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ECOSYSTEMS

Broadleaf Litter Controls Feather Moss Growth in Black Spruce and Birch Forests of Interior Alaska

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ABSTRACT

Plant–soil feedbacks can maintain or reinforce alternative states within ecological systems. In Alaskan boreal forests, changes in fire characteristics have stimulated the replacement of needle-leaf black spruce (*Picea mariana*) by broadleaf deciduous trees. Feather mosses have strong associations with forest type: They dominate black spruce forest understories and are uncommon in broadleaf stands, with consequences for nutrient cycling and carbon storage. Here we test a long-standing hypothesis that broadleaf litter directly excludes mosses with a field experiment in broadleaf paper birch (*Betula neoalaskana*) and black spruce stands. We established 30 plots (15 each in birch and spruce dominated areas) with three *Hylocomium splendens* transplants treated with one of three treatments in each plot (ambient leaf litter deposition, birch leaf litter exclusion or addition), and 30 natural *H. splendens* areas. We measured moss growth and reproductive potential over 3 years. A 1-year experiment assessed leaf leachate and physical structure impacts on moss growth. Moss shoot growth in natural patches was larger in spruce than in birch stands (24.8 vs. 17.3 mg) and *H. splendens* made large contributions to ecosystem productivity in spruce stands. In both stand types, we observed a 40% reduction in moss biomass between litter addition and exclusion treatments and litter additions decreased sporophyte production. We found no difference in growth for mosses treated for 1 year with leaf leachates or physical litter structures. Leaf litter effects appear strong enough to exclude mosses from broadleaf forests, providing experimental support for hypothesized plant–soil interactions that may stabilize alternate forest types.

Key words: Plant–plant interactions; plant–soil interactions; bryophyte; feather moss growth; canopy effect; leaf litter; boreal forest.

HIGHLIGHTS

- Mosses contribute substantially to stand-level productivity in spruce but not in birch stands.
- Birch litter addition severely decreased moss growth after 3 years of experiment.

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Authors' contributions MJ led the field, laboratory, and data analyses and drafted the manuscript with guidance from JFJ. AMM led the field and laboratory work in 2012 when the experiment was established. JFJ, MCM, and AMM conceived the ideas, study approach, and designed the methodology. All authors contributed to manuscript drafts and gave final approval for publication.

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- Deposition of broadleaf litter alters moss growth to shape plant–soil feedbacks.

INTRODUCTION

Complex biological processes and feedbacks underlie stable biological communities in natural systems. Plant–soil feedbacks occur when plants affect soils through physical, chemical, or biological processes in ways that in turn affect plant communities. Such feedbacks influence the ecological resilience of terrestrial ecosystems, with effects ranging in scale from microbial communities to entire ecosystems (Gunderson 2000; Ehrenfeld and others 2005). Ground-covering bryophytes are at the interface between above and belowground processes and play key roles in plant–soil feedbacks (Lindo and others 2013). Bryophytes such as feather mosses and *Sphagnum* play a dominant role in boreal ecosystems because they produce low-bulk-density recalcitrant litter that leads to the accumulation of thick organic layers and promotes cold, wet, and nutrient-poor soils (Rochefort 2000; Frego 2007; Turetsky and others 2012). This, in turn, limits vascular plant productivity and influences species composition (for example, Turetsky and others 2010). Some bryophytes host dinitrogen (N_2)-fixing cyanobacteria, which provide a source of nitrogen (N) in nutrient-poor ecosystems such as boreal forests (DeLuca and others 2002, 2007). Because of these characteristics, bryophyte-mediated plant–soil feedbacks are likely to serve an important functional role in ecosystems at high latitudes where bryophytes are often abundant (Turetsky 2003; Turetsky and others 2012).

Fire is the dominant disturbance in boreal forests and its interactions with moss accumulation on the forest floor shape patterns of plant recovery after fire (Payette 1992). In upland forests of interior Alaska, two main forest types establish following wildfire disturbance: coniferous forests dominated by black spruce (*Picea mariana* [Mill.] B.S.P.), which have historically been the dominant forest type, and deciduous broadleaf forests dominated by trembling aspen (*Populus tremuloides* Michx.) or Alaska paper birch (*Betula neoalaskana* Sarg.) (Chapin and others 2006). Both forest types share the same species pool, but plant interactions driven by canopy composition lead to diverging understory plant communities (De Grandpré and others (1993); Hart and Chen 2006, Jean and others 2017a). In black spruce forests, low needle-leaf litter inputs and shaded, cool, and moist forest floors promote the establishment of feather mosses 20–40 years after fire (Jean and others 2017a). These mosses contribute to the resilience of black spruce forests by producing recalcitrant litter that results in accumulation of thick organic layers that further retain moisture and do not combust well during fire (Miyanishi and Johnson 2002; Johnstone and others 2010a). After fire, residual burned organic matter provides a poor-quality seedbed, but black spruce overcomes this constraint through its large seed bank in semi-serotinous cones (Johnstone and Chapin 2006; Greene and others 2007). In contrast, broadleaf forests do not support an extensive moss cover and annually produce broadleaf litter inputs that blanket the forest floor. Soils in broadleaf stands are characterized by shallow organic layers, warmer temperatures, and fast decomposition and nutrient turnover rates (Melvin and others 2015), all conditions that do not favor moss establishment. Observed changes in fire severity (deeper combustion of soil organic layers) that expose high-quality mineral seedbeds can lead to shifts in post-fire canopy dominance from black spruce to broadleaf species, which are expected to reduce moss cover and alter plant–soil feedbacks (Johnstone and others 2010a, b).

Differences in moss abundance between deciduous broadleaf and coniferous forests could be due to differences in leaf litter inputs or other environmental conditions between the two stand types. Deciduous broadleaf leaf litter has long been hypothesized as a major factor limiting establishment and productivity of forest floor mosses because they are susceptible to being buried (Van Cleve and others 1983b; Oechel and Van Cleve 1986; Sveinbjornsson and Oechel 1992). Impacts of leaf litter on bryophytes can be through physical damage, such as crushing, shading, or barriers to establishment (Van Cleve and others 1983b; Startsev and others 2008). Litter chemistry can also have impacts, for example through leaching of allelopathic compounds like phenols (Startsev and others 2008). Observations of low moss cover in early successional stages dominated by deciduous shrubs (Oechel and Van Cleve 1986; Turetsky and others 2010) or patchy distribution of mosses in areas of low litter inputs (Sveinbjornsson and Oechel 1992) support these hypotheses. However, we are aware of only one experimental test of leaf litter effects on boreal mosses where addition of aspen leaves and leachates led to a decrease in feather moss growth and survival (Startsev and others 2008). Nevertheless, understanding the mechanisms regulating moss abundance is critical to our understanding of boreal ecosystem function (Turetsky and others 2010). If mosses are highly sensitive to leaf litter effects, then changes in tree composition that affect litter deposition could reinforce and stabilize fire-driven changes in forest states (Johnstone and others 2010a). Alternatively, if environmental conditions are the dominant factors shaping moss abundance, then feather mosses should establish and grow better in stands or sites that have suitable environmental conditions, such as colder and moister soils in spruce stands. Teasing apart the relative importance of environmental conditions and leaf litter as mechanisms that drive patterns of moss abundance and biomass production under broadleaf deciduous and coniferous canopies is necessary to understand major stabilizing plant–soil feedbacks of Alaskan boreal forests.

