

Effects of Soil Abiotic and Biotic Factors on Tree Seedling Regeneration Following a Boreal Forest Wildfire

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ABSTRACT

Wildfire disturbance is important for tree regeneration in boreal ecosystems. A considerable amount of literature has been published on how wildfires affect boreal forest regeneration. However, we lack understanding about how soil-mediated effects of fire disturbance on seedlings occur via soil abiotic properties *versus* soil biota. We collected soil from stands with three different severities of burning (high, low and unburned) and conducted two greenhouse experiments to explore how seedlings of tree species (*Betula pendula*, *Pinus sylvestris* and *Picea abies*) performed in live soils and in sterilized soil inoculated by live soil from each of the three burning severities. Seedlings grown in live soil grew best in unburned soil. When sterilized soils were reinoculated with live soil, seedlings of *P. abies* and *P. sylvestris* grew better in soil from low burn severity stands than soil from either high severity or unburned stands, demonstrating that fire dis-

turbance may favor post-fire regeneration of conifers in part due to the presence of soil biota that persists when fire severity is low or recovers quickly post-fire. *Betula pendula* did not respond to soil biota and was instead driven by changes in abiotic soil properties following fire. Our study provides strong evidence that high fire severity creates soil conditions that are adverse for seedling regeneration, but that low burn severity promotes soil biota that stimulates growth and potential regeneration of conifers. It also shows that species-specific responses to abiotic and biotic soil characteristics are altered by variation in fire severity. This has important implications for tree regeneration because it points to the role of plant–soil–microbial feedbacks in promoting successful establishment, and potentially successional trajectories and species dominance in boreal forests in the future as fire regimes become increasingly severe through climate change.

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Key words: Abiotic and biotic soil characteristics; *Betula pendula*; Boreal forest; Burn severity; Climate change; *Picea abies*; *Pinus sylvestris*; Plant–soil interactions; Tree seedling regeneration; Wildfire.

HIGHLIGHTS

- High burn severity created conditions adverse for seedlings growth.
- Low burn severity promoted soil biota that enhanced growth of *Pinus sylvestris* and *Picea abies*.
- *Betula pendula* growth was driven by changes in abiotic soil properties.

INTRODUCTION

Fire is a recurrent natural disturbance in northern coniferous forests that controls vegetation dynamics, structure, diversity and function. While boreal forests are shaped by and adapted to fire, natural fire regimes are rapidly changing as a consequence of global climate change (Kasischke and Turetsky 2006; Soja and others 2007; Balshi and others 2009; Ponomarev and others 2016). For many parts of the boreal region, burn probability, fire area and fire intensity are projected to increase and become more common as the climate warms (de Groot and others 2013). This is in part due to increasing duration of extreme fire-promoting conditions, such as warmer temperatures (Gillett and others 2004). These changes in fire regime are predicted to alter plant and soil community structure and cause elevated tree mortality (Stephens and others 2013), alter soil organic matter content (Czimczik and others 2005) and alter functioning of soil microbial communities due to increased loss of organic material (Allison and Treseder 2011). More frequent and higher intensity fires are also likely to induce shifts in how boreal forests will regenerate and recover from fire disturbances (Johnstone and others 2010; Alexander and others 2018), in part as a consequence of fire-induced effects on loss of soil organic matter and survival of mycorrhizal fungi needed for tree seedling regeneration (Dahlberg and others 2001; Dahlberg 2002).

Fires in boreal forests of Eurasia typically occur as low-intensity ground surface fires, to which many of the dominant tree species are adapted (Angelstam and Kuuluvainen 2004). In Sweden, older Scots pine (*Pinus sylvestris*) trees frequently survive ground fire because of their thick bark and high crown base height (Zackrisson 1977; Hellberg and others 2003), and deciduous trees such as birch (*Betula pendula* and *Betula pubescens*) are well adapted to ground fires because the high position of the crown and their ability to resprout vegetatively after fire (Atkinson 1992). In contrast, Norway

spruce (*Picea abies*) trees are usually consumed by fire because of their thin bark and low branches (Zackrisson 1977). Post-fire regeneration by *P. sylvestris* and *B. pendula* occurs from seeds that are dropped on site shortly after fire from surviving trees, and seeds of *B. pendula* can also be spread over long distances, while *P. abies* typically recolonizes slowly post-fire by seeds originating from outside burned areas. (Granström 1991; Hellberg and others 2003). Fire is often necessary for new forest tree cohorts to regenerate in these ecosystems (Lampainen and others 2004), and this is associated with the reduction or loss of understory vegetation and shifts in soil properties such as increased concentrations of inorganic nitrogen (that is, NH_4^+) (DeLuca and others 2002; Gómez-Rey and Gonzalez-Prieto 2013). However, the extent of post-fire tree regeneration is also regulated by soil burn severity (Bansal and others 2014), because higher severity burns cause greater loss of organic material and soil biota (Certini 2005) and higher mortality rates of trees which may lead to slower tree regeneration. Although much is already known about the impact of fire on plant mortality and post-fire successions in boreal forests, less is known about how variation in fire behavior and tree mortality impacts aboveground-belowground linkages and soil microbial communities, which may have important consequences for forest regeneration (but see Bergner and others 2004; Treseder and others 2004; Holden and others 2013; Sun and others 2015; Hewitt and others 2020).

Soil microorganisms, and notably saprotrophic microbes and ectomycorrhizal fungi, are critical components for nutrient turnover and seedling establishment and growth in boreal forest (Read and others 2004), and their response to fire disturbance can therefore impact on post-fire recovery of trees (Hewitt and others 2017). The extent to which the organic layer is combusted or lost from fire has major impacts on the soil biota and the speed of its post-fire recovery. Communities of ectomycorrhizal fungi can survive low burn severity fires when the organic layer is not completely consumed (Dahlberg 2002; Holden and others 2016). Survival and short-term recovery of ectomycorrhizal fungi may, however, depend not only on the remaining organic layer, but also on the degree of fire-induced mortality of overstorey trees (Dahlberg 2002; Pérez-Izquierdo and others 2021). With regard to saprotrophic soil microbes, bacteria in general appear to be more resistant than fungi to fire because they are better adapted to resist fire-generated heat (Certini 2005; Mataix-Solera and others 2009). The release of organic

nutrients after fire can stimulate the recovery rate of bacterial communities (Bárcenas-Moreno and others 2011), leading to accelerated short-term release of inorganic soil nutrients that favors tree regeneration. In contrast, higher burn severity may strongly reduce the microbial communities and thereby soil organic matter decomposition, reducing the availability of nutrients needed for tree growth (Holden and others 2016). In total, tree seedling responses to fire depend on how the fire affects both the soil microbes and the abiotic soil properties, as well as the interaction between them. However, the effects of belowground biotic and abiotic changes caused by fire on tree seedling regeneration have mostly been investigated in isolation from one another.

