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**Original Article**



# Planted seedling regeneration using gap-based silviculture without herbicide in a wildfire-impacted forest of the Sierra Nevada

Robert York[1,2,*], Amber Lennon[1], Miranda Redmond[2], Brandon Collins[2,3]

[1]Blodgett Forest Research Station, Berkeley Forests, University of California, 4501 Blodgett Forest Road, Georgetown, CA 95634, United States
[2]Department of Environmental Science Policy and Management, University of California, 151 Hilgard Hall, Berkeley, CA 94720, United States
[3]USDA Forest Service, Pacific Southwest Region, 1323 Club Drive, Vallejo, CA 94592, United States

[*]Corresponding author. Blodgett Forest Research Station, Berkeley Forests, University of California, 4501 Blodgett Forest Road, Georgetown, CA 95634, USA. E-mail: ryork@berkeley.edu.

## Abstract

Gap-based silviculture, which we define as the creation and maintenance of multi-aged stands through the periodic harvesting of discrete canopy gaps, provides a potential mechanism for converting previously high-graded stands into more heterogeneous, multi-aged structures. An advantage of small canopy gaps, relative to even-aged regeneration methods, is their potential to suppress shrub competition while allowing seedling growth without the use of herbicides or other means of managing shrub competition. While this idea has been proposed in principle, it has not been tested. The objective of this study was to evaluate the use of small canopy gaps, which were 0.08 ha in size with a mean ratio of gap diameter to border tree height of 1.3, as a method to regenerate four mixed-conifer tree species. Gaps were randomly treated either with or without herbicide in a Sierra Nevada mixed-conifer forest. Our hypothesis was that, if this opening size provided sufficient edge effect to control shrub competition, there would be no or little difference in seedling growth between herbicide-treated and control gaps. For all species planted, height and basal diameter growth trends over time were very similar between gaps treated with and without herbicide. The similarity in seedling growth occurred despite a substantial difference in shrub cover between untreated (43%) and treated gaps (3%). We interpret this as evidence that a gap structure such as the one tested can allow a co-occurrence of mediated shrub development and seedling recruitment and that the primary limitation on seedling growth comes from overstory trees, not shrubs. We demonstrate an example of the difference in seedling growth that can be expected between small gaps and clearcuts in order to discuss tradeoffs between these silvicultural systems. Following repeated measurements of seedlings for 7 years following planting, a wildfire burned across the study area, allowing for an additional assessment of wildfire-related seedling damage and mortality in gaps with differing levels of shrub abundance. Substantial mortality of study trees occurred following wildfire (62% mortality 1-year post-fire), but mortality was similar between treated and control gaps. This suggests that shrubs do not have a negative impact with respect to fire related mortality in small canopy gaps despite higher shrub cover. Gap-based silviculture could be a valuable tool for developing multi-aged, multi-species stands without the use of herbicide.

*Keywords:* regeneration; gap-based; silviculture; herbicides; wildfire-impacted forest; Sierra Nevada

## Introduction

Sierra Nevada mixed-conifer forests of North America have severely departed from historical conditions, including large shifts in species composition and tree densification (Stephens et al. 2015). Low- and moderate-severity fires were frequent throughout many dry forest types in North America, including mixed-conifer forests (Stephens and Collins 2004, Beaty and Taylor 2008). The pre-colonization fire regime in mixed-conifer forests has been disrupted by over a century of fire suppression and exclusion policies (Stephens and Ruth 2005). In principle, the structural and compositional changes associated with an alteration to a disturbance regime can be mitigated with silvicultural systems that are designed to replace many of the key structural elements that are absent (Palik and D'Amato 2024). In mixed-conifer forests, however, prevailing systems tend to result in canopy disturbance scales that are either small (<0.1 ha) or large (>10 ha) relative to scales that fire once maintained in what were historically multi-aged stands (York 2024).

A justification used for even-aged systems that disturb canopies at larger scales, despite the incongruence with the disturbance regime, is the history of large tree removal. Following the forced displacement of Indigenous peoples and removal of their land stewardship culture by European settlers, an era of exploitative and extractive forest practices followed that resulted in the selective harvesting of old and large trees (Beesley 1996). The preferential removal of large trees is commonly known as high-grading, a practice that may be suitable for some forest types (Buongiorno et al. 2000) but is commonly thought of as antithetical to best practices (Helms 1998). Modern silvicultural practices that focus on large tree removal have been criticized in frequent fire forests where high-grading results in increasing wildfire hazard, bottlenecking of species composition toward

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shade-tolerants, and decreasing long-term productivity (York 2015). These issues in high-graded stands can arguably be addressed by creating young stands of planted seedlings with even-aged silvicultural systems. High-graded stands can be replaced with those that have a desired genetic and species composition, along with an assumed higher future growth potential. Thus, they represent the opportunity to correct historical and more recent management legacies by "starting over." Young, planted forests that are a result of even-aged management systems, however, have inherent structural attributes that present challenges in forests that are historically fire-frequent and multi-aged (Safford and Stevens 2017). Across diverse ownerships in mixed-conifer forests, high-severity fire has occurred more readily on, and directly adjacent to, private-industrial forests (Levine et al. 2022) where even-aged systems are prevalent. While density management (i.e. precommercial thinning) is the conventional approach for reducing vulnerability of planted forests to wildfires, empirical studies have thus far suggested that fire severity is insensitive to or even positively associated with pre-wildfire density reduction treatments (Lyons-Tinsley and Peterson 2012, Zhang et al. 2019). Because of fast colonization of large, disturbed patches by competitive shrub species, the application of herbicide is a common tool used to facilitate accepted levels of early tree growth (McDonald and Fiddler 2010). Complex health, socio-economic, and environmental impact tradeoffs notwithstanding, the lack of an analog for herbicide in the historical disturbance regime suggests that it should at least be critically evaluated by managers trying to use the disturbance regime as a guide for silvicultural systems (Seymour et al. 2002). Where herbicide is not preferred, regardless of the reason, alternative silvicultural systems that do not rely on herbicide would need to be developed.

Gap-based silviculture is an alternative that we define as the creation and maintenance of multi-aged stands through the periodic harvesting of groups of trees to create discrete canopy gaps (Coates and Burton 1997, York et al. 2021). The forested space in between gaps may or may not be treated during any given gap-creation treatment depending on other objectives. As we define and apply it here, canopy gaps can be created within a matrix of mature trees that are either dense or sparse. Relative to this matrix, canopy gaps as we envision them in our definition are defined by the absence of trees and result in high levels of resource availability for new regeneration to occur and recruit into the canopy. The creation of discrete canopy gaps in order to regenerate shade-intolerant pine species, along with prescribed fire, is a common thread among silvicultural systems currently proposed as ecologically informed in dry, frequent-fire forests across North America (Palik and D'Amato 2024). Beyond the broad goal of restoring missing elements of a disturbance regime, heterogeneity that develops from gap-based silviculture may have the practical benefits of increasing resilience to wildfire (Stephens et al. 2008, Koontz et al. 2020) and providing revenue that can help cover treatment costs. Revenue can be reinvested into spatially broad surface fuel reduction treatments that provide stand-level scales of resilience (York et al. 2022). For stands that are known to have been impacted by high-grading, gap-based silviculture provides a potential, but not commonly tested, tool for introducing desired genetic and species composition. If it can regenerate a variety of planted species while also being capable of withstanding wildfire, gap-based silviculture offers an alternative method of regeneration that avoids some of the downsides of even-aged systems.

A major uncertainty with gap-based silviculture is related to the competition that seedlings experience following gap creation. Mixed-conifer seedling regeneration is co-limited by light availability (North et al. 2005) and soil moisture (Gray et al. 2005), both of which are impacted by shrub cover. Because of heavy competition from shrubs following high severity disturbances (Battles et al. 2001, Coppoletta et al. 2016), substantially reducing competing vegetation is suggested as necessary to grow young seedlings quickly and economically in planted forests (McDonald and Fiddler 1993, Finley and Zhang 2019). Consequently, the control of shrubs with herbicide has become a standard component of reforestation efforts across ownership types (Stewart 2021). Smaller gap openings, alternatively, create a different competitive environment for regenerating seedlings. Driven by increased edge-effects that cover significant proportions of gap areas, there is less light and water availability across gaps as opening size decreases from 1.0 to 0.1 ha (York et al. 2003). While there may be an ideal gap size that both suppresses shrub development and allows for regenerating trees, so far experimental gap studies in the mixed-conifer forest have either controlled shrubs across all replications (e.g. York et al. 2003) or not at all (e.g. McDonald et al. 1997). Hence, it is unclear whether gap-based silviculture represents an opportunity to avoid herbicide treatments while still achieving acceptable survival and growth of regeneration.