In this study, we used feather moss transplants in black spruce and Alaska paper birch stands, combined with birch litter manipulations (addition and exclusion), to compare the effects of leaf litter versus other associated environmental drivers (for example, moisture, temperature, and pH) on moss growth, reproductive potential, and biomass accumulation. Specifically, we tested the following hypotheses and predictions. (1) Leaf litter is the dominant mechanism limiting moss abundance in deciduous stands because of its physical and chemical detrimental impacts on mosses. Therefore, mosses subjected to broadleaf litter additions in both forest types should present lower growth and reproductive potential. (2) Environmental conditions other than leaf litter are the dominant mechanisms driving patterns of moss abundance and growth because mosses tend to thrive under cool and moist conditions (represented by forest type in our analyses). Therefore, mosses should grow better in spruce stands, which tend to present those favorable environmental conditions more than birch stands. Both mechanisms are likely involved, but their relative importance is unknown. To further investigate specific mechanisms of broadleaf litter impacts on mosses, we conducted a second experiment where we manipulated the form of leaf litter applied to separate chemical impacts (leachates) from the physical impacts of weight and shading (previously leached leaves). Additionally, our data fills a large geographical gap in our understanding of feather moss growth and sporophyte production since the focus has been in Scandinavia (for example, Økland 1995; Rydgren and Økland 2002a, b). Testing mechanisms that drive patterns of moss abundance in contrasting boreal forest stands provides a direct experimental assessment of how changes in forest types may be stabilized by plant–soil feedbacks.

METHODS

Study Area and Site Description

Our study area is in the Tanana Valley State Forest at the base of Murphy Dome near Fairbanks (64°53′N, 148°23′W), interior Alaska, in an area of forest that established following fire in 1958. Interior Alaska has a continental climate with growing seasons that last about 135 days (Hinzman and others 2006). The long-term average air temperature is − 3.1°C with 287 mm of total annual precipitation (65% as rain; Hinzman and others 2006). Two major vegetation types dominate the forest landscape of interior Alaska: evergreen conifer stands of black spruce (39% of the landscape) and deciduous broadleaf stands dominated by aspen or birch (24%). Other vegetation types include forests dominated by mixed deciduous and coniferous trees (6%) or white spruce (10%, *Picea glauca* (Moench) Voss), and non-forested tundra (27%) (Yarie and Billings 2002; Calef and others 2005). In 2012, we established our experiments at three sites (labeled A, B, and C) containing pairs of adjacent black spruce- and Alaska paper birch-dominated stands. Sites A and B were on north-facing slopes about 900 m apart. Site C was about 3 km away and on a shallower slope adjacent to a creek. Five plots (10 m × 10 m) were randomly established in each of the six stands (15 plots dominated by each forest type, 30 plots total). We selected birch as our target broadleaf deciduous species for logistical reasons, since it is generally found on colder and wetter slopes than aspen and more likely to be adjacent to black spruce stands. No studies to our knowledge have investigated birch impacts on feather mosses.

Mean annual air temperature from July 2012 to June 2015 was − 1.6°C and mean annual soil temperatures were 0.7°C in our spruce and 2.0°C in our birch stands (‘‘online resources Appendix 1’’). The organic layer was deeper (16.4 cm ± 0.9 vs. 7.6 cm ± 0.4 SE) and the soil pH lower (4.33 ± 0.09 vs. 4.98 ± 0.10 SE) in spruce than in birch stands (Melvin and others 2015). Stand composition and leaf litter production and quality were described by Melvin and others (2015). Black spruce constituted 79% of all woody biomass in spruce stands from our sites, while Alaska paper birch made up 97% in birch stands, with the remainder being tall shrubs like alder (*Alnus viridis* (Chaix) DC. ssp. *crispa* (Aiton) Turrill) and willows (*Salix spp.*) or other tree species (Melvin and others 2015). Canopy cover (%) was measured with hemispherical pictures taken 30 cm above the surface of each of the 120 moss sampling units (see below) in July 2014 and processed with Gap Light Analyzer (Frazer and others 1999). Annual litter production in birch stands was assessed using three litter collection baskets in each plot (62.2 cm × 45.4 cm laundry baskets in birch stands lined with fiberglass window screen) and litter was collected each fall. Litter inputs in birch stands were dominated by birch leaves (Melvin and others 2015). In spruce stands, litter inputs were half of that of birch stands and composed of about 60% spruce needles with the rest being wood or shrub and birch leaves (Melvin and others 2015). The forest floor bryophyte community was characterized using point-intercept sampling at 10 random locations within each plot (50 cm × 50 cm frame with 16 grid intersections, $n = 300$ intersections). At each intersection, hits on leaf litter or mosses (species or genus level) were recorded.

Moss Transplant Experiment

In June 2012, we excavated six patches dominated by *H. splendens* down to the lower part of the fibric horizon within each of the 15 black spruce plots (30.5 cm diameter, approximately 15 cm depth). *Hylocomium splendens* is a common moss in boreal forests (Van Cleve and others 1983a) and it has a modular growth form which facilitates monitoring (Tamm 1953; Økland 1995). Every year, new segments grow on the segment grown the previous year, reaching full length and width after about 1.5–2 years. The segments become buried in the soil organic layer after about 3–4 years, photosynthesis stops, and decomposition begins. Growth of multiple segments in a year or emergence from older segments was reported as rare in Scandinavia (Tamm 1953; Økland 1995).

Moss patches were randomly assigned to be transplanted to either birch or spruce stands in their site of origin. In spruce stands, mosses were transplanted back into three harvested locations per plot. In birch stands, the forest floor was removed to the mineral soil at three random locations before installing the transplants. Moss transplants were randomly assigned to one of three litter treatments: all broadleaf litter exclusion, birch leaf litter addition, or ambient litter deposition (Figure 1). In the litter exclusion and addition treatments, natural broadleaf leaf litter was prevented from falling on the transplants using plastic mesh tents (mesh size 1.3 × 1.3 cm) during leaf senescence. In the birch leaf litter addition treatment, sorted fresh birch leaves from our litter collection baskets (mix of all sites) were added on moss transplants each October (2012–2014) at a rate of 224.8 g dry leaf litter m^{-2} $year^{-1}$ (ambient rate measured in birch stands in 2012). Starting in October 2013, loose nets were installed over the addition treatments to hold the litter in place until spring (plastic mesh, 1.3 × 1.3 cm). In the ambient litter treatment, the transplants received natural litter fall from the stand type they were placed in, that is, high input of broadleaf litter in birch stands and low input dominated by needles in spruce stands (Figure 1). These ambient treatments were not subjected to tenting, had a more variable leaf litter cover, and the transplants in spruce plots served as the procedural control. In each plot, we also identified an unmanipulated control moss area where *H. splendens* was naturally abundant (30.5 cm in diameter, hereafter named control) to assess transplanting impacts on moss growth. In birch stands, these areas were often small or on decomposing logs. The 90 moss transplants and 30 control moss areas are referred to as sampling units (SUs). Leaf litter cover on each of the 120 SUs was recorded by taking pictures in August 2015 that were processed using Adobe Photoshop CS5 (Adobe Systems, Mountain View, CA) and allowed the use of leaf litter as both a categorical (treatment; multi-year analyses) and continuous (%) variable (total growth from 2013 to 2015). Extensive fungal hyphae colonization of the moss surface below leaf litter was first observed in 2014 and widespread in 2015. As a result, fungal cover (%) of the mosses within the SUs was quantified through visual percent cover estimates in August 2015 with any leaf litter cover removed.

