

The Roles of the Moss Layer in Mediating Tree Seedling Environmental Stress, Mercury Exposure, and Regeneration in High-Elevation Conifer Forests

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ABSTRACT

The persistence of future forests depends on the success of tree seedlings which are experiencing increasing physiological stress from changing climate and air pollution. Although the moss layer can serve as an important substrate for tree seedlings, its potential for reducing environmental stress and enhancing the establishment of seedlings remains poorly understood. We tested if the moss layer decreased environmental stress and increased the abundance of balsam fir seedlings dominant in high-elevation forests of northeastern United States that are sensitive to changing climate and mercury deposition. We surveyed balsam fir seedling density by substrate (moss, litter, other) on 120 quadrats

(1 × 1 m) in two contrasting canopy environments (in gaps and under canopies), measured seedling stress, and quantified mercury content in seedlings and substrates. We observed that, in both canopy environments, tree seedlings established on moss exhibited (i) increased density, (ii) decreased physiological stress, and (iii) higher potential to recruit into larger size classes, compared to seedlings established in litter. Regardless of canopy environment, seedling foliar mercury levels did not correspond to substrate mercury despite large differences in substrate mercury concentrations (relative to moss, litter concentrations were ~ 4-times greater and soil concentrations were ~ 6-times greater), likely reflecting the dominance of foliar over root uptake of mercury. Because the moss layer appeared to mitigate seedling drought stress, and to increase seedling establishment and recruitment compared to other substrates, these microsite effects should be considered in models predicting forest regeneration and dynamics under increased drought stress associated with the ongoing climate warming.

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MB conceived the research, collected and processed the data, performed statistical analyses, and led the writing of the manuscript; MD provided critical feedback on the research design and data analysis, and participated in writing; RK and CD provided advice on data collection and analysis, and critical help reviewing the manuscript.

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Key words: tree seedling establishment; drought stress; mercury exposure; montane forests; seedling substrates; seedling bank; moss layer; balsam fir (*Abies balsamea*).

HIGHLIGHTS

- The moss layer is a common substrate for tree seedlings in montane conifer forests.
- The moss layer supported greater seedling density than other substrates.
- By enhancing seedling recruitment, the moss layer has a key role in forest dynamics.

INTRODUCTION

Climate warming and pollution are two pervasive components of global environmental change and human-induced environmental stress (*sensu* Vitousek 1994; Dietz and others 2017) and montane forest ecosystems are particularly sensitive to both climate change and air pollution. Climate warming tends to shift species climatic envelopes upslope (for example, Wason and others 2017a), whereas the deposition of atmospheric pollutants can undermine plant physiology (Driscoll and others 2001) and contaminate forests with pollutants such as mercury (Driscoll and others 2007). Although canopy trees have been shown to be sensitive to both climate and air pollution (for example, acidic deposition; Wason and others 2019), tree seedling responses to these interacting global change drivers are often less clear despite the key role that tree seedlings play in forest dynamics (Clark and others 1999; Fisichelli and others 2013).

Due to their small stature and shallow roots, tree seedlings are susceptible to climate warming at fine spatial scales related to heterogeneous microsite conditions that affect their light, water, and nutrient availability. For instance, increasing temperatures cause greater heat and drought stress that can vary with canopy openness and substrate type, locally hampering tree seedling establishment (Castro and others 2004; Tourville and others 2022). Similarly, atmospheric deposition and accumulation of pollutants, such as mercury, also varies at fine spatial scales as it is affected by both forests structure (Blackwell and Driscoll 2014, 2015) and substrate type (compare Pahlsson 1989). Thus, fine scale microsite conditions affect seedling growth and survival, and thus ultimately tree seedling

distributions on the forest floor (Dovčiak and others 2003; Mori and others 2004; Bače and others 2012). However, various microsite conditions such as substrate type and canopy openness often covary in complex ways (Jonsson and others 2015; Berdugo and Dovciak 2019), underscoring the importance of better understanding how fine-scale processes may affect responses of tree seedling banks to global environmental change (Fisichelli and others 2014).

Due to the complexity of integrating fine and broad spatial-temporal scales in ecosystem processes (Carpenter and Turner 2000), most studies investigating the effects of global environmental change in forest regeneration tend to consider broader-scale factors (Petrie and others 2016 and references therein; Maréchaux and others 2021) and while often neglecting microsite variables such as substrate type (McCarthy 2001). Compared to much better studied fine-scale effects of forest gaps on light, microclimate, nutrient cycling, microclimate, and forest regeneration (for example, Sprugel 1976; Prescott 2002; Abd Latif and Blackburn 2010; Muscolo and others 2014), the effects of substrate type on tree seedlings are less well understood. Yet, substrate can influence moisture and nutrient availability (Oleskog and Sahlén 2000; Mori and others 2004), exposure to pollutants (Delach and Kimmerer 2002), and ultimately tree seedling survivorship (Cornett and others 1998; Mori and others 2004) and abundance (Simard and others 1998; Mori and others 2004).

The forest-floor moss layer has been posited as a substrate which facilitates forest regeneration (Simard and others 1998; Wright and others 1998; Dovčiak and others 2003) by enhancing seedling establishment via increased water holding capacity and improved seedling nutrition and hydration (Lett and others 2017). However, the effects of moss on seedlings can be complex and species-dependent (for example, Soudzilovskaia and others 2011; Lett and others 2017) both, in terms of moss and seedling species. Yet, most models of forest dynamics fail to consider the role of the moss layer in shaping the composition and abundance of tree seedling banks (compare Pacala and others 1993; Clark and others 1999; Maréchaux and others 2021). Given the ability of mosses to store moisture (Lett and others 2017), better understanding of their roles in forest regeneration is needed particularly under globally increasing heat and drought stress (Will and others 2013).

