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Stand density, drought, and herbivory constrain ponderosa pine regeneration pulse[1]

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Abstract: Trees in dry forests often regenerate in episodic pulses when wet periods coincide with ample seed production. Factors leading to success or failure of regeneration pulses are poorly understood. We investigated the impacts of stand thinning on survival and growth of the 2013 cohort of ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) seedlings in northern Arizona, United States. We measured seedling survival and growth over the first five growing seasons after germination in six stand basal areas (BAs; 0, 7, 14, 23, 34, and 66 (unthinned) m²·ha⁻¹) produced by long-term experimental thinnings. Five-year survival averaged 2.5% and varied among BAs. Mean survival duration was longer in intermediate BAs (11 to 16 months) than in clearings and high BAs (5 months). The BAs of 7, 14, and 23 m²·ha⁻¹ had >2600 5-year-old seedlings·ha⁻¹. In contrast, regeneration was lower in the clearing (666 seedlings·ha⁻¹) and failed completely in the 34 m²·ha⁻¹ and unthinned treatments. Seedling survival was highest during wet years and lowest during drought years. Many surviving seedlings had no net height growth between years 4 and 5 because of stem browsing. Results indicate that natural regeneration of ponderosa pine is influenced by stand BA, drought, herbivory, and interactions between extreme climatic events.

Key words: Pinus ponderosa, thinning, tree seedling establishment, seedling mortality, stand management.

Résumé : Les arbres des forêts sèches se régénèrent souvent en vagues épisodiques lorsque des périodes humides coïncident avec une production abondante de graines. On connaît mal les facteurs responsables du succès ou de l'échec des vagues de régénération. Nous avons étudié les effets de l'éclaircie des peuplements sur la survie et la croissance de la cohorte de semis de pin ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) établie en 2013 dans le nord de l'Arizona, aux États-Unis. Nous avons mesuré la survie et la croissance des semis au cours des cinq premières saisons de croissance après leur germination en fonction de six classes de surface terrière (0, 7, 14, 23, 34 et 66 (non éclairci) m²·ha⁻¹) provenant d'un dispositif expérimental suivi à long terme. Le taux de survie à 5 ans était en moyenne de 2,5 % et variait selon la surface terrière. La durée de survie moyenne était plus longue pour les surfaces terrières intermédiaires (11 à 15 mois) que dans les zones coupées à blanc et celles où la surface terrière était élevée (5 mois). Les surfaces terrières de 7, 14 et 23 m²·ha⁻¹ avaient plus de 2600 semis·ha⁻¹ âgés de 5 ans. En revanche, la régénération était plus faible dans les zones coupées à blanc (666 semis·ha⁻¹) et était complètement absente dans le traitement à 34 m²·ha⁻¹ et les zones non éclaircies. La survie des semis était la plus élevée pendant les années humides et la plus faible pendant les années de sécheresse. La croissance nette en hauteur de nombreux semis survivants a été nulle entre la quatrième et la cinquième année en raison du broutement. Les résultats indiquent que la régénération naturelle du pin ponderosa est influencée par la surface terrière du peuplement, la sécheresse, l'herbivorisme et les interactions entre les événements climatiques extrêmes. [Traduit par la Rédaction]

Mots-clés : Pinus ponderosa, éclaircie, établissement des semis, mortalité des semis, aménagement des peuplements.

Introduction

Many coniferous forests of western North America are experiencing large-scale mortality of mature trees from drought, wildfire, and bark beetle (*Dendroctonus ponderosae* Hopkins, 1902) attacks (Cohen et al. 2016; Hicke et al. 2016), and this mortality is expected to increase with climate warming (McDowell et al. 2016). There is growing evidence that many of these forests have inadequate regeneration (Bell et al. 2014; Stevens-Rumann et al. 2018), raising concerns about future forest sustainability. These trends and concerns highlight the need for better understanding of forest regeneration processes and constraints.

This study focuses on ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) in the southwestern United States. Ponderosa pine is currently the dominant tree species of high-elevation forests in the region, yet its range is projected to shrink in the future because of disturbance and stress driven by climate warming (Rehfeldt et al. 2014). Ponderosa pine typically regenerates in distinct pulses when high cone production is followed by a cool, wet summer that promotes early germination and rapid root growth (Savage et al. 1996; League and Veblen 2006; Rother and Veblen 2017). Ponderosa pine seedling establishment is limited by many factors, including herbivory (Zwolak et al. 2010), drought