On 31 of July 2014, a large accidental wildfire in east-central Sweden, known as the Västmanland burn started (Gustafsson and others 2019). It was initiated and spread fast due to an extended period of unusually hot and dry weather; it burned more than 13,000 ha of forest and was the largest fire in Swedish modern history (Lidskog and others 2019). For a large part of this area, the fire was intense and caused widespread tree death and loss of the organic layer. Within this area, some forest stands were severely burned, some stands were less severely burned, and some stands were not burned at all, creating a mosaic of stands across the landscape with differing fire severity. We collected soils from forest stands of low burn severity, high burn severity and unburned stands for use in each of two greenhouse experiments that were set up to better understand how growth of three different seedling species (*P. abies*, *P. sylvestris*, *B. pendula*) respond to different burn severities. In the first greenhouse experiment we planted seedlings in live (non-sterile) soil from each burn severity class, and the difference in seedling growth between burn severity treatments could be due to either soil abiotic properties (that is, pH, nutrients, organic matter content, or texture) or biotic properties (that is, composition and biomass of organisms present); this experiment did not allow us to disentangle the role of these two mechanisms. In the second greenhouse experiment, we planted seedlings in sterilized soils that had been inoculated with live soil (that is, containing live soil biota) from each stand burn severity class. Doing this allowed us to separate how soil abiotic versus biotic properties influenced seedling growth and thus shed insights into the mechanisms underpinning the first experiment.

Through these two experiments, we sought to test how the abiotic and biotic components of soil

impact tree seedling growth when soils are subjected to different levels of burn severity. For the first experiment, we hypothesized that seedlings will grow better in living soil from stands subjected to low burn severity relative to soils from either unburned or high burn severity stands. We expected this because burning would enhance nutrient availability (Wan and others 2001), and mild burning would enhance nutrient availability without impairing the ectomycorrhizal fungal community or stimulate succession of fire adapted fungal species. Further, we expected this effect to be greater for pioneering fast-growing species (*P. sylvestris* and *B. pendula*) that can better exploit these inorganic resources relative to late-successional species (*P. abies*) because of their rapid root growth and photosynthesis (Pumpanen and others 2009; Nilsson and others 2012). For our second experiment, we hypothesized that tree seedlings planted in sterilized soils would grow the largest when inoculated with soil from stands with live trees present (that is, stands subjected to low severity burning or unburned stands), and that this would occur irrespective of the burn severity class of the sterilized soil. We expected this because high burn severity soils should mostly lack live tree roots (Pérez-Izquierdo and others 2019) and thus are unlikely to harbor a living ectomycorrhizal fungal community (Dahlberg 2002; Pérez-Izquierdo and others 2021) that is essential for plant nutrient acquisition (Smith and Read 2008). Further, we expected that the positive effect of inoculation with unburned or low burn severity soils would be greatest for *P. sylvestris* seedlings because it was the dominant tree cover in these stands before and after fire, and would likely promote an ectomycorrhizal community that is most suitable for *P. sylvestris* and includes fire-adapted early colonizing fungi. Additionally, we would expect conifers to benefit from late-successional fungi present in unburned soils. Testing these hypotheses in combination contributes to a mechanistic understanding of how tree regeneration success following wildfire varies in response to burn severity in boreal forests, and how this is determined by abiotic versus biotic soil properties.

METHODS

Selection of Burn Severity Stands

Within the Västmanland burn, we selected 25 burned forest stands that were each about 0.25 ha and had undergone one thinning operation prior to the fire (stem density of < 1000 stems per hectare).

tare); they were all on podzolized soils, had a site index of 22–24 m (that is, the estimated dominant height at age 100 years) and represented a gradient in burn severity. They occurred within an area of approximately 60 km², with each stand separated at least 300 m from all other stands. Prior to the fire, the stands were dominated (87%) by 40–50-year-old Scots pine (*P. sylvestris*) production forests with scattered (11%) Norway spruce (*P. abies*) and (2%) birch (*Betula* spp.) trees and an understory vegetation dominated by ericaceous dwarf shrubs (*Vaccinium vitis-idaea*, *V. myrtillus* and *Calluna vulgaris*) and mosses (mainly *Pleurozium schreberi*).

In April 2016, data for stand characteristics of the 25 burned stands were collected within a circular plot of 314 m² (radius = 10 m) in the center of each stand. Tree mortality was determined by visual inspection (for example, the lack of green needles present) and calculated as the percentage of dead trees versus all (dead and alive) trees within the plot. The number of trees with stem scorch visible (for example, trees that had bark that had fallen off the stem) was also counted. Flame length was determined as the average charring height of stems for 20 *P. sylvestris* trees per plot, and for these, the level of crown scorching (that is, the proportion of needles killed or consumed by fire throughout the whole crown) was also estimated. For each plot, the total organic (humus) depth (that is, Oa and Oe horizons) and the depth of the charred layer in the soil profile were measured at 25 random positions by vertically inserting a ruler in the ground. In addition, in four randomly allocated positions within each plot, the amount of charcoal deposited on the topsoil was collected within a circular area (radius = 8 cm) and converted to dry mass per area. With the use of these data (that is, tree mortality, flame height, stem scorch, crown scorch, humus depth, depth of charred soil, coarse charcoal on surface and fine charcoal on surface) for each of the 25 stands, we then classified the stands into burn severity classes by using Principal Component Analysis (PCA) followed by K-mean clustering. From this analysis we selected seven stands of high burn severity and seven stands of low burn severity for further use (Supporting Information Figure S1; Table S1). The major differences between high burn and low burn severity stands result from high burn stands having a higher tree mortality, larger flame height, a higher number of stem and crown scorches of trees and a larger reduction of humus thickness from humus combustion (Table 1). In addition, seven unburned stands distributed around the burned area (within 500 m of the fire perimeter) were also selected for

this study. The three burn severity class stands (unburned, high burned and low burned in total 21 stands) were randomly distributed across the burned area, allowing each stand to serve as an independent replicate, with seven randomly distributed stands in each burn severity class. Prior to the fire, there were no major differences in mean tree height, tree basal area, tree biomass or tree species composition among burn severity classes (Pérez-Izquierdo and others, Unpublished Manuscript).

Soil Chemistry of Forest Stands

On May 22–26, 2018 we randomly collected five circular soil cores of mineral soil (radius = 5 cm; depth = 10 cm) and five circular soil cores of the organic layer (radius = 15 cm) to the full organic layer depth from each 21 stands. The organic (humus) layer included the Oa and Oe horizon, while the Oi horizon was excluded from the soil samples. The five soil cores were bulked to represent one sample per stand. Roots and small debris were removed from the soil. For a subsample of each sample, the total concentration of phosphorus (P) was determined by Kjeldahl acid digestion (G-189-97 Rev. 3, multitest MT7) using an Auto Analyzer 3 Spectrophotometer (Omniprocess, Solna, Sweden). Total soil carbon (C) and nitrogen (N) concentrations were analyzed by drying (70 °C, 18 h) and grinding samples followed by dry combustion using an EA-IRMS Elemental Analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). For another subsample, soil pH was determined by using a solution-to soil ratio suspension of 0.01 M CaCl₂ mixed with mineral soil (1:1) or humus (1:10) following Thomas (1996).

