

RESEARCH ARTICLE

FIRE ENHANCES WHITEBARK PINE SEEDLING ESTABLISHMENT, SURVIVAL, AND GROWTH

Judy L. Perkins

University of Montana, Division of Biological Sciences,
32 Campus Drive HS 104, Missoula, Montana 59812, USA

Current address: Bureau of Land Management, Colorado River Valley Field Office,
2300 River Frontage Road, Silt, Colorado 81652, USA
Tel.: +1-970-876-9054; e-mail: jlperkins@blm.gov

ABSTRACT

Periodic fire is thought to improve whitebark pine (*Pinus albicaulis* Engelm.) regeneration by reducing competition and creating openings, but the mechanisms by which fire affects seedling establishment are poorly understood. I compared seedling vegetation production in adjacent sites, one last burned in 1880 and the other in 1988, to test the hypothesis that recent fire increases whitebark pine seedling growth. I experimentally tested effects of fire on seedling recruitment and growth by planting seeds in prescribed burned and nearby unburned sites. Experimental results showed nearly three times greater seed germination and seedling survival in recently prescribed burn plots. Seedling vegetation production in the 1880 and 1988 burn sites were measured using stem diameter and number of new needle bundles. Stem diameter was approximately 26% greater after the more recent fire in the 1988 burn site, and new needle bundle production was approximately 40% greater in this site relative to seedlings in the adjacent site that was last burned in 1880. Seedling growth, measured as both above- and below-

RESUMEN

La mejora de la regeneración del pino de corteza blanca (*Pinus albicaulis* Engelm.) es atribuida a los incendios periódicos, al reducir la competencia y crear aperturas o claros, aunque los mecanismos mediante los cuales el fuego afecta el establecimiento de sus plantines no se comprenden bien. En este trabajo he comparado la producción de plantines en sitios adyacentes, uno de ellos quemado por última vez en 1880 y el otro en 1988, para probar la hipótesis de que los fuegos recientes incrementan el crecimiento de plantines del pino de corteza blanca. He probado experimentalmente los efectos del fuego en el reclutamiento y crecimiento de los plantines, sembrando esta especie en sitios con quemas prescritas y en otros adyacentes sin quemar. Los resultados experimentales mostraron casi el triple de germinación y supervivencia de plantines en las parcelas con quemas prescritas recientes. La producción de plantines en los sitios quemados en 1880 y 1988 fueron medidos utilizando el diámetro del tallo y la cantidad de ramilletes de acículas nuevas. El diámetro del tallo fue de aproximadamente 26% más grande después del fuego más reciente, en el sitio quemado en 1988, y la producción de ramilletes de acículas fue aproximadamente un 40% más grande en este sitio en relación con los plantines en el sitio adyacente que fue quemado por última vez en 1880. El crecimiento de los plantines medido como la biomasa aérea y subterránea

ground biomass, was approximately 57% greater in a recently prescribed burn site relative to growth in an adjacent site that was unburned since 1910. Higher growth rates after prescribed fire corresponded with greater soil NO_3^- and soil-available P concentrations relative to unburned controls. However, high N concentrations in leaves of seedlings in unburned plots indicated that whitebark pine seedlings were not N-limited. Higher P, increased light availability, and earlier snowmelt after fire may be important factors in general post-fire success of whitebark pine.

fue aproximadamente un 57% mayor en un sitio con una quema prescrita reciente en relación al crecimiento en un sitio adyacente que permaneció sin quemar desde 1910. Las tasas de crecimiento más altas luego de la quema prescrita se corresponden con una mayor cantidad de NO_3^- y de concentraciones de P disponible en el suelo en comparación con controles sin quemar. Sin embargo, altas concentraciones de N en las hojas de plantines de parcelas sin quemar, indicaron que el pino de corteza blanca no presentó limitaciones de N. Los altos contenidos de P, el aumento de la disponibilidad de luz, y el derretimiento temprano de la nieve tras el fuego pueden ser factores importantes en el éxito general post-fuego del pino de corteza blanca.

Keywords: fire effects, growth response, Idaho, Montana, nutrients, *Pinus albicaulis*, Rocky Mountains, seedling recruitment

Citation: Perkins, J.L. 2015. Fire enhances whitebark pine seedling establishment, survival, and growth. *Fire Ecology* 11(2): 84–99. doi: 10.4996/fireecology.1102084

INTRODUCTION

Fire has shaped the structure and composition of forests throughout the northern Rocky Mountains (Habeck and Mutch 1973, Arno 1980, Agee 1993). The most important effect of natural wildfires, combined with Native American burning, was the maintenance of disturbance regimes favoring stands dominated by seral conifers (Arno 1980, Barrett and Arno 1982, Morris 1992, Agee 1993). Following the 1910 fires in northern Idaho and northwestern Montana, aggressive fire suppression and changing land use altered historical fire regimes and greatly increased mean fire return intervals, particularly at lower elevations (Arno 1980, 1986; Keane *et al.* 1994; Keane 2001). Whitebark pine forests generally experienced mixed severity fire regimes prior to fire suppression implementation, and in some areas successional replacement of whitebark pine by more shade-tolerant species has increased due to fire suppression (Arno 2001).

While whitebark pine can form pure stands in the upper subalpine zones above the range of other conifers, it is a seral species in the mixed conifer forests of the lower subalpine zone (Arno 1986). Presettlement fire regimes in whitebark pine stands included both low-severity surface fires and high-severity stand-replacing fires in a mixed severity fire regime. Comparing presettlement fire intervals with those since implementation of fire suppression policies, Brown *et al.* (1994) found 2.4 times greater area burned in whitebark pine forests prior to fire suppression implementation in the Selway-Bitterroot Wilderness, Montana, USA. A fire history study by Murray *et al.* (1998), in subalpine forests of the West Big Hole Range spur of the Bitterroot Mountains, found increasing fire rotation intervals and fire severity in the post-settlement period, but with differences between east-side and west-side forests. Another fire history study in the Selway-Bitterroot Wilderness subalpine forests found an average presettlement fire return interval of

139 to 341 years (Kipfmüller 2003, Brunelle *et al.* 2005).

Whitebark pine is a keystone subalpine species, which is rapidly declining due to the introduced disease, white pine blister rust (*Cronartium ribicola* A. Dietr.) (McDonald and Hoff 2001), combined with mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemics exacerbated by climate change and associated drought. Fire suppression and subsequent increase in successional replacement of whitebark pine are believed to have contributed to this decline (Keane *et al.* 1994). Due to this decline, whitebark pine is currently listed as an endangered species in Canada (GOC 2015) and as a candidate for federal listing under the Endangered Species Act in the United States (USFWS 2015).

Disturbance is considered important to whitebark pines in lower subalpine forests, both for opening up the forest canopy to facilitate seedling regeneration, and for preventing successional replacement of whitebark pines (Arno 2001). Whitebark pine seedlings can establish beneath a forest canopy, but without adequate sunlight they generally remain stunted, failing to reach reproductive maturity (Keane *et al.* 2007). Fire is important for removing shade-tolerant species such as subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Englemann spruce (*Picea englemannii* Parry ex Englm.) that can reduce light availability for whitebark pine in undisturbed lower subalpine stands (Arno 1986, Arno and Weaver 1990, Arno and Allison-Bunnell 2002). Whitebark pine seedling regeneration frequently occurs in burned sites, at least partially due to preferential seed caching habits of Clark's nutcrackers (*Nucifraga columbiana* A. Wilson), the tree's primary seed disperser (Tomback 1994). Fire appears to have indirect benefits for whitebark pine forests through its negative effects on competitors and its positive effects on mutualists.

