

Small beginnings: Interactions between fire timing and the giant sequoia seedling generation niche

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Research Article

Keywords: dispersal, fire, giant sequoia, microhabitat, niche, post-fire regeneration, propagule pressure, seedling

Posted Date: March 26th, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-4062409/v1>

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Abstract

Background:

As fire regimes change under a warming climate, ideal tree seedling recruitment locations and conditions are important to understand for forest management and restoration. In forests adapted to frequent, low-intensity fire, reintroduction of fire is often the preferred or recommended management approach. Little work, however, has explored the interacting roles of local-scale microhabitat and fire severity in determining post-fire recruitment. Here we use a back burn applied to a giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) grove in Yosemite National Park, California, to ask how sub-meter microhabitat variation influences seedling establishment and growth following fire.

Results

Post-fire *S. giganteum* seedling establishment was greatest in microhabitats with lower burn severity, higher post-fire sequoia litter, higher moss cover, and higher presence of sequoia cones.

Conclusion

These results indicate the importance of burn severity coupled with propagule pressure and post-fire surface organic matter in defining the seedling regeneration niche. These attributes should be incorporated in future fire management and seedling recruitment plans.

Background

How even the largest, long-lived species begin their lives can have critical consequences on their future success. As temperatures increase and precipitation becomes increasingly variable under a warming climate (IPCC, 2014), tree habitat requirements and ideal recruitment conditions may shift (Moran et al., 2019). For instance, projected increases in fire frequency and intensity in the Sierra Nevada of California (Westerling et al., 2006) may be expected to alter the direction and degree of correlation between important factors such as fire regime and seedling success. Further, with prescribed fire increasingly being used as a management tool, defining productive post-fire seedling niches and understanding how burn severity and habitat interact to drive seedling success can improve targeted management before, during, and after burns, increasing the likelihood of tree grove persistence under climate change.

Giant sequoias (*Sequoiadendron giganteum* [Lindl.] Buchholz) are an iconic California endemic tree species and classified as endangered by the IUCN (Schmid and Farjon, 2013). They are distributed entirely in small, isolated groves throughout the California Sierra Nevada. Persistence of these groves depends on successful reproduction, survival and recruitment of seedlings into the adult cohort. However, reproduction and recruitment has been declining in *S. giganteum* groves over the last century,

likely due to altered fire regimes (Meyer and Safford, 2011; Stephenson, 1996; York et al., 2013b). Current groves are often found in “microclimatic refugia”—locations with sufficient late summer soil moisture (Rundel, 1972) coupled with a short historical fire return interval. Indeed, dendrochronological reconstructions of fire histories in *S. giganteum* groves demonstrate a positive relationship between fire frequency and grove health (Swetnam, 1993; Stephenson and Demetry, 1995; McGraw, 2000; Stephenson, 2000; Carroll et al., 2014). Accordingly, reintroduction of fire to *S. giganteum* groves has been recommended across their distribution, and applied with varying degrees of success (Kilgore and Biswell, 1971; Meyer and Safford, 2011; Parsons, 1993). However, fire intensity and its effects on forest regeneration are highly heterogeneous (Jenkins et al., 2011; Ne’eman et al., 1999; Nesmith et al., 2011). Thus, it is critical to consider an individual species’ biology and fire ecology in the context of current conditions for successful management.

Sequoiadendron giganteum can live more than 3200 years (Stephenson and Demetry, 1995), and such long lifespans allow for numerous, potential reproductive events. Nevertheless, a recent survey found no recruitment in multiple groves over the entire *S. giganteum* range from 2010–2017 (Sillett et al., 2019), a period that included severe droughts and wildfires. Moreover, estimates of the species’ historical range point to significant declines since the Pleistocene (Dodd and DeSilva, 2016). One proposed mechanism of reduced recruitment is the absence of the historical fire regime to which *S. giganteum* is adapted. Reduced fire return intervals have allowed colonization of groves by shade-tolerant and fire-intolerant species such as *Abies concolor* (or *A. lowiana*), decreasing suitable gaps for *S. giganteum* seedling colonization. Thus, reintroduction of historical fire regimes is considered a primary tool in the management of *S. giganteum* groves.

The Sierra Nevada is considered a highly fire-adapted landscape, with numerous shade-intolerant species such as *Pinus ponderosa* and *S. giganteum* requiring regular fire to clear understory vegetation and allow growth in canopy gaps with low competition. In this vein, the re-introduction of prescribed fire has been shown to increase forest resilience to drought stress by reducing competition for surviving trees (Harrod et al., 2008; van Mantgem et al., 2016). Reproduction in *S. giganteum* is fire-dependent (Hartesveldt et al., 1975); fire opens the serotinous cones and allows dispersal while simultaneously creating colonizable canopy gaps and bare mineral soil (Harvey et al., 1980; Weatherspoon, 1990; Swetnam et al., 1991; Swetnam, 1993; Chorover et al., 1994; Demetry and Duriscoe, 1996; Swetnam et al., 2009; York et al., 2010; Meyer and Safford, 2011; York et al., 2011; Nesmith et al., 2015; Stephenson, 1996; York et al., 2013b) in which seeds can germinate and receive adequate light for growth (Shelhammer and Shellhammer, 2006). However, post-fire regeneration in temperate coniferous forests is highly spatially variable; seedling density and growth depend not only on fire severity and distance to a seed source, but also microhabitat (Stevens-Rumann and Morgan, 2019).

Post-fire recovery and general enhancement of recruitment of the threatened *S. giganteum* is of paramount importance as fire regimes continue to intensify. The 2015–2017 fire seasons, which included the Rough Fire (2015) and the Pier and Railroad Fires (2017), saw 75–100% mortality of large, legacy giant sequoia trees (> 1.2m DBH) in high-severity burn patches, including observed lagged

mortality up to three years following the Pier Fire (Shive et al., 2022b). The 2020 and 2021 fire seasons damaged *S. giganteum* populations to an even greater extent, with 7,500 to 10,600 large trees estimated to be lost in the 2020 Castle Fire alone (Stephenson et al., 2021), and between 2,261 and 3,637 large trees estimated to be lost in the 2021 Windy and KNP Complex Fires, respectively (Shive et al., 2022a).

