DISSERTATION

JUVENILE TREE DYNAMICS IN CHANGING LANDSCAPES: EFFECTS OF OVERSTORY-MEDIATED MICROCLIMATES ON DRYLAND TREE RECRUITMENT VARY ACROSS CLIMATIC GRADIENTS

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ABSTRACT

JUVENILE TREE DYNAMICS IN CHANGING LANDSCAPES: EFFECTS OF OVERSTORY-MEDIATED MICROCLIMATES ON DRYLAND TREE RECRUITMENT VARY ACROSS CLIMATIC GRADIENTS

Climate change impacts the future viability of plant species and communities directly through effects on demographic processes and indirectly through structural dynamics. Regeneration, establishment, growth, and survival of juvenile trees can be especially vulnerable processes in forest and woodland community development because juvenile trees are typically not able to tolerate abiotic stress as effectively as more mature trees. Because of this elevated sensitivity to climate-related stressors, juvenile establishment patterns are fundamental to understanding long-term species persistence. Overstory tree structure is an important mediating influence of the impacts of climate change in forest and woodland communities, particularly through influences on resource availability. Fine-scale variation in overstory tree size, density, and species influence primary plant resource requirements, including light availability, atmospheric heat and moisture, precipitation throughfall and soil water availability, and soil nutrient availability. Juvenile trees of different species can benefit from buffering of microclimate conditions by overstory trees, like direct radiation and extreme temperature variation, and experience competitive interactions for light and soil resources, especially in resource-limited communities. Yet, juvenile trees can span a range of sizes and physical maturity and vary in their capacity to acquire resources or tolerate resource limitations, and therefore can differ in facilitative versus competitive relationships with overstory conditions. Amplifying the complexity of these

relationships, interannual variation in weather conditions, such as drier or wetter years than normal, influences the degree to which juvenile trees experience facilitative or competitive relationships with overstory trees. Indeed, the extent of microclimate effects on regeneration processes depend in part on the complex covariance of air temperature and humidity (thus, vapor pressure deficit), moisture availability (precipitation and soil moisture), and photosynthetically active radiation (i.e., light). In the absence of temperature and moisture limitations, trees may benefit from additional light availability for photosynthesis; alternatively, if temperature or moisture conditions are limiting, juveniles may benefit more from buffering influences of overstory, at the expense of decreased light availability. For dry forests and woodlands of the western U.S. which are at the forefront of climate change-driven tree recruitment vulnerabilities, greater resolution into juvenile relationships with overstory structure, and microclimate buffering, will substantially enhance the ability to evaluate and predict the effects of increasingly marginal climate space on their persistence.

In this dissertation, I evaluated juvenile tree regeneration, growth, and survival in dryland forest and woodland systems relative to the mediating influences of overstory trees, across ranges of juvenile sizes, interannual weather variation, and broad climatic and elevational environmental gradients. In Chapter 1, I investigated survival and growth of ponderosa pine and Douglas-fir newly germinated seedlings, and older, larger seedlings to variation in overstory structure and associated microclimate conditions at fine-spatial scales. This study showed that while newly germinated seedlings were more sensitive to interannual variation in microclimates, overall survival and growth of younger and older seedlings were highest in microclimates with above-average warm and dry air during early-growing season months, and above-average light conditions. Importantly, the structural and microclimate influences on survival and growth over

three years of study were primarily associated with the first year of study during which spring weather was abnormally cool and more humid. These results illustrated the environmental context for the initiation of survival and growth trajectories observed in this study, and demonstrate both spatially and temporally narrow conditions in which survival and growth was collectively greatest for both species.

In Chapters 2 and 3, I investigated physiological and growth differences of juvenile piñon pine in dead and live overstory microenvironments over two years following experimentally-induced mortality of overstory trees. In Chapter 2, I measured photosynthetic and stomatal conductance rates of juveniles from among the smallest to largest individuals present in a middle-elevation piñon-juniper site in the core of the geographic distribution of two-needle piñon pine. Larger juveniles in dead overstory environments showed the highest photosynthetic and stomatal conductance rates. However, juveniles of all sizes were overall similarly limited by lower soil moisture and hot and dry microclimate conditions in both live and dead overstory environments. Given these limitations, the results of this study demonstrate the susceptibility of all juvenile piñon trees to hot and dry microclimates, which can be exacerbated both by mortality of overstory trees and by projections of future hotter and drier climate in these woodlands. In Chapter 3, I measured branch growth of juvenile piñon trees at six different sites spanning a gradient of latitudinal climate differences from hotter and drier southern locations to cooler and dry northern locations, and local elevation gradients from low to mid to high elevation piñon-juniper woodlands. Growth in post-overstory mortality years relative to mean growth prior to overstory mortality ("growth ratios") of juveniles across sizes was consistently higher in dead compared to live overstory environments only for middle- and high-elevation sites in our mid-latitude study region of southwestern Colorado, which had cooler and wetter post-overstory mortality weather conditions compared to

other regions. Moreover, differences among sites were likely also related to typical climate differences associated both with latitude, where drier sites at southern and northern latitudes showed little growth responses to overstory mortality, and associated with elevation, where growth ratios were highest at the highest elevation site which has more moderate temperature and precipitation conditions on average.

The results of this dissertation provide evidence for microclimate and juvenile tree survival outcomes in a dry forest restoration treatment and show the impact of acute structural change following overstory tree die-off on physiological and growth activity of juvenile piñon pine. The findings presented here provide ecologists and land managers with new information on the nuances of spatially and temporally narrow regeneration niches of species in dry mixed-conifer forests, and potential patterns and mechanisms of juvenile piñon pine resilience – but also potential future sensitivity – following overstory mortality. Importantly, results of these studies emphasize the role of interannual variation in weather conditions in driving specific forest and woodland development trajectories.

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CHAPTER 1

INTRODUCTION

Climate warming affects plant species' distributions through demographic processes such as the capacity to regenerate, grow, and survive (Kroiss and HilleRisLambers, 2015; Paquette and Hargreaves, 2021; Shriver et al., 2021). For tree species, distributions are typically weighted heavily in data for correlative climate- and environment-based relationships with mature trees at coarse spatial scales (e.g. the forest stand scale and above, approx. ≥60-90 m resolution) (Lembrechts et al., 2019; Maclean, 2020). Yet, there is a growing body of evidence for the differentiation of climatic and environmental controls on tree occurrence based on tree life-stage (Kroiss and HilleRisLambers, 2015; Máliš et al., 2016). Specifically, juvenile trees of a given species typically occupy a climatic and environmental subset of the conditions in which their mature counterparts occur, particularly in water-limited, dry forest types (Bell et al., 2014; Copenhaver-Parry et al., 2017; Dobrowski et al., 2015). Yet, juvenile trees progress through stages of physical and physiological maturity in the process of establishment (ontogeny), and it is unlikely that younger, smaller juveniles and older, larger juveniles experience equivalent impacts of limiting environmental conditions such as temperature- and moisture-related stresses (Clark et al., 1999; Ibáñez et al., 2007). Because juveniles of a species provide the foundation for future reproductive cohorts, evaluating controls on regeneration processes is crucial for management planning and ecological insight (i.e., prediction) related to the impacts of climate warming on the persistence of a species in a given location.

Climate conditions in a given location may be mediated, or buffered, by biophysical features such as topographic variation and overstory tree structure, resulting in microclimate

conditions which are a subset of the broader climate conditions (De Frenne et al., 2021; Dobrowski, 2011; Lembrechts et al., 2019). These microclimates can be more suitable for tree regeneration processes which are dependent on more moderate abiotic conditions, and therefore are crucial for forest and woodland community dynamics (Copenhaver-Parry et al., 2017; Dobrowski et al., 2015). Overstory tree structure, for example, can impact primary resource conditions which juvenile trees experience, including air temperature and humidity, water availability (both in relation to precipitation throughfall and soil moisture availability), and the amount of light available for photosynthesis (reviewed in De Frenne et al., 2021). Microclimate conditions mediated by the presence and structure of overstory trees can vary at fine spatial scales corresponding to overstory tree density, size, and species variation, and are subject to rapid changes resulting from disturbances which affect the presence or structure of overstory trees (Lenoir et al., 2017; Lusk and Laughlin, 2017). For instance, severe wildfire or drought can result in extensive loss of live overstory trees, with varying outcomes on the presence of remaining dead trees or patches of surviving overstory or juvenile trees (Krawchuk et al., 2020). Such disturbances are becoming more frequent and severe with ongoing climate warming, threatening the continuity and persistence of overstory trees and resulting microclimates which may be especially important for juvenile regeneration, growth, and survival (Redmond et al., 2018; Rodman et al., 2020; Wooten et al., 2022). Indeed, forest resilience to disturbances like wildfire and drought is disproportionately dependent on the presence and distribution of forest structural heterogeneity, such as in refugia following wildfire (Chapman et al., 2020; Coop et al., 2019; Downing et al., 2020; Krawchuk et al., 2020), microenvironmental conditions mediated by forest structure in ecotones (Ettinger and HilleRisLambers, 2017; Malanson et al., 2017; Oldfather et al., 2020; Stohlgren et al., 1998), and structural heterogeneity (e.g., canopy cover)

which mediates diverse microclimatic conditions supporting understory plant communities, including new tree regeneration (Gray et al., 2002; Lembrechts et al., 2019; Serra-Diaz et al., 2015). It is therefore imperative to better understand how fine-scale variation in structure and microclimates, and changes to overstory through disturbance, affect regeneration processes and juvenile dynamics, and thus forest and woodland development trajectories.

The magnitude and extent of microclimate effects on regeneration processes depend in part on the complex covariance of primary resource conditions for juvenile trees affected by overstory buffering. These resource conditions include, namely, air temperature and humidity (or, vapor pressure deficit), moisture availability (precipitation and soil moisture), and photosynthetically active radiation (i.e., light) (De Frenne et al., 2021). The extent or intensity of influence of each of these variables on juvenile survival and growth will depend on the magnitude of the other variables, which results from climate and weather conditions (seasonal, interannual) and spatial variation in overstory structure (Davis et al., 2019b; Grossnickle, 2018; Ibáñez et al., 2007; Lenoir et al., 2017; Lusk and Laughlin, 2017; Von Arx et al., 2013). For example, considering a range of daytime temperatures and moisture availability experienced during a typical growing season in a semi-arid forest or woodland, there likely exists a range or balance among these conditions in which the probability of juvenile survival and growth is highest, and the importance of increased light availability (assuming no additional changes to temperatures and evaporative demand) is highest – i.e., little to no limitations of temperature and moisture allows juveniles to benefit from additional light for elevated growth activity (see Figure 1 for a conceptual representation of these relationships). While the precise balance in which these conditions occur will in part depend on variation at the level of species and individuals (Holmgren et al., 2012; Ibáñez et al., 2007; Lusk and Laughlin, 2017), the general concept of this

balance is best illustrated by the definition of reference points or boundaries of known limitations (Figure 1.1).

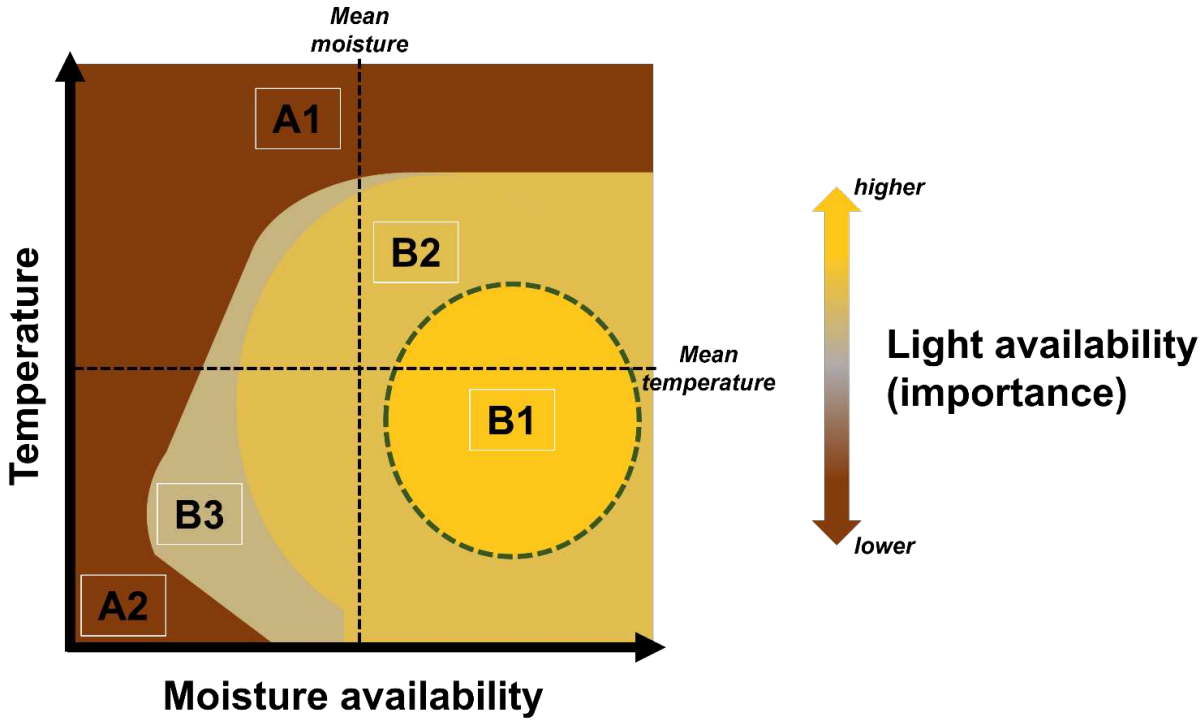

Figure 1.1. *Conceptual representation of the covarying impacts among microclimate temperature, moisture availability (e.g., soil moisture), and light availability for juvenile tree survival and growth in a given semi-arid forest or woodland. Ranges of these variables and black dashed lines indicating mean conditions are assumed to represent typical growing season daytime conditions for a given semi-arid forest or woodland, such as ponderosa pine-dominated dry conifer forests or piñon-juniper woodlands. Juvenile tree survival and growth within these systems can be especially limited by high temperature conditions, such as high temperatures which limit physiological activity and result in high demand for plant water use (e.g., represented by "A1") even when moisture is abundant (upper right corner of A1 area); similarly, juvenile tree survival and growth can be especially limited by low moisture availability both when temperatures are high (upper left corner of A1 area) or when temperatures are more moderate (represented by area "A2"). In these conditions, given the limitations imposed by temperature and moisture availability, the importance of light availability is likely low. In contrast, when temperature and moisture conditions are not limiting, particularly when moisture is abundant (above-average) and temperatures are facilitative of growth activity but not overly high (average, or below-average), the availability of light is likely to be most important in this region (represented by area "B1") as available light can be transformed into photosynthates. This covariance among conditions may represent some range of optimal balance among these primary resource conditions for juvenile survival and growth (B1, with dark green dashed outline). These conditions likely reflect those in which prior studies have identified regeneration pulses and higher growth of trees in semi-arid forest and woodland systems (see text for citations). Outside of this potential optimal range, when moisture availability is high and temperature is not limiting, the availability of light for photosynthesis likely remains relatively high*

(represented by area "B2"). The importance of light availability diminishes as temperatures and moisture availability become limiting (represented by area "B3"), but it is possible that at lower moisture availability temperatures are not as limiting for survival and growth and light availability may still be influential (thus a "hump" of moderate light importance in the lower left plot quadrant, area B3).