Greenhouse Experiment, Experimental Design and Soil Chemistry of Greenhouse Soil

We performed a greenhouse experiment using soils from each of the three burn severity classes of stands. From September 29 to October 2, 2017 we randomly collected approximately ten circular soil cores (radius = 5 cm; depth = 10 cm) within the 314 m² (radius = 10 m) circular area of each of the 21 stands. The different burn severities between stands resulted in variable thickness of the organic horizon, with high severity stands having little or no remaining humus (Mean 20.0 ± SE 1.7 mm), low burn severity stands having some organic layer (24.1 ± 1.9 mm) and unburned stands having thick organic layer (93.9 ± 5.5 mm). In order to

Table 1. Measures of Burn Severity of the Forest Stands.

Burn severity measures	df ¹	Burn severity class of forest stand		F-value	P-value
		High	Low		
Tree mortality (%)	1, 12	100.0 ± 0.0 ^a	32.1 ± 5.0 ^b	186.85	< 0.001
Flame height (m)	1, 12	6.8 ± 1.1 ^a	1.0 ± 0.1 ^b	25.62	< 0.001
Stem scorch (%)	1, 12	13.1 ± 3.6 ^a	2.9 ± 1.9 ^b	6.48	0.026
Crown scorch (%)	1, 12	99.4 ± 0.4 ^a	27.9 ± 2.4 ^b	846.74	< 0.001
Humus depth ² (mm)	2, 18	20.0 ± 1.7 ^a	24.1 ± 1.9 ^a	142.42	< 0.001
Depth of charred soil profile layer (mm)	1, 12	10.3 ± 0.8 ^a	12.8 ± 0.8 ^b	5.03	0.045
Charcoal on soil surface (g/m ²)	1, 12	120 ± 25	75 ± 25	1.50	0.244

Mean ± SE.

Bold F- and P-values are significant at an alpha value of 0.05.

Numbers within rows accompanied by different letters differ significantly at $P \leq 0.05$ (following ANOVA).

¹Numerator degrees of freedom, denominator degrees of freedom.

²The mean ± SE depth of unburned humus was 93.9 ± 5.5 mm and was statistical significantly higher than both high and low burned soils at $P \leq 0.001$ (Bonferroni post hoc test following ANOVA).

achieve a representative sample of the conditions that the roots of a developing seedling would experience, we sampled to a fixed depth (10 cm) at each site which included the humus that was present and the underlying mineral soil. As such, the proportion of organic (humus) soil to mineral soil varied across stands, with the highly burned sites having a low amount of humus relative to the unburned sites. For each stand, all the soil cores were bulked to create a single sample which was then passed twice through a 4.0-mm sieve, placed in a polyethylene bag and transported to Umeå in cooling boxes and stored at 2 °C until the start of the experiment on October 17, 2017. Two-thirds of the sieved soil from each stand was sent in cooling boxes to SynergyHealth (Etten-Leur, Netherlands), for gamma irradiation at a dose of 43.0–78.8 kGy. This sterilization treatment was chosen to effectively kill all the soil biota while creating minimal disturbance to physical soil structure (McNamara and others 2003).

To distinguish between the effects of soil biota and soil abiotic properties on seedling performance, two separate greenhouse experiments were set up in which tree seedlings were grown in the field collected soils. In the first experiment that tested for the effects of soil properties including live biota, we used unsterilized soil from the field sites to perform a factorial experiment consisting of three soil burn severity classes (that is, high burn, low burn and unburned) × three tree seedlings species (*P. abies*, *P. sylvestris*, or *B. pendula*) × seven replicates (that is, the seven stands per burn severity class), resulting in a total of 63 pots. For the second experiment that tested for the separated effects of soil biota and abiotic properties, we used sterilized

soil originating from the same sites as the first experiment and applied soil community inoculation treatments consisting of live soil from each of the different burn severity classes (Figure 1). The experiment was set up in a factorial design in which pots were filled with sterilized soil from three burn severity classes (high burn, low burn or unburned) and planted with each of three plant species (*P. abies*, *P. sylvestris* or *B. pendula*); these soils then were inoculated with four burn severity inoculum class treatments. The four inoculum treatments consisted of live inoculum from each class, as well as a sterile control, resulting in 252 pots in total (Figure 1). The experimental units were randomly arranged into blocks, by including one stand of each burn severity class in each block. Thus, each block consisted of 12 pots (three burn severity classes × four burn severity inoculum classes). Because our research question was focused on local microbial communities and we aimed to generalize results from our experiment to the entire burned landscape we sampled, burn severity inoculum class derived from each stand was kept separate (Gundale and others 2017) and was randomly assigned to receiving soils originating from different stands (Gundale and others 2014). Our inoculation approach therefore followed experiment Type D described by Gundale and others (2017, 2019).

For both experiments, we used 800 ml pots (8 × 8 × 8.5 cm) with holes in the bottom to allow excess water drainage. Pots were filled with 2/3 experimental soil (that is, live soil for the first experiment; sterilized soil + live inoculum for the second experiment) and 1/3 with autoclaved quartz sand to improve drainage after watering. For

the second experiment, 10% of the soil volume in each pot with sterilized soil was replaced with soil containing live biota (burn severity inoculum class treatments). This soil was also mixed with autoclaved quartz sand, resulting in an inoculation amount of approximately 6.6% of the total pot volume. Both unsterilized and sterilized soil from each stand, following mixing with quartz sand, was analyzed for nutrient concentration (NH_4^+ , NO_3^+ , PO_4^{3-}) using standard protocols (Gundale and others 2011).

All pots were set up on tables in a greenhouse and planted with *P. abies*, *P. sylvestris* or *B. pendula* seedlings. The seeds were obtained from tree nurseries in Sweden and consisted of genetic provenances that corresponded to our field sites.

The seeds were sterilized in 5% hypochlorite and rinsed with deionized water and then placed on autoclaved quartz sand for pre-germination for seven days. Two seedlings per species were then planted in each pot, and after one month the smallest seedling was removed. During this first month new seedlings were planted if both seedlings in a pot died. After this period, 100% seedling survival was obtained. The tables were rotated once a week to avoid unwanted effects of greenhouse gradients. Both experiments were run for 4.5 months, and seedlings were watered every day with tap water. The ambient conditions within the greenhouse involved a 18:6 h light/dark photoperiod with a relative air humidity of 40%. The temperature ranged between 25 °C (day) and

