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Impacts of increased soil burn severity on larch forest regeneration on permafrost soils of far northeastern Siberia

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ABSTRACT

Fire severity is increasing across the boreal forest biome as climate warms, and initial post-fire changes in tree demographic processes could be important determinants of long-term forest structure and carbon dynamics. To examine soil burn severity impacts on tree regeneration, we conducted experimental burns in summer 2012 that created a gradient of residual post-fire soil organic layer (SOL) depth within a mature, sparse-canopy Cajander larch (*Larix cajanderi* Mayr.) forest in the Eastern Siberian Arctic. Each fall from 2012 to 2016, we added larch seeds to plots along the burn severity gradient. We tracked density of new larch germinants and established seedlings (alive ≥ 1 year) during subsequent growing seasons, along with changes in seedbed conditions (permafrost thaw depth, moisture, and temperature). Over the study, a cumulative total of 17 and 18 new germinants m^{-2} occurred in high and moderate severity treatments, respectively, while germinants were rare in unburned and low severity treatments (< 0.5 germinants m^{-2}). Most seedlings ($> 50\%$) germinated in summer 2017, following a mast event in fall 2016, suggesting safe sites for germination were not fully occupied in previous years despite seed additions. By 2017, established seedling density was ~5 times higher on moderate and high severity treatments compared to other treatments. Cumulative total density of new germinants and established seedlings increased linearly with decreasing residual SOL depth, as did thaw depth, soil moisture, and soil temperature. Our findings suggest that increased soil burn severity could improve seedbed conditions and increase larch recruitment, assuming seed sources are available. If these demographic changes persist as stands mature, a climate-driven increase in soil burn severity could shift forest structure from sparse-canopy stands, which dominate this region of the Siberian Arctic, to high density stands, with potential implications for carbon, energy, and water cycling.

1. Introduction

In recent decades, fire frequency, extent, and severity have increased across much of the boreal forest biome in conjunction with climate warming (Kasischke et al., 2010; Ponomarev et al., 2016; Soja et al., 2007). Because boreal forests contain a large proportion of global terrestrial carbon (C) stocks (Pan et al., 2011), there has been great interest in understanding the effects of an altered fire regime on these ecosystems and potential feedbacks to climate warming (Beck et al., 2011; Bond-Lamberty et al., 2007; Johnstone et al., 2010; Randerson et al., 2006). Directly, increased fire activity can combust C stored in vegetation and organic soils and increase atmospheric CO_2 emissions, creating a positive feedback to climate warming (Bond-Lamberty et al., 2007; Harden et al., 2000). However, fires can also initiate an array of indirect effects on forest regrowth and permafrost stability that can magnify or offset direct fire effects by influencing net ecosystem carbon balance (NECB; (Chapin et al., 2006)).

An important way that intensifying fire activity can impact boreal forest stand dynamics and C pools is by altering demographic processes during early succession, thereby initiating a post-fire successional

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trajectory that results in a mature stand with a different structure than that of the pre-fire stand. Across the boreal forest, post-fire recruitment of trees and large shrubs is strongly influenced by the depth of the soil organic layer (SOL) (Greene et al., 1999, 2007; Greene and Johnson, 2000; Johnstone and Chapin III, 2006), a thick layer of undecomposed dead mosses, lichens, leaf litter, and fine roots (Dyrness, 1982) that accumulates in cold, moist conditions. In mature forests, the SOL is typically thick and porous, so seedlings experience strong fluctuations in moisture and temperature (Johnstone and Chapin III, 2006) and often desiccate before roots reach the stable moisture environment provided by underlying mineral soils (Brown and Johnstone, 2012; Hollingsworth et al., 2013; Johnstone and Chapin III, 2006). Boreal fires are largely fueled by combustion of the SOL, and the proportion of SOL consumed by fire is a major determinant of fire severity (i.e., amount of organic material consumed by fire; (Rowe, 1983), referred to as soil burn severity (Johnstone and Chapin III, 2006). Increased soil burn severity often correlates with decreased SOL depth and increased mineral soil exposure (Johnstone and Kasischke, 2005; Turetsky et al., 2011), which improves seedbed conditions for many boreal plants (Johnstone and Chapin III, 2006; Tautenhahn et al., 2016). For example, recruitment of boreal trees in North America and Scandinavia increased when fire reduced the SOL to < 2.5 cm (Johnstone and Chapin III, 2006). As long as seed sources are available, high soil burn severity can improve post-fire tree recruitment for decades until the understory and SOL reestablish (Nilsson and Wardle, 2005). Given that soil burn severity is predicted to increase with increased climate warming (Schaphoff et al., 2016; Turetsky et al., 2011), this change in the seedbed could have long-lasting implications for future stand dynamics across the boreal region.

Fire-driven changes in SOL depth also influence permafrost stability due to the SOL's insulating properties (Abaimov et al., 2002a,b), which in turn, can impact tree regeneration through impacts on soil growing conditions and germination microsites. The SOL acts as a thermal insulator and decouples air temperatures from those of the mineral soil (Sofronov and Volokitina, 2010). As such, a post-fire reduction in SOL depth can increase soil temperature, deepen the active layer (Kasischke and Johnstone, 2005; Yoshikawa et al., 2002), and increase unfrozen soil volume, allowing roots to access water and nutrients in deeper soils (Kajimoto et al., 2003). Increased soil temperatures may also speed up decomposition rates and increase soil nutrient availability (Biasi et al., 2008; Schimel et al., 2004). In addition, fire removal of the SOL may promote soil subsidence and thermokarst formation (Brown, 1983; Kharuk et al., 2005; Viereck, 1973), which could expose mineral seedbeds and increase favorable microsites for germination. Conversely, if permafrost is ice-rich, deepening of the active layer and thermokarsting could waterlog soils, thereby reducing seedling establishment. Thus, changes in exploitable space and resources within permafrost soils due to increased fire severity and a shallower SOL depth could further influence the rate and magnitude of forest regrowth post-fire.

Over the post-fire successional interval, fire removal of the SOL and subsequent changes in forest regrowth may impact long-term successional trajectories of forest stands because of the tendency for initial post-fire recruitment patterns to predict future stand dynamics (Johnstone et al., 2004, 2010). Different successional trajectories may, in turn, lead to variability in C storage because of differences in forest stand structure, productivity, longevity, litter availability, and flammability. For example, in boreal Alaska, high severity fires that reduce SOL depth and expose mineral soils can shift forest successional trajectories away from black spruce (*Picea mariana*), an evergreen conifer, to pathways with greater deciduous dominance (Johnstone et al., 2011; Johnstone and Chapin III, 2006; Johnstone and Kasischke, 2005). This shift leads to greater aboveground C storage because deciduous stands accumulate more C in live and dead trees than black spruce stands (Alexander et al., 2012a; Alexander and Mack, 2016). Ultimately, forest recruitment patterns can determine whether C lost during fire is reaccumulated during the post-fire successional interval.