In semi-arid forests and woodlands of the western U.S., numerous studies have identified generally moderate weather conditions – such as below-average temperatures or above-average precipitation – as years in which establishment of juvenile trees in these systems is most likely (Betancourt et al., 1993; Brown and Wu, 2005; Clifford et al., 2011; Davis et al., 2019a; League and Veblen, 2006; Petrie et al., 2016; Romme et al., 2009; Savage et al., 1996) and growth activity may be elevated (Cailleret et al., 2019; Hankin et al., 2019; Kannenberg et al., 2024; Macalady and Bugmann, 2014; Peltier et al., 2018; Redmond et al., 2017). In these conditions in which the general balance of temperature and moisture weather conditions, relative to normal climate conditions, are most facilitative of regeneration and growth, it is likely that individuals would benefit most from light availability (again, absent additional heat or moisture limitation resulting from higher light availability) (Figure 1.1 area B1). Furthermore, regions of covariance between temperature and moisture in which temperatures are high or precipitation represent likely boundaries at which associated limitation to tree physiological activity (e.g., photosynthesis and stomatal conductance) results in little importance of additional light availability for juvenile survival and growth (Figure 1.1 areas A1 and A2). High temperatures (Figure 1.1 area A1), especially in semi-arid systems, during typical growing days and seasons result in stomatal closure (Adams et al., 2015; Grossiord et al., 2020) and even protein denaturation and whole-tissue death (Kolb and Robberecht, 1996), even when moisture is available (Grossiord et al., 2017; Rother et al., 2015), and are associated with limited regeneration generally (Davis et al., 2019a; Petrie et al., 2017, 2016). Similarly, periods of limited moisture availability (Figure 1.1 area A2) can reduce growth activity (e.g., carbon

uptake) and survival in these systems, both with and without high temperatures (Davis et al., 2019a; Grossiord et al., 2017; Kannenberg et al., 2024; Petrie et al., 2017; Rother et al., 2015). In this way, the role of overstory cover and structure in affecting juvenile tree survival and growth, from competitive (negative) to facilitative (positive), depends on the extent to which these factors covary, determined by weather, and mediated by species traits and individual variation. While these examples are useful illustrations, the complexity of covariance among temperature-, moisture-, and light-related resource conditions emphasizes the importance of the understanding the environmental context in which juvenile regeneration, survival, and growth occur (Grossnickle, 2018; Ibáñez et al., 2007; Lusk and Laughlin, 2017; Merges et al., 2020).

Research Outline

The work presented in this dissertation evaluates juvenile tree regeneration, growth, and survival in different forest and woodland systems relative to the mediating influences of overstory trees, across ranges of juvenile sizes, interannual weather variation, and broad climatic and elevational environmental gradients. In addressing juvenile responses over multiple seasons of weather variation, including seasons of normal, below-normal, and above-normal abiotic limitations (relative to long-term, 30-year climate normals), this work seeks to elucidate varying impacts of temperature-, moisture-, and light-related influences on juvenile trees, relative to species and juvenile size differences. This work took place in dryland forest and woodland systems: a dry, ponderosa pine-dominated mixed conifer forest on the Colorado Front Range; and, piñon-juniper woodlands in the southwestern U.S. The particular vulnerability of dry forest systems in the western U.S. to climate changed-induced increases in drought and disturbance frequency emphasizes the need for more complete evidence for microclimate controls on juvenile life-stages in these forests. Dry forest types, such pinyon pine- and ponderosa pine-

dominated systems, are likely to experience more disturbance events – namely drought and fire – in progressively warmer climate conditions, which can result in widespread tree mortality (Bradford et al., 2020) and limited conditions suitable for regeneration (Davis et al., 2019a, 2020; Littlefield et al., 2020; Rodman et al., 2020; Stevens-Rumann et al., 2018). Unlike more productive, higher-elevation forest systems, climate change-pressures on dry forest types result in the risk of system type conversions (i.e., non-forested) following severe disturbance. In these systems, forest recovery through regeneration of new cohorts will be increasingly dependent on spatial and temporal microclimate conditions in which juveniles of different species and life-stages are able to persist (Breshears et al., 1997; Oldfather et al., 2020). Thus, the study of spatial and temporal variation in microclimate conditions in these forest types, and how they may differ across environmental gradients like climate and elevation, is central to evaluating and predicting juvenile establishment successes and failures into the future (Lembrechts et al., 2019; Littlefield et al., 2020; Oldfather et al., 2020).

In Chapter 2, I investigated survival and growth of seedlings at two young life-stages, including newly germinated seedlings and larger one-year old seedlings, to variation in overstory structural conditions at fine spatial scales (e.g., < 20 m) and associated microclimate vapor pressure deficit, soil moisture, and light conditions. These relationships were investigated for two species with contrasting traits, such as tolerance of heat and moisture deficits, including ponderosa pine and Douglas-fir in a dry forest restoration treatment with a wide range of tree grouping and non-tree opening sizes, across various topographic positions. This study occurred across three growing seasons of differing weather conditions, and consequently differing microclimate conditions, ranging from a cool and wet spring in one year to a very hot and dry mid-summer in another year. This study addresses the varying roles of overstory-mediate

microclimates across these different growing seasons, and the apparent balance of temperature, soil moisture, and light conditions in which survival and growth were highest for the two species.

In Chapters 3 and 4, I investigated physiological and growth responses of a wide range of juvenile piñon pine tree sizes and maturity, in relation to live and dead overstory cover. Specifically, Chapter 3 examines photosynthetic and stomatal conductance rates of juveniles across a range of sizes at a single site, over multiple growing seasons and sampling periods, in both live and dead overstory environments. This chapter seeks to address potential near-term responses of juveniles to changes in overstory structure and resulting microclimate conditions which occur with overstory mortality, relative to intact, live overstory environments. In this way, juvenile responses to these environments were assessed relative to potential differences in covarying temperature, soil moisture, and light (from live and dead overstory differences). For Chapter 4, juvenile piñon pine growth was assessed within the same framework across a wide range of juvenile sizes and in live and dead overstory environments. This chapter investigates juveniles in six different locations, encompassing broad gradients in climate conditions, such as monsoon precipitation and climatic moisture deficit, and elevational differences, reflecting both climate and differences in overstory structure (e.g., tree density). As with the previous chapter, this chapter seeks to address how juvenile growth responses to overstory mortality, relative to live overstory, may differ in relation to broad environmental gradients, in addition to interannual weather conditions for multiple years of growth following overstory mortality.

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CHAPTER 2

CANOPY-MEDIATED MICROCLIMATE REFUGIA DO NOT MATCH NARROW REGENERATION NICHES IN A MANAGED DRY CONIFER FOREST[1]

INTRODUCTION

Regeneration, survival, and maturation of juvenile trees are critical for species' population persistence (Buckley et al., 2010; Clark et al., 1999). Juvenile life-stages are highly vulnerable to drought and disturbance (Hessburg et al., 2019; Petrie et al., 2017; Rodman et al., 2020) because they lack adequate physical and physiological means to cope with intense environmental stress compared to adults (Clark et al., 1999; Grossnickle, 2012). Thus, tree regeneration niches (*sensu* Grubb, 1977) are typically characterized by narrower ranges of climatic conditions than adult trees and are more sensitive to changing climate (Bell et al., 2014; Copenhaver-Parry et al., 2017; Dobrowski et al., 2015). The progression of juvenile regeneration, survival, and maturation is partly determined by the capacity for forest canopies to buffer macroclimate conditions and provide suitable microclimates. Microclimates may serve as refugia for juvenile life-stages from unfavorable changes brought by climate warming, and thus carry great importance in maintaining juvenile niches and driving forest development as changes in climate progress (Johnson et al., 2011; Lembrechts et al., 2019; Merges et al., 2020). However, in many forest types, there is currently little evidence linking juvenile tree survival and growth to

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spatial and temporal microclimate variability, and at different stages of maturity.

Recent global forest microclimate research suggests that canopy cover mitigates temperature extremes, humidity fluctuations, and seasonal variation in soil moisture compared to conditions without canopy cover (De Frenne et al., 2021). Canopy-mediated conditions influence vegetation community dynamics (De Pauw et al., 2022; Downing et al., 2020; Lenoir et al., 2017), but juvenile tree responses to microclimate variation remains understudied for most forest types. Elements of forest structure such as tree size, density, and crown architecture vary at fine scales (e.g. 1-20 m) and may affect regeneration patterns through corresponding effects on resource availability from moisture uptake, interception, and runoff, and radiation and temperature fluctuations (Breshears et al., 1997; De Frenne et al., 2021). Moreover, the magnitude of microclimate buffering under forest canopies can vary with seasonal and yearly weather conditions (De Frenne et al., 2021), with buffering being weaker in dry periods and climates compared to wetter periods and climates (Davis et al., 2019b; Hoylman et al., 2018). Thus the relative importance of microclimate buffering for juveniles may change over time (Johnson et al., 2011).

The sensitivity of juvenile trees to temperature and moisture stress varies with the stage of physical development (e.g., age or life-stage) and species traits. Differences in stress tolerance can change across juvenile life-stages due to differences in mechanistic maturity (e.g., lignified stem tissue, leaf cuticle development, and stomatal control) or biomass allocation (Davis and Jacobs, 2005; Dranski et al., 2015; Grossnickle, 2012). Early juvenile life-stages of many species prioritize shorter-term carbon gain over more nuanced stress tolerance strategies (Augustine and Reinhardt, 2019; Lazarus et al., 2018), such as stomatal control, and therefore often require more consistent moisture availability (Kolb and Robberecht, 1996). As juveniles age, their resilience to

environmental stresses typically increases as growth in roots, height, and leaf area contribute to greater moisture, nutrient, and light resource capture (Bachofen et al., 2018; Pirtel et al., 2021). However, the nature of these changes occurring with juvenile physical development may differ among species with contrasting life-history traits related to stress tolerance and acclimation, and phenological plasticity (Davis and Pinto, 2021; Pirtel et al., 2021). Faster-growing, light-adapted species may quickly develop tolerance to heat or drought via leaf traits and stomatal control compared to slower-growing, shade-adapted species. Both life-stage and species trait differences are fundamental components of regeneration niches which likely result in distinct regeneration outcomes relative to fine-scale microclimate variation, but these outcomes are unresolved for many forest types.

The role of microclimate buffering for sustaining regeneration niches via juvenile regeneration, survival, and maturation may be particularly important in forest types characterized by seasonally hot and dry conditions that limit natural regeneration, especially where stand-replacing disturbances exacerbate regeneration failure (Allen et al., 2015; McDowell et al., 2020). For example, dry conifer forests of the interior western U.S. have experienced widespread recruitment failure following high severity wildfires, due in part to loss of canopy cover (Davis et al., 2019a; Rodman et al., 2020; Wooten et al., 2022). Reflecting the importance of canopy cover for seed and site amelioration, Coop et al. (2019) describe how post-wildfire resilience of these forests can be disproportionately dependent on patches of surviving overstory trees as small as 0.01 ha. Current forest restoration treatments in dry conifer forests typically emphasize creating fine-scale structural heterogeneity analogous to historical attributes and patterns (Churchill et al., 2013; Ritter et al., 2020). Despite the assumption that restoration treatments reflect more natural and resilient conditions (Addington et al., 2018; Stephens et al., 2021), it is

unclear how fine-scale variation in structure influences regeneration niches and recruitment dynamics among species with divergent life-history strategies and over varying microclimate conditions.

Disentangling how juvenile trees rely on the moderating effects of canopy buffering requires understanding how survival and growth vary in relation to biophysical conditions and seasonal weather variation (Alba et al., 2019; Hill et al., 2018; Loranger et al., 2016). In this study we assess fine-scale microclimate effects on seedling establishment, survival, and growth for two species with contrasting life-history traits (i.e., regeneration niches) in a heterogeneous, dry conifer forest restoration treatment. The specific objectives of the study were to:

(1) Evaluate relationships between fine-scale variation in forest structure, topography, and microclimate conditions over three consecutive growing seasons

(2) Assess how fine-scale variation in forest structure, topography, and microclimate conditions through influences germination, survival, and growth of (*Pinus ponderosa* var. *scopulorum*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) juveniles

Regeneration niches of ponderosa pine and Douglas-fir are largely dissimilar, including strong differences in the capacity to withstand consistently elevated temperatures and moisture deficits (e.g., Pirtel et al., 2021; Rother et al., 2015), which are likely to result in distinct responses to variation in structure and microclimate conditions. Ponderosa pine is a light-adapted species (Boyden et al., 2005; Chen, 1997; Shepperd et al., 2006) unlikely to survive in the most light-limited conditions; in contrast, Douglas-fir is more shade-tolerant and unlikely to survive in the most exposed, hottest and driest microclimates (Fialko et al., 2020; Rother et al., 2015). We expected survival and growth of both species to be moisture limited, with the lowest survival in the hottest and driest microclimates (e.g., those lacking canopy cover) and seasons (e.g., mid-

late growing season) (Davis et al., 2019a; Rodman et al., 2021; Rother and Veblen, 2017). Additionally, given generally greater plasticity in developmental responses (Pirtel et al., 2021; Rodman et al., 2020a), we expected Douglas-fir survivorship and growth to be more strongly influenced by both favorable and unfavorable periods of weather conditions. Furthermore, we expected new germinants of both species to survive in narrower ranges of conditions compared to older, more physically mature seedlings.

METHODS

Site description

We conducted this study (dataset available at [dataset] Hill et al. 2023) from 2019-2021 in a lower-montane, dry mixed-conifer forest in the Colorado Front Range located in the upper South Platte River watershed near Denver, Colorado, USA (39.437639, -105.256528). The 2.25 ha study site (Figure 2.1) was located within a spatially heterogenous forest restoration treatment, completed in 2018, designed to retain various sizes of tree groupings and openings (see Appendix 1:Supplementary Material and Slack et al., 2021 for additional treatment details). Topographic variation in the study site included only minimal elevation gain (~2,116 – 2,134 m) and multiple slope aspects, predominantly southeast and northwest, situated on a broader northeasterly slope. Ponderosa pine and Douglas-fir were the two dominant tree species in the study site. Rocky Mountain juniper (*Juniperus scopulorum*) was targeted for near complete removal in the restoration treatment. The understory plant community consisted of patchy occurrences of herbaceous and shrub vegetation, though bare, gravelly soil was the predominant ground condition (mean percent cover per study plot was 1.4% ±3.4 for all non-tree vegetation, and 96.1% ±4.6 no vegetation; see below Methods for plot details and see Appendix

1:Supplementary Material for additional vegetation and soils details).

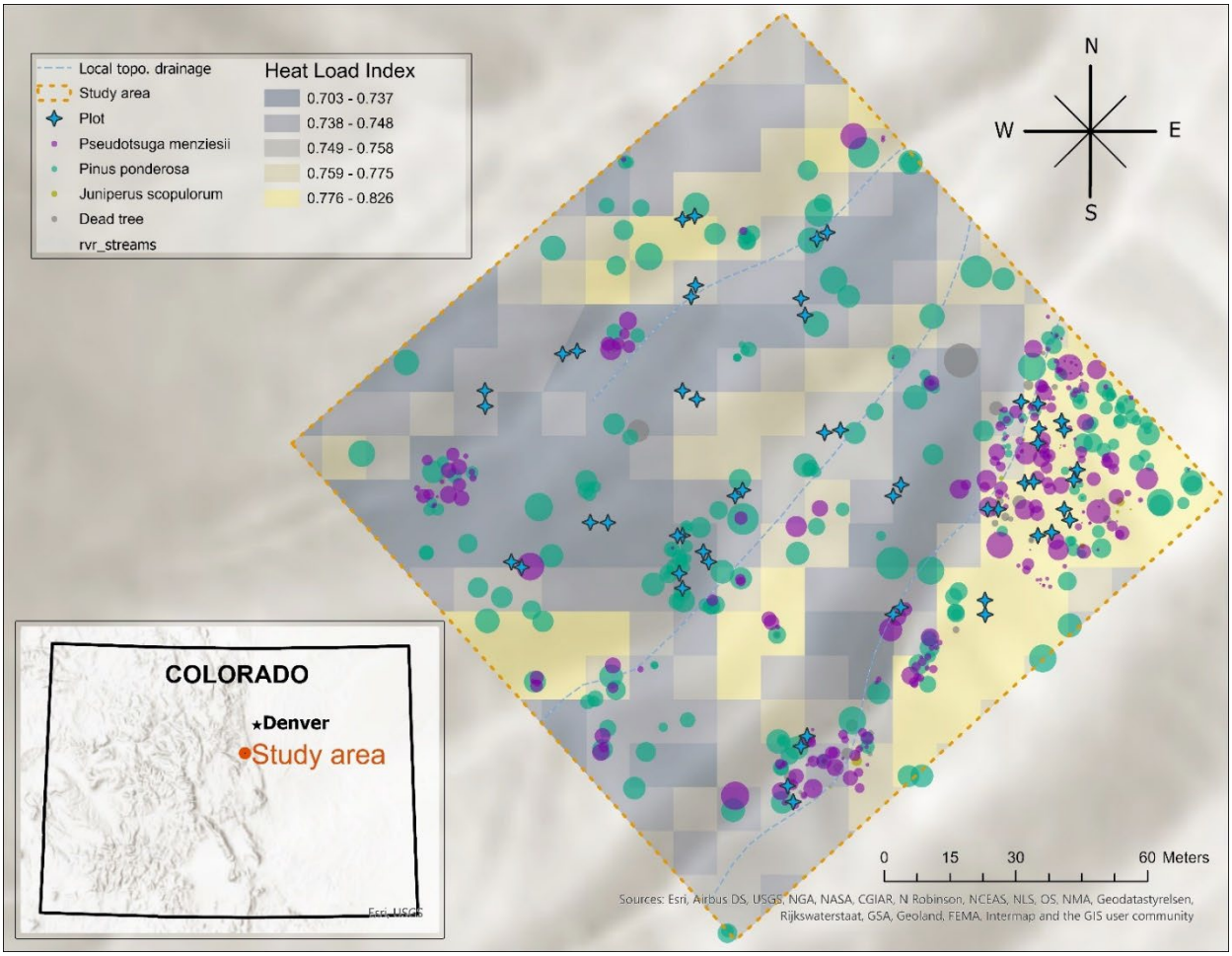

Figure 2.2. *Study area within a large, spatially heterogeneous forest restoration treatment (area not shown) in the Colorado Front Range. Circles denote tree locations of ponderosa pine (green) and Douglas-fir (purple), where the size of the circle corresponds to tree size (diameter at breast height). Topographic heat load index is represented by a blue to yellow shading gradient, indicating cooler and hotter topographic positions, respectively. Plot locations (blue stars) were established using a stratified random design to capture gradients in overstory tree density and topographic solar radiation exposure.*

Average annual precipitation in the study area is 58 cm (± 9.3), concentrated in winter and early spring (~ 85% of annual). Annual mean temperature is 8.6 °C (± 0.6), with cold winters (-0.3 °C ± 1.0) and hot summers (18.4 °C ± 0.9). Weather conditions in the study area observed during the study (2019-2021) varied considerably each year (Figure 2.2). At the start of the study (May 2019), conditions were exceptionally cool, with vapor pressure deficit (VPD) nearly 2 standard deviations below the long-term climate record (Figure 2.2A), though precipitation was

average (Figure 2.2B). By the end (September) of the 2019 growing season, VPD was particularly high at nearly 2 standard deviations above the long-term average. In contrast, VPD conditions during the 2020 growing season were overall higher than the long-term climate record, with an especially hot and dry August 2020 (2 standard deviations above the long-term average). The 2021 growing season was broadly average and included a particularly wet May and high VPD conditions in September. All climate data were accessed from the ClimateNA project website (http://climatena.ca/, 01/03/2022; Wang et al., 2016).