Fig. 1. Taylor Woods levels of growing stock experiment located at the Fort Valley Experimental Forest, Arizona. Each basal area (BA) level (m²·ha⁻¹) is represented by three replicate plots. Asterisks (*) indicate BA treatment levels investigated in this study. Adapted from Schubert (1971) with permission of the Society of American Foresters and from Bailey (2008). [Color online.]
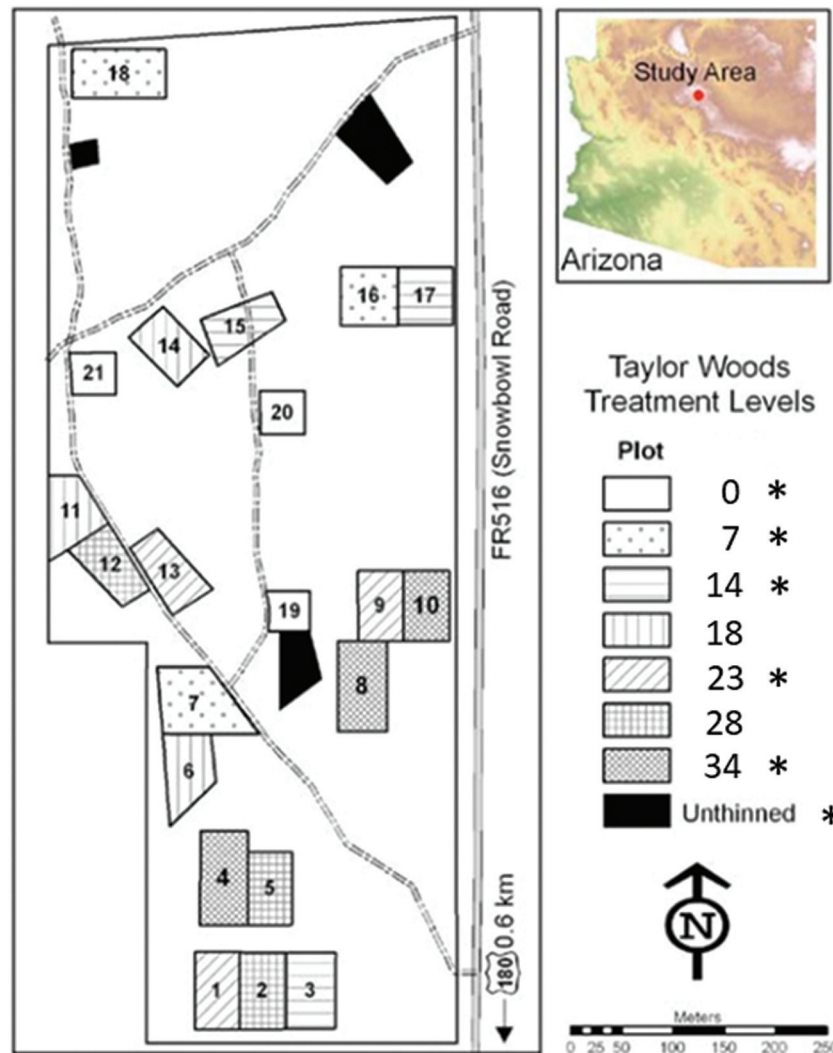
(Puhlick et al. 2012; Davis et al. 2019), grass competition (Larson and Schubert 1969), density of mature trees (Schubert 1971; Flathers et al. 2016), and frost heaving (Heidmann and Thorud 1976). Climate change is also emerging as a potential limitation. A recent model projected that impacts of climate change on ponderosa pine regeneration will shift from an initial increase in the first half of the 21st century to a decrease in the second half of the 21st century because of increasing limitations to seedling survival from high temperature and water stress (Petrie et al. 2017). A recent literature review based mostly on greenhouse experiments found that ponderosa pine seedling establishment is positively associated with precipitation, mean air temperature, and soil temperature and negatively related to maximum air temperature (Petrie et al. 2016). The review also emphasized the need for more field experiments that investigate influences on seedling establishment.

The objectives of this study were to understand constraints on the success of a recent ponderosa pine regeneration pulse in northern Arizona, United States, using a combination of experimental and observational approaches. We used repeated observations on seedling survival and growth over the first 5 years after germination in a long-term thinning experiment that controlled stand basal area (BA). The measurement period (2013–2018) in-

cluded wet and dry years, providing insight about constraints related to drought.

Materials and methods

Study area

We performed the study in the 35 ha Taylor Woods thinning experiment (elevation 2266 m) located in the Fort Valley Experimental Forest, 14 km northwest of Flagstaff, Arizona (Fig. 1). Past (1981–2010) annual precipitation at the study area averaged 57 cm, with approximately half of the precipitation occurring as snow during winter (November–March) and most of the remainder as late-summer rain. May and June are normally dry (1.6 and 0.9 cm of precipitation, respectively). The mean annual temperature is 8.1 °C, and mean monthly temperatures range from –0.9 °C in January to 19.1 °C in July. Soils are a montmorillontic complex of frigid Typic Argiborolls derived from basalt. The A horizon is shallow (10 cm), and maximum soil depth is 152 cm above fractured basalt bedrock (Ronco et al. 1985). The site has a gentle (4%) southwest-facing slope in the habitat type of *Pinus ponderosa* and *Festuca arizonica* Vasey. The site index is 22 based on height in metres at a base age of 100 (Ronco et al. 1985).

Fig. 2. BA treatment levels investigated in the study: (*a*) 0, (*b*) 7, (*c*) 14, (*d*) 23, (*e*) 34, and (*f*) 66 (unthinned) m²·ha⁻¹.
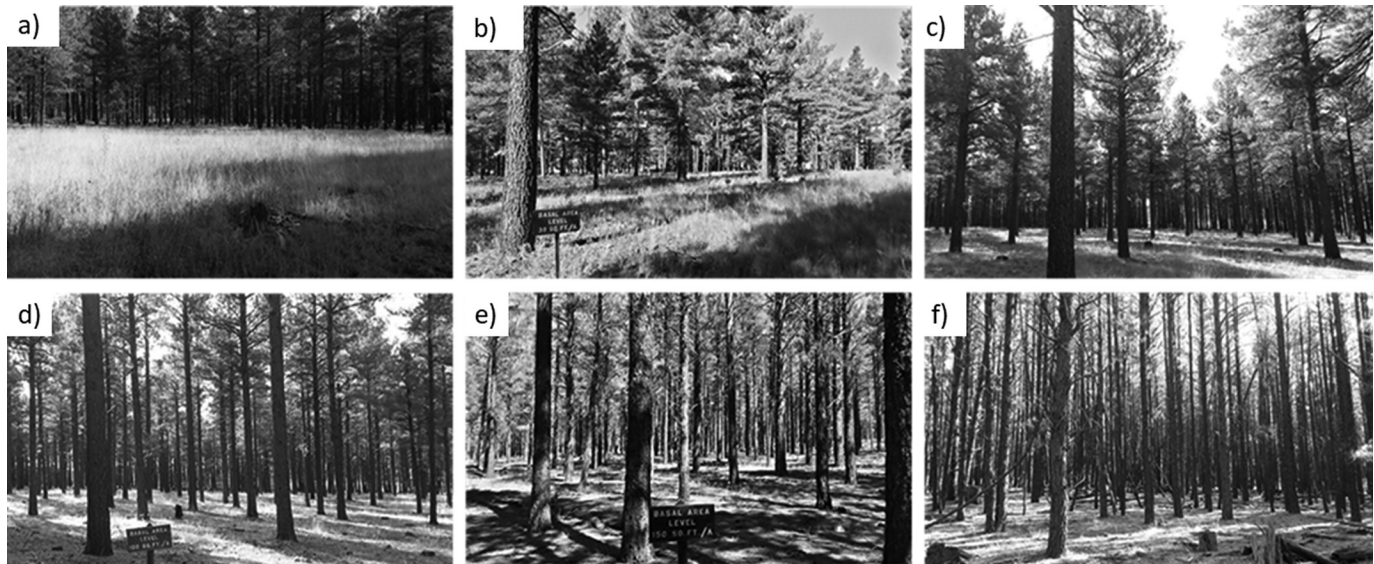
The thinning experiment started in 1962 when the site contained an overstory of older trees and dense understory of saplings and poles, which established in 1919 (Ronco et al. 1985). The first cut in 1962 removed all overstory trees to leave an even-aged stand of 43-year-old saplings and poles. Seven target BA levels (0, 7, 14, 18, 23, 28, and 34 m²·ha⁻¹) and an unthinned control were created later in 1962 by spacing-based thinning in three replicate stands per treatment level. The target BAs were originally designed as growing stock levels, or the BA when mean tree diameter is 25 cm (Myers 1967). The growing stock levels became the same as BA once stands obtained a mean tree diameter of 25 cm in the 1970s or 1980s. Each replicate stand is 0.3–0.5 ha, except the clearcuts (0 m²·ha⁻¹), which were 0.1 or 0.2 ha. Target BAs were maintained in the 7, 14, 18, 23, 28, and 34 m²·ha⁻¹ treatments by subsequent thinnings approximately every decade (1972, 1982, 1992, 2003, and 2017). No subsequent thinning or treatment occurred in the clear-cut (0 m²·ha⁻¹) and unthinned treatment levels. Logs from the thinnings were removed from the site, and slash was either lopped and scattered or piled outside the experimental plots, depending on the year of thinning.