The primary objective of this research is to increase our understanding of post-fire forest successional dynamics by investigating if increased soil burn severity could alter patterns of tree regeneration (i.e., germination and seedling establishment for at least 1 year) on permafrost soils within Cajander larch (*Larix cajanderi* Mayr.) forests of the Siberian Arctic when seed sources were available. To address our objective, we conducted experimental burns of varying soil burn severity in a mature, sparse-canopy larch stand, representative of a 'typical' forest in this region having low-density and aboveground biomass (Alexander et al., 2012b; Berner et al., 2012). Each fall from 2012 to 2016, we added larch seeds and monitored larch regeneration and seedbed conditions (permafrost thaw depth, soil moisture, and soil temperature) for five subsequent growing seasons. We focused on Siberian larch forests because they comprise 20% of the world's boreal forests (Osawa et al., 2010), grow on top of C- and ice-rich, loess-like sediments called Yedoma permafrost or Ice Complex in Russia (Schirrmeister et al., 2013; Sher, 1971; Zimov et al., 2006), and contain a quarter of the C in high latitude permafrost soils (Loranty et al., 2016). These forests span much of Arctic treeline in Siberia (Zyryanova et al., 2007), and the ability of larch to recruit in both the presence or absence of fire will be a primary determinant of whether boreal forests respond to climate warming via treeline migration or retrogression (MacDonald et al., 2008). Further, despite the global importance of larch forests and the potential for an altered fire regime to modify regeneration patterns and future forest cover, larch forests of Eurasia remain largely understudied compared to boreal forests of North America. This study aims to fill this knowledge gap by providing experimental data of how variable soil burn severity impacts larch forest recruitment and successional pathways.

2. Methods

2.1. Study area

Research was conducted near the Northeast Science Station (NESS) in Cherskiy, Sakha Republic, Russia in far northeastern Siberia (68.74° N, 161.40° E), which is located on the Kolyma River, ~250 km north of the Arctic Circle and ~130 km south of the Arctic Ocean. Climate is continental, with warm summers (July average = 12 °C), cold winters (January average = −33 °C), and average annual temperature of −11.6 °C. Annual precipitation is low (230 mm yr^{-1}, with ~ half falling during summer (Cherskiy Meteorological Station, https://rp5.ru/Weather_archive_in_Cherskiy). Forests in this region of the Russian Far East are typically open-canopy, sparse stands dominated by Cajander larch (Alexander et al., 2012b; Berner et al., 2012; Loranty et al., 2016), a deciduous needleleaf conifer, which is adapted to growth on continuous permafrost and a short, cool growing season (Abaimov, 2010). Trees in this region rarely exceed 10 m tall, and stands tend to have relatively low aboveground biomass ($< 1,200$ g m^{-2}) (Berner et al., 2012). Seeds are produced annually, with heavy mast events every 2–3 yr and seed dissemination beginning in early autumn (Abaimov, 2010). Ground vegetation consists of deciduous shrubs (*Betula nana* L. ssp. *exilis* (Sukaczev) Hultén, *B. divaricata* Ledeb., *Salix* spp.), evergreen shrubs (*Vaccinium vitis-idaea* L., *V. uligosium* L., *Empetrum nigrum* L., *Ledum subarcticum* (Ait.) Lodd. ex Steud., herbs (*Artemisia tilesii* Ledeb., *Chamerion angustifolium* (L.) Scop., *Equisetum scirpoides* Michx., *Luzula multiflora* (Ehrh.) Lej., *Pedicularis lapponica* L.), grasses (*Calamagrostis neglecta* (Timm.) *Koeler*), mosses (e.g., *Aulacomnium turgidum* (Wahlenb.) Schwägr. (which is dominant)), *Dicranum* spp., *Polytrichum* spp.), and lichens (e.g., *Cetraria cuculata* (Bellardi) Ach., *Cladonia rangiferina* (L.) Nyl., *Peltigera* spp.).

Current fire return interval in the Russian Far East is 80–200 years (Ponomarev et al., 2016), with an annual burned area of ~2.0 Mha yr^{-1} (Rogers et al., 2015), but fire frequency and extent are increasing across the region (Ponomarev et al., 2016). Most fires are

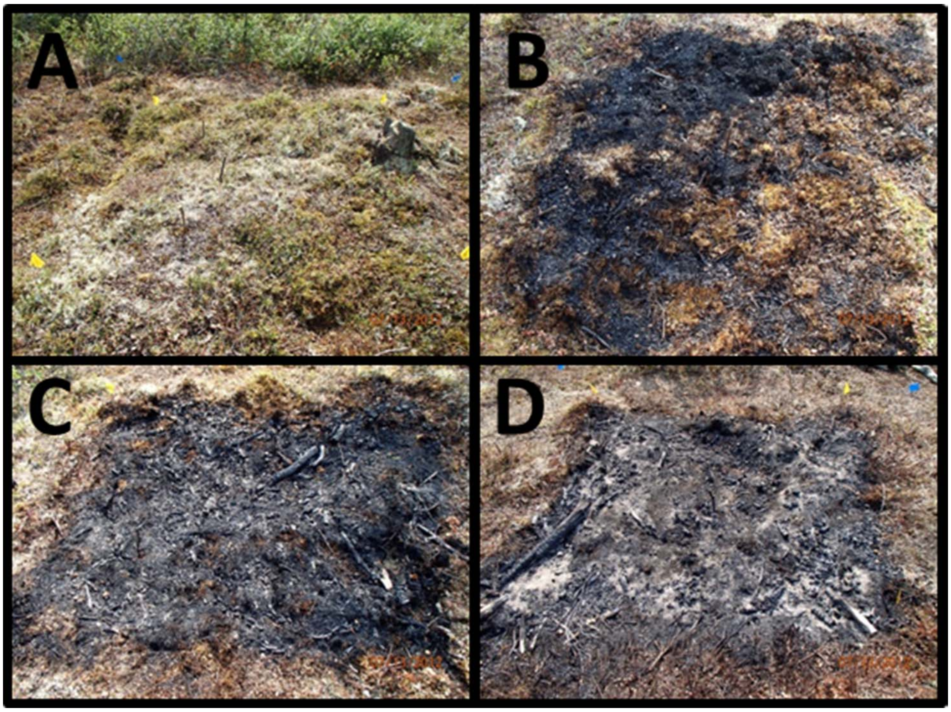

Fig. 1. Soil burn severity gradient obtained with plot-level (4-m^2) experimental burns conducted on July 6–7, 2012 in a Cajander larch forest near the Northeast Science Station, Cherskiy, Russia. (A) Unburned control (residual moss + SOL depth ~12 cm), (B) low-severity (residual moss + SOL depth ~10 cm), (C) moderate-severity (residual moss + SOL depth ~7 cm), and (D) high-severity (residual moss + SOL depth ~3 cm).

surface fires that cause 60–75% stand mortality (Krylov et al., 2014; Rogers et al., 2015; Shuman et al., 2017). Larch leaves have a high moisture content that tends to suppress crown fires (Rogers et al., 2015); most tree mortality is because of root damage. Most of the area burned is due to large fires burning over 2000 ha, and stand-replacing fires are becoming more frequent (Schaphoff et al., 2016).