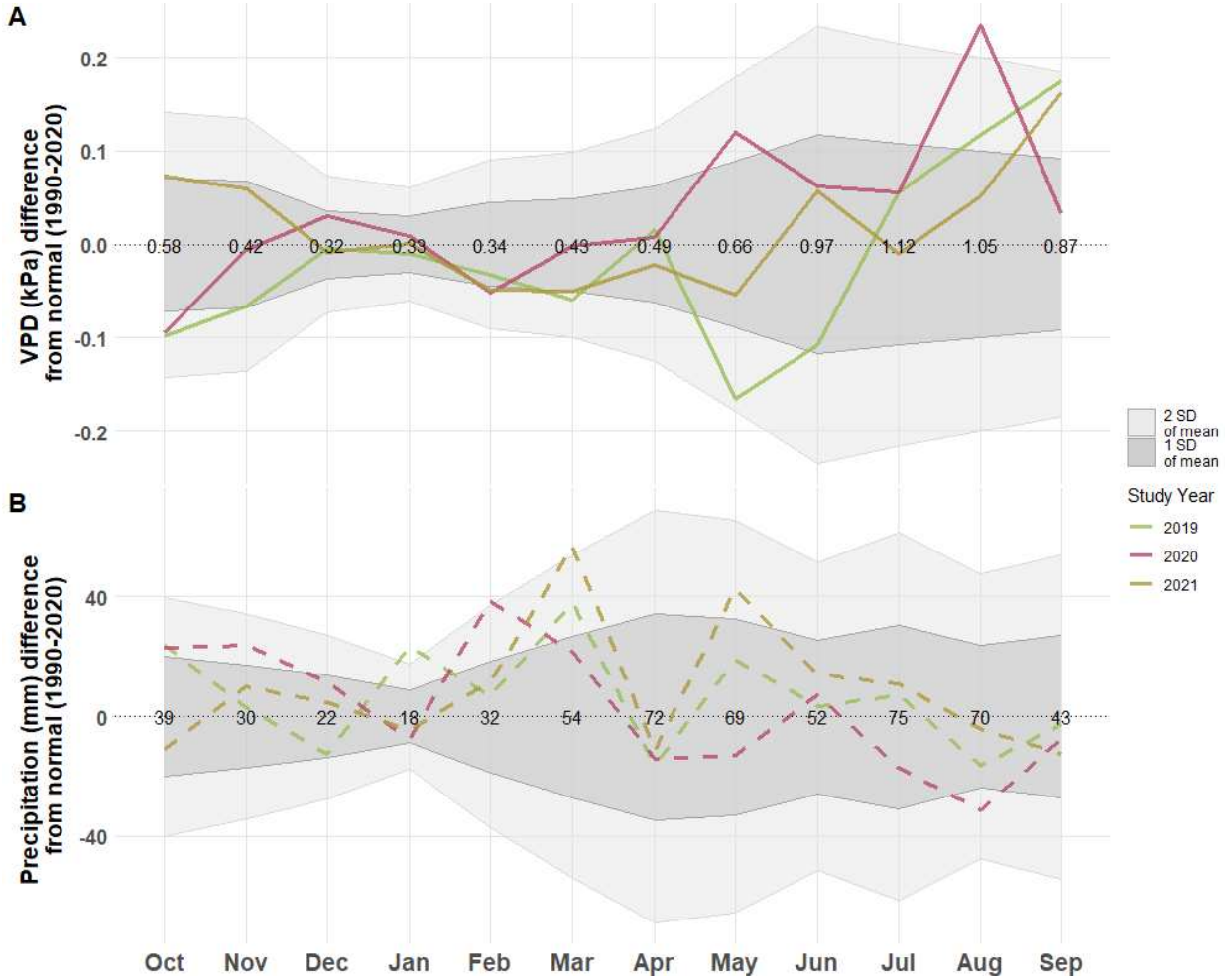

Figure 2.3. *Climate conditions for the study area expressed as differences from 30-year monthly averages (1990-2020) over the water year (October of the previous year – September of the current year). Climate variables shown are vapor pressure deficit (VPD; panel A, solid lines) and precipitation (panel B, dashed lines). Conditions for each year of this study are shown with colored lines: 2019 (green), 2020*

(red), and 2021 (brown). Gray shadings indicate 1 standard deviation (darker gray) and 2 standard deviations (lighter gray) from the 30-year average. For reference, actual mean monthly values for VPD and precipitation are displayed along the zero line in each panel. All climate data were accessed from the ClimateNA project website (http://climatena.ca/, 01/03/2022; Wang et al., 2016).

Experimental design and field sampling

To understand how fine-scale variation in overstory structure buffers weather conditions and influences stand dynamics, we monitored microclimate conditions and juvenile germination, survival, and growth across a broad range of topographic positions and local tree densities. We established 54 plots using a stratified random sampling design to capture fine-scale spatial variation in tree structure and topography in our 2.25 ha study site (Figure 2.1). To accomplish this, we stem-mapped all trees > 2 cm diameter at breast height (dbh) across the site. Using the stem-map and solar radiation data, we divided our study site into five strata of overstory tree density (using a 15 m neighborhood) and two strata of topographic mean daily solar radiation exposure (see Appendix 1:Supplementary Material). We randomly located 26 plots across the resulting 10 strata combinations at a minimum inter-plot distance of 15 m. We then used locations of each initial plot to locate a second set of 26 plots with a random azimuth and distance between 2-4 m to further capture fine-scale variations in microclimate conditions potentially meaningful for tree regeneration.

Structure, topography, and microclimates (Objective 1).

At each plot, we quantified elements of overstory structure and topography expected to influence the regeneration environment (e.g., light, temperature, and moisture). We took hemispherical photographs at 30 cm above ground height (representative of seedling growing environments) at each plot and derived estimates of canopy openness (“SKY”, %; complement of canopy cover; WinSCANOPY Pro 2016a software, Regent Instruments, Inc., Québec, Canada) to use in analyses of structural effects on regeneration responses. We also calculated

basal area ("BA", m^2 per plot) at 5-20m radii for each plot but kept only 5m values ("5m BA") for subsequent analysis (in addition to canopy openness) since all larger radii were highly correlated (Pearson's $|r| >= 0.70$) with canopy openness. To estimate topographic variation, we took field measurements of slope aspect and angle to calculate heat load index ("HLI"; McCune and Keon, 2002) at each plot.

From May 2019 through September 2021 (excluding October-April each year), we used an array of environmental sensors to monitor microclimates at each plot. We affixed air temperature and humidity sensors (iButton Hygrochron, Maxim Integrated Products, Santa Rosa, CA), recording at 0.5 hr timesteps, in gill-style radiation shields (Holden et al., 2013). We secured sensors to small posts 15 cm above the ground surface to sample microclimate conditions representative of what small juvenile trees experience, and because these near-surface conditions can be more strongly buffered by canopy cover compared to conditions further from the ground surface (Campbell and Norman, 2012; Davis et al., 2019b). We used temperature and humidity measurements to calculate corresponding VPD values for each timestep. We used mean daily VPD and maximum VPD ("MaxVPD") in all subsequent analyses given the importance of VPD in driving plant stress (e.g., Grossiord et al., 2020). Additionally, we sampled soil moisture (7 cm depth) and soil temperature (soil surface) at each plot location 24 times (weekly) for the first growing season (May-September 2019), using soil capacitance and temperature sensors (SoilWatch 10, Pino-Tech, Strachocin, Zachodniopomorskie, Poland) connected to an Arduino microcontroller (Sparkfun, Niwot, CO) (Cannon et al., 2022). Due to personnel availability, we reduced the number of soil moisture samples taken to 12 in the 2020 season, and 3 (May, July, September) in the 2021 season. Sensor capacitance values were converted to soil volumetric water content ("soil VWC") using a lab calibration procedure (see Appendix 1:Supplementary

Material). We then summarized microclimate data to daily mean values for all variables (VPD, MaxVPD, soil VWC, soil T) at each plot, and calculated the monthly (May-September) and yearly (2019-2021) averages to be used in analyses.

Juvenile life-stages, survival, and growth (Objective 2).

To assess how microclimate affects seedling germination, growth, and survival across multiple weather years, we seeded both ponderosa pine and Douglas-fir in multiple years and planted seedlings at each plot. Although non-tree vegetation cover was minimal and patchy on our study site, we chose to scarify each plot prior to planting in the first year of study (2019) to limit the influence of any vegetation on establishment (see Appendix 1:Supplementary Material for additional details on vegetation). We sowed 32 seeds (untreated, see Appendix 1:Supplementary Material) per species per plot and protected seeds with rodent exclosures at the beginning (28 April – 1 May) of the 2019 and 2020 growing seasons ("new germinant seedlings"; n = 1,728 per species per year). At the beginning of the 2019 season, we also planted three 1-year old, greenhouse-grown (US Forest Service Bessey Nursery, Halsey, NE) seedlings of each species ("older seedlings") in each plot (n = 162 per species). Placement of seeds and plantings were randomized in cells of a 3x3 grid within each 1 m^2 plot, excluding the center cell of the grid which was used for sampling soil moisture (see Appendix 1:Supplementary Figure S2.1). Population sources for seeds and older seedlings of each species were from USFS Pike National Forest collections obtained from the USFS Bessey Nursery (Halsey, NE). We monitored germination of seeds throughout each growing season (May-September) at the same time as sampling soil moisture, and recorded survival of new germinant seedlings and older seedlings at the end of each season. Lastly, to assess how older seedling growth varied in relation to biophysical conditions, we measured basal diameter for all older seedlings at the time of planting

(2019) and the conclusion of the final growing season (2021) (Davis and Jacobs, 2005).

Analysis

Structure, topography, and microclimates (Objective 1).

To understand how fine-scale structural, topographic, and microclimate variation affect tree regeneration, we assessed bivariate relationships between all variables of interest. We computed correlations (Pearson's *r*) between overstory structure (canopy openness and 5m BA), topography (HLI), and all temporal variants of our microclimate variables (monthly and yearly averages of VPD, MaxVPD, soil VWC, and soil T). We used this information to evaluate general patterns and the strength of canopy-driven microclimate buffering, and to inform our interpretation of survival and growth model results.

Juvenile life-stages, survival, and growth (Objective 2).

We used a series of generalized linear models to assess how fine-scale spatial variation in biophysical conditions influence survival of ponderosa pine and Douglas-fir at different stages of physical maturity. We first evaluated separate models for each species, life-stage (first-year new germinant seedlings, and older seedlings), and year of study (2019, 2020, 2021). Survival was analyzed separately for each life-stage and year of study to evaluate the potential for distinct responses over time, given that limiting conditions may not have been equivalent across years and life-stages. Due to low survival and resulting sample sizes, we were unable to fit models for germinant seedlings surviving beyond their first season. We also constructed survival models inclusive of all years of survival data for each life-stage ("integrated survival models"). We used these integrated survival models to test whether structure, topography, and microclimate consistently influenced survival throughout the study (e.g., the potential for May conditions to be important for survival outcomes within each year). All survival responses were modeled in a

generalized linear model framework, with a binomial error distribution and a logit link function using "glm" in the *stats* package of R (R Core Team, 2020). We modeled survival as a proportion in each plot, adjusted for the number of cases (individual trees) using the "weights" argument. For the integrated survival models, we included year of study as a random intercept ("glmer" in the *lme4* package; Bates et al., 2023) in older seedling models and as a fixed effect in germinant seedling models, the latter due to model convergence issues with the more complex mixed-model form. To simplify our results and discussion, we focus largely on integrated survival models and include details for all models in Appendix 1:Supplementary material.

For all survival models, we considered two separate sets of potential predictor variables: (1) stand structure and topographic variables, and (2) microclimate variables. This separation was made to fully address study objectives, since microclimate variables were often highly correlated with structural variation. For structural-topographic models, we fit models including canopy openness (% SKY) and local tree density (5m BA), to evaluate overstory structure effects at both broader and very fine (localized) spatial extents, and a topographic variable (HLI). We also evaluated relative support for the inclusion of an interaction between HLI and both structural variables; we included any interaction when supported above models excluding the interactions ($\Delta AIC_c < 2$). For microclimate variables, we chose variables to retain for fitting final models with a dimension reduction process. In this process, we first evaluated all model subsets (i.e., monthly and yearly time periods) within each category of microclimate variable (VPD, including MaxVPD; soil VWC; and soil T). If multiple univariate models had similar support in the best model subset for each category of microclimate variable, we chose the variable with the highest correlation with the response variable to use in a final model. Due to strong collinearity with VPD, soil T variables were only considered in a few microclimate models across species

and life stages. In final microclimate models, we considered inclusion of two-way interaction terms between (Max)VPD and VWC variables. For both structural-topographic and microclimate models, we visually inspected data for evidence of non-linear relationships between the response variable and predictor variables and included quadratic terms in models when these relationships were strongly evident. For older seedling models, we included basal diameter (measured at the time of planting) as a fixed effect in all models to control for its strong influence on survival outcomes (Davis and Jacobs, 2005).

After selecting terms to include in each set of final models, we fit the resulting models. We inspected variance inflation factors ("vif" function in the *car* package; Fox and Weisberg, 2019) and removed variables with high inflation factors until all resulting inflation factors were ≤ 2.5, a conservative threshold for smaller data sets. We assessed the importance of estimated model effects by looking at confidence intervals (bootstrapped) and standardized effect sizes. Estimated model effects with confidence intervals that overlapped zero were considered insignificant. All covariate data were standardized (scaled and centered) prior to model fitting to directly compare relative importance via effect size. Finally, to assess fit of each logistic survival model, we computed receiver operating characteristic curves and area under the curve (AUC, Fawcett, 2006; "multiclass.roc" function in the *pROC* package, Robin et al., 2011).

To evaluate influences of overstory structure, topography, and microclimate on seedling growth, we calculated the relative basal diameter growth of older seedlings at each plot by calculating growth over the study period (2021 size minus 2019 size at planting) and dividing by the 2019 size at planting for each older seedling. We assessed structural–topographic, and microclimate influences on growth using linear models with weights corresponding to number of individuals, verifying that errors were normally distributed. Variable selection, model fitting, and

model evaluation followed the same processes as survival models, except that linear model fits were assessed with adjusted R^2 values.

