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The aboveground and belowground growth characteristics of juvenile conifers in the southwestern United States

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Abstract. Juvenile tree survival will play an important role in the persistence of coniferous forests and woodlands in the southwestern United States (SWUS). Vulnerability to climatic and environmental stress declines as trees grow, such that larger, more deeply rooted juveniles are less likely to experience mortality. It is unclear how juvenile conifers partition the aboveground and belowground components of early growth, if growth differs between species and ecosystem types, and what environmental factors influence juvenile carbon allocation above- or belowground. We developed a novel data set for four juvenile conifer groups (junipers, piñon pines, ponderosa pines, firs; 1121 juveniles sampled, 221 destructively) in three height classes (<150 mm, 150–300 mm, and 300+ mm), across 25 SWUS sites. We compared growth characteristics across groups and height classes and related differences to climatic and environmental factors. As tree height increased from <150 mm to 300+ mm, belowground growth increased, root:shoot ratio declined, and specific leaf area declined for all conifers except firs. Maximum rooting depth was shallower than previous estimates (<~400 mm). Lower elevation juveniles were frequently located in sheltered microsites that provided high shading, whereas mid- and higher elevation juveniles were frequently unsheltered. Across all forest and woodland sites, herbaceous cover was positively correlated with aboveground growth. At study locations comprised of multiple sites, differences in aboveground growth were best explained by ecosystem type (piñon pine-juniper woodland, ponderosa pine forest, mixed-conifer forest) and local environmental variation. Our results indicate generally more belowground early growth and more aboveground later growth, but specific allocation patterns varied among ecosystem (greater proportional shoot growth at lower and mid-elevations compared with higher elevations). Juvenile conifers had similar magnitudes of proportional growth across conifer groups, displaying limited capacity to acclimate growth to differences in climate that control ecosystem type. If juvenile conifers also do not acclimate physiologically to their environment, our findings suggest that local environmental variation will play a primary role in regulating forest and woodland persistence and modify the effects of climate change in the SWUS.

Key words: Douglas fir; juniper; piñon pine; pinyon pine; ponderosa pine; regeneration; sapling; seedling; tree; white fir.

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INTRODUCTION

Dryland ecosystems dominated by coniferous trees encompass nearly 30% of global dryland landmasses (Bastin et al. 2017). In the southwestern United States (SWUS), these ecosystems range from lower elevation and relatively water-limited piñon pine-juniper woodlands, mid-elevation ponderosa pine forests that experience a wide range of environmental conditions, up to higher elevation mixed-conifer forests that are strongly influenced by snowpack dynamics and seasonal variation in energy limitation (Comer et al. 2003, Koehn et al. 2021). Forests and woodlands in the SWUS have been strongly influenced by disturbance over the past 60 yr, especially during periods of low precipitation, high temperatures, and the secondary disturbances including wildfire and insect outbreaks that are associated with these events (Allen et al. 2010, Cohen et al. 2016, Hicke et al. 2016, Stevens-Rumann et al. 2018). Although some climate change effects in the SWUS are uncertain, temperature is uniformly projected to continue rising throughout the 21st century (Collins et al. 2013, Hartmann et al. 2013), and weather variability is expected to continue to increase (Diffenbaugh et al. 2017). Future projections of precipitation are less certain (Collins et al. 2013), but the combination of increased temperature and enhanced weather variability alone will likely result in increased drought severity (Prein et al. 2017, Ukkola et al. 2018, Cook et al. 2020). Consequently, current trends in forest and woodland declines are likely to continue and perhaps intensify over the 21st century (van Mantgem et al. 2009, Thorne et al. 2018). Yet, even the most recent severe droughts in the SWUS have had varied effects on tree mortality due to local environmental heterogeneity (Breshears et al. 2009), and it follows that climate change effects to these ecosystems are likely to be heterogeneous and shaped by multiple factors that vary across fine spatial scales (Royer et al. 2012, Gleason et al. 2017, Xu et al. 2020). Better understanding of the interactive effects of these different factors, and the spatiotemporal scales over which they occur, is needed to anticipate the future persistence of forests and woodlands in the SWUS.

Research on forest and woodland persistence has focused predominantly on the effects of climate changes and associated disturbances on mature trees. An additional process with potentially broad implications affecting the persistence of forests and woodlands is declines in area suitable for tree regeneration both before (Puhlick et al. 2012, Petrie et al. 2017) and after severe stand disturbance (Redmond and Barger 2013, Davis et al. 2019). Regeneration is an episodic and multiyear process that involves successful seed production, seed germination, and seedling and sapling (juvenile, hereafter) survival to adulthood (Feddema et al. 2013, Savage et al. 2013, Petrie et al. 2017). The climatic and environmental requirements for juvenile conifer establishment differ from the requirements for the survival and health of mature trees (i.e., the regeneration niche; Grubb 1977), but fine-scale mechanistic information about juveniles is scarce because the episodic nature of regeneration proves difficult to integrate into forest and woodland monitoring programs. Regeneration has therefore received limited research attention until recently (Petrie et al. 2016, Kemp et al. 2019). Of the demographic stages of regeneration, juvenile tree survival in the years following germination likely imparts the strongest control of forest and woodland persistence (Johnson et al. 2011) and may be severely reduced as climatic conditions become even more restrictive in the future (Petrie et al. 2017, Davis et al. 2019, Hansen and Turner 2019). Indeed, regeneration success and failure are predicted to increasingly influence the persistence of forests and woodlands in landscapes both with disturbance (Redmond and Barger 2013, Davis et al. 2019) and without disturbance (Bell et al. 2014*a*, Petrie et al. 2017), as the occurrence of favorable climatic conditions for juvenile growth and survival declines over the next century.

Forecasts for declining forest and woodland persistence are limited by incomplete understanding of how juvenile survival varies within the understory microclimates where regeneration occurs, and how survival is shaped by juvenile tree growth and stress tolerance (Bell et al. 2014*a*, Kane et al. 2015, Hudson et al. 2018), despite recent research that has identified some abiotic (heat stress, moisture availability) and biotic (juvenile density, diameter growth) factors that may impact juvenile tree survival (Shriver et al. 2021).

In the years following germination, juvenile conifers are small (often <250 mm in height), are located close to the soil surface which is often hotter and drier than the surrounding environment, and have limited ability to influence their surroundings (Johnson et al. 2011). Juvenile mortality can therefore be initiated by many events including periods of high temperatures and reduced soil moisture (Kolb and Robberecht 1996), winter freezing and frost heaving (Oliver and Ryker 1990, Puhlick et al. 2012), herbivory (Pearson 1950, Vickers et al. 2019), and competition for light and soil resources (Elliott and White 1987, North et al. 2019). Juvenile conifers growing at lower elevations and/or warmer microclimates in particular have been found to exhibit lower specific leaf areas, slower growth rates, and invest more in root infrastructure as adaptive avoidance mechanisms of drought and temperature stress (Kerr et al. 2015, Dixit and Kolb 2020, Kolb et al. 2020). In contrast, those located at higher elevations and/or cooler microclimates exhibit variation in height, root collar diameter, and leaf area that maximize light acquisition and decrease competition for light with understory vegetation (Dixit and Kolb 2020). Thus, a tree's need to balance photosynthetic CO_2 uptake against potential water loss and soil resource availability is vital for survival and highly dependent on its local environment (Vance and Running 1985, Johnson et al. 2011). Yet, greater allocation of growth belowground may incur a cost of less leaf area that reduces whole-plant photosynthesis and the ability to compete for light, while greater allocation of growth aboveground may enhance vulnerability to evaporative moisture and temperature stress (Johnson et al. 2011, Simeone et al. 2018) that reduces the ability of juveniles to compete for water and soil nutrients (Schubert 1974, Plamboeck et al. 2008). Because most juvenile conifers die before adulthood, we expect juvenile growth characteristics—especially the partitioning of aboveground and belowground growth—to be influenced by environmental stressors such as water limitation (supporting greater belowground growth) or light limitation (supporting greater aboveground growth). In addition, variability in environmental conditions across the SWUS means that juvenile growth may differ between tree species that comprise major forest and woodland ecosystem types, and also between populations growing in different environments.

Declines of lower elevation piñon pine-juniper woodlands (although they may be expanding in other regions of the western United States: see Weisberg et al. 2007), mid-elevation ponderosa pine-dominated forests, and higher elevation mixed-conifer forests are expected in the SWUS (Rehfeldt et al. 2006, 2014*a*, Allen et al. 2010). Across the western United States, the future geographic range of these ecosystems may include northward movement and a contraction toward higher elevations when feasible (Rehfeldt et al. 1999, Bell et al. 2014*a*) and is expected to be increasingly shaped by post-disturbance reestablishment, especially following wildfire (Stevens-Rumann et al. 2018, Davis et al. 2019). Incorporation of the conditions required for successful regeneration improves estimates of current forest and woodland ranges produced by species distribution models (SDMs) for diverse ecosystems of the western United States, suggesting that analogous information for juvenile conifers could improve forecasts of ranges in the SWUS as well (Jackson et al. 2009, Bell et al. 2014*b*, Schlaepfer et al. 2015). Because growth characteristics can inform the types of environmental stress juvenile conifers experience, incorporation of these characteristics in SDMs through direct measurements of destructive sampling of growth characteristics or indirectly through the correlation of nondestructive sampling to growth characteristics may improve estimates of future regeneration. Specifically, we propose that by incorporating quantitative information on how different tree species and populations grow at early life stages through direct measurements or indirect correlations, and determining to what degree these characteristics are shaped by variation in environmental factors, it will be possible to enhance and expand legacy data sets that will ultimately refine understanding of where and under what conditions meaningful changes to regeneration-associated persistence are most likely to occur.

In this study, we assessed the growth characteristics of juvenile conifers and determined if and why their growth characteristics differed among conifer types and across environmental conditions. We quantified above- and belowground growth characteristics of seven coniferous tree species across 25 forest and woodland sites in the SWUS (*Juniperus monosperma*, *Juniperus osteosperma*, *Pinus edulis*, *Pinus monophylla*, *Pinus ponderosa*, *Abies concolor*, and *Pseudotsuga menziesii*). We organized these species into four groups (junipers, piñon pines, ponderosa pines, and firs; 1121 total juveniles sampled, 221 destructively). We selected sites to capture variation in regeneration, physiography, stand characteristics, elevation, and climate conditions. Our objectives were to: (1) determine if above- and belowground growth characteristics differed across conifer groups; (2) determine if within-group growth differed between tree size classes (<150 mm, 150–300 mm, 300+ mm height); (3) quantify the maximum rooting depth of juvenile conifers; (4) determine if height and root collar diameter field measurements can explain patterns of juvenile growth characteristics; and (5) investigate to what degree variation in growth characteristics was attributable to broad-scale, regional climate, and landscape factors that vary across the SWUS, vs. factors that vary across finer local scales. We hypothesized that differences in climate would impart the strongest control on juvenile growth characteristics, such that junipers and piñon pines at lower elevations would exhibit higher belowground proportional growth due to their need to access soil moisture in drier environments (Burns 1983, Meeuwig et al. 1990), whereas ponderosa pines and firs in higher elevation mixed-conifer forests with dense overstory canopy cover would exhibit higher aboveground proportional growth due to their need to access light (Oliver and Ryker 1990, Briggs et al. 2015, Cannon et al. 2019). We expected that these differences would be maintained across tree height classes, underscoring the sustained importance of resource limitation for juvenile conifers in these different environments, and supporting the conclusion that juvenile growth characteristics would largely be controlled by climatic factors and elevation across the SWUS.

