Canadian Science Publishing

ARTICLE

Post-fire early successional vegetation buffers surface microclimate and increases survival of planted conifer seedlings in the southwestern United States

Joseph L. Crockett and Matthew D. Hurteau

Abstract: Climate change and fire exclusion have increased the flammability of western United States forests, leading to forest cover loss when wildfires occur under severe weather conditions. Increasingly large high-severity burn patches limit natural regeneration because of dispersal distance, increasing the chance of conversion to non-forest. Post-fire planting can overcome dispersal limitations, yet warmer and drier post-fire conditions can still reduce survival. We examined how two shrub species with different structures affect below-shrub microclimate and survival rates of planted tree seedlings (*Pinus ponderosa* Lawson & C. Lawson, *Pinus edulis* Engelm., *Pinus strobiformis* Engelm., *Pseudotsuga menziesii* (Mirb.) Franco) following a high-severity fire in northern New Mexico. We expected that Gambel oak (*Querus gambelii* Nutt.), with its denser canopy, would buffer below-shrub climate causing higher survival rates of planted seedlings more than the lower canopy density New Mexico locust (*Robinia neomexicana* A. Gray). Seedlings planted under Gambel oak had survival rates 10% to 35% greater than those planted under New Mexico locust. Higher light availability beneath New Mexico locust corresponded to higher temperatures, lower humidity, and higher vapor pressure deficit, impacting the mortality of planted tree seedlings. These results indicate that by waiting for post-fire shrub establishment, selective use of shrubs can buffer microclimate and increase post-fire planting success in the southwestern United States.

Key words: climate change, forest transition, post-fire management, Gambel oak, New Mexico locust, early successional vegetation.

Résumé : Le changement climatique et la suppression des incendies ont accru l'inflammabilité des forêts de l'ouest des États-Unis, entraînant la perte de couvert forestier lorsque les feux de forêt surviennent en présence de conditions météorologiques sévères. Les feux de forte intensité qui brûlent des zones de plus en plus vastes limitent la régénération naturelle parce que leur dimension excède la distance de dispersion des graines, ce qui augmente les risques de conversion en zone non forestière. La plantation après feu peut surmonter les contraintes associées à la distance de dispersion, mais des conditions après feu plus chaudes et plus sèches peuvent toujours réduire la survie. Nous avons étudié de quelle façon deux espèces d'arbustes qui ont différentes structures influencent le microclimat et le taux de survie des semis d'arbre (*Pinus ponderosa* Lawson & C. Lawson, *Pinus edulis* Engelm., *Pinus strobiformis* Engelm., *Pseudotsuga menziesii* (Mirb.) Franco) plantés sous le couvert de ces arbustes à la suite d'un feu de forte intensité dans le nord du Nouveau Mexique. Nous nous attendions à ce que le chêne de Gambel (*Quercus gambelii* Nutt.), étant donné son couvert forestier plus dense, tempère le climat sous les arbustes, entraînant des taux de survie plus élevés des semis plantés que le couvert forestier moins dense du robinier du Nouveau Mexique (*Robinia neomexicana* A. Gray). Les semis plantés sous le chêne de Gambel avaient un taux de survie 10 à 35 % supérieur à ceux qui avaient été plantés sous le robinier du Nouveau Mexique. La plus grande disponibilité de la lumière sous le robinier du Nouveau Mexique correspondait à des températures plus élevées, une plus faible humidité et un déficit de saturation plus élevé, ce qui avait un impact sur la mortalité des semis d'arbre plantés. Ces résultats indiquent qu'en attendant l'établissement après feu d'arbustes l'utilisation sélective d'arbustes peut protéger le microclimat et augmenter le succès de la plantation après feu dans le sud-ouest des États-Unis. [Traduit par la Rédaction]

Mots-clés : changement climatique, transition forestière, aménagement après feu, chêne de Gambel, robinier du Nouveau Mexique, végétation de début de succession.

1. Introduction

The ongoing warming associated with climate change is increasing the flammability of western United States (US) dry forests, which is compounding the problems associated with increased biomass from land-use change and fire exclusion (Hurteau et al. 2014; Abatzoglou and Williams 2016). As larger fractions of the landscape are impacted by high-severity fire, the potential exists for forests to convert to non-forest (Guiterman et al. 2018; Singleton et al. 2019;

Coop et al. 2020). Early successional post-fire vegetation is common in high-severity patches, but tree seedling establishment is highly variable because establishment is dependent on dispersal, soil, and climatic conditions conducive to germination and growth (Savage and Mast 2005; Haire and McGarigal 2010). Post-fire tree planting can overcome dispersal limitations, but the warmer and drier conditions that follow stand-replacing wildfire can limit survival (Hankin et al. 2019; Stevens-Rumann et al. 2018). While early successional post-fire vegetation can modify surface microclimate by mitigating

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the effects of incoming solar radiation, it is unclear if the microclimatic buffering is sufficient to increase planted seedling survival in southwestern US forests.

In the southwestern US, frequent fire historically maintained the majority of forest ecosystems and following a century of fire exclusion, the area burned by high-severity fire has increased (Singleton et al. 2019). At the beginning of the 20th century, increased grazing reduced fine fuels and decreased surface fires that maintained a heterogeneous forest structure (Allen et al. 2002). The fire exclusion that followed further changed fuel conditions by increasing tree density and the continuity of fuels from the ground to the forest canopy (Covington and Moore 1994). Warmer temperatures and increased aridity due to ongoing climate change have lengthened the fire season and increased the flammability of fuel loads in these semi-arid forests (Abatzoglou and Williams 2016; Westerling 2016; Parks and Abatzoglou 2020). Consequently, high-severity patch size and total area burned at high severity have increased (Singleton et al. 2019). Warmer and drier conditions have also negatively influenced post-fire tree regeneration, raising concerns about the potential for southwestern forests to convert to non-forest (Guiterman et al. 2018; Hankin et al. 2019; Coop et al. 2020; Rodman et al. 2020a).