RESULTS

Structure, topography, and microclimates (Objective 1)

Overall, microclimate VPD conditions were strongly related to overstory structure, but not topography, and these relationships varied in strength seasonally and yearly (Figure 2.3). Reflecting the spatial heterogeneity of overstory structural conditions at the site, canopy openness ranged between 22.1 and 73.5% with a mean of 47.5% (± 14.9) and BA ranged 0.00 to 0.43 m^2 (per 5m radius plot) with a mean of 0.12 m^2 (± 0.11) (see Appendix 1:Supplementary Table S2.1 for a detailed summary of all variables). Spatial variation in mean growing season VPD was strongly related to canopy openness (r = 0.73) but only moderately (r = -0.44) with local tree density (BA at 5m) (Figure 2.3A). The strongest correlations between mean daily VPD and canopy openness occurred when monthly VPD was highest (1.68 kPa ± 0.11, July-August 2020; r = 0.74-0.77) and lowest (0.55 kPa ± 0.05, May 2019; r = 0.75) (Figure 2.3A-B). In contrast to the overall strong relationships between overstory structure and VPD, correlations between VPD and HLI (which had limited variability, ranging 0.74 - 0.97) were low (r = -0.14 overall). Relationships between overstory structure and soil T were similar to VPD but were much more moderate for mean daily MaxVPD on average (r = 0.45; Figure 2.3A).

Relationships between soil VWC (7 cm depth) and overstory structure were less consistent than those of VPD (Figure 2.3A) and were both negative and positive at different times of the study. Soil VWC was strongly and negatively associated with canopy openness (r = -0.57) during the hottest and driest period of the study (July 2020) but was not associated with

canopy openness during other hot and dry periods (e.g., Aug-Sep 2020 and Sep 2021; Figure 2.3A-B). The relationship between soil VWC and canopy openness for all other periods in the study was positive, but minimal in strength (r = 0.13-0.35).

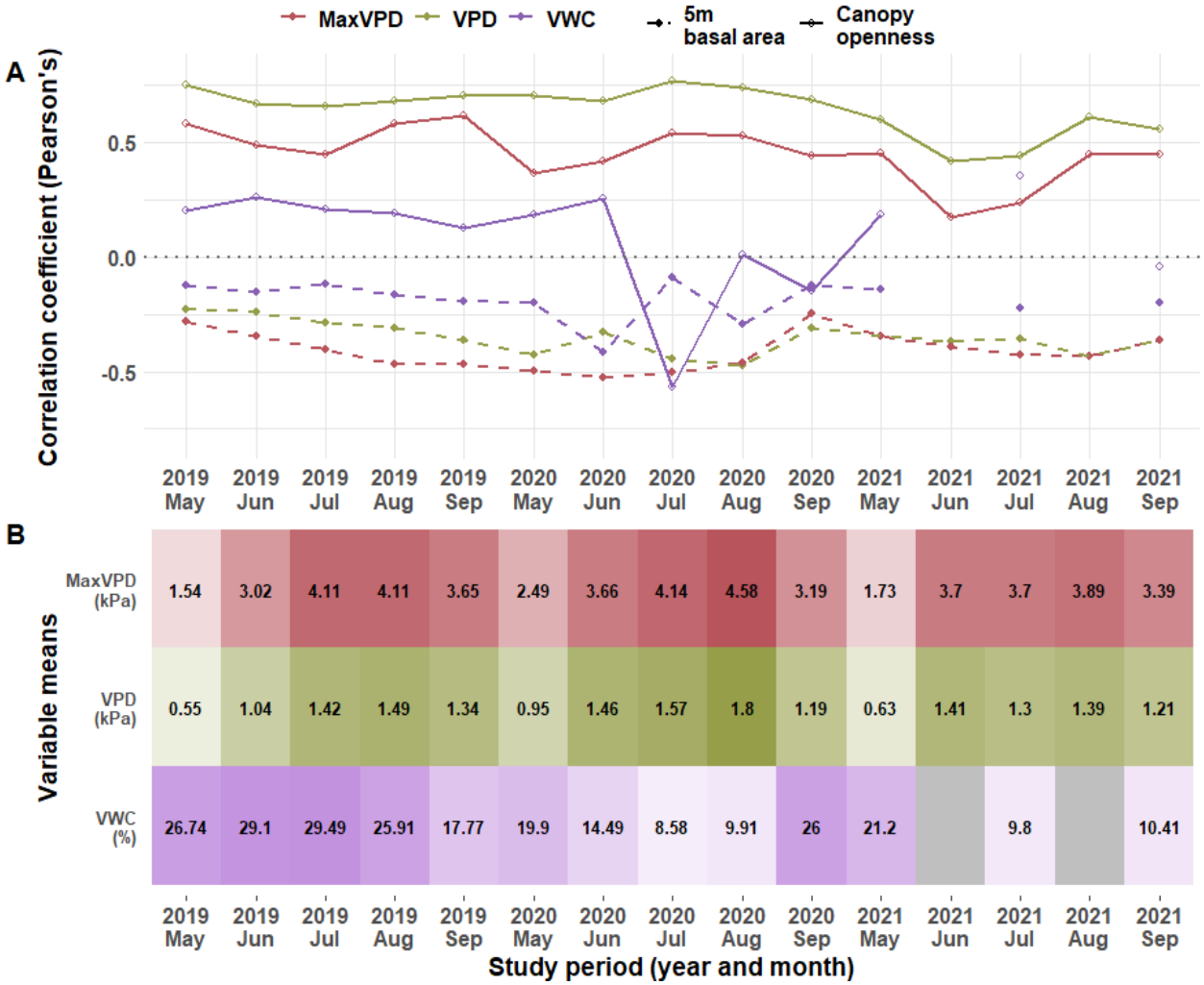

Figure 2.4. *Correlations (Pearson's r) for select microclimate variables and overstory structural variables (A), and mean values for select microclimate variables (B), over the course of the study (May-September in 2019-2021, x-axis). Variable shadings for mean values (B) correspond to monthly magnitude differences across the study period for mean values within each variable, illustrating periods of aligned above- and belowground abiotic stress or relative lack thereof (sampling of soil VWC did not occur in June and August 2021, indicated by gray shading). Mean daily (green) and maximum (red) VPD showed different but consistent correlations with both canopy openness (A, solid lines) and 5m basal area (A, dashed lines), while soil VWC (purple) correlations were generally more variable with both overstory structure variables. The strongest correlations (A) across microclimate variables occurred in the hottest and driest period of study (B), in July-August 2020.*

Juvenile life-stages, survival, and growth (Objective 2)

New germinant seedling survival.

Overall, across both species and years in which seeds were sown (2019 and 2020), germination rates ranged from 3-19%, first-year survival of new germinant seedlings was low (< 6%), and only individuals seeded in 2019 survived beyond their first growing season (see Appendix 1:Supplementary Table S2.2 for detailed survival data). First-year survival of new germinant seedlings in 2019 was 5.4% (±17.2 of those that germinated, n = 266) for ponderosa pine and 1.5% (± 6.7 of those that germinated, n = 322) for Douglas-fir. After the first year, subsequent survival (2020-2021 seasons) of individuals of both species from this 2019 cohort was generally high (>45%). For new germinants seeded in 2020, first-year survival for ponderosa pine was 4.3% (± 15.3, n = 51) and for Douglas-fir was 3.8% (± 10.5, n = 142). No individuals of the 2020 seeded cohort for either species survived into subsequent seasons.

New germinant survival was predicted by structural–topographic, and early- and late-season microclimate variables for both species (Table 2.1 and Figures 2.4-2.5). Integrated survival models for ponderosa pine showed a significant positive relationship with canopy openness, with survival highest above 50%, and a quadratic relationship with 5m BA, peaking at ~ 0.20-0.25 m^2 (per 5m radius plot) (Figure 2.4A-B). Individual year modeled effects were similar (Appendix 1:Supplementary Table S2.3), except survival in 2020 tended to be highest at plots with low (< 35%) canopy openness. In microclimate models, ponderosa pine had a significant quadratic relationship with May VPD (Figure 2.4C), with modeled survival peaking just above mean conditions across the three study years, though actual survival between years occurred in substantially different ranges. Douglas-fir new germinant survival was not associated with any of the structural variables in the integrated models but was negatively associated with HLI (Figure 2.5A). In addition, Douglas-fir germinant survival was highest in plots with

moderate-to-high canopy openness in 2019 and low canopy openness in 2020, similar to ponderosa pine (Appendix 1:Supplementary Table S2.3). Douglas-fir also had a significant quadratic relationship with May VPD conditions similar to ponderosa pine, though for Douglas-fir this relationship occurred with maximum VPD (Figure 2.5B). Douglas-fir germinant survival also showed a significant negative relationship with September mean VPD (Figure 2.5C), and a significant positive relationship with September soil VWC (Figure 2.5D). In 2020, Douglas-fir germinant survival was also negatively associated with August soil temperature (Appendix 1:Supplementary Table S2.3).

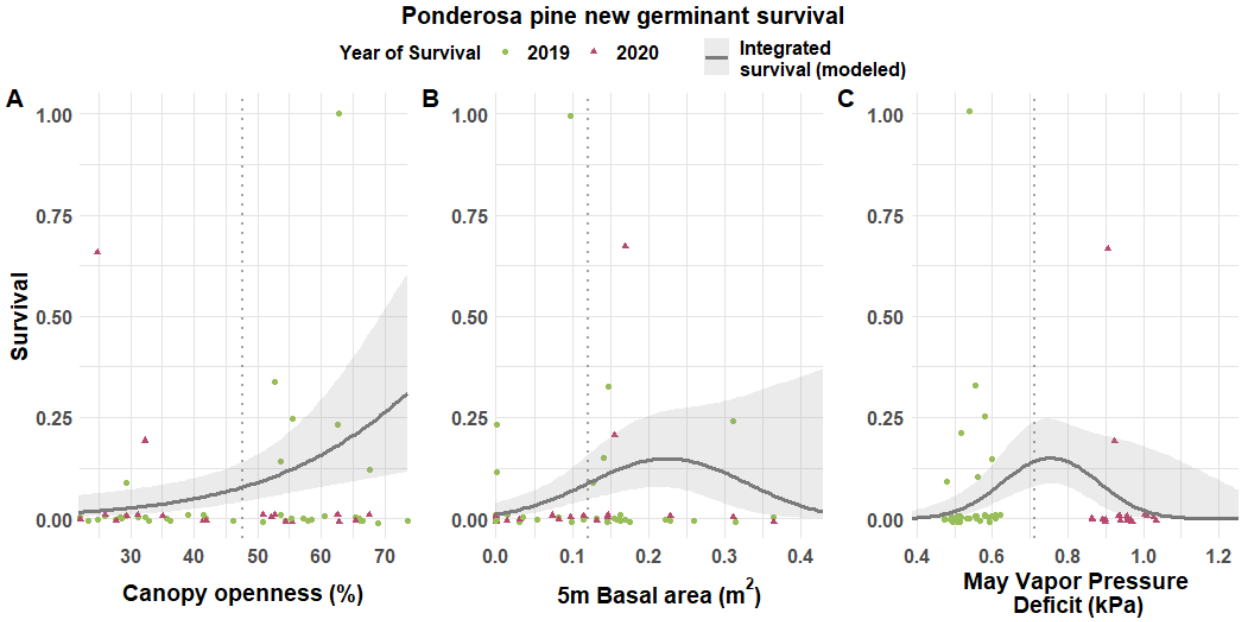

Figure 2.5. *Marginal effects of significant predictor variables for ponderosa pine new germinant survival. Predicted survival probability is indicated by solid gray lines, with gray shading showing prediction uncertainty (standard errors). Significant predictors include canopy openness (A), 5m basal area (B), and May mean daily VPD (C). Actual survival data are shown with points (proportion survival in a plot) corresponding to individual years of first-year survival data, for seeds planted in 2019 (green) and 2020 (red). Vertical black dotted lines indicate the mean value observed for each significant predictor variable.*

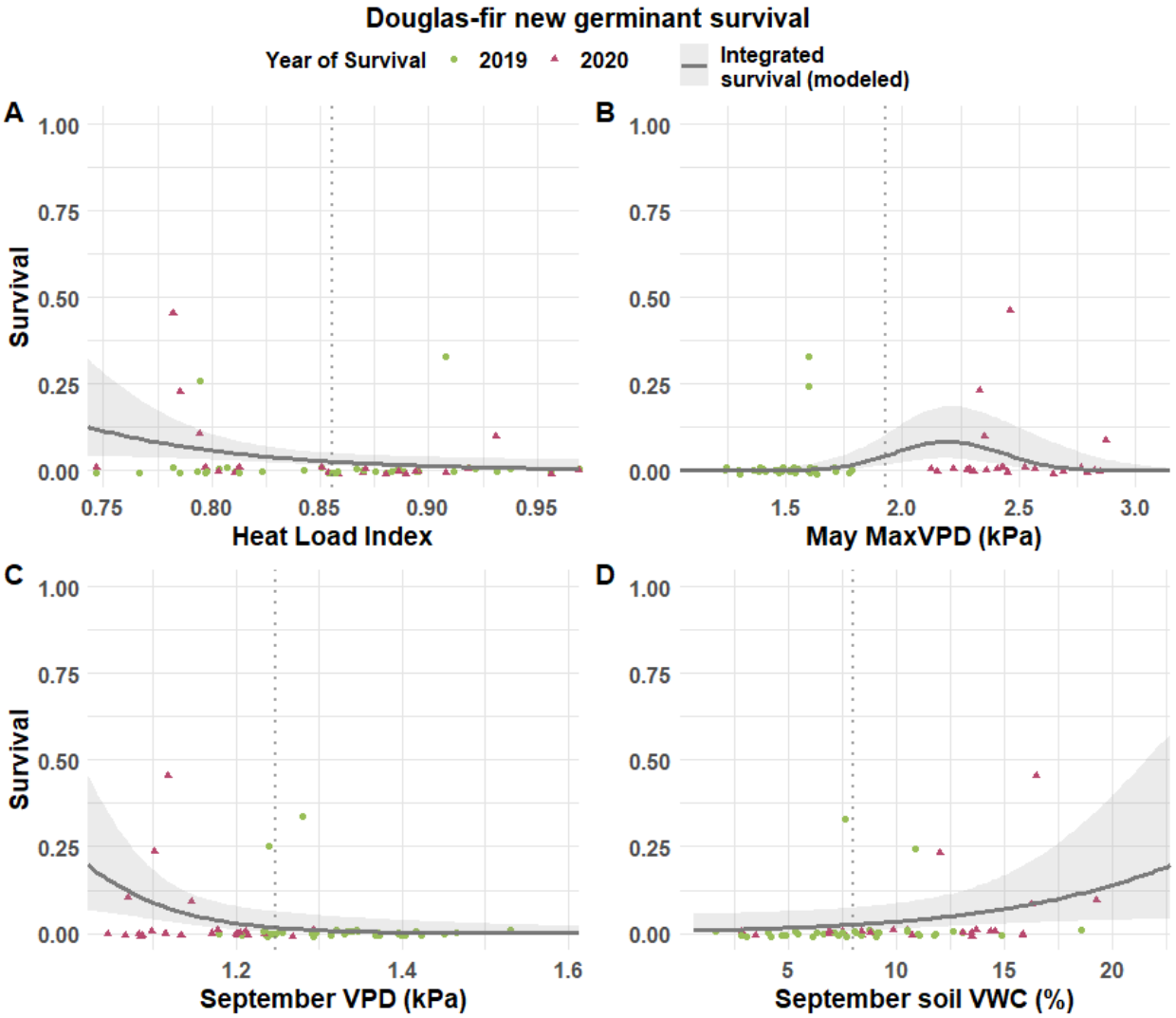

Figure 2.6. *Marginal effects of significant predictor variables for Douglas-fir new germinant survival. Predicted survival probability is indicated by solid gray lines, with gray shading showing prediction uncertainty (standard errors). Significant predictors include topographic heat load index (A), May mean daily maximum VPD (B), September mean daily VPD (C), and September soil VWC (D). Actual survival data are shown with points (proportion survival in a plot) corresponding to individual years of first-year survival data, for seeds planted in 2019 (green) and 2020 (red). Vertical black dotted lines indicate the mean value observed for each significant predictor variable.*

Table 2.1. *Integrated survival and growth model results for all life-stages and species. Results are organized by model type ("structure-topography" and "microclimate" models) and variable type considered in each model. Microclimate model results also include detail for the time period of significant predictors in parentheses. Quadratic model terms are also indicated in parentheses. Directionality of significant effects are shown by "+" and "-." Non-significant effects are designated as "ns," while "NA" is used to indicate where terms were not included in models (due to high multicollinearity with other variables or otherwise not applicable to a given model). Older seedling models for both species also included significant positive effects of basal diameter (not shown).*

Model and Variable Types		Ponderosa Pine			Douglas-fir		
		First-year new germinant seedlings	***Older Seedlings****	***Growth (proportional)***	***First-year new germinant seedlings***	***Older Seedlings****	***Growth (proportional)***
		Integrated	*Integrated*	*2019-2021*	*Integrated*	*Integrated*	*2019-2021*
Structure-topography	***Canopy Openness (SKY)***	+	-	+	ns	ns	+
	5m Basal Area (5m BA)	+/- (quadratic)	ns	ns	ns	+/- (quadratic)	ns
	Topographic HLI	ns	ns	+	-	ns	+
	Structure * HLI (SKY or 5m BA * HLI)	NA	- (5m BA * HLI)	ns	NA	- (5m BA * HLI)	+ (SKY * HLI)
Microclimate	***Vapor pressure deficit (VPD and MaxVPD)***	+/- (May VPD, quadratic)	- (Sep VPD)	ns	+/- (May MaxVPD, quadratic) - (Sep VPD)	- (Sep VPD)	- (Sep 2021 VPD)
	Soil moisture (VWC)	ns	ns	ns	+ (Sep)	- (May)	ns
	Soil temperature	ns	ns	+ (May 2019) - (Aug 2020)	ns	ns	+ (May 2019) - (Aug 2020)

** Older seedling models included significant positive effects of basal diameter (at time of planting)*

Older seedling survival and growth.