METHODS

Site description and study site determination

Our research focused on three generalized ecosystem types in the SWUS: piñon pine-juniper woodlands (southern Nevada, northern New Mexico), ponderosa pine forests (northern Arizona, southern Colorado, southern Nevada, northern New Mexico), and subalpine mixed-conifer forests (southern Nevada, northern New Mexico; Fig. 1). Piñon pine-juniper woodland sites were located at lower elevations (1955–2459 m) and were dominated by either *Pinus edulis* (two-needle piñon pine) in AZ and NM or *Pinus monophylla* (single-leaf piñon pine) in NV, and by either *Juniperus monosperma* (oneseed juniper) in NM or *Juniperus osteosperma* (Utah juniper) in AZ and NV (Thompson et al. 1999, Cole et al. 2008, Rehfeldt et al. 2014*a*). Ponderosa pine forest sites were located at intermediate elevations (2173–2536 m) and were dominated by *Pinus ponderosa* var. *scopulorum* (Rocky Mountain ponderosa pine). At higher elevation mixed-conifer forest sites (2516–2776 m), dominant tree species included *Abies concolor* (white fir) and *Pseudotsuga menziesii* var. *glauca* (Rocky Mountain Douglas fir). Our study sites were located on moderate slopes (with the exception of some in southern NV) and exhibited a wide range of basal areas, canopy covers, and understory cover (cone densities, herbaceous, shrub, woody debris, litter; Appendix S1: Tables S1 and S2). Soils collected in the upper 10 cm at our study sites were of intermediate texture (sandy loam, sandy clay loam) and had a wide range in soil organic matter content (Appendix S1: Table S1).

Annual total precipitation in the southern portion of the SWUS (AZ, NM) is summer monsoon dominated, with a greater proportion of precipitation falling in the summer than winter (Barry and Chorley 1998). Winter is the primary season of precipitation in NV, with summer monsoonal rain events occurring episodically in some years (Blainey et al. 2007). Precipitation in the northern portion of the SWUS (CO) is more evenly distributed throughout the year (Whitlock and Bartlein 1993). Based on climate estimates from the Parameter-elevation Regressions of Independent Slopes Model (PRISM; https://prism.oregonstate.edu/), mean annual temperature (MAT: °C; 1980–2019) across our study sites ranged from 5.3 to 11.7°C and mean annual precipitation (MAP: mm; 1980–2019) ranged from 366 to 687 mm (Appendix S1: Table S1). Lower elevation piñon pine-juniper woodlands generally experienced higher MAT and lower MAP than other sites, and higher elevation mixed-conifer forests

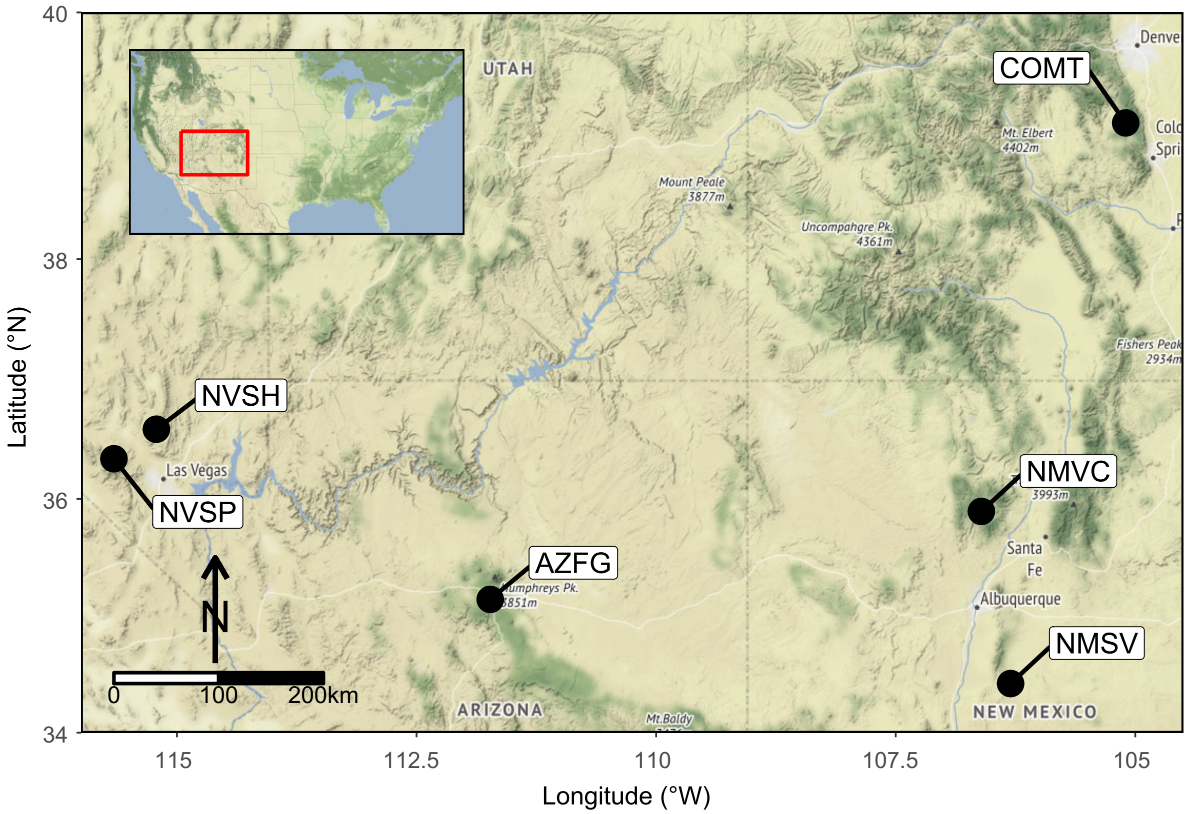

Fig. 1. Study area map including the location of six sampling locations in the SWUS including the Northern Arizona University Centennial Forest in Flagstaff, Arizona (AZFG), the Manitou Experimental Forest, Colorado (COMT), the Sevilleta National Wildlife Refuge and Mountainair, New Mexico (NMSV), Valles Caldera National Preserve, New Mexico (NMVC), the Desert National Wildlife Refuge Sheep Mountains, Nevada (NVSH), and the Humboldt-Toiyabe National Forest Spring Mountains, Nevada (NVSP).

experienced lower MAT and higher MAP (Appendix S1: Table S1). Forest and woodland ecosystems across the SWUS experience a broad range of climates, landscapes, and disturbance and management histories. Our study sites included a range of natural and human influences including experimental piñon pine girdling and induced mortality (NMSV-PJ-1), a bark beetle outbreak (NMSV-PJ-2), understory burning (AZFG-PP,1,2,3; COMT-PP-4), and experimental manipulations of stand structure to produce sites varying in forest density (COMT-PP-1,2,3; NVSP-PP-1; NVSP-MC-1).

We selected six locations to encompass a wide range of regional climate conditions. Within each location, we selected sites (25 total) to capture diversity in local factors expected to influence regeneration including topography, adult tree density, vegetation characteristics, management action, and disturbance (Appendix S1: Tables S1 and S2). Our sampling focused on characterizing the environment of each site, quantifying the density of living juveniles of each present species, and measuring the above- and belowground growth characteristics of a subset of juveniles using both nondestructive and destructive sampling. All study sites contained at least 1 living or dead juvenile conifer. Regeneration across our sites ranged from very low (NVSH-PJ-1: 7 juveniles) to very high (AZFG-PP-2: 700 juveniles; Table 1).

Plot design and site characterization

We conducted our study in the summer (June–August) of 2019. At each sampling site, we established a circular plot with a 5.0–20.0 m radius (Appendix S1: Fig. S1). For sites with very high

Table 1. Location, count, and microsite location of juvenile conifers across our 25 study sites and six sampling locations (AZFG, COMT, NMSV, NMVC, NVSH, and NVSP).

			Conifer group No. sampled (No. destructively)				Microsite	
Site	Latitude (°N)	Longitude (°W)	Juniper	Piñon	Ponderosa	Fir	Sheltered (%)	Unsheltered (%)
AZFG-PP-1	35.1467	111.731	–	–	324 (12)	–	21	79
AZFG-PP-2	35.1457	111.731	–	–	700 (12)	–	0	100
AZFG-PP-3	35.1447	111.7315	–	–	577 (12)	–	2	98
COMT-PP-1	39.1115	105.0877	–	–	37 (10)	–	0	100
COMT-PP-2	39.1118	105.0875	–	–	182 (8)	–	0	100
COMT-PP-3	39.1122	105.0871	–	–	21 (9)	1 (0)	0	100
COMT-PP-4	39.101	105.1130	–	–	0 (8)	–	–	–
COMT-PP-5	39.1009	105.1119	–	–	472 (8)	–	0	100
COMT-PP-6	39.1265	105.1136	–	–	102 (8)	–	2	98
NMSV-PJ-1	34.4455	106.2152	15 (4)	31 (8)	–	–	87.5	12.5
NMSV-PJ-2	34.4453	106.2155	11 (0)	40 (0)	–	–	84	16
NMSV-PJ-3	34.4371	106.2391	13 (2)	64 (10)	–	–	66	34
NMSV-PJ-4	34.368	106.5347	5 (4)	12 (8)	–	–	76.5	23.5
NMVC-PP-1	35.865	106.5962	–	–	48 (12)	1 (0)	0	100
NMVC-MC-1	35.9217	106.6159	2 (0)	–	1 (2)	30 (7)	51.5	48.5
NVSH-PJ-1	36.5725	115.2043	–	7 (0)	–	–	86	14
NVSH-PJ-2	36.59	115.2137	8 (0)	103 (0)	–	–	56	44
NVSH-PJ-3	36.5939	115.2263	–	13 (0)	–	–	92	8
NVSP-PJ-1	36.3806	115.6116	14 (3)	59 (9)	–	–	90	10
NVSP-PJ-2	36.3723	115.6281	15 (4)	120 (8)	–	–	83	17
NVSP-PP-1	36.3093	115.6877	–	–	8 (3)	4 (5)	11	89
NVSP-PP-2	36.3327	115.664	–	40 (12)	–	–	88	12
NVSP-MC-1	36.3172	115.6797	–	–	6 (1)	75 (11)	56	44
NVSP-MC-2	36.3179	115.6814	–	–	8 (2)	89 (7)	15	85
NVSP-MC-3	36.3331	115.6510	0 (1)	–	1 (2)	65 (9)	5	95
		Tree totals	83 (18)	489 (55)	2487 (109)	265 (39)		