Despite the critical importance recruitment stages represent, little is often known about the microhabitat requirements of tree seedlings (Guo et al., 2020). For *S. giganteum*, there is some evidence that post-fire gap size (York et al., 2004; Meyer and Safford, 2011), substrate quality (Harvey and Shellhammer, 1991), and resource gradients within gaps (York et al., 2003) all interact in varying ways to influence seedling success depending on fire intensity, timing, and management history (Shive et al., 2013). Microhabitat traits collectively define the *S. giganteum* post-fire seedling niche, which may differ from that of later life stages, thus representing a “life history niche” (Terradas et al., 2009) or “regeneration niche” (Grubb, 1977). If successful germination and subsequent growth are driven by different microhabitat conditions, this may also represent a case of “habitat filtering” (Baldeck et al., 2013), whereby different patches offer big differences in recruitment opportunities (Li et al., 2018). Seed limitation (i.e., low propagule pressure) within tree groves may also limit regeneration responses after fire. A niche cannot be filled without seeds to fill it. Identifying the post-fire *S. giganteum* seedling germination, survival, and recruitment niche would lead to increased ability to target fire pre-treatment areas, to forecast post-burn recovery and to assist in identification and preparation of sites for planting in restoration and assisted migration activities (Williams and Dumroese, 2013).

Here we used post-fire monitoring of seedling abundance and estimated microhabitat variables and local burn severity after a low intensity back fire during the 2013 Rim Fire in —Yosemite National Park to understand the giant sequoia seedling niche. We asked: which characteristics predict *S. giganteum* seedling presence, density, and persistence following prescribed fire activity? In doing so, we estimated a post-fire sequoia seedling regeneration niche, and evaluated the regeneration niche within habitat filtering and seed limitation contexts.

Methods

Site location

This study was conducted at Tuolumne Grove of Giant Sequoias within Yosemite National Park. Tuolumne Grove is located in the western portion of the park (Figure 1), and ranges from 1678-1771 m—approximately near the mean elevation of the species distribution within Sierran mixed conifer forest. Previous surveys in summer 2013 documented 24 large adult (>200cm diameter at breast height [DBH]), 7 small adult (100-200cm DBH), 86 juvenile (20-100cm DBH), 118 sapling (2-20cm DBH), and 15 seedling (<2cm DBH) sequoias, just prior to the 2013 Rim Fire backfire (Kuhn, 2014). Both the Tuolumne and Merced groves showed depressed seedling recruitment, with only 15 seedlings each in 2013, compared to 3084 seedlings found in nearby Mariposa grove. The 2013 Rim Fire—104,131 ha fire at final containment—burned with high intensity and severity toward the western park boundary, prompting

National Park Service (NPS) managers to ignite a backfire within the Tuolumne grove to limit potential catastrophic fire and damage to sequoias (Figure 2A). This burn was low intensity, yielding bare mineral soil and potential seed drop in adult *S. giganteum*, with limited canopy opening beyond needle cast from adult *Pinus lambertiana* in the years following the fire. All sampling was conducted after this burn, with burn severity data gathered in 2014 and 2015, and microhabitat and seedling data collected in 2015 and 2016.

Seedling surveys and microhabitat

We evaluated twelve previously surveyed (Kuhn, 2014) canopy gaps in the Tuolumne Grove burn area (Figure 1) for seedling density and microhabitat. These survey areas were re-established by locating prior plot centroids using a method of triangulation from reference adult trees (Kuhn 2014) in 2015. Each canopy gap contained a variable number of 4m² subplots, based on canopy gap size and shape, with subplots laid out along the four cardinal directions from a plot center, extending outward in each direction and terminating at the canopy gap edge (Figure 3A). Data collected in 4m² subplots included the following: *S. giganteum* seedling counts, individual seedling height and width (greatest horizontal diameter), canopy cover (estimated as percent cover), duff depth (mm), and soil volumetric water content (VWC) measured at 3, 5, and 10 in depth using a FieldScout TDR 350 soil moisture probe (Spectrum Technologies, Inc., Aurora, IL, USA). Some plots did not have deep enough soil to measure VWC at all probe depths. We also estimated Daubenmire cover classes of sequoia-specific duff, moss, herb, shrub, tree, woody debris, general duff, bare ground, and rock cover. In 2016, we added two 1m² subplots (also referred to as "sub-subplots") within each 4m² subplot to relate microhabitat data to seedling performance. We also established 19 1m² plots containing *S. giganteum* outside the original study plots (Figure 2B, 2C, 3B), which we added to increase microhabitat variation beyond that found within the original canopy gaps. The 1m² subplots were located with a "blind" toss to a random point within the 4m² subplot from subplot center. From the random point, we located the nearest seedling and established a 1m² subplot center 10 cm (in a randomly chosen direction) from that seedling. If too few seedlings occurred for two 1m² subplots (i.e., only one seedling), we established a second 1m² subplot in a random point without seedlings. Data taken in 1m² subplots included the following: number of seedlings, sequoia cone presence or absence (Figure 2D), seedling height and width, duff depth (Figure 2D), soil VWC, and light (lux, lumen/m²) and temperature (°C) recorded on a HOBO pendant light/temperature 64K data logger (OnSet, Bourne, MA, USA). A total of 114 HOBO units were placed in 114 1m² plots: 22 without seedlings, 56 with seedlings, and 36 plots that had seedlings in 2015 but not in 2016 surveys. Of these 114 plots, 4 plots had HOBO units that were not recoverable due to damage or loss, resulting in a total of 110 final plots included in analysis. HOBO units were placed 5cm off the ground using bamboo stakes to elevate them above duff or organic matter. Aboveground light and temperature were recorded every thirty minutes from August 2016-June 2017.

Burn Severity

Burn severity was estimated following the National Park Service Fire Monitoring Handbook (USDI National Park Service, 2003) protocol (Appendix S1). Burn severity was estimated separately for substrate (S) and vegetation (V). Substrate burn severity represents combustion of soil organic material and transformation of soil material into ash, whereas vegetation burn severity represents degree of vegetation directly burned or damaged by the fire. Burn severity was coded as follows: 0 = Not Applicable (represents inorganic or non-vegetated surfaces), 5 = unburned, 4 = scorched, 3 = lightly burned, 2 = moderately burned, and 1 = heavily burned. No plots had substrate burn severity of 5 (unburned). More complete descriptions of the burn severity codes can be found in Table 2. Burn severity was estimated only in 2015 and used for analysis of 2016 seedling densities and traits.