Fire may also have more direct benefits for whitebark pine seedling recruitment (Moody

2006, Keane and Parsons 2010a) and survival and growth of planted seedlings (Izlar 2007). Fire may, depending on severity, reduce or remove understory plant cover (Romme *et al.* 1995, Potash and Agee 1998) and litter that can inhibit seedling recruitment (McCaughy 1994). Fire may also temporarily increase soil nutrient cycling, particularly of nitrogen, by oxidizing organic matter (Lathrop 1994). Subalpine forest soils are generally considered nitrogen limited (Körner 1999), and soil nutrient flushes following fire (Lynham *et al.* 1998, Driscoll *et al.* 1999) could increase seedling growth rates. Higher nutrient availability could be particularly important at high elevation sites because rapid initial growth can improve over-winter survival of young conifer seedlings (Little *et al.* 1994). However, there has been no experimental testing or measurement of whitebark pine seedling mineral nutrition in relation to seedling establishment and growth following fire. Current restoration protocols for whitebark pine include the use of prescribed fire, mechanical thinning in lieu of fire, and planting of rust-resistant seedlings (Hoff *et al.* 2001, Keane and Arno 2001, Keane and Parsons 2010b). Understanding the relationship between fire and whitebark pine regeneration can aid efforts to restore this ecologically important and declining species.

My objectives in this study were to determine if: 1) whitebark pine seedling growth is greater within recently burned areas than in unburned areas, and 2) if post-fire release of soil N and P might benefit whitebark pine seedlings.

METHODS

Seedling Growth at Paired Fire Sites

To test whether seedlings have increased growth in recently burned sites, I measured vegetative production represented by terminal stem diameter and number of new needle bundles produced by whitebark pine seedlings in

the Smith Creek 1880 burn and the adjacent Smith Creek 1988 burn. These two burn sites were located approximately 15 km west of Stevensville, Montana, USA, at 46° 28' N, 114° 15' W. The site elevation is 2100 m to 2150 m. Both sites burned in 1880, with a partial re-burn in 1988 up to a constructed fire line separating the two survey sites. Both burn sites had similar soils. The 1880 burn site had generally east- to southeast-facing aspects, with 0% to 24% slopes. The 1988 burn site also had east- to southeast-facing aspects, although more of it was southeast facing than in the 1880 burn site. Slopes in the 1988 burn were 1% to 17%. The 1988 burn was a high-severity burn, which removed all soil organic matter down to mineral soil, and killed all trees in the study area. The severity of the 1880 burn is uncertain, due to its age and lack of records. At the time of sampling, the 1880 burn site had a mature canopy consisting of subalpine fir, lodgepole pine (*Pinus contorta* Douglas ex Loudon), whitebark pine, and an occasional Englemann spruce. Whitebark pine regeneration was occurring beneath this canopy, with individuals ranging from <0.5 m in height to small trees 2 cm to 8 cm diameter at breast height (DBH) in light gaps. Although whitebark pine growth can be severely suppressed beneath a canopy (Arno and Hoff 1990, Keane *et al.* 1994, Campbell and Antos 2003), trees that are <0.5 m in height are unlikely to have been present prior to the 1880 fire, and so they were considered to be post-fire regeneration. Blister rust was present on this site, but whitebark pine cone production still occurred.

I made vegetation production measurements on 23 seedlings per burn site in June 2000 consisting of: 1) terminal internode stem diameter from the top of the seedling, taken at the top internode and representing growth in 1999; and 2) number of new needle bundles in the top whorl of all branches, representing growth in 2000. I considered all trees <0.5 m in height to be seedlings for this study. I also

sampled leaf tissue, from needle bundles produced in 1999, from each of these seedlings to measure total N content. The single, previous year measurement of stem diameter was used rather than overall height, since trees of the same height differed greatly in age between the 1880 and 1988 burns. Internode distances were tightly clumped in many of the seedlings in the 1880 burn, making it difficult to ascertain numbers of nodes and distances between them.

To control for possible confounding influences from adjacent understory plant effects, and to test for potential effects, I sampled seedlings growing with different common understory plants, as well as those growing on bare ground within the 1988 burn. Within the species associations, sampling was random. The associated species and sample sizes within the 1880 burn were: beargrass (*Xerophyllum tenax* [Pursh] Nutt.), $n = 8$; grouse whortleberry (*Vaccinium scoparium* Leiberg ex Coville), $n = 10$; and Hitchcock's smooth woodrush (*Luzula glabrata* [Hoppe ex Rostk.] Desv. var. *hitchcockii* [Hämnet-Ahti] Dorn), $n = 5$. Within the 1988 burn, the associated species and sample sizes were: beargrass, $n = 4$; grouse whortleberry, $n = 9$; bare ground, $n = 10$. No whitebark pine seedlings occurred adjacent to Hitchcock's smooth woodrush within the 1988 burn, and fewer occurred adjacent to beargrass in the 1988 burn than in the 1880 burn. Due to the severity of the 1988 burn, much of the ground surface was bare, whereas vegetation covered nearly the entire 1880 burn area ground surface. To minimize the effect of size differences on growth rates, I selected seedlings 25 cm to 30 cm in height with three to five whorls of side branches per seedling, within each burn site.

Experimental Seed Planting

The effects of fire on natural whitebark pine regeneration are confounded by blister rust reduction of seed availability (Tomback *et*

al. 1995) and Clark's nutcracker caching preferences (Tomback *et al.* 1993). To test the effects of fire on whitebark pine seedling recruitment, survival, and growth without these confounding factors, I performed a seed planting experiment at Beaver Ridge Experimental Site, Bitterroot Mountains, Idaho, USA (Keane and Arno 2001, Keane and Parsons 2010b). As part of a larger whitebark pine natural regeneration study, a portion of this site was prescribed burned to mimic a wildfire in September 1999, with fuel added to increase burn severity (R. Keane, RMRS Forestry Sciences Lab, Missoula, Montana, USA; personal communication). The fire severity was sufficient to kill nearly all trees on the site and much of the understory species aboveground plant material, and produced patches of hydrophobic soil. A large area of nearby mature forest, last burned in 1910, served as an experimental control (Keane and Arno 2001). No records exist of the 1910 fire severity on this site but, at the time of the experiment, a mature canopy of whitebark pine, subalpine fir, and Englemann spruce covered much of the site, interspersed with open patches of varying size. The understory plant community was well developed, dominated by common subalpine species including beargrass, grouse whortleberry, elk sedge (*Carex geyeri* Boott), and Hitchcock's smooth woodrush. The proximity of the two fire ages at the same site provided me with the opportunity to study fire effects while minimizing other site effects. This site is located at an elevation of 2050 m to 2200 m, along a south-facing slope. Soils are granitic, derived from the Idaho Batholith. The site receives heavy winter snowfall and is usually snow free from early July through early October (R. Keane; personal communication).

