remove soil particles. Below- and aboveground parts were dried (60 °C) and weighed separately.

Table 1
General characteristics and environmental conditions associated with the four experiments.

	Location	Duration	Additional treatment	Period	Temperature			Air humidity		
					Mean	Range	SD	Mean	Range	SD
Germination	Greenhouse	4 weeks	–	May 2015	21.2 °C	11.9–33.6 °C	3.7 °C	60.8%	13.3–100.0%	23.7%
Early seedling growth	Greenhouse	6 months	Fertilization (2 levels)	June 2015 to Nov. 2015	21.2 °C	11.9–33.6 °C	3.7 °C	60.8%	13.3–100.0%	23.7%
2–3-year-old seedling growth	Greenhouse	7 months	Fertilization (2 levels)	May 2015 to Nov. 2015	21.5 °C	12.6–39.6 °C	4.1 °C	60.2%	10.8–100.0%	24.4%
	Field	18 months	Shading (2 levels) Fertilization (2 levels)	July 2014 to Oct. 2014	10.8 °C	−10.5 to 41.8 °C	9.4 °C	90.8%	19.3–100.0%	17.2%
				Nov. 2014 to May 2015	−0.7 °C	−12.9 to 32.5 °C	6.5 °C	81.3%	1.0–100.0%	14.4%
				May 2015 to Oct. 2015	15.0 °C	−9.1 to 46.5 °C	9.6 °C	88.6%	15.1–100.0%	17.8%

The daily cycles of light and temperature were not manipulated in the two greenhouse experiments. Temperature and air humidity were recorded every hour from May to November 2015 (Table 1) using HOBO® data loggers (HOBO® U23 PRO V2, Onset Data Loggers, Bourne, MA).

2.4. Field experiment: three-year-old black spruce growth

The field experiment took place in the boreal forest of western Quebec, in a pure *Picea mariana* [Mill.] B.S.P. stand located on lacustrine clay deposits (49°44′N, 79°17′W) and originating from a fire that occurred in 1976. Average annual temperature (1981–2010) is 0 ± 2.9 °C and average annual precipitation is 909.1 mm (Joutel, Quebec; Environment Canada, 2017). Understory plant species, including mosses and Ericaceae, were the same as mentioned above. The ground layer was composed of alternating feather and *Sphagnum* spp. moss patches (1–5 m wide). The field plantation site (about 1 ha) originated from a fire that occurred in 1976 and presented evident signs of paludification, including low stand aboveground biomass (15.4 Mg·ha^{-1}) and a thick organic layer (70 cm on average).

Seventy 2-year-old spruce seedlings were weighed and planted with their root plug in May 2014. Thirty spruces were planted in feather mosses, 30 in *Sphagnum* spp. mosses, and 10 in bare organic soil where feather mosses had been removed. There were no more than two planted seedlings per patch of one ground cover type. Patches of the two moss types were well-dispersed in the site, and seedlings were considered as randomly distributed (no clumping by moss type). Five additional spruce seedlings were used to calculate a fresh to dry conversion factor. Contrary to the greenhouse experiment 2, spruce roots were not washed before field planting to favor their survival in harsh field conditions. Each type of ground cover was homogeneous within a radius of at least 50 cm around the spruce seedling. Before planting, the aboveground parts of Ericaceae were removed by cutting the stems at the soil surface. Ericaceae roots were not removed to avoid ground cover disturbance. To account for a possible bias in light availability due to the higher abundance of *Sphagnum* spp. mosses in forest openings (Fenton and Bergeron, 2006), canopy closure was measured in July 2014 using fish-eye photos at each seedling location. Photos were analyzed in terms of percentage of pixels attributable to trees using Adobe Photoshop Elements software. This analysis revealed an average canopy closure of 75% with no significant differences between ground cover types (F-value = 0.08, p-value > 0.1).

Controlled-release fertilizer (2 g; 20% nitrogen, 7% phosphorus and 10% potassium, granulated form, Plant-prod Smartcote®) was administered to 10 seedlings per ground cover type, except for bare soil, in May 2015. As forest cover affects light availability, temperature and humidity in the understory, it is likely to have an impact on moss metabolism (Swanson and Flanagan, 2001; Gundale et al., 2012; Stuiver et al., 2015), and thus modify the effects of ground layer composition on spruce seedling growth in the field. A 50% shade cloth (standard perforated net used in horticulture) was used to simulate the impact of a closed forest canopy on the moss layer only. Because this study focuses exclusively on the effects of the moss layer, the direct effect of shade on seedling growth was not tested. The shade cover was positioned 15 cm above the ground cover (below the 2-year-old seedling foliage) in a third of the *Sphagnum* spp. and feather moss plots (10 plots per ground cover type) and half of the bare soil plots (5 plots) at the beginning of the field experiment (May 2014).