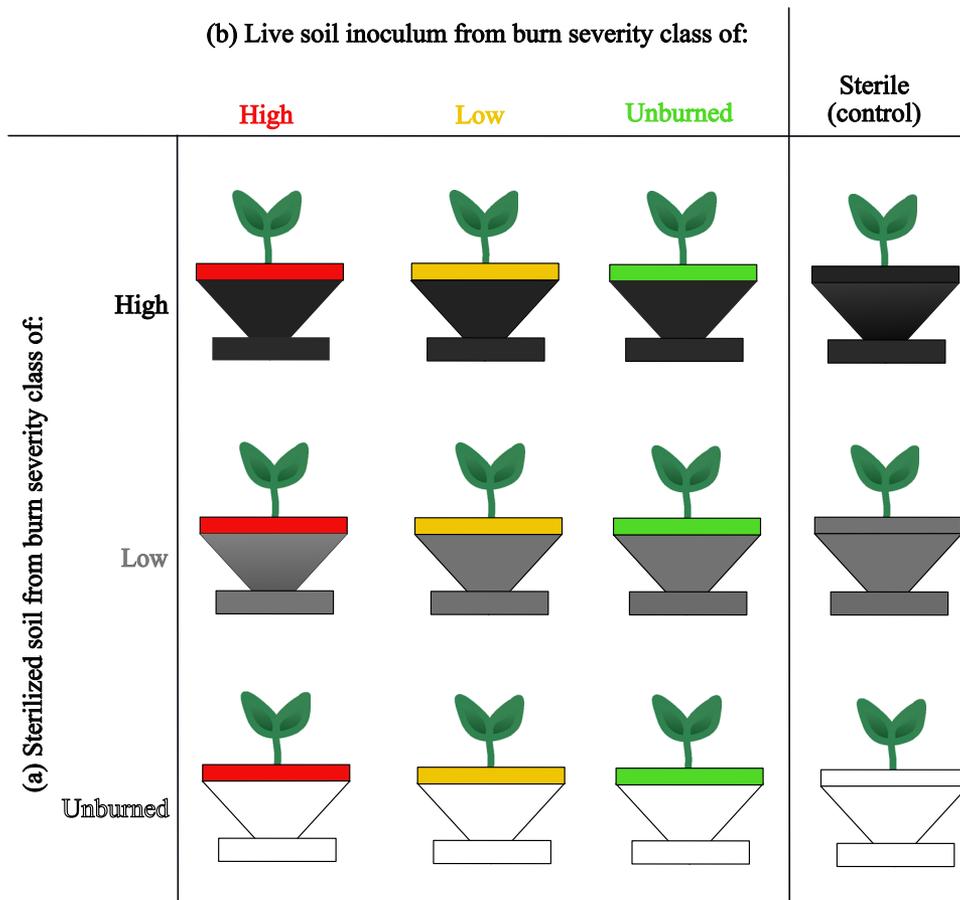


Figure 1. Schematic figure of Experiment 2, which aims to separate the soil biotic and abiotic effects of soils from forest stands subjected to high and low burn severity as well as from unburned stands on the growth of tree seedlings. **a** Pots with sterilized soil from high burn severity (black pots), low burn severity (gray pots) and unburned (white pots) stands receiving, **b** live soil inoculum from high severity (red), low severity (yellow) and unburned (green; top vertical) stands. Pots arranged vertically to the far right consist of sterile soil without added inoculum (sterile controls). Each pot was planted with seedling of *Picea abies*, *Pinus sylvestris* or *Betula pendula*. The 12 pots depicted represent one block for one species; in total seven blocks were set up for each of the three species. There were 12 (pots) × 3 (species) × 7 replicates (blocks), resulting in a total of 252 pots for this experiment. The percentage of total soil in each pot that was added live inoculum was 6.6%, except for the sterile control pots where it was 0%.

15 °C (night). At the end of the experiment we harvested the seedlings by eliminating soil from roots with water and cut the plant at the soil surface to separate aboveground from belowground biomass. Plants were put in paper bags and oven-dried at 65 °C for 48 h and weighed to obtain measures of aboveground, belowground and total biomass.

Statistical Analysis

For the first experiment, statistical analysis was performed by using split plot ANOVA with burn severity class as a fixed factor and plant species as a subplot factor. For the second experiment we used a blocked design followed by split plot ANOVA with burn severity class and burn severity inoculum class as fixed factors and plant species as a subplot factor. The sites were randomly selected in the field, and we therefore performed the data analysis with an assumption that the data is randomly distributed. To satisfy assumptions of homogeneity of variance, all data were $\log(x)$ transformed. Data for burn severity and soil characteristics of the forest stands, and nutrient concentrations in soil used in greenhouse, were analyzed using one-way ANOVA. For both experiments, stand characteristic and greenhouse soil data, Bonferroni post hoc test was used at $\alpha = 0.05$, to further explore pairwise differences between treatment means. All data were statistically analyzed in SPSS version 24 (IBM Corp., Armonk, NY, USA). Raw data are stored as Supplementary material (S3). Figure 1 was created in Affinity Designer 1.8.3.

RESULTS

Soil Chemical Properties

In 2018, four years after the fire, we found no significant differences in concentrations or ratios of total soil C, N, C:N and P in mineral soil or organic layer between stands of different burn severities (Table S2). Meanwhile, mineral soil pH of high burn severity stands ($\text{pH} = 3.89 \pm 0.06$; mean \pm SE) and low severity stands ($\text{pH} = 3.78 \pm 0.07$) were both significantly higher than that for unburned stands ($\text{pH} = 3.31 \pm 0.12$) but did not differ from each other ($F_{2,18} = 12.20$, P -value ≤ 0.001). For the humus, pH in low burn severity stands ($\text{pH} = 3.30 \pm 0.08$) was significantly higher than for unburned stands ($\text{pH} = 3.04 \pm 0.04$) ($F_{1,12} = 8.53$, P -value = 0.013); humus pH could not be determined for the high severity stands due to insufficient humus remaining as a consequence of the fire.

For the soil used for the greenhouse experiment, NH_4^+ and PO_4^{3-} were overall greatest in soil from the unburned stands, whereas NO_3^- was unresponsive to burn severity (Table 2; Figure 2). We also found that sterilization increased NH_4^+ in all soils with the strongest effects on unburned soil. Sterilization also increased soil concentrations of PO_4^{3-} , but only in unburned soil, and had no effect on NO_3^- (Table 2; Figure 2).

Greenhouse Experiments

In the first experiment in which we used unsterilized soil, both burn severity class and plant species identity significantly affected total, aboveground and belowground seedling biomass, and burn severity class also impacted the aboveground-to-belowground biomass ratio (Table 3); there were no interactive effects between these two factors. The effect of plant species identity was because *B. pendula* and *P. sylvestris* produced more aboveground and belowground biomass than did *P. abies* (Figure 3). For the burn severity class effect, seedling biomass were generally greater in the unburned soil compared to the high burn severity soil, with low burn severity soils often showing intermediate seedling growth (Figure 3). The aboveground-to-belowground biomass ratio was lowest in soil from the high burn severity stands, although this effect of burn severity was detected as significant only by the analysis of variance and not the post hoc analysis (Table 3; Figure 3d).