Two burn treatments were used: high-severity burn (prescribed burn with slash fuel added, September 1999) and unburned control (last fire occurred in 1910). For simplicity, these treatments will be referred to as burned and unburned. To control for understory plant

species effects, I planted whitebark pine seeds next to four major understory plant species, with 10 plots of each per burn treatment: grouse whortleberry, beargrass, elk sedge, and Hitchcock's smooth woodrush. I selected these species because they showed either positive (whortleberry and woodrush) or negative (beargrass and sedge) association with whitebark pine seedlings at vegetation survey sites (J.L. Perkins, University of Montana, Missoula, Montana, USA, unpublished data). In the burned site, I located an additional 10 plots in patches of bare ground. I established a total of 90 1 m × 1 m plots, with 50 plots in the burned area and 40 plots in the unburned control. Plots were located along two bands, perpendicular to the slope, in parallel with each other and approximately 50 m apart in elevation. Plant association plots were spread evenly across the sites. Plots were located away from bases of mature trees and snags to minimize effects on light availability. Mean overhead canopy of unburned plots did not differ significantly from that of burned plots, as measured with a concave spherical densiometer (*t*-test: mean canopy <2%, $P = 0.446$, $n = 90$). However, unburned plots received less light on a full-day basis than burned plots due to morning and afternoon shade from neighboring trees. Average overall understory plant canopy within the burned plots was 33%, and within the unburned plots was 75%. Plots were protected from rodent predation by hardware cloth enclosures following the design of McCaughey (1990).

I planted a total of 3330 whitebark pine seeds (37 seeds per plot) on 27 and 28 June 2001. The whitebark pine seeds came from seed lot WBP-14-7425, collected at 2800 m elevation from Union Pass, Shoshone National Forest, Wyoming, USA, in September 1999. The distance of the seed source from the experimental site might have affected overall germination and seedling success, but did not prevent testing of treatment effects within the site. Seeds were processed by the USFS-

Coeur d'Alene Nursery, Coeur d'Alene, Idaho, USA, following the procedures of Burr *et al.* (2001), and remained in cold storage at the USFS-Coeur d'Alene nursery until preparation for planting. Whitebark pine seeds have delayed embryo maturation, and usually require two to three cold-warm stratification cycles to reach maturity (Tomback *et al.* 2001). The seeds used in this experiment were x-rayed at the nursery to check that embryo development was sufficient for planting (K. Burr, USFS-Coeur d'Alene Nursery, Coeur d'Alene, Idaho, USA; personal communication). Seeds are normally cached by Clark's nutcrackers in late August (Tomback 2001), but the unusually long fire season of 2000 followed by early October snows curtailed site access and prevented fall seed planting. To compensate for the delayed planting date, I provided seeds with one warm stratification, following the guidelines of Burr *et al.* (2001), in September 2000, then returned them to cold storage for the 2000-2001 winter. I re-warmed the seeds and placed them in a 48 hr running water soak immediately prior to planting. I planted seeds within or immediately adjacent to target understory plant species, at 2 cm depth to mimic nutcracker cache depths (Tomback 2001). Due to the delayed planting date (27 and 28 June 2001, after snowmelt), I simulated snowmelt conditions by hand-watering plots with on-site spring water every three days for the first two weeks after planting. I placed two one-gallon plastic water jugs, with pin-prick holes along their bottom edges, on the uphill side of each plot to provide slow water seepage into the plots between hand-watering.

I monitored seedling emergence and survival weekly for the first month after planting, and every two weeks for the remainder of the first growing season and through the second growing season (mid-July through early September 2002). No new germination occurred during 2003, but I continued to monitor survival monthly through the summer growing season. I marked seedlings with color-coded

toothpicks and located them on plot maps upon their emergence in order to monitor survival. I calculated survival as total surviving seedlings relative to total emergence. Emergence included all seed germinants, even if they produced no more than cotyledons.

Seedling Growth and Nutrient Concentrations

At the end of the experiment, I removed all remaining surviving seedlings on 25 September 2003 by digging a plug 20 cm in diameter and 35 cm deep around each seedling and lifting it from the ground, trying to keep the roots intact. Due to the rocky nature of the soil and fragility of the roots, some root damage occurred on most of the seedlings, but the bulk of the roots were removed intact. I kept seedlings refrigerated in their soil plugs until the roots were cleaned. After cleaning, I clipped seedlings at the top of the root mass to separate above- and belowground biomass, and dried each for 48 hr at 80°C. I weighed aboveground and belowground biomasses separately. For plots with more than one surviving seedling at harvest, I used averages of all seedlings per plot for biomass quantification and leaf N analysis.

After weighing, I separated all dried seedling needles from fascicles and ground them to a fine powder with steel ball bearings in microcentrifuge tubes placed on a paint shaker. I weighed powdered needle samples of 3 mg in tin capsules on an analytical balance, and sent them to the UC Davis Stable Isotope Facility for total N and $\delta^{15}\text{N}$ analyses.

Soil Nutrients

I assessed soil NH_4^+ , NO_3^- , and available P at the Beaver Ridge experimental site using ionic resin capsules (Unibest, Bozeman, Montana, USA) buried (one per plot) in mineral soil at 5 cm depth for one year to capture nutrients moving through by mass flow and diffusion (Binkley and Vitousek 1989). I in-

stalled one capsule per plot, in both burned and unburned treatments, on 16 July 2001 and removed them on 4 August 2002. I extracted ionic nutrients within 24 hours of removal by three successive 30 min agitated rinses with 2 M KCl (Kjønaas 1999, Morse *et al.* 2000). I centrifuged the decanted KCl extract from the three successive rinses at 3000 RPM for 10 min. I measured NH_4^+ nitrogen and NO_3^- nitrogen using a Technicon Autoanalyzer™ II single-channel colorimeter system (Technicon Instruments Corp., Tarrytown, New York, USA) following standard methodology for this instrumentation. I measured PO_4^{3-} phosphorous by the ascorbic acid colorimetric method (Page *et al.* 1982).

Statistical Analysis

I analyzed seedling vegetation production differences between the Smith Creek 1880 burn and 1988 burn survey sites with *t*-tests, and plant association effects within burn sites using one-way ANOVA. I analyzed leaf nitrogen differences with a Kruska-Wallis test due to violation of homogeneity of variances for my data. I used one-way ANOVA, with plant association as the main factor, to analyze plant association effects on emergence, aboveground growth, and total leaf nitrogen in the burned plots at Beaver Ridge. By the time seedlings were harvested, only six seedlings remained alive in the unburned treatment, and due to both low germination and low survival, plant species effects within the unburned site could not be determined. Only one seedling that germinated in 2001 remained alive at harvest, and was not included in biomass calculations to avoid confounding the data. All biomass means are for seedlings germinating in 2002. I pooled data from all plots within each of the burn treatments and used *t*-tests to test the effects of burn treatment on total number of seedlings emerged, aboveground biomass, total plant leaf nitrogen, and nutrients. I analyzed survival, belowground biomass, and per-

cent leaf nitrogen of whitebark pine seedlings at Beaver Ridge using a Kruska-Wallis test, because survival and belowground growth violated assumptions of variance homogeneity. I normalized soil nitrate and available phosphorus data with ln transformations. I used *t*-tests to compare burn treatment effects on soil nutrients, and two-way ANOVA, with burn treatment and plant association as main factors, to test plant association effects. For all statistical tests, I adopted an α of 0.05 as my basis for mean separation.