Older seedling survival for both species was high throughout the study period and variable relative to observed biophysical conditions, and total (3-year) survival was twice as high for ponderosa (64%) compared to Douglas-fir (32%). In individual years, survival of ponderosa pine older seedlings was 83% (n = 162), 83% (n = 134), and 92% (n = 111) in years 2019-2021, respectively. Survival of Douglas-fir older seedlings was 48% (n = 161), 73% (n = 77), and 93% (n = 56) in years 2019-2021, respectively.

Integrated survival models for older seedlings showed strong similarities between species for structural-topographic and microclimate influences (Figures 2.6-2.7), and these results were nearly the same as 2019 individual year modeled effects, while other individual year models showed almost no significant effects (Appendix 1:Supplementary Table S2.3). Integrated ponderosa pine survival was negatively correlated with canopy openness especially at values > 60% (Figure 2.6A). Ponderosa pine survival also had a significant relationship with the interaction of 5m BA and HLI (Figures 2.6B), where survival declined as local tree density increased on hotter topographic positions, while remaining relatively high on cooler topographic positions with increased density. In microclimate integrated survival models, ponderosa pine had a significant negative relationship with September VPD (Figures 2.6C). Lastly, basal diameter (at the time of planting) had a very strong, significant positive effect on ponderosa pine survival (Figures 2.6D). Survival of Douglas-fir older seedlings was related to the interaction of 5m BA and HLI in the same manner as ponderosa pine (Figure 2.7A), though Douglas-fir survival also had a quadric relationship with 5m BA, with survival highest near the mean 5m BA across plots (~0.1-0.25 m^2 per 5m radius plot). Douglas-fir survival was negatively related to May soil VWC (Figure 2.7B) and, like ponderosa pine, with September VPD (Figure 2.7C). For Douglas-fir, the

positive effect of basal diameter (at the time of planting) on survival (Figure 2.7D) was stronger than that for ponderosa pine.

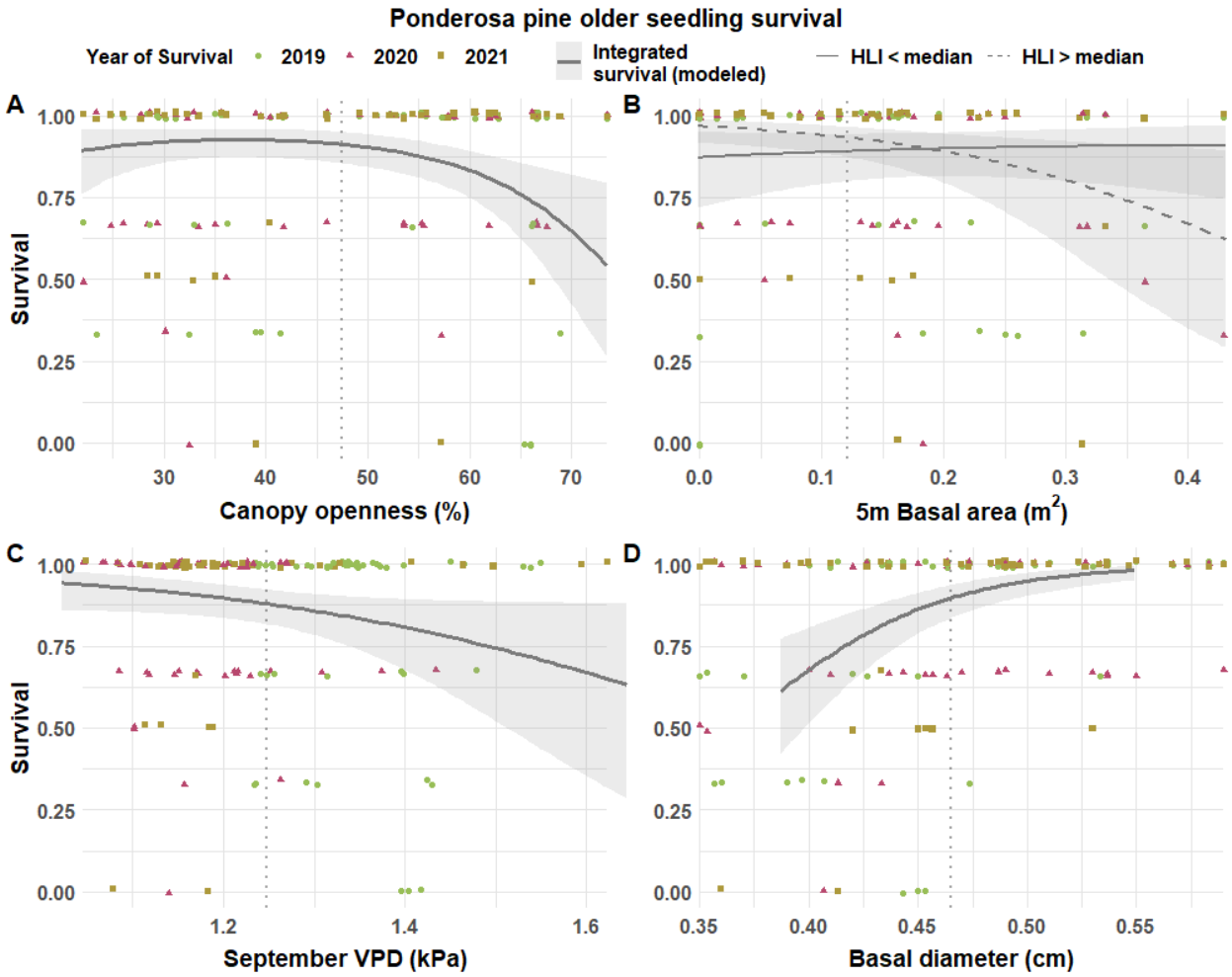

Figure 2.7. *Marginal effects of significant predictor variables for ponderosa pine older seedling survival. Predicted survival probability is indicated by gray fit lines, with gray shading showing prediction uncertainty (standard errors). Significant predictors include canopy openness (A), the interaction of 5m basal area and HLI (B), September mean daily VPD (C), and basal diameter at the time of planting (D). The interaction of 5m basal area and HLI is shown with fit lines indicating predictions below the median HLI (solid line) and above the median HLI (dashed line). Actual survival data are shown with points (proportion survival in a plot) corresponding to each year in which older seedlings survival was monitored, including 2019 (green), 2020 (red), and 2021 (yellow). Vertical black dotted lines indicate the mean value observed for each significant predictor variable.*

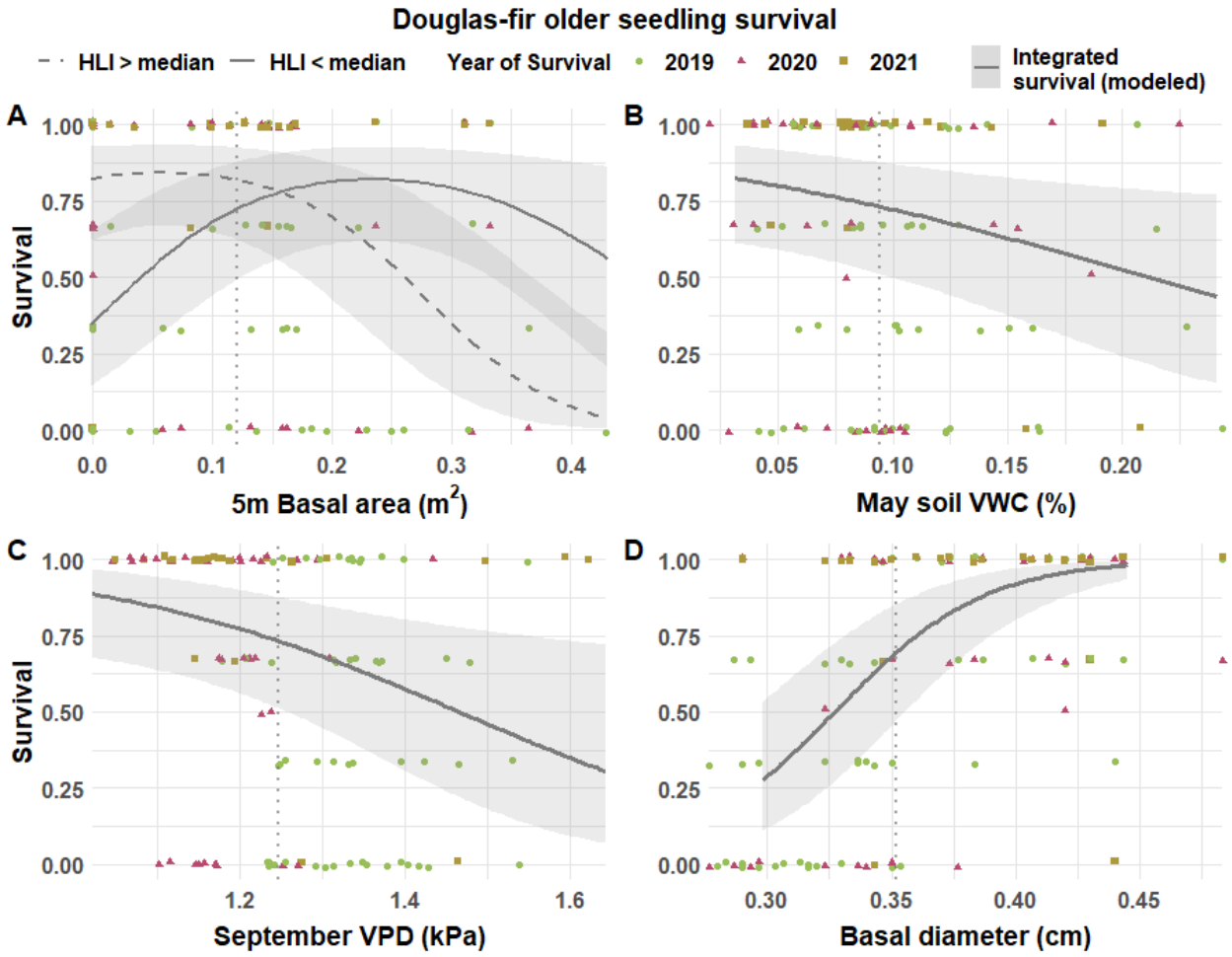

Figure 2.8. *Marginal effects of significant predictor variables for Douglas-fir older seedling survival. Predicted survival probability is indicated by gray fit lines, with gray shading showing prediction uncertainty (standard errors). Significant predictors include interaction of 5m basal area and HLI (A), May mean soil VWC (B), September mean daily VPD (C), and basal diameter at the time of planting (D). The interaction of 5m basal area and HLI is shown with fit lines indicating predictions below the median HLI (solid line) and above the median HLI (dashed line). Actual survival data are shown with points (proportion survival in a plot) corresponding to each year in which older seedlings survival was monitored, including 2019 (green), 2020 (red), and 2021 (yellow). Vertical black dotted lines indicate the mean value observed for each significant predictor variable.*

Basal diameter growth for both species was highest in less dense, relatively warmer and drier microclimates (Figures 2.8-2.9). Growth of ponderosa pine was strongly and positively influenced by canopy openness (Figure 2.8A), with the highest growth occurring at >50%, and less strongly by HLI (Figure 2.8B). For microclimate variables, ponderosa pine growth was not associated with VPD nor soil VWC but was significantly positively associated with warmer soil

T in May 2019 and negatively with warmer soil T in August 2020 (Figure 2.8C and 2.8D, respectively). Douglas-fir growth was interactively influenced by canopy openness and HLI, with the greatest growth occurring at >50% openness on cooler but not hotter topographic positions (Figure 2.9A). In microclimate models, Douglas-fir growth was significantly affected by the same soil temperature variables as ponderosa pine (Figure 2.9B-C). Overall, effect sizes were much larger for the faster-growing ponderosa pine, and smaller for the slower-growing Douglas-fir (Appendix 1:Supplementary Table S2.3).

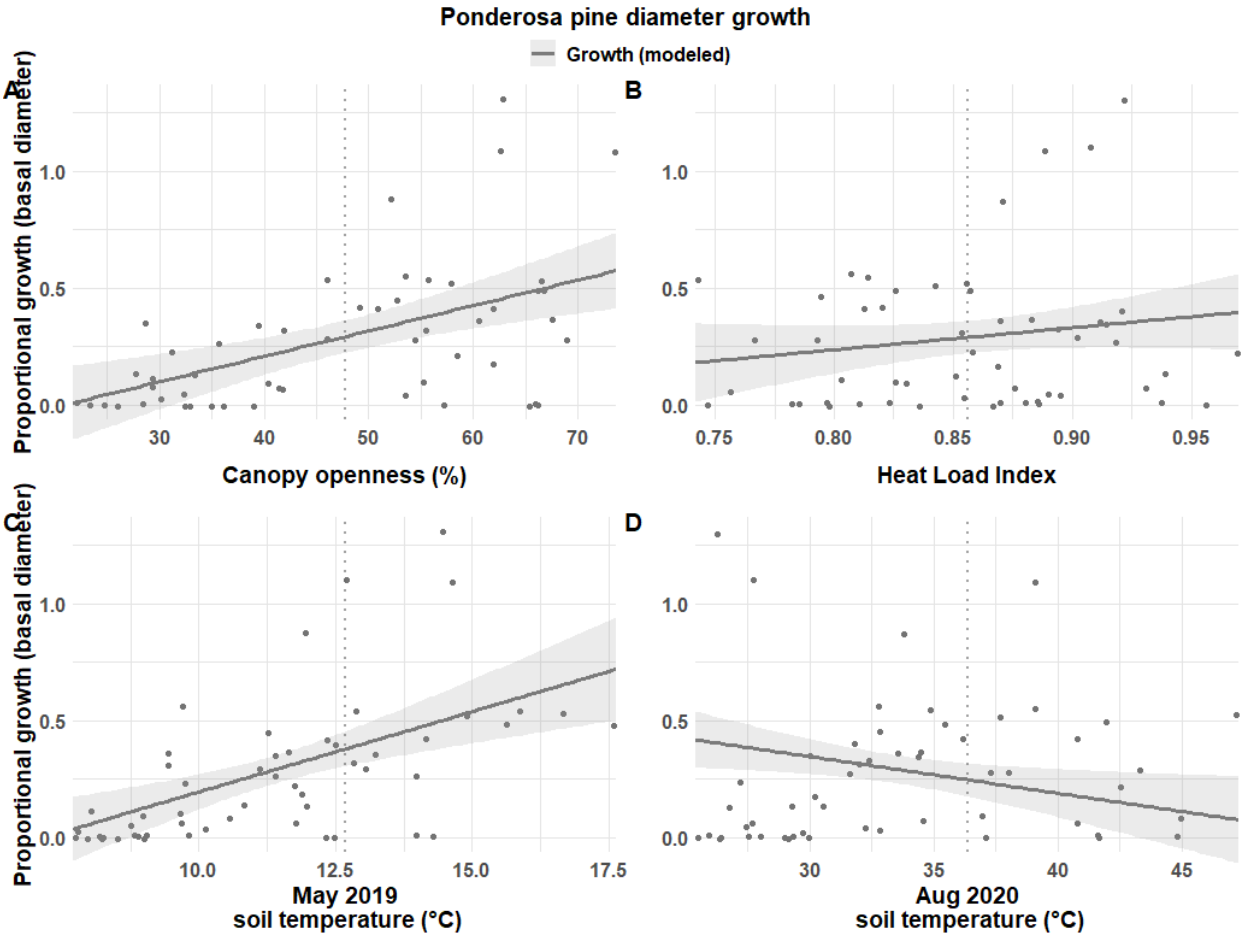

Figure 2.9. *Marginal effects of significant predictor variables for ponderosa pine older seedling basal diameter growth. Predicted growth is indicated by gray fit lines, with gray shading showing prediction uncertainty (standard errors). Significant predictors include canopy openness (A), topographic heat load index (B), mean May 2019 soil temperature (C), mean August 2020 soil temperature (D). Actual growth data are shown with gray points. Vertical black dotted lines indicate the mean value observed for each significant predictor variable.*