Experimental and sample design

We investigated five BA levels (0, 7, 14, 23, and 34 m²·ha⁻¹) plus the unthinned control, for a total of six levels that span the range of BA and tree density at Taylor Woods (Fig. 2). We included all three replicate stands of each of the six levels for a total of 18 stands. Recent stand measurements show that the target BA levels are approximations of actual conditions for the thinned levels (Table 1). For example, in 2015 (before the last thinning), actual BAs were a few square metres per hectare higher than targets, but relative differences among levels were maintained. The last thinning in 2017 produced BAs close to the targets for most levels.

We extended the earlier measurements by Flathers et al. (2016) of survival and growth of the 2013 seedling cohort, which covered only the first 2 years after germination, for another 3 years until November 2018. We used the same sample design and plots established by Flathers et al. (2016). In brief, this design consisted of a network of 10 systematically and evenly spaced plots (1 m²) within each of the 18 stands established in April 2014, which was the first spring after the late-summer germination and initial establishment of the 2013 cohort. We installed plots in the middle of each stand with a 10 m buffer from all stand edges. To allow repeated measurements between 2014 and 2018, we marked plots by rebar, flagging, and Global Positioning System (GPS) and mapped and

Table 1. Mean basal area (BA) for treatment targets in 2015 (before the last thinning) and in 2018 (after the last thinning).

Target BA, m²·ha⁻¹	2015 BA, m²·ha⁻¹	2018 BA, m²·ha⁻¹
0	0.0 (0.00)	0 (0.0)
7	13.6 (1.07)	8.1 (0.22)
14	16.3 (0.13)	16.5 (0.12)
23	28.2 (1.88)	25.4 (0.10)
34	42.0 (1.73)	38.3 (0.39)
66 (unthinned)	65.7 (5.86)	67.9 (5.64)

Note: Values in parentheses are standard errors.

labeled each seedling with a small metal tag. We assessed seedling survival in spring, summer, and fall in the first 2 years (2014–2015) and then every fall for the last 3 years (2016–2018). We classified seedlings as dead when they were 100% brown, red, or black or were missing from plots. In the fall of each year between 2015 and 2018, we measured seedling height with a ruler and stem base diameter (0.5 cm above the forest floor) using a digital caliper. We also measured seedlings from cohorts other than the 2013 cohort, but their frequency was low (see Results), and consequently they were not included in the statistical comparisons.

Soil water content (SWC)

We measured volumetric SWC between May 2014 and November 2018 in one replicate stand of each BA level. In each stand, we installed two Decagon ECH₂O 5TM time-domain reflectometry sensors (METER Group, Pullman, Wash., USA) at a depth of 15 cm and two sensors at a depth of 40 cm. SWC data in each stand were recorded every hour on a Decagon data logger. This resulted in >30 000 hourly observations in each stand. Data gaps, which were generally less than 2 months long and comprised less than 20% of all observations, occurred occasionally because of loss of power to the data logger; gaps were not filled. We averaged the two hourly values over the two depths in each stand.

Data analysis

We used survival analysis to assess whether the BA levels affected seedling survival between April 2014 and October 2018. The outcome variable was months until seedling death. The survival data are interval-censored, meaning that the exact time of death is known to have occurred only within a particular duration of time (Singh and Totawattage 2013). The data are also right-censored, referring to a particular case of interval-censored data in which

Fig. 3. Survival proportion of ponderosa pine seedlings from the 2013 cohort over 55 months (April 2014 to November 2018) in six BA levels (m²·ha⁻¹). Text above the lines is the month and year of measurement. UT, unthinned.
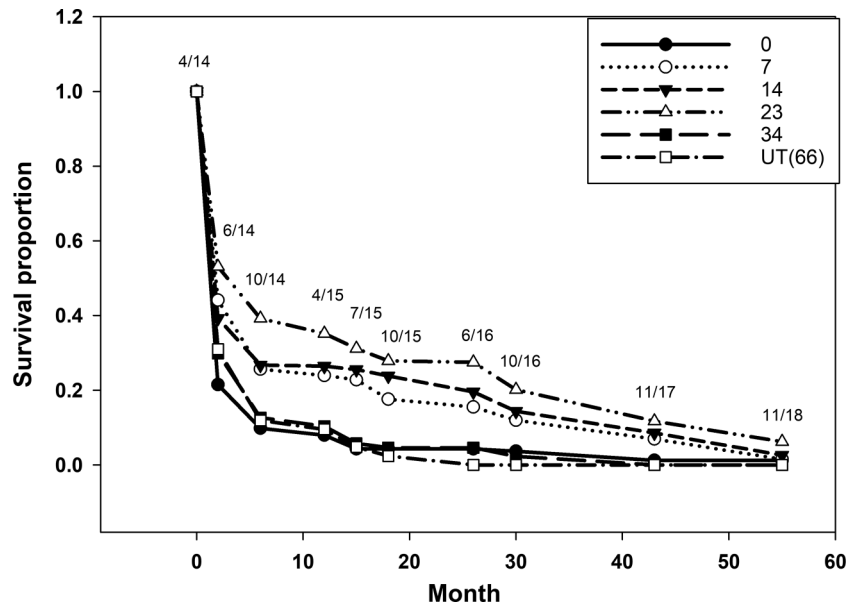
the time of the event for some observations does not occur within the study period, as is the case when seedlings survive past the end of the study (Singh and Totawattage 2013). We used Kaplan–Meier survival curves to show differences in survival among BA levels through time (Harrell 2001) and logrank tests to evaluate the strength of differences in survival among BA levels.