Mercury is a potent, highly toxic global pollutant with considerable mobility among environmental compartments (for example, soil, vegetation,

wildlife; Sauer and others 2020) and a long atmospheric lifetime (Chen and Driscoll 2018; Driscoll and others 2013, 2007). Airborne mercury released from several anthropogenic activities is the main source of this pollutant globally (Driscoll and others 2007). In forest ecosystems, interacting environmental factors such as soil pH, microbial community, and climate influence plant uptake of trace metals (Påhlsson 1989), but empirical data on mercury uptake by tree seedlings in natural settings are scarce (Godbold 1991). Yet, mercury has been shown to accumulate over time in forests due to a local cycle through trees and their litter (Blackwell and others 2014; Jiskra and others 2018; Yanai and others 2020; Zhou and others 2021). In forested watersheds, mercury moves through trophic webs to bioaccumulate in wildlife (Sauer and others 2020). The moss layer can trap airborne particles, including plant nutrients (for example, Lindo and Gonzalez 2010) and trace metals (Schröder and Pesch 2010; Zhou and others 2017). Interestingly, it has been reported that moss can reduce mercury accumulation in forest fungal fruiting bodies at the microsite scale (Nasr and Arp 2011), suggesting that mossy microsites may limit seedling exposure to mercury by controlling mercury evasion from forest soils (Yang and others 2019). The role of the moss layer in mercury uptake by tree seedlings in natural settings, to our knowledge, has not been investigated (but see Nyman and Lindau 2016).

To improve the understanding of the complex effects of the moss layer on forest regeneration under changing environmental conditions, we studied moss-tree seedling interactions in high-elevation balsam fir (*Abies balsamea* (L.) Mill.) dominated forests in northeastern United States that are particularly sensitive to both changing climate (Wason and others 2017a) and deposition of mercury (Gerson and others 2017). Importantly, these high-elevation forests are characterized by fir wave regeneration dynamics that consist of alternating contrasting canopy environments—elongated gaps and closed canopies (fir waves)—formed by wind and ice abrasion in mountains in northeastern United States and around the world (Bekker and Malanson 2008; Sprugel 1976). These distinct canopy environments interact with both atmospheric deposition of mercury (higher under forest canopies where litter with mercury accumulates; Hanson and others 1995; Blackwell and others 2014) and climate-change-induced heat and drought stress (higher in gaps where solar radiation is higher; Will and others 2013). Thus, these high-elevation forests provide a ‘natural experiment’ (with two treatments: gap and closed canopy) that

allow investigation of how fine-scale (microsite) variation in canopy conditions and substrate may interact with broad-scale factors such as climate and atmospheric pollution to affect forest regeneration, tree population dynamics (demography) and regional forest composition (landscape demography; Gurevitch and others 2016).

To elucidate the role of the moss layer in the dynamics of high-elevation balsam fir forests, we tested four hypotheses across the two contrasting canopy environments (gaps, closed canopies) defining this balsam fir-dominated forest: Seedling density (H1) and seedling recruitment rates into taller seedling size class (H2) are higher on moss than on other substrates; and seedlings established on the moss layer experience less instant physiological stress (H3) and less exposure to mercury (H4) than seedlings on other substrates. We anticipate that the moss layer, with similar thickness and species composition in both canopy environments (Berdugo and Dovciak 2019), favors seedling establishment by creating microsites that mitigate seedling stress and reduce mercury exposure compared to other dominant substrates (leaf litter). We also expect differences in the size of the moss-effect between closed canopies and forest gaps as a warmer microclimate in forest gaps (Berdugo and Dovciak 2019) suggests a more stressful environment for seedlings.

METHODS

Study Area

This study was conducted in the high elevation fir-dominated forests on Whiteface Mountain (44.22° N and 73.54° W) in northeastern United States. Details of the study area were previously described in Berdugo and Dovciak (2019) and elsewhere (for example, Battles and others 2003; Wason and others 2017b, 2021). Briefly, Whiteface Mountain is an isolated massif with the summit at 1,485 m above sea level (asl) and well-developed elevational climatic and vegetation zones whose ecology has been extensively studied over the past half century (for example, Sprugel 1976; Battles and others 2003; Aleksic and others 2009; Wason and others 2017b). The vegetation of the area belongs to the Adirondack-New England Highlands ecosystem province (Bailey 2014) and is representative of regional forest communities with northern hardwood forests occurring below ~ 800 m asl, spruce-fir forests between ~ 800 and ~ 1300 m asl, and alpine communities above ~ 1350 m asl (Battles and others 2003). Balsam fir (*Abies bal-*

Table 1. Climate Records for the Fir Wave Zone on Whiteface Mountain

Climate parameter	Observed value and unit	Elevation (m)	Measurement period	Source
Mean annual precipitation	1560 mm	1050	1986–1996	Friedland and Miller (1999)
Mean annual air temperature	8 °C	1095	2001–2002	Richardson and others (2004)
Mean air temperature of the warmest month	13 (Jul.) °C	1095	2001–2002	Richardson and others (2004)
Mean air temperature of the coldest month	– 9 (Feb.) °C	1095	2001–2002	Richardson and others (2004)
Soil mean annual temperature [†]	8 °C	1095	2001–2002	Richardson and others (2004)
Growing season mean air temperature*	13.84 ± 0.12 °C	1198–1276	2014	Berdugo and Dovciak (2019)
Growing season mean RH*	90.42 ± 0.70%	1198–1276	2014	Berdugo and Dovciak (2019)
Growing season mean VPD*	– 0.21 ± 0.02 Pa	1198–1276	2014	Berdugo and Dovciak (2019)

[†]Recorded at 15 cm depth.

*Recorded at 30 cm above the ground surface during the growing season (May–Sept.). RH relative humidity, VPD vapor pressure deficit.

samea (L.) Mill.) is a dominant tree species between ~ 1100 and ~ 1250 m asl where recurring linear openings in the forest canopy, known as fir waves, facilitate fir regeneration (Sprugel 1976; Silvertown and Dodd 1999). Soils in the area are mainly Histosols derived from the accumulation of organic material due to slow decomposition and slow weathering of anorthosite (Witty and Arnold 1970; Sprugel 1976).

