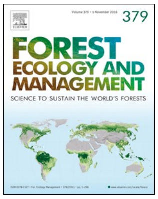
Forest Ecology and Management 478 (2020) 118523

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Topographic position amplifies consequences of short-interval stand-replacing fires on postfire tree establishment in subalpine conifer forests

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ARTICLE INFO

Keywords:
Aspect
Douglas-fir
Disturbance interactions
Fire
Lodgepole pine
Microclimate
Seed germination
Seedling survival

ABSTRACT

Stand-replacing fires burned at 100 to 300-year intervals for millennia in subalpine conifer forests of western North America, but forests are burning more frequently as climate warms. Postfire tree regeneration is reduced when young forests reburn before recovering from previous fires or when drought occurs during postfire years. However, whether seedling vulnerabilities to harsh microclimate conditions may be amplified in short-interval (< 30 years) fires is unclear. We conducted a field experiment to answer three questions: (1) How do germination, survival, and establishment of lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) vary by aspect following high-severity, short-interval fires? (2) What environmental factors control germination, survival, and establishment of both species? (3) Based on our experimental evidence, what proportion of available seed would be expected to establish across landscapes that burned in these short-interval fires? One year postfire, we planted seeds of both species in north-facing, south-facing and flat plots at four sites across the Greater Yellowstone Ecosystem (Wyoming, USA). Soil microclimate was monitored continuously. Seed germination and seedling survival were measured every two weeks during the following growing season and at the beginning and end of the second growing season. Germination did not vary with aspect but increased with early-season soil moisture and temperature. Survival and establishment were low on south-facing aspects (< 1% of seeds established for both species) and declined with warmer soil temperatures and drier soils. For lodgepole pine, we predicted establishment rates of < 1% of available seed over 25% of the reburned landscape. Soil temperatures in short-interval fires were 2°C warmer than similar areas of long-interval fire, with maximum temperatures frequently exceeding 40 °C. Topographic variation will mediate the consequences of short-interval fire for seedling establishment, leading to patchier tree regeneration as climate warming raises the likelihood of short-interval fires.

1. Introduction

Subalpine and boreal forests across the northern hemisphere have coexisted with infrequent, high-severity wildfires for millennia (Bowman et al., 2009), and the adaptative traits of many native species confer ecosystem resilience (ability to rebound following disturbance) to high-severity fires (Frelich, 2002, Johnson and Miyanishi, 2007, Baker, 2009, Turner, 2010, Johnstone et al., 2016). Central to forest resilience is robust postfire regeneration because establishment in the first few years after fire shapes forest structure and composition for decades to centuries (Kashian et al., 2005, 2013, Braziunas et al., 2018, Johnstone et al., 2020). However, anthropogenic warming is increasing fire size, frequency, and severity beyond historical ranges (Jolly et al., 2015, Harvey et al., 2016a, Westerling, 2016, Abatzoglou and Williams, 2016) and these trends are expected to continue through the mid-to-late 21st century (Westerling et al., 2006). It remains unresolved how postfire tree regeneration in subalpine forests will respond to interactions among rapidly changing environmental conditions.

Increased frequency of stand-replacing fires alone could threaten the capacity for subalpine forests to regenerate naturally (Keeley et al., 1999, Brown and Johnstone, 2012, Prichard et al., 2017, Turner et al., 2019). Warm, dry postfire conditions further elevate the risk of regeneration failure (Trumbore et al., 2015, Seidl et al., 2017) because most establishment occurs within the first decade after fire during years of adequate soil moisture (Harvey et al., 2016b, Stevens-Rumann et al., 2018, Hansen and Turner, 2019). Short-interval fires depress postfire tree regeneration via reduced seed supply because young immature trees (that established after an initial fire) may not produce a sufficient

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https://doi.org/10.1016/j.foreco.2020.118523
Received 2 June 2020; Received in revised form 18 August 2020; Accepted 19 August 2020
0378-1127/

supply of seeds (Keeley et al., 1999, Brown and Johnstone, 2012, Enright et al., 2015). Further, seed produced by young stands may be consumed when small trees are completely combusted (Turner et al., 2019), and dispersal from unburned patches and edges is often insufficient for tree regeneration when unburned trees are young and thus short-statured (Gill et al., in press).

Broad-scale effects of climate variability on subalpine forest regeneration in mountainous landscapes are further mediated by fine-scale (< 1 km) variation in microclimate arising from topographic position. Topographic positions characterized by warm, dry microclimates, such as south-facing aspects, convex slopes and lower treeline, are more vulnerable to postfire regeneration failure than buffered positions on north-facing aspects or concave slopes (Donato et al., 2016, Rother and Veblen, 2016, Davis et al., 2019a). However, whether such differences may be exacerbated by shorter fire intervals has not been explored. Under historical fire-return intervals (100–300 years), fire-killed trees remain standing and provide shade for decades (Frock and Turner, 2018). After short-interval fires, complete combustion of aboveground material leaves few legacy structures to buffer the seedling microclimate from temporal (daily, seasonal) and spatial (topographic) variability (Brown and Johnstone, 2012, Turner et al., 2019). Canopy cover buffers microclimate in unburned forests by decreasing maximum temperatures in the understory (Zellweger, 2020; Davis, et al., 2019b). Loss of "structural legacies" in burned forests may increase the likelihood that thresholds of soil temperature and moisture are exceeded, causing postfire conifer regeneration to fail, especially on south-facing aspects and during drought years (Davis et al., 2019a, Hansen and Turner, 2019). Experimental studies in areas of short-interval fire with different microclimates could resolve whether interactions among these drivers could push historically fire-resilient forests into alternative states.