At large spatial scales, there has been a decrease in post-fire tree regeneration because of ongoing climate change (Rodman et al. 2020b; Stevens-Rumann et al. 2018). Regeneration within burned areas is highly variable with limited to no establishment within large high-severity patches in some fires (Savage and Mast 2005; Haire and McGarigal 2010; Ouzts et al. 2015). Larger high-severity patches can influence tree regeneration by reducing the mitigating effect of forest canopy on incoming solar radiation and regional climate (Davis et al. 2019a). As ongoing climate change increases temperature and aridity, surface microclimates more similar to regional climate can subject seedlings to conditions that exceed their physiological thresholds (Bell et al. 2014; Dobrowski et al. 2015). High temperatures increase leaf level vapor pressure deficit (VPD) that can cause catastrophic xylem embolism or carbon starvation, particularly in water-stressed seedlings whose sensitivity to such conditions is greater than adults (Will et al. 2013). Attenuating incoming solar radiation can buffer microclimate temperature extremes while increasing relative humidity, which reduces the atmospheric demand on plant hydraulics (i.e., VPD) (Davis et al. 2019a).

The structure of early post-fire successional communities can alter microclimatic conditions within high-severity patches, influencing tree regeneration. Shrub facilitation of seedling establishment has been observed in arid and semi-arid landscapes including Gambel oak (*Quercus gambelii* Nutt.) and Apache plume (*Fallugia paradoxa* (D. Don) Endl. ex Torr.) on piñon pine (*Pinus edulis* Engelm.). Yet, shrub interactions have also been described as competitive, particularly between ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Gambel oak (Floyd 1982; Sthultz et al. 2007; Singleton et al. 2021). Shrubs increase shading that alters temperatures and moisture availability/stress below the shrub, which can facilitate planted and natural conifer regeneration (Gómez-Aparicio et al. 2004; Marsh et al. 2022). Further, the potential benefits from shrub facilitation arise as abiotic stresses increase, and experimental manipulation of canopy structure indicates that aboveground buffering of abiotic stressors drive the facilitation effect (Sthultz et al. 2007). However, structure and phenology differ between shrub species. It is then possible that this generally positive response could hinge on species-specific characteristics, particularly during periods of regional abiotic stress. As changing regional temperature and aridity shift the distribution of post-fire successional communities, determining if different shrub species can facilitate seedling establishment during periods of abiotic stress can help inform post-fire planting practices.

Table 1. Selected ecological characteristics of Gambel oak and New Mexico locust (from https://plants.usda.gov/).

Characteristic	New Mexico locust	Gambel oak
Growth form	Multiple stem	Single crown
Summer foliage porosity	Porous	Moderate
Nitrogen fixation	Low	None
Moisture use	Low	Low

Gambel oak is associated with higher rates of successful germination of piñon pine, but other shrub species that co-occur with Gambel oak may not mitigate aboveground abiotic stress to the same degree (Floyd 1982). Gambel oak and New Mexico locust (*Robinia neomexicana*) are common in severely burned areas in the region and are characterized by distinct growth forms (Krofcheck et al. 2019). New Mexico locust can maintain leaf cover during a large portion of the growing season, but unlike Gambel oak, leaves are completely senesced during the winter and dispersed by wind, reducing coverage in the beginning of the following growing season. Gambel oak in contrast holds senesced leaves until the beginning of the growing season and accumulates denser litter. In high-severity burned areas in the Jemez Mountains, Gambel oak and New Mexico locust intermix, suggesting that their presence does not necessarily indicate a difference in soils or topography. Thus, it is reasonable to assume that structural differences between shrub species common to early successional communities may have distinct effects on microclimate variability and first-year seedling survival (Krofcheck et al. 2019).

Given the potential for shrubs to modify microclimate in post-fire landscapes, we asked — How does first-year tree seedling survival vary when planted under two different shrub species that are common following high-severity wildfire in the southwest? We expected that Gambel oak would have a greater effect on buffering below-shrub climate than shrubs with a lower density canopy during the growing season. Consequently, tree seedlings of species common to the area planted under Gambel oak would have higher overall survival rates relative to those planted under New Mexico locust.

2. Materials and methods

2.1. Study area

Our experiment was located in the Jemez Mountains of Northern New Mexico at a location in which two successive fires, the Dome fire in 1996 and the Las Conchas fire in 2011, burned through the area at high severity (MTBS Data Access: Fire Level Geospatial Data 2017). Following the Dome fire, shrubs colonized much of the area and their range extended after the Las Conchas fire (Guiterman et al. 2018). Two species, Gambel oak and New Mexico locust are common deciduous species found in the area (see Table 1 for further descriptions).

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine, southwestern white pine (*Pinus strobiformis* Engelm.), and piñon pine were common prior to the fires. Southwestern white pine and Douglas-fir grow primarily on north-facing slopes and in wetter areas, piñon pine grows at lower elevations and on south-facing slopes, and ponderosa pine occurred throughout the experiment location (see Table 2 for selected ecological characteristics).

Soils are a mixture of Laventana, Lacueva, and Bearsprings peak families (Soil Survey Staff 2019). The climate is characteristic of the mountainous Southwest with hot, dry summers and 50% of the annual precipitation occurring during late summer rains from the North American Monsoon (Sheppard et al. 2002). From 1981 to 2010 annual precipitation was 477 mm and mean annual temperature was 9.1 °C (supplementary Fig. S1[1]). Summer temperature normals range from nighttime lows of 12.4 °C to daytime highs of 26 °C

Table 2. Selected ecological characteristics of seedling species.

	Ponderosa pine	Douglas-fir	Southwestern white pine	Piñon pine
Shade tolerance	Intolerant[*]	Intermediate[*]	Intermediate[†]	Intolerant[*]
Drought tolerance	High[*]	Low[*]	Low[†]	High[*]
Moisture use	Medium[*]	Medium[*]	High[†]	Low[*]
Mean seedling height (cm)[‡]	11.9±3.0	22.0±2.5	15.1±3.0	11.2±2.6

[*]https://plants.usda.gov/.
[†]Barton and Teeri (1993).
[‡]Seedling height measured May 2018.