The character of the moss layer in high-elevation fir forests of Whiteface Mtn. is relatively unresponsive to the microclimatic and other environmental changes caused by gaps dynamics (Berdugo and Dovciak 2019). Moss layer here typically covers 57.5 ± 2.2% of the forest floor surface, it is about 2.5 cm thick, and it tends to contain ca. 5 species per square meter both in gaps and under closed canopies (Berdugo and Dovciak 2019). Notwithstanding, two aspects of the moss layer differed between canopy environments: *Dicranum fuscescens* Turner, *Hypnum imponens* Hedw., and *Tetraphis pellucida* Hedw. are more abundant under closed canopies than in gaps, making these moss species indicator species for closed canopies in the area; and functional dispersion (derived from growth form and the Ellenberg indicator values for soil fertility and acidity) is higher under closed canopies than in gaps (Berdugo and Dovciak 2019). While the moss layer in the study area includes up to 25 bryophyte species (Table S2.2 in Berdugo and Dovciak 2019), those identified as seedling sub-

strates in the current study corresponded to the liverwort *Lophozia ventricosa* (Dicks.) Dumort. and four mosses, *D. fuscescens*, *H. imponens*, *Pleurozium schreberi* (Brid.) Mitt., and *Polytrichastrum alpinum* (Hedw.) G. L. Sm. In all our observations, mats of *H. imponens* held sparse fertile shoots of *Pohlia nutans* (Hedw.) Lindb.

Climate on Whiteface Mountain has been characterized in several studies (Table 1) and it can be considered a high-elevation form of a modified continental climate (McNab and others 2007) experiencing the warming climate trend typical of the northeastern United States (Huntington and others 2009; Wason and others 2017a). The climate records specific for the fir wave zone (1100–1250 m asl) are rather sporadic compared to those at the summit (1485 m asl) and the shoulder (~ 600 m asl) of the mountain where climate stations are located (Schwab and others 2015). The weather on Whiteface Mountain during the study period (in September 2015, see “Study design and field data collection”) was mild, but the month was considerably drier in 2015 (48.0 mm of precipitation) than long-term average (93.6 mm, mean September precipitation for 1985–2019 period) (National Atmospheric Deposition Program 2020).

Study Design and Field Data Collection

To assess the relevance of the moss layer for forest regeneration, we selected a total of 40 study plots

using a stratified sampling design with two strata (forest gaps, closed canopy) that represented the two typical canopy environments in these high elevation forests (fir waves; Sprugel 1976). We selected 20 fir waves and placed one plot in each canopy gap and another plot under the forest canopy nearby (on average within 50.2 ± 3.9 m, mean \pm SE, from the closest gap). Each plot consisted of three 1-m² survey quadrats placed along a transect in the gap center and parallel to the gap length; minimum spacing between survey quadrats was 5.6 m. Transect lengths varied between *ca.* 14 m and 25 m long, depending on the gap length while transects under forest canopy were consistently 25 m long. The total number of surveyed quadrats was 120 (3 quadrats \times 40 plots).

Seedling Bank Surveys

We characterized tree seedling abundance and composition on all quadrats in 2014 (May–September) by counting the number of tree seedlings (≥ 5 and ≤ 25 cm tall) by species, height class, and substrate. Based on specific aging methods developed to describe the seedling bank structure of balsam fir (Parent and others 2003), this height range likely captures about 98% of balsam fir seedling bank, composed of seedlings recruited in, at least, the previous 10 years. Balsam fir also dominated the seedling bank as it was found in all plots and represented about 95% of all surveyed seedlings. The remaining 5% of tree seedlings was split among other four species (*Picea rubens* Sarg., *Betula papyrifera* var. *cordifolia* (Regel) Regel, *B. alleghaniensis* Britton, and *Populus tremuloides* Michx.) that were present on less than half of the plots. Seedlings were divided into two height classes: small (≥ 5 and ≤ 10 cm tall) and large (> 10 and ≤ 25 cm tall). Seedling substrate, characterized as moss, litter, and other (decaying logs, bare soil, peat, and rocks), were sampled to a depth ≤ 5 cm to collect the substrate under the moss layer (with thickness of 2.5 ± 0.3 cm, mean \pm SE; Berdugo and Dovciak 2019) while accommodating the generally shallow soil depth (< 10 cm deep; Gerson and others 2017). The two most common seedling substrates were moss and litter (Figure S1).

Microsite Characteristics

In addition to seedling substrate (see above), other environmental characteristics potentially affecting tree seedlings were also measured on all quadrats. Canopy cover (%) was measured with a concave spherical densiometer (Forestry Supplies Inc.,

Jackson, Mississippi, USA) at 50 cm above the ground. Despite lower accuracy under closed canopies, densiometer measurements of canopy cover (or openness) were shown to provide satisfactory contrast between closed forest canopies and open canopies such as those in forest gaps (Rus-savage and others 2021). We also measured tree stem (≥ 2 m tall) density and height by species, density of standing dead trees, tree diameter at the breast height (DBH) by species, and the density of balsam fir saplings (individuals > 25 cm but < 2 m tall). We estimated the cover (%) of understory vegetation, coarse woody debris (CWD; the largest diameter > 5 cm), and fine woody debris (FWD; the largest diameter < 5 cm) within < 30 cm height from the ground surface. We also estimated the overall cover (%) for seedling substrates for each quadrat (substrate details are given in Sect. “Seedling Bank Surveys” above). Balsam fir does not build persistent seed banks (Houle 1992), but its seedling banks can instead stagnate under closed canopies and rapidly grow under canopy gaps (Sprugel 1976; Parent and others 2000; Parent and others 2001; Parent and others 2003). Given these dynamics, most years do not seem to have a strong effect on the structure of fir seedling banks (Parent and others 2003).

Seedling Physiological Stress

To estimate the instantaneous physiological stress that seedlings experienced in the two main substrates (moss, litter) under both canopy environments (closed canopies, gaps), we contrasted the efficiency of heat dissipation (non-photochemical quenching—NPQ, Maxwell and Johnson 2000) in seedling needles. We calculated NPQ for a subsample of 186 seedlings from the seedling bank survey to achieve comparable seedling numbers on the two dominant substrates (95 on moss, 91 on litter) and in the two canopy environments (98 under forest canopy, 88 in gaps) by selecting the most accessible ten study plots (five under the canopy, five in gaps) among the selected fir waves (see Sect. “Study Design and Field Data Collection”).

The efficiency of heat dissipation, NPQ, is calculated from non-invasive fluorescence measurements relative to dark-adapted conditions (Murchie and Lawson 2013). Therefore, we recorded chlorophyll fluorescence on seedling needles in both dark and light conditions. Dark-adapted seedling needles (Figure S2a) were excited with a pulse of 100 steps, each lasting 1.8 μ s, of an intense saturating light (20,000 μ mol m⁻² s⁻¹) and light-

adapted seedling needles (Figure S2b) were excited with this light pulse while recording ambient photosynthetically active radiation (PAR; measured in $\mu\text{mol m}^{-2} \text{s}^{-1}$). Using the Pulse Modulated Chlorophyll Fluorometer Model FMS2 (Hansatech Instruments Ltd, Northfork, United Kingdom), we completed these instantaneous measurements before noon between September 7 and 11, 2015.