Subalpine tree seedlings are more sensitive to climate conditions than their mature counterparts (Jackson et al., 2009, Johnson et al., 2011, Bell et al., 2014), and seedling responses to environmental conditions vary with developmental stage. Germination depends on antecedent conditions that prime seeds (stratification) and appropriate temperature, moisture, and light regimes following snowmelt. Emerged germinants (first-year seedlings) are vulnerable to environmental variability because they have shallow roots without symbiotic associations of adult trees, are easily buried or uprooted by shifting substrates, are sensitive to temperature extremes, and lack carbon reserves to buffer them from photosynthetic constraints (Johnson et al., 2011). Thus, first-year seedling survival requires suitable microclimate conditions. Mortality in seedlings that experience low soil moisture can be driven by xylem cavitation and embolism (Hacke and Sperry, 2001), or by carbon starvation, when high evaporative demand induces seedlings to shut down daytime respiration to avoid desiccation (McDowell, 2008). Moreover, hydraulic failure and carbon starvation can affect seedlings concurrently, such that impaired hydraulic function reduces a plant's ability to draw on carbon reserves and induce starvation before carbon reserves are depleted (Sala et al., 2010). As seedlings establish (survive the first growing season), competition becomes important. Belowground competition for water and nutrients may constrain seedlings on drier sites, whereas light availability is more limiting on mesic sites (Coomes and Grubb, 2000). Whether seedling vulnerabilities may be amplified in short-interval fires is unknown.

Unusually short fire-return intervals (< 30 years) in the Greater Yellowstone Ecosystem, WY, USA in 2016 offered an opportunity to determine whether effects of aspect on soil microclimate and tree regeneration could be amplified in areas of short-interval high-severity fire. We conducted a two-year field experiment with two dominant subalpine conifers [lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*)] (Baker, 2009) to answer three questions: (1) How do germination, survival, and thus establishment, of lodgepole pine and Douglas-fir vary by aspect following high-severity, short-interval fires? (2) What environmental factors control germination, survival, and establishment of both species? (3) Based on our experimental evidence, what proportion of available seed would be expected to establish across landscapes that burned in these short-interval fires? Finally, to quantify differences in soil conditions in short- vs. long-interval fires, we also measured soil temperature and moisture in three locations where paired plots of similar condition were present. We expected similar germination rates among aspects because seeds typically germinate in late spring after snowmelt, as soils warm but remain saturated. Later in the growing season, we expected lower seedling survival and establishment on south-facing aspects, where summer warming and drying in the absence of standing dead trees might exceed thresholds of tolerance. We expected soil moisture and soil temperature to be dominant determinants of seedling establishment relative to soil properties and competition with herbaceous vegetation. Across our study area, we hypothesized variable proportions of tree seedling establishment in short-interval burns due to differences in aspect.

2. Materials and Methods

2.1. Study area

Yellowstone and Grand Teton National Parks (Wyoming, USA) comprise the core of the Greater Yellowstone Ecosystem (GYE). The climate is continental, with mild dry summers (23.8 °C July mean maximum temperature), and cold snowy winters (-17.6 °C December mean minimum temperature; 592 mm mean annual total precipitation; from 1981 to 2010 at Old Faithful, Wyoming [station #486845], Western Regional Climate Center). Most precipitation falls as snow, and precipitation increases with elevation (Dirks and Martner, 1982). Soils are nutrient poor and derived from Quaternary rhyolite or andesite bedrock. Vegetation is closely associated with topographic gradients in temperature and precipitation (Baker, 2009). Low-elevation grasslands and shrub-steppe valleys transition upslope to montane woodlands of Douglas-fir and aspen (*Populus tremuloides*) and then to subalpine forests dominated by lodgepole pine. These forests persisted during the Holocene under a regime of infrequent (every 100–300 years) high-severity fire (Romme, 1982, Millspaugh et al., 2000, Higuera et al., 2011, Stegner et al., 2019). Subalpine forests in the GYE were resilient to 20th-century fire, including the large 1988 fires (Romme et al., 2011). Whether forests will maintain resilience to climate warming and increased fire remains unresolved (Westerling, 2011; Hansen et al., 2018; Hansen et al., 2020; Turner et al., 2019).

Fires in the GYE during summer 2016 (Fig. S1) included short-interval (< 30 years) burns representative of projected future conditions (Westerling et al. 2011) and revealed greater burn severity and lower tree regeneration than observed following previous long-interval fires (Turner et al., 2019). The 2016 fires created an opportunity to evaluate how microclimate varies with aspect in areas of short-interval fires and how this variation influences tree seedling establishment. The 2016 fires included > 18,000 ha of short-interval burns. The 8400-ha Berry Fire in reburned areas of both 28-yr old lodgepole pines that regenerated after 1988 and 16-yr old lodgepole pines that regenerated after 2000; the 18,400-ha Maple Fire burned 28-yr old lodgepole pine forests that regenerated after 1988; and the 5100-ha Buffalo Fire reburned lodgepole pine and Douglas-fir forests that burned in 1988.

2.2. Experimental design and field methods

In 2017, we established plots and deployed environmental sensors in four sites of stand-replacing short-interval fires that burned in 2016 (n = 12 plots; Fig. S1, Table S1). These sites spanned a gradient from Douglas-fir forests at lower tree line (~1900 m in the Buffalo Fire) to lodgepole pine forests in the subalpine zone (~2200 m in the Maple and Berry Fires). At each site, we categorized areas of high-severity, stand-replacing fire by aspect as north-facing, south-facing or flat. Within