Notes: Tree counts include all juveniles in each study site, and the number of destructively sampled juveniles in parentheses. The percentage of juveniles in sheltered and unsheltered microsites was calculated from a subset of up to 48 field-measured juveniles at each site. COMT-PP-4 was a burned area with no within plot juveniles, so destructively sampled individuals were obtained from a nearby location outside the plot boundary. We did not destructively sample juveniles at NVSH due to low regeneration.

juvenile density, we used a 5 m plot radius. For sites with lower density, we increased the plot radius outwards from 5 m in increments of 2.5 m until plots contained approximately 100 juvenile conifers, reached a maximum radius of 20 m, or was restricted by physiographic features (e.g., cliff edges, change in slope exceeding >~20°). We subdivided each plot into four quadrants along North-South and East-West transects, and located 4, 1-m^2 quadrats evenly along each transect (eight total; Appendix S1: Fig. S1). Measurements made across the entire circular plot (i.e., plot measurements) included elevation (m), slope (°), aspect (°), basal area with a 10-factor prism (m^2/ha), and canopy cover using a concave spherical densiometer (%). Measurements made in each of the four quadrants (i.e., quadrant measurements) included adult and juvenile tree count (no. of individuals), physical soil characteristics from 0 to 10 cm, and four volumetric soil moisture measurements in the upper 12 cm of mineral soil (%; HydroSense II, Campbell Scientific, Inc., Logan, UT, USA). Measurements made in each of the eight quadrats (i.e., quadrat measurements) included conifer cone density on the forest floor (no./m^2), woody and herbaceous vegetation cover (%), litter cover (%), and litter depth (O horizon; cm).

To measure soil texture and soil organic carbon concentration (SOC: %), we collected soil samples in the upper 10 cm of soil (four samples per site). We ground and sieved soil in the laboratory to <710 μm and used the sedimentation soil particle size analysis of Bouyoucos (1962) to determine soil texture. We estimated SOC using loss on ignition (LOI), where 5 g of soil collected from each site was heated at 100°C for 24 h, weighed, then heated in a muffle furnace at 450°C for 6 h, and weighed again (Abella and Zimmer 2007).

Juvenile survey and nondestructive sampling of growth characteristics

We sampled the height (mm), root collar diameter (mm), and microsite location (visually determined to be sheltered or unsheltered by near-surface features including woody debris, large rocks, and near-surface tree and shrub canopies that provided high shading) of juvenile conifers at each study site (up to 12 trees in each plot quadrant, 48 maximum per site). In total, we measured 900 juveniles (64 junipers, 284 piñon pines, 395 ponderosa pines, and 157 firs; Table 1). We organized field-measured juveniles by tree group (junipers, piñon pines, ponderosa pines, firs) and by tree height (<150 mm, 150–300 mm, 300+ mm). We counted any remaining trees but did not measure them (3324 total counted).

Destructively sampled juvenile growth characteristics

We destructively sampled 8–12 juvenile conifers at each site located near and outside of plot boundaries, except sites with sparse regeneration (NVSH-PJ-1,2,3). Destructive sampling totaled 221 juveniles (18 junipers, 55 piñon pines, 109 ponderosa pines, and 39 firs; Table 1). We marked the location of the root collar where it met the soil surface on each tree to separate the aboveground stem and belowground roots, and then excavated it from the soil surface until the main taproot was <1 mm in diameter, or the taproot was broken. Once excavated, we measured the diameter of the excavated root from the root collar to the end of the taproot in 1 cm increments to determine how root diameter tapered along the length of the root (we used the mean of two measurements taken at each 1 cm increment with a 90° rotation to account for variation in root shape). We measured the diameter of lateral roots at their intersection with the main taproot using the same methodology, but did not excavate lateral roots because it was often necessary to break them to completely excavate the main taproot and to minimize soil disturbance.

We estimated the maximum rooting depth of each destructively sampled tree individually based on the relationship between incremental root diameter and root length. We approximated a minimum root diameter for all juveniles at three diameters (0.5 mm, 0.75 mm, 1.0 mm), which corresponded to the minimum root diameter from juveniles with roots that were completely excavated. To better understand the relationships between taproot length and taproot diameter across tree groups and height classes, we evaluated four diameter-length fit equations for each individual tree (Appendix S1: Table S3). We determined the best fit equation for each height class and conifer type by evaluating the R^2 statistic (highest average), root mean squared error (RMSE; lowest average), and proportion of trees with a significant P-value ($P \leq 0.05$; highest proportion of equations) for each of the four fit equations. This method determined the equation that provided the best approximation of root diameter and root length across the entire root profile (Appendix S1: Table S3). Additionally, we evaluated the difference between destructively sampled root diameters and fit equation estimates at the three minimum root diameters (0.5 mm, 0.75 mm, and 1.0 mm) to determine the fit equation that converged most accurately to root length by having the lowest average error (Appendix S1: Table S3). Since we could not fully excavate most juveniles to 0.5 mm diameter, using three diameters allowed us to increase our sample size and provide greater confidence in our estimation of maximum rooting depth.

For each destructively sampled tree, we measured the leaf, stem, and root proportions by dry weight (g) and area (cm^2) and calculated specific leaf area (SLA: cm^2/g) for each tree as photosynthetic leaf area divided by leaf weight. We calculated root:shoot ratios by weight and by area. For area measurements, we used the leaf area analysis protocol of Glozer (2008) with CanScan LiDE 300 generated images. To prepare destructively sampled juveniles for image analysis, we separated photosynthetic leaves from the stem and cut roots at the root collar. Samples were dehydrated in a VWR High-Performance Horizontal Air Flow Oven at 50°C for 72 h. Many analyses of leaf area use undried samples (Gonzalez-Benecke et al. 2018, Hudson et al. 2018), but this was not feasible for the large number of samples in our study due to the time required to process them, and we therefore analyzed oven-dried samples. Comparison of undried and dried leaf area from a separate set of juvenile conifers showed a mean difference of 31 ± 2.5% between undried and dried samples. We increased leaf area values by 31% to account for this difference.

Juvenile tree ring counts

We cut a cross section of each destructively sampled tree at the soil surface end of the aboveground stem, and hand sanded the cross section with up to 2000 grit sandpaper. We examined and hand counted rings under a dissecting microscope. Juniper ring counts were most uncertain due to commonly formed absent and false rings, especially in summer monsoon-dominated landscapes like much of the SWUS (Derose et al. 2016). At some sites (such as AZFG), tree rings corresponded to known regeneration years (2012–2013), whereas at other sites, they were difficult to ascertain and highly variable. We therefore quantified relationships between ring count and height and diameter, but did not focus on age differences in our analysis. Further research focused on juvenile age and ring counts is needed before ring counts can be used to accurately pinpoint germination years (see Hankin et al. (2019) for analysis of ponderosa pine and Douglas fir).

Height class determination and analysis

Our analyses focused on juvenile growth characteristics between different tree groups (junipers, piñon pines, ponderosa pines, firs), different height classes (<150 mm, 150–300 mm, 300+ mm), and different environments. Our analyses of juvenile height, diameter, and growth ratio were conducted for field-measured juveniles, and all other analyses were conducted for destructively sampled juvenile trees. We did not combine field-measured and destructively sampled data (except when comparing the variation in height and diameter between microsite locations) because we prioritized smaller individuals in our destructive sampling. In cases where <7 juvenile conifers of the same group were in a single height class (300+ mm, for example), we added these samples to the lower height class for analysis (150–300+ mm) or did not include these classes in our statistical analysis when we deemed it inappropriate (e.g., a case where adding 300+ mm samples to the 150–300 mm group would result in erroneous significance). We did not destructively sample any fir juveniles >300 mm in height.

We conducted an analysis to determine linear relationships between the height and root collar diameter of destructively sampled juveniles (independent variables) and their above- and belowground growth characteristics (dependent variables). When significant ($P \leq 0.05$), we report these relationships and used them to estimate the minimum and maximum values of growth characteristics of field-measured juveniles (Appendix S1: Tables S4–S7). We forced these equations through the origin when linear regression equations estimated negative values at very low height and diameter.

To evaluate the relative growth of juvenile trees between our study sites, we calculated the relative height ratio and relative diameter ratio of each tree as its measured value divided by the mean value of all individuals of the same tree group in the same height class pooled across sites. This provides a ratio scale measure of how much taller or larger trees were at a site compared with all other sites, while accounting for differences in the composition and size of juvenile trees.

Statistical analysis

We determined significant differences in the mean of growth characteristics as well as relative height and diameter ratios using one-way analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) test ($P \leq 0.05$). We used the statistical program R for all analyses and created figures using the packages *ggplot2* and *corrplot* (Team 2019). In all boxplots, error bars represent the minimum and maximum values above and below the lower (Quartile 1 − (1.5·interquartile range)) and upper fences (Quartile 3 + (1.5·interquartile range)), respectively.