NPQ was calculated as $(F_m - F'_m)/F'_m$ in light-adapted samples, where F'_m is the maximum fluorescence yield in light-adapted conditions and F_m is the maximum fluorescence yield in dark-adapted conditions (Murchie and Lawson 2013). We used a single F_m value for seedlings in equivalent conditions (substrate, canopy environment) by averaging the measurements. Long-term seedling stress was avoided by targeting only healthy seedlings and was verified with a ratio between variable and maximum fluorescence (F_v/F_m) in dark-adapted needles > 0.8 (Maxwell and Johnson 2000; Murchie and Lawson 2013) as the average F_v/F_m of dark-adapted needles of seedling established in both substrates and in both environments ($n = 74$) was 0.84 ± 0.05 (mean \pm SD). Ruling out long-term seedling stress allows us to assume that differences in efficiency of heat dissipation (NPQ) may result from short-term stress drivers (Murchie and Lawson 2013), such as climate.

Climatic Stressors

To identify potentially climatically stressful conditions for tree seedlings, we monitored instantaneous microclimate during the time when seedling instantaneous physiological stress (chlorophyll fluorescence) was measured (that is, September 7–11, 2015). Air temperature (T) and relative humidity (RH) were measured using iButton data loggers (Model DS1923; Maxim Integrated Products, Inc., Sunnyvale, California) on each plot every 15 min with 0.5 °C resolution for temperature and 0.6% for relative humidity. Each iButton was placed at 30 cm above the ground within a hand-made gill shield (~ 12 cm height \times 9 cm diameter) to measure ambient microclimate (T , RH) while shielding the sensor against solar radiation and allowing for adequate ventilation (Tarara and Hoheisel 2007).

Exposure to Mercury

We quantified total mercury in seedling needles and dominant substrates (moss, litter) on the plots used for monitoring seedling instantaneous physiological stress (see above). Assuming mercury accumulation in conifer needles overtime (Black-

well and others 2014) by quantifying total mercury, we indirectly measured seedling exposure to mercury (Parent and others 2003). We selected 53 seedlings using stratified random sampling to represent the combinations of substrate (litter, moss) and canopy environment (forest canopy, gap) and collected samples of both seedling needles and associated substrates (both surface and subsurface). Sample collection followed the protocol for environmental sampling of low-level trace metals (EPA Method 1669; US EPA 1995) adapted for solid samples. Briefly, a two-member team wearing clean nitrile gloves split sampling tasks. “Clean hands” only handled the plastic bag containing the final sample. “Dirty hands” prepared sample containers, collected samples by operating pruning scissors and a soil sampling tube, cleaned these tools by rinsing them with trace metal grade HCl, and handled secondary container bags and shipping containers. All needles were collected from each seedling along with the associated seedling substrate(s). A substrate sample was collected when a single substrate was present within the 5 cm depth from the surface. Another separate substrate sample was collected if a different substrate was present within 5 cm of the substrate surface (that is, subsurface substrate included moss, litter, or soil A horizon; Fig. S1). Seedling roots and substrate sections contaminated by the adjacent substrates were discarded. Thus, a total of 125 samples were collected and transported on ice to the Center for Environmental Systems Engineering (CESE) at Syracuse University where they were kept frozen until processed. Samples were freeze-dried to a constant weight and hand homogenized to a fine powder (any twigs, stems, or rocks were removed from the samples). Homogenized samples were analyzed for total mercury concentration following the EPA Method 7473 (US EPA 2007) with an Advance Mercury Analyzer AMA 254 (Leco Corporation, Saint Joseph, Michigan); details on quality control according to the EPA Method 7473 (US EPA 2007) are described in Appendix S1 in supporting information.

Data Analyses and Hypothesis Testing

To test our hypothesis H1, whether the moss layer had a positive effect on tree seedling density, we used a multivariate approach by fitting generalized linear models (GLM). We modeled maximum count of fir seedlings per square meter for two seedling height classes, small (≥ 5 and ≤ 10 cm tall) and large (> 10 cm and ≤ 25 cm tall) at the plot level ($n = 40$) with a Poisson error distribution

and 'log' link function. These two height classes allowed us to target seedlings established in, at least, the last decade (Parent and others 2003). The full model predictor set included the percentage moss cover, four uncorrelated forest structural metrics ($P > 0.05$ and $\rho < 0.300$; see Appendix S2)—canopy openness, fir sapling density, fir tree density, and density of other tree species—and the interaction between the moss cover and canopy openness. Because the forest structural metrics accounted for the structural differences among the plots, neither random nor categorical effects by canopy environment (that is, gap vs. canopy) were included in the model; consistently including plot as a random effect did not change the model selection. We did not include the cover of litter (the other dominant substrate) in the model to avoid collinearity since moss and litter covers were highly and negatively correlated (Pearson correlation coefficient = -0.538 , $P < 0.001$). We fitted all possible models and the best model was selected using delta AIC corrected for small sample size (ΔAICc ; Anderson and Burnham 2002); models within $\Delta\text{AICc} < 2$ were considered equivalent.

To test our hypothesis H2, whether the moss layer had positive effects on seedling recruitment into the larger size class, we calculated an index of seedling recruitment potential. The index was calculated as a demographic ratio between large (> 10 and ≤ 25 cm tall) and small seedlings (≥ 5 and ≤ 10 cm tall) for those quadrats where both seedling height classes were present, that is, recruitment potential was calculated for 54 of the 120 sampling quadrats. The differences in seedling recruitment potential between the two dominant substrates were analyzed with the Kruskal–Wallis tests as data did not follow a normal distribution.