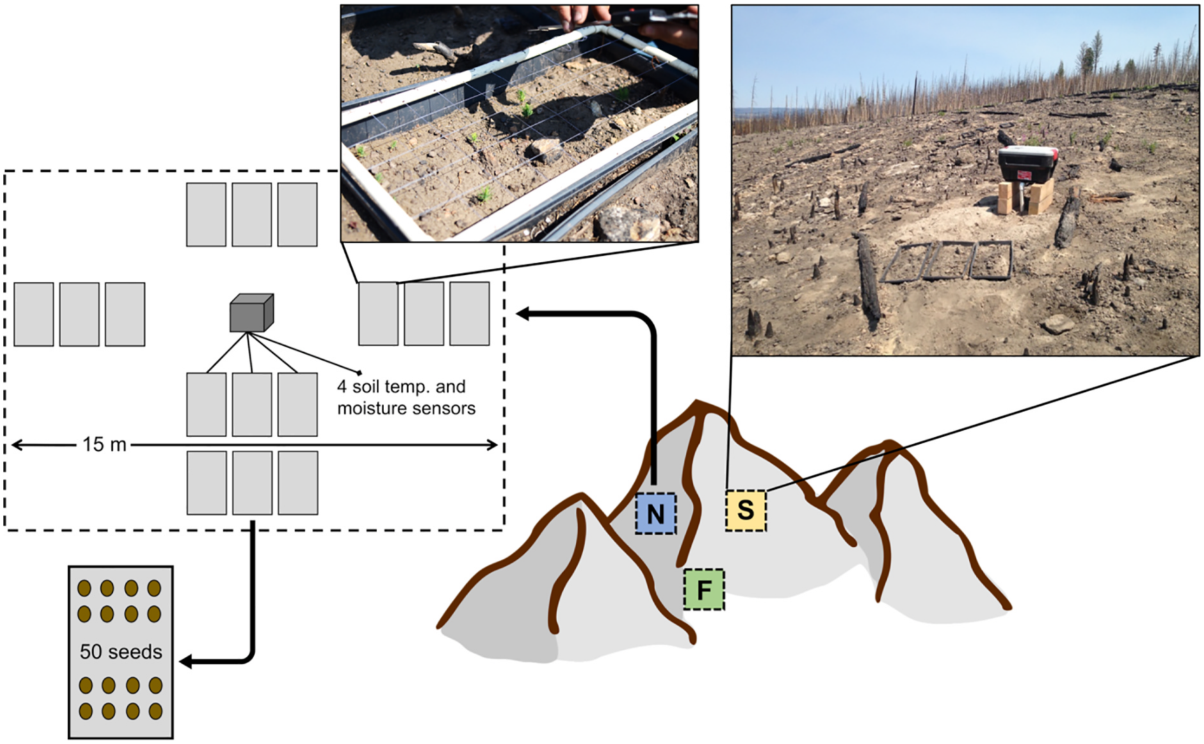

Fig. 1. Schematic of experimental plot design. Seedling trays, shown by grey boxes, were randomly assigned to be planted with Douglas-fir or lodgepole pine, or left unseeded as controls. Schematic is not to scale.

each aspect category at each site, we established a circular plot (15-m diameter) of similar burn severity (complete overstory mortality, nearly complete consumption of woody biomass, exposed mineral soil) and moderate slope ($< 20^\circ$). Areas of high burn severity where the 2016 Buffalo fire overlapped 1988 fire perimeters were inaccessible; thus, we located our plots in areas of severe-surface fire within the Buffalo fire that included sparse Douglas-fir trees, some of which survived the 2016 fire. We retained this site in our study because of the warmer, drier conditions at lower elevation (Hansen and Turner, 2019), and note that the presence of live trees could lessen the effects of aspect on microclimate.

In each plot, we installed five groups of three plastic trays with bottoms removed (50 × 25 cm, $n = 15$ trays per plot) in exposed mineral soil, with one group at plot center and the others positioned 7.5 m from the center in each cardinal direction (Fig. 1). No vegetation was present in any tray. The three trays in each group randomly received seeds of lodgepole pine, Douglas-fir, or were assigned as a control. Four soil moisture and temperature sensors (ECH$_2$O 5TM; Meter Group, Pullman, WA) and a data logger were installed at each plot center, with a sensor buried 5 cm beneath each tray in the center-group and one sensor buried ~1 m away from the trays. Data were recorded hourly for the duration of the experiment. In addition to *in situ* measurements, we characterized mean (1980–2010) growing season temperature and precipitation based on time series collected at the West Yellowstone, Montana (station USC00248857) and Moran, Wyoming (station USC00486440) weather stations near our sites (accessible via National Centers for Environmental Information; https://www.ncdc.noaa.gov/).

Prompted by observations during summer 2018, we augmented measurements in our experimental plots by installing sensors in north-facing, south-facing and flat plots in areas of the Berry Fire that had burned mature forest (> 150 years old; Fig. S1). In contrast to areas of short-interval fire, fire-killed trees were large and standing (Fig. 2-B), and additional sensors allowed us to compare soil microclimate in areas that burned at short and long intervals.

During July 2017, we collected soil samples (15-cm depth) from three locations in each plot to assess texture and nutrient content. Samples were composited, dried at 60 °C for 24 h, and sieved through 2 mm screen before analysis at the University of Wisconsin Soil and Forage Analysis Laboratory.

Consistent with seed-rain phenology, we planted 50 lodgepole pine and 50 Douglas-fir seeds in September 2017 ($n = 250$ seeds species^{-1} plot^{-1}, and 3000 total seeds species^{-1}); control trays were unseeded. Seeds were locally sourced from the USDA Forest Service Lucky Peak seed extractory and originated in the nearby Shoshone National Forest. Seeds were equally spaced 5 cm apart and planted 5 mm below the soil surface. Prior to sowing, we estimated optimal germination rates by placing seeds in petri dishes on filter paper kept damp, in a lab at 21 °C. Grow lights matched growing-season daylength in the study area, and trials ran for eight weeks. The proportion of seeds that germinated was 0.79 for lodgepole pine and 0.70 for Douglas-fir.

We recorded the presence and survival of every seedling every two weeks from June-August 2018, at the end of the first growing season (October 2018), and at the beginning and end of the second growing season (June and October 2019). During each visit, we recorded germination (new seedling emergence) and seedling survival (green foliage visible) or mortality. We inspected each control tray for the presence of seedlings that seeded naturally; no such germination occurred in the control trays. Any aboveground biomass of other species (e.g., graminoids or forbs) in any tray was trimmed to the ground surface during each visit; we did not remove roots to avoid disturbing the seedlings. Ground cover outside the trays was characterized during July 2018, near annual peak biomass, by recording percent cover of forbs, grasses, litter, bare ground, rock, charred material, or moss in 15 quadrats (50 × 25 cm) per plot. Percent cover of forbs and grasses was summed to estimate herbaceous vegetation cover.