In the second experiment involving soil sterilization and inoculation of live biota, we found that burn severity class, burn severity inoculum class and plant species identity nearly always had significant effects on seedling total, aboveground and belowground biomass, and on the ratio of aboveground to belowground biomass (Table 4). The plant species effect occurred because *B. pendula* produced the most biomass, while *P. abies* produced the least; *B. pendula* seedlings also had the lowest aboveground-to-belowground biomass ratio (Figure 4). The burn severity effect occurred because seedling growth variables were always highest in unburned soils and usually least in high burn severity soils (Figure 4a–d). For the significant burn severity inoculum class effects, low burn severity inoculum class often stimulated the highest seedling biomass, and the aboveground-to-belowground biomass ratio, the most out of all inoculum classes (Figure 4e–h). The interactive effect of burn severity and plant species identity was significant for all variables except aboveground biomass (Table 4), which was due to the stronger overall pos-

Table 2. Results from Analysis of Variance Comparing Main and Interactive Effects of Burn Severity Class (BSC) and Sterilization (S), of Soil Used in the Greenhouse, for NO_3^- , NH_4^+ and PO_4^{3-} .

	df ¹	NO_3^-		NH_4^+		PO_4^{3-}	
		F-value	P-value	F-value	P-value	F-value	P-value
Burn severity class (BSC)	2, 18	2.470	0.099	13.747	< 0.001	9.045	0.001
Sterilization (S)	1, 12	3.457	0.071	167.441	< 0.001	5.554	0.024
BSC × S	2, 18	2.431	0.102	17.864	< 0.001	6.010	0.006

Bold F- and P-values are significant at an alpha value of 0.05.

¹Numerator degrees of freedom, denominator degrees of freedom.

itive effect of burn severity on *B. pendula* biomass, and on the aboveground-to-belowground biomass ratio for *P. sylvestris* and *P. abies* (Figure 4a–d). We also observed a two-way interactive effect of burn severity inoculum class and plant species and a three-way interactive effect of these two variables and burn severity, on both aboveground biomass and the ratio of aboveground to belowground biomass (Table 4). The two-way interaction (Figure 4e–h) occurred because *B. pendula* responded less to burn severity inoculum class than did the two conifer species. Meanwhile, the three-way interaction occurred because the two conifer species responded stronger to low burn severity inoculum class when grown in the unburned soil compared to the other burn severity classes.

DISCUSSION

We aimed to test how the abiotic and biotic properties of soil, collected from stands subjected to different burn severity, impact tree seedling growth. Overall, we found that effects of burn severity on both soil biotic and abiotic properties were important for seedling growth, but that effects of soil abiotic properties were overall more important, although seedlings of different tree species varied in their responses to only soil biotic properties. Our findings elucidate how fire may affect seedling performance via its effects on the soil and soil biota, thus providing insights into key mechanisms underlying tree regeneration after wildfire.

Effects of Non-sterile Burn Severity Soil on Tree Seedling Growth

In our first experiment, where live (non-sterile) soil from each stand was used, we found that both burn severity and plant species identity were important for explaining seedling growth. However, we did not find any interactive effect between burn severity and species identity, meaning that the

three species responded similarly to the burn severity treatments. We found that all seedlings grew worse in high burn severity soils and best in unburned soils, with the fast-growing *P. sylvestris* and *B. pendula* seedlings achieving a higher final biomass than those of *P. abies*. These findings contradict those from field experiments showing ground burning of intermediate severity to be more beneficial to growth of pioneer species relative to their growth in unburned soil (Bansal and others 2014). In our study, there were no major differences in concentrations of NH_4^+ , NO_3^- and PO_4^{3-} in live soils at the time of collection, probably because we collected our soils four years post-fire, and the expected flush of nutrients immediately following fire (Gundale and others 2005) may have dissipated. However, the greater seedling growth in unburned soils suggests higher nutrient availability in those soils, likely because these soils had a higher proportion of organic material that could be rapidly mineralized in the greenhouse environment.

The seedlings may also have grown largest in the unburned soils because these soils would likely support more ectomycorrhizal and saprotrophic fungi that would stimulate organic matter decomposition and plant access to nutrients which should benefit seedling growth (Holden and others 2016). It has also been suggested that high availability of C in the root zone from root exudates may stimulate bacterial breakdown of complex sources of N (Clarholm 1985), meaning that mineralization rates should be higher in soils with active plant roots. At the same time, lower growth of seedlings in high burn severity stands could be due not only to lower resource availability and loss of mutualistic biota, but also to greater levels of fungal pathogens (Hewitt and others 2016). However, our Experiment 1 is unable to separate between the likely abiotic and biotic mechanisms contributing to these effects.

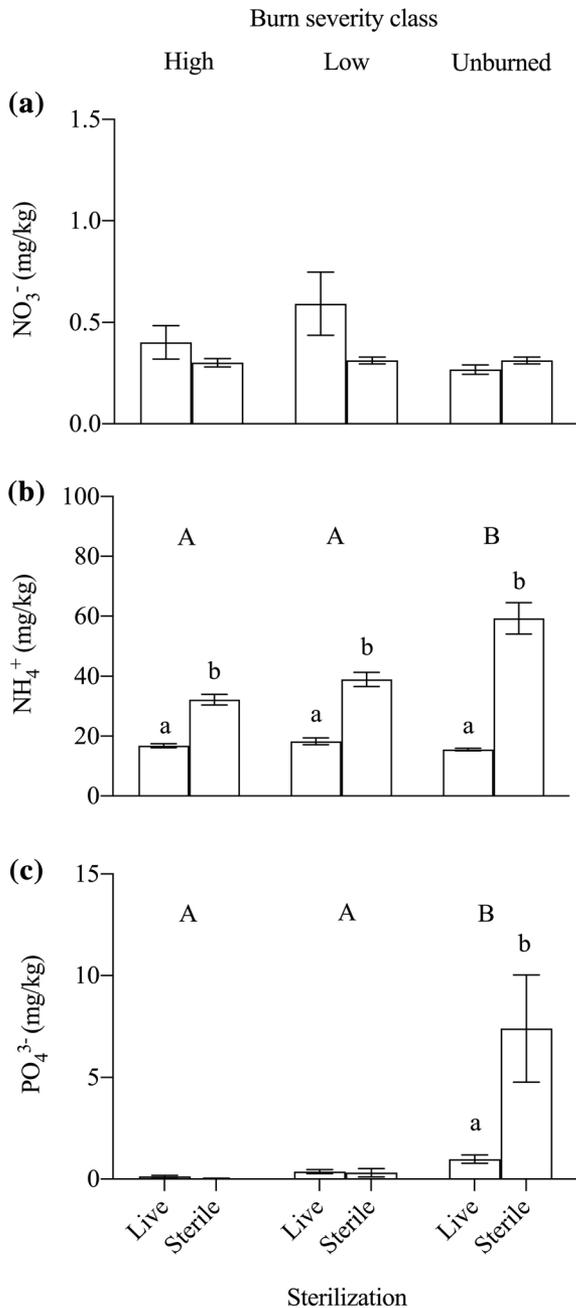


Figure 2. Mean \pm SE of NO_3^- (a), NH_4^+ (b) and PO_4^{3-} (c) of live or sterilized mixtures of humus and mineral soil from different forest stand fire severity classes. All soil was mixed with autoclaved sand, at a 2:1 ratio. Different capital letters above pairs of bars indicate significant differences between burn severity classes, and different lower case letters indicate significant differences between live and sterile soil, according to Bonferroni post hoc tests at $P \leq 0.05$. Corresponding two-way ANOVA results (F - and P -values) are reported in Table 2.

