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Effects of various fire treatments on the regeneration of Jeffrey pine in the northern Sierra Nevada

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ABSTRACT

Fire suppression in montane regions has allowed dense second-growth conifer stands to form following logging. This has increased the likelihood of severe wildfire. Fire plays a key role in conifer seedling recruitment, nutrient cycling, and plant growth in coniferous forests. Thinning followed by prescribed burning has become an increasingly popular solution to increase forest resilience, structure, and regeneration. From 2016 to 2023 in the Sagehen Creek Experimental Forest, California, the US Forest Service conducted four fire treatments: surface burn, pile burn, unburned lop and scatter, lop and scatter with surface burn. In this study, we compared post-fire Jeffrey pine (*Pinus jeffreyi)* seedling densities and pre-fire Jeffrey pine seedling new growth between the four fire treatments to test the impacts of these treatments on post-fire Jeffrey pine recruitment and regeneration. Our study revealed that the unburned lop and scatter treatment site had the lowest density of post-fire Jeffrey pine seedlings among the four treatment types. No pre-fire treatment had a greater impact than burning in any plot. Considering the limited time and resources available to implement effective fuels management strategies, we recommend prioritizing fire-based treatments in conifer forests to promote conifer seedling recruitment. We believe the surface burn treatment is the most cost-effective among the four fire treatments.

Keywords: Jeffrey pine *(Pinus jeffreyi)*; SPLAT; seedling density; forest regeneration; post-burn succession

INTRODUCTION

Fire has shaped biodiversity, plant diversification, and ecosystem dynamics worldwide for millions of years (Rundel et al. 2018, Kelly et al. 2020). Low-intensity fire provides vital ecosystem services and is a key contributor to biodiversity (Van Wagtendonk 2006, Prepas et al. 2009, Pausas and Keeley, 2019). Low-intensity fire is fueled by the combination of litter, woody fuel, shrubs, and low vegetation, but remains on the forest floor and does not reach the canopy. The presence of natural and indigenously stewarded low-intensity fire has been well documented for its ability to reduce plant biomass, introduce limiting resources into the soil, and stimulate post-fire plant growth in montane forest communities (McShea 2003, Jordan et al. 2003, Harper et al. 2016). These effects have contributed to high species richness levels and increased the presence of native species (He et al. 2019). However, despite the abundant benefits of regular fire, management practices have rarely

considered its vital role in maintaining ecological biodiversity.

The disruption of indigenous forestry practices has led to over a century of fire suppression and subsequent negative impacts on forest ecosystems (Chang 1996, Thonicke et al. 2001, Keane et al. 2002, Pyne 2016, Kromer 2022). Although these mandates aimed to reduce the adverse effects of fires, they worsened them (Kreider et al. 2024). Large-scale fire suppression drastically alters the natural biodiversity of fire-adapted ecosystems, establishing avenues for non-native plant species to invade or for fast-growing shrubs and grasses to dominate and outcompete other species (Gilliam and Platt 1999, Shlisky et al. 2007, Stephens et al. 2009, Larson et al. 2013). This can create highly homogeneous and monocultured forests that are more susceptible and vulnerable to disease outbreaks, drought pressure, and high competition for limited resources (Scasta 2015, Voelker et al. 2019). Furthermore, the absence of low-intensity fire allows large amounts of plant biomass to accumulate, often resulting in high-severity fires that severely damage forest environments (Hai et al., 2023). Before a controlled burn is implemented, time, goals, scale, fuel, weather, and forest conditions are all carefully considered to create a fire plan (Dye 2022, “Wildland Fire” 2025). Before a burn, sites undergo treatment that alters the landscape to ensure the success and safety of the burn (Weir et al., 2013).

Prescribed fire treatment is implemented through four primary means in California forests: surface burn, pile burn, unburned lop and scatter, and lop and scatter with surface burn (Table 1). Each of these methods requires various amounts of treatment effort to implement. Treatment effort includes the monetary cost of time, manpower, equipment and permits required to carry out a treatment (Ott et al., 2023). The surface fire treatment utilizes fuel breaks--naturally occurring or man-made gaps such as cleared areas, rivers, and roads--to prevent the rapid spread of fire and maintain control. This method requires the least amount of treatment effort and costs approximately $302 per hectare (Loomis and González-Cabán 2010, Shamsoshoara et al. 2021). Pile burn treatment is used in areas with high vegetation cover where surface burns may be unsafe. Ignition fuel is mechanically or manually collected and piled together (Redmond et al. 2014). This treatment requires a moderately high amount of treatment effort and costs approximately $579 per hectare. The lop and scatter treatment requires personnel to delimb and cut trees, then scatter material across the forest floor. This treatment focuses on changing the size and arrangement of fuels to facilitate decomposition, decrease fire severity, and increase forest stand fire resilience (Halbrook et al. 2006). The lop and scatter treatment requires substantially higher treatment effort and costs approximately $2,486 per hectare (Kim et al. 2026). Lastly, the lop and scatter with surface burn treatment combines both the lop and scatter and surface burn treatment methods to redistribute fuel load and minimize fire intensity (Ascoli et al. 2018). This treatment requires the highest amount of treatment effort and costs approximately $2,788 per hectare (Loomis et al. 2019, Kim et al. 2026).

Table 1. Description of four SPLAT treatments within Sagehen Experimental Forest in Truckee, CA.