Statistical Analysis

We used stepwise multiple regression to evaluate significance of microhabitat variables in predicting seedling density based on 1m² plot data collected in 2016. Because of a high number of 0-seedling plots, seedling density was modeled as a negative binomial response to microhabitat variables. We chose to model seedling density as a negative binomial response as opposed to a zero-inflated Poisson or quasi-Poisson due to the ability of negative binomial models to account for over-dispersion and account for the effects of low seedling density versus high seedling density more effectively than a Poisson model (Lindén and Mäntyniemi, 2011) or quasi-Poisson model (Hoef and Boveng, 2007). We also tested multi-level models that added random intercepts for subplot and subsubplot to account for spatial autocorrelation.

Predictors included in the preliminary models (Appendix S2) included all measured microhabitat cover class variables (% cover of moss, herbaceous vegetation, shrubs, small trees, woody debris, total duff, bare ground, and sequoia-specific duff), duff depth (mm), and fire severity. For light and temperature, we calculated maximum, minimum, and standard deviation across the entire continuously monitored period, as opposed to calculating any integrated measures of light or temperature (e.g. growing degree days). This was done in consideration of a recent model of Sierran conifer seedling growth and survival that showed that sequoia seedling growth was negatively correlated with simple maximum July temperature (Moran et al. 2019), and because our light measurements were in lux units (lumen/m²), which does not allow direct calculation of more physiologically significant measures of light availability such as photosynthetically active radiation (PAR).

Stepwise model reduction was performed using Akaike's information criterion (AIC), with final models chosen when AIC reduction was negligible when a variable was removed. Data were first trimmed to remove plots with burn severity coded as a 0, which represents inorganic or non-vegetated surfaces. This resulted in 17 subplots being dropped from final models, with a final n of 97 subplots. Due to the large number of variables and the stratified random design of HOB0 placement, we first ran a model using all measured cover class and fire severity variables and ran successive models removing non-significant variables until the lowest AIC was reached (Supplemental Materials). A second microclimate model was then run using only HOB0 data and reduced via stepwise reduction as described above (Appendix S2).

Due to soil moisture not being able to be measured at all soil depths within each plot, a separate model of seedling count only as a function of soil moisture at all three depths was run on a subset of plots for which all soil moisture data were available, as well as a model using only the shallowest depth of soil moisture measurement as this was the most data-rich dataset. A final model was then run using variables selected via variable reduction in the preliminary models, with final included variables listed in Table 1. Models were built using the `glmer.nb` function in the `lme4` package (Ripley et al., 2019; Venables and Ripley, 2002) in R Version 3.5.3 (R Development Core Team, 2020). We checked final models for variance inflation using the `car` package (Fox et al., 2019).

Finally, we tested for density-dependent seedling growth using generalized linear models with seedling height as a response. We chose only to use seedling height and not diameter as we were assessing seedling vigor and potential for recruitment, which depends on outcompeting nearby competitors at the seedling stage. Seedling height was modeled using a gamma distribution due to significant right skewness. Predictors in these models included all original microhabitat variables and seedling density. We then used stepwise reduction using AIC to determine the final model.

We also assessed the effect of spatial subplot location within canopy gaps because of the finding by Meyer and Safford (2011) that *S. giganteum* density after fire and thinning was higher in locations further from the canopy gap edge. Locations of 1 m² plots were coded according to cardinal direction and distances from gap center and the effect of gap location on each of the significant habitat variables from the seedling density models was tested using a generalized linear model using only cartesian plot location as predictors. We excluded the 19 additional 1 m² plots outside of canopy gaps from this analysis.

Results

The most significant predictors of post-fire seedling density (Table 1) were sequoia cone presence ($\beta = 0.976$, $p = 0.052$), moss cover ($\beta = 0.622$, $p = 0.001$), vegetation burn severity ($\beta = 0.370$, $p = 0.082$), sequoia-specific duff cover ($\beta = 0.507$, $p = 0.006$), and maximum temperature ($\beta = 0.049$, $p = 0.068$). Note that burn severity is an inverse scale, with low numbers representing high severity. Seedling density was greatest in plots with “lightly burned” substrate (burn severity 3, Figure 4), and “scorched” vegetation, but also with the highest moss cover (Figure 4A,) and sequoia-specific duff cover (Figure 4B). Presence of sequoia cones in a plot was also significantly positively associated with seedling density. Temperature was weakly positively associated with seedling density at high and moderate burn severity ($\beta = 0.049$, $p = 0.076$), but negatively at moderate-to-high and low severities. Soil moisture was not a significant predictor of seedling density in final models ($p = 0.720$ for 5cm depth, 0.703 for 10cm, and 0.932 for 20cm, respectively), nor was mean or total light availability ($p = 0.484$ and 0.852, respectively).

Seedling height did not exhibit density dependence (seedling density $p = 0.958$). Significant predictors of seedling height had small effect sizes (Table 2) and included the following: substrate burn severity ($\beta = 0.045$, $p < 0.001$), woody debris cover ($\beta = -0.059$, $p = 0.010$), herb cover ($\beta = -0.013$, $p = 0.028$), and duff

depth ($\beta = 0.002$, $p = 0.002$). Seedling height was predicted to be greatest in plots with low tree cover, woody debris cover, herb cover and substrate burn severity, but high duff depth (Figure 5). We found no significant effect of gap distance or subplot location on seedling density.

Discussion

In this study we tested the role microhabitat variation plays in predicting seedling abundance and growth. Post-fire natural sequoia seedling density was best predicted by cone presence, high moss cover, low burn severity, and high sequoia-specific duff cover. Post-fire recruitment success was higher in areas of greater post-fire propagule pressure, evidenced by the cone presence, rather than in certain abiotic microclimates such as areas with higher soil moisture. In this vein, the sequoia grove displayed broad nursery effects given sufficient seed rain, consistent with both theoretical and empirical evidence of propagule pressure-driven regeneration in other forests following fire (Stewart et al., 2020). Post-fire duff cover may serve a facilitative mulching role, which is a promising future goal for restoration experiments.