Leachates Experiment

In 2014, we initiated a second experiment to separate the chemical and physical effects of birch leaf litter on *H. splendens*. A total of five plots (2 × 2 m) were established in areas that had a continuous cover of feather mosses near the transplant experiment plots in the black spruce stand of site A. Four subplots (50 × 50 cm) were randomly assigned to a treatment: leached leaves, leaf leachates, fresh leaf litter, and control. No manipulations were conducted on the control subplots, and we used the transplant experiment leaf litter input rate (224.8 g dry leaf litter m^{-2} $year^{-1}$, sorted fresh leaf litter from all litter collection baskets) for the three other treatments. The fresh leaf litter treatment was equivalent to the addition treatment in the transplant experiment. The leached leaves treatment consisted of adding birch leaves that had been leached in deionized water at room temperature

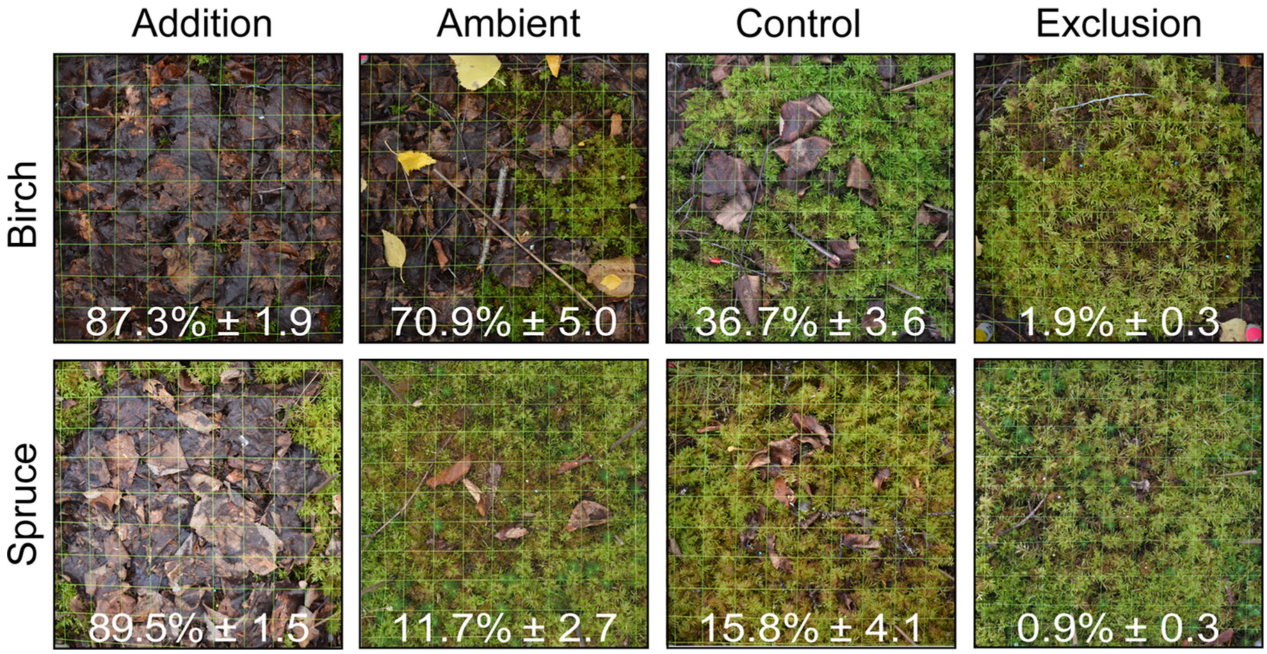

Figure 1. Deciduous leaf litter cover (%) on the sampling units according to leaf litter treatments in spruce and birch stands from September 2012 to 2015 (four measurements per sampling unit, mean ± SE). Each photograph (pictures by M. Jean) is an example of the treatment effects in both forest types. The fine grid visible in the photographs is fishing line (3 cm apart) used to locate moss individuals.

(20°C) for 7 days to remove water-soluble, leachable components from the leaves but keep their physical structure intact. The water was changed three times a day and stirred both before and after each change. The leaves were dried at room temperature for 24 h before application. In the leaf leachate treatment, we leached birch leaves (total of 281 g dry leaf litter for the 5 subplots) with 5 L of rainwater for 24 h at room temperature, manually stirring the leaf litter for 2 min every 4 h. We applied 800 mL of the filtered solution in a single application to each leachate treatment subplot and the same volume of rainwater all other subplots in September 2014, June 2015, and August 2015. This ratio of water to leaves was selected to immerse all leaves and is similar to other leaching experiments (for example, Nilsson and Zackrisson 1992). Dried leaf litter was preserved frozen at − 20°C to make a new solution for each application.

MOSS MEASUREMENTS

Marked Individuals, Biomass and Allometry

We marked the uppermost segment on five randomly selected *H. splendens* shoots in each of the 120 SUs of the moss transplant experiment in June 2013 and an additional five shoots in September 2013 (total $n = 1200$). Ten individuals of *H. splendens* were marked in each subplot of the leachate experiment in September 2014 (total $n = 200$). Slit, colored PVC rings (HAMA plastic beads, Malte Haaning Plastics Co., Denmark; outer diameter 2.5 mm and inner diameter 1 mm) were placed at the base of the moss segments using tweezers (Økland 1995). The location of all moss shoots within SUs was recorded using a grid system. Marked individuals were measured in September 2013 (transplant experiment only), September 2014, and August 2015. New PVC rings of different colors were added to emerging segments over the years. For each moss shoot, the length and width of each segment were measured to the nearest millimeter using a ruler. When multiple branches occurred, their length and width were also measured. In 2013 and 2014, we tagged new moss shoots to replace those broken by experimenters or not relocated (~ 3% of moss individuals).

All shoots were destructively harvested in August 2015, and their dimensions, dry weights, and sporophyte counts were recorded in the laboratory. Moss biomass was measured directly in 2015, and we used allometric equations to estimate biomass in 2013 and 2014. In September 2013, June 2014, and September 2014, we collected a core of *H. splendens* (100 cm^2) in the proximity of each plot in the transplant experiment ($n = 30$) for estimates of shoot density and biomass allometry. We used 5 to 20 moss shoots from each core to build allometric equations between the length, width, and weight of the five uppermost *H. splendens* segments (details presented in Jean 2017) to estimate *H. splendens* biomass in 2013 and 2014. There was a close match between predicted values created by our equations and measured moss biomass in August 2015 ($r^2 = 0.97$, $p < 0.0001$).

Statistical Analyses

Unless otherwise stated, all of our analyses were mixed model conducted using the library *lme4* (Bates and others 2014) and *lmerTest* (Kuznetsova and others 2015) in R (R Development Core Team 2016). This type of model was selected to account for the hierarchical nesting of our sampling design (moss shoots when applicable, nested within SUs, nested within plots) and is similar to a randomized block experiment. Because site only had three levels, it was considered a fixed effect (Bolker and others 2009). Nonsignificant interactions were removed from final models. Units of replication were moss sampling units in the transplant ($n = 120$) and leachates experiments ($n = 20$). Tukey's Honest Significant Difference (HSD) post hoc tests were used when applicable. Our data are available online (Jean and others 2017b, c, d, e) and complete statistical tables are provided in ''online resources Appendix 2''. Our models test for the respective impacts of birch leaf litter (both as treatments and percent covers) and other environmental variables associated with the two stand types (encompassed in the forest type variable in our analyses) on variables associated with moss growth and reproductive output.