Lop & Scatter (2016)	Focuses on changing the size and arrangement of the fuels to allow the material to decompose more rapidly. Refers to removal of tree, brush, and dead branch material. No fuel is burned.
Lop & Scatter with Surface Burn (2016)	Following fuel rearrangement, the fuels are consumed in place through burning, generally burning at a low intensity .
Pile Burn (2018)	Natural and mechanically collected fuels are placed in a pile for burning following a year-long drying process. Designed to mimic underburning in places where understory is too dense to keep fire under control.
Surface Burn (2023)	A fire that burns live and dead fuels on the surface of the ground. Designed to consume surface debris and standing deadwood.

Within Sagehen Experiment Forest in Truckee, CA, the California Department of Forestry and Fire Protection (CAL FIRE) and the US Forest Service (USFS) used these strategically placed area land area treatments (SPLATs) to reduce fuel cover and promote conifer regeneration (Boden et al. 2023). These SPLATs consisted of a surface burn treatment in 2023, a pile burn treatment in 2018, an unburned lop and scatter treatment in 2016, and a lop and scatter with surface fire treatment also in 2016 (Bancroft et al. 2024, Smith et al. 2024). The US Forest Service claimed that these fire treatments would increase conifer regeneration within the Sagehen Basin (Boatner et. al 2013). Despite these assertions from the Forest Service, the true impact of these treatments on conifer regeneration in the long term has not been studied. Given the extremely variable costs of these different prescribed fire treatments, managers must understand their individual effectiveness in the long term. We chose to study Jeffrey Pine (*Pinus Jeffreyi*) as a proxy for measuring these effects, as it is highly abundant within every treatment site in the Sagehen Experimental Forest.

Jeffrey pine is a prominent California conifer tree species that benefits from controlled burns and prescribed fire treatments (Kouba et al. 2025). It is a shade-intolerant conifer that is fire-resistant due to thick bark and tall growth (Bova and Dickinson 2005, Pausas and Keeley 2019). These characteristics allow Jeffrey pine to thrive in post-fire environments that lack dense woody shrubs and canopy cover. Treatments that use fire increase sun exposure, nutrient availability, and improve

soil conditions for Jeffrey pine seedling recruitment (Keeley et al. 2011). Pre-fire mechanical thinning can enhance this positive effect on seedling recruitment by further minimizing competing shrub presence, clearing the forest floor, and opening up the tree canopy (Hood et al. 2017, Baird et al. 1999). The lop and scatter with surface burn treatment combines fire and mechanical thinning to create the most suitable growing conditions for Jeffrey pine seedlings.

At Sagehen, we sampled multiple plots at each of the four prescribed fire treatment methods. Our primary objectives were to: 1) determine the long-term effects of different prescribed fire treatments on the density of post-fire Jeffrey pine seedlings and 2) ascertain if different fire treatment methods affect pre-fire Jeffrey pine seedling new growth (growth that occurred within the past year). We predict that due to Jeffrey pine's shade intolerance and tendency to establish in open areas (Jenkinson 1990), post-fire Jeffrey pine seedling density will be greater in the lop and scatter with surface fire treatment site. Similarly, we predict that pre-fire Jeffrey pine saplings will have the greatest amount of new growth in the lop and scatter with surface fire treatment site as well.

METHODS

Our study was conducted from July 30 to August 2, 2026 at Sagehen Creek Field Station in the Sierra Nevadas in California (39.431861, -120.240556). Sagehen Creek is located at the floor of the Sagehen basin. The surrounding 3640-hectare experimental forest ranges from 1877 to 2262 m in elevation ("UC Nature" 2026). A majority of the basin is an Experimental Forest and is currently managed by the USDA Forest Service's Pacific Southwest Research Station and the Tahoe National Forest (Sagehen Experimental Forest | US Forest Service Research and Development 2023). The forest is located 16 km north of Truckee, CA on the east side of the Sierra Nevada Range. The forest has a Mediterranean climate with warm and dry summers. Annual precipitation is around 84 cm, with over 80 percent of precipitation coming from snow (Sagehen Experimental Forest | US Forest Service Research and Development 2023). The mixed conifer stands consist mainly of ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), and western white pine (*Pinus monticola*) (Moriarty et al. 2011, Boatner et al. 2013). The understory is composed of woody plants such as greenleaf manzanita (*Arctostaphylos patula)* and snowbrush ceanothus (*Ceanothus velutinus),* which thrive in disturbed environments (McDonald et al. 1997, Anderson 2001, Johnson et al. 2005).

The Sagehen Basin has a long history of disturbance (UC Nature 2026). Sheep and cattle grazing occurred from the 1860s to 2008 (Boatner et al. 2013). The area was intensely logged from the 1870s through the 1930s until it was acquired by the Forest Service in 1936. The basin was culturally burned by the Washoe tribe every 2.5 years on average for nearly 1000 years (UC Nature 2026). When settlers arrived, cultural and natural fire was suppressed in the following 150 years (Beaty and Taylor 2008, Long and Heritage 2019). The combination of logging and the lack of disturbance created a dense, second-growth forest plantation. In 1960, the Donner Ridge Fire—the highest intensity fire the basin had experienced—burned one third of the basin.

Wildfire severity and concern about forest stand diversity within the Eastern Sierra Nevada led the US Forest Service and CAL Fire to implement fire treatments in Sagehen Experimental Forest (Boatner et al. 2013). Selected sites within the basin were all mixed conifer forests. In 2016, the lop and scatter treatment was carried out on site with a southeast-facing, high relief aspect at approximately 2,200 m elevation in the northwest of the basin (Outside Inc. 2026; Fig. 2). In 2016, the lop and scatter with surface burn treatment was implemented on a southeast-facing site at approximately 2,200 m elevation. This site was completely burnt in the Donner Ridge fire (UC Nature 2026). In 2018 and 2023, the pile burn and surface burn treatments were implemented on flat sites in the northeast of the experimental forest at a similar 200 m range in elevation (Outside Inc. 2026). These two sites have clear signs of volcanic activity, with andesite flows obscuring the ground in many places (UC Nature 2026). White fir and Jeffrey pine are the primary trees present in all sites.