(https://www.ncdc.noaa.gov/cdo-web/datatools/normals, Los Alamos station, NM; 2262.8 m above sea level). The winter prior to when we planted the experiment, winter 2018 (December 2017 to February 2018) precipitation was approximately 30% of normal total seasonal precipitation and 18% of normal snowfall relative to the 1981–2010 seasonal normals (68 mm precipitation, 810 mm snowfall, https://www.ncdc.noaa.gov/cdo-web/datatools/normals, Los Alamos station, NM; 2262.8 m).

2.2. Experimental design

We planted 64 individual seedlings each of four tree species (Douglas-fir, ponderosa pine, southwestern white pine, and piñon pine) in a 2-km-long zone between 2400 and 2750 m above sea level, in five general planting locations. These planting locations were identified by their proximity to long-term weather stations (see Marsh et al. 2022 for details). We then planted seedlings within 30–50 m of the weather stations under Gambel oak and New Mexico locust that were adjacent to each other and growing on relatively flat topography to limit its effects on solar insolation. Each location contained eight to 24 seedlings of each species, with half planted under New Mexico locust and half planted under Gambel oak, and arranged so that two seedlings per species were planted beneath a single shrub. We assumed that since the two shrub species were intermixed at each planting location that abiotic factors, such as soil conditions, were consistent under the different species of shrub.

Seedlings were grown at the John T. Harrington Forestry Research Center of New Mexico State University and planted during March 2018. Douglas-fir and ponderosa pine seeds were gathered from sources in the Jemez Mountains, New Mexico; southwestern white pine seeds were gathered from sources on the Lincoln National Forest; and piñon pine seeds were gathered from sources near Gallup, New Mexico. The seed sources were selected to meet seed transfer guidelines and included mixing of five seed sources. Seedlings were grown in cone-tainers for one growth year and allowed to harden before being manually planted. Seedlings were not provided with supplemental water after planting. Planted seedlings were protected with Vexar tubing to reduce herbivory. We conducted seven live–dead surveys at irregular intervals throughout the 2018 growing season that ended October 2018 and classified seedlings as dead if 100% of needles were not green. All seedlings were visited on the same day during each survey.

We instrumented five representative Gambel oak and five representative New Mexico locust, one individual of each in the five planting areas, with upward facing game cameras (Moultrie D-80) and iButton® temperature/humidity logger (model No. DS1923; temperature accuracy ± 0.5 °C; humidity resolution 0.6%; https://www.maximintegrated.com/en/products/ibutton-one-wire-dataloggers/DS1923.html) under each shrub (i.e., 10 iButton and 10 game cameras). The instrumented shrubs were in the center of each planting area. Non-instrumented shrubs were within approximately 50 m of the instrumented shrub in each planting area. We also instrumented five adjacent open-space areas with iButtons. Game cameras were programmed to take one picture every 30 min and were leveled on the ground with the lens upward. The iButtons were placed in non-aspirated reflective shielding

(Tarara and Hoheisel 2007). Fire closures in the Santa Fe National Forest restricted access until late June, thus 2018 microclimate and imagery measurements were taken between 26 June and 1 November 2018.

2.3. Data analysis

To answer the question — How does first-year tree seedling survival vary between two different shrub species that are common following high-severity wildfire in the southwest? — we conducted three analyses. First, we developed semi-parametric interval censored hazard models to describe differences between seedlings planted under each species. Second, to compare how shrub species alter microclimates, we calculated the differences of microclimate means between shrub and open space microclimate variables and modeled the relationship between canopy coverage and microclimate variables. Finally, to determine how the cumulative stress that seedlings experienced contributed to mortality, we calculated the cumulative daily mean temperatures and VPD from the time of planting to each live–dead survey date during the growing season.

We developed Cox proportional hazard models to describe the likelihood of death for each seedling species by shrub species. Due to the irregular intervals and unobserved time of death, seedlings required the use of interval censored hazard models. The hazard function $h(t)$ describes the instantaneous failure rate at time t can be extended to a proportional hazards regression model:

$$(1) \qquad h(t|X,B) = h_o(t)e^{B'X}$$

where h_o is the baseline hazard function and $h(t|X,B)$ is the hazard conditional on regression parameters B and covariates X. Due to the sensitivity of parametric interval censored models to the selection of a baseline distribution and because we are using these models for inference, we opted to develop semi-parametric Cox proportional hazard models with the ic_sp function from the icenReg package in R (Anderson-Bergman 2017). In icenReg a non-parametric maximum-likelihood estimator is used as a computationally efficient means to determine semi-parametric estimators for Cox proportional hazard models where interval censuring exists. We developed models for each seedling species with shrub species as the single covariate.

The icenReg package does not provide functions to extract Schoenfeld residuals, a standard way to detect nonproportional hazards in semi-parametric models, but we examined covariate effects using the diag_covar function to assess whether the assumption of proportional hazard was met (see Anderson-Bergman (2017) for a description of the procedure and rationale; supplementary Fig. S2[1]). We used the interval during which the event occurred as our response variable, the standard format used in icenReg, which satisfies the assumption of independent observations. We extracted the median time until mortality for the baseline hazard and each covariate. Because multiple hazard curves maximize the likelihood of interval-censored data, we produced two curves per covariate that represent the upper and lower boundaries of estimates.