To test our hypothesis H3, whether tree seedling stress varied by substrate, we performed several comparisons. We assessed the difference of the instant desiccation potential of the air between canopy environments, the difference of instant physiological stress of seedling between substrates within each canopy environment, and the interaction between substrate and canopy environment on the instant physiological stress. Instant microclimate and instant physiological stress, synchronized by their time record, were positively correlated (Pearson's correlation coefficient between instant air desiccation potential—VPD—and efficiency of heat dissipation—NPQ: $\rho = 0.21$, $P < 0.001$, $n = 186$). Field measurements of temperature (T) and relative humidity (RH) were combined to calculate instant vapor pressure deficit (VPD), a measure of the desiccation potential (Will

and others 2013). VPD was calculated as the difference between saturation vapor pressure (SVP) and actual vapor pressure (AVP) at a given temperature following Ward and Trimble (2003), where $\text{SVP} = \exp(16.78 \times T - 116.9) / T + 237.3$, and $\text{AVP} = \text{SVP} \times RH/100$. Seedling physiological stress was estimated as non-photochemical quenching (NPQ, see Sect. "Seedling Physiological Stress"). Because NPQ data were non-normal (Shapiro–Wilk: $W = 0.40$, $P < 0.001$) and variance homogeneity was not met for either substrate (Bartlett: $\chi^2_{(1)} = 112.9$, $P < 0.001$) or canopy environment (Bartlett: $\chi^2_{(1)} = 11.2$, $P < 0.001$), we used nonparametric Kruskal–Wallis test followed by Friedman test (Friedman 1937) for the interaction between substrate and canopy environment.

Finally, to assess whether exposure to mercury differs between seedling substrates (H4), we tested the differences in total mercury concentrations (THg) both in (i) seedling needles (by substrate and canopy environment) and (ii) among the sampled substrates (moss, litter, and soil by canopy environment). Unlike instant physiological stress, exposure to mercury is cumulative as mercury concentration in plant tissues increases over time (Driscoll and others 2013). Samples from quadrats were averaged at the plot level for each sample type (seedling needles, moss, litter, and soil). Because seedling total mercury concentrations met the assumptions of normality (Shapiro–Wilk: $W = 0.92$; $P = 0.150$) and variance homogeneity (between substrates, Bartlett: $\chi^2_{(1)} = 0.00$; $P = 0.958$; and between environments Bartlett: $\chi^2_{(1)} = 0.43$, $P = 0.512$), we used two-way ANOVA to test whether tree seedling total mercury differed by substrate in the forest as a whole and between canopy environments, while considering also the interaction between substrate and canopy environment. Finally, we tested for the differences in total mercury among seedling substrates using a Kruskal–Wallis test since substrate total mercury concentrations were not normally distributed (Shapiro–Wilk: $W = 0.90$; $P = 0.01$) and their variances were not homogeneous ($\chi^2_{(1)} = 12.03$, $P = 0.003$). We evaluated the main effect of canopy environment on the total mercury concentration in each substrate using one-way ANOVA since the data for each substrate separately complied with normality (Shapiro–Wilk: $W < 0.93$; $P > 0.05$).

All analyses were performed in R (R Core Team 2018) with the 'stats' package as well as with additional specific packages; 'lme4' (Bates and others 2015), 'MuMIn' (Barton 2020), and 'arm' (Gelman and Su 2020) for model fit and selection.

RESULTS

We found support for hypothesis H1 as the density of small fir seedlings (5–10 cm tall) established on moss was 5.01 ± 1.19 (mean \pm SE, stems per m²) compared to 3.06 ± 0.85 for small seedlings on litter (regardless of the canopy environment). The density of large fir seedlings (10–25 cm tall) was one order of magnitude lower than the density of small fir seedlings (0.72 ± 0.18 on moss; and 0.17 ± 0.07 on litter). The density of these seedling height classes differed between canopy environments, with overall higher density of small fir seedlings under closed forest canopy (3.34 ± 0.72) than in gaps (2.06 ± 0.75) ($\chi^2_{(1, N=120)} = 7.91, P < 0.01$), and an opposite pattern of higher density of large fir seedlings under canopy gaps (0.53 ± 0.13) than under closed canopies (0.09 ± 0.03) ($\chi^2_{(1, N=120)} = 8.28, P < 0.01$). The moss layer and closed forest canopy had positive effects on early seedling establishment as the density of small seedlings was related positively to the moss cover and negatively to canopy openness (Figure 1a). In contrast, the density of large seedlings was strongly positively related to canopy openness and unrelated to the moss cover, indicating greater seedling recruitment to the larger height class in canopy gaps (Figure 1b) where the density of large seedlings was positively related to the density of fir saplings and other tree species (Figure 1b). The interaction between canopy openness and moss cover affected only the density of small seedlings which decreased under open canopies (Figure 1ab).

Our hypothesis H2 that moss layer increases seedling recruitment was supported under the

forest canopy but not in canopy gaps (Figure 2ab). Recruitment potential was an order of magnitude greater in canopy gaps than under forest canopy

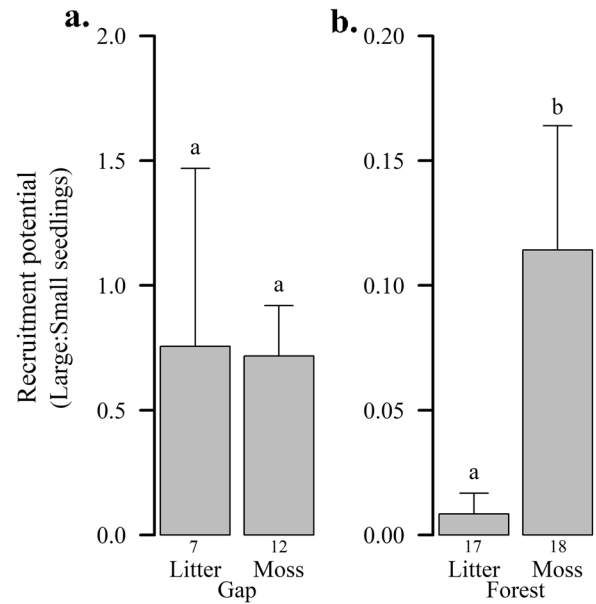


Figure 2. Recruitment potential of fir seedlings established on litter and moss under two canopy environments, gap (a) and forest canopy (b) in high-elevation fir-dominated forests on Whiteface Mountain in the northeastern United States. Recruitment potential was calculated as the number of large seedlings (> 10 and ≤ 25 cm) divided by the number of small seedlings (≥ 5 and ≤ 10 cm); different letters indicate statistically different means; error bars indicate 1 SE; bars indicate mean values; the number of replicates, underneath each bar, varied due to removing plots with missing one of the size-classes (see Sect. “Data Analyses and Hypothesis Testing”). Note that y-axes vary in scale among the plots.