Air temperature and humidity 10 cm above the ground were recorded hourly from July 2014 to October 2015 using HOBO® data loggers (Table 1). Data loggers were not covered by radiation shields, which may explain why maximum temperature measurements for the two growing seasons were very high in the field (Table 1). Spruce 3-year-old seedlings were harvested in October 2015, and roots were washed with water. Below- and aboveground parts were dried at 60 °C and weighed separately.

2.5. Soil nutrient analysis

The effect of ground cover type on soil nutrient availability was estimated for both greenhouse and field experiments. Samples of the substrate used to fill the pots of the greenhouse plantation were harvested before the experiment in May 2015 for soil analyses. Potting soil samples (randomly sampled from the whole pot content) of 10 pots per ground cover type (five fertilized and five non-fertilized) were harvested at the end of the greenhouse experiment 2 in November 2015. In the field experiment, three organic samples per treatment type (top 20 cm of the organic layer) were harvested in October 2015 to analyze the effects of the different treatments on nutrient availability. Organic samples were first sieved at 6 mm to remove large roots and debris, dried at 60 °C, then ground and sieved at 2 mm. NH4-N and NO3-N were extracted with a 2 M KCl solution and analyzed by spectrophotometry (QuikChem R8500 Series 2, Lachat Instruments, Milwaukee, WI). Phosphorus, potassium, calcium, magnesium and sodium were separated with a Mehlich extraction and analyzed by inductively coupled plasma (ICP) using an optical emission spectrometer (OES) (Optima 7300 DV, Perkin Elmer, Waltham, MA). Soil concentration in base cations was estimated by summing potassium, calcium, magnesium and sodium concentrations.

2.6. Statistical analysis

We first tested the effects of ground cover type on spruce germination using a generalized linear model based on a binomial distribution of the dependant variable (germination rate per pot 28 days after sowing). Residual dispersion was estimated at 2.87 and considered in the model analysis. Early seedling growth was estimated by summing the biomass of the three individual 6-month-old seedlings per pot, while the relative growth of the 2-year-old seedlings in the greenhouse and 3-year-old seedlings in the field was calculated as the difference in seedling biomass between the beginning and the end of the experiment, divided by the initial seedling biomass (expressed in %). The effects of ground cover type and fertilization treatment on both early and 2-year-old seedling growth in the greenhouse, as well as the effects of ground cover type, fertilization and ground cover shading on seedling growth in the field were tested using linear models. This statistical method was chosen as it allows the use of contrasts to analyze the effects of ground cover *versus* bare soil in a first phase and to compare the effect of feather and *Sphagnum* spp. mosses in a second phase. Targeted contrasts increase the power of statistical tests and reduce the chance of type I error. For each experiment, treatment effects were tested on below- and aboveground growth separately, total growth, and root allocation, i.e., the difference between final and initial belowground biomass divided by the difference between final and initial total biomass. The effects of ground cover type and fertilization on final potting soil nutrients, as well as the effects of ground cover type, fertilization and shade on nutrient availability at the end of the field experiment were analyzed using linear models.

When necessary, the dependent variables were transformed to respect linear model conditions (square root or log-transformation). When homoscedasticity was not verified for one factor, supplementary parameters were used to estimate the variance associated with each level of a factor and models were analyzed based on the maximum likelihood method. Finally, when data did not accurately fit a specific distribution, we resorted to a bootstrap procedure in which treatment effect significance was deduced from the probability that the associated individual coefficient of the linear or generalized linear model was equal to zero considering the bootstrap confidence intervals (Fox and Weisberg, 2012). All analyses were performed on R/3 software (R Core Team, 2014), using the packages 'nlme' (Pinheiro et al., 2014), 'car' (Fox et al., 2016), and 'MASS' (Ripley et al., 2013). Data are available online ([dataset] Pacé et al., 2017).

3. Results

3.1. Germination and early seedling growth in the greenhouse

A high percentage of seeds (≈85%) germinated in the greenhouse. While the presence of a ground cover had no effect on spruce germination success after 4 weeks in the greenhouse (84 ± 4% *vs* 82 ± 5% on bare soil, $z = 0.49$, p-value > 0.1), germination success was marginally higher in *Sphagnum* spp. than in feather mosses (92 ± 6% against 76 ± 7%, respectively, $z = 1.74$, p-value = 0.0813).