We tested for differences among BA levels using generalized linear models (GLMs), using stand-level values ($N = 18$) of seedling survival proportion (number of live seedlings/total number of seedlings), height, and diameter to avoid pseudoreplication (Hurlbert 1984). We checked assumptions of distribution and homogeneous variance and residuals before analyzing data and used nonnormal error distributions when necessary. We analyzed all data with JMP software (version Pro 14, SAS Institute Inc., Cary, N.C., USA). Although we measured height and diameter repeatedly over several years, we analyzed data separately for each year (2014–2018) because high mortality prevented repeated measurements on most seedlings in all years. We evaluated differences among specific BA levels by contrasts in the GLMs for seedling survival proportion and by Tukey honestly significant difference (HSD) tests for height and diameter.

We did not use inferential statistics for the SWC data because we made measurements in only one replicate stand per BA level. We averaged data over the two sensors at each soil depth in each BA level and plotted trends between 2014 and 2018 to provide insight about soil moisture dynamics over the course of the study. We used monthly mean precipitation and air temperature data obtained from the National Weather Service (https://www.ncdc.noaa.gov/cdo-web/datasets) for Flagstaff Pulliam Airport, which is located 16 km from the study site, to understand the role of climatic factors on seedling performance and SWC. Monthly mean precipitation and air temperature data from Flagstaff Pulliam Airport are strongly correlated with data from a weather station at the Fort Valley Experimental Forest, located 1 km from our study site, which was decommissioned before our study (precipitation: $r = 0.84$, $p < 0.001$; temperature: $r = 0.99$, $p < 0.001$; years 1950 to 2000).

Results

Seedling survival

Survival of the 2013 seedling cohort decreased in every BA level between the start of the census in April 2014 and the end in November 2018 (Fig. 3). The largest decrease in survival was in the first 2 months between April and June 2014, when the surviving proportion was less than 0.6 in every BA level. Large differences in survival among BA levels emerged in October 2014, when survival was higher in the BA levels of 7, 14, and 23 m²·ha⁻¹ than in the levels of 0, 34, and 66 (unthinned) m²·ha⁻¹ (Fig. 3). Survival continued to decrease in all BA levels between 2015 and 2018, during which the BA levels of 7, 14, and 23 m²·ha⁻¹ continued to have higher survival than the other BA levels.

Survival analysis showed significant differences (logrank $\chi^2 = 78.63$, $p < 0.001$) in duration of survival for the 2013 seedling cohort among BA levels (Table 2). Mean survival was shortest in the 0, 34, and 66 (unthinned) m²·ha⁻¹ BA levels, averaging about 5 months, and longer in the intermediate BA levels (7, 14, and 23 m²·ha⁻¹), ranging from 11 to 16 months.

Survival of the 2013 seedling cohort at the end of the study in November 2018 differed significantly ($p < 0.0001$) among BA levels (Table 2). The 34 m²·ha⁻¹ BA and unthinned levels had no survival. Only two seedlings (a proportion of 0.0123 of the initial total) survived in the 0 m²·ha⁻¹ BA level (clearing), which scaled to 666 seedlings·ha⁻¹ in November 2018. Survival proportion was low in the 7 m²·ha⁻¹ BA level (0.0150), which had 2667 seedlings·ha⁻¹ in November 2018 because of the large number of seedlings at the start of the study. The 23 m²·ha⁻¹ BA level had the highest survival proportion (0.0623) and the highest number of seedlings in November 2018 (5667 seedlings·ha⁻¹). The 14 m²·ha⁻¹ BA level had an intermediate survival proportion (0.0260), but had the same number of seedlings per hectare at the end of the study as the 23 m²·ha⁻¹ BA level because it had the largest number of seedlings at the start of the study (Table 2).

We also measured ponderosa pine seedlings from cohorts other than the 2013 cohort (aged by bud scale scars) and found that their frequency was low. For example, only three seedlings from the 2010 cohort occurred at the start of the study over all BA levels, which is 0.17% of all initial seedlings. All three seedlings from the 2010 cohort died: one between October and November 2017 and

Table 2. The number of seedlings in measurement plots at the start (April 2014) and end (November 2018) of the study, survival proportion, mean months of survival, and number of seedlings per hectare at the end of the study for the six basal area (BA) levels.

BA, $m^2 \cdot ha^{-1}$	No. of seedlings		Survival proportion	Mean survival months	No. of seedings per hectare, November 2018
	April 2014	November 2018			
0	163	2	0.0123 (0.0086) a	4.8 (0.65) a	666 (333)
7	535	8	0.0150 (0.0052) a	11.1 (0.69) b	2667 (2186)
14	655	17	0.0260 (0.0062) a	12.3 (0.68) b	5667 (2333)
23	273	17	0.0623 (0.0146) c	15.8 (1.15) c	5667 (3480)
34	87	0	0.0000 (0.00) b	5.3 (0.85) a	0 (0)
66 (unthinned)	42	0	0.0000 (0.00) b	5.2 (1.18) a	0 (0)

Note: No. of seedlings represents the number of seedlings pooled over thirty 1 m^2 plots (10 per each of three stands per BA level). Different lowercase letters denote significant differences among BA levels. Values in parentheses are standard errors. For Survival proportion, $p < 0.0001$ for the effect of BA on stand-level values ($N = 18$) from the general linear model using maximum likelihood with negative exponential distribution. Differences among BA levels were tested by contrasts. For Mean survival months, logrank χ^2 $p < 0.0001$ for differences among BA levels using JMP survival analysis for individual seedling data ($N = 1755$). Differences among BA levels were tested by pairwise survival analysis comparisons.

two between November 2017 and November 2018. The 2012 cohort had 10 seedlings at the start of the study over all BA levels (0.56% of the total); six were alive in November 2018, one died between October and November 2017, and four died between November 2017 and November 2018. The 2015 cohort had three seedlings over all BA levels (0.017% of the total); two were alive in November 2018 and one died between November 2017 and November 2018.