Predictors of Sequoia Seedling Density

The relationship between substrate burn severity and seedling density is consistent with prior hypotheses and observations of fire being beneficial to *S. giganteum* seed germination and seedling density. Meyer and Safford (2011) compared sequoia plots that were thinned and burned with non-managed plots that experienced wildfire and found that wildfire plots had the highest seedling densities. They also found that light environment played a significant role in seedling density, as well as gap distance (distance from canopy gap edge). We did not find significant effects of light environment or gap distance, though it should be noted that our sampled gaps were previously existing, as opposed to gaps created by the fire or management activity.

Our observations that sequoia cone presence, moss cover, and percent sequoia duff cover were positively associated with seedling density, while soil moisture was not, point to potentially important interactions between seedling-scale microhabitat and overstory environment. Although we did not find significant effects of soil moisture on seedling density, counter to prior studies (Meyer and Safford, 2011), this may be due to low variation in soil moisture at a site (grove) of this size, and not necessarily that soil moisture is unimportant. This may also be related to our inability to include all soil moisture measurements at deeper depths in final models due to incomplete sampling. Increased moss cover can indicate shading and lower understory temperatures than plots with less moss cover (Bonan and Korzhin, 1989). Prior work has shown that moss cover may inhibit tree seed germination in dry conditions, but enhance germination under wet conditions by lifting the seed from the over-saturated soil surface (Staunich et al., 2012). Sequoia groves are often found in significantly more mesic habitats than their surroundings, and thus related mechanisms may play a role in our sample plots. The role of soil moisture at different depths on varying life stages of developing sequoia trees is a needed future avenue of research.

We found that total duff depth and cover were not significant indicators of seedling success, whereas sequoia-only duff percent cover was. This points to canopy species composition being an important contributor; sequoia cone presence may indicate that plots with higher seedling density simply represent cone “aggregation” areas (i.e., swales in the landscape), or the combination of cone presence and sequoia litter may indicate that simple distance to parent tree (not measured here) may be a significant driver of seedling density. However, models predicted greater seedling height in plots with high duff depth, but observed values were greatest in plots with low duff depth, but increasing with duff depth as fire severity declined (Fig. 5). Alternatively, wildlife transport of cones or seed to preferred areas may influence cone aggregation. Regardless of the mechanism of cone aggregation, fire intensity or gap size has little effect on sequoia seedling density in the absence of cone and seed dispersal (Stephens et al., 1999). This combination of predictors may point to post-fire surface moisture (potentially driven by both lower duff consumption in lower burn severity areas and higher post-fire sequoia litter input) and litter mulching effects as drivers of successful germination.

Higher seedling density associations with higher levels of sequoia litter could be related to fire insulation, burn severity, or litter moisture. Magalhães and Schwilk (2012) found that *S. giganteum* leaf litter’s primary contribution to multivariate models of fire intensity, duration, and a suite of other factors, was a reduction in fire temperature integration (a term representing duration of combustion and temperature to represent total heat release). In other words, higher sequoia duff cover was associated with lower heat release for a given burn severity. Belcher (2016) performed an experimental assessment of total and peak heat and burn duration of litter of various species and found that *S. giganteum* had a significantly higher peak burn intensity than many co-occurring species but lower burn duration. Thus, plots with high sequoia duff cover may have burned hotter, but not for as long as plots with less sequoia duff. Post-fire litter inputs from surrounding adult *S. giganteum* (i.e. “spontaneous mulching,” Oliveira et al. 2019) may have also contributed to patterns we observed. Hille and Stephens (2005) found higher forest duff depth and higher general cover in forest gaps only in cases when burns were ignited under moist conditions after the first significant precipitation event. They hypothesized this is because higher precipitation throughfall in gaps was associated with higher litter moisture and lower total litter combustion. Our data were collected from a burn ignited in late August, with no appreciable precipitation prior to the burn.

Predictors of Sequoia Seedling Height

Seedling height was greatest in plots with similar conditions as those with higher seedling density, but there was no detectable correlation between height and density in our plots, counter to observations of lower growth at higher densities in planted areas (York et al., 2013a).. We observed a weakly positive relationship between duff depth and height, lending further support to the potential for both decreased duff consumption and increased post-fire duff accumulation to be important predictors of seedling success. Shellhammer and Shellhammer (2006) found that tree height was highly correlated with sunlight and less so with moisture. Both soil moisture and light were important to establishment of trees, but growth in the first four decades appeared to be more dependent upon sunlight. We did not find

evidence of light environment predicting seedling growth but did find that small tree cover was negatively correlated with seedling growth.

Regeneration Niche, Habitat Filtering, and Seed Limitation

The significance of cone presence provides further evidence in support of propagule pressure driving successful regeneration. For *Pinus nigra*, prior work has shown significant influence of microhabitat on recruitment (Ordóñez et al., 2004), but dispersal limitation appears to be the primary driver (Christopoulou et al., 2014). In this vein, successful recruitment depends first and foremost on seed presence, but becomes particularly significant when considering forest dynamics under climate change. Climate and propagule pressure interact, with a higher number of propagules being required for successful post-fire forest regeneration as aridity increases (Tepley et al., 2017). However, here we have also shown that microhabitat plays a role. Thus, the regeneration niche exists, but filling of the niche is constrained by seed limitation.

The similarities between conditions associated with seedling density and seedling growth, and our observation of no correlation between sunlight and growth indicate that the significance of habitat filtering may vary by growth stage and trait, with a lack of potential habitat filtering at the young seedling stage, but a large role in seedling growth. For example, prior observations of *S. giganteum* growth being limited by sunlight (Shellhammer and Shellhammer, 2006) point to future potential habitat filtering in older trees.

Management Implications

The results presented here provide important considerations for managers in both *S. giganteum* stands and fire-dependent forests in general. We demonstrate that post-fire seedling recruitment is indeed a function of habitat filtering, as it is highly dependent on the seedling niche (for both presence and growth), but also on propagule pressure (for general presence), with substantial variability in micro-scale site conditions that determine seedling germination success. The data suggest that the timing of prescribed burns should further be taken in consideration if surface moisture may be a driving factor in seedling establishment and persistence. Cool spring burns may target smaller diameter fuels and not significantly reduce larger fuels, whereas fall burns would likely reduce both (Knapp et al., 2005). If there is limited duff, moss and moisture after a spring burn, seedlings are much less likely to establish because of limited surface water availability. In a fall burn, there is time for duff, litter, and moss to accumulate and extend the critical wet period for seedling establishment until the next dry cycle. However, extending this logic, burning during drought (as was done here) would be expected to not maximize opportunities for seedling establishment, but we found significant seedling establishment as a result of this burn, demonstrating potential interactions among available niche space, duff and litter presence, and not only seed presence but also selection for fast-rooting seedlings (i.e. simply a function of these seeds being “in the right place at the right time”). The importance of duff is also a consideration as climate continues to become warmer and drier. These results indicate that seedlings in the future may

need to be managed more directly at the local scale, with considerations of specific duff depths for mulching, especially relative to the degree of drought at the location of interest.