RESULTS

Aboveground growth characteristics

Significant linear correlations occurred among height, root collar diameter, and tree ring number ($P < 0.01$; Fig. 2). We note that the absolute

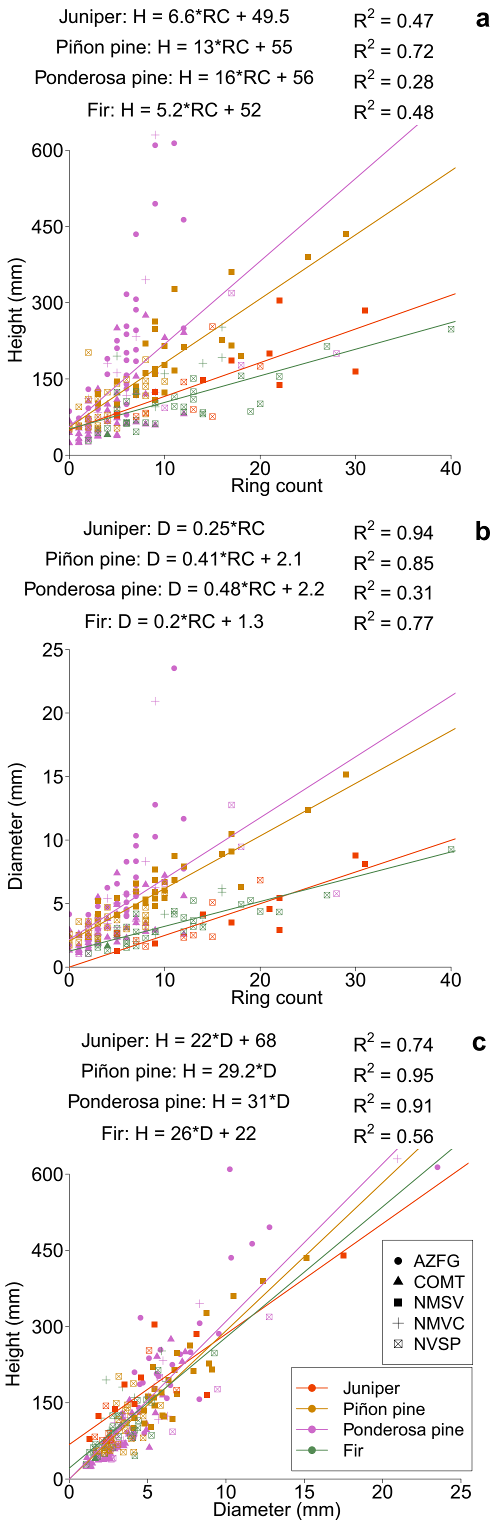

Fig. 2. Linear correlations between juvenile conifer ring number and juvenile height (mm; Panel a), ring number and root collar diameter (mm; Panel b), and root collar diameter and height (mm; Panel c) for juniper, piñon pine, ponderosa pine, and fir tree groups. All correlations are significant at $P < 0.01$.

tree ring number is somewhat uncertain for individuals with >10 rings (we approximated an average uncertainty of 1–3 rings for many of these trees). All junipers had uncertain ring numbers. The slope of tree height–diameter relationships was similar for all tree groups and was most highly correlated for piñon pines and ponderosa pines ($R^2 = 0.95$ and 0.91, respectively; Fig. 2). Firs had a lower slope of ring-height and ring-diameter relationships compared with other tree groups (Fig. 2a, b) and had the lowest height–diameter correlation ($R^2 = 0.56$; Fig. 2c).

The height and root collar diameter of juvenile conifers increased significantly from the smallest (<150 mm) to largest (300+ mm) height class (Fig. 3, Table 2). Generally, junipers and piñon pines were significantly taller and larger in diameter than ponderosa pines and firs within each height class (Fig. 3). We did not observe consistent differences in diameter between juvenile trees in sheltered vs. unsheltered microsites (Fig. 3). However, juveniles located in unsheltered microsites (resulting in high shading) were significantly taller than those in sheltered microsites in two instances (150–300 mm piñon pines, <150 mm firs; Fig. 3c, g), and juveniles located in unsheltered microsites were significantly larger in diameter than those in sheltered microsites in four instances (150–300 mm junipers, 150–300 mm and 300+ mm piñon pines, 300+ mm firs; Fig. 3b, d, h). We observed one instance where sheltered juveniles were taller than unsheltered juveniles (<150 mm firs; Fig. 3g).

Piñon pine and ponderosa pine SLA declined significantly with increasing tree height ($P \leq 0.05$), but SLA did not change significantly for firs (Fig. 4, Table 2). Junipers showed a similar pattern of decreasing SLA between the <150 mm and 150–300 mm height classes, but SLA increased when juveniles were 300+ mm tall. Piñon pines and firs had significantly higher SLA

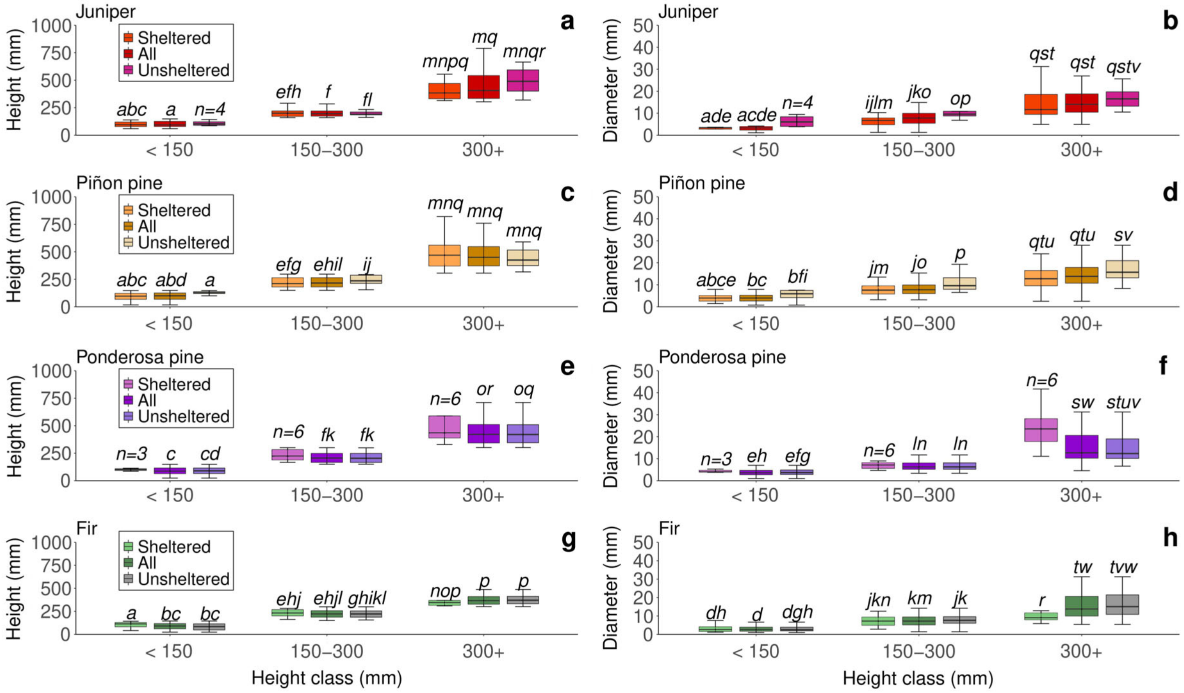

Fig. 3. Boxplots illustrating significant differences in juvenile conifer height (Panels a, c, e, g) and root collar diameter (Panels b, d, f, h) between height classes (<150, 150–300, 300+ mm) of juniper, piñon pine, ponderosa pine, and fir tree groups. Analysis includes all juvenile trees (field-measured and destructively sampled), juvenile trees in sheltered microsites providing high shading (field-measured), and juvenile trees in unsheltered microsites (field-measured). Letters indicate significant differences ($P \leq 0.05$, Tukey's HSD test) among all boxes and panels.

than junipers and ponderosa pines at <150 mm height, whereas firs had significantly higher SLA at 150–300 mm (Fig. 4). We did not estimate the range of SLA values for field-measured juveniles because neither height nor diameter was significantly correlated to SLA. Instead, leaf mass and leaf area can be estimated from their relationships with tree height and diameter (Appendix S1: Fig. S2).

Belowground growth characteristics

Root mass and root area increased significantly across height classes (Fig. 5, Table 2). Piñon pines had significantly higher root mass than ponderosa pines and firs at <150 mm height, higher root mass than ponderosa pines 150–300 mm, and higher root area than all other tree groups <150 mm height ($P \leq 0.05$; Fig. 5). Ponderosa pines <150 mm height had significantly higher root mass than firs (Fig. 5).

Log-functions provided the most accurate fit of juvenile taproot diameter (Appendix S1: Fig. S3, Table S3). Third-order polynomial functions provided the best estimates of maximum rooting depth for all tree groups at <150 mm height, and 2nd-order polynomial functions provided the best estimates of maximum rooting depth at 150–300 and 300+ mm height (Table 3, Appendix S1: Table S3). Using these equations and a minimum root diameter of 0.5 mm, we estimated that maximum rooting depth significantly increased with height for piñon pines and ponderosa pines (Fig. 6, Table 2). At <150 mm height, ponderosa pines had significantly shallower maximum rooting depth than other tree groups ($P \leq 0.05$), but maximum rooting depth was similar across tree groups for all other height classes (Fig. 6).

Proportional aboveground and belowground growth

Root:shoot ratios calculated by weight and by area decreased significantly between <150 mm

Table 2. Mean and standard deviation of growth characteristics for destructively sampled juniper, piñon pine, ponderosa pine, and fir juvenile trees, organized into three height classes (<150 mm, 150–300 mm, 300+ mm).

Conifer group	No.	Height class (mm)	Height (mm)	Diameter (mm)	Ring count (No.)	Specific leaf area (cm^2/g)	Root mass (g)	Root area (cm^2)	Rooting depth (mm)	R:S weight	R:S area
Juniper	10	<150	103.6 ± 30.9	2.4 ± 0.8	11.0 ± 5.3	47.4 ± 8.5	0.7 ± 0.8	7.1 ± 3.2	307.3 ± 155.3	0.9 ± 0.8	0.3 ± 0.2
	6	150–300	210.7 ± 47.7	6.2 ± 2.1	22.3 ± 6.7	27.8 ± 7.2	3.5 ± 2.2	109.7 ± 210.1	303.1 ± 119.14	0.4 ± 0.2	0.3 ± 0.2
	2	300+	372 ± 96.2	11.5 ± 8.5	22.0	107.5 ± 122.7	20.7 ± 26.4	47.7 ± 39.7	344.0 ± 81.7	0.5 ± 0.2	0.08 ± 0.07
Piñon	36	<150	97.1 ± 33.3	3.7 ± 1.3	4.4 ± 2.9	91.3 ± 15.3	0.8 ± 0.6	9.1 ± 4.7	227.8 ± 117.5	0.9 ± 0.4	0.2 ± 0.2
	15	150–300	201.5 ± 31.3	6.3 ± 1.7	10.4 ± 4.1	67.1 ± 10	2.4 ± 1.3	20.1 ± 9.4	305.6 ± 99.5	0.5 ± 0.2	0.1 ± 0.05
	4	300+	387 ± 45.9	11.7 ± 2.7	20.5 ± 8.1	51.9 ± 6.8	10.8 ± 6.2	49.3 ± 26.3	261.0 ± 219.1	0.3 ± 0.1	0.05 ± 0.03
Ponderosa	73	<150	73.1 ± 31.3	3.0 ± 1.2	3.6 ± 2.5	82.2 ± 16.1	0.3 ± 0.4	5.8 ± 4.4	145.6 ± 68.4	0.6 ± 0.3	0.2 ± 0.1
	25	150–300	210.6 ± 38.6	6.2 ± 1.5	8.0 ± 5.2	69.4 ± 9.9	1.6 ± 1.3	18.3 ± 6.7	278.1 ± 106.4	0.4 ± 0.2	0.1 ± 0.1
	10	300+	453.5 ± 130.6	12.3 ± 5.8	9.5 ± 3.2	61.7 ± 11.7	8.9 ± 11	41.7 ± 24	367.9 ± 83	0.3 ± 0.2	0.09 ± 0.08
Fir	30	<150	81.3 ± 28.1	2.8 ± 1.1	8.5 ± 4.6	90.5 ± 16.3	0.5 ± 0.4	6.1 ± 2.4	226.7 ± 112.3	0.9 ± 0.3	0.2 ± 0.1
	10	150–300	190.4 ± 37.6	5.1 ± 1.9	18.1 ± 9.8	88.5 ± 22.7	2.4 ± 2.3	17.2 ± 12.3	322.1 ± 160.4	0.7 ± 0.3	0.2 ± 0.1

Notes: Growth characteristics include juvenile height (mm), root collar diameter (mm), ring count (No.), specific leaf area (cm^2/g), root mass (g), root area (cm^2), rooting depth (mm), root:shoot ratio by weight, and root:shoot ratio by area. Maximum rooting depth was estimated from equations developed in this work (see Table 3).