Moss Biomass and Growth form Responses to Forest Type and Leaf Litter

We analyzed average biomass and the total number of segments per moss shoot according to forest type, leaf litter treatment, and sampling year. Significant three-way interactions were followed by separate models for each year with a Bonferroni correction (Crawley 2007). Moss biomass and averaged number of segments were transformed to ensure normality using natural logarithm and square root transformations, respectively. Partial R^2 calculated using the Kenward Rogers method was used as a measure of the relative impacts of leaf litter treatment and forest types on moss growth (package *r2glmm;* Johnson 2014, Jaeger 2016). Afterward, we investigated how moss growth (June 2013 to August 2015), measured as biomass and segment production, varied according to leaf litter and canopy cover as continuous variables and forest type. No data transformations were needed. Akaike's information criterion (AIC) was used to select the most parsimonious model from a series of nested models (Crawley 2007). A Spearman rank correlation was used to investigate the relationship between leaf litter and fungus cover, as their relationship was monotonic and nonlinear, and a Pearson correlation was used for fungus cover and moss growth.

In the transplant experiment, we calculated the proportion of moss segments from which more than one growth point emerged in 2013–2014 and 2014–2015 (thus producing more than one segment) and the proportion of moss biomass allocated to new segment production versus expansion of existing segments in 2014–2015. Only segments from the main axis were used to identify each segment with certainty. Of the 1136 moss shoots remaining in 2015 (some were broken by experimenters or lost), 55 were removed from the analyses of biomass allocation because they showed no growth, mostly due to mechanical damage and branch loss, and allocation could not be determined. The proportion of segments producing multiple growth points and allocation proportions were compared among forest types and leaf litter treatments using a generalized linear model (multiple growth points at the SU level) and mixed models (allocation at the shoot level) with a binomial family and a logit link function (Bates and others 2014).

Moss Fitness Responses to Forest Type and Leaf Litter

To assess the impacts of forest type and leaf litter on moss fitness, we counted the total number of sporophytes measured on marked shoots in each transplant, relative to the number of shoots (marked for biomass estimates, $n = 5$–13, average of 9). To account for possible phenotypic differences in sporophyte production among mosses originating from different stand types, we ran one model on controls and a separate model on transplants (all transplant mosses originated from spruce stands). We used generalized linear models with a Poisson distribution for zero-inflated and over dispersed count data to analyze control data (package *pscl*; Zeileis and others 2008) and a mixed-model approach for the transplant data (package glmmADMB; Skaug and others 2011). An interaction between forest type and leaf litter treatment could not be included in the model due to sample size limitations, so percent leaf litter cover was used as a continuous variable instead of treatment, as this variable captured the difference in leaf litter cover in the two ambient treatments.

Physical, Chemical, and Biotic Mechanisms of Leaf Litter Impacts on Mosses

We compared *H. splendens* growth (final biomass data from September 2015) in the four experimental leachate treatments using mixed models with plot as a random effect. Initial moss measurements (September 2014) were included in the model to account for pre-experiment differences in moss size. To comply with distribution assumptions, moss biomass was square-root-transformed.

Contribution of Mosses to Ecosystem Net Primary Production

We estimated total biomass per unit area produced by *H. splendens* under all combinations of forest types and transplant treatments using average moss growth per shoot per year (g moss shoot^{-1}, 2014 to 2015), cover (%), and shoot density (growing points m^{-2}). All segments marked since 2013 were included because the oldest ones still showed a 39% weight increase in 2015. The contribution of *H. splendens* biomass was compared to stand-level aboveground net primary productivity (ANPP) measured at our study sites by Melvin and others (2015).

RESULTS

Canopy and Forest Floor Characteristics

Canopy cover was higher (80.9% ± 0.6 and 62.3% ± 2.3 SE, respectively) and annual light availability lower in birch than in spruce stands (''online resources Appendix 1''). Moss percent cover was higher in spruce than in birch stands (94.3% ± 1.1 and 12.5% ± 1.6 SE, respectively) and dominated by the feather mosses *Hylocomium splendens* (Hewd) Schimp. and *Pleurozium schreberi* (Brid.) Mitt.. Broadleaf litter covered most of the ground in birch stands (95.5% ± 1.0 SE) compared to half of the ground surface (often with mosses below) in spruce stands (50.0% ± 3.2 SE; ''online resources Appendix 1'').

MOSS GROWTH RESPONSES TO FOREST TYPE AND LEAF LITTER

Moss Biomass and Segment Production

The way that forest type and leaf litter treatment interacted to affect moss biomass varied among years (three-way interaction, Table 1a, Figure 2A, ''online resources Appendix 2.1''). In 2013, only the impact of forest type was detectable ($P < 0.0001$; partial R^2 of 0.50 vs. 0.06 for treatment), with larger mosses in spruce (8.7 ± 0.2 mg) than in birch stands (6.9 ± 0.2 mg [raw data averages ± SE]). In 2014, mosses were still larger in spruce than in birch stands (18.2 ± 0.7 and 13.3 ± 0.5 mg, respectively; $P < 0.0001$; partial R^2 of 0.50). Mosses in the leaf litter addition (13.4 ± 0.7 mg) and ambient (15.0 ± 1.0 mg) treatments in 2014 were smaller than the ones in the exclusion (16.6 ± 0.9 mg) treatments and the controls (17.8 ± 0.9 mg; $P < 0.0001$; partial R^2 of 0.25). In 2015, the effect of treatment varied according to forest type (two-way interaction; $P = 0.0079$), but the relative impact of leaf litter treatment was slightly larger than that of forest type (partial R^2 of 0.48 and 0.43, respectively; interaction partial R^2 of 0.13). Indeed, there was no difference in moss biomass between controls in birch and spruce stands, compared to large biomass differences between moss subjected to low and high leaf litter cover in both forest types (Figure 2A). Mosses with low leaf litter cover (both exclusions and controls, plus ambient in spruce) weighed on average 32.6 ± 1.2 mg, while mosses under a high leaf litter cover (both additions, plus ambient in birch) weighed only about 18.9 ± 1.1 mg (Table 1a; Figure 2A; ''online resources Appendix 2.1'').

Changes in moss biomass from 2013 to 2015 were negatively affected by leaf litter percent cover (as a continuous variable, $P < 0.0001$) and growth was larger for mosses in spruce (increase of 24.8 ± 1.5 mg) than in birch stands (increase of 17.3 ± 1.1 mg; $P = 0.0034$; Table 2a; Figure 3). Leaf litter cover had a larger relative impact on moss growth than forest type (partial marginal R^2 of 0.43 and 0.22, respectively). Differences in canopy cover among spruce and birch stands did not affect moss growth ($P = 0.1937$). Site had a significant effect in all our biomass models (Table 1, Table 2a), with the largest mosses found at site C and the smallest found at site A. There was a strong positive correlation between leaf litter and fungal hyphae cover on mosses (Spearman's $\rho = 0.87$, $P < 0.0001$), and moss growth was negatively

Table 1. Results from the Linear Mixed Models Comparing (a) Moss Biomass and (b) Number of Segments According to Leaf Litter Treatment, Forest Type, and Sampling Time.