2.2. Experimental design

To assess the effects of soil burn severity on seedbed conditions (thaw depth, moisture, and temperature) and larch regeneration, experimental burns were conducted on July 6 and 7, 2012 in a low-density (0.03 trees m^{-2}), low canopy cover (~6%), mature (~178 yr old) larch stand on a south-facing slope (15°) located ~0.5 km east of the NESS. Prior to treatment, soil burn severity level (unburned, low, medium, and high) was randomly assigned to each of 16 4-m^2 plots. Each burn plot was located > 2 m from a mature larch tree and > 2 m distant from each other. Plots were aligned in two rows, parallel to the slope, and did not overlap. Soil burn severity treatments were created by varying fuel loads added to each plot. The goal was to obtain a gradient of soil burn severities based on residual SOL depths that represented the range of depths reported in the literature as being important for impacting larch regeneration in other regions (Sofronov and Volokitina, 2010): 2–4 cm (high severity), 6–8 cm (moderate severity), and > 10 cm (low severity).

Fuel loads were based on preliminary burn trials conducted in Alaska, which showed that these quantities were needed to create different levels of soil burn severity when the SOL was moist (i.e., non-drought conditions), which was the forest condition when burns were conducted. Presumably, lower fuel loads would have been needed in drier conditions to produce similar reductions in the SOL. We did not intend to mimic natural fuel loads, which are estimated at 8 kg m^{-2} based on live vegetation, snag, woody debris, and SOL pool estimates in mature, low-density stands (Alexander et al., 2012b). Natural fuels collected from forested and riparian areas near the NESS were dried in a sauna for several days pre-burn. Low severity treatments received 2.25 kg m^{-2} fine twigs (< 1 cm diameter) and leaves. Moderate severity treatments received 2 kg m^{-2} fine twigs and leaves, 2.5 kg m^{-2} small twigs (1–2 cm diameter), and 5 kg m^{-2} coarse twigs (2–5 cm diameter), for a total of 9.5 kg m^{-2} fuels. High severity treatments received 5.5 kg m^{-2} fine twigs and leaves, 5 kg m^{-2} small twigs, 5 kg m^{-2} coarse twigs, and 21.5 kg m^{-2} logs (> 5 cm diameter), for a total of 37 kg m^{-2} fuels.

One day prior to burning, a 0.5-m buffer zone was created around the edge of each plot where all woody vegetation was clipped to create a fire line and minimize potential for fire spread. All woody ground vegetation (mostly *B. divaricata* Ledeb., *L. decumbens* (Ait.) Lodd. ex Steud., *V. vitis-idaea* L., and *V. uligosium* L.) inside each plot was also clipped because we were burning in relatively wet conditions, and moisture in these live fuels likely would have prevented the fires from igniting. In natural wildfires, forest ground vegetation is a main fuel source (Ivanova et al., 2011) and is typically top-killed by the fire (Zyryanova et al., 2007). Our clipping likely produced a similar effect. Plots designated as controls were also clipped (hereafter referred to as "unburned"). Air-dry biomass of clipped vegetation was measured, and a subsample was oven-dried to obtain an air:oven dry conversion factor and total dry biomass/plot. Biomass averaged 291 ± 22 g dry wt m^{-2}, and there were no pre-treatment differences among fire-treated and unburned control plots ($p = 0.16$). Biomass removed from each plot to be fire treated was returned to the plot prior to burning; these weights were factored into the totals for fuel addition mentioned above. At the end of 2013 sampling season, we added control plots with no clipping manipulations because of recent studies indicating effects of shrub removal on active layer conditions (Blok et al., 2010; Myers-Smith and Hik, 2013); these plots are hereafter referred to as "unmanipulated." Fires were started using fire starters, which are dried hay-like material covered with parafilm, and were allowed to burn out naturally. No outside fuel sources (i.e., gasoline) beyond the biomass additions described above were used in these burns because drip-torches could not be brought into Russia and because we anticipated future radiocarbon work. Fuels were mostly consumed on low and moderate severity plots, but unburned charcoal covered ~30% of high severity plots, and ash was abundant (Fig. 1).

2.3. Soil conditions

One-day prior to burning, green moss and SOL (distance from the bottom of green moss to the top of the mineral layer) depth were measured at five locations around the edges of plots (to minimize disturbance). Moss and SOL depth were measured by carefully removing a monolith from the live moss surface to the mineral-organic layer boundary and measuring their depth with a ruler. One-day post-burn, these same measurements were acquired at five locations within the plot.

Thaw depth (depth from bottom of green moss to top of frozen soil) was acquired one day pre-fire and weekly during the field season from 2012 to 2017. Thaw depth was measured by inserting a hand-held metal probe until frozen soil/ice resistance was felt at 2–5 locations within the plot (fewer locations were sampled as study progressed to minimize disturbance on plots). Reported thaw depth measurements in burned plots included a correction to account for the depth of moss and SOL consumed during the fire; analysis of uncorrected data produced similar statistical results. On several occasions in moderate and high severity plots, especially in the last two study years, thaw depth extended beyond the reach of the probe, and depth was recorded as the maximum probe depth (115 cm).

From 2012 to 2017, surface (~5-cm depth) volumetric soil moisture (site-calibrated) and temperature were measured weekly during the field season adjacent to thaw depth measurements using a soil moisture sensor attached to a digital readout (GS-3 and ProCheck, Decagon Devices, Pullman, WA) and a thermocouple thermometer (Amprobe TMD-52, Everett, WA) with a K-type probe, respectively. In 2012, soil moisture was measured only twice, and soil temperature was not recorded due to a malfunction of the probe.