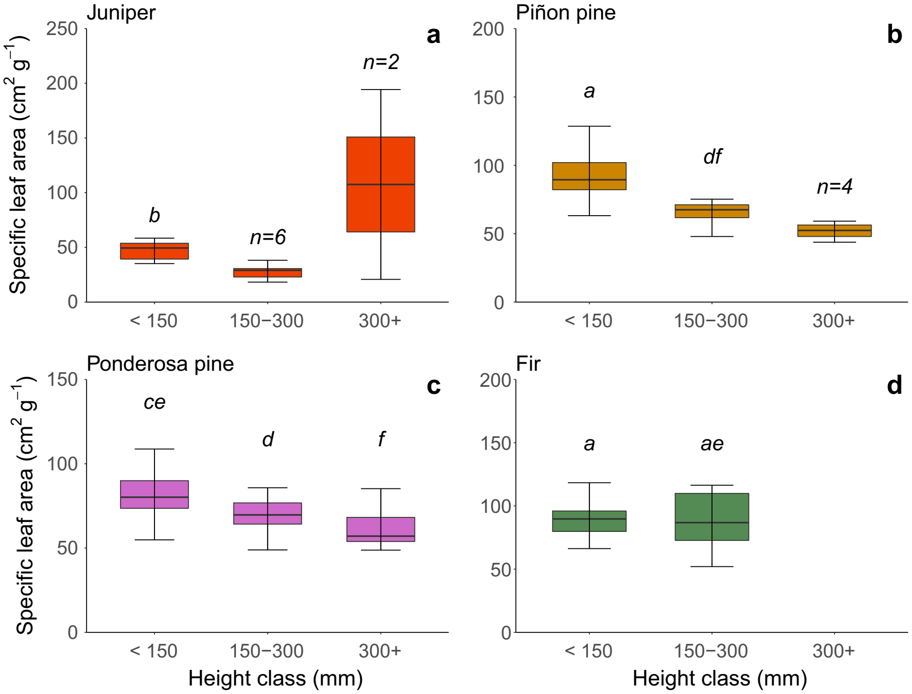

Fig. 4. Boxplots illustrating significant differences in specific leaf area (SLA: cm^2/g) between height classes (<150, 150–300, 300+ mm) of juniper (Panel a), piñon pine (Panel b), ponderosa pine (Panel c), and fir (Panel d) tree groups. Analysis includes destructively sampled juvenile trees. Letters indicate significant differences ($P \leq 0.05$, Tukey's HSD test) among all boxes and panels. The y-axis scale differs between panels for visualization of significant differences.

and 150–300 mm height classes, but did not decline further at 300+ mm height (Fig. 7, Table 2). At <150 mm and 150–300 mm height, firs had significantly higher root:shoot ratio by weight than piñon pines and ponderosa pines, and at <150 mm height, piñon pines had significantly

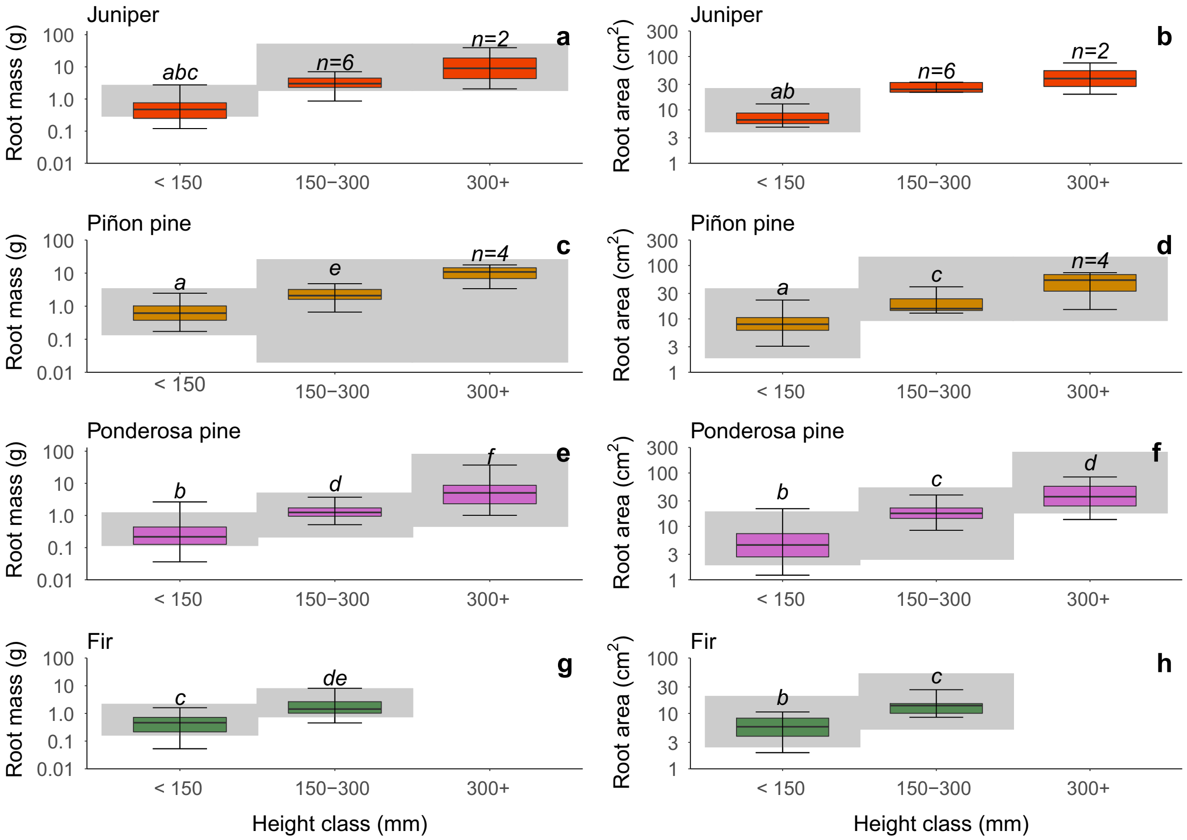

Fig. 5. Boxplots illustrating significant differences in root mass (g; Panels a, c, e, g) and root area (cm^2; Panels b, d, f, h) between height classes (<150, 150–300, 300+ mm) of juniper, piñon pine, ponderosa pine, and fir tree groups. Root mass and root area axes are in log scale. Analysis includes destructively sampled juvenile trees, and the estimated potential range of these values for field-measured juvenile trees is illustrated by gray boxes. Letters indicate significant differences ($P \leq 0.05$, Tukey's HSD test) among all boxes and panels. The y-axis scale differs between panels for visualization of significant differences.

Table 3. Summary of 3rd-degree (trees <150 mm in height) and 2nd-degree (150–300+ mm) polynomial equations determined to best estimate maximum rooting depth as a function of root collar diameter [d: mm] for destructively sampled juvenile conifers.

Height class (mm)	*n*	Equation	Root diameter (mm)	Mean max root depth (mm)		Mean error (mm)
				Field	Equation	
<150	**48**	$\mathbf{depth = -0.9 \cdot d^3 - 40.2 \cdot d^2 + 175.1 \cdot d - 214.4}$	**0.5**	**133.1 ± 61.1**	**137 ± 60.7**	**−3.9 ± 14.8**
	90	$\text{depth} = -8.4 \cdot d^3 - 10 \cdot d^2 + 148.4 \cdot d - 228.7$	0.75	122.9 ± 61.2	126.6 ± 60	−3.7 ± 16.3
	122	$\text{depth} = -6.9 \cdot d^3 - 5.4 \cdot d^2 + 134.7 \cdot d - 234.1$	1	106.1 ± 56.8	111.8 ± 57.6	−5.7 ± 15.5
150–300+	**8**	$\mathbf{depth = -13.1 \cdot d^2 + 132.5 \cdot d - 351.1}$	**0.5**	**291.3 ± 67.7**	**288.1 ± 64.7**	**3.2 ± 29.3**
	15	$\text{depth} = -11.7 \cdot d^2 + 124.9 \cdot d - 320.2$	0.75	229.3 ± 72.2	233 ± 62.6	−3.7 ± 21.8
	30	$\text{depth} = -10.5 \cdot d^2 + 116.3 \cdot d - 322.7$	1	212.3 ± 63.6	216.9 ± 56.1	−4.6 ± 21.3

Notes: Results are presented for comparisons of field-measured and estimated maximum rooting depth for three minimum root diameters (0.5, 0.75, 1.0 mm). Equation accuracies are the mean and standard deviation of differences (error) of observed minus estimated maximum rooting depth. Positive rooting depth error indicates underestimation (shallower than observed) of rooting depth equations and negative error indicates overestimation (deeper than observed) of rooting depth equations. Recommended equations are illustrated in bold.