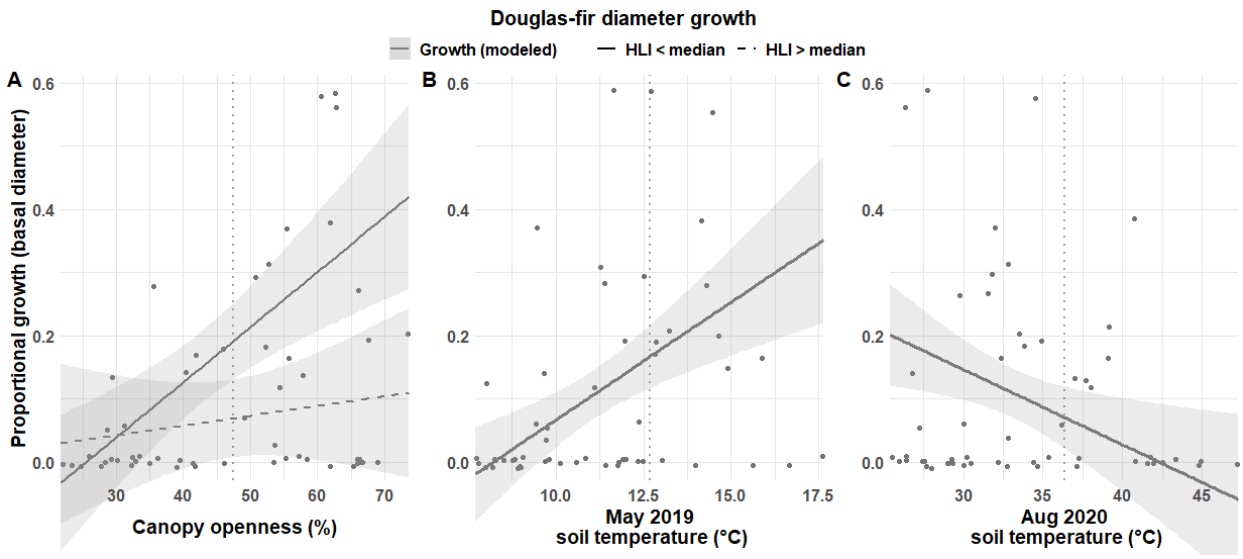

Figure 2.10. *Marginal effects of significant predictor variables for Douglas-fir seedling basal diameter growth. Predicted growth is indicated by gray fit lines, with gray shading showing prediction uncertainty (standard errors). Significant predictors include the interaction of canopy openness and HLI (A), May 2019 mean soil temperature (B), and August 2020 mean soil temperature (C). The interaction of canopy openness and HLI is shown with fit lines indicating predictions below the median HLI (solid line) and above the median HLI (dashed line). Actual growth data are shown with gray points. Vertical black dotted lines indicate the mean value observed for each significant predictor variable.*

DISCUSSION

Although our results support the importance of canopy cover for buffering environmental conditions, especially VPD, we did not find that the buffering effect promoted seedling survival and growth. Despite refuge from high VPD provided by higher canopy cover, survival and growth across life-stages and species were collectively highest in above-average canopy openness with warm and dry microclimates. These patterns seem to be driven by juvenile sensitivity to light availability and early-season warmth, but also result in exposure to later-season hot and dry microclimate conditions. The confluence of explanatory effects across life-stages and species suggests that this tradeoff provides the best opportunity for young individuals to survive and grow over time. These results do not invalidate the potential benefits of canopy-mediated microclimate refugia for tree regeneration, but provide evidence for more nuanced examination of regeneration patterns in which canopy buffering influences and interannual

weather variation may produce distinct regeneration pathways.

Structure, topography, and microclimate relationships (Objective 1)

Canopy openness had a strong and positive relationship with mean daily VPD, highlighting the substantial and reliable moderation of microclimate conditions provided by canopy cover, as found in other studies (Davis et al., 2019b; Von Arx et al., 2013). For more punctuated, extreme VPD conditions (MaxVPD), weaker relationships with canopy openness (Figure 2.3A) may suggest a diminished importance of overstory structure for ameliorating peak abiotic stress for young trees. However, the relatively stronger relationship between local (5m) basal area and maximum VPD, as compared to mean VPD, may indicate more localized moderation of diurnal VPD extremes. These results contrast with prior findings of strong canopy buffering of maximum VPD in a similar forest type (Davis et al., 2019b), likely due to a much smaller spatial scale of analysis and lower site productivity (i.e., site water balance) in this study. Instead, our results may correspond more closely with large changes in radiation penetration (and thus temperature and humidity fluctuations) that occur with relatively small changes in canopy cover (Cannon et al., 2019). This could suggest that smaller tree groupings, or smaller areas of structural variation within larger tree groups have some influence on regeneration outcomes which are sensitive to variation in maximum VPD.

The observed relationships between overstory structure and soil moisture over the study show inconsistent canopy buffering of soil moisture availability on which juvenile trees of our study species are especially dependent (Kolb and Robberecht, 1996; Sapes et al., 2019). The weakness of these relationships may be due in part to unobserved interactions such as water-use by sporadic non-tree vegetation cover and variation in soil moisture with depth (Williams et al., 2018). Recent studies in similar dry conifer forests and woodlands have demonstrated

consistently drier and less variable soil moisture patterns at shallow (<25 cm) compared to deeper soil depths, and especially in higher overstory tree density (Belmonte et al., 2022; Petrie and Savage, 2022). While we aimed to capture soil moisture patterns at a shallow depth where our young study trees' roots would likely be active, deeper moisture sources are typically more important for growth over time in these forests (Andrews et al., 2020), and should be addressed in future work. We observed only one time period with a strong relationship between canopy openness and shallow soil moisture (Figure 2.3A), which showed the opposite relationship (open microenvironments were associated with less soil moisture) of the overall trend and occurred during the hottest and driest period of the study (Figure 2.3B). This is likely due to concurrent effects of reduced soil water evaporation beneath tree canopies (De Frenne et al., 2021), little understory vegetation cover and use of shallow moisture sources (Grossiord et al., 2019), and limited transpiration by overstory trees, as they were likely more physiologically dormant at this time. Both ponderosa pine and Douglas-fir are broadly isohydric in their water-use strategies and limit water use during hot and dry periods to maintain hydraulic safety (Hubbard et al., 2001; Ruehr et al., 2014). Overall, our findings suggest that canopy cover may facilitate shallow moisture availability during very hot and dry conditions and highlight the complexity with which fine-scale spatial and temporal variations in microclimates can occur in these types of dry forests.

Survival and growth across juvenile life-stages and species (Objective 2)

Survival and growth of both species and life-stages were collectively greatest in a spatially and temporally narrow range of microenvironmental conditions: moderate-high canopy openness (~ 50-60%) and moderate local tree density (~ 0.1-0.2 m^2 basal area per 5m radius plot), with warm and dry air conditions early in growing seasons (May) and cooler, more humid

air later in growing seasons (August-September). The juxtaposition of positive responses to early-season warm and dry conditions with negative responses to later-season warm and dry conditions emphasizes the foundational role of spring conditions in shaping fine-scale spatial patterns of regeneration establishment which subsequently intersect with late-season conditions. The observed benefits of warmer and drier air conditions early in the growing season likely relate to the initiation of growing-season phenology, when trees can be highly active in their metabolic processes, especially for growth and maturation, requiring carbon gain and water movement throughout the plant (Augustine and Reinhardt, 2019; Pinto et al., 2016). Germination and establishment of ponderosa pine have been identified as benefitting from increasing mean temperatures up to 25-30 °C (Petrie et al., 2016), and juvenile trees may be especially driven by carbon acquisition and fixation for growth and later-season stress mitigation during which they may be reliant on carbon reserves (Augustine and Reinhardt, 2019; Dixit et al., 2022). Additionally, warmer and drier conditions early in the growing season are likely to accelerate snowmelt and thus the availability of soil water, especially in less dense canopy cover (Belmonte et al., 2022). Likewise, May microclimates with higher shallow soil moisture might also reflect growth constraints from lower temperatures and longer snowpack retention, leading to the observation of a negative influence of May soil moisture on Douglas-fir older seedling survival (Figure 2.7B). These results generally agree with a number of studies that identify moderate climate conditions (e.g., higher than average precipitation, lower than average temperatures) as significant predictors of ponderosa pine recruitment, especially conditions occurring in spring (reviewed in Petrie et al., 2016; see also Davis et al., 2019a and Hankin et al., 2019) and related to canopy cover (Puhlick et al., 2012). Our results suggest that these important landscape-scale factors can also mediate regeneration patterns within fine-scale, spatially heterogeneous

structural and microclimate conditions.

The intersection of microclimate effects on survival with effects on growth of both species provide insight into the role of growth and seedling size in early juvenile life-stages for coping with abiotic stresses experienced later in growing seasons. The spatial patterns of survival established by sensitivity to early-season warmth and moisture availability in this study were incongruent with refuge provided by greater canopy cover during mid-late season periods when mean VPD was highest and soil moisture was lowest. High VPD conditions have been demonstrated to be detrimental to tree survival and growth in many settings (e.g., Rother et al., 2015), and are especially acute when available water is insufficient for transpirative cooling (Grossiord et al., 2020; Kolb and Robberecht, 1996). Consequently, these juvenile trees must overcome periods of acute stress through species heat-tolerance and water-use traits (Hubbard et al., 2001) or avoid these periods of stress through growth (Pirtel et al., 2021). For older seedlings in our study, it is likely that the exceptionally large influence of seedling diameter (at the time of planting) on survival contributed to the greater range of conditions in which they survived as compared to new germinant seedlings (Hill and Ex, 2020; Shepperd et al., 2006). Because basal diameter is highly related to plant traits like root biomass (Grossnickle and Ivetić, 2022; Rose et al., 1997), these results illustrate the role of growth in young seedlings for overcoming stress induced by microclimate and environmental variation and subsequently sustaining survival through older life-stages (Stein and Kimberling, 2003; Warwell and Shaw, 2019). Because growth of both species, like survival, was strongly related to open, warmer and drier conditions, and limited by high late-season VPD and soil temperatures, these findings underscore the tradeoff that occurs with the need for carbon gain at these vulnerable young life-stages.

While our main results mirror those of others which have documented the contribution of

greater light availability (Hill and Ex, 2020; Owen et al., 2020) and warm temperatures (Balisky and Burton, 1997; Carroll et al., 2021) to higher survival and growth rates for these species, they conflict with studies which show a strong dependence of survival and growth on facilitative conditions. Recent analyses of seedling survival in similar forest types in the southern Rocky Mountain region have provided evidence of higher survival rates dependent on greater degrees of facilitating shade, and lower VPD conditions (Crockett and Hurteau, 2021; Marsh et al., 2022). While our study includes spatial and temporal occurrences of high-stress microenvironments, our study location experiences substantially more annual precipitation on average and our study did not take place following an abnormally dry winter, as did outplanting in those examples. Indeed, as demonstrated elsewhere, the role of facilitating influences may be heavily dependent on weather conditions in which establishment processes occur (Alba et al., 2019; Hill and Ex, 2020). Ultimately, our study results suggest that despite the capacity for fine-scale overstory structural variation to provide microclimate refugia, especially in the hottest and driest periods (e.g., July-August 2020), those refugia do not align with conditions which are more generally supportive of survival and growth in this comparatively wetter dry conifer forest.

The significant influences for integrated survival in our study are clearly influenced by the abnormally cool and humid conditions in May of the first year of study (2019), and illustrate how different juvenile establishment and development trajectories may be initiated through varying interactions of weather and microclimates (Loranger et al., 2016; Werner et al., 2019). This is highlighted by the diverging results from the two cohorts of new germinant seedlings in our study, where the effects of canopy openness on juvenile survival were nearly opposite between the two years (Appendix 1:Supplementary Table S2.3). Moreover, the only individuals to survive into subsequent seasons for both species were from the 2019 cohort, the year with

exceptionally cool and wet early-season conditions (Appendix 1:Supplementary Table S2.2). These results are consistent with a pulse model of regeneration patterns observed in longer-term, landscape-scale reconstructions in similar dry conifer forests, where regeneration cohorts have typically been associated with periods of above-average precipitation and below-average temperatures (League and Veblen, 2006; Savage et al., 1996). Although climate data indicate that precipitation was average in 2019 (Figure 2.2B), we did observe the highest overall soil moisture availability in 2019 relative to other years, which coincided with abnormally low VPD conditions. Therefore, our results reflect a particular regeneration trajectory initiated in below-average VPD conditions which resulted in survival resilience for both life-stages across subsequent periods of our study, including the above-average hot and dry September 2019 and May-August 2020 (Figure 2.2A).

Effects of microclimates on survival identified in this study are also similar to climate thresholds recently demonstrated by Davis et al. (2019a) for ponderosa pine and Douglas-fir recruitment events in the northern Rocky Mountain region. In their work, the authors identified ponderosa pine recruitment success dependent on VPD below 1 standard deviation of the normal climate mean and soil moisture greater than 6.5% in the driest month; in our study, new ponderosa germinants survived predominantly below this same threshold and did not experience soil moisture below 6.5%. Our observed conditions (Appendix 1:Supplementary Table S2.1) did not exceed identified surface (soil) temperature thresholds identified by Davis et al. (2019a) for Douglas-fir recruitment, and our early-season moisture was similar to their 28% spring moisture threshold, though their definition for spring also included prior, historically wetter months (versus only May in our study). In contrast, all of these thresholds were exceeded in 2020; while older seedlings, having established in 2019, were largely able to sustain survival through this

period, new germinant seedlings of the 2020 cohort did not establish. With these broad similarities, our results demonstrate the narrow spatial conditions of overstory structure which can facilitate, or fail to facilitate, these favorable abiotic conditions at fine spatial scales within the scope of individual management units.

CONCLUSIONS

Dry conifer forest restoration treatments aim to create fine-scale variation in the spatial arrangement of overstory trees. Yet, the effects of these spatial structures on microclimates and regeneration niches are unresolved and can inform how treatments both promote and inhibit regeneration. Our results highlight that heterogeneous forest structures create a broad range of microclimate conditions, with particularly strong relationships with vapor pressure deficit but notably weak relationships with shallow soil moisture. We documented opposing early- and late-season microclimate effects on juvenile tree survival, resulting in a narrow range of structural conditions that promote regeneration niches, largely inconsistent with the strongest canopy buffering of microclimate conditions. These effects were notably similar for both new germinant seedlings and more physically mature older seedlings, as well as for our different study species, ponderosa pine and Douglas-fir. As warranted by management needs, the limits of these optimal ranges of structural conditions may in part be overcome through use of greenhouse-grown, more physically developed seedlings, which in our study had much greater tolerance of microenvironmental variation than did new germinant seedlings. Yet, if climate changes result in shortened favorable early-season conditions or unfavorable hot and dry periods occurring earlier, the narrow temporal window for successful regeneration for any juvenile life-stage observed in this study may be further restricted and future persistence threatened.

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CHAPTER 3

JUVENILE PIÑON PINE VIGOR FOLLOWING OVERSTORY TREE DIE-OFF IS HIGHEST FOR LARGER JUVENILES AND LIMITED BY MICROCLIMATE CONDITIONS

INTRODUCTION

Climate change impacts the future viability of certain plant species and communities directly through effects on demographic processes and indirectly through structural dynamics, such as enhanced competition for increasingly limited resources (Paquette and Hargreaves, 2021). Impacts on demographic patterns are relatively easily interpreted, such as elevated mortality resulting from increasingly frequent drought, but generally less is known about how community structural development and recovery from disturbance (e.g., biotic interactions) mediate broader outcomes of climate change (Bisbing et al., 2021; Copenhaver-Parry et al., 2017; Ma et al., 2023). Importantly, climate change is driving more frequent and severe disturbances on plant communities globally, resulting in extensive plant mortality, sudden and dramatic alterations to resource conditions, and uncertainty in subsequent community development and potential recovery (Allen et al., 2015; McDowell et al., 2020). In forest and woodland communities, widespread tree mortality from disturbances like wildfire and drought have resulted in limited tree regeneration in many instances, emphasizing the need to better understand patterns and mechanisms of recovery of affected tree species and communities (Redmond et al., 2018; Stevens-Rumann et al., 2022). Near-term responses of surviving trees to altered resource conditions are critical to better understand future community development

pathways, including opportunities for recovery or potential for transitions to alternative ecological states.