2.4. Larch seed germination rates and seedling establishment

To assess larch seed germination rates and density of new germinants (i.e., number of new seedlings each year) and established seedlings (i.e., number of germinants that survived for ≥1 year) in response to post-fire soil conditions and in the presence of seed sources, we collected larch seeds during 2012 and 2014 near the NESS in late-August/early-September when needles were yellowing (Lobanov, 1985), as seeds are typically fully developed by this time (Shearer, 2008). Larch cones were picked directly from trees, allowed to dry and open, and run through a shaker to remove the seeds (Krechetova et al., 1978; Minnin, 1949; Moscow, 1993). To test seed germination rates, we exposed seeds collected in 2012 to different pre-germination treatments (untreated, soaked in paper towels, or soaked in water), growth substrates (moist paper towel or top soil), and air temperatures (20 and 30 °C). Germination rates were determined by counting the number of germinated seeds over a 30-day period.

Each fall from 2012 to 2016, seeds were broadcast by hand (250 seeds m^{-2}) onto the burn plots as evenly as possible at their natural dispersal time, in late-August/early-September. This seedfall rate is slightly lower than average seed production rates (300–400 seeds m^{-2}) for the western race of Dahurian larch (*L. gmelinlii* (Rupr.) Rupr.) (Pozdnyakov, 1975) but similar to mid-value estimates of seed production reported for North American western larch (*L. occidentalis* Nutt.) (Roe, 1976; Stoehr, 2000). Seeds collected in 2012 were used in 2012 and 2013, and those collected in 2014 were used in 2014–2017. Seeds that were not sown immediately following collection were stored in the dark and in a freezer at 1 °C until subsequent summers when they were brought to room temperature, weighed (2.5 g = 1000 seeds), and placed on plots. Previous work has shown that most larch species do not require cold stratification (Shearer, 2008) and storage between 1 and 3 °C for 25 years had little to no impact on larch germination (Gordon and Faulkner, 1992). One plot of each burn treatment was left unseeded to monitor natural seedling establishment in the absence of outside seed inputs; we used only one plot because of logistical constraints associated with conducting burns. From 2013 to 2017, during ~4 weeks in July, new germinants were marked with a small flag labeled with establishment year and enumerated on each plot; seedlings that established in previous years and were still alive were also counted.

2.5. Data analyses

Treatment impacts on residual moss + SOL depth were analyzed as a two-way repeated measures ANOVA (repeated measure = plot; compound symmetry = covariance structure) with treatment and sampling date (1-day pre-burn vs 1-day post-burn) as fixed effects and plot nested within treatment as a random effect. Variations in mean thaw depth, soil moisture, and soil temperature for each treatment and sampling date (including the one pre-burn sampling date) are presented, but statistical analyses were used only to compare treatment effects for pre-burn values and values averaged over the study period because of the inconsistency of sampling dates across the years, which makes year-to-year comparisons difficult to interpret. Annual density of new germinants and established seedlings were analyzed using a two-way repeated measures ANOVA (repeated measure = plot; compound symmetry = covariance structure) with treatment and sampling year as a fixed effects and plot nested within treatment as a random effect. Cumulative total seedling density and survival rates (ratio of established/new germinants × 100) at the end of the study period were analyzed as a one-way ANOVA with treatment as a fixed effect and plot nested within treatment as a random effect. Percentage of larch seeds germinating over the 30-day incubation period was compared using a three-way ANOVA with pre-treatment exposure, substrate, air temperature, and all interactions as model effects. Data not meeting the underlying assumptions of normality and homogeneity of variance were log + 1 (thaw depth) or sqrt + 1 (moisture and temperature) transformed prior to analyses. When a significant ($p < 0.05$) main effect or interaction was detected, a LSD Student's *t* test was used for post hoc comparisons between treatments.

Relationships between residual post-fire SOL depth and soil conditions (thaw depth, soil temperature, and soil moisture) averaged over the study period, total cumulative germinant density, and total cumulative established seedling density were analyzed using a mixed linear model, with plot nested within treatment as a random effect and SOL depth as a fixed effect. We did not explicitly explore thaw depth, soil moisture, and soil temperature relationships with seedling density as these parameters were significantly linearly correlated with SOL depth, and as such, were not independent variables. We present findings from unseeded plots for reference, but because we did not replicate these plots, we performed no statistical analyses on the results and caution interpretation of these data beyond general trends. All analyses were performed using PROC MIXED in SAS v. 9.4.

3. Results

3.1. Soil conditions

Burning led to a significant decrease (treatment, $p < 0.0001$; date, $p < 0.0001$; treatment∗date, $p = 0.0003$) in residual moss + SOL depth (Fig. 2). Average pre-burn moss + SOL depth was ~12.8 ± 0.5 cm across the treatments, and there were no pre-burn treatment differences among plots ($p > 0.20$ for all comparisons). One day post-burn, depths were significantly shallower on high severity plots (3.3 ± 0.4 cm) compared to other treatments ($p < 0.0001$ for all comparisons). Moderate severity plots had significantly shallower depths (6.7 ± 0.6 cm) than low severity (9.8 ± 0.7 cm; $p = 0.01$) and unburned (11.6 ± 0.7 cm; $p = 0.0006$) plots, but low severity plots did not differ from those left unburned ($p = 0.24$).

Permafrost thaw depth, soil moisture, and soil temperature varied within and across sampling years, but in general, increased with increasing soil burn severity (Fig. 3). Pre-burn, thaw depth was similar

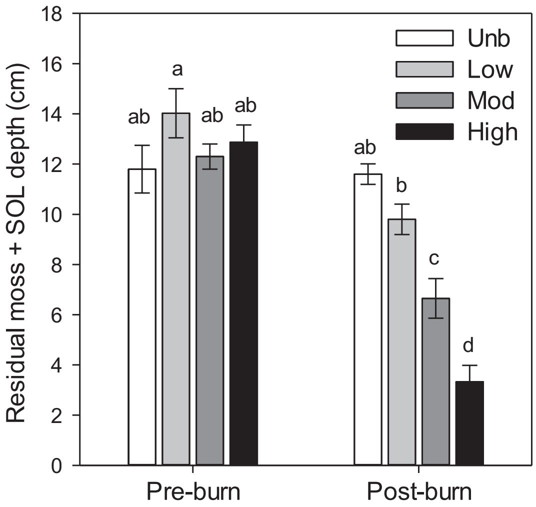

Fig. 2. Mean moss + soil organic layer (SOL) depth (± SE) in unburned (Unb), low, moderate (Mod), and high soil burn severity plots prior to burn treatment on July 6, 2012 and 1-day post-burn in a Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Different letters denote significant differences ($p < 0.05$).

(22–25 cm) across treatments ($p = 0.91$). By 1-day post-burn, thaw depth on burned plots was generally deeper compared to those left unburned, and depth tended to increase with increased soil burn severity; this trend persisted over the study period (Fig. 3A). Regardless of treatment, thaw depth generally increased over the growing season within each year; thaw depth also appeared to increase over the study period. Surface soil moisture and temperature were more irregular than thaw depth but also tended to increase with increased burn severity (Fig. 3B and 3C, respectively).