We compared climatic factors with seedling survival to investigate the role of drought in seedling mortality (Fig. 4). The highest annual mortality occurred to young seedlings in the first 6 months of observation (April–October 2014), during which survival proportion over all BA levels was 0.257. The annual Palmer drought severity index (PDSI) for 2014 was 1.24 (https://wrcc.dri.edu/wwdt/time/), indicating slightly wet conditions primarily produced by a cool, wet summer. Survival was high in 2015 (0.752) and 2016 (0.745) during continuing cool, wet conditions (PDSI 3.32 in 2015 and 2.28 in 2016). Survival decreased to 0.572 in 2017, during which there was moderate drought (PDSI –2.51) and a late summer and fall that were notably hot and dry. Drought continued in 2018 (PDSI –2.27), and survival decreased to 0.357 even though seedlings were 5 years old. Drought in 2018 was caused by abnormally warm and dry conditions in fall 2017 and winter 2018 (Fig. 4). Fall precipitation in 2017 was the lowest ever measured in the region (0.03 cm over October–December).

Mortality factors

Interpretation of our visual observations of seedling mortality agents is clearer for the first 2 years of the study (2014–2015), during which we made measurements every spring, summer, and fall, than for the last 3 years (2016–2018), during which we made measurements only in the fall. In the first 2 years, the majority (>90%) of seedling mortality was attributed to desiccation (visually observed dry seedlings), with minor amounts (<10%) of mortality from trampling by elk (*Cervus elaphus* Linnaeus, 1758), burial in the soil from gopher (Geomyidae Bonaparte, 1845) digging, and rodent herbivory. Observation of mortality factors was impossible for about half of the seedlings that died in the last 3 years of the study; tags were located, but only dried fragments, or no physical evidence, of seedlings remained. The dead seedlings we located had evidence of desiccation, base clipping, or top browse. Of the seedlings alive in fall 2018 over all BA levels, 43% had a reduction in height >0.5 cm between 2017 and 2018 and visual evidence of top-browse damage. Many of these browsed, living seedlings had resprouted shoots from lateral buds.

SWC

Drought in 2017 and 2018 caused unusually dry soil in all BA levels. Figure 5 shows temporal trends in SWC in four of the BA

levels ranging from the treatment with no overstory (0 $m^2 \cdot ha^{-1}$) to the densest overstory (unthinned). SWC in the nondrought years of 2015 and 2016 varied among wet in winter, drying in spring or early summer, and rewetting in late summer. In 2017, however, soil rewetting during late summer was less than in earlier years. Drying soil in fall 2017, during a period of near-zero precipitation and hot temperatures, led to the lowest SWC of the entire study period in late November 2017. The below-average precipitation of winter 2018 wetted the surface soil (15 cm) but failed to recharge deep (40 cm) soil water, resulting in an unusually long period of dry deep soil between late winter and summer 2018.

SWC at 40 cm is particularly relevant to understanding drought impacts on ponderosa pine seedlings given that their taproot can penetrate soil to a depth of 58 cm in the first growing season (Larson 1963). Stands with higher BA had drier deep soil (40 cm) during seasonally dry periods than stands with lower BA (Fig. 5). For example, between 2014 and 2016, SWC of deep soil in the 23 $m^2 \cdot ha^{-1}$ BA level (Fig. 5c) and unthinned level (Fig. 5d) dropped below 0.15 $m^3 \cdot m^{-3}$ every summer, whereas SWC of deep soil in the 0 (Fig. 5a) and 7 $m^2 \cdot ha^{-1}$ BA levels (Fig. 5b) was greater than 0.15 $m^3 \cdot m^{-3}$ between 2014 and 2016. In 2017, the 23 $m^2 \cdot ha^{-1}$ BA and unthinned levels had lower SWC in deep soil during the late-fall drought, and less recharge during late-summer rains, than the 7 $m^2 \cdot ha^{-1}$ BA level and, to a lesser extent, the 0 $m^2 \cdot ha^{-1}$ BA level.

Seedling growth

Seedling size differed among BA levels in some measurement years (Fig. 6). In fall 2015, the end of the second growing season after germination, the sample size of stand-level means used in the analysis was high ($N = 14$ stands), and each BA level was represented by at least two stands, except unthinned, which was represented by one stand. In fall 2015, seedlings in the unthinned level had the greatest height (Fig. 6a) but smallest stem diameter (Fig. 6b) compared with those in the other BA levels. Seedlings in all BA levels increased in size between fall 2015 and fall 2016, but seedlings in the 34 $m^2 \cdot ha^{-1}$ BA and unthinned levels did not survive beyond 2016. Sample size dropped further in fall 2017 to 13 stands, with all BA levels represented by two or three stands, except the 34 $m^2 \cdot ha^{-1}$ BA and unthinned levels, which were represented by one stand each. Significant differences (F test: $p < 0.05$) among BA levels occurred in fall 2017; height and diameter were highest in the 0 $m^2 \cdot ha^{-1}$ BA level and lowest in the 23 $m^2 \cdot ha^{-1}$ BA level. Seedling size was similar over BA levels in fall 2018 when overall sample size dropped to nine stands. Mean height decreased slightly in most BA levels between fall 2017 and fall 2018. This decrease in mean height was due to a reduction in height between 2017 and 2018 on 43% of the seedlings alive in fall 2018.