Only 5.3% of the seedlings died in the 6 months that followed germination. Belowground, aboveground and total dry seedling biomass per pot was significantly higher in the presence of a ground cover but did not differ between feather and *Sphagnum* spp. mosses (Table 2, Fig. 1). Root allocation was significantly higher in bare soil than in *Sphagnum* spp. and feather mosses (Table 2). Belowground, aboveground and total 6-month-old seedling growth was significantly enhanced by fertilization and this effect did not differ among the three ground cover types (Table 2 and Fig. 1). Nutrient supply increased total biomass of the 6-month-old seedlings by 149 mg on average (+70%), without significantly affecting seedling root allocation (Table 2).

3.2. Two-year-old seedling growth in the greenhouse

Belowground and total growth of the greenhouse 2-year-old seedlings was significantly reduced in the presence of a ground cover, while aboveground growth was not affected (Table 2 and Fig. 2). Contrary to belowground growth that did not differ between the two moss types, aboveground and total growth were significantly higher in feather than in *Sphagnum* spp. mosses (Table 2 and Fig. 2). Spruce allocated a greater proportion of biomass to roots in *Sphagnum* spp. than in feather mosses (62 ± 3% and 52 ± 2%, respectively; Table 2).

Greenhouse 2-year-old seedling growth was positively affected by fertilization in all the ground cover types, especially in *Sphagnum* spp. mosses where the positive effect of nutrient supply was higher than in feather mosses (significant effect of the interaction, Table 2 and Fig. 2). Root allocation in greenhouse 2-year-old seedlings was significantly reduced in the case of fertilization (regardless of the ground cover type, 49 ± 2% for fertilized seedlings against 62 ± 2% for non-fertilized seedlings) and this effect was similar for all ground cover types (Table 2).

3.3. Three-year-old seedling growth in the field

We only considered healthy trees for the statistical analyses ($N = 64$) and discarded seedlings that had died in the field (9% of the total, Fig. 2). The large thermal variations observed in the field (Table 1) may have been the cause of thermal stress in the seedlings, leading in some cases to seedling mortality. Relative belowground growth and root allocation were significantly lower in bare soil than in the presence of a ground cover (root allocation: 56 ± 6% and 61 ± 2%, respectively). This result, however, relies on a small number of control trees (only four per shading treatments) and thus should be considered with caution. Spruce growth and root allocation in the field did not differ between feather and *Sphagnum* spp. mosses (Table 2 and Fig. 2).

Three-year-old seedling total growth was only marginally increased by nutrient supply (Table 2). Although it was less clear than in the greenhouse experiment 2, field belowground growth tended to be more stimulated by fertilization in *Sphagnum* spp. than in feather mosses (marginal effect of the interaction, Table 2). Root allocation in field seedlings was not affected by nutrient supply.

Ground cover shading effect on belowground biomass differed according to ground cover type (marginal and significant interaction effects, Table 2). Ground cover shading significantly increased 3-year-old seedling root allocation, especially in bare soil and *Sphagnum* spp. mosses (+19% and +7%, respectively), but did not affect spruce total growth (Table 2 and Fig. 3).

3.4. Nutrient analysis

While nitrogen content (NH_4^+ and NO_3^-) was not affected by ground cover type, phosphorus and base cation contents of the greenhouse 2-year-old seedling pots were lower under *Sphagnum* spp. than under feather mosses (Tables 3 and 4). Fertilization of the greenhouse seedlings only increased NO_3^- content in the pots. In the field, none of the nutrients were affected by ground cover type, and fertilization tended to reduce soil concentration in phosphorus (marginal effect) and base cations (significant effect) at the end of the experiment (Table 4). There was no detectable nitrate in the field organic soil samples. Ground cover shading did not modify any of the field nutrient concentrations we measured (Table 4).

4. Discussion

4.1. Influence of ground cover type on spruce germination and growth

In our greenhouse experiment, 6-month-old seedlings grew better in the presence of a ground cover. Compared with bare soil conditions, the presence of a moss layer may have maintained favorable micro-environmental conditions that protected seedlings from high daily or seasonal variations in temperature and/or moisture (Wheeler et al., 2011; Soudzilovskaia et al., 2013). Although the lower water-holding capacity of feather mosses has been identified as an important limiting factor of seedling growth in several previous studies, whether it be in controlled conditions (Lavoie et al., 2007a) or in the field (Lavoie et al., 2007b; Groot and Adams, 1994), the two moss types had no differential effects on germination and early seedling growth in the good moisture conditions of our greenhouse experiment.