All temperature (T, °C), relative humidity (RH, %), and game camera imagery were visually and quantitatively assessed for

errors. We visually inspected and removed any T ($n = 326$) and RH ($n = 27$) data points exceeding three standard deviations of the mean, leaving 93 491 T data points and 93 805 RH data points for analysis. At each time-step, we calculated Vapor Pressure Deficit (VPD, kPa) as the difference (eq. 2) between saturated (eq. 3; P_{sat}) and effective water pressure of the air (eq. 4; P_{air}).

$$(2) \qquad VPD = P_{sat} - P_{air}$$

$$(3) \qquad P_{sat} = 0.6112 \times e^{\frac{(17.62 \times T)}{(T+243.12)}}$$

$$(4) \qquad P_{air} = P_{sat} \times \frac{RH}{100}$$

We then aggregated T, RH, and VPD to daily daytime and night-time means and compared the values for each shrub species to open space values using nonparametric Wilcoxon signed-rank tests. Instrumented sites were adjacent to Spectrum Technologies Watchdog® 2700 weather stations ($n = 5$, https://www.specmeters.com/brands/watchdog/watchdog2700/) that were placed in Fall 2016 and record at 30 min intervals. To fill microclimate data gaps, we developed linear mixed models between daily iButton and weather station daily aggregates (mean and maximums) using the lmer function in the lme4 package in R and selected the most parsimonious model using AICc (Hurvich and Tsai 1993; Bates et al. 2015). We used weather station T, RH, precipitation, and shrub species as fixed effects, and a categorical variable for site as a random effect. We applied 10-fold cross validation to assess model fit and used models to gap-fill where necessary (supplementary Tables S1 and S2[1]). We note that weather station values are consistently lower than iButton values due to the Weather stations recording at approximately 1.5 m above ground level, compared to the iButtons at ground level (Dingman et al. 2013). We used the gap-filled T and VPD daily means to calculate the cumulative daily microclimate means at each live–dead survey time point.

We used a workflow in R (version 4.1.0) to identify blurred game camera images using a Laplacian filter (R Core Team 2021). We inspected and removed blurred imagery (266 images) and selected quality imagery during daylight hours (1845 images). To compare the amount of light likely to be experienced under each shrub species, we calculated the gap fraction (amount of visible sky) by applying a unimodal threshold to the blue band to differentiate sky pixels from vegetation pixels, then divided the number of sky pixels by the total pixels in the image (Martin 2015). From this, we calculated daily mean gap fraction.

To compare how shrub species offset microclimates from adjacent open locations, we calculated the differences of means between shrub and open space microclimate variables using non-gap-filled values. We then developed generalized linear mixed models relating maximum daily gap fraction to daytime and nighttime differences in mean RH, T, and VPD between shrub and open space using the glmmTMB package in R (Brooks et al. 2017). We used Gaussian family distributions for RH, VPD, and T and designated shrub species and iButton location as random effects. To assess model fit, we calculated root mean squared error (RMSE) using a 10-fold cross-validation framework and calculated Nakagawa's R^2 for marginal effects.

We used the gap-filled values to calculate the cumulative daily mean and the mean study period daily mean temperatures and VPD from the time of planting to each live–dead survey date during the growing season. We then compared the temperatures and VPD experienced by seedlings that died during each period to those experienced by seedlings that survived with Wilcoxon tests. While we did not instrument every seedling, the instrumented shrubs were in close proximity to non-instrumented shrubs in planting areas. We thus included all seedlings in this analysis rather than just those planted under instrumented shrubs.

3. Results

We found differential survival by seedling species and shrub species by the end of the 2018 growing season with individuals planted under Gambel oak having higher survival (Douglas-fir, 29.7%; ponderosa pine, 45.3%; piñon pine, 29.7%; southwestern white pine, 23.4%) than individuals planted under New Mexico locust (Douglas-fir, 0%; ponderosa pine, 12.5%; piñon pine, 7.8%; southwestern white pine, 1.6%). Over the 2018 growing season (May to October), seedlings planted below New Mexico locust had greater hazard than those planted below Gambel oak. Median time to mortality based on the baseline hazard was 15.82 weeks (Douglas-fir), 16.03 weeks (ponderosa pine), 15.66 weeks (southwestern white pine), and 15.38 weeks (piñon pine). However, New Mexico locust increased hazard coefficients by 5.85 (95% CI = [3.22, 10.62], z-score = 5.80, $p < 0.0001$) for Douglas-fir, 5.84 (95% CI = [2.19, 96.76], z-score = 4.70, $p < 0.0001$) for ponderosa pine, 5.84 (95% CI = [2.62, 10.70], z-score = 4.64, $p < 0.0001$) for southwestern white pine, and 2.64 (95% CI = [1.47, 4.73], z-score = 3.26, $p = 0.001$) for piñon pine, which decreased the median time until mortality for each seedling species (Douglas-fir, 13.07 weeks; ponderosa pine, 13.40 weeks; southwestern white pine, 12.72 weeks; piñon pine, 13.67 weeks) (Fig. 1; supplementary Table S3[1]). By the end of the growing season, Douglas-fir planted under New Mexico locust had 100% mortality (Fig. 1).

Gambel oak buffered microclimate to a greater extent than New Mexico locust (Figs. 2 and 3), Estimated differences between daytime temperature below Gambel oak and in adjacent open locations were approximately −2.07 ± 2.50 °C (Wilcoxon test: $V = 3008$, $p < 0.0001$) and below New Mexico locust the difference was closer to but different from 0 (−0.42 ± 1.80 °C; Wilcoxon test: $V = 13401$, $p < 0.0001$) (Figs. 2 and 3). Mean humidity difference from open was higher under Gambel oak (1.6% ± 6.69%; Wilcoxon test: $V = 6303$, $p < 0.0001$) than under New Mexico locust (−0.72% ± 6.71%; Wilcoxon test: $V = 14732$, $p < 0.0001$) (Fig. 2B). Daytime VPD under New Mexico locust was closer to open (−0.10 ± 0.512 kPa; Wilcoxon test: $V = 20438$, $p = 0.22$) than open to Gambel oak (−0.42 ± 0.74 kPa; Wilcoxon test: $V = 26594$, $p < 0.0001$) (Fig. 2C). Nighttime mean T, rH, and VPD had opposite trends to daytime values: T and VPD were greater than open spaces under Gambel oak at night, and rH was lower, than under New Mexico locust. Daytime mean T and VPD were different between shrubs as well (Wilcoxon test: $V = 59182$, $p = 0.04$; $V = 58606$, $p = 0.03$, respectively), while daytime and nighttime mean humidity, and nighttime mean T and VPD were not dissimilar (Wilcoxon test: $p = 0.12$, $V = 69111$; $p = 0.11$, $V = 60306$; $p = 0.09$, $V = 69472$; $p = 0.13$, $V = 68987$, respectively).