Fig. 4. (*a*) Proportion of normal precipitation and (*b*) deviation from mean normal air temperature between January 2014 and November 2018 for the study region. In panel *a*, text above the line is the proportion of surviving seedlings for the year preceding each fall measurement. Normals are shown by the horizontal line in each panel. Data were obtained from the National Weather Service, Flagstaff Pulliam Airport, Flagstaff, Ariz., USA.
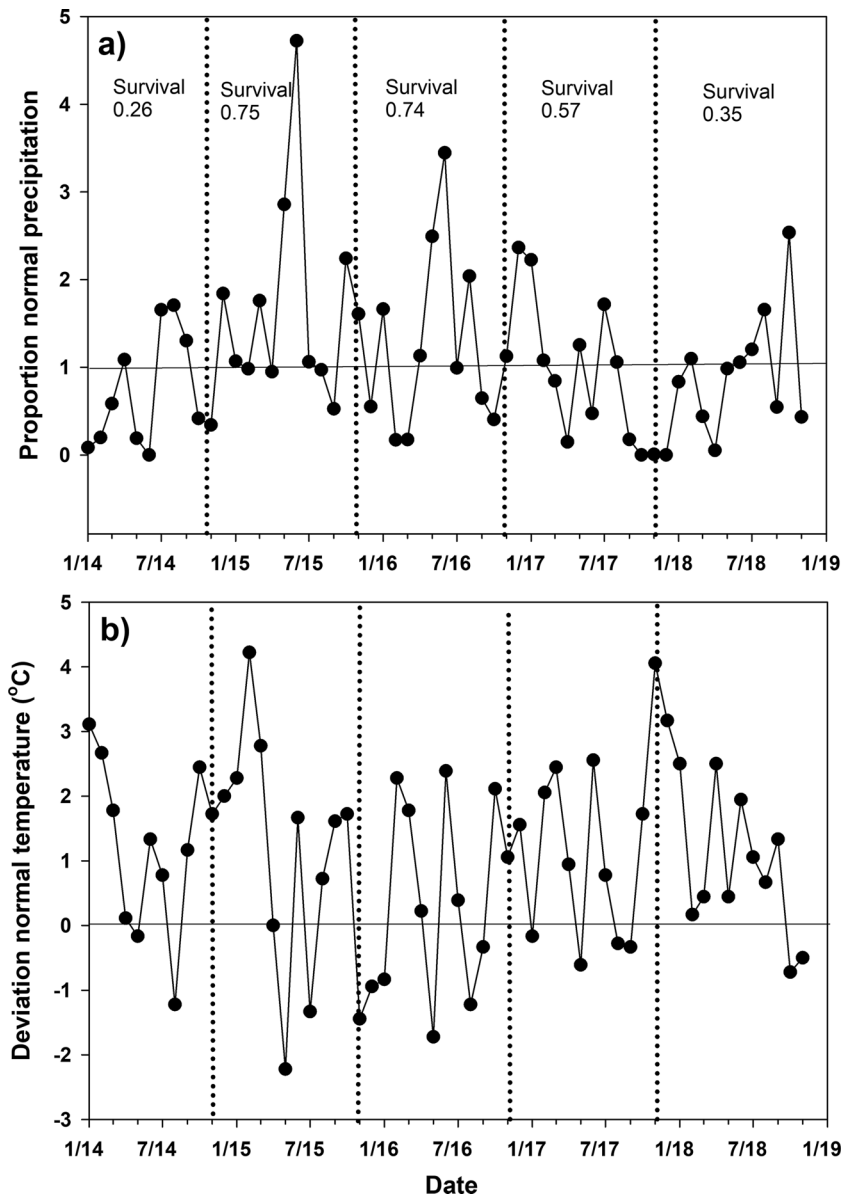
The mean decrease for these shrinking seedlings was 1.8 cm, supporting a role of top browsing in limiting height growth. Mean diameter did not change between 2017 and 2018 in the 14 and 23 m²·ha⁻¹ BA levels and increased about 1 mm in the 0 and 7 m²·ha⁻¹ BA levels (Fig. 6*b*).

Discussion

The 2013 regeneration pulse of ponderosa pine in northern Arizona produced many seedlings at our study site and across the region. Factors that drove this pulse appear to be similar to factors described for earlier regeneration events in northern Arizona. Similar to the 1919 regeneration event (Savage et al. 1996), a heavy cone crop occurred in fall 2012 (Kolb et al. 2016), which provided many seeds for germination in summer 2013. Also similar to the 1919 event, July precipitation in the germination year (2013) was extremely high (19 cm), tying the historical maximum that occurred in 1919. Early and ample summer precipitation is important for rapid germination and fast root development of ponderosa pine, which increases seedling resistance to frost heaving and drought (Schubert 1974). Above-average precipitation and cool temperature in the year of germination have been associated with pulses of ponderosa pine seedling establishment throughout the intermountain western United States (Petrie et al. 2016; Rother and Veblen 2017; Hankin et al. 2019).

Stand BA level strongly influenced the duration of seedling survival. Mean survival was shortest at 5 months in both the clearings (0 m²·ha⁻¹) and highest BA treatments (34 m²·ha⁻¹ and unthinned), intermediate at 12 months in the 7 and 14 m²·ha⁻¹ BA treatments, and longest at 16 months in the 23 m²·ha⁻¹ BA treatment. An earlier analysis found that second-year seedling survival at our study site was negatively associated with stand BA and positively associated with litter cover and SWC (Flathers et al. 2016). Low seedling survival in the herbaceous-dominated clearings in our study can be attributed to resource competition (Larson and