2.3. Analyses

Environmental conditions (microclimate, soil properties, vegetation

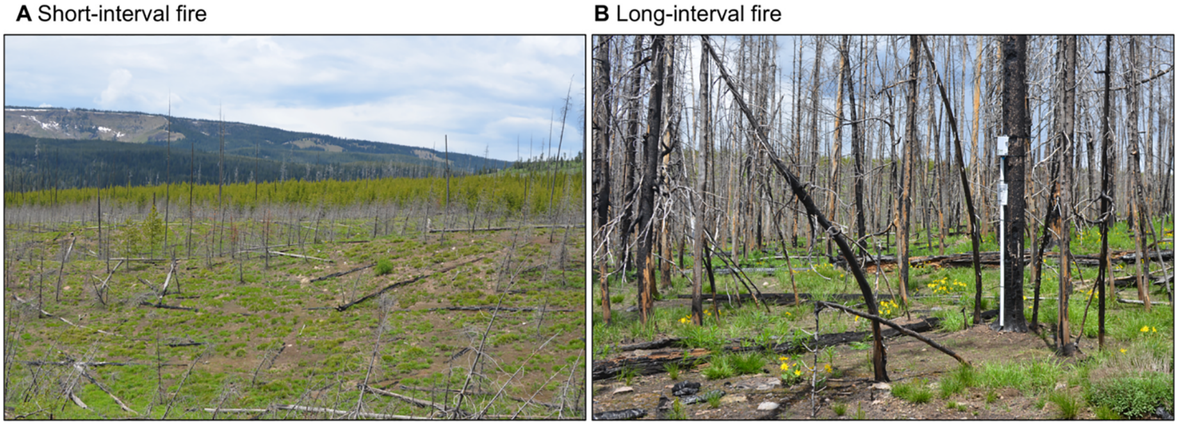

Fig. 2. Areas burned by short-interval (16-year) fire were characterized by limited standing or downed woody debris and low vegetation cover (A), whereas adjacent areas burned by long-interval (> 150-year) fire were characterized by abundant legacy structure (B). Soil temperatures in the short-interval fire were > 2 °C (10%) warmer and soil moisture was up to 0.05 m^3 m^{-3} (25%) lower than the long-interval fire (Fig S2), which were separated by < 500 m.

cover) were summarized by plot. Readings from soil sensors buried away from trays were indistinguishable from other sensors, indicating no effect of the trays on soil moisture or temperature. Soil temperature and moisture data were summarized as the daily mean of hourly readings and compared among aspect classes. Soil temperature and moisture data were also compared between the short- and long-interval plots in the Berry fire.

All data analyses were conducted at the plot level. Germination, first and second year survival, and establishment by species are reported as the plot-level mean of the proportion of successes in each tray. Successful establishment was defined as germination and survival through both years, i.e., through October 2019. Differences among aspects (Question 1) were assessed using a one-way analysis of variance (ANOVA, $\alpha = 0.05$) of logit-transformed proportions for each response (germination, survival in year one, survival in year two, and establishment) independently. When aspect was significant, pairwise differences between aspects were evaluated using Tukey's range test ($\alpha = 0.05$).

Generalized linear models with a logit link function and binomial errors were used to quantify effects of environmental variation on germination, survival and establishment (Question 2). We considered soil microclimate, soil properties and herbaceous vegetation cover (Table S2) and selected predictors based on a priori expectations for each seedling life stage. For germination, we used median soil temperature (°C) and moisture (VWC, m^3 m^{-3}) during the period of germination (June 1 – June 15, 2018), and soil organic matter content (SOM, %). For survival and establishment, we used median soil temperature and moisture during the first (July 1 – October 1, 2018) and second (June 1 – October 1, 2019) growing seasons, total soil nitrogen (N; %), SOM, and herbaceous vegetation cover. Models were estimated with standardized predictors centered on zero, the number of predictors in a given model was limited to two, and colinear predictors ($R^2 > 0.6$) were not included in the same models. We used AICc (Burnham and Anderson, 2002) to rank all possible models for each response, and models within two AICc units of the most predictive model were retained. Mean coefficient estimates were calculated for each term from all retained models that included the term. P-values were derived from analysis of deviance tables of a global model (response as a function of all predictors without interactions) using a likelihood-ratio test. Odds-ratios were calculated from models estimated using the same procedure, but on the original predictor scale. All analyses were conducted in R using functions from base (R Core Team, 2018) and MuMIn (Barton, 2020) packages.

To explore spatial patterns of vulnerability in postfire tree establishment due to topographic position throughout areas of recent short-interval fire (Question 3), we estimated models for second-year lodgepole pine seedling establishment from topographic indices. We replaced field-measured environmental predictors with topographic position metrics, including aspect (transformed to an index; Beers, Dress, & Wensel, 1966), elevation, topographic position index (TPI; Wilson, O'Connell, Brown, Guinan, & Grehan, 2007), and heat load index (HLI; McCune & Keon, 2002). All predictors were derived from a ~30 m-resolution digital elevation model (National Elevation Dataset). We made predictions using the most predictive two-term model based on AICc. We predicted relative establishment rates (proportion of available seed) within perimeters of 2016 short-interval fire where our experimental results are most applicable; grasslands, lakes, and exposed bedrock were excluded. Cumulative frequency distributions were used to estimate the proportion of the reburned landscape falling in classes of estimated relative establishment probability.

3. Results

3.1. Environmental conditions

Growing season climate. Based on permanent climate stations near our plots, growing season air temperatures were near 1980–2010 means during the two years of our experiment, but precipitation varied (Fig. S2). July and September were dry during the first year of our experiment (2018), with precipitation 0–22% of the 30-yr mean; August precipitation was near the mean (Fig. S2). During the second year (2019), precipitation was near the mean during July, low in August, and above the mean in September (Fig. S2).

Soil microclimate. Based on data collected by in situ sensors installed at each plot, soils were cool and wet during the germination period and similar across aspects, averaging 14.4 °C and 0.129 m^3 m^{-3}. Soils were warm and dry during the growing seasons, particularly on south aspects. Mean temperatures were 2.5 °C warmer in 2018 and 2.1 °C warmer in 2019 on south aspects than on north aspects. Maximum soil temperatures were also higher at south-facing plots than other aspects. Soil moisture declined through the growing season and was consistently lower at south-facing plots. During the growing season, mean soil moisture was 0.022 m^3 m^{-3} (25%) lower in 2018 and 0.029 m^3 m^{-3} (21%) lower in 2019 on south aspects than on north aspects. Differences in soil temperature and moisture among aspects were most pronounced at the lowest elevation site.