Our results have further utility in models of post-fire forest behavior that influence current management activities. For example, Demetry et al. (1998) used natural wildfire gaps as a model for revegetating sequoia groves in Sequoia National Park following removal of buildings and pavement in the Giant Forest. Our results demonstrate the role and importance of the local-scale sequoia seedling post-fire niche. Including niche effects could inform whether prescribed fire and other management activities are sufficient, or whether more aggressive measures (i.e., assisted migration, direct planting, and seed banking; e.g., McLane and Aitken, 2012; Lunt et al., 2013; Williams and Dumroese, 2013; Grady et al., 2015; Hällfors et al., 2016, Sillett et al. 2019) are necessary to encourage trees and groves that will persist in the future.

Using prescribed fire to restore sequoias should yield high seedling densities, but with caveats. Density of germinated seedlings does not always predict successful growth and establishment. Our models found that woody debris, small tree cover, and herb cover were all negatively associated with seedling height, but that duff depth was positively associated. All of these effects, particularly duff depth ($\beta = 0.002$), were very small, but point to light environment and potentially soil surface moisture being associated with potential growth and recruitment of seedlings. York et al. (2011) found in an experimental growth trial that sequoia seedling survival post-fire varied significantly with gap size and light environment, with growth saturating above 70% light but increasing linearly with soil nutrient content, demonstrating the need for large canopy gaps and sufficient soil nutrient cycling for sequoia growth and establishment. York et al. (2013a) further argued that low-intensity fire, as occurred here, should be expected to reduce seedling density and enhance seedling growth. Nevertheless, continued measurement of seedlings through the sapling stage to recruitment into the adult population is necessary to determine the ultimate success of individuals.

We measured seedling heights in the peak of extreme drought, and seedlings may have been allocating more resources belowground than to aboveground growth. The California drought of 2012–2016 was the most intense in approximately 1200 years (Griffin and Anchukaitis, 2014), and was associated with mass tree mortality in the Sierra Nevada (USDA, n.d.), primarily due to bark beetle-induced death of drought-weakened pines (Fettig et al., 2019). Although *S. giganteum* has not shown extensive mortality as a result of the drought, extensive foliage dieback was observed in adult trees (Nydick et al., 2018; Stephenson et al., 2018), and soil moisture was extremely limited during this time period. Our seedlings were sampled in 2015, just after the peak of the drought, and again in 2016—a year with slight recovery in soil water but not at depths accessible by seedlings (Bales et al., 2018). Further studies should examine soil moisture recovery and seedling response. Moreover, fire features (intensity, frequency, season of occurrence) can modify growth and soil nutrient cycles substantially under different climatic regimes. In Mediterranean forests in particular, these fire-drought interactions can determine the post-fire recovery capacity (resilience) of aboveground (e.g., productivity) and belowground (e.g., nutrient cycling) processes (Alfaro-Sánchez et al., 2016).

Finally, the significance of propagule pressure in determining seedling presence can drive prescribed burn timing decisions by incorporating knowledge of masting patterns in target forests. Cone fertilization and maturation in conifers can take multiple years. In *S. giganteum*, for example, maturation has been shown to occur late in the year after the year of fertilization (Hartesveldt et al., 1975). Our results demonstrate that incorporating cone crop size estimates as well as microhabitat considerations into burn plans the year prior to a burn can potentially boost seedling germination prospects, even in a serotinous species that holds cone crops in its canopy, such as *S. giganteum*.

Conclusions

Our work demonstrates the significance of both micro-scale variation and propagule presence in determining post-fire seedling germination success and growth. Further, our work demonstrates that broad conclusions regarding the factors predicting efficacy of prescribed burns must be tempered by understanding of micro-habitat and its interactions with species-specific niches across life history stages. Inclusion of micro-habitat variables in plans for restoration projects can increase the likelihood of successful recovery, decreased project cost, and overall greater target species persistence.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

Data are not yet available, but following acceptance for publication, will be stored for public access on the corresponding author's GitHub repository and/or on Dryad, as well as be available upon request.

Competing interests

We declare no financial or non-financial competing interests.

Funding

This work was supported by a grant from the Yosemite Conservancy through Save our Sequoias to MS and JS and UC Merced Student Success Internships to ACM, YL, and AT. Work was conducted on NPS Permit # YOSE-2016-SCI-0124.

Authors' contributions

JS, MS, GD, and TR conceived of the study and led data collection. MS, YL, OM, TS, JH, ACM, AT, and TR conducted field data collection, lab processing, and preliminary analysis. JL, CR, and ACC conducted statistical analyses. JL, MS, and JS drafted the manuscript. All authors reviewed and contributed revisions to the final manuscript.

Acknowledgements

We thank: Asmeret Berhe for advice the soil sampling protocols; Steve Hart and Morgan Barnes for assistance with soil processing techniques and access to equipment for soil analysis; Molly Downer with the National Park Service (NPS) for help coordinating NPS volunteers for initial surveys; the Sierra Nevada Research Institute, and organized research unit of the University of California Merced, for equipment use; and Erin Dickman (NPS) for HOBO field deployment assistance.