	Df	*F* value	*P* value
(a) Moss biomass			
Full model (2013–2015; marginal $R^2 = 0.82$, conditional $R^2 = 0.94$)			
Forest type	1, 26	27.062	< **0.0001**
Treatment	3, 84	13.858	< **0.0001**
Sampling year	2, 224	1869.868	< **0.0001**
Sites	2,26	9.854	**0.0007**
Forest type × Treatment	3, 84	2.276	**0.0856**
Forest type × Sampling year	2, 224	3.176	**0.0436**
Treatment × Sampling year	6, 224	22.404	< **0.0001**
Forest type × Treatment*Sampling year	6, 224	5.711	< **0.0001**
September 2013 (marginal $R^2 = 0.41$, conditional $R^2 = 0.54$)			
Forest type	1, 26	25.794	< **0.0001**
Treatment	3, 87	1.9872	0.1403
Sites	2,26	10.924	**0.0004**
September 2014 (marginal $R^2 = 0.47$, conditional $R^2 = 0.59$)			
Forest type	1, 26	26.904	< **0.0001**
Treatment	3, 84	9.866	< **0.0001**
Sites	2, 26	10.265	**0.0005**
August 2015 (marginal $R^2 = 0.51$, conditional $R^2 = 0.61$)			
Forest type	1, 26	18.329	**0.0002**
Treatment	3, 84	25.961	< **0.0001**
Sites	2, 26	6.546	**0.0050**
Forest type × Treatment	3, 84	4.212	**0.0079**
(b) Number of moss segments (marginal $R^2 = 0.82$, conditional $R^2 = 0.90$)			
Forest type	1, 26	6.418	**0.0177**
Treatment	3, 87	12.595	< **0.0001**
Sampling year	2, 232	1339.170	< **0.0001**
Sites	2, 26	2.910	0.0724
Treatment × Sampling year	6, 232	8.262	< **0.0001**

Analysis of variance tables for linear mixed models with repeated measures (type III, Satterthwaite approximation for degrees of freedom). Degrees of freedom of the numerator are followed by degrees of freedom of the denominator. Biomass data were log transformed and segment data were square-root-transformed. A Bonferroni correction was applied for the monthly analyses with a critical p value of 0.017. Significant effects are shown in bold font. Nonsignificant interactions were removed from the final models. Coefficient estimates and standard errors are presented in ''online resources Appendix 2.1''.

associated with fungus cover ($r^2 = -0.54$, $P < 0.0001$).

Moss segment counts were slightly higher in spruce than in birch stands (4.3 ± 0.1 vs. 4.1 ± 0.1 segments; $P = 0.0177$) and treatment impacts varied according to sampling year (two-way interaction; $P < 0.0001$; Table 1b). In 2013, segments per moss shoot were similar among all treatments (1.8 ± 0.02; Figure 2b). At the end of the experiment (2015), mosses in leaf litter addition treatments had the fewest number of segments (3.8 ± 0.2 in spruce and 3.4 ± 0.3 in birch), followed by ambient (4.4 ± 0.2 in spruce and 3.9 ± 0.2 in birch) and exclusion (4.5 ± 0.2 in spruce and 4.1 ± 0.1 in birch) treatments. Mosses in controls had the most segments (4.6 ± 0.2 in spruce and 5.0 ± 0.2 in birch; Figure 2b). Leaf litter cover had a negative impact on total segment production between 2013 and 2015 (Table 2b). However, the small but significant difference found according to forest type for moss segment counts was not reflected when looking at segment production between 2013 and 2015 (3.1 ± 0.1 in spruce vs. 3.0 ± 0.1 in birch; Table 2b). Production of multiple segments in a year was relatively common; 3.1% of samples in 2014 and 15.3% in 2015 produced a least one segment with multiple growth points (Table 3). Neither forest type nor treatment affected the production of multiple segments in 2014; in 2015 fewer multiple segments were produced in the leaf litter addition and ambient leaf litter treatments ($P < 0.001$; ''online resources Appendix 2.4'').

Litter treatments had a significant impact on moss biomass allocation by decreasing segment production in favor of elongating old segments,

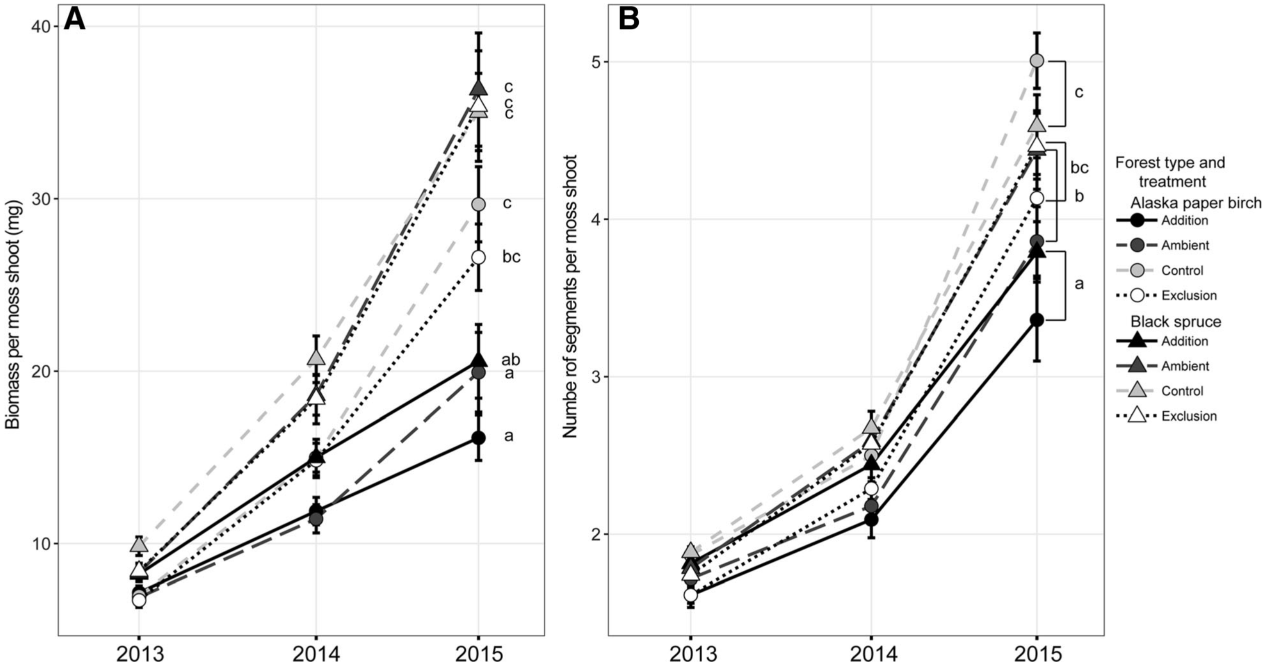

Figure 2. **A** Average biomass of individual moss shoots (± SE) and **B** number of segments per moss shoot (± SE) according to sampling time (September 2013, September 2014, and August 2015; $n = 120$ per sampling time). Symbols indicate forest type and colors and line types indicate leaf litter treatment. Different letters indicate that the treatments within each forest type (8 levels) were significantly different in 2015 (Tukey's HSD post hoc test, $P < 0.05$, details presented in ''online resources Appendix 2.2''). Note that raw data are presented here, whereas statistical analyses used the natural log of biomass and square root of segment number as well as the nesting structure of the data as random effects in the models (sampling units within plots).