RESULTS

Seedling Growth

At the Smith Creek site, burn year affected seedling vegetation production. Although all seedlings were similar in overall size, seedlings in the 1988 burn had approximately 24% larger terminal stem diameters ($P < 0.001$), 40% more needle bundles ($P < 0.001$), and 9% greater leaf N concentrations than seedlings in the adjacent site that had not burned since 1880 ($P = 0.032$, Figure 1). There were no significant differences in the vegetation production measurements or leaf N concentrations relative to understory plant species associations.

Seedling Emergence, Survival, Growth

Very low germination rates of the 3330 planted seeds occurred during the first growing season (2001 germination: burn $n = 13$ of 1850 planted; unburned $n = 7$ of 1480 planted) but, by the end of the second growing season, 11% of the seeds had germinated (combined 2001 and 2002 germination: burn $n = 197$; unburned $n = 67$). I observed no additional recruitment during the third season. Total germination was almost double in the burned plots compared to the unburned plots (12% vs. 7%, $P = 0.004$; Figure 2a). Survival of seedlings, regardless of germination date, was

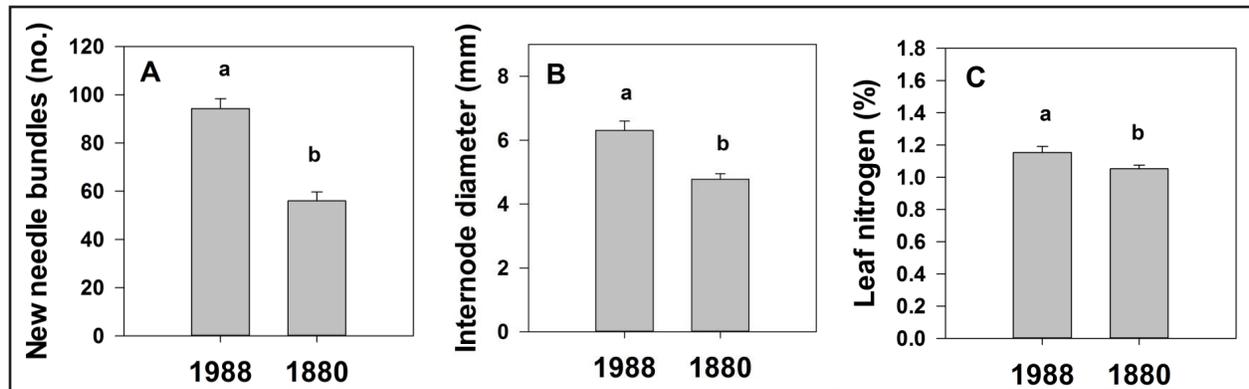


Figure 1. Comparison of A) new needle production, B) internode diameter, and C) leaf nitrogen concentration of whitebark pine seedlings (25 cm to 30 cm height with three to five side-branch whorls) in the Smith Creek 1988 burn (12 yr old) and Smith Creek 1880 burn (120 yr old) sites, with $n = 23$ at each site. Different letters denote significance at $P < 0.05$. Error bars show one standard error from the mean.

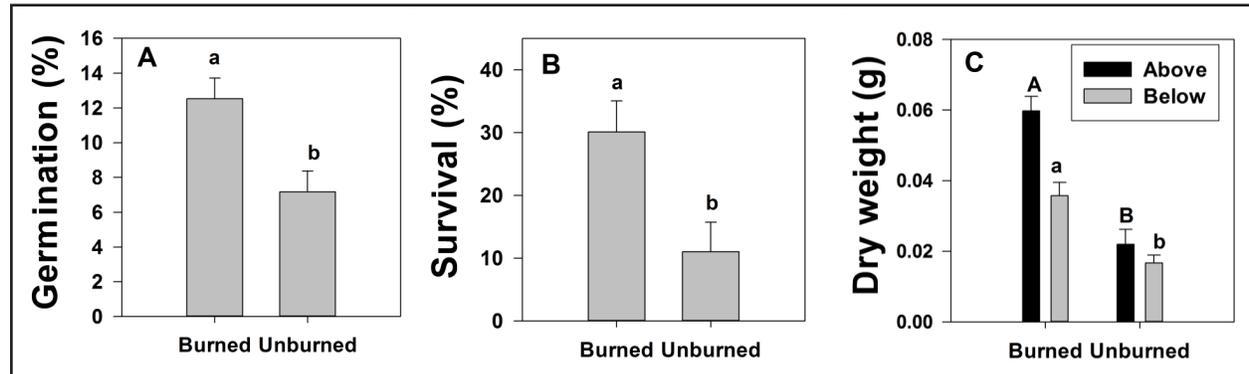


Figure 2. Comparison of A) germination rates, B) survival rates, and C) dry weights of whitebark pine seedlings grown from out-planted seed in burned and unburned treatments at Beaver Ridge Experimental Site, Idaho, USA. Dark bars show aboveground biomass, and light bars show belowground biomass. Treatment sample sizes for dry weights were: burned treatment $n = 28$; unburned treatment $n = 5$. Different letters denote significance at $P < 0.05$. Error bars show one standard error from the mean.

nearly 150% greater in the burned vs. unburned treatment (Kruska-Wallis $P = 0.004$; Figure 2b). By the September 2003 harvest, only one 2001 germinant remained in the unburned treatment, and none of the 2001 burned treatment germinants remained. Numbers of seedlings surviving from 2002 germination until 2003 harvest were: burned $n = 50$, unburned $n = 6$. Both aboveground and belowground seedling biomass in the burned treatment were more than double the seedling biomass in the unburned treatment ($P = 0.001$, $P = 0.01$; Figure 2c).

Neither seed germination nor survival differed among seeds planted with different understory neighbors, but, in burned plots, average total seedling dry biomass was significantly lower when seedlings grew in association with beargrass (71.3 mg) and elk sedge (76.4 mg) than in bare ground (144.5 mg) (Kruskal-Wallis test: $P = 0.03$; Mann-Whitney U test: $P = 0.019$ [beargrass], $P = 0.016$ [elk sedge]). Average total seedling dry biomass was of intermediate value in association with grouse whortleberry (107.9 mg) and with Hitchcock's smooth woodrush (100.5 mg).

Distribution of the surviving seedlings across plant treatment plots at harvest were approximately equal in the unburned treatment (one plot each for grouse whortleberry and elk sedge treatments, and two plots each for beargrass and smooth woodrush treatments). Within the burn treatment, surviving seedlings were distributed across a greater number of plots with elk sedge ($n = 8$), grouse whortleberry ($n = 7$), and beargrass ($n = 6$), than with Hitchcock's smooth woodrush ($n = 4$) or bare ground ($n = 4$).