Even if gap-based silvicultural systems can be developed that achieve conifer regeneration without shrub control, the influence of shrubs on fire-caused mortality of regeneration remains a central question. This is true in the contexts of both wildfire and prescribed fire. Shrubs are a critical component of vegetation communities in mixed-conifer forests and were historically found concentrated in canopy gaps (Knapp et al. 2013). However, shrub dominance can be associated with higher burn severities that reinforce shrub dominance at the expense of tree regeneration (Coppoletta et al. 2016). Well-developed heavy shrub cover can increase woody fuel loads, acting as a heat source that increases fire intensity during extreme weather conditions (McGinnis et al. 2010). If live fuel moisture is high, however, shrubs may act as a heat sink, reducing fire intensity (Stephens et al. 2018). Understanding shrub influences on fire-related mortality of regeneration is therefore an important component of evaluating the feasibility of gap-based systems.

In this study, we evaluate the use of 0.08 ha canopy gaps as a method to regenerate multiple tree species with and without the use of herbicide to control shrubs in a Sierra Nevada mixed-conifer forest. Further, we analyze the interaction of the experimental treatments with a wildfire that burned across the entire study area. Following visual observations of tree growth and shrub development where gap-based silviculture had been previously applied, we hypothesized that 0.08 ha circular gaps would have the best chance of controlling shrub competition using edge effects, and that shrub control via herbicide would therefore have little or no impact on seedling growth. In the same year that we created the 0.08 ha experimental gaps we also regenerated two nearby stands with 5-ha clearcuts, one treated with herbicide and one not treated. As a demonstration, we use these clearcuts as a companion to the gap study to provide managers with an example of the differences in early growth that may occur between even-aged and small gap-based systems for this forest type. The study objective was to test gap-based silviculture as an alternative approach to vegetation control by addressing two questions: (1) Does the control of shrub development via herbicide application influence seedling survival and/or growth in small canopy gaps? (2) Does the level of shrub development that occurs in small canopy gaps influence the effect of wildfire on seedlings? If reducing shrub abundance with herbicides positively influences seedling growth and/or reduces fire-related mortality or damage, then it would suggest that either our hypothesized gap size did not represent the best choice of gap size, or that there may not be any existing gap size that can facilitate acceptable tree regeneration without the control of shrub development. We discuss the results within the context of using gap-based silviculture without herbicide in stands that have been high-graded or stands where heterogeneity and regeneration of shade-intolerant species is desired.

## Materials and methods

### Study site

This study took place at Blodgett Forest Research Station (BFRS) in the Sierra Nevada mountain range in California, USA (38°91′N, 120°66′W). This region has a Mediterranean climate and receives an average of 165 cm of rainfall per year. The study site ranges from 1305 to 1340 m above sea level. Overstory species composition is mixed-conifer with five conifer species: white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), incense cedar (*Calocedrus decurrens* [Torr.] Florin), ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), and sugar pine (*Pinus lambertiana* Douglas) and one hardwood species: California black oak (*Quercus kelloggii* Newberry). Soils are deep and well drained, originating from granodioritic and volcanic rock. BFRS is classified as having high site productivity, representative of other areas of the Sierra Nevada that are similar in elevation and precipitation.

The Nisenan, Miwok, Maidu, and Washoe peoples have inhabited and stewarded the land in this region since time immemorial. The historical (pre-European settlement) disturbance regime was dominated by low- to moderate-severity fire from both Indigenous and lightning ignitions (Anderson 2018). The median fire return interval was <6 to 14 years at the 3–5 ha spatial scale in the study site (Stephens and Collins 2004). When used as the guiding framework for ecological silvicultural systems in this forest type, the disturbance regime of frequent, low-severity fires result in management objectives that generally promote low stocking densities, patchiness, and large-tree dominance (York 2024). Mixed-conifer forests in this region were heavily logged in the 19th and early 20th centuries (Beesley 1996), including at our study site. This resulted in the initiation of a new cohort, which now occupy the upper canopies of many forests. These "second growth" trees are still young relative to their maximum lifespan (York 2024).

### Experimental design

Prior to the treatments installed for this study, the site was harvested twice with a diameter-limit prescription. All trees above 60 cm diameter at breast height (DBH) were removed in 1984 and again in 2003 using conventional harvesting methods. The diameter-limit cutting was different than high-grading in that only the best-formed trees from species with the greatest economic value were removed. However, the removal of the largest trees available, regardless of their form or species, still resulted in the negative outcomes associated with high-grading. Specifically, timber growth and yield was only half as productive as in stands where smaller trees were preferentially removed, and species composition trended markedly toward shade-tolerant species (York 2015). In 2014, the silvicultural system was transformed into an experimental gap-based system that could address some of the negative outcomes of the previous system. The current study was started by harvesting 20, circular 0.08 ha canopy gaps. Prior to this gap-creation harvest, the structure was dominated by a continuous canopy of co-dominant trees of all species and a dense layer of mid-story trees that were primarily white fir and incense cedar. The harvest was done with mechanized cutting and whole tree yarding. About 10% of the stand was converted to distributed, small canopy gaps. Re-entry periods of 10–20 years are planned, equating to a rotation age of ∼165 years. Merchantable and sub-merchantable trees were harvested from the gaps, leaving them cleared and without substantial harvest-related fuels. Following the harvest in 2014, Douglas-fir, incense cedar, ponderosa pine, and sugar pine were planted in parallel rows (one species per row, 2.5 m spacing within and between rows) running from the north to south edges of gaps. There were nine to 14 seedlings planted per species, per gap. Variation stemmed from slight variations in gap size and geometry. A total of 886 seedlings were planted.

A common method of standardizing gap size across forests of different heights is to express gap size relative to surrounding canopy stature. We did this by measuring the heights of mature trees immediately adjacent to gaps at 40° intervals from gap center. These border trees were at least 20 cm DBH and had at least 50% of their crowns exposed to the gap interior. The resulting mean ratio of gap diameter (32 m) to border tree height (24 m) was 1.3; this same ratio in a taller forest would occur with a larger gap size. Our speculation that 0.08 ha could result in the desired amount of edge-effects that mediated shrub competition was derived from an early gap-based silviculture study that used 0.08 ha as the lower end of a range of gap sizes (McDonald et al. 1997). Their results did not confirm that small gaps of this size could be used to control shrubs at their study site, but they posited that future experimental work could confirm it. We also did pilot measurements, observing limited shrub development in similar sized canopy gaps across BFRS where gap-based silviculture was used.

A simple experimental design (herbicide application versus no-application controls) that maximized replication of one targeted gap size and relied on a high frequency of repeated measurements was intended to maximize experimental power and to capture the variability that would be expected at operational scales. Eleven gaps were randomly assigned to the herbicide treatment, leaving 9 gaps as the controls. In spring of 2017 (3 years after cutting and planting), the 11 treatment gaps were sprayed with 4% glyphosate, receiving a secondary 3% glyphosate treatment in spring of 2018. Herbicide application was targeted to woody shrubs known to be competitive with conifer seedlings, including deerbrush (*Ceanothus integerrimus*, Hook. & Arn.), whitethorn (*Ceanothus cordulatus*, Kellogg), whiteleaf manzanita (*Arctostaphylos viscida*, Parry), and greenleaf manzanita (*Arctostaphylos patula*, Greene). This sequence of planting followed by herbicide application (i.e. a "release treatment") is a common form of vegetation control in this region, where shrubs occupy disturbed sites quickly and then grow aggressively under conditions with high-resource availability.