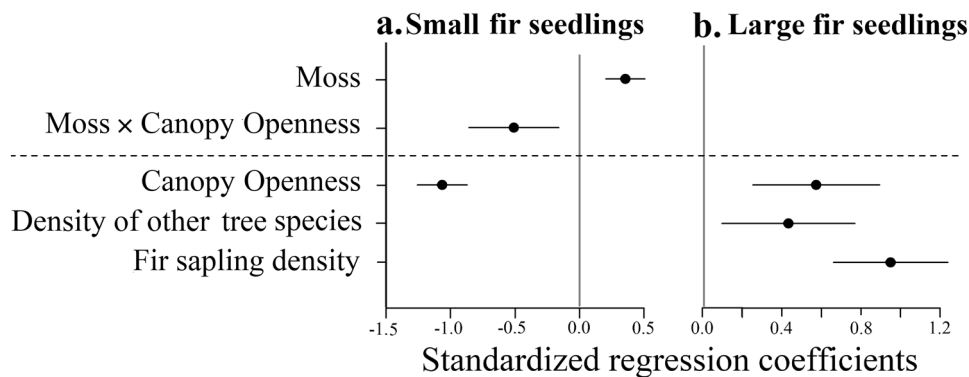


Figure 1. Standardized coefficients of the best models fitted to test the effect of the moss substrate (above the dashed line) and forest structure (below the dashed line) on the maximum abundance of tree seedlings in the high-elevation fir-dominated forests on Whiteface Mountain in the northeastern United States. The density for small (≥ 5 and ≤ 10 cm, a) and large (> 10 and ≤ 25 cm, b) seedlings was modeled using GLMs. Error bars show 95% CI of the coefficient estimates. Model intercept estimates are not shown for brevity. Fir saplings = individuals > 50 cm and < 2 m tall. Appendix S3 in supporting information provides additional details on the GLM models and statistics.

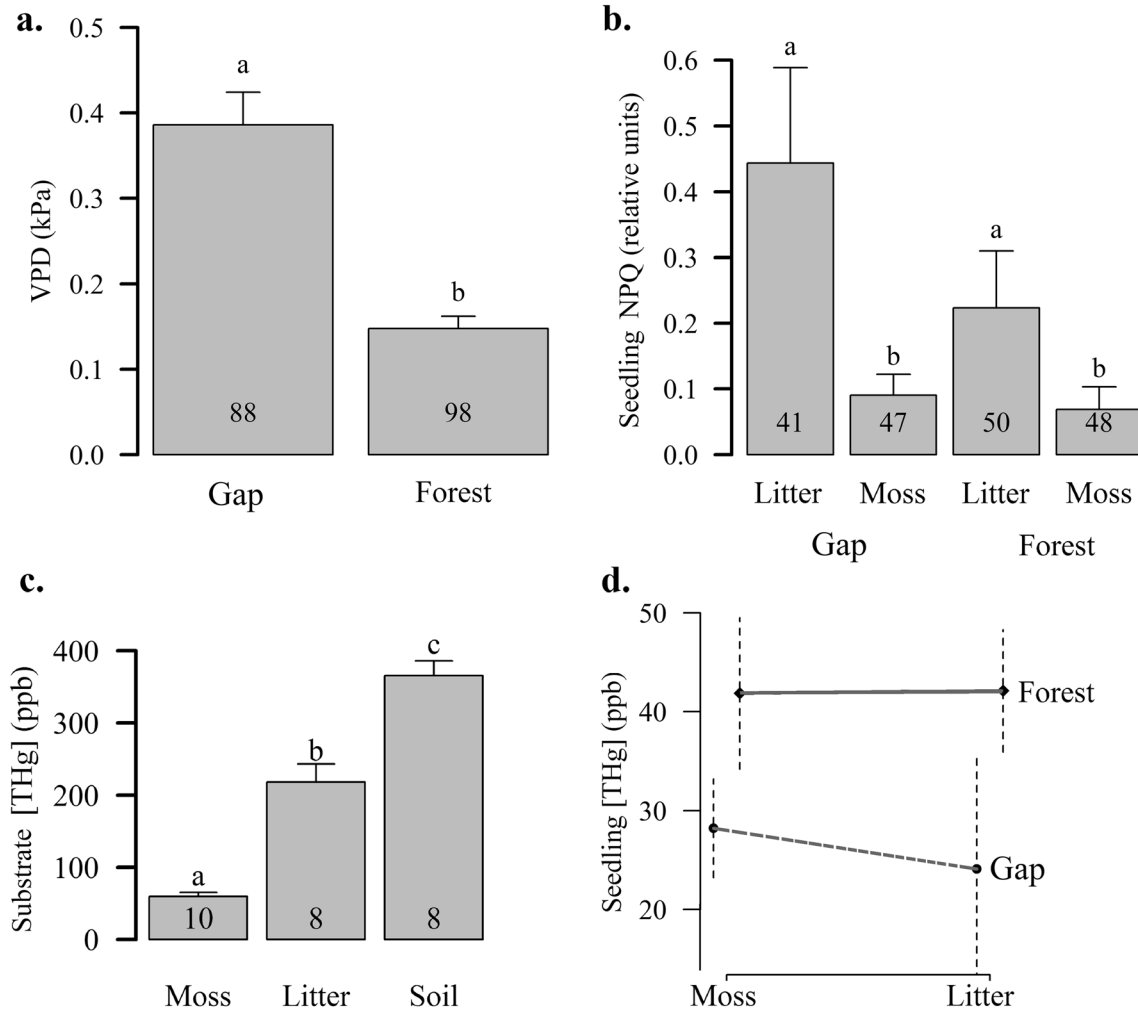


Figure 3. Environmental and physiological stress caused by climate, vapor pressure deficit, (a and b) and pollution, mercury, (c and d) of fir seedlings ≤ 25 cm tall in the high-elevation forests on Whiteface Mountain in the northeastern United States. VPD = Vapor pressure deficit. NPQ = Non-photochemical quenching (a measure of plant physiological stress). Seedlings mercury exposure was estimated as mercury concentrations in their surface (moss, litter) and subsurface (moss, litter, and soil) substrates (c). The chronic stress by mercury was measured as mercury concentrations in seedling needles (d). In (a) and (b), the numbers within each bar indicate the number of seedlings for which physiological stress was assessed. Because THg of seedling substrate was aggregated at the plot level, numbers within each bar in (c) indicate the number of plots where those substrates were collected. In (c) and (d), THg = Total mercury concentration. Bars indicate mean values; error bars indicate 1 SE; different letters indicate statistically different means; numbers within each bar indicate the number of replicate measurements used to calculate mean values. Higher values of VPD and NPQ indicate higher desiccation potential and higher physiological stress, respectively.