Our first experiment also revealed that increases in soil pH associated with fire could indirectly ex-

plain seedling growth response to fire, because the burned soil had both the highest soil pH and the lowest seedling growth. This may be because higher soil pH can disfavor communities of fungi (Day and others 2019), which would reduce the organic matter decomposition and therefore presumably decrease the availability of nutrients for plant growth (Smith and Read 2008). Our analysis further showed marginally significant statistical differences in seedling aboveground-to-belowground biomass ratios among soil burn severity treatments, and all species tended to have weakly lower ratios when grown in high burn severity soils compared to when grown in low severity and unburned soils, which could reflect greater soil resource limitation. Since the high burn severity soil had much less organic material than in the other soils, it is likely to contain fewer saprotrophic microbes and mycorrhizal fungi needed for promoting nutrient availability for the seedlings, which may have caused them to allocate more biomass to the rooting zone (Ledo and others 2018).

Separating Soil Biotic and Abiotic Influence on Seedling Growth

Our second experiment (Experiment 2) compared growth of seedlings in sterilized soils across the three burn severity treatments and in sterilized soils that had been reinoculated with live soils (that is, containing live soil biota) from each of the burn severity treatments. This set up enabled us to disentangle the effects of abiotic soil properties from that of live biota.

Similar to the first experiment, we found that burn severity had a highly significant influence on seedling growth of all species, in that seedlings in soil originating from unburned stands grew the most and those in soil from the high burn severity stands grew the least, even when soils were sterilized. We therefore suggest that the availability of nutrients (that is, abiotic soil properties) was the primary driver of growth differences among soils in both experiments. This effect may have occurred in Experiment 1 because there was more organic material in pots with unburned soil that could be mineralized and in Experiment 2 because the sterilization of the soil released nutrients of NH_4^+ and PO_4^{3-} . The higher PO_4^{3-} levels of sterilized unburned soil in our greenhouse experiment may also have contributed to higher uptake of NH_4^+ by seedlings. Blanes and others (2012) showed, although in a field experiment, that when limitation by P was alleviated, *Abies pinsapo* seedlings increased their N uptake. Although we cannot com-

Table 3. Results from Analysis of Variance Comparing the Main and Interactive Effects of Burn Severity Class (BSC) and Plant Species (PS) on the Total, Aboveground and Belowground Biomass Including the Ratio of Aboveground to Belowground Biomass.

	df ¹	Total biomass ²		Aboveground biomass ²		Belowground biomass ²		Aboveground/belowground ^{2,3}	
		F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Burn severity class (BSC)	2, 18	7.823	0.004	10.673	0.001	4.085	0.034	3.981	0.037
Plant species (PS)	2, 36	7.900	< 0.001	6.050	0.005	9.512	< 0.001	3.071	0.059
BSC × PS	4, 36	1.115	0.365	0.857	0.499	1.215	0.321	0.308	0.997

Seedlings of *Picea abies*, *Pinus sylvestris* and *Betula pendula* were grown on unsterilized soils from three burn severity classes, that is, from stands of high or low burn severity, or from intact unburned stands.

Bold F- and P-values are significant at an alpha value of 0.05.

¹Numerator degrees of freedom, denominator degrees of freedom.

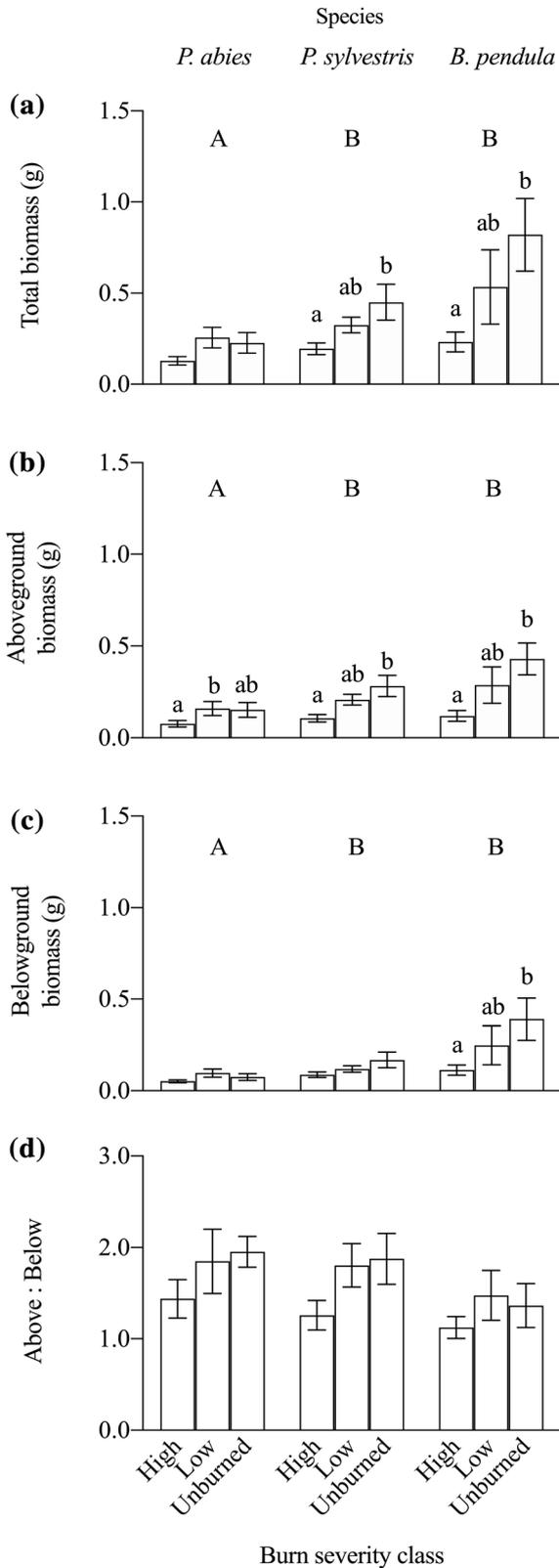
²Data were transformed ($\log(x)$) prior to analysis.

³The ratio of aboveground to belowground biomass.

pletely exclude the possibility that the responses to soil abiotic conditions could also be because of variation in soil physical properties across our stands, we believe this effect to be minimal and unlikely to vary much among our burn severity treatments. As such, the field collected soil was mixed with 1/3 autoclaved quartz sand to assure water drainage in each pot and to minimize the influence of variation of soil physical properties across our stands.