Table 2
Treatment effects on spruce growth in the greenhouse and field experiments. Significant p-values (95% confidence interval) are given in bold (†p-value < 0.1). Transformation of the response variable is indicated in italics for each model. Interaction effects that were not at least marginally significant were not considered in the models.

	Belowground			Aboveground			Total			Root allocation		
	β	t	*p*-value	β	t	*p*-value	β	t	*p*-value	β	t	*p*-value
Greenhouse 6-month-old seedlings	*(log)*			*(log)*			*(log)*					
Ground cover *vs* bare soil	0.36	11.25	< **.0001**	0.44	12.22	< **.0001**	0.41	12.10	< **.0001**	−1.68	−5.28	< **.0001**
Sphagnum spp. *vs* feather mosses	0.05	0.91	0.3660	0.06	0.94	0.3490	0.06	0.95	0.3470	−0.17	−0.31	0.7560
Fertilization	0.46	5.04	< **.0001**	0.51	5.01	< **.0001**	0.49	5.11	< **.0001**	−1.05	−1.16	0.2510
Greenhouse 2-year-old seedlings	*(log)*			*(log)*			*(log)*					
Ground cover *vs* bare soil (1)	−0.08	−2.09	**0.0415**	−0.10	−1.86	0.0690†	−0.08	−2.12	**0.0386**	0.05	0.04	0.9677
Sphagnum spp. *vs* feather mosses (2)	−0.09	−1.04	0.3048	−0.45	−3.69	**0.0005**	−0.21	−2.38	**0.0208**	7.58	3.60	**0.0007**
Fertilization (3)	0.37	4.09	**0.0001**	0.96	7.75	< **.0001**	0.61	6.81	< **.0001**	−13.30	−5.47	< **.0001**
Interaction (1) × (3)	0.05	0.86	0.3916	−0.07	−1.01	0.3187	−0.02	−0.47	0.6393	3.25	1.89	0.0637†
Interaction (2) × (3)	0.23	1.82	0.0738†	0.46	2.65	**0.0106**	0.29	2.25	**0.0283**	−4.45	−1.49	0.1409
Field 3-year-old seedlings				*(log)*								
Ground cover *vs* bare soil (1)	42.43	2.25	**0.0286**	−1.09	−0.18	0.8550	8.31	0.89	0.3785	0.09	2.38	**0.0208**
Sphagnum spp. *vs* feather mosses (2)	−23.33	−0.97	0.3385	0.21	0.04	0.9720	−10.81	−0.90	0.3706	−0.01	−0.23	0.8204
Fertilization (3)	56.66	1.65	0.1039	21.49	1.45	0.1530	33.21	1.95	0.0557†	−0.03	−0.43	0.6670
Shade (4)	53.75	1.64	0.1070	−16.31	−1.21	0.2300	0.88	0.05	0.9570	0.15	2.27	**0.0271**
Interaction (2) × (3)	67.00	1.96	0.0556†	–	–	–	24.23	1.43	0.1594	0.04	0.62	0.5351
Interaction (1) × (4)	−52.51	1.98	0.0532†	–	–	–	−8.93	−0.68	0.5007	−0.10	−1.78	0.0811†
Interaction (2) × (4)	70.53	2.12	**0.0386**	–	–	–	27.72	1.68	0.0988†	0.04	0.64	0.5271

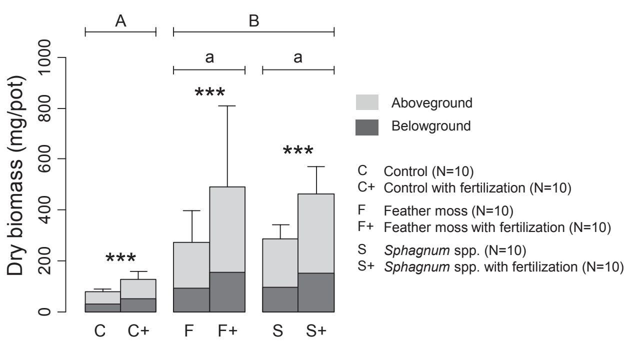

Fig. 1. Ground cover type and fertilization effects on greenhouse spruce 6-month-old seedling final biomass (3 seedlings per pot). Vertical lines correspond to standard deviations of the total biomass. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A–B), while the differences between *Sphagnum* spp. and feather moss treatments are indicated by lowercase letters (a–b). Difference between fertilization treatments are indicated for each ground cover type by asterisks (*** significant at 0.01%).