Table 2. Results from the Linear Mixed models Comparing (a) Total Moss Growth and (b) Increase in the Number of Segments (June 2013 to August 2015) According to Leaf Litter Cover, Forest Type, and Canopy Cover.

	Estimate	Standard error	Df	*T* value	*P* value
(a) Moss growth (2013–2015; marginal R^2 = 0.52, conditional R^2 = 0.56)[a]					
Intercept	14.311	5.237	53.6	2.733	**0.0085**
Leaf litter cover (%)	− 0.156	0.019	90.3	− 8.252	< **0.0001**
Canopy cover (%)	0.081	0.062	57.3	1.315	0.1937
Forest type (spruce)	6.372	2.018	33.2	3.158	**0.0034**
Site (B)	2.909	1.970	23.9	1.477	0.1528
Site (C)	8.184	1.996	24.2	4.101	**0.0004**
(b) Number of segments (2013–2015; marginal R^2 = 0.21, conditional R^2 = 0.21)[a]					
Intercept	2.477	0.507	113	4.887	< **0.0001**
Leaf litter (%)	− 0.009	0.002	113	− 4.488	< **0.0001**
Canopy cover (%)	0.009	0.006	113	1.504	0.1352
Forest type (spruce)	0.201	0.189	113	1.063	0.2900
Site (B)	0.147	0.180	113	0.813	0.4178
Site (C)	0.451	0.183	113	2.465	**0.0152**

Analysis of variance tables for linear mixed models (type III, Satterthwaite approximation for degrees of freedom. Degrees of freedom of the numerator are followed by degrees of freedom of the denominator. Significant effects are shown in bold font. Nonsignificant interactions were removed from the final models.

[a] *This model was run while excluding one outlier (control, site B, birch stands, plot 2). Results from the model run on the complete dataset are presented in ''online resources Appendix 2.3''.*

with significant differences in the addition treatment compared to the controls and exclusion treatments ($P = 0.0127$, $P = 0.0068$; ''online resources Appendix 2.5''). Typical biomass allocation in controls was 20.0% ± 1.8 SE to new segments versus 79.2% ± 2.1 SE to elongate existing seg-

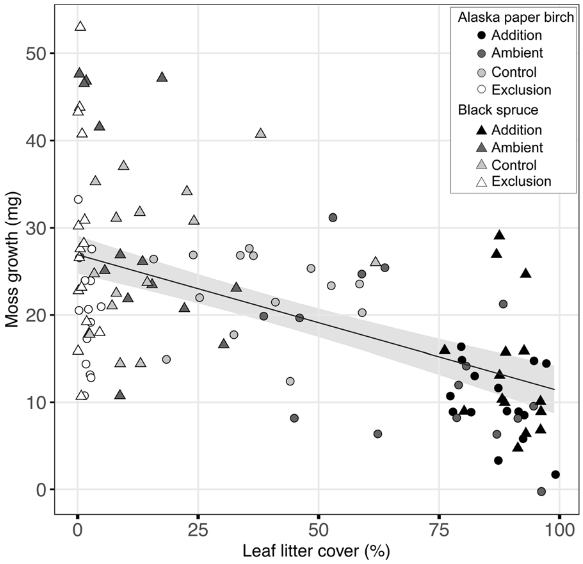

Figure 3. Moss growth between June 2013 and August 2015 (mg) in relation to leaf litter cover (%). Points are the averages of moss shoot growth per transplant, symbols represent forest types, and colors represent leaf litter treatments (total $n = 120$). The line represents the fixed effect of leaf litter with a 95% confidence interval shading (Table 2).

ments. Similar biomass allocation to new segments occurred in exclusion (20.7% ± 1.8 SE) and ambient treatments (16.8% ± 2.0 SE). With litter addition, mosses decreased biomass allocation to new segments (11.9% ± 1.7 SE), consistent with lower segment production in addition treatments. Under high leaf litter cover, mosses produced long and narrow segments with few side branches (''online resources Appendix 3'').

Physical and Chemical Mechanisms of Leaf Litter Impacts on Mosses

The 1-year experiment using different forms of leaf litter additions (fresh leaf litter, leachates, and leached leaves) produced nonsignificant treatment effects ($P > 0.05$, ''online resources Appendix 2.6''). Mosses receiving the leached leaves and natural leaf litter treatments were marginally smaller than those in the controls ($P = 0.0763$ and $P = 0.0959$), while growth was similar in control and leaf leachates plots ($P = 0.5545$; ''online resources Appendix 2.6''; Figure 4).

Moss Fitness Responses to Forest Type and Leaf Litter

Sporophytes

A least one sporophyte was produced on 6.1% and 1.8% of measured moss segments in the controls of spruce and birch stands, respectively. However, sporophyte count (on measured mosses per SU) was similar between the controls of birch and spruce stands ($z = -0.21$, $P = 0.8376$; ''online resources Appendix 2.7''). This lack of difference may be due to one SU in a birch stand having a very high sporophyte count (15 sporophytes; Figure 5). Although sporophyte counts were more variable in spruce than in birch stands, a few sampling units in the latter presented very high counts (Figure 5). In transplants with low leaf litter inputs, at least one sporophyte occurred on between 3.6 to 6.1% of measured moss segments, whereas in transplants with high litter inputs, values were between 0.2

Table 3. Percentage of Moss Shoots (± SE) that Produced More Than One Segment in a Year Along the Main Axis of Growth According to Forest Type and Leaf Litter Treatment.

Forest type	Treatment	Samples that produced more than one segment (%)	
		2013–2014 (1086 moss shoots)	2014–2015 (1136 moss shoots)
Birch	Litter addition	1.3 ± 0.9	8.7 ± 3.1*
	Ambient litter	2.5 ± 1.1	9.0 ± 2.9*
	Control	2.7 ± 1.5	26.1 ± 2.4
	Litter exclusion	6.0 ± 2.4	16.9 ± 2.4
	Birch average	3.1 ± 0.8	15.2 ± 1.6
Spruce	Litter addition	2.7 ± 2.1	10.0 ± 2.6*
	Ambient litter	4.0 ± 1.3	11.6 ± 3.9*
	Control	2.0 ± 1.1	20.4 ± 5.5
	Litter exclusion	4.0 ± 2.4	19.5 ± 4.0
	Spruce average	3.2 ± 0.9	15.4 ± 2.1
	Average	3.1 ± 0.6	15.3 ± 1.3

**Significant treatment effect, see ''online resources Appendix 2.4'' for details.*

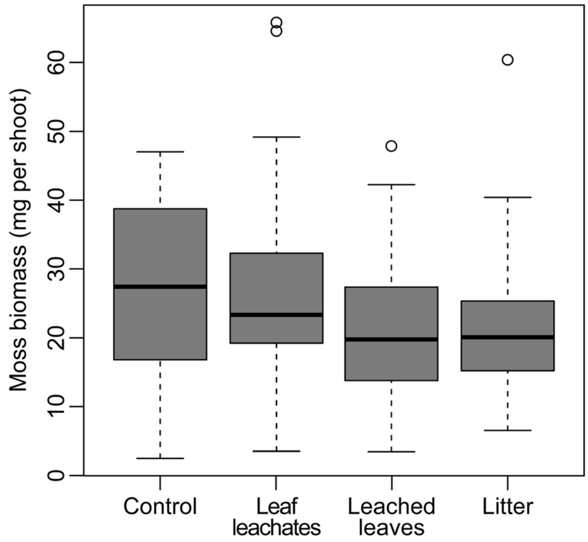

Figure 4. Average weight per shoot (mg) of *Hylocomium splendens* after 1 year of treatment with leaf leachates, leached leaves, or fresh leaf litter (measured in September 2015, total $n = 20$). Medians are indicated by the black horizontal lines, boxes include 25–75% quantiles of the data, and whiskers include 5–95%. Outliers are shown as open circles. Note that raw data are presented whereas statistical analyses comprised a random plot effect and data were square-root-transformed.

and 0.6%. Sporophyte count was higher in transplants in spruce compared to birch stands ($z = 3.79$, $P = 0.0001$), but all transplants with high litter cover (birch ambient and additions in both forest types) had very few sporophytes (Figure 5). Leaf litter cover as a continuous variable had a strong negative impact on sporophyte count ($z = -4.80$, $P < 0.0001$) that was larger than that of forest type alone ($z = 3.79$, $P = 0.0001$; ''online resources Appendix 2.7'').