In September 2022, when seedlings were 8 years old, nearly all of the study area burned in the Mosquito Wildfire. The fire had primarily low-severity effects, resulting in a high mortality of lower canopy trees and limited overstory mortality. Using a network of 18 permanent plots that were in the burn area, we quantified severity by assessing fire-related mortality and crown damage of trees greater than 40 cm DBH. The average percent crown volume that was damaged was 14% and the average mortality was 6%. A small area in the study did not fall within the wildfire footprint. In order to have the entire study site impacted by fire, we burned this area with a prescribed fire 1 month later in October 2022 with similarly low severity effects, although with somewhat lower overstory crown damage (5%) and mortality (0%). We consider both wildfire and prescribed fire severities to be "low" since they both consumed significant surface fuels but have overstory mortality levels that are considered acceptable during standard prescribed burns at BFRS. Heavy equipment used in the wildfire suppression activities impacted two of the gaps that did not receive herbicide treatments. These gaps were excluded from post-fire measurements, leaving nine gaps in each treatment group for the analysis of fire effects.

## Clearcut versus gap demonstration

To provide additional context for managers who use even-aged silviculture and are concerned with the extent to which seedling growth is reduced by using small gaps, we compared seedling growth in the study gaps with growth of seedlings in nearby clearcuts that were regenerated and planted in the same year. Specifically, we planted two 5-ha clearcuts, one that included the application of herbicide to reduce shrub competition and one that did not use any herbicide. The application methods were similar to those described above. Given the lack of replication and the intent to use this as a demonstration, we do not consider this comparison to be part of the study in terms of making inferences from data analyses. We measured seedling height and growth in both clearcuts after 6 years, similar to measurements in the gaps. Seedlings were sampled using 0.04 ha permanent plots that were established on a 60-m grid. We compared height and basal diameter growth between the clearcut with herbicide, clearcut without herbicide, and the canopy gaps from this study using visual comparison of box plots, averaged across all species. Given the results of the gap study, both treated and control gaps were combined for the purposes of comparing growth with clearcuts.

## Measurements

We used line intercept transects spanning the gaps from south to north in 2019 to characterize the level of shrub development in treated versus control gaps. Because the use of herbicide is expected to invariably reduce shrub cover when applied correctly, testing for a difference in shrub cover between treated and untreated gaps does not help answer our study questions. Understanding the difference in shrub development, however, does provide critical context regarding two outcomes: (1) that the herbicide application was indeed applied correctly and thus effective in reducing the shrubs that were present and (2) that shrub development in small gaps is less than shrub development expected to occur in larger disturbances (i.e. clearcuts). The first was confirmed by comparing shrub cover in treated versus control gaps. The second was confirmed by comparing shrub development within the gaps to shrub development in the clearcut without herbicide i.e. described above. Development was characterized by shrub cover, which was expressed as a percent of the transect that was covered by shrubs, and by shrub height, which was measured for each individual shrub crossing the transect and then averaged across the entire transect length. To provide further context related to the expected consequences of either using or not using herbicide, we calculated the Shannon Diversity Index of shrub species for each gap using the transect data. Two thousand nineteenpercent shrub and percent bare ground cover were included as potential model predictors for fire-caused canopy damage, initial mortality, and cumulative mortality (see Section "Data Analysis").

To characterize the change in light availability to newly established seedlings as a result of gap creation and to confirm that sufficient light was available for shade-intolerant species in 0.08 ha gaps, we used hemispherical photography. Photos were taken in a sample of the gaps at their center locations prior to and after gap creation, including post-fires. This post-fire measurement served to further confirm that fire effects were primarily low-severity (since little or no change in light availability following the fire would suggest that the canopy did not change substantially). The light availability data are not useful for statistical analysis, since it is a given that light availability will increase following canopy creation. Importantly, however, we report light availability to allow for broader application of the results to different structural types within the mixed-conifer forest. Generally, variability in surrounding canopy height and leaf area density should be expected to create different levels of light availability for a given gap size (Gersonde et al. 2004). We used 40% as a threshold for light availability i.e. generally thought to be the minimum needed for recruiting all seedlings, including the most shade-intolerant, in this forest type (Annighöfer et al. 2019). Photos were taken using a Nikon 35 mm camera and a Nikkor fisheye lens (8 mm *f*/2.8) to provide a 180° view of the canopy. The camera was placed 1 m above the ground in the center of each gap at dawn or dusk to minimize effects of direct lighting. Photos were then analyzed using the Gap Light Analyzer (version 2.0) software (Frazer et al. 1999) to calculate the percent total transmitted radiation (%TTR). %TTR estimates the percent of incident photosynthetically active radiation transmitted to the understory during the growing season and therefore provides a robust estimate of average light availability. Photos were taken in three gaps pre-harvest in 2014, 20 gaps post-harvest in 2014, 9 gaps post-harvest in 2018, and 18 gaps post-fire in 2023. The variable number of gaps measured over time reflects the above-described purpose of this measurement as well as time limitations. Three photos prior to gap creation is sufficient for generally describing understory light availability, given that the canopy was known to be dense and homogenous prior to the gap harvest. Time was available to measure all 20 gaps following the harvest, and random samples of gaps were measured in 2018. In 2023, the two gaps that were impacted by heavy equipment were not measured.

To assess seedling survival and growth over time, seedling status (alive or dead), height, and basal diameter were measured for all seedlings 2 years following planting in 2016 and then again in 2018, 2019, 2020, and 2022. For simplicity, we refer to these planted seedlings as "seedlings" as they get older, as opposed to saplings. A high frequency of measurements was used to detect the timing of any departure in growth that may have been occurring between herbicide-treated and untreated gaps. If shrub removal with herbicide did have an influence, we wanted to know when it occurred. To explore the potential for shrub cover to influence fire effects on seedling recruitment, post-fire measurements included initial mortality, percent crown volume scorch (PCVS), and percent crown volume torch (PCVT) in fall 2022. PCVS is a measure of the proportion of the crown that was killed via heating from the fire (i.e. brown needles), while PCVT is the proportion that was killed via direct combustion (i.e. charred and black). PCVS and PCVT were assessed visually on each live seedling in fall 2022. PCVS and PCVT were added together, resulting in a measure of total canopy damage (i.e. inclusive of foliage killed via either scorching or torching). Both PCVS and PCVT were recorded between 0% and 100%, where a seedling was presumed dead when total canopy damage was 100% (i.e. there was no green foliage present). Cumulative seedling mortality, which captured delayed mortality, was measured by resurveying status in 2023, 2 years following the fire.

## Data analysis

All statistical analyses were completed in R version 4.3.1 (R Core Team 2023). Two sample *t*-tests were used to compare ground cover differences and Shannon Diversity Index of shrub species between the treatment and control groups. This served to verify that the herbicide treatment had the intended impact of reducing shrub cover and altering shrub species composition. Differences were considered significant when $P < .05$.

To test for non-parallel trends in height and basal diameter growth between herbicide-treated and control gaps, repeated measures multivariate analysis of variance (MANOVA) was used with the MANOVA.RM package (Friedrich et al. 2019). A repeated measures MANOVA has the advantage of avoiding assumptions in the structure of the data but is often not used because of a lack of statistical power. In this case, sample size is relatively large at the gap scale and the analysis of trend differences fits well with the study objectives. This was the primary analysis used for making inferences regarding our first study question. The within subject factor was time (year), and the between subject factor was treatment (herbicide versus control). The parameter of interest was an interaction between time and treatment, testing for a difference in the slope of the growth over time between treatment groups. Non-parallel slopes indicate that the herbicide treatment influenced seedling growth, while parallel slopes indicate that the herbicide treatment had no detected effect. Given our hypothesis that there is no effect of treatment, we also pay close attention to the difference in means between treated and control gaps, and associated confidence intervals. Results were reported for time, treatment, and interaction between time and treatment. Differences were considered significant when $P < .05$. Analyses for the height and basal diameter of each species were done separately.