As already observed in previous field studies (Chrosciewicz, 1976; Ohlson and Zackrisson, 1992; Groot and Adams, 1994; Hörnberg et al., 1997), the high germination success, survival rate and early growth of the seedlings we obtained in *Sphagnum* spp. mosses indicate that this type of ground cover constitutes a high-quality substrate for black spruce germination and early development. Relationship to ground cover type was different for the 2-year-old seedlings that grew best in feather mosses than in *Sphagnum* spp. in the greenhouse experiment. These results are consistent with the theory that *Sphagnum* spp. mosses do not reduce black spruce recruitment but have a negative effect on the growth of the established trees, as already suggested in previous studies (Saint-Denis et al., 2010, Pacé et al., 2017b).

The lack of significant ground cover effect on spruce growth in our paludified field experiment forces us, however, to consider the results obtained in the greenhouse with caution. Indeed, our results do not tell us if the effects observed in the greenhouse also exist under the harsher conditions of the field. Since other studies have shown that *Sphagnum* spp. mosses constitute a lower quality substrate than feather mosses for seedling growth in paludified site plantations (Lavoie et al., 2007a; Lafleur et al., 2011), we can suppose that our field experiment was too short in duration to allow seedling acclimation to harsh field conditions. Transplant shock (Struve, 2009) may have been stronger in the field than in the greenhouse and may explain the low response of field seedlings to experimental treatments. Another factor that may explain the greater difference between treatments in the greenhouse experiment is that 2-year-old seedling roots were washed from all soil residues prior to planting in the greenhouse, which made them more sensitive to their new growth environment. In contrast, field seedlings were planted with their root plug, which may have reduced the influence of ground cover treatment in the field experiment.

4.2. *Sphagnum* spp. effect on spruce growth: identification of potential drivers

The long-term effects of *Sphagnum* spp. colonization on organic layer accumulation and hydric regime in paludified forests has been largely described in the literature (Lavoie et al., 2005; Fenton et al., 2005, 2006; Fenton and Bergeron, 2006; Simard et al., 2007). However, what we showed in this study is that even a thin transplanted layer of *Sphagnum* spp. has negative effects on spruce growth conditions, suggesting the existence of more direct inhibiting mechanisms, such as the short-term effect of *Sphagnum* spp. on soil nutrient availability.

Several pieces of evidence indicate that greenhouse 2-year-old seedling growth was more limited by nutrient availability in *Sphagnum* spp. mosses than it was in feather mosses, as already suggested in previous studies (Lavoie et al., 2007a, 2007b; Camill et al., 2010; Lafleur et al., 2011). Firstly, the positive effect of fertilization on greenhouse 2-year-old seedling growth was higher in *Sphagnum* spp. than in feather mosses. Secondly, greenhouse 2-year-old seedlings allocated more biomass to roots when they grew in *Sphagnum* spp. compared to those that grew in feather mosses, suggesting a greater limitation in soil resources. Finally, although there was no difference in final soil NH_4^+ and NO_3^- concentrations, *Sphagnum* spp. pots contained significantly less available phosphorus and base cations at the end of the greenhouse experiment than the feather moss pots. *Sphagnum* spp. mosses have been shown to have a higher ion exchange capacity than feather mosses and vascular plants (Clymo, 1963; Chapin et al., 1987). Therefore, the low nutrient availability in the *Sphagnum* spp. pots may have been related to nutrient absorption and retention in the moss tissues. These results are coherent with those of Lavoie et al. (2007b) who measured lower foliar nitrogen and phosphorus concentrations in seedlings that grew in *Sphagnum* spp. than in seedlings that grew in feather mosses.