In partial agreement with our second hypothesis, we found that seedling growth was affected by addition of live inoculum from stands of different burn severities, but in a different way to what we observed for live soil in the first experiment. Specifically, for the two conifer species, we found stronger positive seedling growth responses when inoculum originated from low burn severity sites than from either unburned or high burn severity sites, pointing to the beneficial effects of a low intensity of burning. A possible mechanism is that soil microbes, including ectomycorrhizal fungi, can survive when the organic layer is not completely consumed in a low severity fire (Dahlberg 2002; Holden and others 2016; Day and others 2019), as opposed to in a high severity fire. Further, when overstory trees survive a low severity fire, these trees can maintain the symbiotic relationship with the ectomycorrhizal community (Dahlberg 2002; Pérez-Izquierdo and others 2019), which could allow new seedlings to easily develop new ectomycorrhizal networks after a low burn compared to after a high burn severity fire. Fire may also induce a functional shift in microbial community composition (Clemmensen and others 2015) toward taxa that are more beneficial for seedling growth. For

example, Pérez-Izquierdo and others (2021) showed that soils of burned stands, from the same stands as those utilized in this study, were inhabited by ectomycorrhizal species of the genera *Sphaerospora* and *Laccaria* that are known to be fire-adapted and possibly having a higher affinity for inorganic N (LeDuc and others 2013). It is therefore possible that these or other fire-resistant or fire-adapted ectomycorrhizal fungal species, when transferred to the unburned soils, would have benefitted seedlings by improving their access to inorganic N from this soil. Alternatively, non-mycorrhizal saprotrophs could also have contributed to these effects. As such, our results suggest that conifer tree seedlings are likely to be constrained by the availability of beneficial root associated soil biota (such as non-fire adapted ectomycorrhizal species) or particular saprotrophic microbes in sites that have experienced severe wildfire but not where fire has been less intense (Pérez-Izquierdo and others 2021). This could result in a slow post-fire recovery of important soil biota, and the tree seedlings that depend on them. Finally, soil inoculum from unburned soils had no positive effect on seedling growth of any species in our study. This inoculum is likely to host late-successional ectomycorrhizal fungi such as *Russula* and *Cortinarius* (Pérez-Izquierdo and others 2021) important for mobilizing nutrients bound in organic matter complexes (Lindahl and Tunlid 2015). When this inoculum was transplanted to burned soils in the greenhouse, it is plausible that they utilized host plants as their primary source of metabolic C (Corrêa and others 2011), and therefore drainage of C of seedling origin could have contributed to explain the lower biomass increment of



◀ **Figure 3.** Mean \pm SE of total biomass (a), aboveground biomass (b), belowground biomass (c) and the ratio of aboveground to belowground biomass (d) for tree seedlings of *Picea abies*, *Pinus sylvestris* and *Betula pendula*. Seedlings were grown on unsterilized soil originating from stands differing in burn severity (that is, high, low or unburned). Different capital letters above bars indicate significant differences between plant species across burn severity classes, and different lower case letters indicate significant differences between burn severity classes within species, according to Bonferroni post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (F - and P -values) are reported in Table 3.

seedling grown in burned soils receiving unburned inoculum.

Contrary to our expectations, the late-successional *P. abies* showed the strongest positive response of all three species to soil inoculation (because it responded significantly more to inoculum from low severity burned stands than that from both high burned and unburned stands), with *P. sylvestris* showing an intermediate response, and *B. pendula* showing no response. We expected *P. sylvestris* to respond most strongly to soil burn severity inoculum because of the dominance of this species at our experimental sites, and because live adult trees often facilitate growth of regenerating tree seedlings of the same species (Jonsson and others 1999; Andivia and others 2018), in part through shared ectomycorrhizal connections. However, it is recognized that ectomycorrhizal communities associated with *P. abies* and *P. sylvestris* partially overlap (Menkis and others 2005), which could explain why seedlings of both conifers (but not *B. pendula*) responded positively to the low burn severity inoculum class relative to at least some of the other inoculum treatments. Our finding that *P. abies* and *P. sylvestris* do not perform well on highly burned soils in the absence of a live community of microorganisms may explain regeneration of conifers is sometimes disfavored following fire in Swedish forests (Elfving 1983; Kardell and Laestadius 1987). Unlike the two conifer species, *B. pendula* never responded to soil inoculation treatments. *B. pendula* is a fast-colonizing species on fire disturbed areas (Hellberg and others 2003; Gustafsson and others 2019), and its post-fire abundance has often been interpreted in terms of it being a good resource competitor (Dehlin and others 2004) that is effective at exploiting initial elevated levels of inorganic N resulting from fire disturbance (Gundale and others 2005). Findings from our study suggest *B. pendula*

Table 4. Results from Analysis of Variance Comparing the Main and Interactive Effects of Burn Severity Class (BSC), Burn Severity Inoculum Class (IC) and Plant Species (PS) on the Total, Aboveground and Belowground Tree Seedling Biomass, and the Ratio of Aboveground to Belowground Seedling Biomass.

	df ¹	Total biomass ²		Aboveground biomass ²		Belowground biomass ²		Aboveground/belowground ^{2,3}	
		F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Burn severity class (BSC)	2, 66	50.402	< 0.001	58.972	< 0.001	38.331	< 0.001	27.900	< 0.001
Burn severity inoculum class (IC)	3, 66	2.993	0.037	3.534	0.019	2.002	0.122	3.134	0.031
Plant species (PS)	2, 144	189.502	< 0.001	165.750	< 0.001	198.825	< 0.001	23.050	< 0.001
BSC × IC	6, 66	1.331	0.256	1.235	0.300	1.362	0.243	0.174	0.983
BSC × PS	4, 144	3.092	0.018	1.717	0.149	4.878	0.001	3.390	0.011
IC × PS	6, 144	1.189	0.087	2.703	0.016	0.990	0.434	2.701	0.016
BSC × IC × PS	12, 144	1.469	0.142	1.941	0.034	1.167	0.312	2.883	0.001
Block	12, 66	4.400	0.006	3.620	0.004	2.849	0.016	1.972	0.082

Bold F- and P-values are significant at an alpha value of 0.05. Seedlings of *Picea abies*, *Pinus sylvestris* and *Betula pendula* were grown on sterilized (gamma irradiated) soils from three burn severity classes, that is, from stands with high or low burn severity, or, from unburned stands. In order to separate effects of abiotic drivers (burn severity) and biotic drivers (soil biota) on seedling growth, all sterilized soils were reinoculated with live soil from different classes (that is, stands with high burn severity, low burn severity or unburned) or with sterile soil.

¹Numerator degrees of freedom, denominator degrees of freedom.

²Data were transformed ($\log(x)$) prior to analysis.