Moss Growth Contribution to Ecosystem Net Primary Productivity

Hylocomium splendens ANPP, as estimated from measurements of shoot growth and density, was one order of magnitude higher in the controls of spruce (43.8 g m^{-2} $year^{-1}$) than in birch stands (3.0 g m^{-2} $year^{-1}$; Table 4). Contribution of *H. splendens* to stand level ANPP was estimated at 0.65% in birch stands, and 17.7% in spruce stands. Mosses transplanted into birch stands produced amounts of biomass and a proportion of stand-level ANPP more similar to the controls in birch than those in spruce stands. Contribution to stand-level ANPP of mosses in the exclusion treatments was very similar to that of mosses in the controls in both forest types (Table 4). Experimental and ambient birch litter inputs in spruce and birch stands led to large decreases in moss biomass production and contribution to stand-level ANPP, with estimates being between 17 and 39% of the controls (Table 4).

DISCUSSION

Addition of birch leaf litter to *H. splendens* transplants led to significant reductions in moss growth, biomass accumulation, and sporophyte production in both birch and black spruce stands. Experimental results from this study suggest that broadleaf deciduous leaf litter is likely a more important

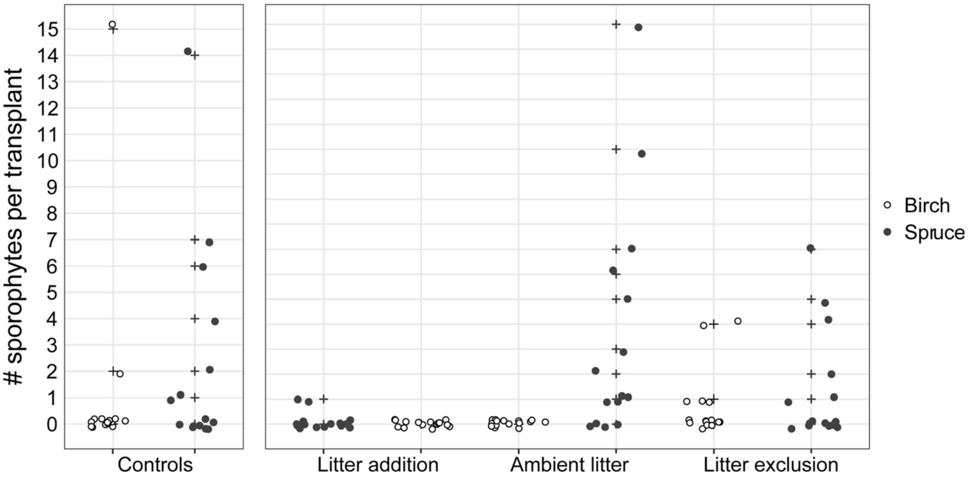

Figure 5. Number of sporophytes on moss segments produced between 2013 and 2015 per transplant according to treatment and forest type ($n = 15$ per forest type × treatment) in August 2015. Points have been randomly offset to avoid overlap around the central crosses that represent the sporophyte count.

Table 4. Estimates of Moss Biomass Production per Year (g m^{-2} $year^{-1}$) Estimated from Individual Moss Shoot Growth in 2014–2015, Moss Cover, and Moss Shoot Density (Growing Points).

Treatment	Site	Moss cover (%)[a]	Moss density[b]	Biomass production per sample[c]	Growing points per sample	Biomass production[d]		Percent of annual ANPP[e]
Alaska paper birch, ANPP estimates[d]								465
Control	A	7.25	555.8	15.6	2.15	4.03	3.00	0.65
	B	12.6	751.2	15.8	2.69	4.41		
	C	1.75	112.3	12.6	2.49	0.57		
Litter addition	A			3.51	1.88	1.04	1.13	0.24
	B	[f]	[f]	4.26	1.57	2.04		
	C			5.16	1.85	0.32		
Ambient litter	A			6.58	1.67	2.19	1.88	0.11
	B	[f]	[f]	8.47	2.16	2.95		
	C			10.5	2.35	0.51		
Litter exclusion	A			9.33	1.76	2.95	2.78	0.60
	B	[f]	[f]	10.8	1.79	4.53		
	C			15.8	2.37	0.86		
Black spruce, ANPP estimates (g m^{-2} $year^{-1}$)[e]								247
Control	A	58.3	8046	14.7	1.75	67.58	43.8	17.7
	B	52.8	4714	12.8	1.57	38.43		
	C	47.0	3920	17.8	2.76	25.28		
Litter addition	A			6.33	1.88	27.09	16.9	6.84
	B	[f]	[f]	2.41	1.85	6.14		
	C			7.93	1.78	17.46		
Ambient litter	A			13.4	1.71	63.05	46.3	18.7
	B	[f]	[f]	13.4	1.85	34.14		
	C			25.9	2.44	41.61		
Litter exclusion	A			11.0	1.49	59.50	45.0	18.2
	B	[f]	[f]	15.6	2.20	33.42		
	C			24.6	2.30	41.92		

[a] *Absolute percent cover for H. splendens.*

[b] *Growing points m^{-2}. These values are the same throughout the table and were obtained from a core of H. splendens (100 cm2) collected in the proximity of each plot in birch and spruce stands at all sites.*

[c] *mg $shoot^{-1}$ $year^{-1}$.*

[d] *g m^{-2} $year^{-1}$.*

[e] *g. m^{-2} $year^{-1}$. Annual net primary productivity (ANPP) estimates from Melvin and others (2015) for the tree data. We added our estimates of average moss productivity from the controls to get the complete ANPP for each stand type.*

[f] *The values are the same throughout the table. Moss cover was obtained at 10 random locations within each plot using point-intercept sampling (50 cm × 50 cm frame with 16 grid intersections, see ''online resources Appendix 1'' for additional information).*

mechanism limiting the growth and abundance of *H. splendens* in deciduous stands in interior Alaska than stand type and other associated differences in environmental conditions. Our results are consistent with other experiments using aspen (*Populus tremuloides*) litter in Alberta (Startsev and others 2008) and support the long-standing hypothesis of the detrimental effect of deciduous broadleaf litter on mosses (for example, Van Cleve and others 1983b). Canopy effects of deciduous broadleaf litter on moss abundance and accumulation of soil organic material represent a dynamic set of plant–soil interactions that may stabilize deciduous and coniferous stands and shape patterns of carbon accumulation in the boreal forest (Johnstone and others 2010a; Trugman and others 2016). In black spruce stands, low birch and other broadleaf leaf litter inputs favor high moss productivity that produces slowly decomposing moss and thick organic layers, whereas in deciduous stands, leaf litter inputs maintain low moss cover and productivity, thus driving the persistence of shallow organic layers. Indeed, ANPP of *H. splendens* alone accounted for up to 18.7% of ANPP in spruce stands but accounted for a negligible proportion in birch stands (< 1%; Table 4).