To determine if seedlings were established before or after their respective fire treatment, we tested if height could be used as a proxy for seedling age. Seedlings were identified as any Jeffrey pine tree that was less than 90 cm tall or less than 5.1 cm in diameter at breast height (dbh) ("NAL Agricultural Thesaurus: NALT: seedlings" 2018). We sampled 15 Jeffrey pine seedlings from a 2023 surface burn site within Sagehen Experimental Forest (39.432415, -120.240712). Jeffrey pine seedling heights were measured, cut at the base of their trunks, and the cross-sections were sanded with 120 and 180-grit sandpaper. After water was applied to the cross-section, a hand-lens was used to count the rings of the tree to determine seedling age. We then ran a linear regression that correlated height to age ($y = 0.307*\text{height} - 2.548$, $R^2 = 0.845$, $p < 0.001$; Fig. 1). From that linear regression, we estimated that 10-year-old seedlings were at most 40 cm tall, 8-year-old seedlings were at most 35 cm tall, and 3-year-old seedlings were at most 18 cm tall. We used this regression in the field to classify each seedling as a pre-fire or post-fire seedling depending on the year of the site's fire treatment and seedling height.

We randomly surveyed eighty total plots at four fire treatment sites in Sagehen Experimental Forest: surface burn, pile burn, unburned lop and scatter, and lop and scatter with surface burn (Fig. 2). At each fire treatment site, twenty 20x20 meter plots were randomly chosen with no overlap between plots and set up using a rangefinder, compass, and four pin flags (Fig. 2). Within each plot, we counted the total number of post-fire Jeffrey pine seedlings and calculated the density (Tortorelli et al. 2024). We then measured in centimeters the current year's new growth of all pre-fire seedlings, which are less than 90 cm tall or less than 5.1 cm dbh ("NAL Agricultural Thesaurus: NALT: seedlings" 2018). New growth was identified by a distinct color and texture difference from the woody light brown main stem to the tender, bright green apical bud (Fig. 3).

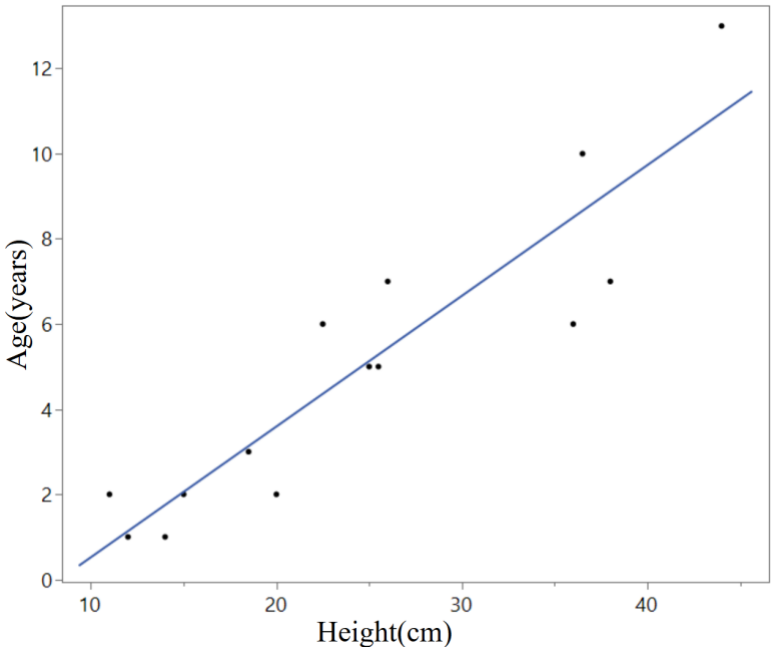


Figure 1. Height increases with age in Jeffrey pine seedlings. Data was collected in Sagehen Experimental Forest in Truckee, CA on July 30, 2026. A total of 14 Jeffrey pine seedlings were cut at the base of the trunk, and tree rings were counted to estimate the age of each seedling ($y = 0.307*\text{height} - 2.548$, $R^2 = 0.845$, $p < 0.001$).