Mean fire-related damage and mortality are reported to understand fire effects across gaps. To assess damage caused by the fire, beta regression models were used to predict percent canopy damage as a continuous proportion between 0 and 1. For proportions to fall within the open interval (0,1), proportions were transformed (Douma and Weedon 2019) (Equation 1). To run the beta regression model, the glmmTMB package was used (Brooks et al. 2017). Predictors tested included treatment, seedling height, seedling basal diameter, percent shrub cover, and percent bare ground cover. Gap was included as a random effect. The null model included an intercept and a random effect. Models were run at the gap level ($n = 18$) for each species individually. The model was also ran for all species combined, the inference being for mixed species cohorts that regenerate within gaps impacted by fires. Model performance was evaluated using the MuMIn package and the dredge function for automated model selection (Bartón 2023). This function ranks models based on the corrected Akaike Information Criterion (AICc), which is used when sample size is <40 (Anderson and Burnham 2002). To understand mortality caused by the fire, beta regression models were again used to predict both percent initial and cumulative mortality for each species individually and for all species combined at the gap level ($n = 18$). The same transformation formula (Equation 1), random effect, predictor variables, and evaluation method were used:

$$p^* = \frac{(p\,(n-1) + 0.5)}{n} \tag{1}$$

$p^*$ is the transformed proportional value, $p$ is the proportional value, and $n$ is the number of observations.

# Results

## Shrub cover

Confirming the herbicide treatment's effects, shrub cover was lower in gaps that received the herbicide treatment compared to untreated gaps. This was true both before the fire (in 2019; $P = .003$) and after the fire (in 2023; $P = .019$). The difference was substantial, with gaps treated with herbicide having a mean shrub cover of 3% and mean shrub height of 16 cm prior to the fire, and increasing to 12% and 28 cm following the fire. Meanwhile, control gaps had a mean shrub cover of 43% before the fire, changing only slightly to 41% following the fire. Control gaps had mean shrub height of 49 cm pre-fire and 60 cm post-fire. The most abundant shrub species across all gaps was deerbrush, which was present in 88.9% of all gaps post-fire. As expected, shrub diversity was lower in gaps treated with herbicide ($P = .008$). Mean Shannon Diversity Index was 1.1 (SE = 0.12) for control gaps and 0.06 (SE = 0.14) for gaps treated with herbicide.

## Light availability

Across all gaps, average light availability (%TTR) increased from 21% to 68% following the 0.08 ha gap creation in 2014, but decreased somewhat between 2018 and 2023 (Fig. 1). This dramatic increase is expected with gap creation, as is the decline over time, as surrounding trees respond to increased resource availability by growing laterally toward gaps and densifying their crowns. The post-fire mean light availability in herbicide treated gaps was 66%, and the post-fire mean light availability in gaps that were not treated was 64%, confirming that overstory light availability was similar across treatment groups and that the canopy—not the understory—was controlling light availability. Gap creation also pushed light availability above our reference level of 40%, suggesting that enough light resources were available for all species to regenerate given adequate moisture and nutrient availability. Lastly, the light availability change from pre- to post-fire confirm that the fires did not disturb the surrounding canopies at a meaningful level since %TTR in gaps did not increase following the fires.

## Shrub control influences on seedling growth

For all species, time had a significant influence ($P < .001$) on height growth, as expected. Between 2016 and 2022, height increased by 235%, 203%, 358%, and 277% for Douglas-fir, incense cedar, ponderosa pine, and sugar pine, respectively (Fig. 2). Similarly, for all species, time had a significant influence ($P < .001$) on basal diameter growth. Between 2016 and 2022, basal diameter increased by 329%, 388%, 387%, and 358% for Douglas-fir, incense cedar, ponderosa pine, and sugar pine, respectively (Fig. 3). These results confirm that there was sufficient light and underground resource availability to facilitate steady rates of recruitment toward the canopy.

Treatment had a significant influence on one species: sugar pine height growth across time ($P = .021$). Sugar pine seedlings in gaps that did not receive herbicide were slightly taller (2022 mean = 113.4 cm, SE = 6.6) than seedlings in gaps that did receive herbicide (2022 mean = 105.5 cm, SE = 9.2). Treatment did not have a significant influence on height growth for the other species: Douglas-fir ($P = .22$), incense cedar ($P = .14$), and ponderosa pine

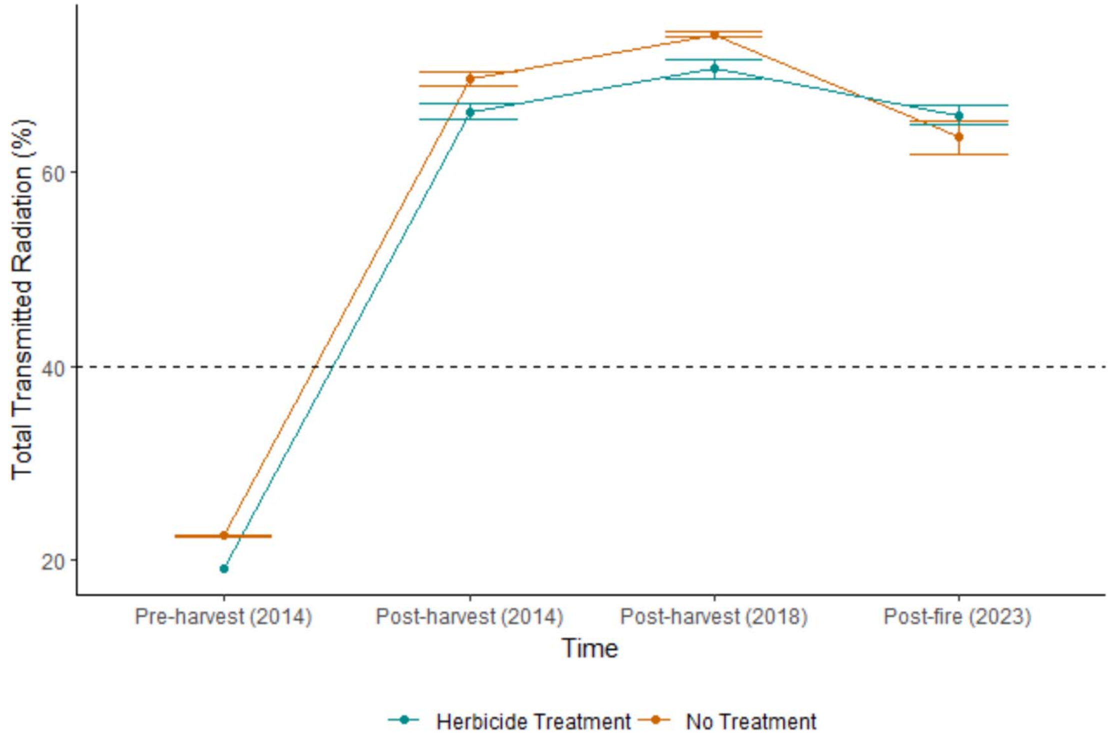


**Figure 1.** Mean %TTR available in herbicide-treated and control gaps at BFRS. Error bars represent 95% confidence intervals of the mean total transmitted radiation. $N = 3$ pre-harvest (2014), 20 post-harvest (2014), 9 post-harvest (2018), and 18 post-fire (2023). The dashed line at 40% TTR represents the reference light availability needed in this forest type to recruit seedlings.