(Figure 2ab), corroborating the idea of increased recruitment in canopy gaps. However, the recruitment potential in gaps is similar between the two dominant substrates, moss layer and litter (Figure 2a). In contrast, recruitment potential under the forest canopy was much higher for seedlings established on moss than for seedlings established on litter, although still lower than recruitment potential in gaps (Figure 2b).

Seedling established on the moss layer experienced less instant physiological stress than those

established on litter (H3). Interestingly, although instant desiccation potential of the air (vapor pressure deficit, VPD) was ca. three-fold greater, in canopy gaps than under forest canopies ($\chi^2_{(1, N = 186)} = 18.95, P < 0.001$; Figure 3a), canopy environment did not affect seedling instant physiological stress (NPQ: $\chi^2_{(1, N = 186)} = 2.46, P = 0.117$; with non-significant substrate \times canopy interaction: $\chi^2_{(1, N = 4)} = 2.00, P = 0.157$). However, seedling physiological stress differed substantially by substrate as seedlings established on moss

experienced less instant physiological stress than seedlings on litter ($\chi^2_{(1, N = 186)} = 4.68, P = 0.03$; Figure 3b).

Mercury concentrations varied substantially by substrate ($\chi^2_{(2, N = 26)} = 21.13, P < 0.001$) and they were lowest in the moss layer, intermediate in the litter layer (about four-times as high as in moss), and highest in soil (about six-times as high as in moss and nearly twice as high as in litter) (Figure 3c). However, despite these substantial differences among the substrates, mercury concentrations in seedlings did not differ by substrate ($F_{(1,13)} = 0.04; P = 0.855$) in either of the two canopy environments ($\chi^2_{(1, N = 186)} = 2.46, P > 0.05$; non-significant substrate \times canopy interaction: $F_{(1,13)} = 0.08; P = 0.776$) (Figure 3d). In contrast, seedlings under forest canopy appeared to contain greater mercury concentrations than seedlings in canopy gaps (Figure 3d) but this was not significant ($F_{(1,13)} = 4.44; P = 0.055$). Therefore, we did not find support for our last hypothesis.

DISCUSSION

Our results provide multiple lines of evidence for the importance of the moss layer in forest regeneration, corroborating previous indirect inferences from other studies (Simard and others 1998; Dovčiak and others 2003; Soudzilovskaia and others 2011; Bače and others 2012). Moreover, our findings suggest that forest dynamics studies that do not consider the role of the moss layer may be missing an important driver of forest regeneration (Clark and others 1999; Pacala and others 1993; Maréchaux and others 2021). We found that, compared to litter, the moss layer positively affected forest regeneration in the high-elevation conifer forests by providing microsites: (i) where tree seedlings experienced less instant physiological stress; (ii) that supported a greater abundance of small seedlings, suggesting greater seedling establishment and early survival on moss; and (iii) where greater recruitment potential of tree seedlings occurred under forest canopies. However, the mechanisms by which mossy substrates reduce instant physiological stress remain unclear. We observed that even under the warmer and more desiccating conditions of forest canopy gaps, seedlings established on mossy substrates dissipate heat with the same efficiency as those established under cooler and less desiccating conditions of the closed canopy forest (Figure 3a, b), but we did not find an effect of canopy environment on instant physiological stress of seedlings. Interestingly, despite the

moss layer containing far lower mercury concentrations than litter or soil, seedlings' foliar mercury concentration did not differ per seedling substrate, consistent with the foliar pathway of mercury uptake reported for adult trees of conifer species in natural settings (Blackwell and others 2014; Yang and others 2019).

Role of Moss Layer in Fir Wave Regeneration

The affinity of small balsam fir seedlings with the moss layer that we document here has been suggested in the past by other authors, although often with less direct evidence when moss cover effects on seedlings were not explicitly quantified but only mentioned as one of potentially important features of seedling microsites (for example, Simard and others 1998; Parent and others 2003). Moisture is an important limiting factor for seedling establishment and survival (for example, Cornett and others 1998) and even a thin moss layer has been suggested to both store moisture within its tissues and capillary spaces and reduce moisture loss from underlying substrates (Lindo and Gonzalez 2010; Lett and others 2017; Soudzilovskaia and others 2013) to positively affect balsam fir seedling abundance (Cornett and others 1997). Although previous studies of high-elevation fir-dominated forests in northeastern United States and elsewhere have shown the importance of canopy gaps in forest regeneration dynamics (Sprugel 1976; Bekker and Malanson 2008; Fig. S3), our study expands that classic work by elaborating on the importance of the moss layer for the initial establishment and recruitment of the dense seedling bank under the forest canopy (prior to the formation of fir wave canopy gap). Our results show how the biology of balsam fir, a species with a shade tolerant seedling bank, explains the synchronous recruitment into larger size classes once canopy gaps allow more light penetration into forest understory. Thus, our results corroborate and expand early fir wave studies (Sprugel 1976) that documented the importance of canopy gaps in fir regeneration.

Seedling Climatic Stress and Mitigating Effects of the Moss Layer

Even in a high-elevation ecosystem where frequent clouds provide a moisture source (Richardson and others 2004), canopy gaps could be potentially stressful environments for fir seedlings compared to under closed forest canopies. We observed desic-

cation potential (vapor pressure deficit, VPD) in canopy gaps to be significantly higher (by $\sim 60\%$) than under forest canopy. However, we did not observe a similar difference in physiological stress in seedlings growing in forest gaps and under forest canopies—perhaps because grouping seedlings in disregard of their substrate reduces the signal to noise ratio. The medium-term seasonal desiccation potential is relatively low in these moist high-elevation forests and it does not differ dramatically between forest canopies and canopy gaps (Berdugo and Dovciak 2019). Indeed, some studies suggested that these high-elevation montane forests are linked to the occurrence of cloud ceiling with high atmospheric moisture content (Richardson and others 2004).