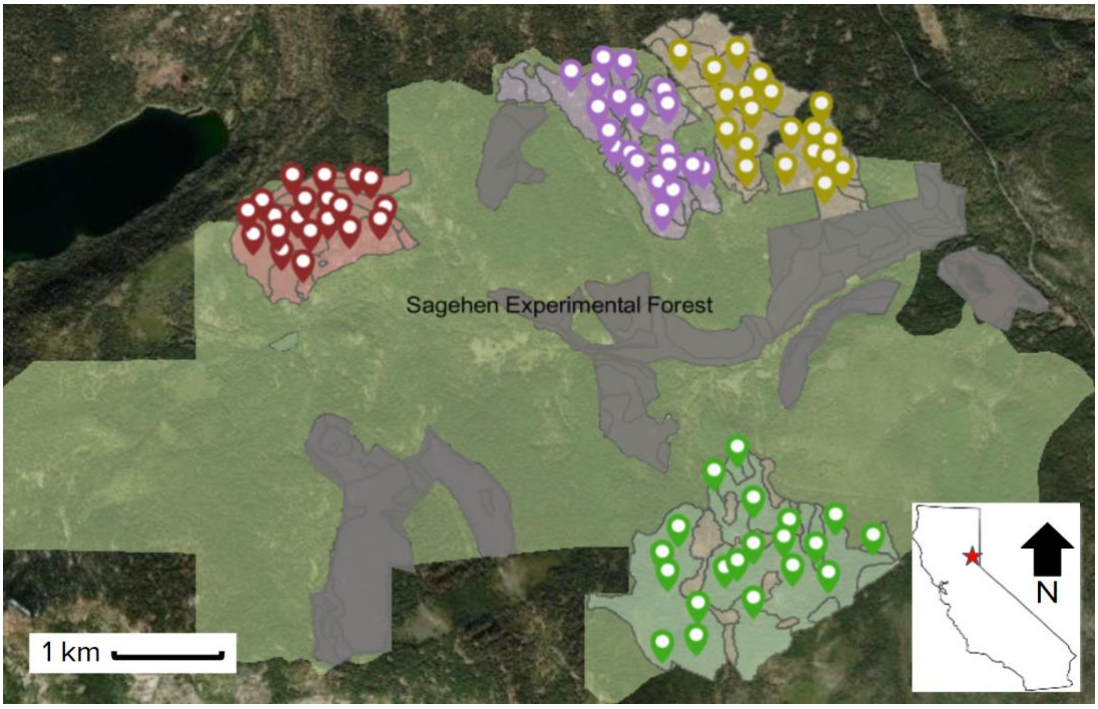


Figure 2. Fire treatment sites in Sagehen Experimental Forest (3640 hectares). Site is situated 16 km northwest of Truckee, California within Sierra and Nevada counties. Points represent the southwest corner of each 20 x 20 m plot, with each plot oriented to the north. Red points represent lop and scatter (1.09 km^2), green points represent lop and scatter with surface burn (2.64 km^2), purple points represent pile burn (0.77 km^2), and tan points represent surface burn (1.40 km^2). Grey represents treated sites that were not sampled.



Figure 3. New growth in Jeffrey pine seedlings can be distinguished as a lighter, brighter green than darker, older brown plant growth. The yellow bar demarcates the delineation of new growth compared to old growth. Sample was taken on July 30, 2026, at Sagehen Creek Field Station (39.431861, -120.240556).

We used an ANOVA with a Tukey HSD post-hoc test to compare Jeffrey pine post-fire seedling density between the four fire treatments. We also used an ANOVA with plot as a random effect to compare pre-fire Jeffrey pine seedling new growth between each of the four fire treatments. We used a Wilcoxon rank-sum nonparametric analysis for median comparison to compare pre-fire seedling density between the four fire treatments. All statistical analyses were conducted using JMP statistical software v18 (2026 JMP® Version 18. JMP Statistical Discovery LLC, Cary, NC.).

RESULTS

The unburned lop and scatter treatment site had the lowest density of post-fire Jeffrey pine seedlings. The lop and scatter with surface burn, pile burn, and surface burn treatment sites were similar in seedling density ($N = 20$, $F = 3.39$, $p = 0.022$; Fig. 4). Site location drives Jeffrey pine new growth, not fire treatment ($N = 86$, $F = 4.68$, $p = 0.32$). There was no effect of fire treatment on pre-fire seedling density ($N = 86$. $X^2 = 0.38$, $p = 0.94$).

We observed high amounts of woody plant cover in the lop and scatter with surface burn site, and the unburned lop and scatter site. Greenleaf manzanita (*Arctostaphylos patula*) and snowbrush ceanothus (*Ceanothus velutinus*) were among the most common woody shrubs, oftentimes growing in dense patches. Substrate composition varied amongst survey plots of all fire treatment types, from rocky and compact to loamy and soft. Duff depth varied from 1 to 15 cm deep.

DISCUSSION

Our study did not support the prediction that post-fire Jeffrey pine seedling density would be greater in the lop and scatter with surface burn treatment site. Instead, we found that the unburned lop and scatter treatment site had the lowest post-fire Jeffrey pine seedling density due to a lack of fire. Fire improved post-fire Jeffrey pine seedling germination and recruitment because Jeffrey pine seedling density did not differ among sites before treatment. After treatment, burned sites had greater seedling densities than the lop and scatter site that lacked fire.