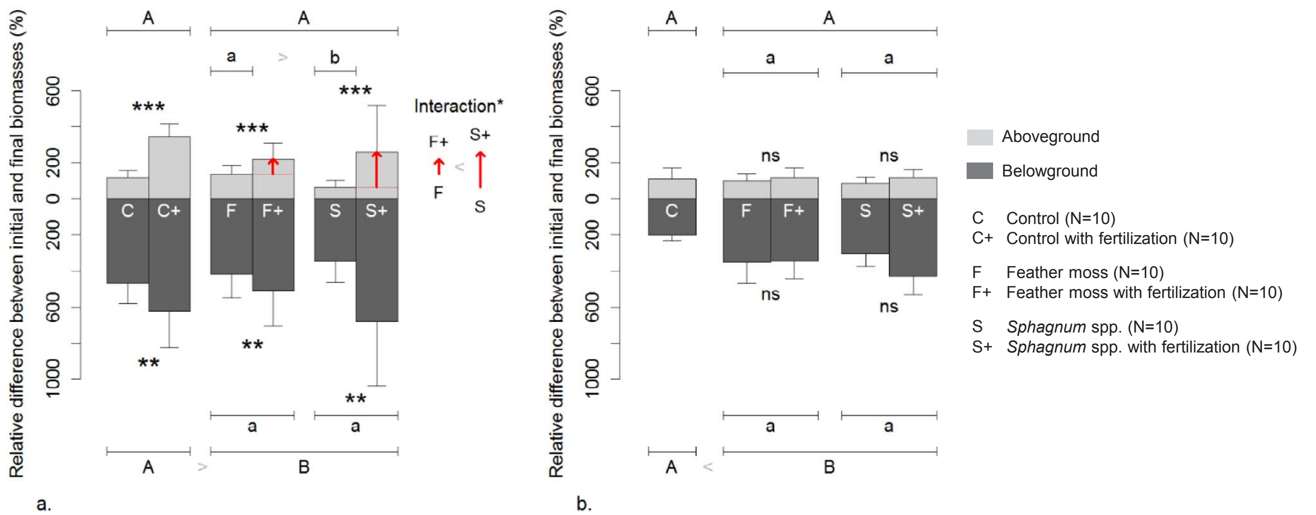

Fig. 2. Effects of ground cover type and fertilization on the growth of (a) greenhouse 2-year-old seedlings and (b) field 3-year-old seedlings. Vertical lines correspond to standard deviations in the above- and belowground growth. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A–B), while the differences between *Sphagnum* spp. and feather moss treatments are indicated by lowercase letters (a–b). In case of a significant interaction between ground cover types and fertilization treatment, letters indicate differences for non-fertilized treatment only. Red arrows are used to highlight the difference in fertilization effect between ground cover types, and the interaction effect is indicated on the right-hand side of the figure. Differences between fertilization treatments are indicated for each ground cover type by asterisks (*** significant at 0.1%, ** significant at 1%, * significant at 5%, ns: non-significant). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fertilization had a positive impact on greenhouse seedling growth in all ground cover types, indicating that spruce growth was limited by nutrients regardless of the ground cover treatment. However, the strong positive effect of the presence of a moss layer on early seedling growth suggests that micro-environmental conditions were as crucial as nutrient availability at this stage of spruce development. Vertical growth of the moss layer in the greenhouse seedling experience had no significant impact on tree seedling access to light.

Interestingly, it seems that greenhouse fertilization inversed the effects of feather moss and *Sphagnum* spp. on spruce 2-year-old seedling growth, i.e. the fertilized seedlings tended to be smaller in feather mosses than in *Sphagnum* spp. mosses and control pots. This may indicate that the positive effect of feather mosses on non-fertilized black spruce growth compared with *Sphagnum* spp. was mainly related to their positive effect on soil nutrient availability. When nutrient limitation was removed, feather mosses turned out to be a less suitable substrate for black spruce growth than bare soil or *Sphagnum* spp., suggesting that feather mosses are more likely to affect tree growth through other potential drivers such as chemical interference (Steijlen et al., 1995; Michel et al., 2011) than *Sphagnum* spp.

The effect of fertilization on spruce seedling growth was not as important in the field as it was in the greenhouse experiment. Soil nitrogen and phosphorus concentrations at the end of the field experiment were not increased by fertilization, and soil phosphorus even