When areas that burned at short (16 years) or long intervals (> 150 years) were compared, soil temperatures at north- and south-facing plots in the short-interval fire were generally > 2 °C warmer and soil moisture was up to 0.05 m^3 m^{-3} (25%) lower than areas of long-interval fire (Fig. 3). Within-season trends in daily soil temperature and moisture were similar, but short-interval fires reached higher

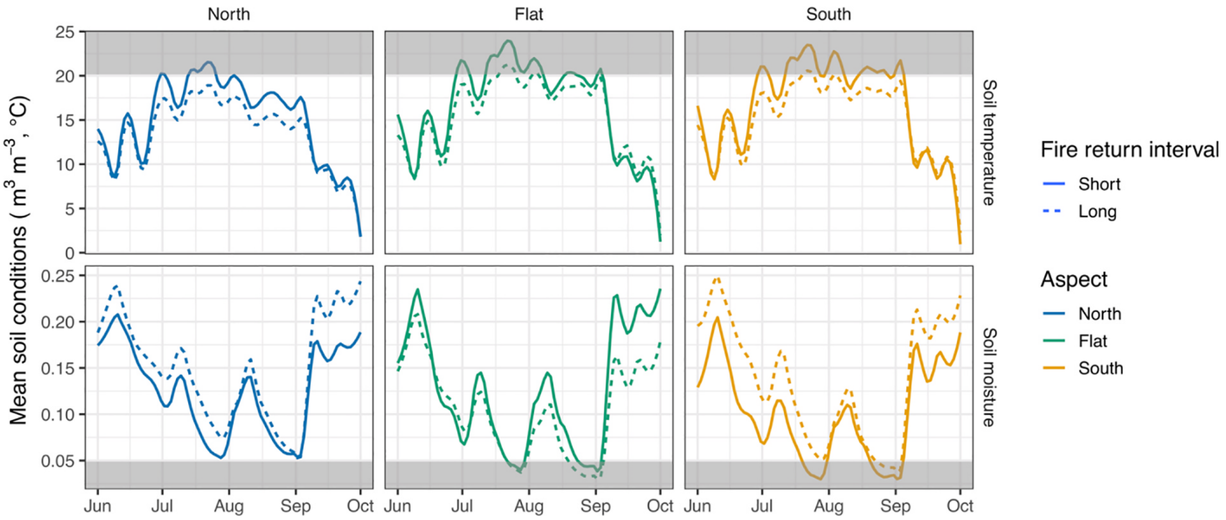

Fig. 3. Soil conditions from June 1 – October 1, 2019 in forests that burned under short (16 years, solid line) vs. long (> 150 years, dashed line) fire return intervals. Values are smoothed 14-day means of daily mean values. Line color indicates slope aspect where sensor was located (blue = north, green = flat and yellow = south). Grey boxes are a visual cue to highlight differences among panels, and span 0.00–0.05 m^3 m^{-3} soil moisture and 20-25° C soil temperature. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

temperatures and lower soil moisture (Fig. 3). During July and August, daily median soil temperatures frequently exceeded 20 °C on south-facing or flat aspects in short-interval fires but seldom exceeded 20 °C in long-interval fires or on north-facing slopes. During late July, in the middle of the growing season, daily median soil moisture approached zero in south-facing plots in short-interval fire (Fig. 3).

Soil characteristics and vegetative cover. Among all plots, soils were loamy in texture, mean soil organic matter (SOM) was 3.1 ± 0.38%, and mean soil total N 0.17 ± 0.05% (Table S2). Peak herbaceous vegetation cover in 2018 was 33 ± 7% and varied among sites (Table S2). Among sites, soil organic matter, total soil N and herbaceous cover were lowest at the Maple fire.

3.2. *Germination, survival, and establishment by aspect (Question 1)*

The mean proportion of lodgepole pine seeds that germinated among all plots was 0.13 ± 0.03, the proportion of germinants that survived until the end of the experiment (three years postfire) was 0.41 ± 0.08, and the proportion of all planted seeds that established after two years was 0.06 ± 0.02. The proportion of lodgepole pine seeds that germinated did not vary with aspect. However, aspect explained 61–67% of the variation in first and second year survival (Table S3), with over four times as many germinants surviving on north-facing (0.60) and flat (0.53) plots than on south-facing (0.13) plots (Fig. 4). Aspect explained 50% of the variation in establishment of lodgepole pine after two years, with higher establishment on north-facing (0.11 of planted seeds) and flat plots (0.06) and extremely low establishment on south-facing plots (0.01).

The mean proportion of Douglas-fir seeds that germinated was 0.06 ± 0.01 (Fig. 4), less than half the germination of lodgepole pine. The proportion of germinated seedlings that survived until the end of the experiment was only 0.10 ± 0.05, and the proportion of planted seeds that established was 0.01 ± 0.00 (26 seedlings survived until the end of the experiment). Germination, survival and establishment for Douglas-fir did not vary with aspect (Fig. 4, Table S3).

3.3. *Environmental predictors of germination, survival and establishment (Question 2)*

Germination. The proportion of lodgepole pine and Douglas-fir seeds that germinated increased with soil moisture and temperature (Fig. 5). A 0.01 m^3 m^{-3} increase in soil moisture increased the odds of germination by 44% for lodgepole pine and by 28% for Douglas-fir. A 1 °C increase in soil temperature increased the odds of germination by 167% for lodgepole pine and 79% for Douglas-fir.

Survival and establishment. Lodgepole pine survival in both years was greater with cooler soil temperatures during the growing season and lower herbaceous cover, and second-year survival increased with soil moisture (Fig. 5). A 1 °C increase in soil temperature decreased the odds of lodgepole pine survival through year two by 24%, a 0.01 m^3 m^{-3} increase in soil moisture increased the odds of survival by 15%, and a 10% increase in herbaceous cover decreased the odds of survival by 66%. A 0.01 m^3 m^{-3} increase in soil moisture increased the odds of lodgepole pine establishment after two years by 34% and a 1% increase in SOM decreased the odds by 53%.

Douglas-fir survival was higher with greater soil moisture and cooler soil temperatures in both years; survival also increased with SOM in the first year and decreased with herbaceous cover in the second year (Fig. 5). A 1 °C increase in soil temperature decreased the odds of Douglas-fir survival by 60%, a 0.01 m^3 m^{-3} increase in soil moisture increased the odds by 52% and a 10% increase in herbaceous cover decreased the odds by 41%. A 0.01 m^3 m^{-3} increase in soil moisture increased the odds of Douglas-fir establishment after two years by 55%, and a 10% increase in herbaceous cover decreased the odds by 42%.