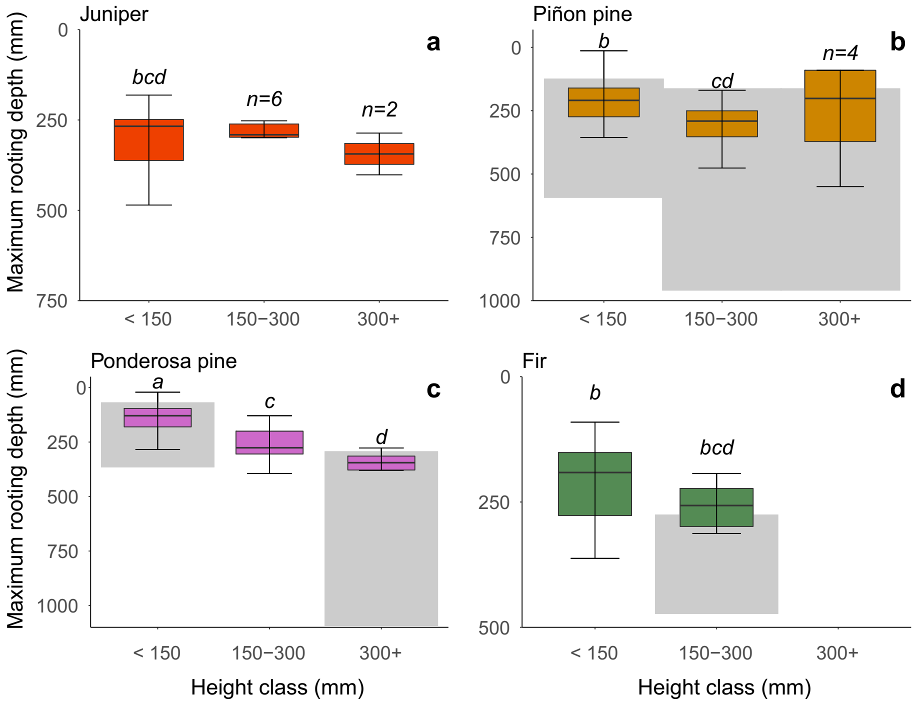

Fig. 6. Boxplots illustrating significant differences in estimated maximum rooting depth (mm) between height classes (<150, 150–300, 300+ mm) of juniper (Panel a), piñon pine (Panel b), ponderosa pine (Panel c), and fir (Panel d) tree groups. Analysis includes destructively sampled juvenile trees, and the estimated potential range of these values for field-measured juvenile trees is illustrated by gray boxes. Maximum rooting depth was estimated using 3rd-order polynomial functions (<150 mm) and 2nd-order polynomial functions (150–300 mm and 300+ mm, respectively). Letters indicate significant differences ($P \leq 0.05$, Tukey's HSD test) among all boxes and panels. The *y*-axis scale differs between panels for visualization of significant differences.

higher root:shoot ratio by weight than ponderosa pines ($P \leq 0.05$; Fig. 7). We did not observe significant differences in root:shoot ratio by area between different tree groups within each height class (Fig. 7).

Estimates of growth characteristics from tree height and diameter

We provide estimates of the above- and belowground growth characteristics of conifer groups from their linear correlation with height and diameter ($P \leq 0.05$; Fig. 8, Appendix S1: Fig. S4, Tables S4–S7). Junipers had the lowest number of significant correlations (Fig. 8, Appendix S1: Fig. S4). Diameter was a better predictor of growth characteristics than height was (6 vs. 9 insignificant correlations respectively), and rooting depth was the least correlated growth characteristic (Fig. 8, Appendix S1: Fig. S4).

Environmental factors associated with growth

At lower elevations, juvenile conifers were frequently located in sheltered microsites, and at mid- and higher elevations, juveniles were frequently located in unsheltered microsites (Table 1). 10 of our 25 study sites had significantly different growth ratios (Fig. 9a, c). We did not find a significant relationship between elevation and growth ratios. Instead, herbaceous cover was positively correlated to relative height ratio across our study sites ($R^2 = 0.25$, $P = 0.007$; Fig. 9b). Differences in relative height ratio and relative diameter ratio may have been more strongly associated with site-level variation within a single study location. At COMT, higher relative height ratio (COMT-PP-6) was associated with lower basal area, lower litter depth, higher SOC concentration, and higher clay content, and higher relative diameter ratio (COMT-PP-1) was

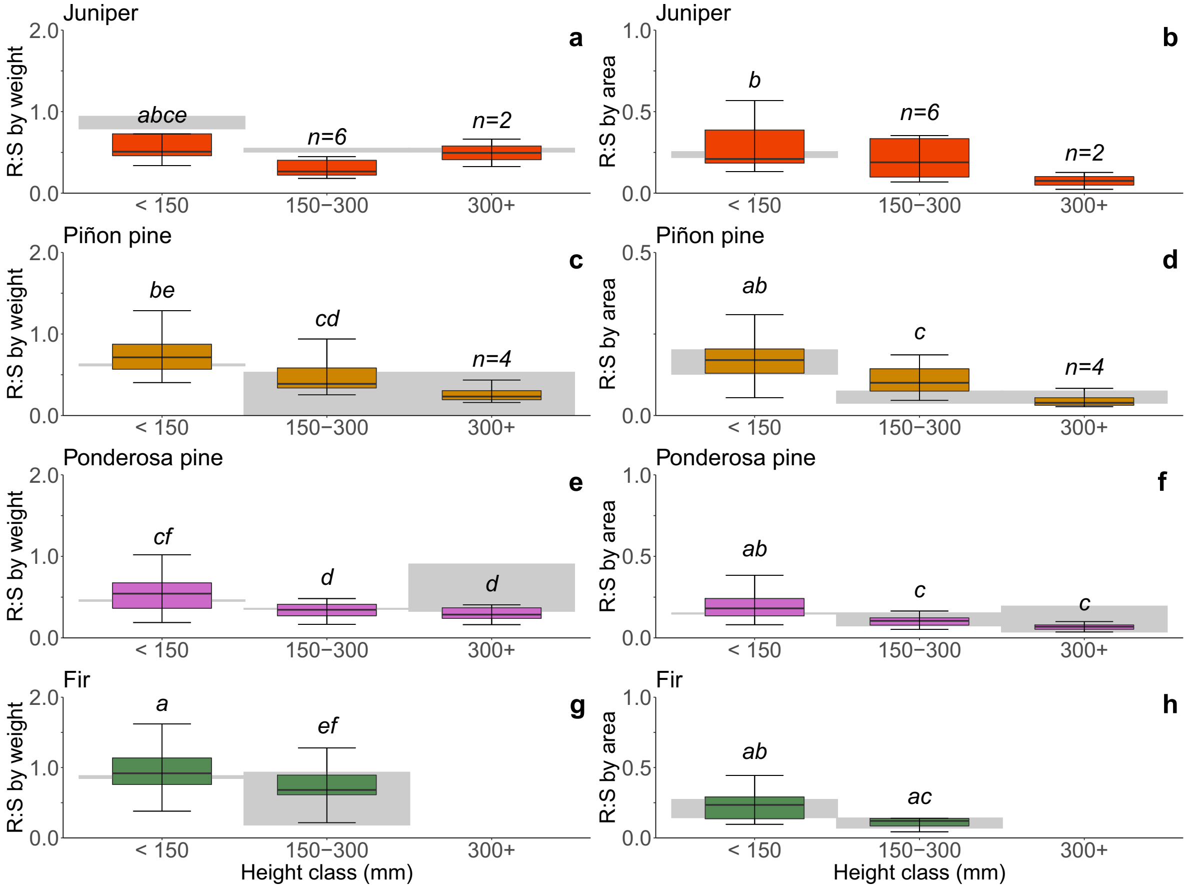

Fig. 7. Boxplots illustrating significant differences in root:shoot ratio by weight (Panels a, c, e, g) and area (Panels b, d, f, h) between height classes (<150, 150–300, 300+ mm) of juniper, piñon pine, ponderosa pine, and fir tree groups. Analysis includes destructively sampled juvenile trees, and the estimated potential range of these values for field-measured juvenile trees is illustrated by gray boxes. Letters indicate significant differences ($P \leq 0.05$, Tukey's HSD test) among all boxes and panels. The y-axis scale differs between panels for visualization of significant differences.

associated with lower canopy cover (Appendix S1: Fig. S5a–e). At NVSP, higher relative diameter ratio (NVSP-MC-3) was associated with higher SOC concentration (Appendix S1: Fig. S5f). At NMSV, higher relative diameter ratio (NMSV-PJ-4) was associated with higher canopy cover, higher number of adult trees in the study site, higher herbaceous cover, and lower litter cover (Appendix S1: Fig. S5g–j).

DISCUSSION

We characterized the aboveground and belowground growth characteristics of juvenile conifers, correlated destructively sampled juvenile growth characteristics to estimate ranges of growth for field-measured juveniles, and investigated the factors shaping differences in the relative growth of juvenile trees growing across 25 diverse SWUS sites. We found that measures of growth increased significantly from the smallest juvenile tree height class (<150 mm) to the largest (300+ mm) across all tree groups (junipers, piñon pines, ponderosa pines, firs) except for SLA and root:shoot ratio, which often declined. Juvenile maximum rooting depth increased with height to an estimated maximum depth of up to ~400 mm. Ponderosa pines exhibited significantly

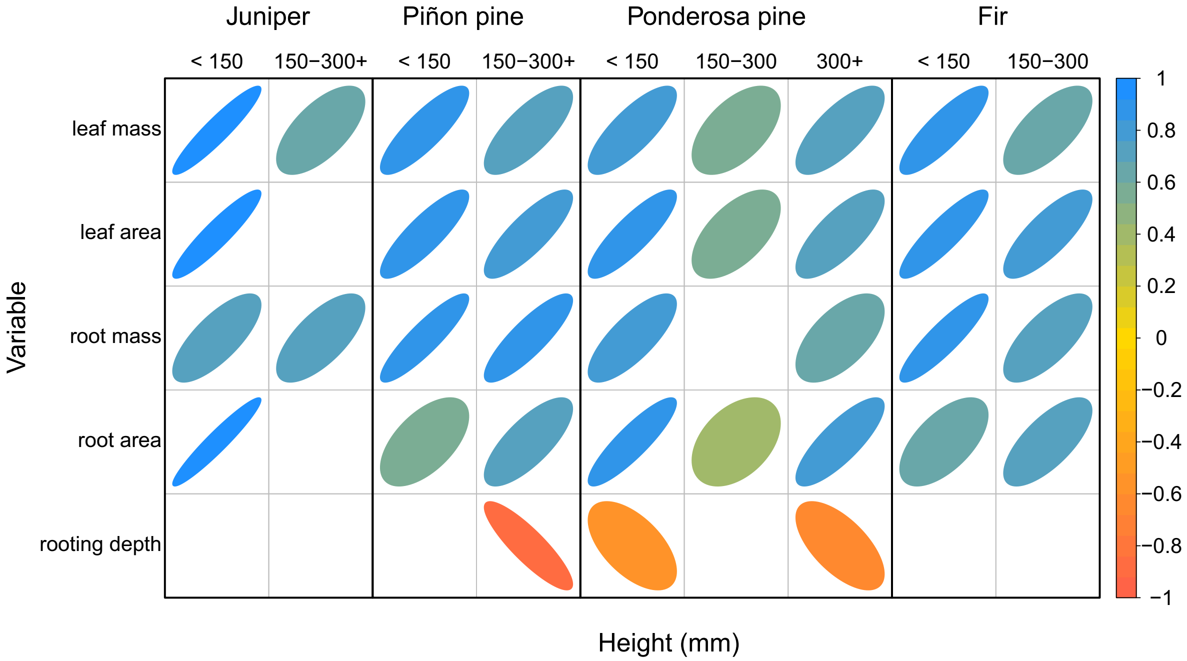

Fig. 8. Correlation matrix illustrating the strength and direction of the correlation between destructively sampled juvenile height (mm) and leaf mass (g), leaf area (cm^2), root mass (g), root area (cm^2), and rooting depth (mm) used to estimate the range of these variables for field-measured juvenile conifers. Each column represents the correlation of variables in each height class (<150 mm, 150–300 mm, 150–300+ mm, 300+ mm) for junipers, piñon pines, ponderosa pines, or firs. Bubble shape, color, and orientation correlate to the R statistic, where bubbles that are narrower and darker red or blue indicate a strong negative or positive correlation ($R \sim 1.0$) between juvenile height and the corresponding growth characteristic, respectively. Insignificant relationships ($P \geq 0.05$) are not shown. See Appendix S1: Fig. S4 and Tables S4–S7 for additional information.

shallower maximum rooting depth than other groups at <150 mm height, which may be attributed to the large number of very young (1–2 yr old) juveniles at some of our sampling sites. Firs maintained a similar maximum rooting depth between <150 mm and 150–300 mm height classes, the only tree group to do so.