Light availability explained some differences in microclimate below the two shrub species. Over the study period, New Mexico locust had higher gap fractions (i.e., lower amount of light interception) than Gambel oak (Fig. 2D; Wilcoxon test: $V = 4909$, $p < 0.0001$). To understand the effect of gap fraction on daytime microclimate differences between shrubs and open spaces, we modeled the mean difference between shrub and open space variables as a response to the interaction of gap fraction and shrub species with iButton location and shrub as random effects (Fig. 3). Marginal Nakagawa R^2 values (i.e., variance explained by fixed effects) for mixed models ranged between 0.05 and 0.26 (Fig. 3; supplementary Tables S4 and S5[1]). The effect of increased gap fraction differed under shrub species, with temperature and VPD slightly decreasing under Gambel oak and increasing under New Mexico locust and humidity increasing under Gambel oak and decreasing under New Mexico locust (Fig. 3).

To determine how the cumulative stress that seedlings experienced contributed to mortality, we calculated the cumulative daily mean temperatures and VPD from the time of planting to each live–dead survey date during the growing season (Fig. 4). Living seedlings tended to experience lower cumulative daily mean

Fig. 1. Cox Proportional Hazard regression models for time since planting for seedlings (A, piñon pine; B, ponderosa pine; C, southwestern white pine; D, Douglas-fir) planted under Gambel oak (solid blue) and New Mexico locust (dashed yellow). Boxes indicate likely range of hazard between observation periods. Multiple hazard curves maximize the likelihood of interval-censured data, and the two curves per covariate represent the upper and lower boundaries of estimates. Horizontal lines beyond week 20 indicate the range of possible survival outcomes in the absence of data. [Colour online.]
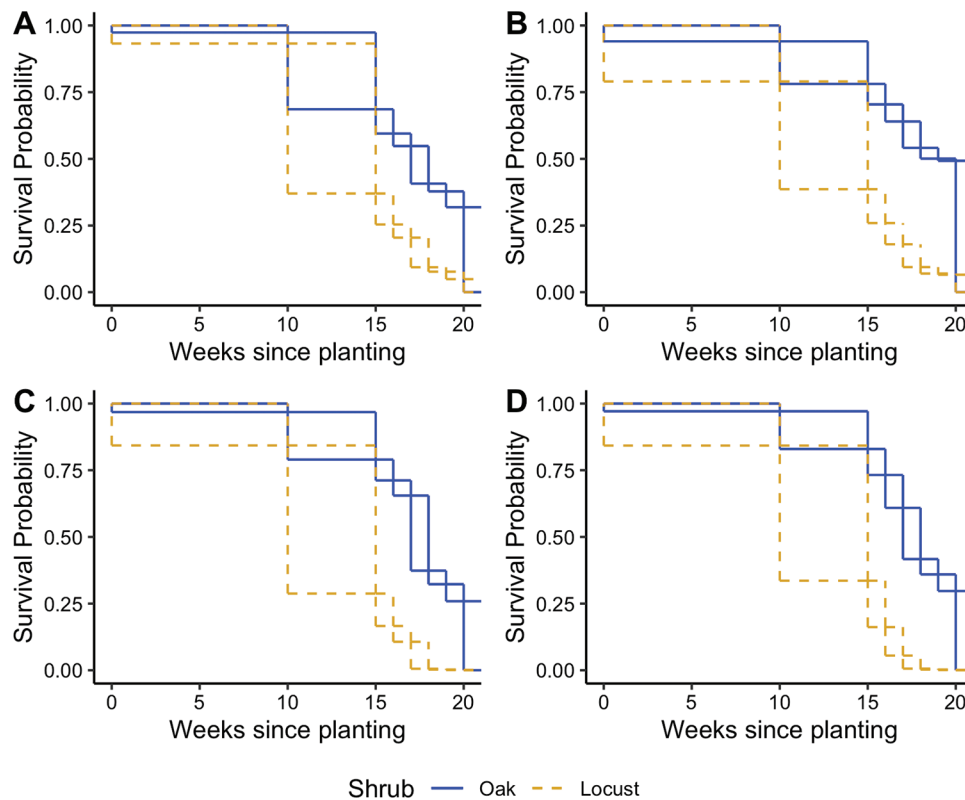
VPD and cumulative daily mean temperature between sampling periods than dead seedlings experienced throughout the first year (Fig. 4). Southwestern white pine and Douglas-fir had a larger number of time periods with significant differences in cumulative VPD and T between living and dead compared to piñon and ponderosa pine. We did not see these differences when comparing mean temperature and VPD between living and dead between survey dates (supplementary Fig. S3[1]), whereas the cumulative stress of moisture deficits had an important role in determining survival.

4. Discussion

The interaction of high-severity wildfire and warming and drying from ongoing climate change is increasing the land area where forest to non-forest transitions are occurring (Coop et al. 2020; Rodman et al. 2020a). In the southwestern US, shrub-dominated patches are a feature of the landscape and are reinforced by fire, a process that can continue even in large high-severity patches (Guiterman et al. 2018; Keyser et al. 2020). High-severity burn patches are often hotter and drier because of overstory tree mortality. However, our results indicate that while some seedling mortality is to be expected, planting under shrubs, such as Gambel oak, can mitigate the climate conditions that reduce tree seedling survival during the first growing season.

Western forests are increasingly likely to have crossed climate thresholds that make tree regeneration unlikely in high-severity burned areas (Davis et al. 2019b). However, despite planting in a dry winter that preceded a warm and dry growing season, we saw 25%–40% of seedlings survive through their first growing season under Gambel oak (Fig. 1). Planted seedling success rates in eight other fires in the southwest averaged 25% five years after the

fires, though those occurred between 2002 and 2005 and may not be representative of more recent climate conditions (Ouzts et al. 2015). We note several explanations for the survival in this study. First, the lower gap fraction helped to decrease below-shrub temperature means while increasing humidity (Fig. 3). Seedlings are sensitive to short-term extreme events and mitigating these may have more influence on survival than decreasing overall means (Reyer et al. 2013; Davis et al. 2019a). Second, lower temperatures coupled with higher humidity reduced daytime VPD, which has a critical role in seedling survival (Will et al. 2013; Davis et al. 2019b). High-severity burned areas experience higher VPD and temperatures than unburnt locations (Wolf et al. 2021). VPD is expected to increase with climate change and these results highlight how directed planting in dense shrubs can affect survival outcomes following future fires (Williams et al. 2013; Ficklin and Novick 2017). New Mexico locust canopy had less effect on temperature and humidity (Fig. 2), and the relatively open structure may have increased wind-driven mixing with the atmosphere, though we did not measure this (Davis et al. 2019a).