3.4. *Landscape patterns of relative lodgepole pine establishment (Question 3)*

The most predictive model of relative establishment rates of lodgepole pine within short-interval fires based on topographic indices included aspect and topographic position index (TPI) as predictors (Table S5). This model of relative establishment rates in reburned areas, given propagules, indicated substantial spatial variation across the landscape (Fig. 6). We estimated establishment rates of available seeds ranging from 0.00 to 0.89 and a landscape-wide median of 0.03 ± 0.00 (Fig. 6). At the upper end, only 5% of the reburned landscape was predicted to have establishment rates > 0.15, but 25% of the reburned landscape had establishment rates ≥0.08 (Fig. 6). At the lower end, 25% of the reburned forest landscape, was predicted to have establishment rates ≤0.01 of available seeds (Fig. 6).

4. Discussion

Our study provides evidence that effects of topographic position on

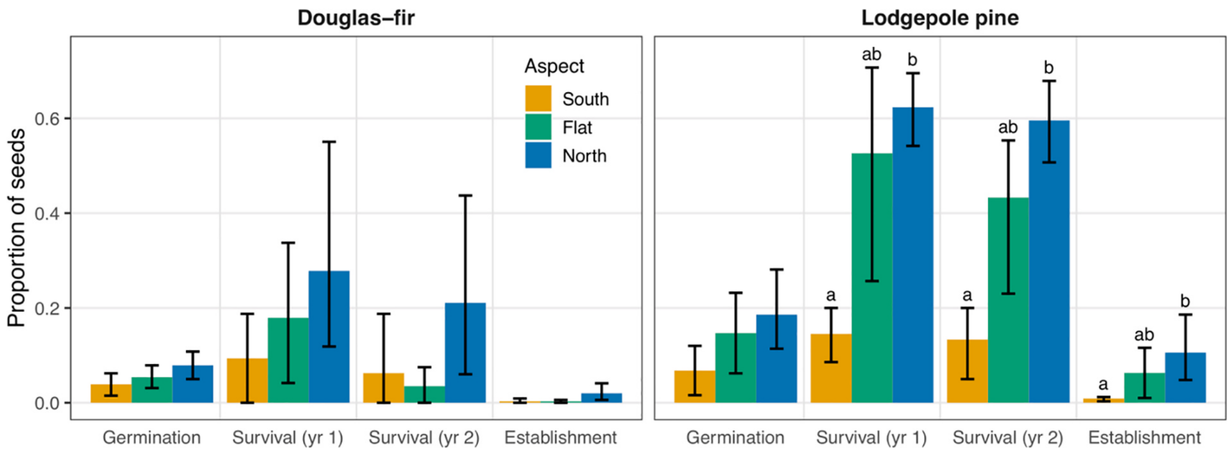

Fig. 4. Proportions of planted lodgepole pine and Douglas-fir seeds that germinated, survived, and established. Colored bars show the mean proportion of seeds in each response by aspect (blue = north, green = flat and yellow = south). Error bars indicate bootstrapped 95% confidence interval, and letters indicate pairwise differences among groups based on a post-hoc Tukey's range test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

soil microclimate and postfire tree seedling establishment were amplified in short-interval fires, where soils were > 2° C warmer and 25% drier than in comparable locations of long-interval fire. Following short-interval fire, establishment of two conifer species was near zero on south-facing aspects, where soils were 2.3 °C warmer and 23% drier than north aspects. Topoedaphic controls on tree regeneration varied by developmental stage, but soil moisture limited germination and survival of both conifers. By extrapolating our findings for lodgepole pine across short-interval burned areas and assuming adequate seed supply, we estimated that establishment could potentially fail across ~25% of short-interval burned areas. Low or absent postfire regeneration could persist for decades or longer (Donato et al., 2016, Hansen et al., 2018). These findings underscore the interactive effects of changing drivers (Paine et al., 1998, Ratajczak et al., 2018) – interactions that may manifest more frequently in the future with directional change in temperature and fire activity (Millar and Stephenson, 2015).

Differences in soil temperature and moisture between north and south aspects were similar in magnitude to the differences between short- and long-interval fires. Our data suggest that their additive effects on microclimate and tree seedling establishment can erode forest resilience on south aspects in short-interval fires. Aspect mediates variation in drought-induced mortality (Schwantes et al., 2018), adult tree growth (Adams et al., 2014) and seedling mortality (Hansen and Turner, 2019). In our experiment, aspect explained > 50% of the variation in lodgepole pine seedling survival and establishment. The effect of aspect is amplified after short-interval fires because these settings lack standing dead trees (Turner et al., 2019) to buffer the microclimate from environmental exposure. The effect of reduced postfire residuals on the seedling microclimate mirrors impacts of residual removal by post-disturbance salvage logging and canopy loss in live forests. Areas salvage-logged after high-severity fire experience higher mean temperatures (Vlassova and Pérez-Cabello, 2016), lower nighttime minimum temperatures and begin to warm earlier in the day (Fontaine et al., 2010). Downed burnt wood can create "nurse" sites that reduce seedling water stress (Marañón-Jiménez et al., 2013). In unburned forests, microclimatic conditions under canopy cover, buffered from regional macroclimate, drive plant community change (Zellweger et al., 2020). After long-interval fires, standing dead trees offer approximately half the buffering capacity of live canopies in western conifer forests (Davis et al., 2019b). We suspect that the added warming and evaporative demand in short-interval fires exceeded physiological thresholds of tolerance in young tree seedlings at south-facing sites.