Soil Nutrients

Nitrate and available P content at the Beaver Ridge experimental site were more than three times higher in soils two to three years post burn than in unburned soils (nitrate $P < 0.001$, phosphorus $P = 0.012$; Figure 3). Soil NH_4^+ nitrogen did not differ between the burned and unburned sites ($P = 0.529$; Figure 3a). Understory plant species associations had no effect on either soil NO_3^- nitrogen or NH_4^+ nitrogen in burned plots. However, available P was greater in association with Hitchcock's smooth woodrush and lower in association

with grouse whortleberry in burned plots, and lower in association with unburned elk sedge plots (ANOVA plant treatment $F = 10.035$, $P = 0.002$; plant \times burn interaction $F = 3.55$, $P = 0.01$).

Plant Nutrients

Total leaf nitrogen concentration, calculated as percent leaf dry weight, was approximately 35% greater in seedlings growing in the unburned plots than in seedlings in burned plots (Kruska-Wallis $P = 0.006$; Figure 3b). However, total plant leaf nitrogen was approximately 34% greater in seedlings from burned plots than in seedlings from unburned plots ($P = 0.035$) (Figure 3c). Understory plant species association had no effect on leaf nitrogen in seedlings from burned plots, and low seedling recruitment was inadequate for analysis of understory plant species effects in the unburned plots. There was no significant difference in $\delta^{15}\text{N}$ between treatments. No correlation was found between soil nutrient availability and any of the whitebark pine recruitment or growth parameters.

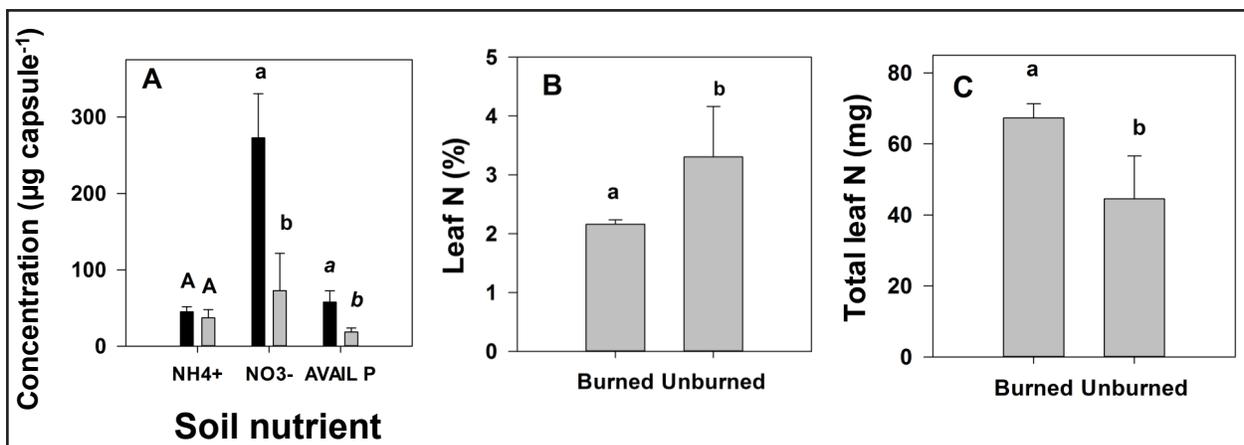


Figure 3. Comparison of A) resin-sorbed NH_4^+ nitrogen, NO_3^- nitrogen, and P as a measure of net N and P mineralization and solubilization, (resins buried for 1 yr in soil at 5 cm depth [dark bars represent burned treatment, light bars represent unburned treatment]), B) whitebark pine leaf nitrogen content, and C) whitebark pine total plant leaf N in burned and unburned treatments at Beaver Ridge Experimental Site, Idaho, USA. Different letters denote significance at $P < 0.05$. Error bars show one standard error from the mean.

DISCUSSION

Overall, my results suggest that while whitebark pine recruitment is not dependent on fire, moderate- to high-severity fire can have a strong positive effect on seedling establishment and growth. Seedling emergence from planted seeds at Beaver Ridge was much greater in the 1999 prescribed burn than in unburned forest, as was seedling survival, supporting the hypothesis that whitebark pine seedling recruitment is improved by fire. McCaughey (1990) tested the effects of seedbed conditions on whitebark pine recruitment from planted seeds and found greater recruitment on unburned mineral soil than on either burned seedbeds or litter. However, the addition of artificial shade increased recruitment in both burned and litter seedbeds by decreasing soil surface temperatures, which in turn reduced evaporation of soil moisture and reduced insolation mortality. Tomback *et al.* (2001) monitored natural whitebark pine seedling recruitment and survival following the 1988 Yellowstone fires and found no effect of fire. Seedling recruitment was correlated with spring precipitation at a dry site, but not at a moist site. This suggests that fire effects interact with precipitation patterns to influence whitebark pine seedling recruitment at individual locations.

Successful whitebark pine regeneration depends on seedling growth as well as recruitment, since whitebark pines growing beneath an established tree canopy may never grow sufficiently to reach reproductive maturity (Keane *et al.* 2007). Results from both the Smith Creek site sampling and from the seed transplant experiment showed greater seedling productivity and growth in recently burned sites than in stands unburned for at least 90 years.

There are several possible mechanisms by which fire could improve whitebark pine seedling growth. First, fire can reduce or remove overstory tree canopy and increase light avail-

ability. Measurements of tree rings indicate that whitebark pine seedlings may be suppressed by overstory trees for up to 150 years and then show a growth release with the loss of the canopy (Campbell and Antos 2003). However, in the Beaver Ridge experiment, seedlings grew more slowly in the unburned plots than in the burned plots, even though all plots were in open areas with no overhead shading. This suggests that factors other than eliminating shade contributed to the effects of fire on the growth of whitebark pine seedlings.

Fire may reduce the competitive effects of understory plants on whitebark pine seedlings. Understory vegetation canopy cover in the Beaver Ridge burned plots was less than half that within the unburned plots. Due to low seedling survival in unburned plots at Beaver Ridge, interactions between specific understory plant species and fire effects on growth could not be assessed. However, in the burn treatment plots, the greatest productivity was measured in seedlings growing on bare ground, suggesting a possible negative effect from competition. Competitive effects varied among understory species, with significantly lower growth rates for seedlings growing with elk sedge or beargrass. These species produce dense root masses, which can have a negative effect on conifer establishment (Abrams and Dickmann 1982, Landhäusser *et al.* 1996).