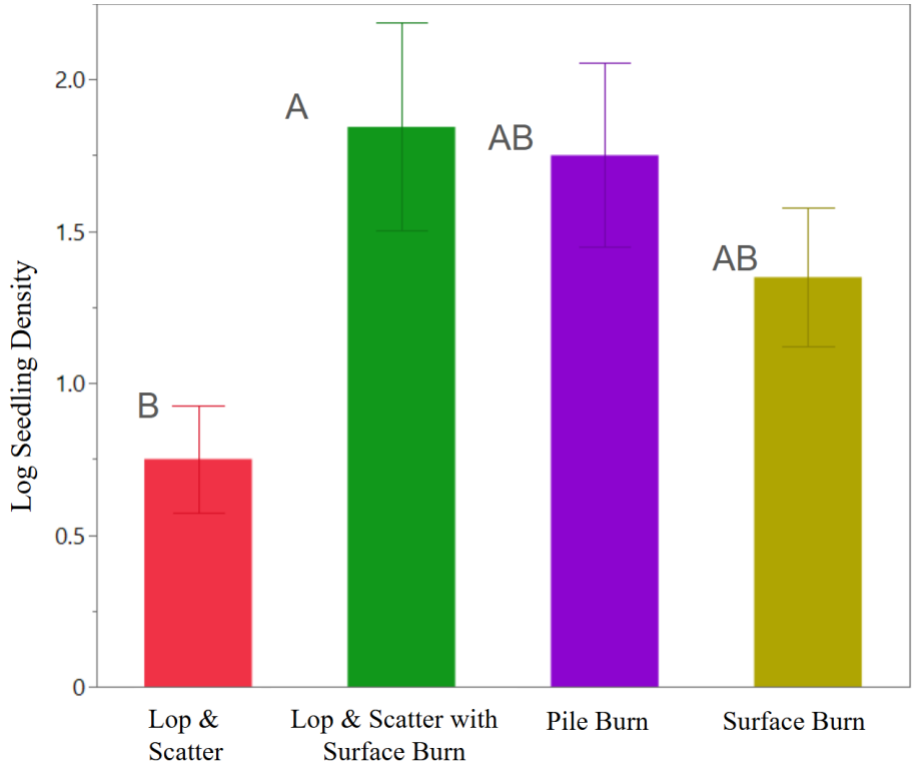


Figure 4. Post-fire Jeffrey pine seedling density was lowest in the unburned lop and scatter site. Data was collected in randomly selected 20x20 plots within treatments in Sagehen Experimental Forest from July 30 to August 2, 2026. Post-fire density was recorded in 20 plots in each of the four treatment sites. Shared letters indicate groups with non-significant differences between them based on a Tukey HSD post-hoc test. Error bars represent one standard error (N= 20, F = 3.39, p = 0.022).

The presence of fire in a mixed-conifer forest can decrease shrub cover density, minimize needle duff thickness, and provide limiting nutrients (Oswald et al. 1998, Johnson et al. 2005, Boatner et al. 2013). These conditions are favorable for Jeffrey pine seedling germination and recruitment. We observed high woody plant cover in the lop and scatter with surface burn treatment site, and the unburned lop and scatter treatment site. In coniferous forests, shrubs can provide suitable microclimates for Jeffrey pine seed germination by offering shade and protection from wind, which increases soil moisture, decreases heat stress, and reduces the risk of desiccation (Legras et al. 2010, Kirk-Davidoff 2026). When the surface burn was implemented directly after the lop and scatter treatment, woody shrubs were burned and created space for both conifer seedlings and shrubs to grow together, rather than compete (Boatner et al. 2013). After the fire, as woody shrubs continued to grow, they may have provided a suitable microclimate for Jeffrey pine seedling germination (Anderson 2001, Legras et al. 2010). This likely allowed dense shrub cover to overtake the landscape and hinder Jeffrey pine seedling recruitment by overshading and depleting soil moisture (McDonald et al. 1997, Tortorelli et al. 2024).

Needle duff was observationally thinner in burned treatment sites than the unburned lop and scatter treatment site. Thick needle duff limits sun exposure and suppresses seed germination (Oswald et al. 1998). As

duff is burned, limiting nutrients such as magnesium, phosphorus, and nitrogen are released into the soil (Jordan et al. 2003, Johnson et al. 2005). The surface burns and pile burn most likely thinned the thick needle duff, increased light availability, and increased nutrient availability for post-fire Jeffrey pine seed germination (Oswald et al. 1998).

We believe that the impact of fire treatment on post-fire conifer seedling density could potentially vary based on tree species serotiny (Neale and Wheeler 2019). Serotinous plants, such as lodgepole pines (*pinus contorta*), rely on fire to open cones and release seeds in postfire environments that are nutrient-rich and lack competition (Welch et al. 2016). Fire plays a larger role in lodgepole pine (*pinus contorta*) seed dispersal than Jeffrey pine ("Wildland Fire in Lodgepole Pine (U.S. National Park Service)" 2021). Future research could compare the post-fire seedling density of serotinous with non-serotinous conifers. This investigation would more specifically inform land managers how fire treatments will benefit specific conifer species within mixed-conifer forests, as well as what species will dominate in the post-fire landscape.

Our study did not support our prediction that pre-fire Jeffrey pine new growth would be greater in the lop and scatter with surface burn treatment site. Our results showed that pre-fire Jeffrey pine seedling growth is not affected by fire treatment type. This may be explained instead by variability in site conditions and fire treatment age.

Besides fire treatment, substrate composition variables such as duff depth and rockiness influence seedling growth (Oswald et al. 1998, Hubbert et al. 2001, Meyer et al. 2007). We observed that duff depth varied by over 10 cm amongst all fire treatment sites. McIver confirmed these results in 2013; ecological variables' response to prescription fires did not depend on the fire treatment type but instead depended more on site-specific variables. In areas where pine seedlings are unable to penetrate their roots as deeply or absorb as much water from their substrate, growth is lessened, and survival rates also decrease (Hubbert et al. 2001, Meyer et al. 2007). The substrate between sites varied in rockiness, soil depth, and composition, all of which have critical roles in supporting Jeffrey pine tree growth.