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Tables

Table 1. Final reduced Seedling Density model results

Predictor	β	Std. Error	z	p
Intercept	-6.972	1.723	-4.047	<0.001
Sequoia Cone Presence	0.976	0.502	1.945	0.052
% Cover Sequoia Duff	0.507	0.184	2.754	0.006
% Moss Cover	0.622	0.191	3.266	0.001
Burn Severity (Vegetation)	0.370	0.213	1.739	0.082
Maximum temperature	0.049	0.027	1.823	0.068

Table 2. Final reduced Seedling Height model results

Predictor	β	Std. Error	z	p
Intercept	0.333	0.057	5.934	<0.001
% Herb Cover	-0.015	0.006	-2.414	0.021
% Woody Debris Cover	-0.060	0.017	-3.572	0.011
Duff Depth (mm)	0.001	0.001	3.215	0.003
Burn Severity (Substrate)	-0.033	0.009	-3.751	<0.001

Figures

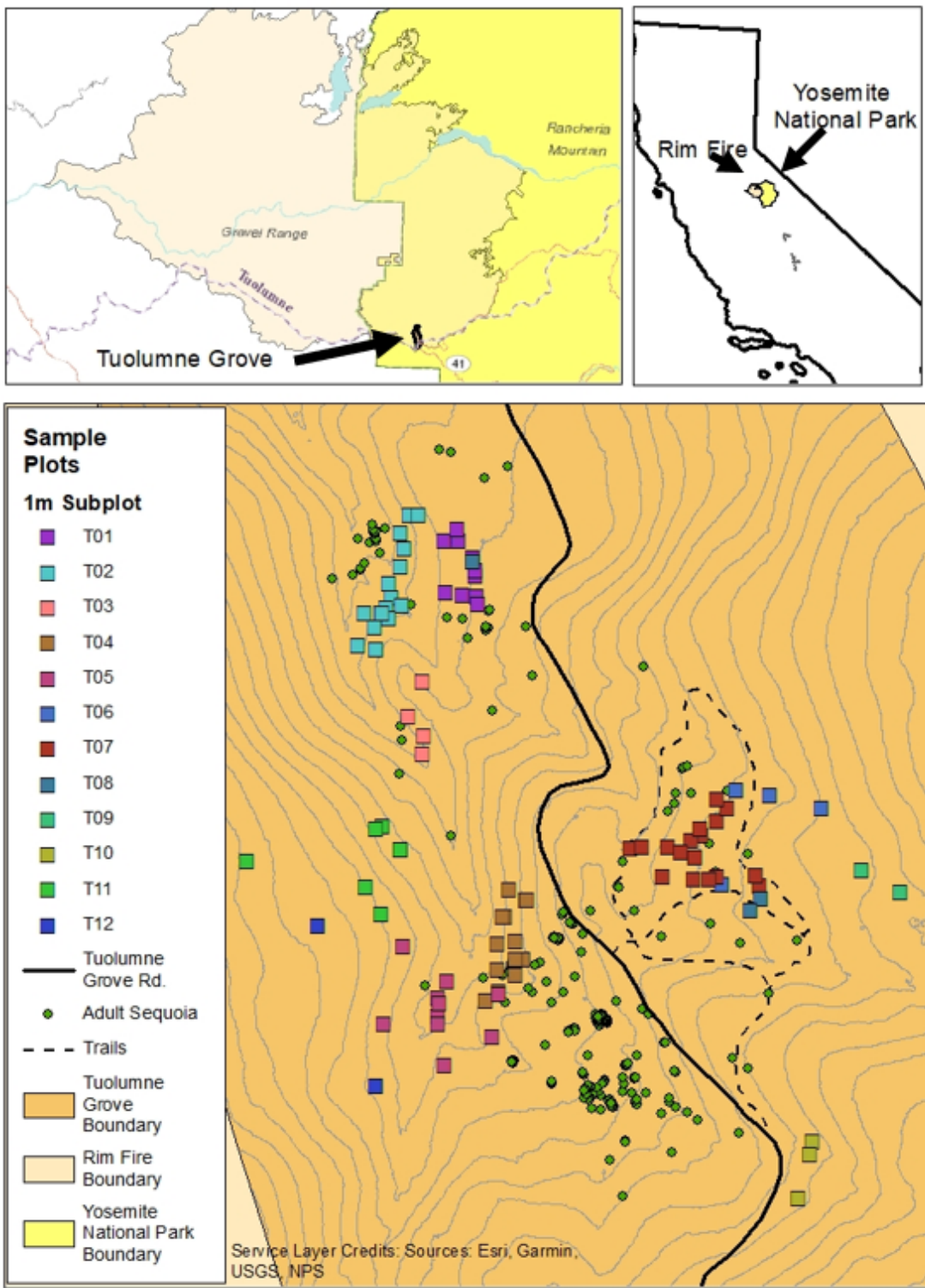


Figure 1

Map of Tuolumne Grove of *Sequoiadendron giganteum* in Yosemite National Park and post-fire canopy gap locations with the grove relative to the Rim Fire. Topographic lines represent 20ft elevation differences. Original tree spatial data credit to Thomas Reyes (Reyes 2014).



Figure 2

A) Backfire ignition in Tuolumne Grove, Yosemite, during the Rim Fire. B) 1m² microplot randomly placed for substrate measurements. C) 1m² microplot during measurement also showing interaction with public explaining purposes of the study. D) SEGI cone and duff development.