Fire may also improve whitebark pine seedling growth through increased soil nutrient availability. High elevation sites are generally considered nutrient limited, particularly in N (Baron *et al.* 1994, Körner 1999, Stevenson and Cole 1999). After fire, some of the nutrients previously locked up in plant biomass may be released, providing a temporary post-fire flush of nutrients into the soil (Agee 1993, Saa *et al.* 1993, Giardina and Rhodes 2001). Seedlings in the 1988 Smith Creek burn had greater leaf nitrogen, corresponding with greater growth, than seedlings in the adjacent 1880 burn. I found no difference in soil NH_4^+ nitrogen between the recently burned

Beaver Ridge site and the adjacent unburned site, but resin-sorbed NO_3^- nitrogen and P were greater in burned than in unburned soils, corresponding with greater seedling biomass in burned plots. However, leaf N concentrations were greater in seedlings from unburned plots. While conifers may prefer NH_4^+ nitrogen (Plassard *et al.* 2000), application of a high NO_3^- fertilizer to nursery-grown whitebark pine seedlings produces robust young seedling growth (K. Eggleston, USFS-Coeur d'Alene Nursery, Coeur d'Alene, Idaho, USA, unpublished nursery records). The lower leaf N concentration in burned treatment seedlings may be the result of growth dilution, since total plant leaf N was greater in seedlings from the burned plots (Figure 3). The seedlings may not have experienced N limitation on Beaver Ridge, since seedlings in the unburned plots had greater leaf N concentrations than seedlings in burned plots, yet showed suppressed growth.

If whitebark pine seedling growth is not N limited, the mechanism for increased growth in burned vs. unburned sites may be the increased availability of P. Leaf P concentrations of seedlings could not be measured due to insufficient leaf material, but soil-available P concentrations were greater in burned plots (Figure 3). Although effects of fire on P availability are highly variable, soil-available P can increase following fire (Saa *et al.* 1993, Simard *et al.* 2001, Ketterings *et al.* 2002). Phosphorus appears particularly important for root growth in young whitebark pine seedlings (K. Burr, personal communication), and inadequate root growth can cause whitebark pine seedling mortality in the field (McCaughey and Schmidt 1990). McCaughey (1990) also observed high mortality in young whitebark pine seedlings due to summer desiccation, indicating that water availability is critical to newly emerged seedlings. Adequate P availability could speed root growth to deeper soil layers with greater water availability, thereby improving seedling survival rates in sites

where surface soil layers are exposed to sun and wind desiccation.

Longer growing seasons are also linked with subalpine conifer establishment (Franklin *et al.* 1971, Larson and Kipfmüller 2010). Increased light availability after fire can increase snowmelt rates and soil temperatures. At Beaver Ridge, snow typically left the burned site at least two weeks earlier than the unburned site during the study period, providing a longer growing season for seedlings. Munn *et al.* (1978) found direct solar radiation in open meadows caused an earlier spring warm-up, higher overall growing season soil temperatures, and a longer growing season relative to forests. Similar patterns were observed for temperature and snowmelt on bare ground relative to tree stands in subalpine sites of British Columbia (Ballard 1972). Jacobs and Weaver (1990) tested the effects of temperature on whitebark pine seed germination and root growth and found highest germination and greatest root growth at temperatures of 25°C to 35°C, although both germination and root growth can occur at 10°C to 40°C.

Adequate soil moisture coinciding with warm spring soil temperatures is important for seedling recruitment (Little *et al.* 1994, Tomback *et al.* 2001). Delaying seed planting until after snowmelt, combined with subsequent low summer precipitation, probably contributed to low seedling emergence during the first year of the Beaver Ridge experiment. Total June through September 2001 precipitation for Savage Pass, Idaho, USA (the nearest SNO-TEL site), was 19 cm, with a mean temperature for this period of 9°C. The following year had much higher recruitment, with a total June through September precipitation of 32 cm, and a mean temperature of 10.7°C (USDA 2004). Using seed collected from a different whitebark pine seed zone, with different climate patterns, may have also contributed to low seed germination.

This is the first study to show that whitebark pine seedlings benefit either directly or

indirectly from fire. The results reported here suggest that reducing both overstory canopy coverage and understory plant density, and perhaps increasing N and P availability, may be important factors in recruitment of whitebark pine after forest fires. However, it is probable that fire also indirectly benefits whitebark pine recruitment and growth by increasing solar radiation to the melting spring snowpack, thus lengthening the growing season and increasing soil temperatures earlier in the spring.

Whitebark pine forests have continued to decline from a combination of bark beetle infestation, white pine blister rust infection, fire suppression, and climate change (Logan *et al.* 2010, Tomback and Achuff 2010). Efforts to restore whitebark forests include the use of prescribed fire and mechanical thinning in lieu of fire. My results suggest that the use of moderate- to high-severity prescribed fire and allowing wildfires to burn in whitebark pine habitats may be beneficial for regeneration, as long as a seed source is present in the vicinity.

ACKNOWLEDGEMENTS

This research was supported by a USFS Research Joint Venture Agreement with W. McCaughey, RMRS-Forestry Sciences Lab, Missoula, Montana, USA, No. 01-JV-11222022-116, supplemented by R. Keane, RMRS-Fire Sciences Lab, Missoula, Montana, USA. Additional funding came from NSF Dissertation Improvement Grant No. DEB-0309223; NSF T-Web Grant No. DGE-9553511; the John Marr Ecology Fund, Boulder, Colorado, USA; and Brown Bear Resources, Missoula, Montana, USA. Dr. A. Sala and Dr. R. Callaway served as my Ph.D. advisors at the University of Montana for this research. M. Vander Meer, M. Gundale, D. Mackenzie, and T. DeLuca at the University of Montana Soils Laboratory provided equipment and guidance. L. Todd, L. McIntyre, K. Hinxman, B. Brown, J. Moran, D. White, A. Darnell, D. Hooper, C. Hall, and J. Howard provided field assistance, and R. Keane, A. Brosten, M. High, Stevensville R.D., and Powell R.D. of the USDA-FS provided field sites.

LITERATURE CITED

- Abrams, M.D., and D.I. Dickmann. 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. *Canadian Journal of Botany* 60: 946–954. doi: [10.1139/b82-120](https://doi.org/10.1139/b82-120)
- Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, D.C., USA.
- Arno, S.F. 1980. Forest fire history in the northern Rockies. *Journal of Forestry* 78: 460–465.
- Arno, S.F. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? *Western Journal of Applied Forestry* 1: 92–94.
- Arno, S.F. 2001. Community types and natural disturbance processes. Pages 74–104 in: D.F. Tomback, S.F. Arno, and R.E. Keane, editors. *Whitebark communities: ecology and restoration*. Island Press, Washington, D.C., USA.
- Arno, S.F., and S. Allison-Bunnell. 2002. *Flames in our forests*. Island Press, Washington, D.C., USA.
- Arno, S.F., and R.J. Hoff. 1990. *Pinus albicaulis* Englm. Whitebark pine. Pages 268–279 in: R.M. Burns and B.H. Honkala, technical coordinators. *Silvics of North America*. Agriculture Handbook 654. Volume 1. USDA Forest Service, Washington, D.C., USA.