Fig. 5. Volumetric soil water content (SWC) at depths of 15 and 40 cm in BA levels of (*a*) 0, (*b*) 7, (*c*) 23, and (*d*) 66 (unthinned) m²·ha⁻¹ between May 2014 and November 2018. The horizontal line at 0.15 m³·m⁻³ is a reference to facilitate comparisons.
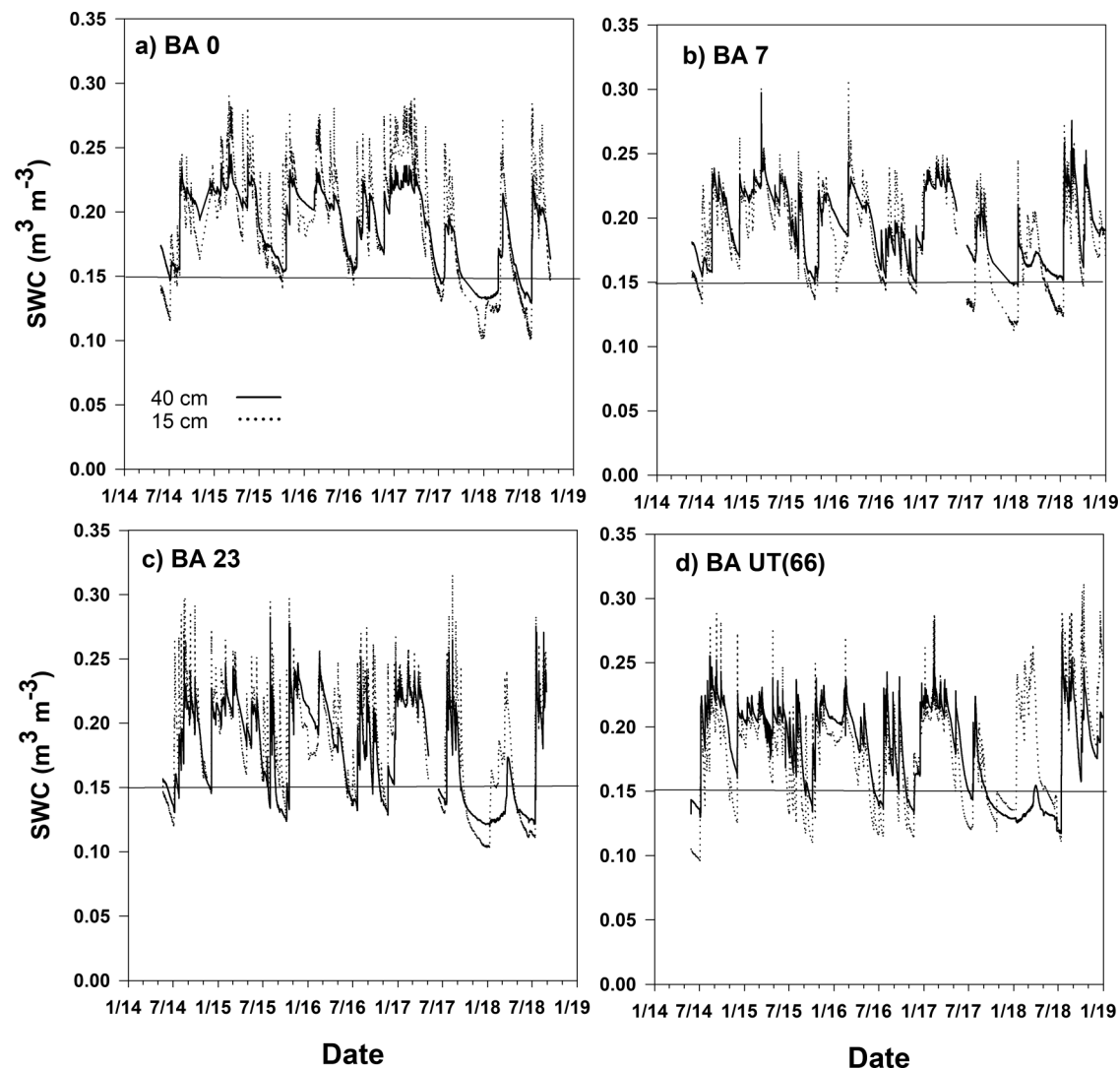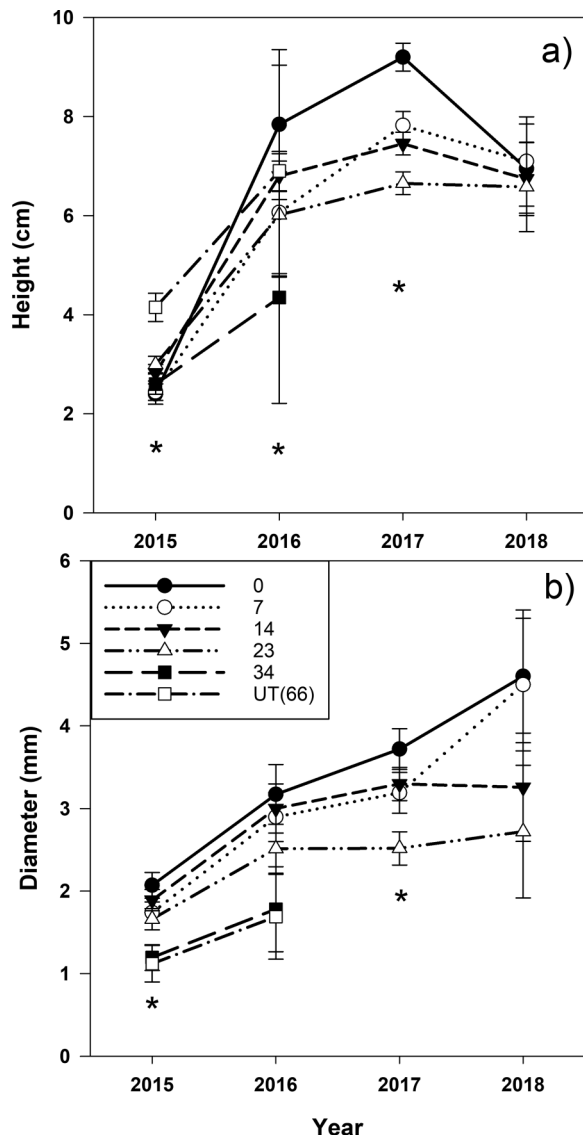

Schubert 1969; Long and Wagner 1992). Low seedling survival in stands with high tree BA can be attributed to resource competition with overstory trees, particularly for light, and to deep litter that prevents roots of new germinants from reaching mineral soil (Pearson 1940; Schubert 1974). The intermediate BA treatments in our study apparently promoted seedling survival by moderating resource competition and by having an intermediate amount of litter that acts as a mulch to limit evaporation of surface soil water.

Stand treatment effects on seedling survival and density in the first 2 years after germination continued through year 5. At the end of the second growing season (2015), all BA levels contained live seedlings, but survival and density were greater in the intermediate BA levels (7, 14, and 23 m²·ha⁻¹) than in the clearing (0 m²·ha⁻¹) and highest BA levels (34 m²·ha⁻¹ and unthinned). At the end of the fifth growing season, no seedlings survived in the highest BA levels; the last seedlings in these treatments died in year 4 during drought. The openings had only two live seedlings over all plots at the end of year 5, which scaled to 666 seedlings·ha⁻¹. Despite decreasing survival over time, the intermediate BA levels had between 2667 and 5667 seedlings·ha⁻¹ at the end of year 5. Our finding of ample ponderosa pine regeneration in intermediate BA levels produced by thinning is consistent

with recent reports for shelterwood cuts and fuel-reduction treatments in Colorado, United States (Shepperd et al. 2006; Francis et al. 2018). The low occurrence of seedlings in the openings in our study is perhaps surprising given that the openings are small (0.1–0.2 ha) and surrounded by seed sources from mature trees. Plenty of seeds should have been dispersed by wind into these small openings based on their close proximity to mature trees (Lentile et al. 2005). The openings, however, support a dense herbaceous community of bunchgrasses and forbs, which limit ponderosa pine seedling establishment by competition (Schubert 1974; Long and Wagner 1992).