When averaged over the study, thaw depth ($p = 0.0031$), soil moisture ($p = 0.0014$), and soil temperature ($p = 0.0068$) increased with increased soil burn severity (Fig. 4). Thaw depth was ∼30% deeper on high severity plots (90 ± 4 cm) than low severity, unburned, and unmanipulated plots ($p < 0.05$ for all comparisons) but statistically similar to moderate severity plots (77 ± 5 cm; $p = 0.25$) (Fig. 4A). Thaw depth on moderate severity plots was deeper than low severity (69 ± 4 cm; $p = 0.06$), unburned (63 ± 4 cm; $p = 0.03$), and unmanipulated plots ($p = 0.0023$). Thaw depth on unburned and unmanipulated plots did not differ ($p = 0.25$). Soil moisture on high severity plots ($0.19 \pm 0.02\ \text{cm}^3\ \text{cm}^{-3}$) was similar to moderate severity plots ($0.15 \pm 0.02\ \text{cm}^3\ \text{cm}^{-3}$; $p = 0.14$) but 30–50% higher ($p > 0.05$ for all comparisons) than low severity, unburned, and unmanipulated plots (0.09–$0.12\ \text{cm}^3\ \text{cm}^{-3}$) (Fig. 4B). Surface soil temperature on high

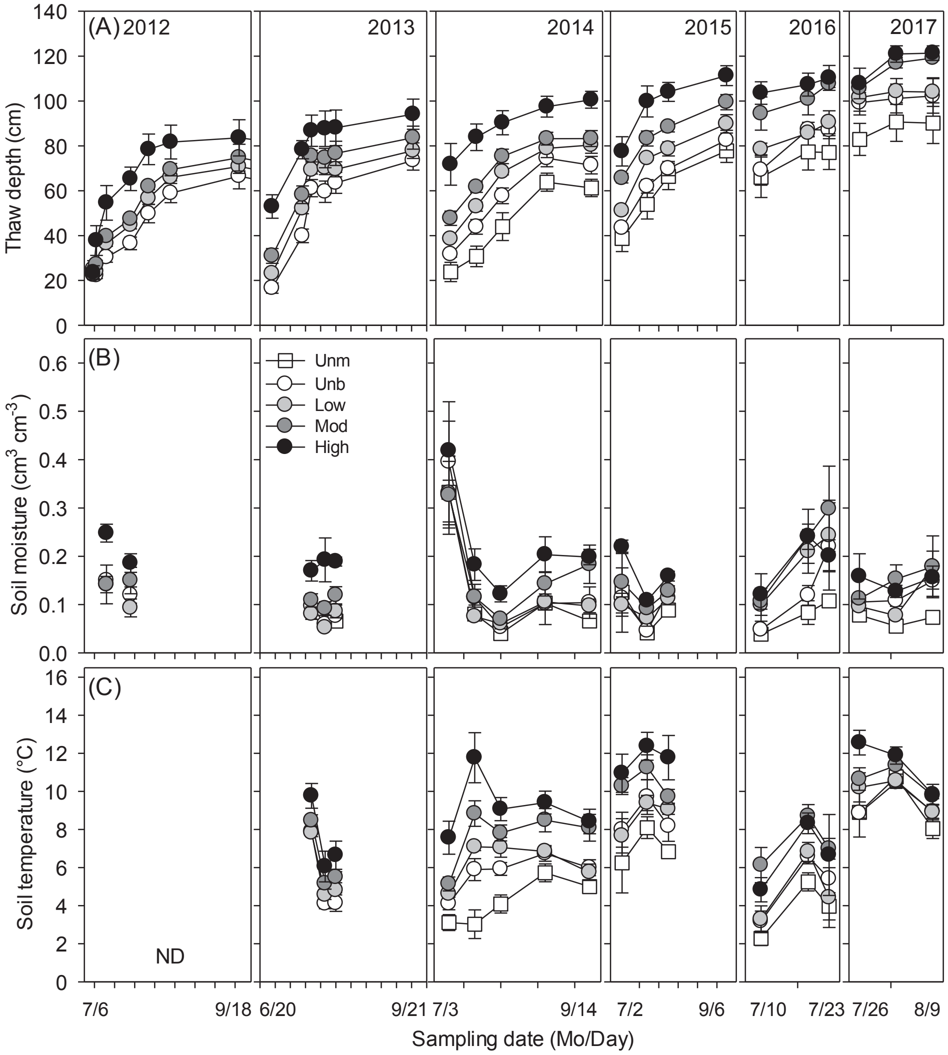

Fig. 3. Mean (± SE) (A) permafrost thaw depth, (B) surface (5-cm depth) soil moisture (site-calibrated), and (C) surface soil temperature on each sampling date from 2012 to 2017 in unmanipulated (Unm), unburned (Unb), low, moderate (Mod), and high severity experimental burn plots in a Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. The first sampling date (July 6, 2012) represents pre-burn data. ND = no data. Unmanipulated plots were not added until the end of the 2013 field season.

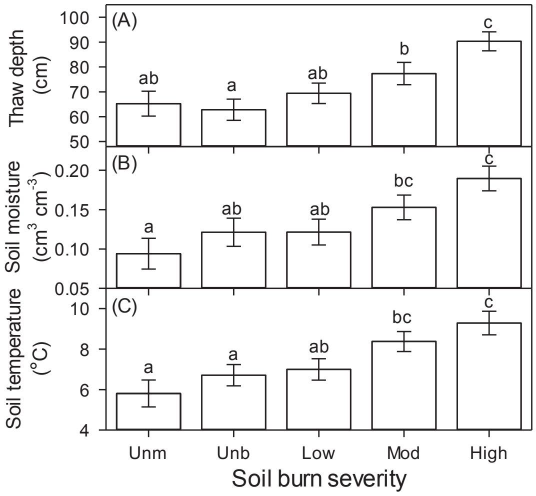

Fig. 4. Mean (± SE) post-treatment (A) permafrost thaw depth, (B) surface (5-cm depth) soil moisture (site-calibrated), and (C) surface soil temperature recorded periodically during the growing season (June – September) then averaged over the study period (2012–2017) in unmanipulated (Unm), unburned (Unb), low, moderate (Mod), and high severity experimental burn plots in a Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Different letters denote significant differences between burn treatments ($p < 0.05$). Unmanipulated plots were not added until the end of the 2013 field season.

severity plots (9.3 ± 0.6 °C) was similar to moderate severity plots (8.4 ± 0.5 °C) ($p = 0.25$) but was 2–3.5 °C warmer than low severity (7.0 ± 0.5 °C; $p = 0.0059$), unburned (6.7 ± 0.5 °C; $p = 0.0024$), and unmanipulated plots (5.8 ± 0.7 °C; $p = 0.0002$) plots, which were statistically similar to one another ($p > 0.05$ for all comparisons) (Fig. 4C).