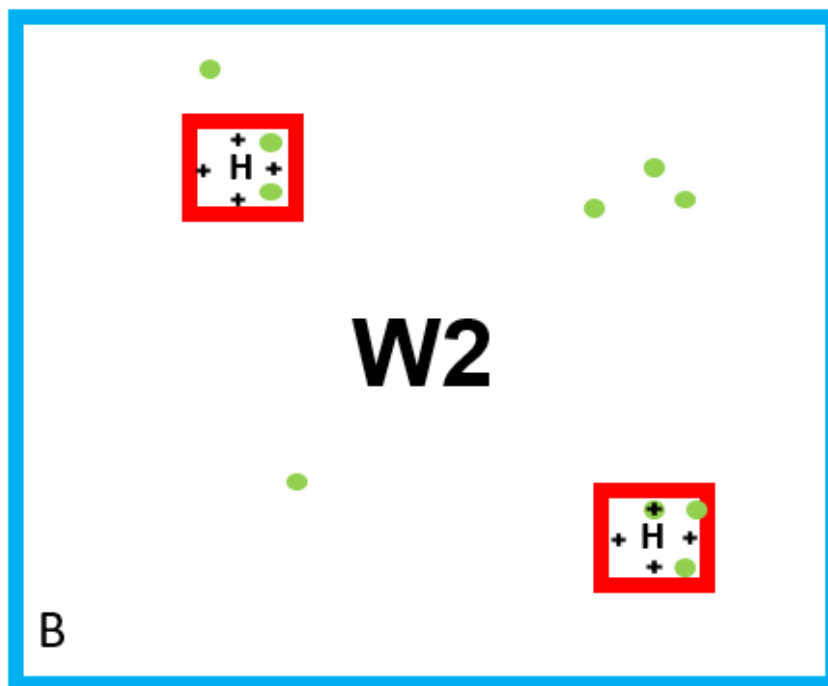
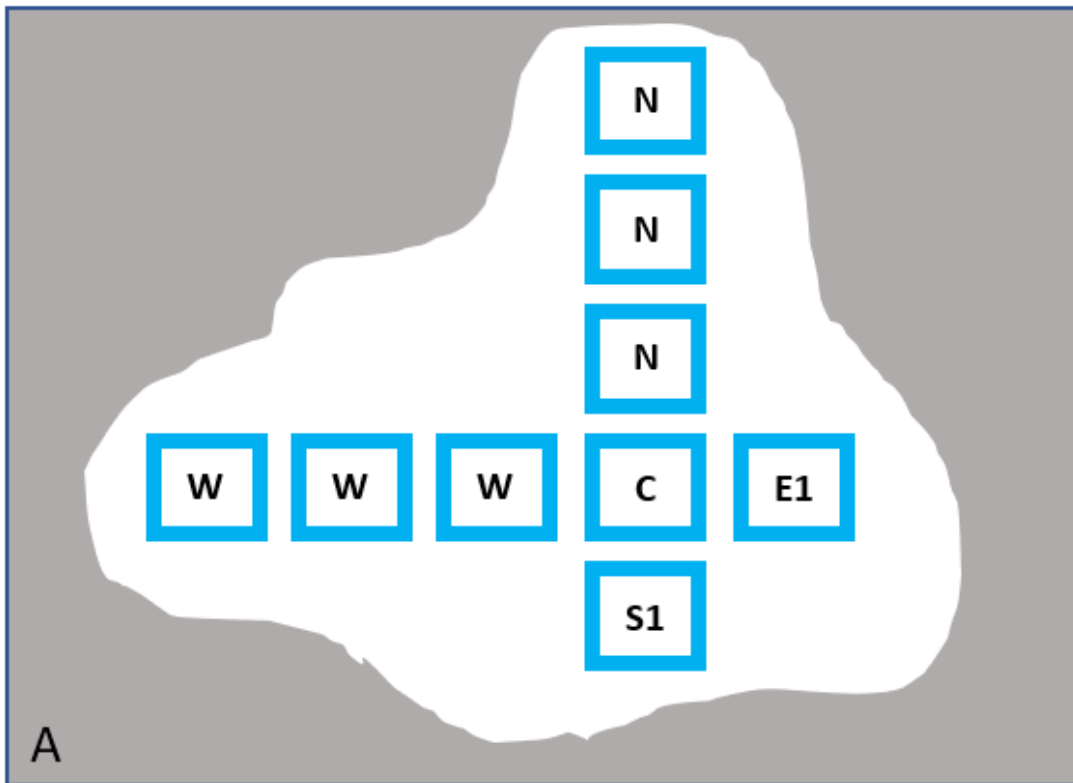


Figure 3

Schematic depicting study plot methodology for locating subplots within canopy gaps T1-T12. A) Example showing a canopy gap (white area) 4m² subplots (blue squares) for gap T1, which has one center subplot, three subplots in the north (N1-N3) and west (W1-W3) cardinal directions, and one subplot each in the east (E1) and south (S2) directions. Subplots were separated by a distance of 8m. B)

Example of 1m² subplots (red squares), located semi-randomly to capture SEGI seedling presence, containing one HOB0 sensor ("H") and four soil cores (+ symbol) in each.