- Arno, S.F., and T. Weaver. 1990. Whitebark pine community types and their patterns on the landscape. Pages 97–105 in: W.C. Schmidt and K.J. McDonald, compilers. Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. USDA Forest Service General Technical Report INT-270, Intermountain Research Station, Ogden, Utah, USA.
- Ballard, T.M. 1972. Subalpine soil temperature regimes in southwestern British Columbia. *Arctic and Alpine Research* 4: 139–146. doi: [10.2307/1550397](https://doi.org/10.2307/1550397)
- Baron, J.S., D.S. Ojima, E.A. Holland, and W.J. Parton. 1994. Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: implications for aquatic systems. *Biogeochemistry* 27: 61–82. doi: [10.1007/BF00002571](https://doi.org/10.1007/BF00002571)
- Barrett, S.W., and S.F. Arno. 1982. Indian fires as an ecological influence in the northern Rockies. *Journal of Forestry* 80: 647–51.
- Binkley, D., and P. Vitousek. 1989. Soil nutrient availability. Pages 75–96 in: R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel, editors. *Plant physiological ecology: field methods and instrumentation*. Chapman and Hall, New York, New York, USA. doi: [10.1007/978-94-009-2221-1_5](https://doi.org/10.1007/978-94-009-2221-1_5)
- Brown, J.K., S.F. Arno, S.W. Barrett, and J.P. Menakis. 1994. Comparing the prescribed natural fire program with presettlement fires in the Selway-Bitterroot Wilderness. *International Journal of Wildland Fire* 4: 157–168. doi: [10.1071/WF9940157](https://doi.org/10.1071/WF9940157)
- Brunelle, A., C. Whitlock, P. Bartlein, and K. Kipfmüller. 2005. Holocene fire and vegetation along environmental gradients in the northern Rocky Mountains. *Quaternary Science Review* 24: 2281–2300. doi: [10.1016/j.quascirev.2004.11.010](https://doi.org/10.1016/j.quascirev.2004.11.010)
- Burr, K.E., A. Eramian, and K. Eggleston. 2001. Growing whitebark pine seedlings for restoration. Pages 325–345 in: D.F. Tomback, S.F. Arno, and R.E. Keane, editors. *Whitebark communities: ecology and restoration*. Island Press, Washington, D.C., USA.
- Campbell, E.M., and J.A. Antos. 2003. Postfire succession in *Pinus albicaulis*-*Abies lasiocarpa* forests of southern British Columbia. *Canadian Journal of Botany* 81: 383–397. doi: [10.1139/b03-040](https://doi.org/10.1139/b03-040)
- Driscoll, K.G., J.M. Arocena, and H.B. Massicotte. 1999. Post-fire soil nitrogen content and vegetation composition in sub-boreal spruce forests of British Columbia's central interior, Canada. *Forest Ecology and Management* 121: 227–237. doi: [10.1016/S0378-1127\(99\)00003-1](https://doi.org/10.1016/S0378-1127(99)00003-1)
- Franklin, J.F., W.H. Moir, G.W. Douglas, and C. Wiberg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic and Alpine Research* 3: 215–224. doi: [10.2307/1550194](https://doi.org/10.2307/1550194)
- Giardina, C.P., and C.C. Rhoades. 2001. Clear cutting and burning affect nitrogen supply, phosphorus fractions and seedling growth in soils from a Wyoming lodgepole pine forest. *Forest Ecology and Management* 140: 19–28. doi: [10.1016/S0378-1127\(00\)00272-3](https://doi.org/10.1016/S0378-1127(00)00272-3)
- GOC [Government of Canada]. 2015. Species at risk public registry. <http://www.sararegistry.gc.ca/species/schedules_e.cfm?id=1>. Accessed 24 January 2015.
- Habeck, J.R., and R.W. Mutch. 1973. Fire-dependent forests in the northern Rocky Mountains. *Quaternary Research* 3: 408–424. doi: [10.1016/0033-5894\(73\)90006-9](https://doi.org/10.1016/0033-5894(73)90006-9)
- Hoff, R.J., D.E. Ferguson, G.I. McDonald, and R.E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. Pages 346–366 in: D.F. Tomback, S.F. Arno, and R.E. Keane, editors. *Whitebark communities: ecology and restoration*. Island Press, Washington D.C., USA.
- Izlar, D.K. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. Thesis, University of Montana, Missoula, USA.

- Jacobs, J., and T. Weaver. 1990. Effects of temperature and temperature preconditioning on seedling performance of whitebark pine. Pages 134–139 in: Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Bozeman, Montana, USA, 29–31 March 1989. USDA Forest Service General Technical Report INT-270, Intermountain Research Station, Ogden, Utah, USA.
- Keane, R.E. 2001. Successional dynamics: modeling an anthropogenic threat. Pages 159–192 in: D.F. Tomback, S.F. Arno, and R.E. Keane, editors. Whitebark communities: ecology and restoration. Island Press, Washington, D.C., USA.
- Keane, R.E., and S.F. Arno. 2001. Restoration concepts and techniques. Pages 367–400 in: D.F. Tomback, S.F. Arno, and R.E. Keane, editors. Whitebark communities: ecology and restoration. Island Press, Washington, D.C., USA.
- Keane, R.E., K.L. Gray, and L.J. Dickinson. 2007. Whitebark pine diameter growth response to removal of competition. USDA Forest Service Research Note RMRS-RN-32, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Keane, R.E., P. Morgan, and J.P. Menakis. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness complex, Montana, USA. Northwest Science 68: 213–229.
- Keane, R.E., and R.A. Parsons. 2010a. Restoring whitebark pine forests of the northern Rocky Mountains, USA. Ecological Restoration 28: 56–70. doi: 10.3368/er.28.1.56
- Keane, R.E., and R.A. Parsons. 2010b. Management guide to ecosystem restoration treatments: whitebark pine forests of the northern Rocky Mountains, USA. USDA Forest Service General Technical Report RMRS-GTR-232, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Ketterings, Q.M., M. van Noordwijk, and J.M. Bigham. 2002. Soil phosphorus availability after slash-and-burn fires of different intensities in rubber agroforests in Sumatra, Indonesia. Agriculture, Ecosystems & Environment 92: 37–48. doi: 10.1016/S0167-8809(01)00287-0
- Kipfmüller, K.F. 2003. Fire-climate-vegetation interactions in subalpine forests of the Selway-Bitterroot Wilderness area, Idaho and Montana, USA. Dissertation, University of Arizona, Tucson, USA.
- Kjønaas, O.J. 1999. Factors affecting stability and efficiency of ion exchange resins in studies of soil nitrogen transformation. Communications in Soil Science and Plant Analysis 30: 2377–2397. doi: 10.1080/00103629909370380
- Körner, C. 1999. Alpine plant life: functional plant ecology of high mountain ecosystems. Springer-Verlag, Berlin, Germany. doi: 10.1007/978-3-642-98018-3
- Landhäuser, S.M., K.J. Stadt, and V.J. Lieffers. 1996. Screening for control of a forest weed: early competition between three replacement species and *Calamagrostis canadensis* or *Picea glauca*. Journal of Applied Ecology 33: 1517–1526. doi: 10.2307/2404790
- Larson, E.R., and K.F. Kipfmüller. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forest Research 40: 476–487. doi: 10.1139/X10-005
- Lathrop, R.G., Jr. 1994. Impacts of the 1988 wildfires on the water quality of Yellowstone and Lewis lakes, Wyoming. International Journal of Wildland Fire 4: 169–175. doi: 10.1071/WF9940169
- Little, R.L., D.L. Peterson, and L.L. Conquest. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: effects of climate and other factors. Canadian Journal of Forest Research 24: 934–944. doi: 10.1139/x94-123