The future of seedlings in the intermediate BA levels is unclear. Seedling density at the end of year 5 in the intermediate BA levels (2667–5667 seedlings·ha⁻¹) suggests that the 2013 cohort will be represented in the future overstory at intermediate BA levels based on current understanding of the amount of regeneration needed to produce a low-density multi-age stand (Mast et al. 1999; Bailey and Covington 2002; Reynolds et al. 2013), as well as a two-aged stand (Long 1996). Yet, the surviving seedlings had a mean height of only 7 cm in 5 years. Most surviving seedlings had no change in height, or lost height, between years 4 and 5 because of herbivory and drought. We expect mortality of these tiny seedlings to continue. Survival of ponderosa pine seedlings 5 or more

Fig. 6. Mean (± standard error) (*a*) height and (*b*) stem base diameter of ponderosa pine seedlings in six BA levels (m²·ha⁻¹) between fall 2015 and fall 2018. Asterisks (*) indicate dates with significant differences (*F* test: $p < 0.05$) among BA levels in Tukey honestly significant difference (HSD) comparisons.

ing which a combination of top-browse herbivory and drought constrained height growth.

Herbivory constrained seedling survival and growth well after germination. Herbivory by insects and rodents was a major source of mortality to young ponderosa pine seedlings in past investigations in northern Arizona (Schubert 1974; Stein and Kimberling 2003). Stein and Kimberling (2003) reported that herbivory from lepidopteran larvae was the second most important source of mortality to ponderosa pine seedlings in the year after germination, behind desiccation. The annual resolution of our observations in the last 3 years of the study prevents accurate estimation of herbivore impact on mortality; about half of the dead seedlings could not be located at tagged locations, suggesting that they were moved by herbivores, wind, or other unknown factors. Yet we observed evidence on the located dead seedlings of both desiccation and herbivory, including browsing of buds, leaves, and the upper stem. We also observed upper-stem browsing and a reduction in height on 4- and 5-year-old live seedlings. In live seedlings that lost height over the last 2 measurement years, the terminal bud and older leaves were often missing, yet the seedlings survived by forming new leaves from a lateral or dormant bud. The capacity of these stunted, browsed seedlings to develop into larger saplings is unresolved and needs more investigation.

Our results suggest that drought constrains seedling survival and growth. Our 5 years of measurements included a range of drought intensity. Year 1 was slightly wet (PDSI 1.24), and only 26% of seedlings survived between spring and fall over all BA levels. Young ponderosa pine seedlings typically have low survival in the first year after germination because of shallow roots that lead to desiccation (Stein and Kimberling 2003; Shepperd et al. 2006; Keyes et al. 2009) and high vulnerability to xylem hydraulic failure (Miller and Johnson, 2017). Seedling survival during the first year of our study was greater than that of Stein and Kimberling (2003), who reported no first-year survival of naturally germinated ponderosa pine seedlings in a northern Arizona forest in 1987. The next 2 years of our study were unusually wet (PDSI 3.32 in 2015 and 2.28 in 2016), and 75% of seedlings alive at the start of each year survived until fall. The last 2 years had unusually warm temperatures and moderate drought (PDSI −2.55 in 2017 and −2.27 in 2018), and survival decreased each year. In 2017, 57% of seedlings alive at the start of the year survived until fall over all BA levels; in 2018, only 35% of seedlings survived. Thus, seedling survival in years 2–5 was negatively associated with drought. This association is consistent with the results of manipulative experiments showing that reductions in soil water availability decrease establishment of ponderosa pine seedlings (Stein and Kimberling 2003; Pinto et al. 2012; Rother et al. 2015).

The low survival of older seedlings in years 4 and 5 of the study is surprising based on seedling age alone. The deeper roots of older seedlings should provide more drought resistance than those of younger seedlings, yet annual survival decreased as seedlings aged beyond year 3. Information about rooting depth of naturally regenerated ponderosa pine seedlings in the region of our study site is scarce beyond Larson's (1963) report that roots can grow to a depth of 58 cm in the first year. An explanation for the low survival of older seedlings in our study is that greater drought stress in years 4 and 5 was more important than the benefits of larger seedling size. SWC in summer of years 4 and 5 approached 0.10 m³·m⁻³, a level causing mortality of ponderosa pine seedlings grown in basalt-derived soils obtained near our study site in earlier experiments (Heidmann and King 1992). Water-release curves for these soils show a soil water potential of about −3 MPa at a water content of 0.10 m³·m⁻³ (Heidmann et al. 1990). Based on measurements of older ponderosa pine trees in northern Arizona, this water potential starts to cause xylem hydraulic failure due to cavitation (Koepke and Kolb 2013). Hydraulic failure is a likely mechanism of mortality for seedlings that died in our study during drought, highlighting the need for more information on cav-

years after germination is poorly understood, but high mortality has been reported through at least the first decade after germination (Shepperd et al. 2006). Ponderosa pine seedlings often grow slowly for decades. For example, naturally established ponderosa pine seedlings in northern Arizona can require up to 25 years to attain a height of 1.37 m (Puhlick et al. 2013).

The temporal pattern of differences in seedling size among BA levels was consistent for diameter but not height. Seedling diameter decreased with increasing BA level in all years and was greatest in the 0 and 7 m²·ha⁻¹ treatments at the end of year 5. Difference in seedling height among BA levels, however, shifted over time. Seedlings in the unthinned treatment were tallest in the first growing season, likely because of shade-induced etiolation, but this superiority was lost in year 2, and all seedlings in this treatment died by year 3. In year 4, height generally decreased with BA, and seedlings were tallest in the 0 m²·ha⁻¹ treatment. Differences in height among BA levels disappeared in year 5, dur-

itation vulnerability of very young seedlings (Miller and Johnson 2017). Moreover, dead seedlings frequently had evidence of both desiccation and herbivory, suggesting that seedling mortality in our study resulted from poorly understood interactions among hydraulic failure, carbon balance, and biotic resistance (Adams et al. 2017).

In summary, our results show a tortuous path of obstacles to ponderosa pine seedling establishment for a natural regeneration pulse in northern Arizona. A strong regeneration pulse at our study site, driven by the co-occurrence of ample seed supply with an extremely wet summer, was muted by subsequent extreme drought, showing the influence of interacting extreme events on regeneration. A seedling's fate over the first 5 years after germination depended on stand BA, drought intensity, and herbivory. The high mortality of 5-year-old seedlings shows that biotic and abiotic constraints to establishment occur for years after germination. More knowledge about constraints to seedling establishment is needed to refine efforts to control regeneration by forest management and to inform efforts to predict future regeneration during climate change.

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