It is important to note that the four fire treatments were implemented multiple years apart. The effects of burned fire treatment on pre-fire seedling new growth may have been more pronounced within the immediate years after the fire than multiple years later (Ganzlin et al. 2016, Knelman et al. 2017, Bancroft et al. 2024). In the younger, 3-year-old surface burn treatment site, we observed an open tree canopy and low shrub density on the forest floor, both of which are favorable for Jeffrey pine seedling growth. In contrast, both the older 10-year-old burned and unburned lop and scatter treatment sites had a less open canopy and were dominated by tall shrubs. Additionally, it was found that post-fire limited nutrients such as nitrogen are most enhanced within the first three years and recede in the long-term (Ganzlin et al. 2016; Knelman 2017). This time difference may have created variable conditions that explain why we saw no difference in pre-fire seedling new growth. Our study gave us a snapshot of post-fire conditions and seedling densities. A future study that observes post-fire seedling growth amongst SPLAT fire treatments of the same age can control for this time variability. For example, in Stephens and

Moghadda's study in 2005, four different treatments involving thinning and prescription fires were randomly applied to plots within a one-month period. Sites were then tested for effects at four different stages of treatment to see how fuel loads and vegetation structure changed over time (Stephens and Moghaddas 2005). A similar temporally uniform study design could provide more accurate observations on the pre-fire new growth of Jeffrey pine seedlings.

Land managers prioritize two questions in fire management decisions: "Will it work?" and "How much does it cost?". Our study showed that treatments that use fire are more effective at increasing Jeffrey pine seedling recruitment than treatments that lack fire, regardless of the use of pre-fire mechanical thinning. In McIver et al. 2013, it was found that burned mechanical thinning treatments had higher post-fire conifer seedling density than unburned mechanical thinning treatments. This study supports our findings that the presence of fire leads to greater Jeffrey pine seedling density. However, our study did not support McIver's findings that pre-fire thinning led to greater conifer seedling density than in the absence of thinning before fire. These observations are advantageous for land managers. Both mechanical and manual thinning are significantly more expensive to implement than surface fire alone (Ascoli et al. 2018, Loomis et al. 2019, Kim et al. 2026).

Overall, our results on post-fire Jeffrey pine seedling density suggest that fire plays a strong role in promoting Jeffrey pine seedling establishment. Fire can determine whether Jeffrey pine seedlings and neighboring woody shrubs coexist or compete (Boatner et al. 2013). Fire may also promote Jeffrey pine seedling recruitment by decreasing duff thickness, amending the soil, and facilitating nutrient cycling (Legras et al. 2010; Oswald et al. 1999). Despite current emphasis on pre-fire thinning, our study indicates that this fire treatment may not contribute to post-fire Jeffrey pine seedling recruitment. Land managers throughout California have limited resources and time to execute fuels management strategies. We recommend land managers prioritize the implementation of fire rather than thinning because it is efficient, cheap, and has been proven to be effective in promoting Jeffrey pine seedling regeneration.

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REFERENCES

Anderson, M. 2001. SPECIES: *Ceanothus velutinus*. U.S. Department of Agriculture. https://www.fs.usda.gov/database/feis/plants/shrub/ceavel/all.html.

Ascoli, D., L. Russo, F. Giannino, C. Siettos, and F. Moreira. 2018. Firebreak and fuelbreak. Pages 1–9 *in* S. L. Manzello, ed. *Encyclopedia of Wildfires and Wildland-Urban Interface (WUI) Fires*. Springer International Publishing, Cham.

Bancroft, K., C. Dayton, Jih-Heng Huang, and N. Ng. 2024. Prescribed burns in a mixed conifer forest

maintain diversity in bird communities. *CEC Research* **8(2)**.

Beaty, R. M., and A. H. Taylor. 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. *Forest Ecology and Management* **255:**707–719.

Boatner, K., T. Cardoza, and S. Conway. 2013. Environmental Assessment Sagehen Project. Page 324. United States Department of Agriculture.

Boden, K., D. Philippus, A. Sytsma, J. Kurzweil, J. Randell, A. M. Kinoshita, and T. S. Hogue. 2023. A multi-scale assessment of forest treatment impacts on evapotranspiration and water yield in the Sierra Nevada. *Ecohydrology* **16:**e2548.

Bova, A. S., and M. B. Dickinson. 2005. Linking surface-fire behavior, stem heating, and tissue necrosis. *Canadian Journal of Forest Research* **35:**814–822.

Chang, C. 1996. Ecosystem responses to fire and variations in fire regimes. *Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Assessments and scientific basis for management options.* Davis: University of California, Centers for Water and Wildland Resources.

Ganzlin, P. W., M. J. Gundale, R. E. Becknell, and C. C. Cleveland. 2016. Forest restoration treatments have subtle long-term effects on soil C and N cycling in mixed conifer forests. *Ecological Applications* **26:**1503–1516.

Gilliam, F. S., and W. J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest. *Plant Ecology* **140:**15–26.

Hai, J., L. Zhang, C. Gao, H. Wang, and J. Wu. 2023. How does fire suppression alter the wildfire regime? A systematic review. *Fire* **6:**424.

Halbrook, J., H.-S. Han, R. T. Graham, T. B. Jain, and R. Denner. 2006. Mastication: A fuel reduction and site preparation alternative. *In*: Chung, W.; Han, H. S., eds. *Proceedings of the 29th Council on Forest Engineering Conference; July 30-August 2, 2006; Coeur d'Alene, ID*. p. 137–146.

Harper, C. A., W. M. Ford, M. A. Lashley, C. E. Moorman, and M. C. Stambaugh. 2016. Fire effects on wildlife in the central hardwoods and Appalachian Regions, USA. *Fire Ecology* **12:**127–159.

He, T., B. B. Lamont, and J. G. Pausas. 2019. Fire as a key driver of Earth's biodiversity. *Biological Reviews* **94:**1983–2010.

Hubbert, K. R., R. C. Graham, and M. A. Anderson. 2001. Soil and Weathered Bedrock: Components of a Jeffrey Pine Plantation Substrate. *Soil Science Society of America Journal* **65:**1255–1262.