Mean residual moss + SOL depth measured 1-day post-burn exhibited an inverse linear relationship with mean thaw depth, soil temperature, and soil moisture averaged over the study period (Fig. 5). Thaw depth decreased linearly with residual moss + SOL depth ($R^2 = 0.67$; $p < 0.0001$), ranging from a high near 103 cm on a high severity plot to a low of 52 cm on an unmanipulated plot (Fig. 5A). Surface soil moisture decreased linearly ($R^2 = 0.58$; $p < 0.0001$) from a high of 0.21 cm^3 cm^{-3} on a high severity plot to lows near 0.08 cm^3 cm^{-3} on unmanipulated plots (Fig. 5B). Surface soil temperature decreased 2-fold over the residual moss + SOL range, from a high of 11 °C on a high severity plot to a low of 5 °C on an unmanipulated plot ($R^2 = 0.66$; $p < 0.0001$; Fig. 5C).

3.2. Larch seed germination rates and seedling establishment

In the germination tests, percentage of larch seeds germinating decreased with increased air temperature ($p = 0.02$), but pre-treatment soaking ($p = 0.17$), germination substrate ($p = 0.34$), and all interactions ($p > 0.05$ for all) had no impact on germination rates (data not shown). Overall, percentage of seeds germinating was low (< 16%), but percentage of larch seeds germinating was 5% higher when seeds were incubated for 30 days at 20 °C (15.6 ± 1.2) compared to incubation at 30 °C (11.5 ± 1.2).

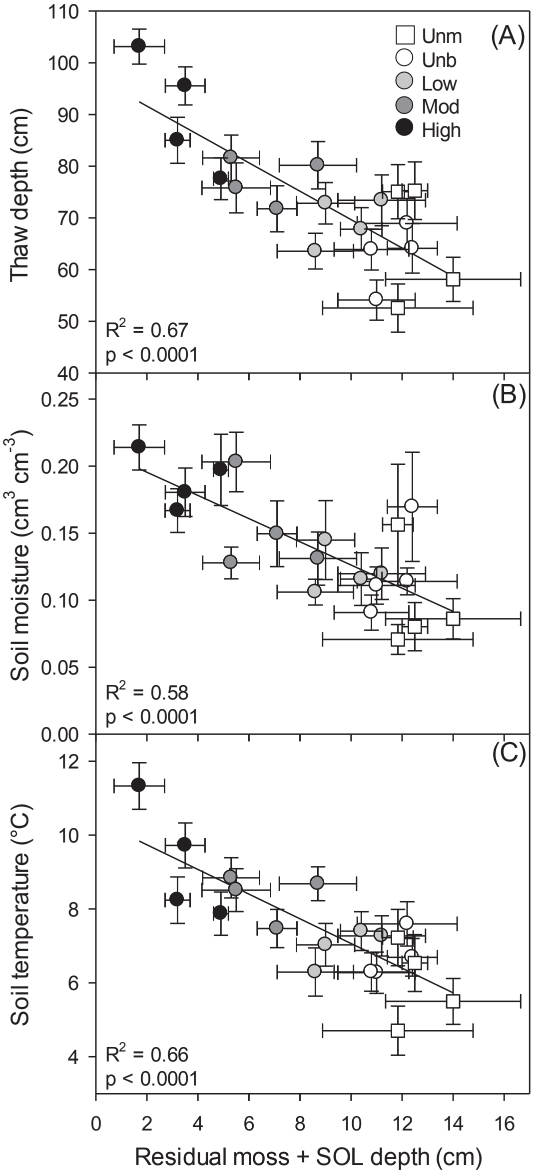

Fig. 5. Mean (A) permafrost thaw depth, (B) surface (5-cm depth) soil moisture (site-calibrated), and (C) surface soil temperature (± SE) recorded periodically during the growing season (June – September) then averaged over the study period (2012–2017) in relation to mean (± SE) residual moss + soil organic layer (SOL) depth measured 1-day post-treatment in unmanipulated (Unm), unburned (Unb), low, moderate (Mod), and high severity experimental burn plots in a Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Unmanipulated plots were not added until the end of the 2013 field season.

Density of new larch germinants increased with increased soil burn severity (Fig. 6A; treatment, $p = 0.0049$), and this trend was consistent across sampling years (treatment ∗ year, $p = 0.5604$), although germinant density was significantly higher in 2017 compared to all other years (year, $p < 0.0001$). High and moderate severity plots had similar germinant density ($p = 0.72$), with 1–2 new germinants m^{-2} yr^{-1} from 2013 to 2016 and about 10 germinants m^{-2} in 2017. A total of 17–18 new germinants m^{-2} were tallied on high and moderate severity plots over the study. New germinant density on low severity, unburned, and unmanipulated plots was significantly lower than moderate and high severity plots ($p < 0.05$ for all comparisons) but statistically similar ($p > 0.15$ for all comparisons) to one another. New germinant density on these plots was < 0.7 new germinants m^{-2} yr^{-1} from 2013 to 2016 compared to 1–4 germinants m^{-2} in 2017.

Similar to new germinants, moderate and high severity plots tended to accumulate more established seedlings over time compared to other treatments (Fig. 6B; treatment, $p = 0.049$). By 2017, these treatments had ~2 established seedlings m^{-2} compared to low severity, unburned, and unmanipulated plots, which had < 0.3 established seedlings m^{-2}. There were no significant treatment differences in percent of seedlings surviving for more than one year ($p = 0.83$; Fig. 6C). We counted only three new germinants on unseeded plots (0–0.25 germinants m^{-2}) from 2013 to 2016; however, in 2017, following a mast year in 2016, we measured 0–7.75 new germinants m^{-2} (Table 1). Density of new germinants on unseeded plots did not appear to vary with soil burn