The ability of shrubs, such as Gambel oak, to buffer climate has implications for seedling survival in burned areas with climate change. The opportunity for successful seedling establishment is likely to decrease as temperature and aridity continue to increase with additional climate change (Davis et al. 2016). Warming will result in a nonlinear increase in VPD. Plants respond to increasing VPD by decreasing stomatal conductance to a threshold point, after which continued high VPD can cause cavitation in xylem (Williams et al. 2013; Grossiord et al. 2020). Seedlings are often more susceptible to these effects than adults due to shallower rooting depths (Padilla and Pugnaire 2007). The mitigation of high temperature

Fig. 2. Difference between daytime and nighttime mean temperature (A), mean relative humidity (B), and mean vapor pressure deficit (VPD, C) under Gambel oak and New Mexico locust and adjacent open spaces, aggregated to the growing season. Negative (positive) values correspond to cooler (warmer), wetter (drier), and lower (higher) VPD than open spaces. The gap fraction difference between shrub species is shown in panel D, ranging from 0 (no visible sky) to 1 (no canopy). Boxplots show median (bold line), mean (+), the interquartile range (vertical line), and points outside the range (points). All groups were distinct from zero (i.e., different from open space microclimate values) except for daytime VPD under New Mexico locust (Wilcoxon test, *p* value >0.1).
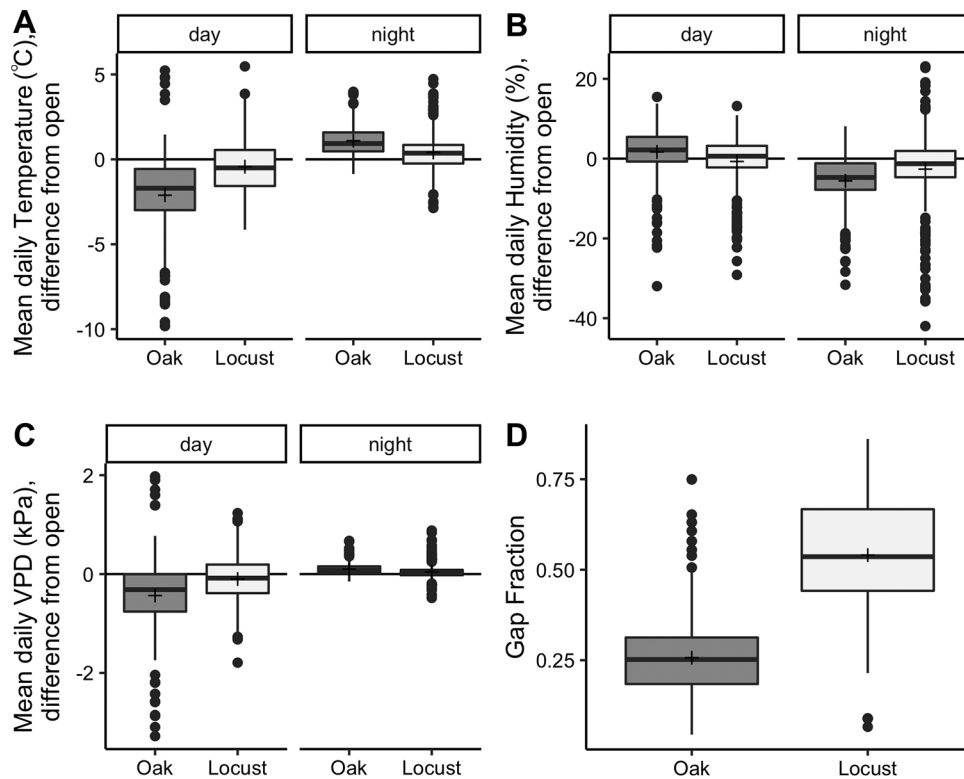
and VPD in the early stages of development may provide seedlings with time to grow to less vulnerable life stages (Urza et al. 2019). By decreasing VPD and temperature relative to open-spaces, Gambel oak provided a climatic buffer during the first growing season.

Climate change is forcing species migration by increasing temperature and aridity beyond that which is conducive to seedling survival (Dobrowski et al. 2013; Maguire et al. 2018). While mature trees can typically tolerate a wide range of climate conditions, their pre-disturbance presence does not necessarily indicate that seedlings of the same species would successfully establish following disturbance (Davis et al. 2019b; Foster et al. 2020; Minott and Kolb 2020). However, our work indicates that post-fire survival of planted seedlings within a species' current range is possible despite environmental conditions that suggest that range is shifting. The survival of Douglas-fir and southwestern white pine below Gambel oak suggests that the shrub provided a local environment that could support species accustomed to cooler and wetter environments as they were approximately as likely to survive as the more drought-tolerant ponderosa and piñon pines (Fig. 1).

The influence of shrubs on seedling survival suggests that these seedling species will have far greater establishment success following high-severity fire if the early successional community is dominated by shrub species that alter microclimate. Out of the four species, piñon pine had the greatest survival rates under both Gambel oak and New Mexico locust (Fig. 1). Floyd (1982) observed this relationship, suggesting that piñon could invade Gambel oak stands without detriment. Their coexistence suggests a facilitative effect, but it could be a neutral one because the sites were still within the climatic niche of piñon. The relatively high levels of survival of piñon pine below New Mexico locust supports

this argument, indicating that while Gambel oak has a stronger facilitative effect, piñon pine would still survive in this area. However, the low survival of Douglas-fir and southwestern white pine under New Mexico locust suggest that these species would not readily colonize severely burned areas in this region, despite its presence in the area pre-fire.