Jenkinson, D. S. 1990. An introduction to the global nitrogen cycle. *Soil Use and Management* **6:**56–61.

Johnson, D. W., J. F. Murphy, R. B. Susfalk, T. G. Caldwell, W. W. Miller, R. F. Walker, and R. F. Powers. 2005. The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. *Forest Ecology and Management* **220:**155–165.

Jordan, M. J., W. A. Patterson, and A. G. Windisch. 2003. Conceptual ecological models for the Long Island pitch pine barrens: implications for managing rare plant communities. *Forest Ecology and Management* **185:**151–168.

Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in the Rocky Mountain ecosystems: a literature review. Page RMRS-GTR-91. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Keeley, J. E., W. J. Bond, R. A. Bradstock, J. G. Pausas, and P. W. Rundel. 2011. *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management. First edition*. Cambridge University Press.

Kelly, L. T., K. M. Giljohann, A. Duane, N. Aquilué, S. Archibald, E. Batllori, A. F. Bennett, S. T. Buckland, Q. Canelles, M. F. Clarke, M.-J. Fortin, V. Hermoso, S. Herrando, R. E. Keane, F. K. Lake, M. A. McCarthy, A. Morán-Ordóñez, C. L. Parr, J. G. Pausas, T. D. Penman, A. Regos, L. Rumpff, J. L. Santos, A. L. Smith, A. D. Syphard, M. W. Tingley, and L. Brotons. 2020. Fire and biodiversity in the Anthropocene. *Science* **370:**eabb0355.

Kim, G., W. Chung, N. M. Anderson, and H. Woo. 2026. Optimizing deployment of mobile biochar production equipment for enhanced slash management. *International Journal of Forest Engineering*:1–15.

Kirk-Davidoff, R. 2026. Nurse shrubs increase *Pinus jeffreyi* seedling survival in Eastern Sierra post-fire plantings. PhD Thesis, University of Nevada, Reno.

Knelman, J., E. Graham, S. Ferrenberg, A. Lecoeuvre, A. Labrado, J. Darcy, D. Nemergut, and S. Schmidt. 2017. Rapid shifts in soil nutrients and decomposition enzyme activity in early succession following forest fire. *Forests* **8:**347.

Kouba, P. V., A. M. Latimer, D. J. N. Young, M. Odkins, D. M. Bell, I. R. Clark, and M. P. North. 2025. Prescribed and natural fire help restore fire-adapted conditions in an Eastern Sierra Jeffrey pine forest. *Forest Ecology and Management* **595:**123010.

Kreider, M. R., P. E. Higuera, S. A. Parks, W. L. Rice, N. White, and A. J. Larson. 2024. Fire suppression makes wildfires more severe and accentuates impacts of climate change and fuel accumulation. *Nature Communications* **15:**2412.

Kromer, M. 2022. Wildfire simulation using agent based modeling: expanding controlled burn season. Senior independent thesis, Wooster University. https://openworks.wooster.edu/independentstudy/9888/

Larson, A. J., R. T. Belote, C. A. Cansler, S. A. Parks, and M. S. Dietz. 2013. Latent resilience in ponderosa pine forest: effects of resumed frequent fire. *Ecological Applications* **23:**1243–1249.

Legras, E. C., S. B. Vander Wall, and D. I. Board. 2010. The role of germination microsite in the establishment of sugar pine and Jeffrey pine seedlings. *Forest Ecology and Management* **260:**806–813.

Long, J., and W. C. Heritage. 2019. Washoe cultural resources vulnerability assessment. Pages 56–61, *in* California Tahoe Conservancy and Catalyst Environmental Solutions, *Technical Memos: Integrated Vulnerability Assessment of Climate Change in the Lake Tahoe Basin*.

Loomis, J., and A. González-Cabán. 2010. Forest service use of nonmarket valuation in fire economics: Past, present, and future. *Journal of Forestry* **108:**389–396.

Loomis, J., J. J. Sánchez, A. González-Cabán, D. Rideout, and R. Reich. 2019. Do fuel treatments reduce wildfire suppression costs and property damages? Analysis of suppression costs and property damages in U.S. National Forests. Gen. Tech. Rep. PSW-GTR-261 (English). Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station **261:**70–84.

McDonald, P. M., and C. S. Abbott. 1997. Vegetation trends in a 31-year-old ponderosa pine plantation: effect of different shrub densities. United States Dept. of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

McIver, J. D., S. L. Stephens, J. K. Agee, J. Barbour, R. E. J. Boerner, C. B. Edminster, K. L. Erickson, K. L. Farris, C. J. Fettig, C. E. Fiedler, S. Haase, S. C. Hart, J. E. Keeley, E. E. Knapp, J. F. Lehmkuhl, J. J. Moghaddas, W. Otrosina, K. W. Outcalt, D. W. Schwilk, C. N. Skinner, T. A. Waldrop, C. P. Weatherspoon, D. A. Yaussy, A. Youngblood, and S. Zack. 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogate study (FFS). *International Journal of Wildland Fire* **22:**63–82.

McShea, W. 2003. *Oak Forest Ecosystems*. Johns Hopkins University Press, Baltimore, Maryland.

Meyer, M. D., M. P. North, A. N. Gray, and H. S. J. Zald. 2007. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. *Plant and Soil* **294:**113–123.

Moriarty, K. M., W. J. Zielinski, and E. D. Forsman. 2011. Decline in American marten occupancy rates at Sagehen Experimental Forest, California. *The Journal of Wildlife Management* **75:**1774–1787.

NAL Agricultural Thesaurus: NALT: seedlings. 2018, May 3. https://lod.nal.usda.gov/nalt/en/ page/32911.