Unlike the canopy environment (gap vs. forest canopy), we found that substrate type made a large difference in instant physiological stress experienced by fir seedlings. Although we did not measure instant moisture in each substrate, we did record that seedlings established on litter dissipated heat two to four times more efficiently than seedlings associated with moss, consistent with the greater water holding capacity of moss. This pattern is not surprising given that balsam fir litter, compared to the moss layer, contains less moisture given both, its particulate size and structure and its concentration of lignin (balsam fir litter is 47% lignin, Klaus 2018); moss mats are rich in capillary spaces and their surfaces rich in cellulose, allowing for water movement and storage in extracellular spaces (Nakamura 1992; Lindo and Gonzalez 2010; Philben and others 2018). In addition, such differences in water holding capacity likely correlate to differences in pH and nutrient concentration, features that we did not study but that could be potentially relevant for seedling survival and recruitment (Wheeler and others 2011; Stuijver and others 2014; Nyman and Lindau 2016; Lett and others 2017).

Thus, although canopy gaps in this high-elevation forest ecosystem have been shown to facilitate seedling recruitment into the canopy (Sprugel 1976), moss patches seem to have a much more important role than canopy gaps do in affecting (ameliorating) fir seedling climatic stress and facilitating copious establishment in the initial stages of fir wave regeneration. Consistently, the higher recruitment potential of seedlings established on the moss layer, compared to seedlings established on litter, highlights the facilitative role of the moss layer in early stages of tree seedling establishment (that is, for seedlings ≥ 5 and ≤ 25 cm tall) under closed forest canopy. The observed patterns of

recruitment potential reflected the patterns in microclimate conditions (Figure 3a) and seedling stress across different substrates (Figure 3b). More adverse microclimate (and potentially somewhat lower seed rain) in canopy gaps likely contributed to a greater seedling establishment under forest canopy (Peguero-Pina and others 2007), where climatic stress was lower, and particularly so on moss layer. On the one hand, the difference in recruitment values between canopy environments (Figure 2) emerges from the life history of balsam fir, as its seedlings can survive in shaded environment under closed forest canopy for a relatively long time until a canopy gap forms above them. On the other hand, similar climate-driven stress levels in seedlings established on mossy substrates in both canopy environments (Figure 3b) suggest that the resilient moss layer of these forests (Berdugo and Dovciak 2019) provides some resilience also to seedlings established on moss.

Decoupling Between Mercury Content of the Moss Layer and Seedlings

The observed low concentration of mercury in the moss layer contrasted with the considerably higher mercury concentration in litter and soil, probably due to the long-term accumulation of this contaminant in soil, compared to litter and plant tissue (Driscoll and others 2013). These observations support that mercury uptake via roots is limited (Grigal 2002) and suggest that soil mercury concentrations and pools may increase as leaf litter accumulates and decomposes over time, as observed in Demers and others (2007). At the same time, our observations suggest that mercury is not easily transferred from these pools (litter and organic soil) into mosses or fir seedlings. In agreement with Zhou and others (2021), we observed that the mercury concentration in fir seedlings was even lower than mercury concentration in the moss layer. This finding agrees with the hypothesis that mercury largely enters canopy trees via atmospheric exchange and deposition (Bushey and others 2008; Blackwell and Driscoll 2015; Zhou and others 2021) and extends this hypothesis to tree seedlings (≤ 25 cm tall) of canopy species. Overall, our measurements of mercury concentrations indicate that bryophytes and conifer seedlings do not represent a significant concern in terms of mercury bioaccumulation relative to mercury concentrations observed in litter or soil.

Although young seedling needles are expected to hold less mercury than older needles of adult trees (Rasmussen and others 1991), we found mercury

concentration in fir seedling needles slightly higher than previously reported for canopy trees of this species (Rasmussen and others 1991; Blackwell and Driscoll 2015). This observation emphasizes the continuous exposure to mercury as time passes in fir seedlings below 25 cm tall, which can be a decade old (Parent and others 2003; see also Obrist and others 2021). Interestingly, the slight difference in seedling mercury concentrations observed between canopy environments can be explained by increased photoreduction of mercury from forest soils (that is, soil mercury evasion) in canopy gaps (Yang and others 2019). The relative similarity in total mercury concentration between seedling needles and bryophytes are likely due to both moss layer and seedlings as components of the forest understory. This forest stratum experiences a local enrichment cycle of mercury (Boening 2000) because losses of mercury from forest soil enter plants via foliage, especially under forest canopies (Bushey and others 2008; Yang and others 2019). Finally, the total mercury concentration that we found in the moss layer agrees with the total mercury concentration reported for pleurocarpous mosses previously (Rasmussen and others 1991).

CONCLUSIONS

Tree seedlings benefit from association with the moss layer in different forest types (for example, Cornett and others 1998; Oleskog and Sahlén 2000; Dovčiak and others 2003) where the moss layer can function as a nurse plant (*sensu* Filazzola and Lortie 2014) in initial stages of forest regeneration (Soudzilovskaia and others 2011). Our findings highlight the importance of the forest moss layer as a tree seedling substrate and thus the need to more explicitly include the moss layer in forest ecosystem models. Recent evidence gathered along elevational gradients in the northeastern United States indicated that moss cover can compensate for the decline in tree seedling species richness with increasing elevation and with increasing understory cover (Dovciak and others 2021). Including moss cover in such models is especially relevant for montane forests where moss cover is abundant (Berdugo and others 2018) and where it interacts with canopy gaps, as shown in our study, to produce often complex forest regeneration dynamics characteristic of many mountain forests around the world (Fig. S3; Sprugel 1976; Bekker and Malanson 2008). After all, the fine-scale intimate interaction of mossy substrates with tree seedlings may influence demographic outcomes at broader forest or landscape scales (compare Gurevitch and others

2016). Our observational contribution suggests that experimental settings may be implemented to assess the mechanisms by which mossy substrates reduce instant physiological stress in tree seedlings.

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DATA AVAILABILITY

The data analyzed in this manuscript are available in DRYAD (<https://doi.org/10.5061/dryad.280gb5msj>).

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