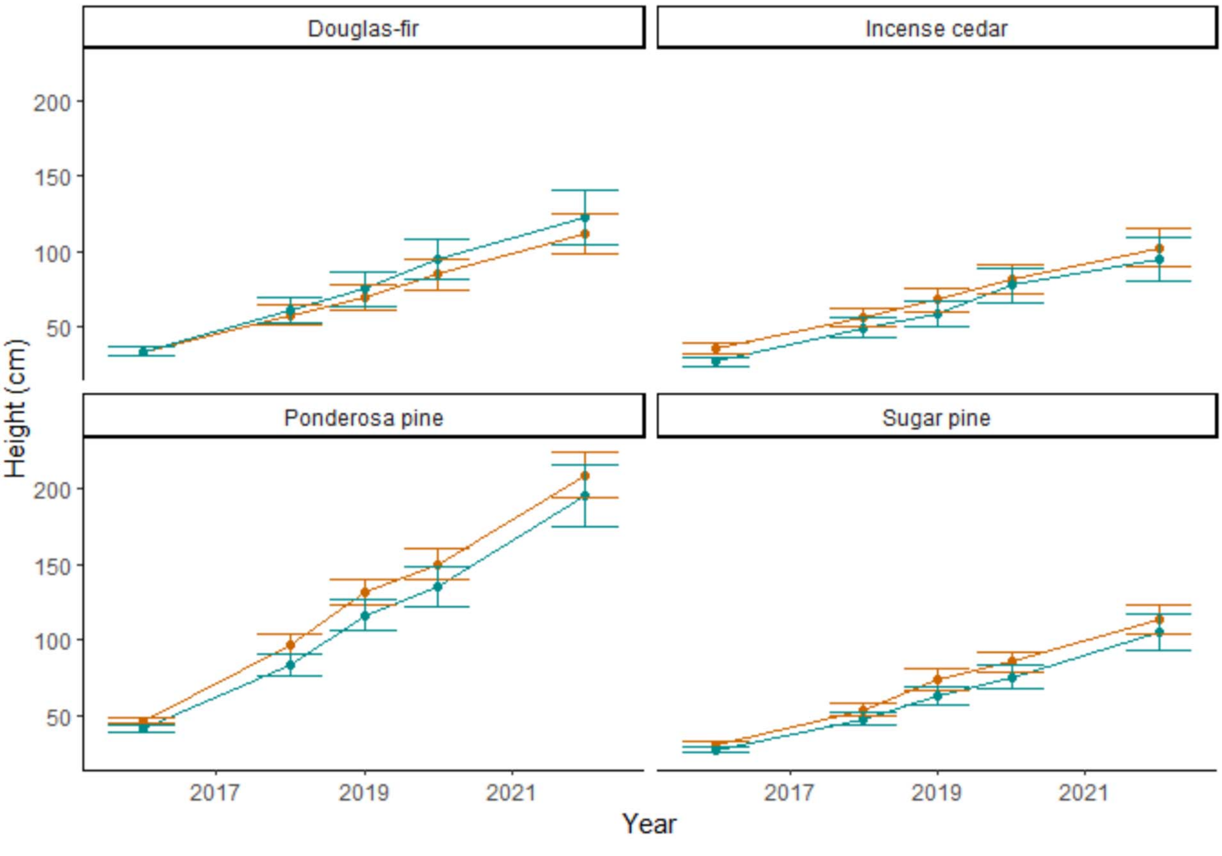


**Figure 2.** Mean height growth for each species between 2016 and 2022. Error bars represent 95% confidence intervals of the mean height. $N = 11$ gaps treated with herbicide and 9 control gaps.

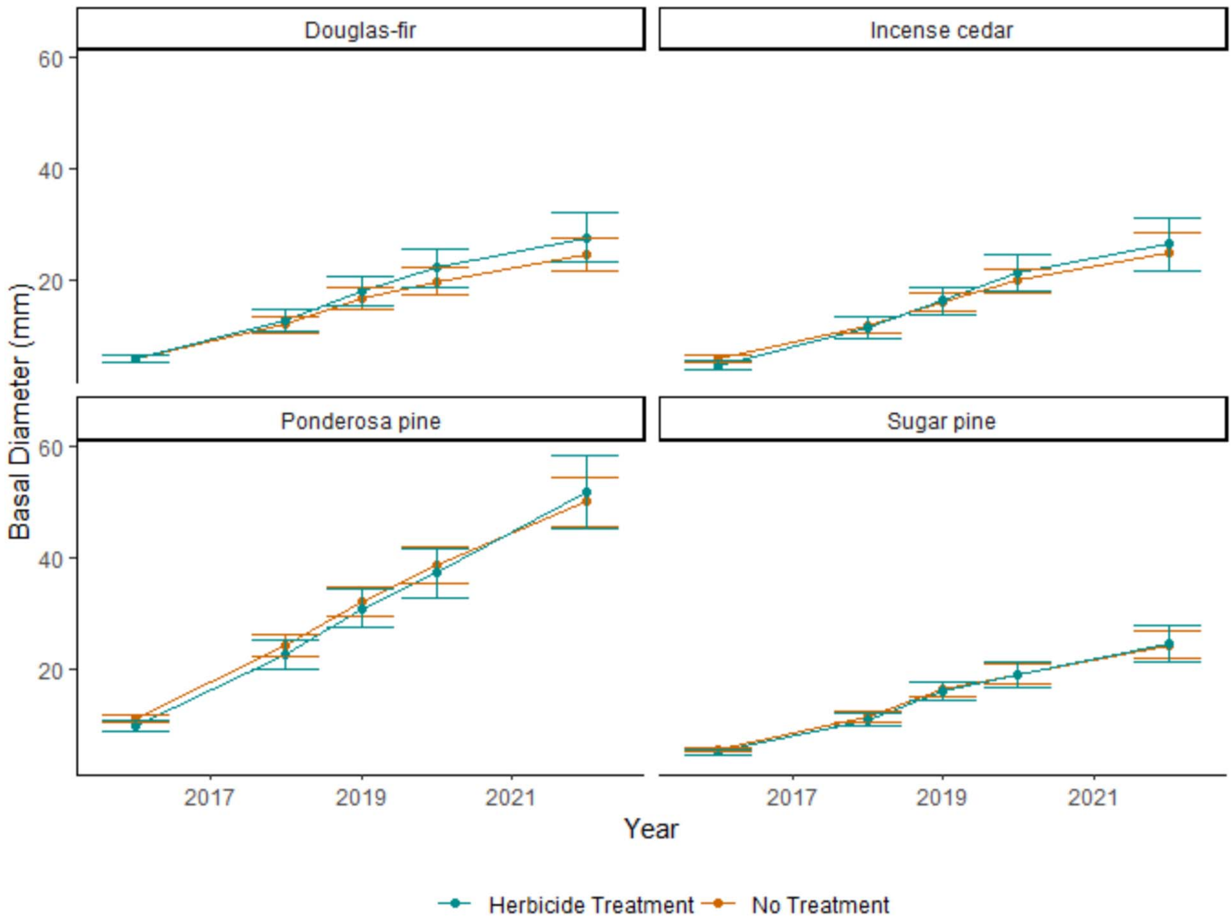


**Figure 3.** Mean basal diameter growth for each species between 2016 and 2022. Error bars represent 95% confidence intervals of the mean basal diameter. $N = 11$ gaps treated with herbicide and 9 control gaps.

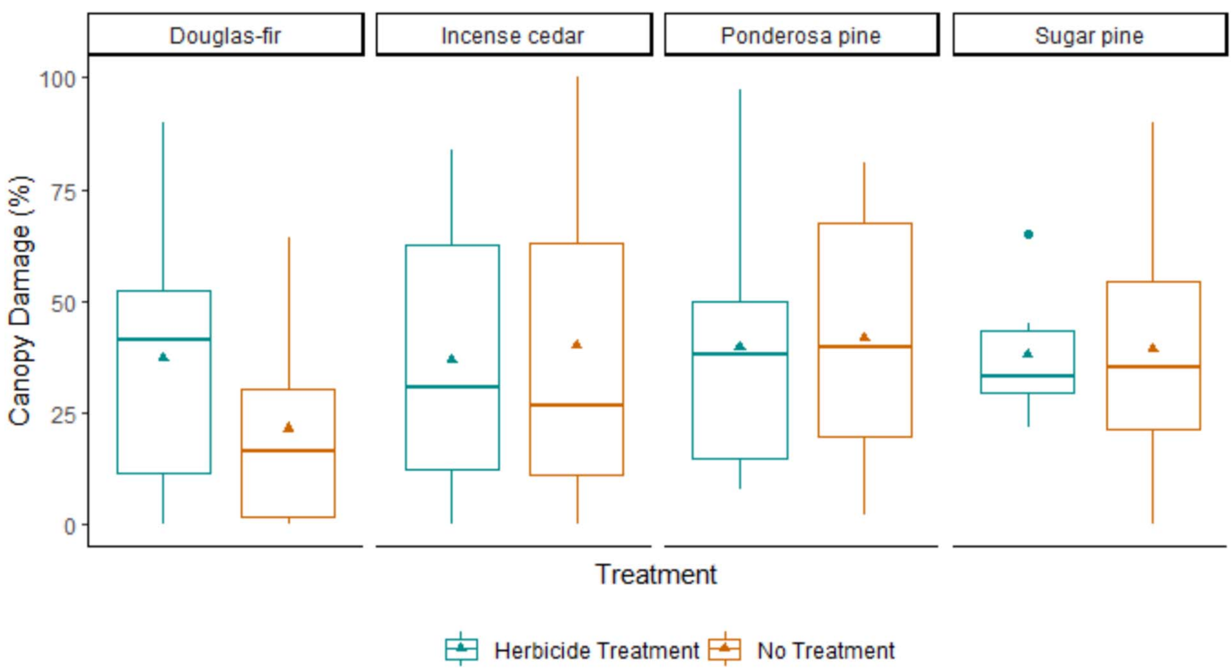


**Figure 4.** Percent canopy damage for each species. The horizontal lines in the boxes represent the medians, and the triangles represent the means. The circle is an outlier. $N = 18$ gaps for each species.