Controls on postfire tree regeneration varied with seedling stage. Our expectation that *germination* of lodgepole pine and Douglas-fir would not be affected by aspect per se was supported, however germination did increase with both soil moisture and temperature. Similar experiments have shown that germination of Engelmann spruce (*Picea*

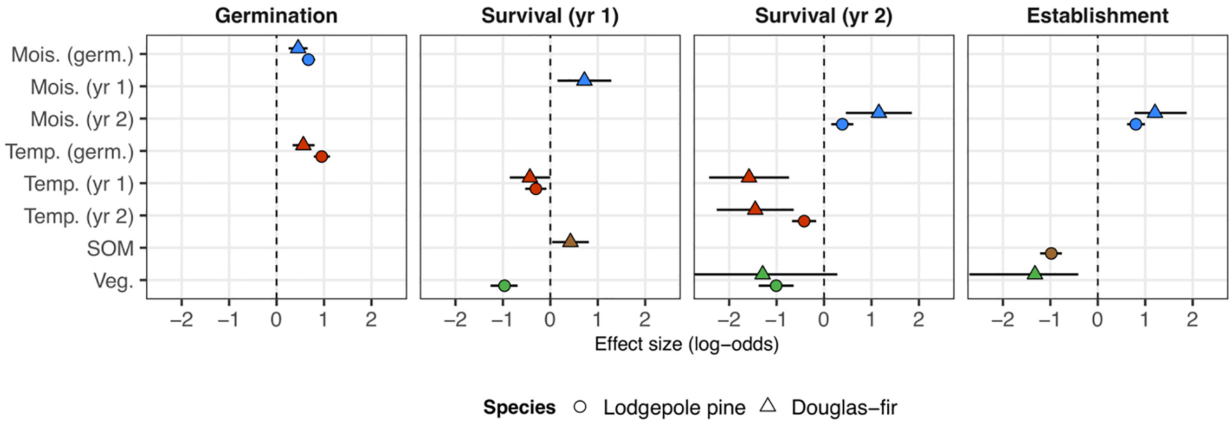

Fig. 5. Standardized coefficient estimates with 95% confidence intervals for median soil moisture (Mois.) and soil temperature (Temp.) during the germination (germ.) period and growing seasons in year one (yr 1) and year two (yr 2), soil organic matter content (SOM), and herbaceous vegetative cover (Veg.) in models of lodgepole pine (circles) and Douglas-fir (triangles) germination, survival, and establishment. Soil total nitrogen was not retained in any of the most predictive models, and not all predictors were available in all models (see Methods).

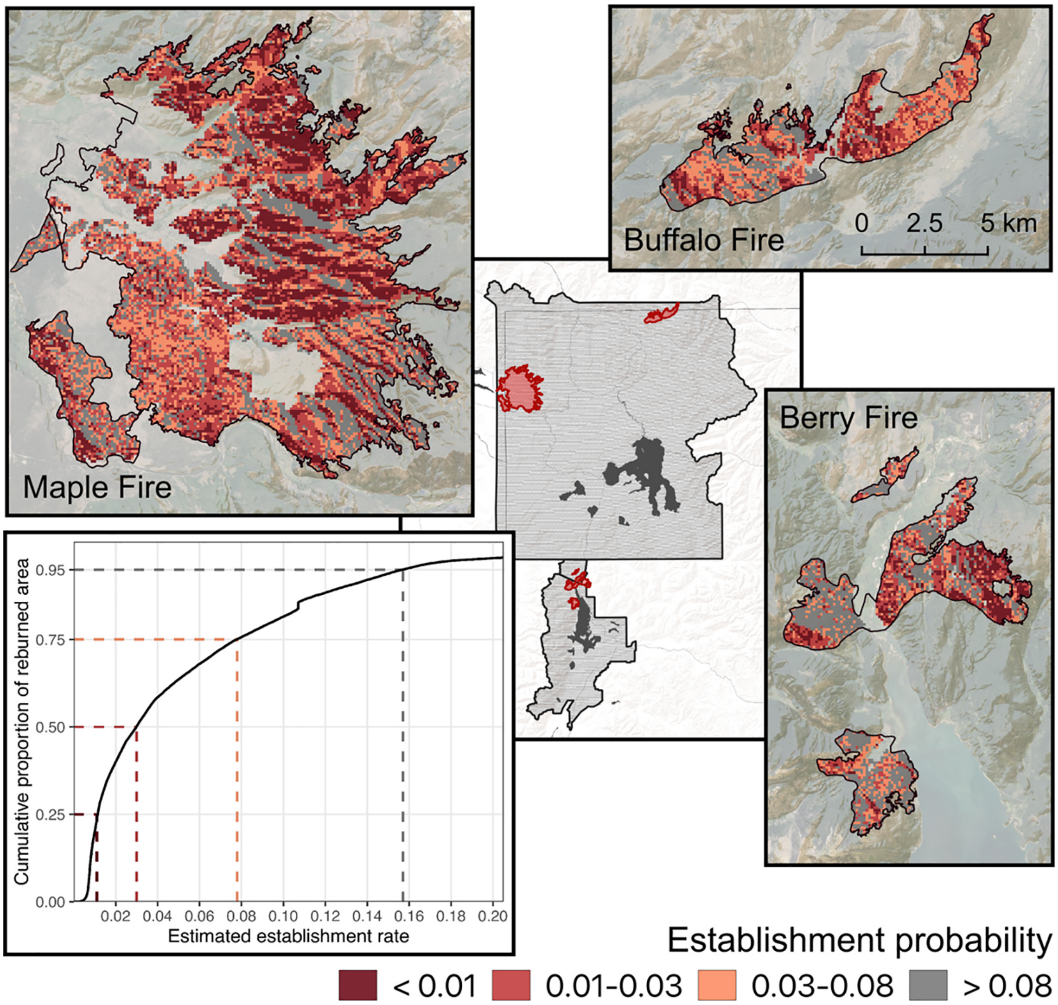

Fig. 6. Map of estimated relative lodgepole pine establishment in areas that reburned in short-interval fires in 2016, based on extrapolation of a GLM (Table S5) of establishment rates as a function of aspect and topographic position index (TPI). Red-grey colors on large-scale maps indicate binned estimates of seedling establishment probability given propagules; uncolored areas within perimeters are non-forested. Dark grey polygons on small-scale map are water bodies, red polygons are reburned areas, and grey polygons are national parks. Base map data © Google and ESRI. Inset figure shows the cumulative density function of estimated lodgepole pine establishment. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