Due to increased need to access water in more arid environments (Burns 1983, Meeuwig et al. 1990), we hypothesized that juveniles in lower elevation piñon pine-juniper woodlands would exhibit higher proportional belowground growth compared with juveniles at higher elevations. However, root:shoot ratio of lower elevation juveniles did not differ from those in higher elevation sites (as assessed by area) or was inconclusive (assessed by weight). This is surprising because conifers are expected to allocate more resources to belowground growth in response to increased climate-driven aridity (Callaway et al. 1994, Olszyk et al. 2003) and in environments with high relative moisture stress (Cregg 1994, Greenwood and Weisberg 2008). Instead of growth differences, our results show that juveniles growing in more arid environments are more likely to be located in sheltered microsites, even if their rate of aboveground growth is lower in sheltered microsites.

Due to increased need to access light in environments with a shorter growing season and greater canopy shading (Oliver and Ryker 1990, Cannon et al. 2019), we hypothesized that juveniles in high elevation mixed-conifer forests would exhibit higher measures of aboveground growth or light capture compared with juveniles located at lower elevations. We found support for this hypothesis for firs which had the highest SLA of all tree groups. However, firs also had a significantly higher root:shoot ratio by weight than other conifer groups, which may indicate

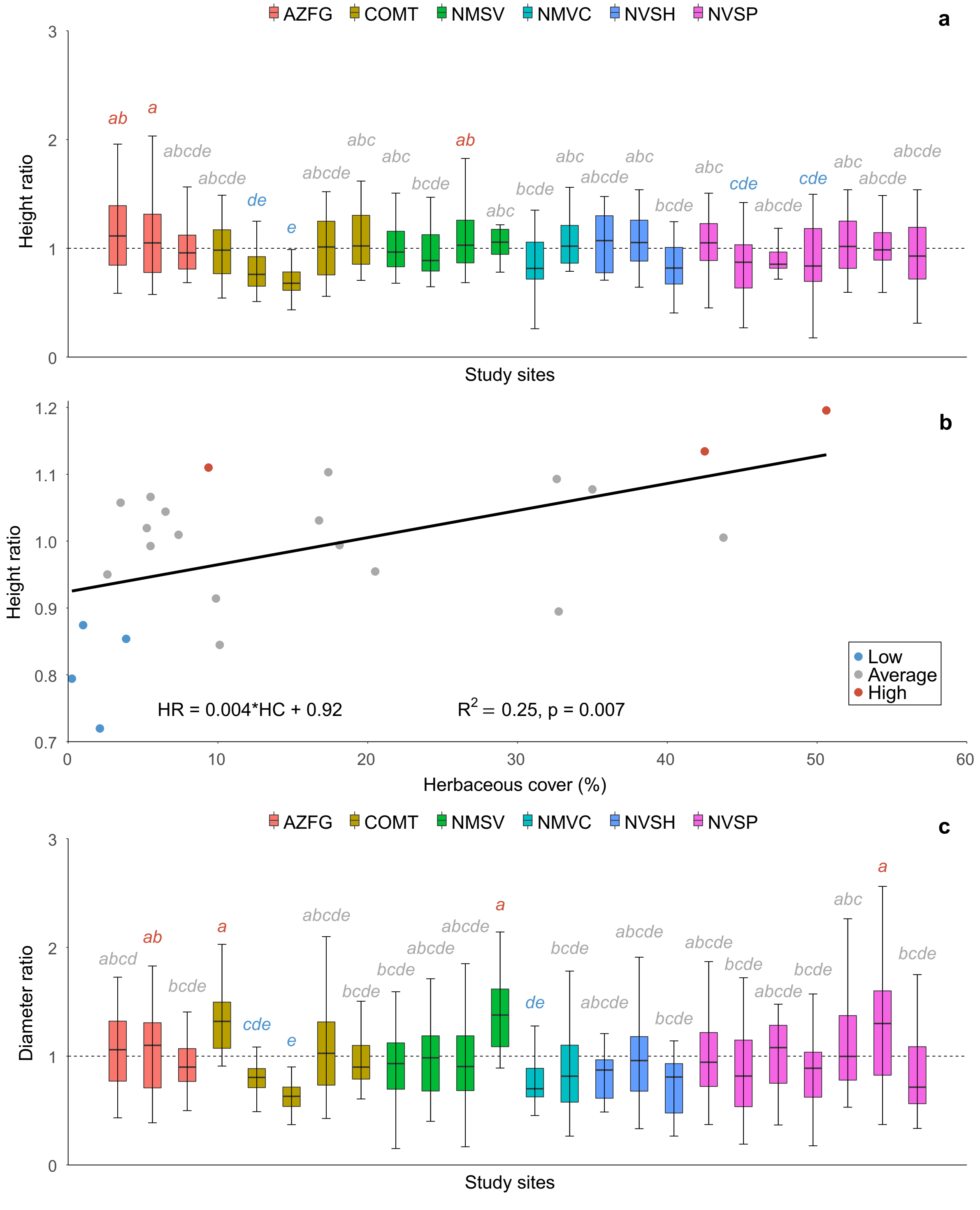

Fig. 9. Boxplot illustrating the relative height ratio (i.e., relative height of juvenile trees at each site compared with similar juvenile trees at all other sites, where 1.0 is average; Panel a), a scatterplot illustrating the significant relationship between site herbaceous cover (%) and relative height ratio (Panel b), and a boxplot illustrating the relative root collar diameter ratio (i.e., relative diameter of juvenile trees at each site compared with similar juvenile trees at all other sites, where 1.0 is average; Panel c). Letters indicate significant differences ($P \leq 0.05$, Tukey's HSD test) within each panel. COMT-PP-4 was not included in this analysis because there were no juvenile trees present at the site.

consistent structural differences of juveniles in high elevation mixed-conifer forests compared with lower elevation ponderosa pine forests and piñon pine-juniper woodlands. The growth characteristics of ponderosa pines were often similar to those of lower elevation conifers (junipers, piñon pines), notably a consistent decline in SLA with increasing height. Although these results highlight the importance of elevation and mean climate conditions for juvenile conifer growth, we found that variation in measures of relative aboveground growth at our study sites was not correlated to broad measures of climate and elevation (see Dobrowski et al. (2015) for similar results). Instead, aboveground growth may be more clearly explained by variation in herbaceous vegetation cover, stand adult tree characteristics, and soil clay and SOC content.

Utility of correlation equations

Our estimates of growth characteristics are intended as reference material to increase the utility of existing and more commonly conducted field measurements of juvenile conifer height and diameter to estimate a broader range of growth characteristics that require destructive sampling. These regression equations of juvenile growth characteristics, especially those that are highly correlated, can describe allocation of growth above- and belowground that can be used in assessments of juvenile vulnerability to environmental stress and to identify potential local morphological adaptations. To this end, our paper provides correlation matrices to help identify components of juvenile growth that are highly correlated to height and root collar diameter, as well as related equations and summary statistics in Appendix S1.

Can juvenile growth characteristics inform contemporary topics in forest and woodland ecosystems?

The persistence of piñon pine-juniper woodlands in the western United States may be dichotomous. In the SWUS, these ecosystems have contracted in response to two major global-change-type drought events in the 1950s and early 2000s, which resulted in large incidence of mortality for the less drought-tolerant variety of piñon pine (*Pinus edulis*) located in this region (Mueller et al. 2005, Breshears et al. 2009). Potential juniper mortality across the SWUS is emerging in 2021, but is not yet fully documented or understood. These piñon pine-juniper woodlands are expected to continue to contract as deleterious climate events intensify in the future (Mcdowell et al. 2016, 2020). Other regions of the western United States are populated by a more drought-tolerant variety of piñon pine (*Pinus monophylla*), which has also experienced large mortality events (Greenwood and Weisberg 2008), yet at higher latitudes these ecosystems are expanding downward into sagebrush-dominated shrublands due to their recovery from past human disturbances and a warming climate (Miller and Rose 1999). Following large adult tree mortality events, piñon pine-juniper woodland reestablishment and recovery depends on advanced regeneration (juvenile establishment that precedes disturbance), particularly for piñon pines reliant on sheltered microsites (Redmond and Barger 2013, Minott and Kolb 2020). Our results corroborate the importance of sheltered microsites for juvenile piñon pines and junipers as found in Minott and Kolb (2020): Both grew more commonly in sheltered environments and also grew larger at sites with higher canopy cover. We found that juveniles of both groups were often smaller in sheltered microsites compared with unsheltered microsites, which we attribute to a small proportion of highly favorable unsheltered microsites at some of our study sites where juveniles were able to survive in interspaces and minimize the trade-off between growth and survival (Chambers et al. 1999). Both tree groups spend a prolonged time period (15+ yr) in the juvenile stage, suggesting that these microsites must be sustained for long time periods for regeneration to occur. In regions where piñon pine-juniper woodlands are expanding, recent research suggests that enhanced belowground growth deeper than 1000 mm in the soil profile (which we did not observe in the more arid sites of our study) helps young juveniles establish a stable water source and reduce desiccation risk (Chesus and Ocheltree 2018). As an additional component of regeneration and juvenile growth characteristics, well-documented differences in the physiological controls of stomatal conductance and leaf water potential employed by piñon pines (isohydric) and junipers (anisohydric) may lead to divergent patterns of survival and mortality even for juveniles located in the same environments (Linton et al. 1998, McDowell et al. 2008, Plaut et al. 2012). We propose that research focused on these physiological differences in juvenile piñon pines and junipers, specifically how regulation of stomatal conductance and xylem cavitation vulnerability may alter a juvenile's susceptibility to stress during natural regeneration, is needed to more comprehensively understand potential changes to the regeneration niche in these ecosystems.