($P = .09$). Furthermore, there was no treatment influence on diameter growth for any of the species: Douglas-fir ($P = .25$), incense cedar ($P = .78$), ponderosa pine ($P = .70$), and sugar pine ($P = .41$).

An interaction between time and treatment, which was the main effect of interest, was not detected as a significant influence on height growth for any of the species: Douglas-fir ($P = .14$), incense cedar ($P = .63$), ponderosa pine ($P = .37$), and sugar pine ($P = .26$). There was also no time and treatment interaction effect on diameter growth, which is typically more sensitive to competition: Douglas-fir ($P = .13$), incense cedar ($P = .19$), ponderosa pine ($P = .29$), and sugar pine ($P = .55$). Importantly, there was no difference in final seedling size of any species between treatment and control gaps that was either statistically or biologically meaningful. Final means were very similar and replication resulted in narrow confidence intervals that overwhelmingly overlapped with each other (Figs 2 and 3).

### Fire-related damage and mortality

While fire-related damage occurred across the entire study area, there were no large differences in its effects between species or treatments (Fig. 4). For all species combined, the best performing model predicting canopy damage was the null model (Supplementary Table S1). For the individual species Douglas-fir, incense cedar, and ponderosa pine, the best performing model was also the null model. The selection of the null model indicates that there was no detectable influence of shrub control on fire-related damage. For sugar pine, the best performing model predicting canopy damage included herbicide use and shrub cover, but the null model was the next best and not substantially different ($\Delta$ AICc = 1.7).

One year after the fire, there was 41.2% mean fire-related mortality (SE = 11.3%) across all gaps with large variation: 0% mortality (minimum) occurred in one gap and 100% mortality (maximum) occurred in two gaps (Fig. 5). For all species combined, the best performing model predicting initial mortality was the null model. For Douglas-fir the best performing model predicting initial mortality included basal diameter, with the null model as next best but not substantially different ($\Delta$AICc = 1.1). For incense cedar, ponderosa pine, and sugar pine, the null model best predicted initial mortality. We were thus unable to detect an effect of herbicide influencing initial fire-related mortality for any of the species, meaning the use of herbicide did not strongly influence fire-related mortality.

The non-significant effect of the herbicide treatment on fire-related mortality continued as cumulative mortality (2 years after the fire) occurred (Fig. 6). On average, there was 61.9% cumulative mortality (SE = 9.9%) across all gaps after the second survey, again with large variation: 13.67% mortality (minimum) occurred in one gap and 100% mortality (maximum) occurred in three gaps (Fig. 6). For all species combined and each species individually, the best performing model predicting cumulative mortality was the null model (Supplementary Table S2).

### Clearcut versus gap demonstration

As expected, compared to growth in gaps, seedling growth was greater in the clearcut when herbicide was used to control shrub competition (Fig. 7). The gain in early growth when using clearcuts and herbicide was substantial for both height (~50% increase) and basal diameter (~100% increase). In the clearcut without herbicide, seedling growth was similar to the small canopy gaps. As typically occurs in this forest type following high-severity disturbances, shrub growth was vigorous following the clearcut. In the plots within the clearcut without herbicide the average shrub cover was 100%, meaning that every plot's seedlings were embedded within a canopy of continuous shrub cover.

## Discussion

The canopy gaps that we tested were small—0.08 ha circular openings with diameters that were 1.3 times the height of the surrounding canopy. The results suggest that creating canopy gaps such as these, despite their small size, is a viable option to regenerate and recruit all species of seedlings in mixed-conifer forests without vegetation control. Because herbicide had no effect on growth or fire-related damage and mortality, the application of herbicide did not confer a detectable benefit within this context of gap-based silviculture. This has broad relevance for situations where an objective is to develop silvicultural systems that avoid the use of herbicide. With particular relevance to previously high-graded stands and the desire to practice disturbance regime-guided silviculture, this gap-based approach with planting created a new cohort of diverse species and introduced heterogeneity at a spatial scale i.e. aligned with a low- to moderate-severity fire regime. Further transformation of the high-graded and even-aged canopy stands used in our study into productive and multi-cohort structures could occur by continuing to introduce canopy gap disturbances that periodically regenerate cohorts in the future. While the low-severity wildfire damaged seedlings and reduced their density, it did not overwhelm the existing trajectory of seedlings recruiting into the overstory. In other words, seedlings were vigorous before the fire, and they were vigorous after the fire.

### Shrub cover and herbicide application

Reforestation practices in the mixed-conifer forest commonly rely on herbicide to limit shrub competition and thus promote seedling establishment and growth following high-severity disturbances such as wildfires and even-aged regeneration harvests (Stewart 2021). Numerous studies document that reducing shrub cover in large openings increases seedling growth (McDonald and Fiddler 2010) and our cursory comparison between clearcuts with and without herbicide (Fig. 7) demonstrate why this practice is common. Presumably, a one-time treatment could be justified when it is practiced in the physical context of a forest structure i.e. already misaligned because of a novel disturbance event. Novel high-severity fires in the mixed-conifer forest have created conditions that native conifer species are not adapted to, producing transitions into non-forested structures at the stand level (Coop et al. 2020) and potentially at the ecosystem level (Cabiyo et al. 2021). To avoid this transition and to develop a structure where low-severity fire can be introduced as soon as possible, herbicide arguably fits within a disturbance regime guided framework if it leads to a structure where the use of prescribed fire or low-severity wildfire can feasibly occur (i.e. pyrosilviculture, *sensu* York et al. 2021). However, in stands that have not yet burned with high-severity fire the use of herbicide can be avoided by transitioning away from even-aged systems and toward multi-aged systems that are based on the disturbance regime to which the mixed-conifer forest is adapted (York 2024).

While the gaps that we created limited shrub development and therefore limited shrubs from competing with seedlings, shrub presence was still substantial (42% cover after 5 years). There are numerous benefits to shrub presence related to ecological processes, including nitrogen fixation by *Ceanothus* (Delwiche et al. 1965) and wildlife habitat (Conard et al. 1985). From an ecological silviculture perspective (*sensu* Palik and D'Amato 2024),

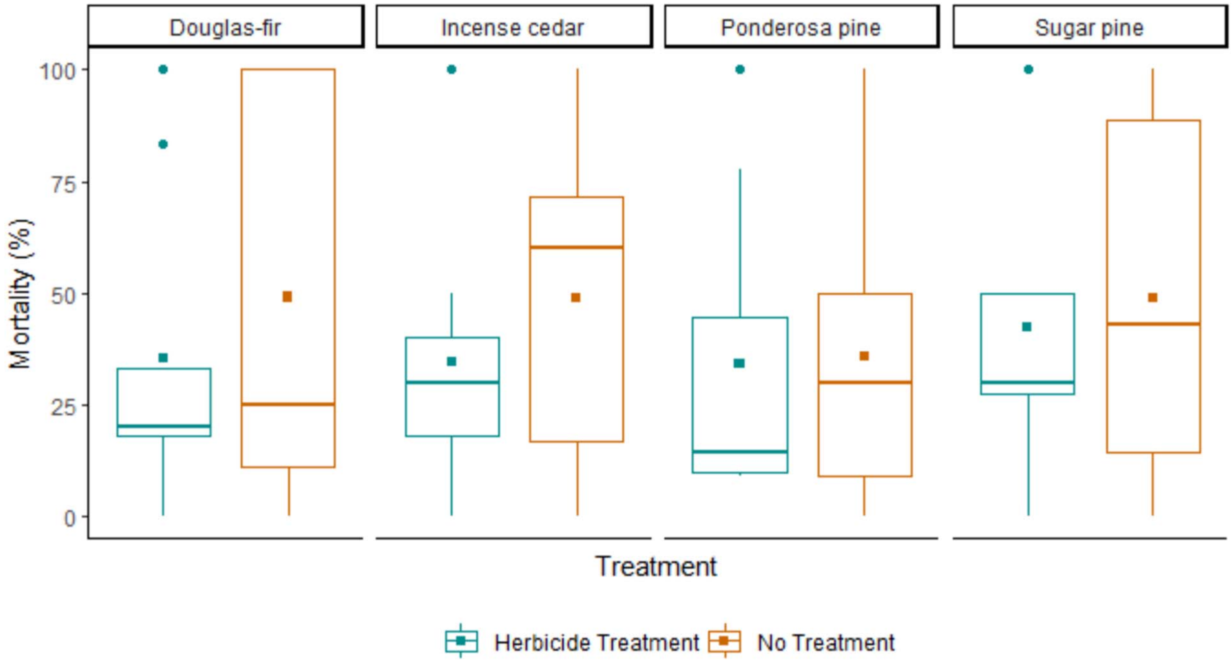


**Figure 5.** Percent mortality for each species 1 year after a fire. The horizontal lines in the boxes represent the medians, and the squares represent the means. The circles are outliers. $N = 18$ gaps for each species.