Overstory tree mortality events result in fundamental resource changes for trees previously occupying sub-canopy or understory environments, and the survival and growth of these (typically juvenile) trees will likely depend on the degree and direction of these resource changes. Increased solar radiation, air temperatures, and soil moisture are three primary conditions that will likely change when the upper tree canopy is lost (De Frenne et al., 2021; Morillas et al., 2017; Wolf et al., 2021). Overstory mortality will have a direct impact on solar radiation, allowing greater incident light for plant photosynthesis to reach juvenile trees, but this canopy loss should also indirectly increase maximum air temperatures, and have more complex outcomes on soil moisture (Petrie and Savage, 2022). While a greater proportion of precipitation typically reaches the soil surface following overstory tree mortality, greater solar radiation and elevated temperatures drive higher rates of evapotranspiration when soil water is abundant, with a shift to direct radiative heat as water becomes scarce (Morillas et al., 2017). Further, post-disturbance increases in dead plant material, such as leaf litter, can influence water infiltration and evaporation from the soil resulting in spatial variability in soil moisture (Morillas et al., 2017; Williams et al., 2018). Adding to the complexity, these direct and indirect changes in microclimates (e.g., increased heat or water availability) will likely be affected by the extent to which dead trees continue to buffer the effects of direct radiation (e.g., standing or fallen dead trees shading portions of the resulting understory environment) (Belmonte et al., 2022; Kane et al., 2015; Phillips et al., 2024). Therefore, it is critical to better understand microclimate outcomes in post-disturbance forest and woodland communities, and how these specific

conditions may affect juvenile tree responses, which are typically more vulnerable to environmental stresses than more mature trees.

Drought-induced tree mortality events often only directly affect overstory trees and thus tree recovery tends to occur through survival and growth of remaining juvenile trees (Redmond et al., 2018, 2015). Yet, the extant population of juvenile trees can vary considerably in physical development (i.e. size, age) resulting in differential responses to changes in resource availability and environmental conditions following overstory tree mortality (Forrester et al., 2022; Luu et al., 2024; Ma et al., 2023). While larger, more mature individuals typically have greater resource access through extensive root systems and larger crowns for acquiring light energy, these larger individuals also more directly interface with environmental stresses (e.g., direct light, high temperatures) and have greater resource requirements than smaller, less physically mature individuals (Camarero et al., 2024; Ma et al., 2023). Unlike larger individuals, younger, less physically mature juvenile trees often display growth and survival strategies characterized by prioritization of carbon-gain above water-use efficiencies, which may ultimately be less responsive to variable post-disturbance microclimate conditions (Augustine and Reinhardt, 2019; Lazarus et al., 2018). Differences in juvenile tree vigor may be evident in basic physiological processes that reflect inherent plant function and resource constraints (e.g., McDowell et al., 2008), especially for individuals at a microenvironmental scale. For example, photosynthetic and stomatal conductance rates can reflect both internal necessities, such as water use for photosynthetic activity and carbon gain and maintenance of cell turgor, and relative resource availability and ambient atmospheric stress, such as maintaining these processes in water-limited environments and during periods of elevated temperatures and atmospheric evaporative demand (Grossiord et al., 2020, 2017). Yet, evidence is needed to identify which juvenile tree sizes or

life-stages may be most capable of capitalizing on "release" from resource competition with overstory trees following their mortality.

In piñon-juniper woodlands of the southwestern U.S., widespread mortality of overstory trees, especially piñon pine (two-needle piñon pine, *Pinus edulis*), has repeatedly occurred at greater frequency and extent due to severe and prolonged hotter droughts over the past 20 years (Breshears et al., 2005; Clifford et al., 2013; Floyd et al., 2009). Because juvenile piñon pine trees germinate, grow, and survive predominantly within the facilitative influences (i.e. favorable microclimates) of overstory cover, these mortality events result in strongly and suddenly divergent resource conditions for surviving juveniles (Chambers, 1999; Kane et al., 2015; Redmond et al., 2018, 2015; Redmond and Barger, 2013). The loss of below-canopy microsites from severe drought in recent decades has resulted in significantly limited new pinyon pine seedling establishment, while older juveniles that established before drought have shown greater resiliency to these losses of canopy microsites (Redmond et al., 2018, 2015; Redmond and Barger, 2013). Because these woodlands exist at the margins of climatic suitability for tree cover in the southwestern U.S. (Shriver et al., 2021), exposure to high light, high temperatures, and dry atmospheric conditions may be especially acute for juveniles which persist following overstory mortality. Indeed, observational studies in these systems indicate lower capacity for recovery in more water-limited environmental conditions (Adams et al., 2015; Redmond et al., 2018). Yet, the potential for woodland recovery appears to be dependent on the growth and survival of these juveniles that established prior to and persist following overstory mortality (Figure 3.1). Given the likelihood of limited favorable weather years (Bradford et al., 2020) which have historically driven widespread tree recruitment events in southwestern piñon-juniper

woodlands, connecting juvenile responses to microclimate change will improve evaluations of resilience and recovery processes and thus future woodland trajectories.

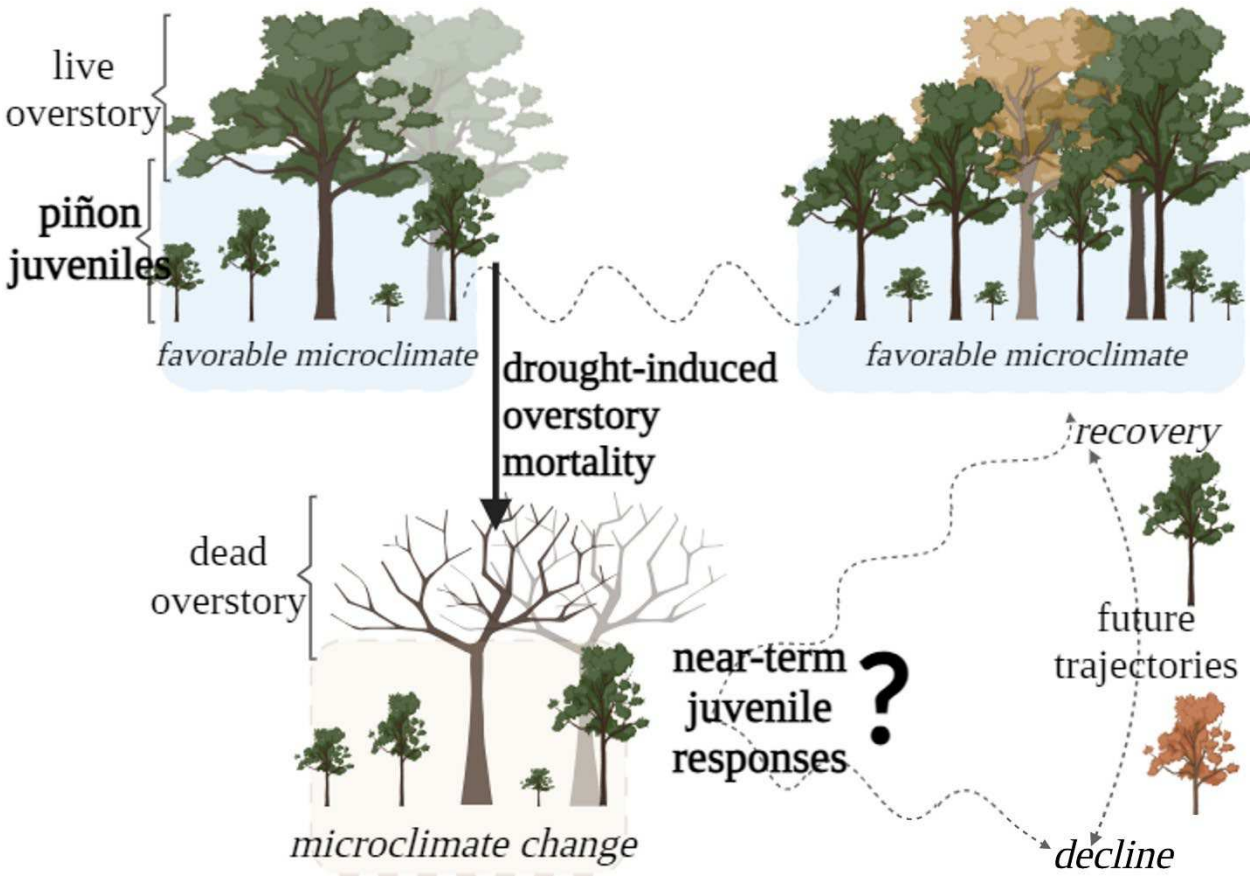

Figure 3.1. *Schematic representation of woodland development (upper) in the absence of severe or extensive disturbance, with juveniles regenerating and growing within facilitative influences of other, overstory trees; and, alternative woodland development initiated by drought-driven overstory mortality (bottom). Following drought-induced overstory mortality, juveniles previously existing in favorable microclimate conditions suddenly encounter new resource conditions including increased incident light and precipitation throughfall, while soil moisture may increase or decrease depending on evaporative demand and non-tree vegetation water-use. The responses of juveniles to these novel conditions may depend on the specific nature of microclimate changes, such as the extent to which greater available light is counterbalanced by increased radiative heat and atmospheric demand for water resources, as well as the stage of physical development and related access to resources for an individual juvenile.*

While observational field studies following overstory mortality events have identified patterns of juvenile tree persistence and recovery (Redmond et al., 2018, 2015; Redmond and Barger, 2013), they are less able to identify mechanisms leading to observed trends. We

conducted a tree girdling experiment to simulate an overstory tree die-off event and measured juvenile pinyon pine responses among a population of juveniles located in our experimental dead overstory vs. adjacent live overstory environments. Our objectives included: (1) evaluate the physiological responses of juvenile piñon pine trees following overstory tree mortality (2) determine how juvenile tree size influences these physiological responses; (3) assess how microclimate conditions mediate juvenile tree physiological responses under live and dead overstory environments. It is clear from prior work on growth patterns in piñon pine that resource stress, namely moisture stress strongly limits growth activity (Adams et al., 2015; Grossiord et al., 2017; Redmond et al., 2017). Moreover, prior work has shown that individuals with an elevated capacity for resource use plasticity are more likely to benefit from periods of favorable conditions (Macalady and Bugmann, 2014; Pangle et al., 2015), which may or may not occur following overstory mortality depending on the degree of abiotic stress which occurs both due to loss of shade and concurrent microclimate conditions. Yet, it is unclear if greater abiotic stress from more exposed microclimates would outweigh newly available resources, or if these opposing forces produce any observable changes in juvenile vigor. Our results ultimately help to understand possible future trajectories of piñon pine structural and demographic development in these woodlands, and thus inform the capacity for woodland resilience relative to drought-driven overstory mortality events.

METHODS

Description of Study Location

To investigate juvenile piñon vigor for this study, we sampled in a model piñon-juniper woodland in the core of the geographic distribution of two-needle piñon pine (*Pinus edulis*) in

southwestern Colorado (37.87, -108.63) and at an elevation approximately midway (2,111 m) between lower elevation woodlands and higher elevation woodlands in the area (Figure 3.2). We used prior knowledge from work in piñon-juniper woodlands in the southwestern U.S. and from this area specifically to inform selection of a specific site (Redmond et al., 2017). Climate conditions at this site are moderate relative to the overall distribution of two-needle piñon pine. Mean annual precipitation during water year months (October-September) is 338 mm (± 90), with monsoon precipitation (July-September) accounting for approximately 33% of total annual precipitation at our study site. Annual mean daily temperatures for water year months are 8.9 °C (± 8.7), with the hottest periods occurring in July on average (21.3 °C ± 1.2 mean daily temperature; 30.0 °C ± 1.4 mean daily maximum temperature), followed by August and June. Vapor pressure deficits (VPD) also typically peak in July at this site (1.23 mean daily kPa ± 0.11). Precipitation during years of study was much more variable, as both April 2021 and May 2022 received precipitation below 1 standard deviation of the long-term mean, and above 1 standard deviation of the long-term mean in July 2021 and June 2022 (Appendix 2:Supplementary Figure S3.1). Monsoon precipitation in these years was higher than average, accounting for 43% and 37% of annual precipitation, respectively. During years of sampling for this study (2021-2022), VPD conditions were not substantially different from the long-term mean and variation (Appendix 2:Supplementary Figure S3.1).

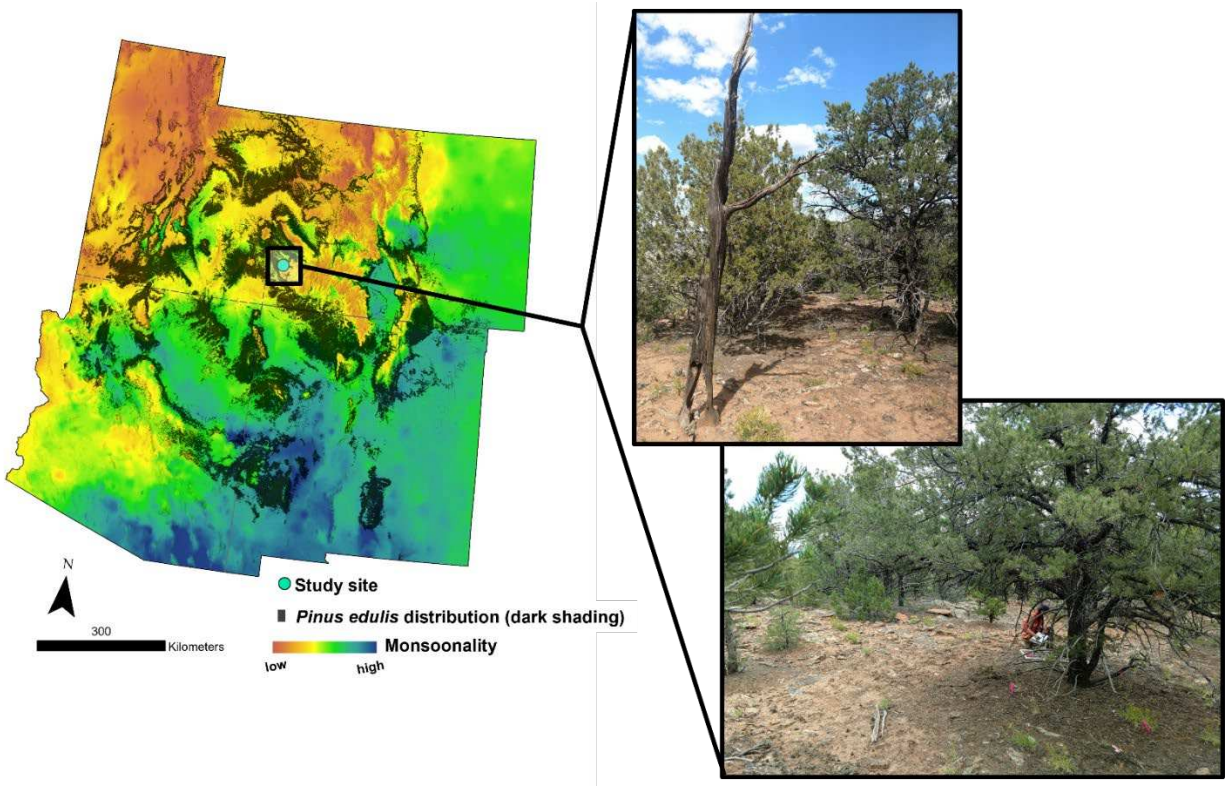

Figure 3.2. *Map (left) showing the study site relative to the distribution of* Pinus edulis *in the four-corner states region (AZ, UT, CO, NM). This study site is situated in the geographic core of* P. edulis *distribution with intermediate climate conditions, such as the strength of monsoonal precipitation (color gradient in map), relative to other areas of its distribution. Photos (right) show examples of site conditions where juvenile vigor was sampled for this study, including structural variation (e.g., treed patches with interspaces), juniper and piñon overstory, and sparse understory.*

The site was situated on a northeasterly aspect, with minimal slope, though the surrounding area is dissected with ephemeral drainages. Soils are predominantly sandy loams, but frequently shallow with bedrock existing at as little as 25 cm deep (USDA NRCS Web Soil Survey, https://websoilsurvey.nrcs.usda.gov/, accessed 3 January 2023). Regarding vegetation, piñon and juniper tree cover was generally patchy (basal area information specific to sampling area provided in sampling description below), with spaces between individual trees and tree patches occupied largely by bare soil and coarse rock, though a variety of herbaceous vegetation were present, in addition to biological soil crust and coarse woody debris. The broader area,

situated on public land, is grazed by cattle, though this site showed little impact, likely owing to minimal cover of herbaceous vegetation.