Across the SWUS, ponderosa pine forests are declining at the lower elevational limits of their distribution (Allen and Breshears 1998, Minott and Kolb 2020) and are experiencing an increasing number of severe disturbance events that they are not recovering from due to inadequate regeneration (Stevens-Rumann et al. 2018, Rodman et al. 2020). As a result, the persistence of ponderosa pine forests increasingly hinges on successful regeneration and juvenile survival, a trend predicted to intensify in a progressively arid future (Petrie et al. 2017). Juvenile ponderosa pines have relatively high drought and heat tolerance (Kolb and Robberecht 1996), but acclimation to stress may come at the cost of decreased growth (Kerr et al. 2015, Augustine and Reinhardt 2019). In a region predicted to incur more frequent episodic climate events such as hot-drought (Overpeck 2013), changes in mean climate that reduce juvenile growth may increase their vulnerability to these events (Johnson et al. 2011). Our study corroborates others reporting low root:shoot ratios for juvenile ponderosa pines (Kolb et al. 2016, Dixit and Kolb 2020), and we report that juvenile rooting depth may actually be shallower than estimated in previous studies (Petrie et al. 2017). Based on our findings, we propose that juvenile ponderosa pines may be less able to compete for belowground resources (Elliott and White 1987) and survive in unfavorable semiarid locations and environmental conditions than previously estimated (Johnson et al. 2011, Rother et al. 2015). In post-disturbance environments, successful regeneration will become increasingly difficult due to the aboveground-focused growth strategy employed by juvenile ponderosa pines (Kemp et al. 2019), which may maximize carbon gain at the expense of reducing stress tolerance (Augustine and Reinhardt 2019). Even in favorable environments (high soil SOC content, for example), the patterns of enhanced aboveground growth that we observed may be offset by climate-induced growth reductions, potentially limiting the ability of edaphic and landscape characteristics to enhance ponderosa pine forest persistence in the same manner as they currently do.

Juvenile trees in mixed-conifer forests often encounter unique environmental challenges including shorter growing seasons, greater photoinhibition, and increased risk of frost damage (Maher and Germino 2006, Bansal and Germino 2008). Although the photosynthetic capacity of higher elevation tree species is often similar to those in lower elevations (Piper et al. 2006), it is often restricted by low temperatures and/or photoinhibition (Germino and Smith 1999). In response, adult firs increase leaf area on branches within the understory to maximize photosynthesis (Borghetti et al. 1986). We found evidence that fir juveniles also seek to maximize light acquisition: They were more likely to be located in unsheltered microsites, they were significantly larger in unsheltered microsites in most cases, and they had significantly higher SLA at 150–300 mm height compared with other conifers. Although they invested in a higher proportion of roots by weight, firs were the only tree group that did not significantly increase maximum rooting depth between <150 mm and 150–300 mm height classes. Rehfeldt et al. (2014*a*,*b*) report greater phenotypic plasticity in belowground allocation of growth in Douglas fir compared to ponderosa pine, which may indicate a greater capacity for fir acclimation and perhaps adaptation to environmental variation. We found unique fir growth characteristics compared with other tree groups, although we caution that we did not sample a large number of mixed-conifer sites in our study. Future research that quantifies the association between fir growth variation and environmental variation (perhaps across elevational gradients) would help to elucidate to what degree plasticity may influence the resilience of mixed-conifer forests in a changing climate.

Informing the future geography of coniferous forests and woodlands

Coniferous forests and woodlands in the western United States are predicted to experience range contractions at lower elevations and latitudes in response to climatic warming and drying by the end of the 21st century (Allen et al. 2010, Bell et al. 2014*b*). Increasing evidence points to the differing requirements for adults vs. juveniles, and overemphasis of adult requirements for persistence in regional SDM projections may not accurately capture the future of these ecosystems in cases where the regeneration niche is substantially different from the adult survival niche (Bell et al. 2014*a*). Our study provides a few novel results that can help to incorporate juvenile survival in SDM approaches. First, on the intermediate textured soils that comprised our study sites, juvenile conifers had relatively shallow rooting depths, and it follows that the soil depths at which drought events and extreme high soil temperature can initiate stress to juveniles is also relatively shallow. Other studies have found deeper rooting depths, in some cases attributable to favorable soil parent material, that support greater water infiltration and deeper root growth (Heidmann and King 1992, Heidmann 1998, Feddema et al. 2013, Chesus and Ocheltree 2018). Second, lower and mid-elevation juvenile conifers (junipers, piñon pines, ponderosa pines) had similar allocation of both above- and belowground growth that did not vary markedly between different site environments, suggesting that these tree types do not proportion their above- and belowground growth to different environments. If mid- and lower elevation juvenile conifers also do not acclimate physiologically to environmental variation (see Augustine and Reinhardt (2019) for a study including ponderosa pine), we postulate that the biotic component of juvenile survival may have relatively uniform influence on ecosystem persistence, although we note that there can be genetic variation in growth allocation to shoots and roots among provenances in the SWUS that may alter this relationship (Kolb et al. 2016, Dixit and Kolb 2020).

The regeneration-associated persistence of coniferous forests and woodlands is likely to be strongly influenced by environmental variation at local scales. Previous research has established the importance of local variation in elevation and topographic heterogeneity on the water balance of forests and woodlands of the SWUS (Bradley and Fleishman 2008, Petrie et al. 2015, Koehn et al. 2021). We found that variation in adult tree density had positive effects on juvenile growth at lower elevations, corroborating results of previous studies (Sthultz et al. 2007, Redmond and Barger 2013, Urza et al. 2019), whereas adult tree density had negative effects on juvenile growth at higher elevations. Additionally, local variation in edaphic properties—especially variables associated with higher SOC content—often corresponded to greater juvenile growth. These findings underscore the importance of local variation in favorable sites for regeneration, and point to the potential for field and modeling-based research to identify and fine-tune the management actions that account for local variation in topography, optimal adult tree density, and edaphic properties (Flathers et al. 2016, Kolb et al. 2020). Flexible design of management actions in ponderosa pine-dominated and mixed-conifer forests may be especially important because favorable regeneration conditions and juvenile growth strategies in these ecosystems contrast strongly with future climate change and disturbance forecasts (Johnson et al. 2011, Davis et al. 2019). An important part of maximizing the distribution and abundance of these ecosystems will be to determine the geography of future regeneration favorability, and focus actions in locations where management can make a difference. For example, in areas where existing microsites are no longer favorable for regeneration or are occupied by adult trees, more complex management strategies may need to be implemented. This can include creating an artificial shifting mosaic landscape where adult trees are cut to reopen favorable soil and geomorphic niche spaces and recolonized by allowing natural seed dispersal by nearby adults or direct planting (Abella et al. 2013). Additionally, better quantitative assessments about the conditions (soil moisture and temperature) that are required for regeneration can enable more accurate assessments of forest and woodland persistence, improve forecasts of the changing geographic distributions of these ecosystems, and contribute to the success of management actions and programs.

Do conifer growth characteristics support the stress gradient hypothesis?

The stress gradient hypothesis suggests that facilitative plant–plant interactions are more common in stressful environments, whereas competitive plant–plant interactions are more common in benign or resource-rich environments (Bertness and Callaway 1994). Nurse plant facilitation comprises a majority of positive plant–plant interactions in lower elevation forests and woodlands (Mueller et al. 2005, Redmond and Barger 2013), and sheltered microsites formed by burned trees and other features provide important microclimates for tree recovery in post-wildfire landscapes (Haffey et al. 2018). In the piñon pine-juniper woodlands of our study, 80.1 ± 12% of juveniles were located in sheltered microsites, supporting previous findings of the important role of facilitation even in cases where these environments may restrict juvenile growth (Chambers 2001, Minott and Kolb 2020). We also found evidence supporting the stress gradient hypothesis prediction of greater competitive interactions in higher elevation ponderosa pine and mixed-conifer forests. Juveniles were more likely to have recruited in unsheltered microsites in these environments (88.7 ± 26.3% in ponderosa pine forests; 68.1 ± 25.6% in mixed-conifer forests), and aboveground growth was negatively correlated with variables associated with high adult tree density. This suggests that competition with adult trees for light and soil resources may restrict locations supporting regeneration in higher elevation ecosystems, whereas adult–juvenile relationships are more facilitative at lower elevations. Additional research elucidating facilitation vs. competition in these ecosystems, especially the spatial scales over which these patterns occur, may help to improve understanding of environmental control on regeneration across a broad range of conifer species and semiarid ecosystem types.

Future directions in juvenile conifer research

We recommend future research in two main areas to improve understanding of juvenile conifers in the SWUS. First, juvenile conifers are more vulnerable to environmental stressors than adult trees (Johnson et al. 2011), but it is unclear to what degree these stressors are imposed by differing microenvironments (such as their position near the soil surface and shallow rooting depth), differences in stress tolerance between juvenile and adult trees, and the uncertainty of interactions between adults and juveniles along a competition-facilitation spectrum. Knowing how the magnitude and duration of environmental stress can exceed the physiological limitations of juvenile conifers would greatly enhance scientific ability to forecast regeneration-associated persistence, and this may be investigated through field and laboratory research, physiological modeling, and field experiments. Second, we stress the need for a more complete understanding of how landscape factors—specifically topography, soil properties, and tree stand and understory characteristics—underlie the growth and survival of juvenile conifers. Doing so may improve estimates of the geography of forest and woodland persistence using high-resolution digital elevation models, spatial data sets and estimates, and species distribution information.

CONCLUSION

We characterized the aboveground and belowground growth characteristics of four juvenile conifer groups (junipers, piñon pines, ponderosa pines, firs) across 25 sites in the SWUS, estimated the range of growth characteristics for field-measured juveniles using correlation equations, and examined the environmental factors associated with variation in juvenile growth across these sites. Lower elevation juvenile conifers were generally located in sheltered microsites, whereas higher elevation juveniles were often unsheltered. Juvenile growth is likely better explained by variation in local environmental factors than by broader climate. Growth increased significantly from the smallest (<150 mm) to the largest (300+ mm) juvenile height class across all groups, but SLA and root:shoot ratio declined. The estimated maximum rooting depth of juvenile conifers was <~400 mm, which is shallower than previously reported for juveniles of similar size. In contrast to other conifers, firs maintained a similar SLA, root:shoot ratio by area, and maximum rooting depth between <150 mm and 150–300 mm height classes. Indeed, we found many similarities between juniper, piñon pine, and ponderosa pine juveniles that were not shared by firs. This finding illustrates the unique growing environment of higher elevation mixed-conifer forests and also portends a limited capacity of mid- and lower elevation conifers to acclimate above- and belowground growth to environmental conditions. If mid- and lower elevation juveniles do not acclimate physiologically to changing environmental conditions, our results suggest that variation in environmental factors such as soil characteristics, adult tree density, and litter depth will play a substantial role in regulating regeneration. This study serves as a resource for information pertaining to the growth characteristics of juvenile conifers, provides foundational information to inform forest and woodland management, improves forecasts of the future persistence of these ecosystems, and guides future research.

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DATA AVAILABILITY

Raw and derived data from this study are available for public access via https://doi.org/10.5281/zenodo.5551031

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3839/full