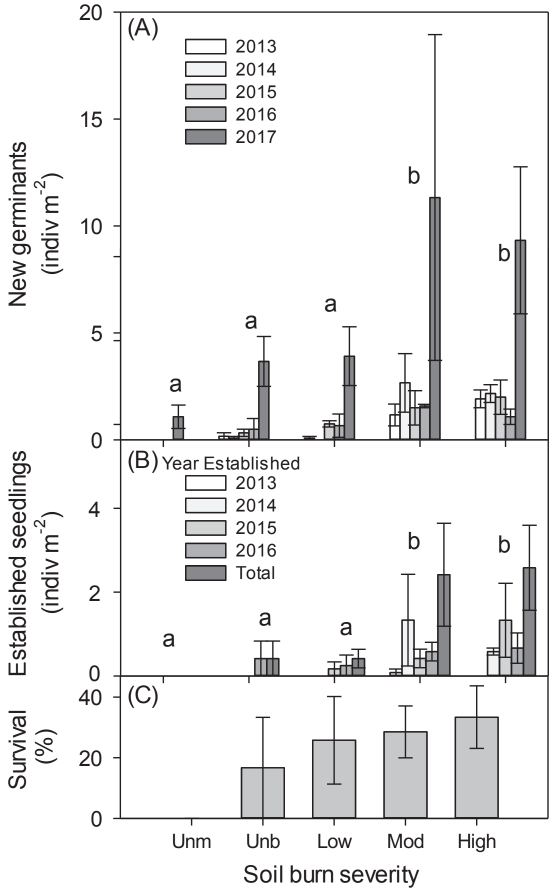

Fig. 6. Mean density of (A) new larch germinants during each study year from 2013 to 2017 and (B) established larch seedlings (alive ≥ 1 year) that germinated in previous years and were still alive in 2017 within unmanipulated (Unm), unburned (Unb), low, moderate (Mod), and high soil burn severity experimental burn plots in a Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Burns were conducted on July 6–7, 2012. Unmanipulated plots were not added until the end of the 2013 field season. No seedlings established on unmanipulated plots; thus, a survival rate was not obtained. Different letters denote significant differences between burn treatments at $p < 0.05$.

Table 1

Density of new larch germinants within unmanipulated (Unm), unburned (Unb), low, moderate (Mod), and high soil burn severity experimental burn plots that were not seeded in a Cajander larch forest near the Northeast Science Station in Cherskiy, Russia. Due to logistical limitations with conducting burns, unseeded plots were not replicated. We present these data only to illustrate that seedling establishment was minimal without seed additions until summer 2017, following a mast year in fall 2016.

	New germinants on unseeded plots (indiv m^{-2})				
Trt	2013	2014	2015	2016	2017
Unm	0	0	0	0	0
Unb	0	0	0	0	1.25
Low	0	0	0.25	0	7.75
Mod	0	0	0	0	4.50
High	0.25	0	0.25	0	0

severity. Total cumulative density of both new germinants and established larch seedlings exhibited a significant ($R^2 = 0.46$, $p = 0.005$ and $R^2 = 0.51$, $p = 0.003$, respectively) linear decrease with depth of the residual SOL (Fig. 7).

4. Discussion

Our results demonstrate that Cajander larch seedling establishment increases with increased soil burn severity when seed sources are available. Each growing season over the 5-year study period, the highest densities of new larch germinants and established seedlings occurred on seeded plots after moderate and high severity fires that left behind a residual SOL depth of 2–8 cm. These findings coincide with those along the Nizhnyaya Tunguska River in central Siberia, where western Dahurian larch seedling establishment was highest (16.5 seedlings m^{-2}) following fires that reduced the SOL to < 4 cm depth and lowest when the SOL was > 8 cm thick (Sofronov and Volokitina, 2010). Post-fire increases in tree seedling establishment with decreased SOL depth to ~2.5 cm have also been documented across boreal forests of Canada and Interior Alaska (Greene et al., 2007; Johnstone et al., 2011; Johnstone and Chapin III, 2006; Johnstone and Kasischke, 2005). Thus, partial consumption of the SOL appears to improve Cajander larch recovery after fire.

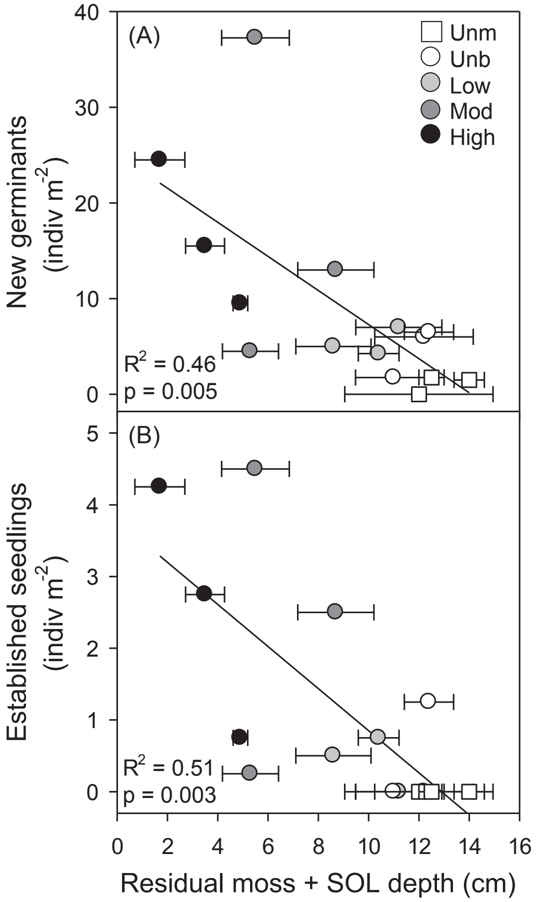

Fig. 7. Cumulative density of (A) new larch germinants over the study period from 2013 to 2017 and (B) established seedlings (seedlings that germinated in previous years and were still alive in 2017) in relation to mean (± SE) residual depth of the moss + soil organic layer (SOL) measured 1 day post-fire within unmanipulated (Unm), unburned (Unb), low, moderate (Mod), and high soil burn severity experimental burn plots in a Cajander larch forest near the Northeast Science Station in Cherskiy, Russia.

Thaw depth, soil moisture, and soil temperature increased with increased soil burn severity and may have contributed to increased larch seedling establishment on more severely burned plots. As soil burn severity increases, residual SOL depth decreases; because the SOL insulates overlying soils, soil temperature and thaw depth increase (Fisher et al., 2016; Hinzman et al., 1991; Jiang et al., 2015; Yoshikawa et al., 2002). Increased soil burn severity is also associated with decreased vegetation cover, which can further increase soil temperature and thaw depth through decreased shading, reduced albedo, and greater snow accumulation, and increase moisture through reduced evapotranspiration rates (Chambers et al., 2005; Fisher et al., 2016).

Albedo may be further reduced by increased char on in severely burned areas, which would also increase soil temperature and thaw (Rocha and Shaver, 2011). Increased thaw depth, soil moisture, and temperature can improve larch regeneration by reducing seed and seedling desiccation (Johnstone and Chapin III, 2006) and increasing rooting volume and nutrient availability (Abaimov et al., 2002a,b). For example, in central Siberia, stem growth of 1-year old Gmelin larch seedlings was higher on warm sites where surface soil (< 5-cm depth) temperatures during the growing season were 8 °C higher (11–19 °C) on average than cold sites (3–10 °C) (Korotkii et al., 2002). Root growth of the same species was limited by both soil temperature and water availability (Prokushkin et al., 2002). Consequently, environmental conditions of the seedbed associated with soil burn severity may be important filters for post-fire Cajander larch seedling establishment when seed sources are available.