- Logan, J.A., W.W. MacFarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications* 20: 895–902. doi: [10.1890/09-0655.1](https://doi.org/10.1890/09-0655.1)
- Lynham, T.J., G.M. Wickware, and J.A. Mason. 1998. Soil chemical changes and plant succession following experimental burning in immature jack pine. *Canadian Journal of Soil Science* 78: 93–104. doi: [10.4141/S97-031](https://doi.org/10.4141/S97-031)
- McCaughey, W.W. 1990. Biotic and microsite factors affecting *Pinus albicaulis* establishment and survival. Dissertation, Montana State University, Bozeman, USA.
- McCaughey, W.W. 1994. Silvicultural treatments and whitebark pine plantation and regeneration trial results. Pages 35–49 in: K.C. Kendall, B. Coen, B. Keane, B. Donner, and K. Brewer, organizers. Workshop proceedings: research and management in whitebark pine ecosystems. USDI, National Biological Survey, Glacier Field Station, Fort Collins, Colorado, USA.
- McCaughey, W.W., and W.C. Schmidt. 1990. Autecology of whitebark pine. Pages 85–96 in: Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Bozeman, Montana, USA, 29–31 March 1989. USDA Forest Service General Technical Report INT-270, Intermountain Research Station, Ogden, Utah, USA.
- McDonald, G.I., and R.J. Hoff. 2001. Blister rust: an introduced plague. Pages 193–220 in: D.F. Tomback, S.F. Arno, and R.E. Keane, editors. Whitebark communities: ecology and restoration. Island Press, Washington, D.C., USA.
- Moody, R.J. 2006. Post-fire regeneration and survival of whitebark pine (*Pinus albicaulis* Engelm.). Thesis, University of British Columbia, Vancouver, Canada.
- Morris, S. 1992. Wildfire as a part of cultural prehistory in Montana and the implications for public land managers. *Archaeology in Montana* 33: 79–91.
- Morse, C.C., I.V. Yevdokimov, and T.H. DeLuca. 2000. *In situ* extraction of rhizosphere organic compounds from contrasting plant communities. *Communications in Soil Science and Plant Analysis* 31: 725–742. doi: [10.1080/00103620009370473](https://doi.org/10.1080/00103620009370473)
- Munn, L.C., B.A. Buchanan, and G.A. Nielsen. 1978. Soil temperatures in adjacent high elevation forests and meadows of Montana. *Soil Science Society of America Journal* 42: 982–983. doi: [10.2136/sssaj1978.03615995004200060033x](https://doi.org/10.2136/sssaj1978.03615995004200060033x)
- Murray, M.P., S.C. Bunting, and P. Morgan. 1998. Fire history of an isolated subalpine mountain range of the Intermountain Region, United States. *Journal of Biogeography* 25: 1071–1080. doi: [10.1046/j.1365-2699.1998.00241.x](https://doi.org/10.1046/j.1365-2699.1998.00241.x)
- Page, A.L., R.H. Miller, and D.R. Keeney, editors. 1982. Methods of soil analysis, part 2. Chemical and microbiological properties. American Society of Agronomy, Madison, Wisconsin, USA.
- Plassard, C., B. Bonafos, and B. Touraine. 2000. Differential effects of mineral and organic N sources, and of ectomycorrhizal infection by *Hebeloma cylindrosporum*, on growth and N utilization in *Pinus pinaster*. *Plant, Cell, and Environment* 23: 1195–1205. doi: [10.1046/j.1365-3040.2000.00630.x](https://doi.org/10.1046/j.1365-3040.2000.00630.x)
- Potash, L.L., and J.K. Agee. 1998. The effect of fire on red heather (*Phyllodoce empetriformis*). *Canadian Journal of Botany* 76: 428–433. doi: [10.1139/b98-005](https://doi.org/10.1139/b98-005)
- Romme, W.H., L. Bohland, C. Persichetty, and T. Caruso. 1995. Germination ecology of some common forest herbs in Yellowstone National Park, Wyoming, USA. *Arctic and Alpine Research* 27: 407–412. doi: [10.2307/1552034](https://doi.org/10.2307/1552034)
- Saa, A., M.C. Trasar-Cepeda, F. Gil-Sotres, and T. Carballas. 1993. Changes in soil phosphorus and acid phosphatase activity immediately following forest fires. *Soil Biology and Biochemistry* 25: 1223–1230. doi: [10.1016/0038-0717\(93\)90218-Z](https://doi.org/10.1016/0038-0717(93)90218-Z)

- Simard, D.G., J.W. Fyles, D. Paré, and T. Nguyen. 2001. Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. *Canadian Journal of Soil Science* 81: 229–237. doi: [10.4141/S00-028](https://doi.org/10.4141/S00-028)
- Stevenson, F.J., and M.A. Cole. 1999. *Cycles of soil: carbon, nitrogen, phosphorus, sulfur, micronutrients*. Second edition. John Wiley & Sons, New York, New York, USA.
- Tomback, D.F. 1994. Ecological relationship between Clark's nutcracker and four wingless-seed *strobis* pines of western North America. Pages 221–225 in: *Proceedings of an international workshop on subalpine stone pines and their environment: the status of our knowledge*. USDA Forest Service General Technical Report INT-GTR-309, Intermountain Research Station, Ogden, Utah, USA.
- Tomback, D.F. 2001. Clark's nutcracker: agent of regeneration. Pages 89–104 in: D.F. Tomback, S.F. Arno, and R.E. Keane, editors. *Whitebark communities: ecology and restoration*. Island Press, Washington, D.C., USA.
- Tomback, D.F., and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. *Forest Pathology* 40: 186–225. doi: [10.1111/j.1439-0329.2010.00655.x](https://doi.org/10.1111/j.1439-0329.2010.00655.x)
- Tomback, D.F., A.J. Anderies, K.S. Carsey, M.L. Powell, and S. Mellman-Brown. 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology* 82: 2587–2600. doi: [10.1890/0012-9658\(2001\)082\[2587:DSGIWP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2587:DSGIWP]2.0.CO;2)
- Tomback, D.F., J.K. Clary, J. Koehler, R.J. Hoff, and S.F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance Burn of northern Idaho (USA.). *Conservation Biology* 9: 654–664. doi: [10.1046/j.1523-1739.1995.09030654.x](https://doi.org/10.1046/j.1523-1739.1995.09030654.x)
- Tomback, D.F., S.K. Sund, and L.A. Hoffmann. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. *Canadian Journal of Forest Research* 23: 113–119. doi: [10.1139/x93-018](https://doi.org/10.1139/x93-018)
- USDA [US Department of Agriculture Natural Resources Conservation Service]. 2004. Snow Telemetry (SNOTEL)—Savage Pass, Idaho. Natural Resources Conservation Service, National Water and Climate Center. <http://www.wcc.nrcs.usda.gov/data/snow/snotel/table/history/idaho/14c04s_p.txt>. Accessed 1 March 2004.
- USFWS [US Fish and Wildlife Service]. 2015. US Fish and Wildlife Service, endangered species: whitebark pine. <<http://www.fws.gov/mountain-prairie/species/plants/whitebarkpine/>>. Accessed 24 January 2015.