Two years were required before the impact of leaf litter treatments on mosses became apparent, and litter effects did not override stand differences as the major driver of moss growth until after 3 years of experimental treatment (Table 1; Figure 2). Time lags in moss responses to litter treatments may reflect the time required to accumulate about three layers of deciduous leaves, an amount similar to that found on the forest floor of mature deciduous stands (Landhäusser and Lieffers 2003). At the end of the experiment, mosses subjected to low leaf litter treatments (control, exclusion and ambient in spruce, and control and exclusion in birch) were on average 1.7 times larger and had produced approximately one more segment than mosses in the high leaf litter cover treatments (ambient and addition in birch, and addition in spruce). Our experimental tests of the mechanisms behind leaf litter impacts on moss growth showed no significant responses, possibly because of the short-term nature of the study (Figure 4). There was a trend toward negative impacts of leached leaves and leaf litter, while leachates alone had no apparent impact on *H. splendens* growth. Similar trends were found for *P. schreberi* in the same experimental plots (Jean 2017). These trends suggest leaf litter impacts may be more associated with physical impacts such as shading and crushing than chemical impacts. However, further testing will be required to more clearly determine mechanisms of litter impacts on mosses, for example using chemical analyses and shading treatments. Observations from our 3-year transplant experiment also raise questions of how changes in moisture, light and nutrient availability due to leaf litter additions may alter biotic interactions in the bryosphere, for example with fungi (Davey and Currah 2006) and litter- and moss-grazing micro- and mesofauna (Kardol and others 2016; Lindo and Gonzalez 2010).

Leaf litter cover was inversely related to moss growth and segment production over the course of the experiment (Table 2, Figure 3). Our results do not support findings of others that intermediate leaf litter inputs may stimulate *H. splendens* growth due to leaves leaching sugars and nutrients (Sveinbjornsson and Oechel 1992). Annual inputs of leaf litter in boreal birch stands (224.8 g dry leaf litter m^{-2} $year^{-1}$) were much higher than in the subarctic forest of Scandinavia (75 g m^{-2} $year^{-1}$), where positive impacts of deciduous leaf litter on moss-associated N_2 fixation have been reported (Sorensen and Michelsen 2011). Evidence from our experiment and the literature suggest that, even if feather mosses are shade-tolerant species (Sulyma and Coxson 2001), the addition of a continuous layer of broadleaf deciduous leaf litter may inhibit their photosynthesis and growth (Startsev and others 2008). Declines in moss greenness observed in our experiment (Jean 2017), along with low moss growth in the leaf litter addition treatments indicated that the long-term effects of leaf litter cover may lead to moss mortality. Leaf litter also affected moss growth form (Table 3), resource allocation, and reproductive effort (Figure 5). Investments in sexual reproduction through sporophyte production were almost eliminated with high litter inputs. Moreover, mosses covered by leaf litter either produced fewer segments or linear segments with no side branches (''online resources Appendix 3''), a morphological response that was also observed by Startsev and others (2008). Therefore, our results support that deciduous broadleaf litter is a key mechanism driving differences in moss growth and abundance among deciduous and coniferous stands.

Overall, mosses grew slightly better in spruce stands, being 1.2 times larger in the controls at the end of the experiment and having produced more biomass (7.5 mg) and segments (0.5 segment) than in birch stands (Figure 2, Tables 1 and 2). Differences in moss shoot density among stands types was not mirrored by patterns of growth rates of moss (Table 4; Figure 2), suggesting that factors other than shoot density were driving the observed differences. At our study sites, spruce stands had higher soil moisture and lower pH compared to birch stands (Melvin and others 2015), which are environmental conditions likely to favor moss growth (Busby and others 1978; Sveinbjornsson and Oechel 1992). In addition, the established moss carpet in spruce stands provides more hydraulic conductivity to support further development of the moss layer and acclimation of moss transplants. Canopy cover had no effect on moss growth, possibly because higher canopy cover could have different impacts in each forest type. For example, in spruce stands, a denser canopy may protect mosses from heat and desiccation, while more shaded conditions in birch stands are likely to increase local broadleaf litter fall. In the absence of leaf litter on the transplants (our exclusion treatment), there was high variability in moss growth, which suggests that other environmental variables also play a role in driving moss growth patterns.

We observed stand-level differences in moss phenotypes between forest types. First, mosses tended to produce more sporophytes in spruce than in birch stands, which may be due to better environmental conditions and higher light availability (Rydgren and Økland 2002a, 2002b), a segment size threshold (Rydgren and others 1998), higher moss density increasing the chance for fertilization (Rydgren and Økland 2001), or genetic differences between populations (Cronberg 2002). Production of sporophytes on mature segments was higher

(6.1% of shoots in spruce stands) than previously reported in Scandinavia: 0.05% in Økland (1995) and 2.8% in Callaghan and others (1978). Unlike Norwegian forests (Økland 1995), the production of more than one growing point in 1 year in the branching cycle of *H. splendens* was relatively common at our Alaska study site.

Feather mosses are important components of the carbon cycle in boreal ecosystems, as they produce large amounts of biomass and recalcitrant litter that builds soil organic layers and contribute up to 80% of C stored in boreal soils (Flanagan and Van Cleve 1983; Apps and others 1993; Kolari and others 2006). The productivity of *H. splendens* was low in birch stands, while it was a significant contributor to stand productivity in black spruce stands (Table 4), which is similar to other estimates from boreal Alaska and Canada (Lindo and others 2013). The difference among stands was mostly due to the high *H. splendens* cover (and therefore shoot density) in spruce stands. Experimental and ambient birch litter inputs decreased moss annual productivity by more than 50%, suggesting that broadleaf litter has a strong impact on the contribution of mosses to ANPP and C storage. Complementary studies that investigate the mechanisms of leaf litter impacts on moss growth as well as effects of length of the growing season, light, moisture, or biotic interactions will improve estimates of moss productivity across the range of feather moss distribution in the boreal forest.

CONCLUSION

This study provides some of the first experimental evidence that multi-year deposition of broadleaf litter reduces feather moss productivity, thus supporting the hypothesis that plant–soil feedbacks mediated by canopy composition effects on moss may stabilize alternative forest types in interior Alaska (Johnstone and others 2010a). Interactions among canopy composition, broadleaf deciduous leaf litter, and moss growth exert a dominant control on differences in feather moss abundance between broadleaf deciduous and coniferous forests. In both black spruce and paper birch stands, we observed significant declines in the growth, health and architecture of mature shoots of *H. splendens* within 3 years of broadleaf litter deposition. Production of large amounts of broadleaf litter in deciduous stands had a large detrimental impact on feather moss and in the absence of leaf litter, mosses tended to grow slightly better in spruce than in birch stands. If future increases in fire severity lead to an increase in broadleaf cover on the landscape (Mann and others 2012), we expect this to dramatically decrease moss growth due to increased broadleaf litter production. Once deciduous broadleaf stands establish, leaf litter inputs are likely to prevent a return to stands dominated by feather mosses under a spruce canopy.

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