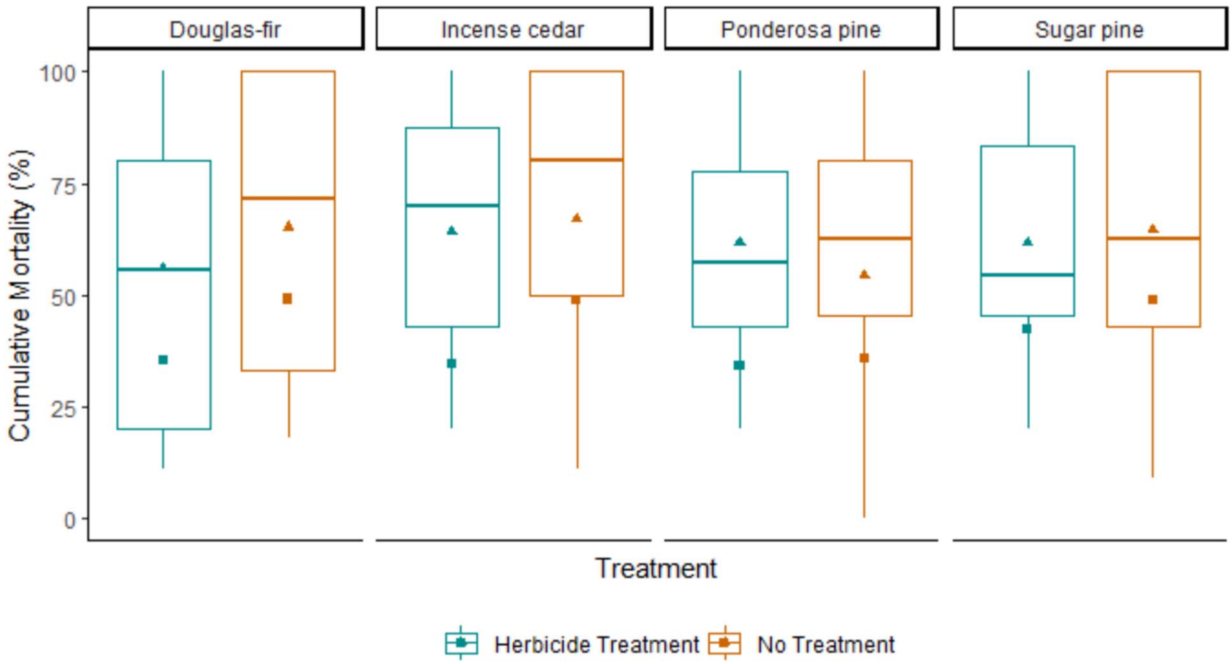


**Figure 6.** Percent cumulative mortality for each species. The horizontal lines in the boxes represent the medians. The triangles represent the mean cumulative mortality, and the squares represent the mean initial mortality. $N = 18$ gaps for each species.

the presence of native shrubs at levels approximating historic conditions would be preferred as long as they are not substantially diminishing primary forest management objectives. Our results complement those from Fertel et al. (2022) who found no relationship between shrub cover and seedling height or basal diameter in small canopy gaps that had developed following hot prescribed fires. It is worth noting that the stand structure of the forests measured by Fertel et al. (2022) included large, mature trees, with presumably small fire-generated gaps. Our direct experimental approach provides an even stronger case that small gaps, by nature of their size and resulting levels of resource availability, can effectively control seedling-shrub competition. Given the higher presence of shrubs in low-density forests that were historically maintained with frequent fires (Knapp et al. 2013, Collins et al. 2015), it is not surprising that mixed-conifer seedlings are adapted to establish and eventually recruit while surrounded by some level of canopy-limited shrub cover. Understanding that there are limits to seedlings' capacity to recruit in heavy shrub dominance is important, however. While shrub cover may initially assist seedling establishment, via protection from direct radiation, few

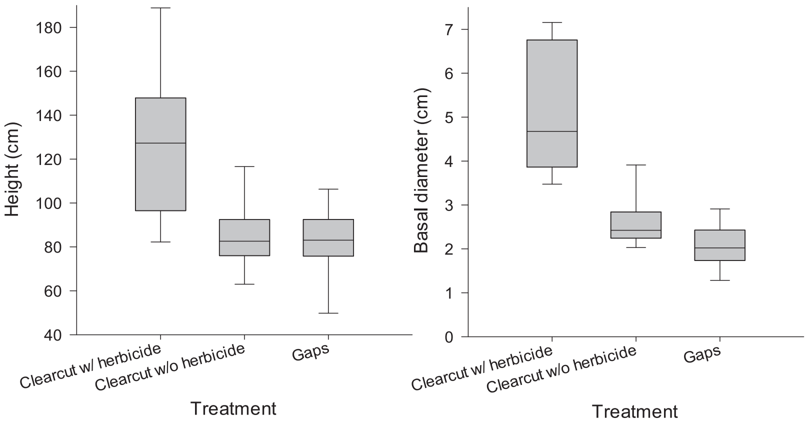


**Figure 7.** Height and diameter growth of seedlings in a clearcut treated with herbicide, a clearcut treated without herbicide, and the twenty 0.08 ha gaps in this study (the treatment and control gaps are averaged).

seedlings are typically found in patches dominated heavily by shrubs (Tortorelli et al. 2024). Other studies have noted species-specific responses to shrub cover that are important for successional trajectories. Juvenile ponderosa pine, e.g. had emergence rates from developing shrubs that exceeded those of white fir (Tubbesing et al. 2022). This is consistent with the differential shade tolerances of ponderosa pine and white fir, where ponderosa pine grows rapidly with high levels of light (i.e. while shrubs are developing), and white fir is able to grow well in low light (i.e. once shrubs have matured). There are various seedling–shrub interactions such as this that can be allowed to occur when a mature canopy's density and spatial arrangement is managed to facilitate regeneration and recruitment while mitigating shrub development. Acknowledging that our study used planted, and not naturally regenerated seedlings, our seedlings may have had a significant "head start" that gave them a competitive edge to persist with shrubs. Further research that compares natural to planted regeneration within gap-based silviculture systems could help resolve the extent to which planting may be necessary.

## Light availability

Prior to gap creation, ~21% of light reaching the canopy was available on the forest floor. While this is greater than the average of 6% at BFRS in fully stocked reserves that were not harvested or treated within the past century (York et al. 2012), it is far below levels of light that would be expected to result in new cohort development (Annighöfer et al. 2019). In another study at BFRS, the creation of 0.1 ha gaps surrounded by dense and tall mature trees (i.e. non-high-graded) resulted in an average light availability of 54% (York et al. 2003). Because of the history of harvests that preferentially removed large trees in our study area, the trees forming the edges of our gaps were relatively short. In practice, this means that smaller gaps can be used to result in sufficient light compared to taller-stature stands. In our study, harvesting small gaps created 68% light availability, indicating that these gaps created sufficient light for survival of ponderosa pine, the most shade-intolerant species planted. The decline in light availability, presumably driven by growth responses of large trees, was minimal (declining to 65% after 4 years). It is important to recall that the mature forest surrounding the gaps was not thinned. Had it been thinned, even smaller gaps would have resulted in the same amount of light availability for the new cohort. Thus, for managers who are able to measure light availability or who can otherwise learn how canopy disturbance translates to light availability with good precision, they can target the creation of 65%–68% light availability to balance seedling growth and shrub development. Otherwise, managers wanting to replicate our result of achieving regeneration without vegetation control may find gap diameter to canopy height ratio to be a more useful target. In our case, this ratio was 1.3.