While Gambel oak played a facilitative role on conifer survival, light availability could affect future growth. Here, a lower light environment below Gambel oak did not appear to have a negative effect on either ponderosa or piñon pine, consistent with similar studies (Gómez-Aparicio et al. 2004). It is possible that growth rates will be altered due to light constraints. However, pine species in semi-arid environments often exhibit slowed growth in response to growing season aridity (Truettner et al. 2018), while low light environments have limited effect on seedling photosynthesis rates (Gray et al. 2005). Even if growth is slower, conifers planted under Gambel oak may be more likely to survive until reaching a growth stage capable of surviving unbuffered climate compared to those planted in the open (Urza et al. 2019).

We expected seedlings planted beneath New Mexico locust to have lower survival rates than Gambel oak. However, we did not expect the almost complete mortality across all species planted beneath New Mexico locust. Seed for the ponderosa pine and Douglas-fir seedlings was gathered from this area, and so we expected some measure of genetic acclimation to local conditions (Kolb et al. 2016). Further, the study location supported all species planted prior to the fires, with naturally germinated individuals of all seedling species in an unburned area adjacent to the planting site. Although microclimate below New Mexico locust appears to be strongly related to survival, shrub facilitation

Fig. 3. Scatterplots showing daily daytime (A, C, E) and nighttime (B, D, F) microclimate mean differences (humidity (top), temperature (middle), and VPD (bottom)) by maximum daily gap fraction and shrub species, with lines indicating the marginal effects of the mixed models. [Colour online.]
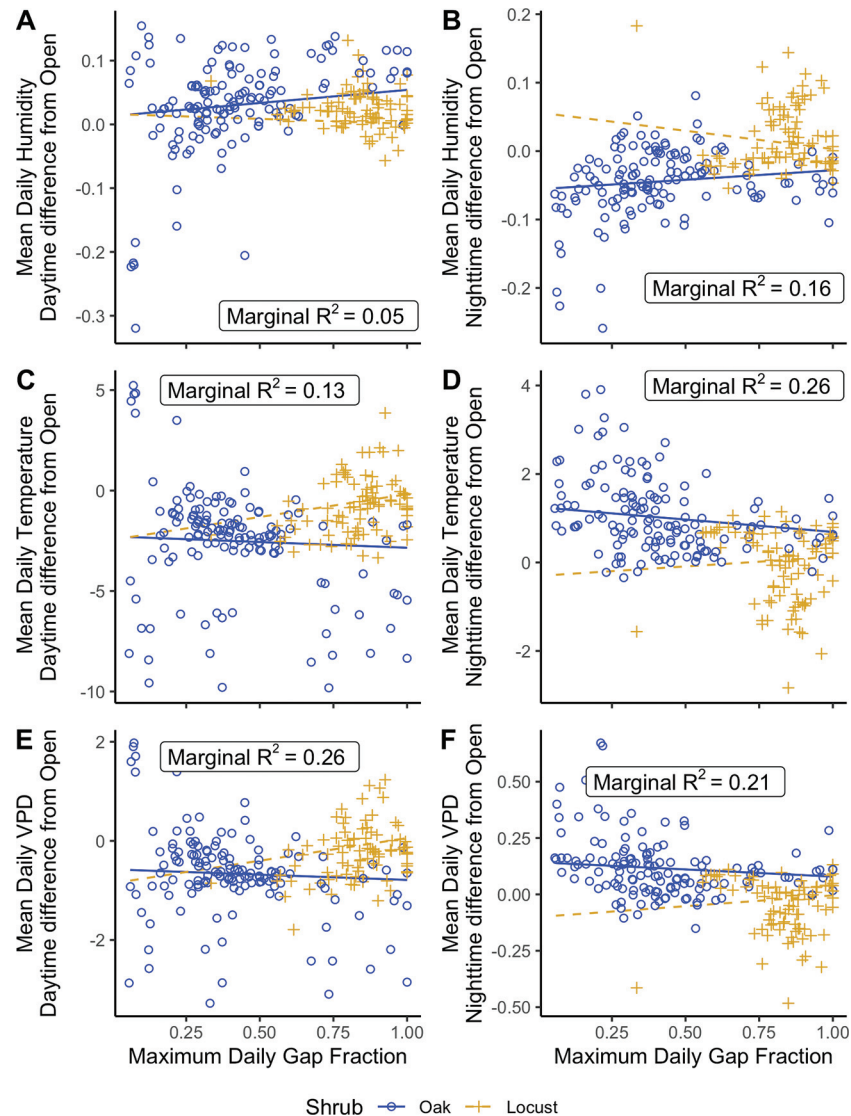

studies offer several other possible explanations for near-total mortality. At intermediate levels of stressful abiotic conditions, facilitation is possible, yet at high levels of stressful abiotic conditions, the effect can be overwhelmed (Sthultz et al. 2007). Further, shrub interactions can have a gradient of facilitative effects depending on the life stage of the seedling (Urza et al. 2019). It is possible that the positive effect of New Mexico locust is key only in very early stages (i.e., germination) or later stages in which its nitrogen-fixation properties assist growth while Gambel oak has a wider facilitative effect that includes the first growing season. We only planted under shrubs, but it is reasonable to suppose that few seedlings would have survived in the open given the small, but significant differences in mean microclimate over the growing season between open and New Mexico locust (Fig. 2).

Another important consideration for future seedling growth when planted below shrubs is competition for water. In other systems, competition for soil moisture between shrubs and seedlings can result in decreased survival until seedling roots access deeper water (Plamboeck et al. 2008). Gambel oak, however, may increase the infiltration and redistribution of moisture throughout the soil column (Oerter and Bowen 2019). We did not measure

soil moisture; however, soil moisture can be as important a determinant of seedling survival as the direct effects of temperature or VPD (Davis et al. 2019*a*; Foster et al. 2020). Thus, quantifying the potential for shrub cover to alter soil moisture and its potential to influence planted seedling survival is worthy of investigation.