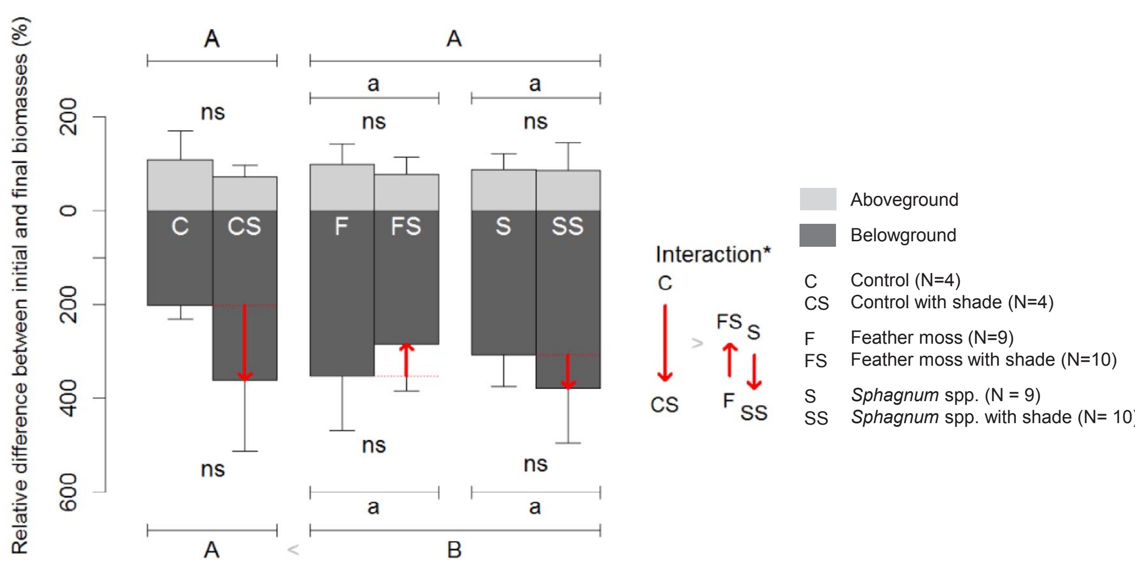

Fig. 3. Effects of ground cover type and shade on field 3-year-old seedling growth. Vertical lines correspond to standard deviations in the above- and belowground growth. Horizontal lines and letters indicate differences between ground cover types. Contrasts were used for the statistical analyses. The differences between ground cover and bare soil treatments are indicated by capital letters (A–B), while the differences between *Sphagnum* spp. and feather moss treatments are indicated by lowercase letters (a–b). In case of a significant interaction between ground cover types and shading treatment, letters indicate differences for non-shaded treatment only. Red arrows are used to highlight the difference in shading effect between ground cover types, and the interaction effect is indicated on the right-hand side of the figure. Differences between shading treatments are indicated for each ground cover type (ns: non-significant). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Final substrate available nutrient concentrations according to treatment and ground cover type (mean ± se). Feather moss values in bold indicate a significant difference between feather and *Sphagnum* spp. mosses (confidence interval = 95%). Significant differences are indicated for ground cover types only, regardless of the secondary treatment (fertilization or ground cover shading).

Experiment	Treatment	Ground cover	NH_4^+ (mg·kg^{-1})	NO_3^- (mg·kg^{-1})	P (mg·kg^{-1})	Major base cations (cmol·kg^{-1})
Greenhouse[a]	Control	Bare soil	77.5 ± 8.1	0	39.0 ± 2.8	12.5 ± 1.3
		Feather mosses	109.3 ± 19.9	1.5 ± 1.1	**43.0 ± 2.9**	**13.8 ± 0.8**
		Sphagnum spp.	80.3 ± 4.3	0.2 ± 0.1	29.8 ± 1.3	12.2 ± 0.7
	Fertilization	Bare soil	182.6 ± 61.0	27.1 ± 18.9	126.6 ± 59.6	11.9 ± 1.5
		Feather mosses	100.2 ± 21.8	5.0 ± 4.6	54.4 ± 8.0	14.4 ± 0.6
		Sphagnum spp.	99.4 ± 25.4	6.3 ± 3.5	32.9 ± 1.6	11.1 ± 2.0
Field	Control	Bare soil	65.8 ± 12.5	0	109.4 ± 22.3	10.0 ± 1.7
		Feather mosses	151.7 ± 22.8	0	126.0 ± 10.8	11.1 ± 2.6
		Sphagnum spp.	111.7 ± 50.1	0	107.6 ± 21.0	14.2 ± 0.5
	Fertilization	Feather mosses	60.8 ± 47.3	0	62.3 ± 30.6	6.0 ± 2.7
		Sphagnum spp.	105.1 ± 37.9	0	97.1 ± 5.5	9.7 ± 0.6
	Shading	Bare soil	103.6 ± 32.7	0	130.7 ± 42.3	10.1 ± 2.5
		Feather mosses	92.9 ± 32.7	0	112.0 ± 17.7	12.4 ± 2.9
		Sphagnum spp.	127.4 ± 6.1	0	105.2 ± 16.1	10.4 ± 0.4

[a] Data for the greenhouse experiment 2; the initial chemical composition of the peat used to fill the greenhouse pots was 138.3 ± 27.7 mg NH_4^+·kg^{-1}, 0.00 ± 0.01 mg NO_3^-·kg^{-1}, 28.3 ± 3.3 mg P·kg^{-1} and 11.9 ± 1.9 cmol base cations·kg^{-1}.

tended to be lower in fertilized plots. Nutrient loss in the field may have resulted from absorption by the neighboring vegetation or microbial communities. The low fertilization effect on field seedling growth may also have resulted from the existence of other more limiting factors in the field, such as unfavorable moisture or temperature conditions, which did not exist in the greenhouse.