engelmannii) declines with warming temperature (Kueppers et al. 2017b) but is mediated by moisture availability (Kueppers et al., 2017a). Our expectation that seedling *survival* would be reduced on south-facing slopes was supported for lodgepole pine, but not for Douglas-fir (noting that our detection ability was limited by low statistical power). Soil moisture was universally important in our experiment, having positive effects on both seed germination and subsequent survival. Few studies separate environmental effects on germination and survival, but our results are consistent with studies across western US conifer forests that identify soil moisture limitations as a primary control of long-term establishment (Moyes et al., 2015, Rother and Veblen, 2016, Lazarus et al., 2018, Andrus et al., 2018, Davis et al., 2019a, Hansen and Turner, 2019). Our results were also consistent with experimental (Rother et al., 2015, Foster et al., 2020) and observational (Hankin et al., 2019, Rodman et al., 2020) evidence from drier, low-elevation Douglas-fir forests. Variability in the controls on postfire regeneration through developmental stages mirrors tree establishment more generally (Schupp, 1995). At arctic and alpine tree line, warming effects are contingent on moisture, soil fertility, herbivory, and competition with surrounding vegetation (Lett and Dorrepaal, 2018).

Herbaceous vegetation cover influenced seedling survival for both species. Although we removed aboveground leaves and stems, we suspect that belowground competition with herbaceous vegetation reduced tree seedling survival. Most herbaceous vegetation in these plots consisted of perennial graminoids (e.g., *Calamagrostis rubescens, Carex rossii, Carex geyeri*) and forbs (e.g., *Arnica cordifolia*, *Lupinus argenteus*, *Achillea millefolium*) that resprouted after the 2016 fires. These plants likely had well developed root systems allowing them to outcompete first-year tree seedlings. Experimentally seeded herbaceous vegetation decreases establishment and growth of lodgepole pine seedlings (Powell, Pitt, & Wikeem, 1994). Competition is frequently as important as warming for tree seedling establishment at treeline (Lett and Dorrepaal, 2018).

Given that soil temperatures in the short-interval fires we studied were often 2 °C warmer than similar areas of long-interval fire, with maximum temperatures frequently exceeding 40 °C, our results strongly suggest that short-interval fires can push conditions beyond thresholds of seedling tolerance in exposed positions. Our findings are consistent with recent work in lower montane forests that found minimal ponderosa pine (*Pinus ponderosa*) and Douglas-fir recruitment when soil moisture was below a threshold of 0.07 $m^3\ m^{-3}$ (Davis et al., 2019a). Previous experiments in our study system also found sharp declines in lodgepole pine seedling establishment when mean growing-season soil temperatures exceeded 16 °C (Hansen and Turner, 2019). By creating warmer microclimates, short-interval fires may accelerate the loss of resilience in subalpine forests.

Reduced regeneration after short-interval fires has been documented in subalpine forests of the western US (Turner et al., 2019), North American boreal forests (Johnstone and Chapin, 2006, Johnstone et al., 2010, Whitman et al., 2019), and eucalypt forests of Australia (Bowman et al., 2014, 2016, Enright et al., 2015), but previous studies had not tested for the interaction between fire interval and topographic position while controlling for seed availability. Our findings call for broader consideration not only of disturbance-disturbance interactions (Paine et al., 1998, Buma, 2015) and disturbance-climate interactions (Stevens-Rumann et al., 2018, Davis et al., 2019a), but also how landscape position can further amplify these effects as short-interval fires become increasingly widespread (Millar and Stephenson, 2015). Our model of relative vulnerability suggests that 25% of the reburned landscape would face establishment rates ≤ 0.01 (1% of seeds), even if seed supply was adequate. We controlled seed supply in our experiment, but recent observations indicate that seed supply is limited in short-interval fires because seed production is low in young forests (Keeley et al., 1999) and seeds do not disperse far from live short-statured trees outside the reburn perimeter (Gill et al., in press).

Our results reveal the extreme environmental conditions to which postfire tree seedlings are exposed. Adult tree distributions can be poor indicators of regeneration potential, given the narrower tolerance of juveniles to environmental variation (Jackson et al., 2009, Bell et al., 2014). Juvenile tree ranges in British Columbia suggest the area suitable for mesic species like lodgepole pine and subalpine fir will be reduced over the next several decades, while drought-adapted species like Douglas-fir will expand (Mathys et al., 2018). The range of drought-tolerant species (or genotypes) is hypothesized to shift upslope or expand under future warming, but experiments suggest they will be constrained by concurrent increases in seedling water stress (Conlisk et al., 2018).

The amplified effect of south-facing aspects in short-interval fires may push some postfire landscapes beyond regeneration thresholds. Interactions between short-interval fire and topography can reduce tree seedling establishment on south aspects even when seed supply is sufficient, suggesting that natural tree regeneration may fail in these areas as the frequency of stand-replacing fires increases. Conversely, north-facing aspects in reburns may still allow for establishment and sustain forest resilience even with some increased fire frequency. Our experiment highlights how disturbances can serve as proximate catalysts of climate-driven forest transitions (Thom et al., 2017, Crausbay et al., 2017). The amplification of topographic effects on soil microclimate and postfire tree regeneration is likely to become even more pronounced as climate warming continues and fires burn more frequently. South-facing slopes in short-interval fires may be harbingers of future subalpine forest conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

MGT and WDH conceived and designed the experiment; TJH and WDH installed the experiment. TJH collected and analyzed the data. TJH and MGT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. We thank Kristen Emmett, Nathan Gill, Jacob Gold and Mathilda Hendin Hoecker for field assistance; Kristin Braziunas, Trond Simensen and two anonymous reviewers for helpful comments on the manuscript; the University of Wyoming-National Park Service Research Station for logistical support; and Yellowstone and Grand Teton National Parks for facilitating this study under National Park Service permits YELL-2017-SCI-5238 and GRTE-2017-SCI-0021.

Funding

This research was funded by the U.S. National Science Foundation (DEB-1719905). TJH acknowledges research support from the Department of Integrative Biology, University of Wisconsin-Madison; MGT acknowledges support from the University of Wisconsin-Madison Vilas Trust, and WDH acknowledges support from Columbia University's Earth Institute and Center for Climate and Life.

Data availability

All data and code will be made publicly available via the Environmental Data Initiative following acceptance for publication.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118523.

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