Neale, D. B., and N. C. Wheeler. 2019. *The Conifers: Genomes, Variation and Evolution*. Springer International Publishing, Cham.

Oswald, B. P., K. Wellner, R. Boyce, and L. F. Neuenschwander. 1998. Germination and initial growth of four coniferous species on varied duff depths in northern Idaho. *Journal of Sustainable Forestry* **8:**11–21.

Ott, J. E., F. F. Kilkenny, and T. B. Jain. 2023. Fuel treatment effectiveness at the landscape scale: a systematic review of simulation studies comparing treatment scenarios in North America. *Fire Ecology* **19:**10.

Outside Inc. 2026. Gaia GPS.

Pausas, J. G., and J. E. Keeley. 2019. Wildfires as an ecosystem service. *Frontiers in Ecology and the Environment* **17:**289–295.

Prepas, E., N. Serediak, G. Putz, and D. W. Smith. 2009. Fires. *In* pages 74–87 *Encyclopedia of Inland Waters*. Elsevier.

Pyne, S. J. 2016. *California: A Fire Survey*. University of Arizona Press, Tucson, Arizona.

Redmond, M. D., T. J. Zelikova, and N. N. Barger. 2014. Limits to understory plant restoration following fuel-reduction treatments in a piñon–juniper woodland. *Environmental Management* **54:**1139–1152.

Rundel, P. W., M. T. K. Arroyo, R. M. Cowling, J. E. Keeley, B. B. Lamont, J. G. Pausas, and P. Vargas. 2018. Fire and plant diversification in Mediterranean-climate regions. *Frontiers in Plant Science* **9:**851.

Sagehen Experimental Forest. 2023, March 21. US Forest Service Research and Development. Text. https://research.fs.usda.gov/psw/forestsandranges/locations/sagehen.

Scasta, J. D. 2015. Fire and Parasites: An under-recognized form of anthropogenic land use change and mechanism of disease exposure. *EcoHealth* **12:**398–403.

Shamsoshoara, A., F. Afghah, A. Razi, L. Zheng, P. Z. Fulé, and E. Blasch. 2021. Aerial imagery pile burn detection using deep learning: The FLAME dataset. *Computer Networks* **193:**108001.

Shlisky, A., A. Alencar, M. Manta, L. Curran, and M. Cochrane. 2009. Overview: Global fire regime conditions, threats, and opportunities for fire management in the tropics. Pages 65–83 *in* M. A. Cochrane, ed. *Tropical Fire Ecology: Climate Change, Land Use and Ecosystem Dynamics*. Springer Praxis Books

Smith, K. A., K. E. Schneider, A. M. Kinoshita, J. Kurzweil, B. Prucha, and T. S. Hogue. 2024. Water yield response to forest treatment patterns in a Sierra Nevada watershed. *Journal of Hydrology: Regional Studies* **53:**101762.

Stephens, S. L., and J. J. Moghaddas. 2005. Experimental fuel treatment impacts on forest structure, potential fire behavior, and predicted tree mortality in a California mixed conifer forest. *Forest Ecology and Management* **215:**21–36.

Stephens, S. L., J. J. Moghaddas, B. R. Hartsough, E. E. Y. Moghaddas, and N. E. Clinton. 2009. Fuel treatment effects on stand-level carbon pools, treatment-related emissions, and fire risk in a Sierra Nevada mixed-conifer forest. Pub. No. 143, National Fire and Fire Surrogate Project. *Canadian Journal of Forest Research* **39:**1538–1547.

Thonicke, K., S. Venevsky, S. Sitch, and W. Cramer. 2001. The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. *Global Ecology and Biogeography* **10:**661–677.

Tortorelli, C. M., D. J. N. Young, M. J. Reilly, R. J. Butz, H. D. Safford, N. E. Venuti, K. R. Welch, and A. M. Latimer. 2024. Post-fire resurveys reveal predictability of long-term conifer recruitment in severely burned California dry forests. *Forest Ecology and Management* **566:**122100.

UC Nature. 2026. Educational, UC Nature, Sagehen Creek Field Station, Truckee, California. https://sagehen.ucnature.org/history/.

Van Wagtendonk, J. W. 2006. Fire as a Physical Process. Pages 38–57 *in* N. Sugihara, editor. *Fire in California's Ecosystems*. University of California Press, Oakland, California.

Voelker, S. L., A. G. Merschel, F. C. Meinzer, D. E. M. Ulrich, T. A. Spies, and C. J. Still. 2019. Fire deficits

have increased drought sensitivity in dry conifer forests: Fire frequency and tree-ring carbon isotope evidence from Central Oregon. *Global Change Biology* **25:**1247–1262.

Weir, J., S. Fuhlendorf, D. Engle, T. Bidwell, D. Cummings, R. Elmore, R. Limb, B. Allred, J. Scasta, and S. Winter. 2013. Patch burning: Integrating fire and grazing to promote heterogeneity. Department of Natural Resource Ecology and Management, Oklahoma Cooperative Extension Service, Oklahoma State University. Extension Circular E-998. Stillwater, Oklahoma.

Welch, K. R., H. D. Safford, and T. P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. *Ecosphere* **7:**e01609.

Wildland Fire in Lodgepole Pine (U.S. National Park Service). 2021. https://www.nps.gov/articles/wildland-fire-lodgepole-pine.htm.

Wildland Fire: What is a Prescribed Fire? (U.S. National Park Service). 2025. https://www.nps.gov/articles/what-is-a-prescribed-fire.htm.