We recognize that adding fuels to the plots could have influenced seedling establishment through impacts on soil nutrient availability and/or pH. In a supporting study (Ludwig et al., in preparation), we measured a brief pulse (8-day post-fire) of elevated nitrogen (N; both dissolved inorganic and organic) that dissipated by 1-year post-fire and a small (from 5.7 in unburned to > 6 in burned plots), but short-lived (< 1 week post-fire), impact on soil pH. Phosphorus (P) availability increased post-fire in all burn plots and remained elevated for at least 1 year. Given the consistency of treatment effects on new germinant and established seedling density over the 5-year study and the fleeting nature of changes in N availability and soil pH, variations in these variables were unlikely to have major impacts on observed seedling establishment patterns.

The peak in new germinant density in 2017 following a heavy mast year in 2016 (Alexander, Personal Observation) and the lack of seedling establishment on unseeded plots in non-mast years suggest that seed abundance is an also an important factor influencing larch forest recovery after fire. While there were clear treatment differences in seedling density on seeded plots, density was 5-fold higher in 2017 than previous years across all treatments. In addition, new germinant density was relatively high (1.25–7.75 indiv m^{-2}) on three unseeded plots (Unb, Low, and Mod) in 2017, which had little to no new germinants in previous years. While mature tree density was low on this site, several seed-bearing trees occurred just uphill of these plots, and likely provided a seed source during the 2016 mast event; there were no seed-bearing trees near the one unseeded high severity plot. These findings suggest that safe sites (i.e., sites suitable for germination and establishment) were not saturated in previous, non-mast event years, even on seeded plots and that safe sites exist on unburned and low severity plots, but are fewer, so require higher seed inputs for successful seedling establishment.

The overall increase in new germinant density following a mast year regardless of soil burn severity or seeding treatment may be because there is a trade-off between safe sites that provide the best environmental conditions and those that protect seeds from predators. Unlike other larch species, Cajander larch disperse seeds in fall; thus, many rodents and birds collect these seeds in preparation for winter, which can substantially impact seed availability, especially in non-mast years (Dokuchaev, 2012). Although we did not measure seed/seedling predation, we did observe increased seed and seedling visibility with increased soil burn severity due to reduced vegetation and SOL structure. This could increase seed/seedling predation in more severely burned areas, thereby negating some of the positive impacts of improved environmental conditions. In contrast, visibility and predation would likely be lower in less severely burned areas, but environmental conditions would be less suitable. Seed/seedling predation has been shown to have a major effect on post-fire black spruce regeneration in eastern Canadian boreal forests (Côté et al., 2003) and in montane conifer forests of Montana (Zwolak et al., 2010) and has been attributed to increased fecundity associated with improved foraging efficiency in burned areas with less structural complexity (Zwolak, 2009; Zwolak et al., 2010). As such, seedling establishment may be more limited by seed/seedling predation with higher soil burn severity, while environmental conditions may be more limiting with lower burn severity.

Based on our germination trials, Cajander larch seeds from our sites have low germination rates (12–16%), which could further increase the need for high seed inputs for successful seedling establishment. These findings are similar to germination rates (18%) of Cajander larch from the Magadan region of the Russian Far East, ~1000 km south of our study site, but lower than average rates (25.2%) reported across larch species of Russia (Abaimov et al., 2002a,b). Thus, even without other influencing factors, ~6–8 seeds would be needed to produce a single seedling. We also found that germination rates decreased with increasing air temperature (from 16% at 20 °C to 12% at 30 °C), suggesting that even higher seed inputs will be needed as climate continues to warm.

The importance of seed availability for post-fire forest recovery is important to consider given that increases in fire extent, frequency, and severity can alter seed abundance through various mechanisms. Increased fire size could limit seed availability by increasing the distance between seed-bearing trees and burned areas. Distance to seed source may be particularly important because larch is a masting species with wind dispersal (Abaimov, 2010), as opposed to many boreal conifers which exhibit cone serotiny and on-site seed sources from fire-opened cones. Increased fire frequency could limit recovery by resetting succession and reducing forest age, hence seed-producing capacity at the landscape level (Zyryanova et al., 2007). Increased canopy fire severity could decrease abundance of individual, seed-bearing trees that survive the fire; these survivors can be major contributors to larch forest recovery (Sofronov and Volokitina, 2010). Thus, if canopy burn severity is high, post-fire regeneration may be low due to low seed availability (Cai et al., 2013; Cai and Yang, 2016). As such, low seed availability could limit post-fire tree regeneration even when appropriate seedbed conditions exist.

5. Conclusions

Our findings suggest that if seed sources are available, increased soil burn severity can improve seedbed conditions and increase larch recruitment, with potentially long-lasting influences on forest structure because of the tendency of initial post-fire demographic patterns to persist as stands age (Johnstone et al., 2004; Johnstone and Chapin III, 2006). Importantly, a climate-driven increase in soil burn severity could cause a shift in forest structure from sparse-canopy stands to high density stands in areas with adequate seed sources, which could feedback to influence a suite of ecosystem processes, including C storage (Alexander et al., 2012b; Berner et al., 2012), surface energy balance (Chang et al., 2015), water cycling (Kropp et al., 2017), and the net feedback of increasing fire activity on the climate system (Loranty et al., 2016).

Although multiple factors impact mature stand density, the distribution of a high density larch stands across the landscape could potentially improve our understanding of fire history in this remote region. While uncommon, high density stands are currently scattered throughout the region (Alexander et al., 2012b; Berner et al., 2012), and the presence of these stands necessitates that two factors converged during early-succession: an appropriate seedbed and ample viable seed. Most likely, moderate to high soil burn severity produced the appropriate seedbed because fire is the only natural mechanism in this region capable of removing the SOL over relatively large and remote areas. As such, high density stands could indicate a historical fire that burned at moderate to high soil burn severity. Thus, the factors that influence initial post-fire demographic properties in larch forests likely determine the impacts of an altered fire regime on both current and future forest dynamics.

Author contributions

HDA: Designed study, performed research, analyzed data, wrote manuscript; SMN: Designed study, performed research, assisted with manuscript preparation; MML: Performed research, assisted with manuscript preparation; MCM: Assisted with study design and manuscript preparation; SL: Assisted with research and manuscript preparation; VS: Assisted with study design and manuscript preparation; SD: Assisted with research and manuscript preparation; NZ: Assisted with research and manuscript preparation; IT: Performed seed germination experiment and assisted with manuscript preparation.

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