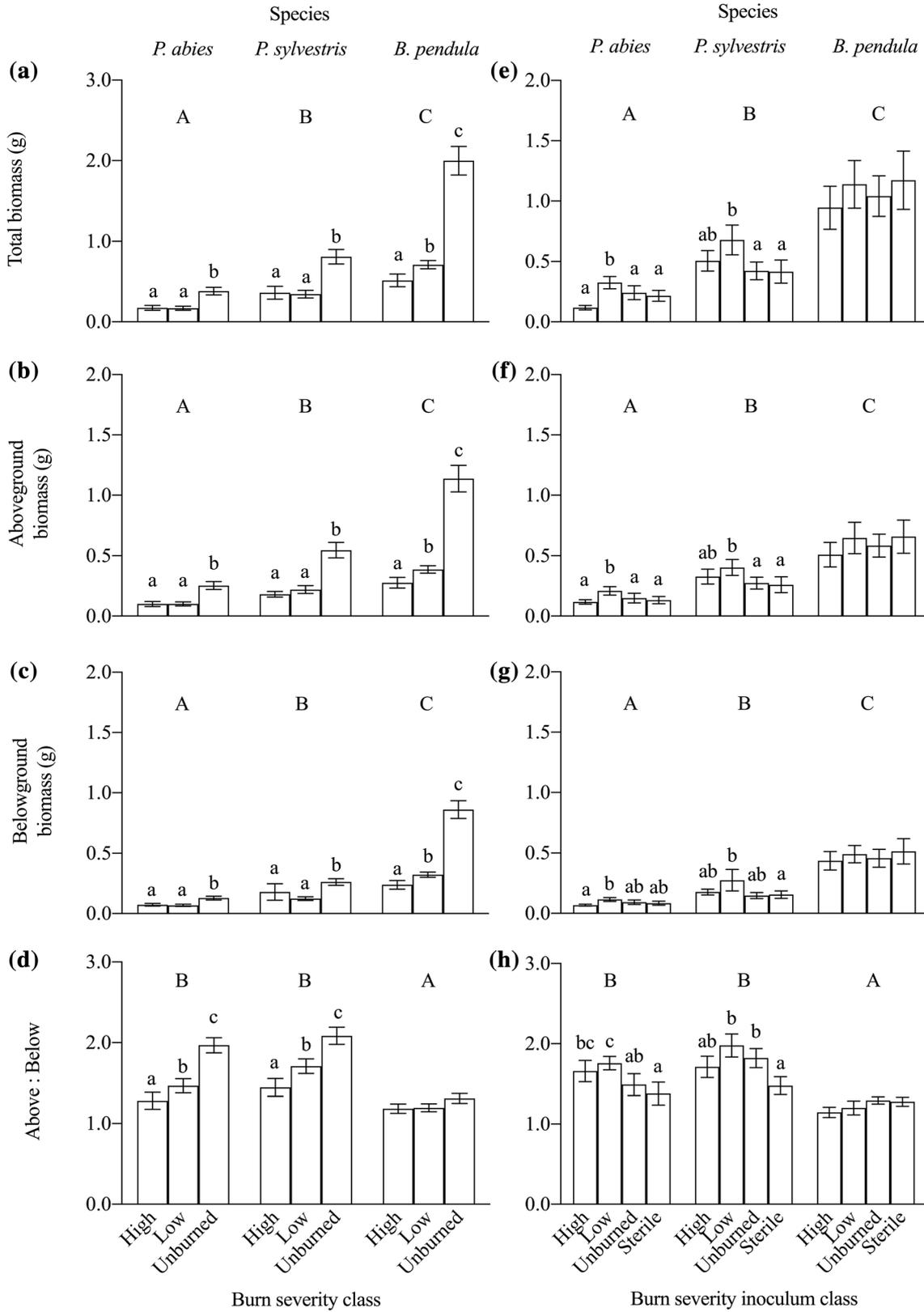
³The ratio of aboveground to belowground biomass.

seedlings responded strongly to conditions of elevated nutrients and appeared less dependent than the conifers on ectomycorrhizal associations or other microorganisms for nutrient uptake during their establishment phase. However, this warrants further exploration given that mycorrhizal fungi have previously been shown to influence growth of *B. pendula* seedlings in boreal forests (Jonsson and others 2001). Deciduous trees such as *B. pendula* are expected to become more dominant in the forested landscape if climate warming increases and higher burn severity conditions prevail (Mekonnen and others 2019; Mack and others 2021). Our study suggests that this is mainly because *Betula pendula* seedlings are largely unresponsive to live soil biota and are therefore positioned to perform well directly after a fire in high burn severity sites even when the soil biota has been lost. *B. pendula* may not be disfavored from the absence of soil biota to the same extent as *P. sylvestris* and *P. abies* may be.

CONCLUSIONS

In this study we disentangled the effect of soil abiotic and biotic properties on tree seedling performance following wildfire to evaluate the effect of fire disturbance on the regeneration of boreal forests and shed light on the underlying mecha-

nisms. Our results have several implications. First, they highlight that regeneration of *B. pendula* is unresponsive to changes in soil biota and is instead mostly driven by changes in abiotic soil properties. In contrast, both *P. abies* and *P. sylvestris* were responsive to soil biota from low burn severity soil relative to biota from the other soils; this demonstrates that low severity fire disturbances in part benefit post-fire regeneration of conifers due to the presence of specific soil biota that benefit from low burn severity fire. However, all seedlings responded positively when soil nutrients were elevated and grew well in the absence of biota, suggesting that soil nutrient conditions following fire would likely have an overriding importance for the regeneration success of all species shortly after fire. Second, studies such as ours can inform on strategic post-fire management decisions that involve restoration or assisted forest regeneration. When low burn severity fires occur, including during management procedures that incorporate prescribed burning prior to forest replanting, there is a need to consider its consequences for soil biota and how this biota in turn impacts on conifer seedling growth and regeneration. Finally, our work provides evidence of the relative importance of biotic and abiotic drivers of tree seedling regeneration following fire disturbance, and how these drivers are in turn



◀Figure 4. Mean \pm SE of total biomass (a, e), aboveground biomass (b, f), belowground biomass (c, g), ratio of aboveground to belowground biomass (d, h) for tree seedlings of *Picea abies*, *Pinus sylvestris* and *Betula pendula*. Seedlings were grown on sterilized (gamma irradiated) soil, originating from stands differing in burn severity (that is, high, low and unburned), and with the sterilized soil then reinoculated with live soil from stands differing in burn severity (high, low and unburned) or with sterile soil. Different capital letters above bar groups indicate significant differences between plant species across burn severity inoculum class treatments, and small letters within bar groups indicate significant differences for burn severity classes (a–d) or burn severity inoculum class treatments (e–h) according to Bonferroni post hoc tests at $P \leq 0.05$. Corresponding ANOVA results (F - and P -values) are reported in Table 4.

impacted by burn severity. Understanding how burn severity impacts the interplay of these abiotic and biotic soil factors is of particular importance in understanding the mechanisms by which future climate change may influence forest regeneration, given that climate warming is expected to lead to both more frequent and more severe fires in the boreal region. As climate warming is being accompanied by novel fire behavior regimes, there is a growing need to further understand the role played by both soil abiotic factors and the soil microbial community in promoting early seedling establishment under different fire scenarios.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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