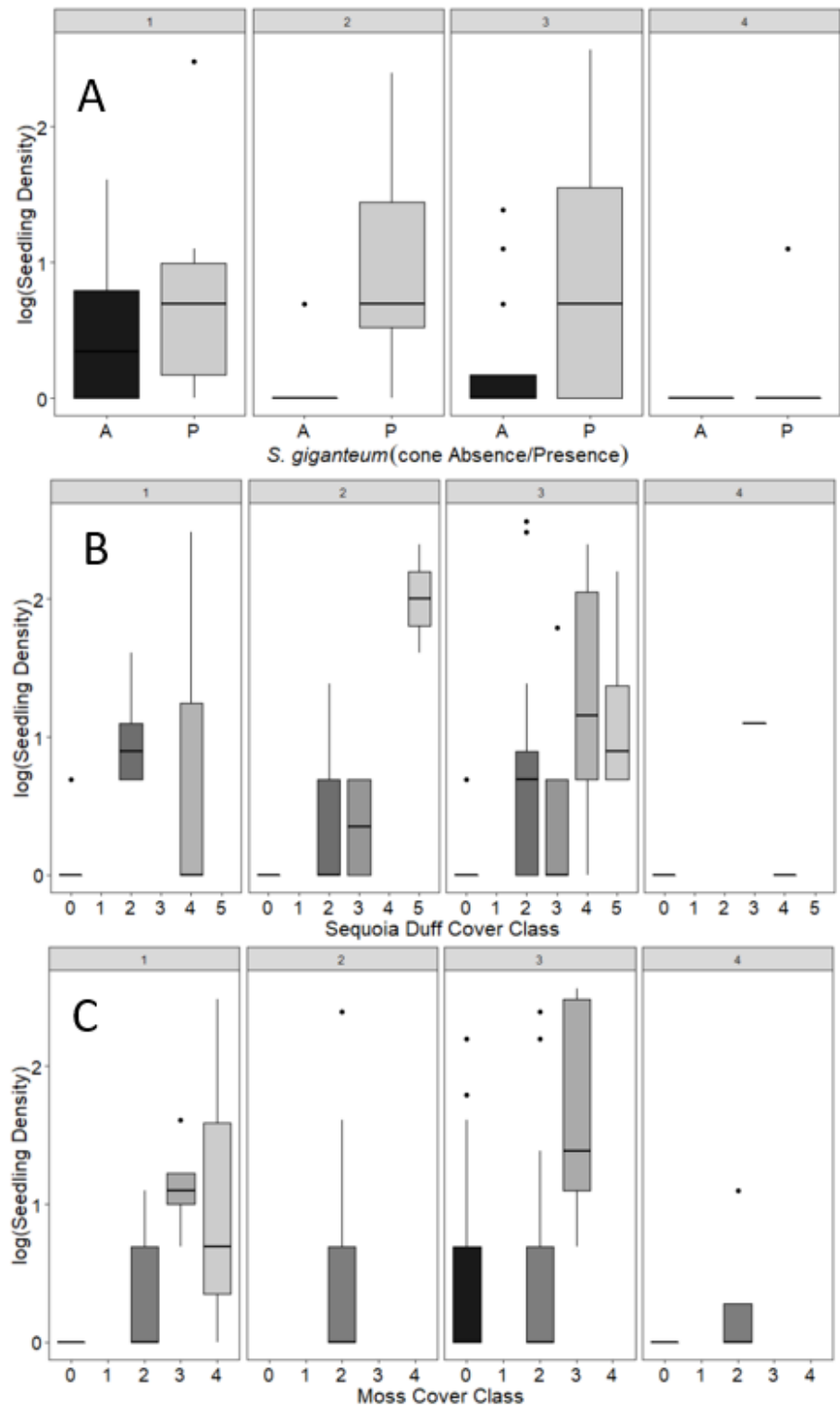


Figure 4

Boxplots of observed *S. giganteum* seedling density relative to significant ($p < 0.05$) predictors from negative binomial regression model. Solid horizontal lines represent median values, boxes represent first and third quartiles, vertical lines represent range, and dots represent outliers (± 1.5 S.D.). The most

significant predictors of seedling density were fire severity (here representing substrate burn severity, numbers in boxes, 1 = high severity, 4 = low severity), *S. giganteum* cone presence (A), Sequoia-specific duff cover class (B), and moss cover class (C). Cover classes: 0 = 0%, 1 = 0-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = >75%.

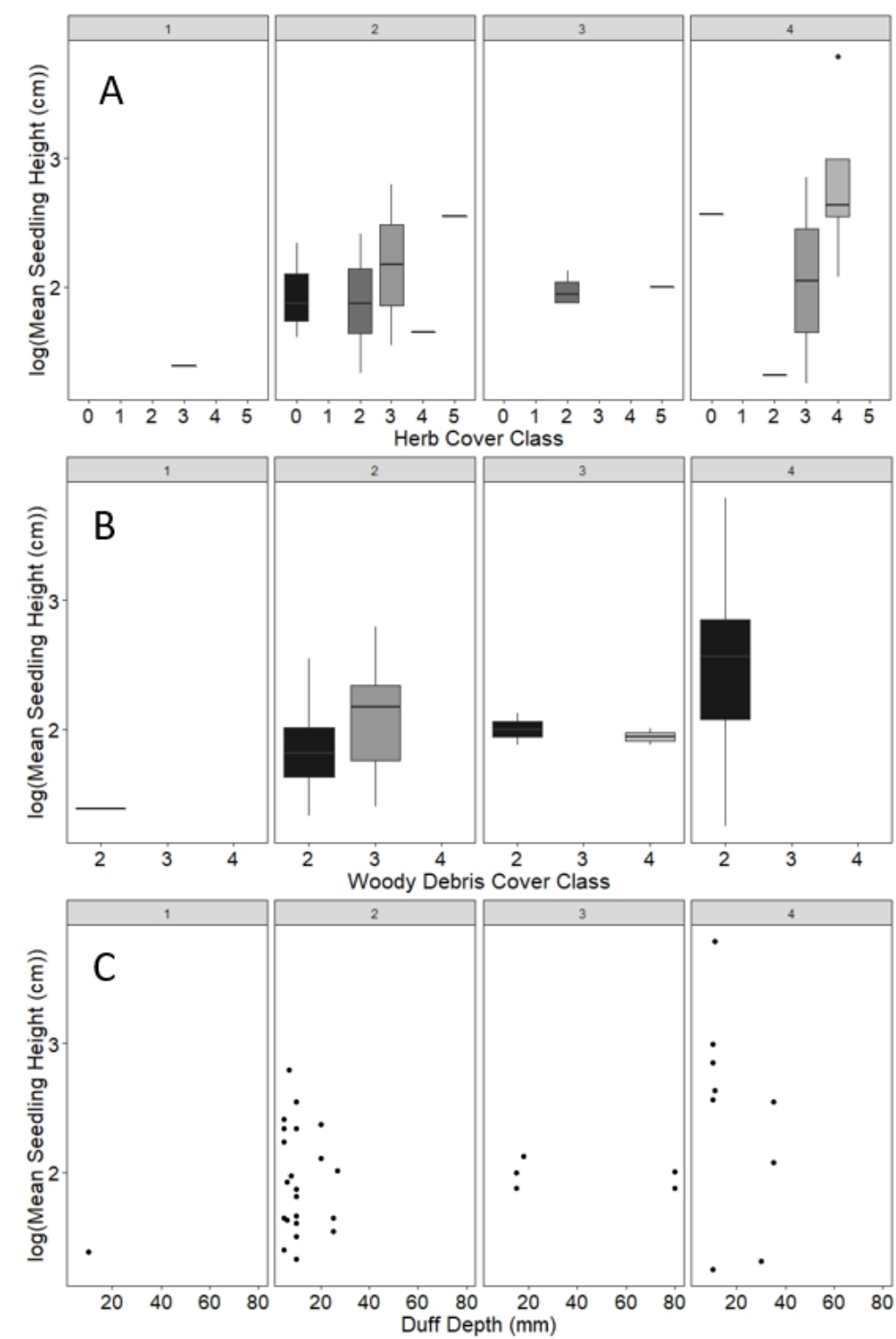


Figure 5

Boxplots (A-B) and scatterplot (C) of observed *S. giganteum* seedling height relative to significant ($p < 0.05$) predictors from negative binomial regression model. Solid horizontal lines represent median values, boxes represent first and third quartiles, vertical lines represent range, and dots represent outliers (± 1.5 S.D). The most significant predictors of seedling density were fire severity (here representing vegetation burn severity, numbers in boxes, 1 = high severity, 4 = low severity), herbaceous plant cover class (A), woody debris cover class (B), and measured duff depth (C). Cover classes: 0 = 0%, 1 = 0-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = >75%.