Planting within shrub patches in the Jemez mountains and similar locales may expose seedlings to additional risk. Historically, frequent fires maintained and expanded Gambel oak patches in the Jemez Mountains due to their prolific resprouting behavior when burned (Abella and Fulé 2008; Guiterman et al. 2018; Coop et al. 2020). Future increases in fire occurrence are likely to expand shrub fields while conifers are unlikely to regenerate at sufficient rates to naturally re-establish pre-fire forest cover (Keyser et al. 2020). Further, planted seedlings have low survival in fires of any severity (Steady et al. 2019). Long fire-free periods are then necessary to ensure successful reestablishment, though this is increasingly unlikely as climate change alters fire frequency and area burned (Abatzoglou and Williams 2016). While shrubs are initially an asset to seedling survival, they can become a liability to survival if fire is present. Conducting such a planting exercise, or any planting in areas of extensive, fire-reinforced shrub fields, may require

Fig. 4. Cumulative daily mean vapor pressure deficit (VPD) (A) and temperature (B) for year 1, grouped by seedlings that were observed as alive at each time point (grey) and those that have died between the previous and current time points. *, indicate statistically significant difference between the groups (Wilcoxon test, *p* value <0.05).
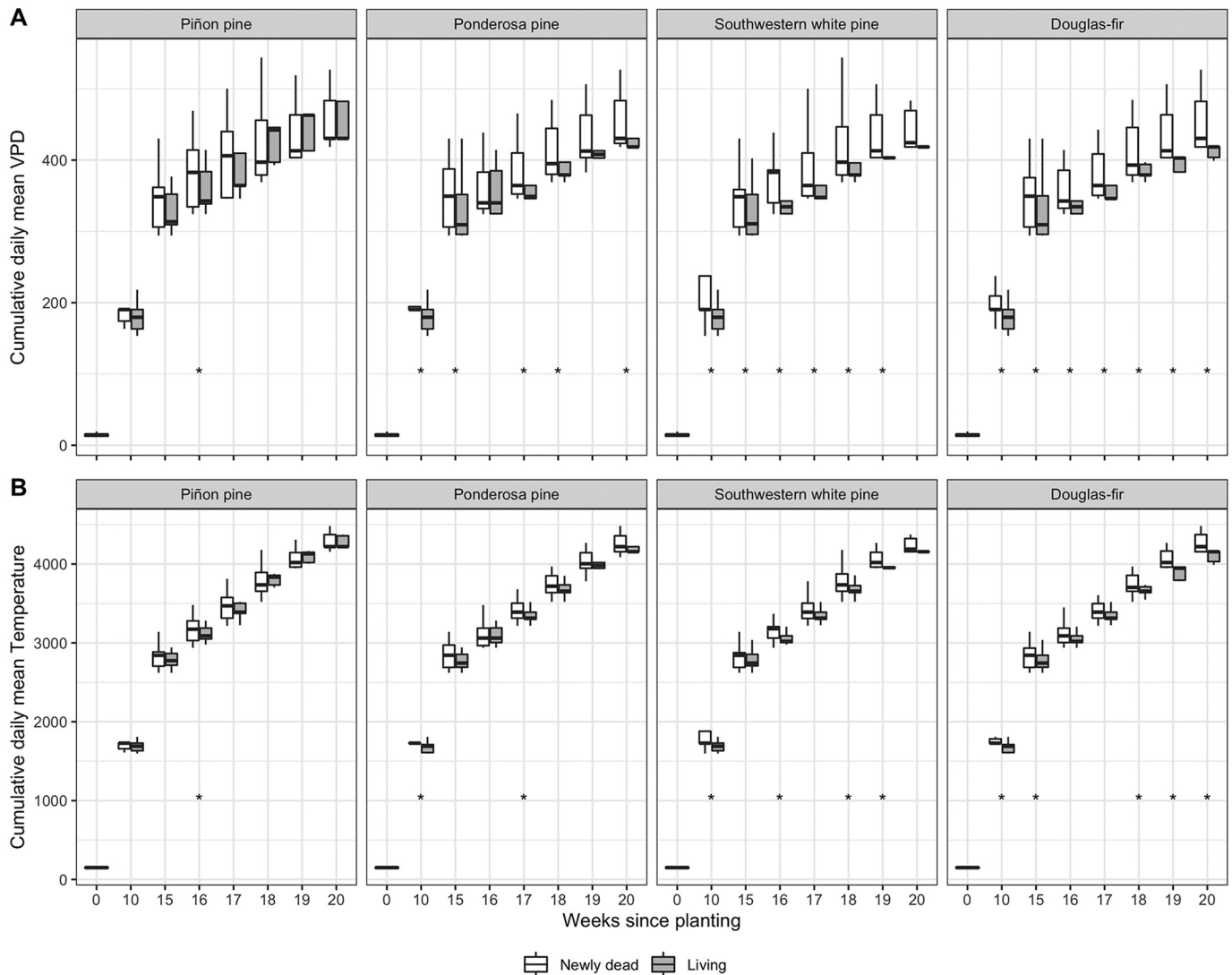
continued active management to avoid fire spread. However, the facilitation effect of shrubs on conifer seedling survival should not be overlooked in the face of this potential risk.

5. Conclusions

Climate change is increasing the likelihood of hotter droughts and drier growing seasons in the southwestern US (Cayan et al. 2010). As the area conducive to tree establishment following fire continues to decrease, post-fire planting will likely be necessary to avoid permanent transitions to non-forest from previously forested areas (Guiterman et al. 2018; Hankin et al. 2019; Coop et al. 2020). Our work highlights how the morphology of shrubs, particularly those with dense canopies, can alter planted seedling survival. Although further work is required to compare planting with and without shrub cover, these results indicate that post-fire planting success in the southwest can be increased by waiting for post-fire shrub establishment and leveraging shrubs to buffer microclimate.

Data availability

Data and code used in this research is available at https://datadryad.org/stash/dataset/doi:10.5061/dryad.hx3ffbgcs.

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