The application of a shading cloth to simulate the shading effect of forest cover on the moss layer did not have any short-term positive impact on total seedling growth. Therefore, our second hypothesis, which postulates that stressing the moss by ground cover shading would increase nutrient release in the soil and favor seedling growth, was not verified. Instead, the positive effect of ground cover shading on seedling root allocation, especially in bare soil and *Sphagnum* spp., suggests that this treatment rather reduced soil resource availability for spruce seedlings. The small number of control seedlings used in this experiment do not allow us, however, to determine the specific role played by the moss layer in these effects. Shade may have reduced surface soil temperature and microbial activity. It may also have reduced atmospheric nitrogen fixation by mosses as this process has been shown to be light-dependent in some bryophyte species (Stuiver et al., 2015).

4.3. Implications for forest management

One of the objectives of forest management is to promote the establishment of productive post-harvest stands (Fenton et al., 2009). Our results in the greenhouse, if confirmed in non-paludified field conditions, suggest that the dominance of *Sphagnum* spp. (including *Sphagnum capillifolium*, *S. angustifolium*, *S. fuscum*, and *S. magellanicum*) in a particular site can be used as an indicator of poor growth conditions, even in the absence of organic layer accumulation. Therefore, total or partial harvesting in forest sites with high *Sphagnum* spp. cover may result in subsequent tree growth problems, regardless of the organic layer thickness. *Sphagnum* spp. cover can be reduced in those sites by prescribed burning or soil preparation (Lavoie et al., 2005; Fenton et al., 2009; Thiffault et al., 2013; Lafleur et al., 2016), followed by high density seeding or plantation to favor a rapid reforestation that would promote a rapid colonization of the understory by feather mosses.

5. Conclusion

Although moss type had no differential effect on field 3-year-old spruce growth in our paludified field experiment, we showed in a greenhouse experiment that transplanted *Sphagnum* spp. mosses (including *Sphagnum capillifolium*, *S. angustifolium*, *S. fuscum*, and *S. magellanicum*) affect 2-year-old seedling growth conditions by providing lower nutrient availability than feather mosses. This nutritional effect exists independently of the long-term effects of *Sphagnum* spp. mosses on excess water and their consequences on soil physical, thermal, chemical and biological conditions in the paludified forest. Based on these results in the greenhouse that remain to be validated in the field, we suggest that the dominance of *Sphagnum* spp. in a particular site can

Table 4
Treatment effects on soil nutrient content for the greenhouse and field experiments. Coefficient estimates that are significantly different from zero are given in bold. Transformation of the response variable is indicated in italics for each model.

	NH_4^+			NO_3^-			P			Base cations		
	β	t-value	p-value	β	t-value	p-value	β	t-value	p-value	β	t-value	p-value
Greenhouse[a]	*(log)*			*(sqrt)*			*(log)*[b]					
Ground cover *vs* bare soil	−0.06	−0.96	0.3460	0.14	1.20	0.2397	−0.05	–	> 0.1	0.24	0.69	0.4965
Sphagnum spp. *vs* feather mosses	−0.06	−0.59	0.5600	−0.21	−1.06	0.3004	−0.20	–	**< .0001**	−1.23	−2.10	**0.0451**
Fertilization	0.20	1.18	0.2480	1.75	2.20	**0.0363**	0.16	–	> 0.1	−0.32	−0.33	0.7443
Field							*(log)*					
Ground cover *vs* bare soil	12.09	1.25	0.2270	–	–	–	−0.01	−0.10	0.9230	0.65	1.13	0.2719
Sphagnum spp. *vs* feather mosses	6.47	0.47	0.6420	–	–	–	0.07	0.71	0.4900	0.79	0.97	0.3458
Fertilization	−38.85	−1.21	0.2410	–	–	–	−0.47	−1.95	0.0660	−4.62	−2.42	**0.0259**
Shade	−1.76	−0.06	0.9490	–	–	–	−0.01	0.03	0.9800	−0.82	−0.51	0.6193

[a] Data for the greenhouse experiment 2.
[b] A bootstrap procedure was used because of the non-normal distribution of the residuals.

be used as an indicator of poor growth conditions, even in the absence of thick organic layer accumulation and waterlogged conditions, and considered as a warning in regard to post-logging productivity. Unless it is followed by soil preparation, harvesting is likely to aggravate tree growth conditions in these sites by favoring *Sphagnum* spp. growth and accentuating paludification.

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