## Seedling growth

Previous studies have demonstrated that seedling growth tends to increase with gap opening size and then levels off, resulting in an asymptotic relationship (e.g. Coates 2000). McDonald and Abbot (1994) described small gaps as an "inhospitable" environment for the growth of natural regeneration, where 0.06 ha gaps had over 3300 ponderosa pine seedlings per ha that were on average only 0.4 m tall after 9 years of growth. That was a much different outcome than our study of 0.08 ha gaps, which had many ponderosa pine seedlings over 2 m tall after eight growing seasons. An important difference is that seedlings in our study were planted, as opposed to naturally regenerated. In the context of historically high-graded stands that were genetically bottle-necked, planting following numerous entries of gap creation could be important for restoring growth potential. Local site productivity could be an additional factor that guides local decisions regarding gap sizes to target. Presumably, this could be found at a local level through trials of different gap sizes followed by monitoring of growth. Generally, if establishment and growth of ponderosa pine is desired while controlling shrub competition with edge effects, we recommend a gap size range of 0.05–0.5 ha be considered for further exploration with trials.

In our study, ponderosa pine was consistently larger in both height and basal diameter compared to other species (Figs 3 and 4). While this may be surprising given assumptions that shade-intolerant species require large canopy openings, our finding is consistent with the life-history strategy of ponderosa pine, as seedlings were able to establish and grow quickly immediately following gap creation when there was sufficient light availability. This rapid growth may allow ponderosa pine seedlings to stay above the shrub canopy, especially in small canopy gaps where our results suggest that the competitive capacity of shrubs is significantly suppressed to the point that they have no detectable influence. McDonald and Fiddler (1993) noted that when seedlings must stay above competing vegetation, they grow tall and thin to reach sunlight. Other work has found this tendency to allocate resources to height growth as a response to competition (e.g. Ritchie 1997). While we considered the possible result that seedlings could grow *taller* in untreated gaps, we did not find substantial evidence for it. Sugar pine seedlings were taller in untreated gaps, but the difference was very small (Fig. 2).

We interpret the positive linear growth in height and basal diameter among all four species (Figs 3 and 4) to mean that active recruitment into the canopy is occurring. During the 6 years following planting, height increased by over 200% and basal area increased by over 300% for all species. Importantly, however, we note that maximizing seedling growth is not necessarily a desirable outcome with multi-aged silviculture. In fact, seedlings growing at their maximum rate could be considered a sign of inefficiency within multi-aged stands because of reduced stand-level growth efficiency (O'Hara and Nagel 2006). In mixed-conifer forests, it has been proposed that smaller gaps may result in increased stand-level growth because of the positive impact of gap creation on the growth of surrounding large trees (York and Battles 2008). While maximizing growth of seedlings should arguably not be a primary objective within a multi-aged silviculture system, it is still likely desirable for most managers to sustain enough growth to result in canopy recruitment of all desired species.

The comparison of seedling growth between the experimental gaps and the nearby clearcuts demonstrates the difference in seedling performance i.e. often expected between even-aged and gap-based multi-aged systems. This comparison further supports our experimental finding that surrounding trees, not shrubs within canopy gaps, are limiting seedling growth. Importantly, these differences in seedling growth between clearcuts and canopy gaps are not assessments of differences in stand growth, which would require long-term and stand-level growth monitoring to make empirically based comparisons. Such robust and long-term comparisons of growth between even-aged and multi-aged systems are rare. The most applicable study that we are aware of for the mixed-conifer forest, because of its geographic proximity and similar disturbance regime, is from pure ponderosa pine stands (O'Hara and Nagel 2006). That study's finding that multi-aged stands had slightly higher growth efficiency than even-aged stands demonstrates the need to avoid the premature conclusion that clearcuts are more productive than small gaps because early growth is greater.

## Fire effects

We did not detect a significant difference in fire-related canopy damage or mortality between treated and untreated gaps. Herbicide and shrub cover were predictors for sugar pine fire-caused canopy damage, but this did not translate to models predicting that shrubs were related to sugar pine mortality. Ponderosa pine seedlings sustained the most canopy damage compared to other species, but this did not translate to elevated ponderosa pine mortality for either treatment group. A related study of wildfire interactions with planted ponderosa pine also found that overall post-fire tree growth was not significantly affected compared to pre-fire growth (Zhang et al. 2019). These results indicate that in practice, young ponderosa pine growth is resilient to low-severity wildfire. Furthermore, if fire-related damage results in an increase in the height to crown base because of the killing of lower branches, then fire-impacted trees will likely be more resistant to damage in the future. Ponderosa pine bark thickens quickly, which can insulate cambium and protect trees from heat damage, allowing even some young trees to withstand low-severity surface fires (Fitzgerald 2005). Another study showed variable mortality rates in young mixed-conifer stands following prescribed fire and concluded that prescribed fire is a feasible treatment in stands as young as 13–14 years old (Bellows et al. 2016). Interestingly, the age of the young stands from Bellows et al. (2016) and from our study is within the median fire return interval in this area (6–14 years), suggesting that there may be some evolutionary context for young trees having adaptations for withstanding fire under a frequent low- to moderate-severity fire regime.

The literature suggests high complexity regarding the role of shrubs in fire-related tree mortality. One study found that fire-related mortality of small trees (<30 cm DBH) was marginally lower in shrub patches (Lutz et al. 2017), where shrubs may have acted as a heat sink. This reduction in fire behavior is likely to occur when fuel moisture is high and fire weather is not extreme (Jaffe et al. 2021). In contrast, another study showed disproportionately more mortality from a wildfire when seedlings were adjacent to or within shrub canopies (Stephens et al. 2008), suggesting that shrubs acted as a heat source. Overall, canopy damage and mortality were similar between treatments for each species, precluding us from asserting either a heat sink or source mechanism. Rather, the relevant result is that the use of herbicide did not lead to a detectable difference in seedling survival following a low severity wildfire. As with survival and growth, there was no benefit of using herbicide to reduce fire-related mortality.

# Conclusion

Much of the Sierra Nevada mixed-conifer forest was high-graded in the early 1900s (Laudenslayer and Darr 1990), leaving a legacy that managers are now forced to address. Small canopy gaps present an opportunity to begin a transformation from even-aged canopies that lack structural heterogeneity and compositional diversity into multi-aged stands that can sustain all tree species. A primary downside to gap-based silviculture is the extra cost of harvest operations, especially related to having to move equipment from one gap to another, as opposed to working in one concentrated area. However, given the emerging pattern of wildfire severity increasing on industrial lands in the mixed-conifer forest, an association that has been suggested to be related to even-aged silviculture (Levine et al. 2022), this operational cost will have to be considered against the financial risks of high-severity fires occurring in planted forests prior to them reaching merchantable size.

Given broad social and ecological concerns around herbicide use, other vegetation control methods may be considered, including prescribed fire (DiTomaso et al. 2006), cattle grazing (Popay and Field 1996), and grubbing to decrease competition and increase individual tree growth (Zald et al. 2022). These treatments each present substantial financial costs and are likely done out of a necessity i.e. derived from the silvicultural system being misaligned with the disturbance regime. Gap-based silviculture, and small canopy gaps in particular, may offer an alternative opportunity for landowners at various scales to develop multi-aged silvicultural systems that restore many of the structural elements of the historic disturbance regime without the need to control shrub competition.

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## Supplementary material

Supplementary material is available at *Forestry Journal* online.

The following supplementary material is available at *Forestry* online: Table S1, providing the model selection results from the analysis of canopy damage for all species combined; Table S2, providing the model selection results from the analysis of 2-year mortality for all species combined.

## Conflict of interest

None declared.

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## Data availability

The data underlying this article will be shared upon reasonable request.

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