Experimental Design and Field Sampling

Our study aimed to experimentally assess how tree mortality affected juvenile response. To set up this experiment, we first established all plots (n = 30) under live overstory tree cover at the beginning of our study in the summer of 2019, and subsequently introduced a mortality treatment to half of our plots with random assignment (hereafter referred to as live and dead overstory plot types). We selected individual, dominant piñon trees on which to center our plots ("focal tree"). We selected these focal trees by identifying apparently healthy (≥ 90% live green foliage, no evidence of insect- or other damage which would indicate decline in health), dominant piñon trees which had an average crown diameter of at least 3 m (based on 2 perpendicular measurements). Focal trees were all greater than 10 m apart from each other to minimize any treatment effects on nearby focal trees. Additionally, we selected against trees on slopes greater than 15%. To quantify overstory woodland structure around selected focal trees, we measured diameter at root collar (or, basal diameter; hereafter, "DRC") of all non-juvenile trees (≥ 9 cm DRC) within a distance of 7m of each focal tree stem, which was approximately 1.25 times the height of focal trees, on average. Overstory density across plots was 72.4 m^2 ha^{-1} (± 31.6) basal area.

In the winter of 2019-2020 (~late November-early March), we initiated a mortality treatment for a random selection of half of our live overstory plots. Our objective with this treatment was to create a physical analogue to drought-induced mortality of overstory piñon trees, as has been seen in many regions throughout the range of piñon-juniper woodlands. As such, we sought to create patches of dead overstory environments with standing dead trees,

leaving as little physical disturbance to remaining live vegetation as possible. We created these dead overstory environments by girdling overstory piñon trees in each plot assigned to the mortality treatment. We chose to only girdle piñon pine because the majority of overstory tree mortality in these woodlands in the preceding years had occurred in piñon pine, and less so in juniper (various spp.). Girdling consisted of using a chainsaw to cut approximately 0.5-2.5 inches deep into the sapwood (dependent on stem diameter and desire to maintain the integrity of the stem to leave standing dead trees) and 3 inches vertically along the stem of all overstory trees (≥ 9 cm DRC) in a given plot. While the girdling treatment resulted in observable mortality (extensive to full crown dieback) by 2020-2021 for girdled trees, the timing in which dead needles fell was slightly more variable. In early 2021, girdled trees still retained approximately 68% (± 21) of needles, but by early 2022 this had fallen to only 3% (± 4) on average. Additionally, non-girdled overstory juniper trees and circumstantial mortality contributed to variation in the structural outcomes of our experiment. While our live overstory plots remained representative of live cover with 87% (±18) live crowns, dead overstory plots also retained some, but highly variable, live cover accounting for 35% (± 25) of total basal area on average across plots.

In order to characterize the microclimate conditions of individual plots we randomly selected 5 plots from both live and dead overstory plot types to install an array of microclimate sensors in the summer of 2020. Our sensor arrays included air temperature and humidity sensors (using a breakout board manufactured using the Sensiron SHT31) housed in gill-style radiation shields 3-D printed using white PETG and placed ~15-20 cm above the ground surface, and soil capacitance sensors (SoilWatch 10, Pino-Tech, Zachodniopomorskie, Poland) at shallow (7 cm) and deeper (20 cm) locations. These microclimate arrays were designed by team members (see

Cannon et al., 2022 for a similar design) to run on microcontrollers (manufactured with the ATmega328P chip) logging sensor readings every hour. Sensor arrays were installed beneath the crown of focal trees at a southwestern or southeastern azimuth, depending on where the sensors could best be situated to sample conditions fully beneath the focal tree crown. We used soil cores to calibrate our soil capacitance sensors to soil volumetric water content by soaking soil cores for 24 hours followed by gradual drying, measuring soil weight and sensor capacitance throughout the process to construct calibration curves based on capacitance readings and volumetric water loss (soil bulk densities were derived with separate bulk density-specific soil samples). We used calibration equations from this process to transform field-derived capacitance readings to volumetric soil water content (Appendix 2:Supplementary Figure S3.2). While we attempted to run sensor arrays throughout the growing season (~May – September) of each year of study, the distance of travel to study sites, weather, and equipment logistics resulted in data gaps in the time-series. To provide robust microclimate data given the data gaps, we pooled data from all plots at which sensors were located to calculate averages for variables of interest for each time period of juvenile vigor sampling (detailed below). Averaged microclimate data for each time period of analysis ultimately included pooled data from 2-3 plots of each live and dead overstory environments. Although we pooled microclimate data across overstory environments for average conditions, we still considered these average microclimate rather than average climate (or weather) data because they reflect conditions influenced by the presence of tree structure, in contrast to open- (or free-) air conditions (e.g., De Frenne et al., 2021). Lastly, we installed a commercially available weather station (ATMOS 41 Weather Station, Meter Group, Pullman, WA, USA) in open conditions at 1.5m above the ground surface for site-wide weather conditions, including temperature, humidity, and precipitation. We used these reference

conditions to qualitatively assess the relative consistency of microclimate sensor patterns, and to assess differences in treed microclimate conditions and sitewide reference weather conditions, for better understanding how treed microclimate conditions related to weather at the site and climate change expectations.

To evaluate how juvenile trees responded to overstory tree mortality, we measured photosynthetic and stomatal conductance rates across a range of juvenile sizes from the smallest we could feasibly measure to the largest juveniles present (without evidence of reproductive maturity, e.g., cone scars). Overall, juveniles ranged in size from 0.3 cm to 8.9 cm basal diameter and were in apparently healthy condition. We ensured that juveniles sampled were comparable in sizes and range in each of our live and dead overstory plot types. We measured photosynthetic and stomatal conductance rates between 8:30 and 11:30 am on 15 individuals each in the live and dead overstory plot types at three periods in 2021, including mid-June, mid-July, and mid-August, capturing earlier- (prior to typical monsoon periods), mid- (typically hottest and driest), and later- (typically following or during monsoon precipitation periods) growing season conditions. Based on our 2021 measurements, trees exhibited minimal physiological activity in July, and so in 2022 we only measured in mid-June and mid-August, but were able to increase our sample size to 25 individuals (within the same range of sizes) in each plot type.

We sampled photosynthetic (A_{net}, μmol CO_2 m^{-2} s^{-1}) and stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) rates with a LiCOR 6400XT model gas exchange analyzer equipped with a model 6400-40 fluorometer chamber head with a 2 cm^2 capacity (LI-COR Environmental, Lincoln, NE, USA), more suitable for needle-leaved trees. For each juvenile, we selected a healthy group of the most fully-formed needles (~ 1-year old) from the middle of the crown on the southerly

aspect, or the healthiest branch from smaller juveniles with no distinct branching (typically < 1 cm DRC). We used the same tree branch on each individual juvenile for each period of sampling to estimate vigor to avoid additional variation potentially present across an individual tree crown. Using the 6400XT, we took a series of point measurements of gas exchange over the course of approximately 10 minutes, and recorded photosynthetic rate (A_{net}, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), and VPD of the air as measured by the 6400XT. We corrected A_{net} and g_s measurements for the amount of leaf area present in the chamber for each sample, and took the average of all measurements for a given individual tree and time period (June, July, August).

To understand the individual-level environmental and physiological context of our point measurements of gas exchange, we supplemented these measurements with both dark-adapted and light-adapted leaf fluorescence measurements using a MINI-PAM Photosynthesis Yield Analyzer (Heinz Walz GmbH, Effeltrich, Germany) from which we extracted (Photosystem II) quantum yield (Φ_{PSII}) estimates. We derived a measure of yield that would simply represent the approximate efficiency of the photosynthetic apparatuses in measured individual juvenile trees. Specifically, we calculated the difference in yield values of light-adapted, representative light conditions (at ~1200 PAR) from the maximum theoretical yield, or dark-adapted, light-saturated conditions (F_M). We expected this variable to efficiently represent how well a given individual could perform in representative light conditions relative to its maximum (Murchie and Lawson, 2013), with larger differences suggesting a predisposition to lower photosynthetic rates in representative light conditions.

Analysis

We used linear mixed models to evaluate A_{net} and g_s ("vigor") of our sampled juvenile piñon trees. To assess whether the effects of tree mortality varied based on tree size, we split juvenile trees into two size classes: small juveniles (<2 cm DRC) and large juveniles (>2 cm DRC). This was based on visual inspections of the data that showed a natural break based on these size classes and is a size cutoff similar to what has been used in other studies to distinguish between small (and younger) and large (and older) juveniles (Redmond and Barger, 2013). Additionally, this cutoff was near the median juvenile size in this study and therefore resulted in nearly equal sample sizes for our separate models. Therefore, our analysis included four models: one for each response variable (A_{net} and g_s) and juvenile size group (smaller trees < 2 cm DRC, and larger trees > 2 cm DRC). For modeling, we used the *lmer* function in the "lme4" package (Bates et al., 2023) in the R statistical computing environment (R Core Team, 2020), using maximum likelihood-based estimates of model coefficients.

We constructed models including covariates for overstory plot type (live and dead), juvenile tree DRC, microclimate variables for soil moisture and VPD (conditions during sampling days), and two control variables (detailed below). For soil moisture microclimate conditions, we chose to average soil VWC across shallow and deeper sampling depths for a total average soil moisture value in each sampling time period. Total soil moisture represented a more integrative and robust reflection of the wetness of environmental conditions during a given sampling period. For VPD, we considered both mean daily and mean daily maximum VPD conditions for inclusion in our models, especially since mean maximum VPD is likely to have the most acute influence on juvenile tree performance. We also included all possible meaningful interactions, including for overstory plot type and juvenile tree DRC, and overstory plot type and each microclimate variable. Control variables included individual photosynthetic yield

efficiency (detailed above) and VPD values from the 6400XT directly associated with each gas exchange measurement (instantaneous VPD). Our control photosynthetic yield efficiency variable helped to account for individual-level physiological differences in photosynthetic capacity not attributable to environmental conditions, thus providing additional context for point measurements of gas exchange, and was used in all models for photosynthesis, but not for stomatal conductance models. We also accounted for instantaneous VPD in order to more directly control for the timing of samples during a given day, since VPD can increase rapidly during morning hours of physiological activity and can strongly affect openness of stomata and therefore gas exchange activity (Figure 3.3). To do this, we scaled and centered the instantaneous VPD values to the range of conditions for each sampling day, with a mean of zero and standard deviation of 1 for each day. For selecting a final model for each size grouping and response variable, we assessed all possible model subsets (*dredge* function in the "MuMIn" package, Bartoń, 2023) to obtain the most parsimonious models (lowest AIC_c) which included, *a priori*, fixed effects for overstory plot type (live and dead), juvenile tree DRC, total soil VWC, and one VPD microclimate variable, in addition to both control variables.

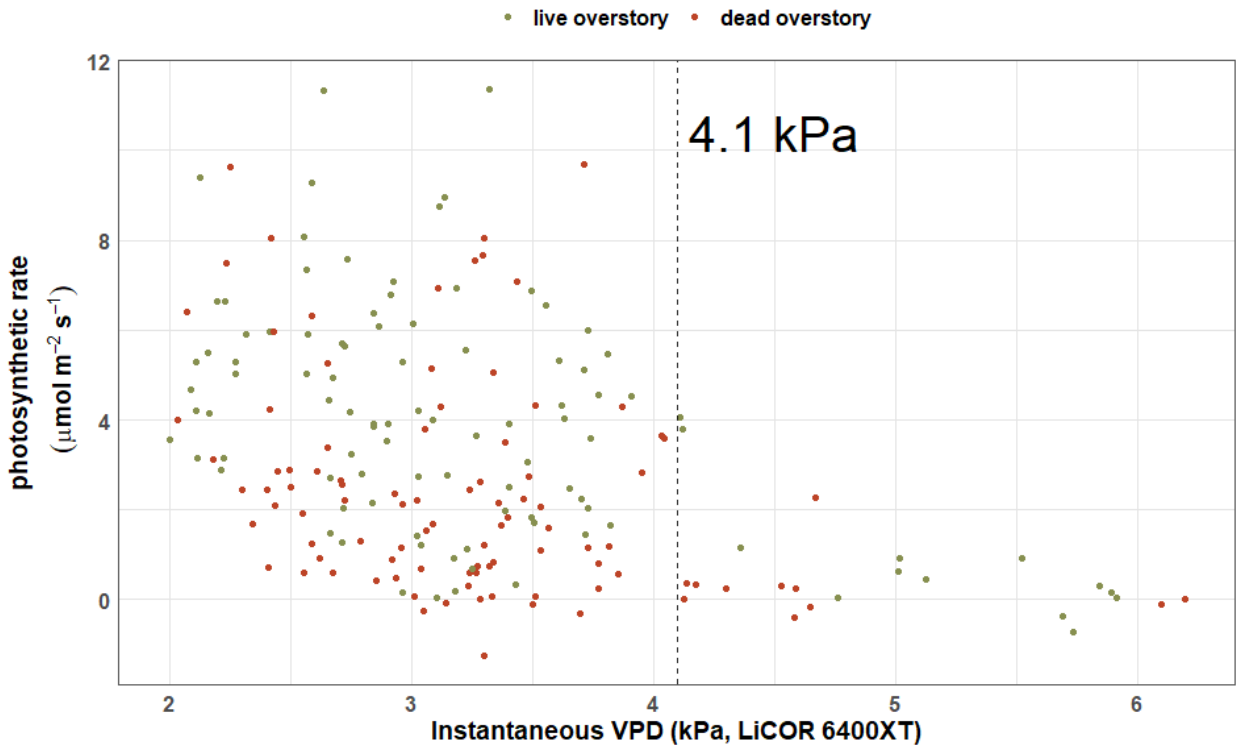

Figure 3.3. *Relationship between measured photosynthetic rate (A_{net}) and vapor pressure deficit at the moment of measurement. We used this instantaneous measurement of VPD (scaled within each day of sampling) as a fixed effect in all models to control for its known influence, in order to make estimates of microclimate and treatment effects more robust. This relationship shows a general pattern that occurred with trees across all sizes and in both live and dead overstory environments across our study. The vertical dashed line at 4.1 kPa appears to be an approximate threshold at which juveniles at this site close stomata and limit physiological activity.*

We scaled and centered all variables to a mean of zero and standard deviation of 1 prior to model fitting to provide an easily interpretable measure of strength of estimated coefficients in each model. The significance of each model covariate was determined by evaluating the overlap of zero of each coefficient confidence interval, where estimates not overlapping zero were considered significant. However, as we used likelihood-based methods to select among model subsets, we also considered that all variables in selected top models had some support, and therefore we report on all results, including variables with insignificant effects as determined by confidence intervals. Overall model fit was assessed through calculating prediction error of the

model as root mean squared error (estimated with *rmse* in the "performance" package, Lüdecke et al., 2021).

RESULTS

Across juvenile sizes and time periods of sampling in this study, A_{net} and g_s were highly variable, ranging from negative values for (presumably) highly stressed individuals to A_{net} over 12 μmol CO_2 m^{-2} s^{-1}. Modeling A_{net} and g_s responses separately for smaller and larger trees showed that these measures of vigor for juvenile piñon trees were distinct for the two size groups (see Supplemental Table S3.1 for full model details, including coefficient estimates, uncertainty, and model fit statistics). Final results and top model selections included highly similar relationships of A_{net} and g_s with variables retained in selected top models; therefore, we focus our presentation of results and discussion of results largely on A_{net}.

A_{net} was significantly higher in dead compared to live overstory plots for larger trees (Figure 3.4C), and although this pattern was also observed for smaller trees (Figure 3.4A) the modeled effect was only marginally significant. A_{net} increased with juvenile tree size among larger juveniles (Figure 3.4D), but not for smaller trees whose responses were relatively unchanged across size (Figure 3.4B). For larger trees, elevated A_{net} responses were especially evident for trees > 4 cm DRC, whereas the transition from 2-4 cm DRC showed relatively similar vigor levels to average responses of the smaller juvenile group (< 2 cm DRC). No top models in our selection process included interactions for overstory plot type and juvenile tree size.

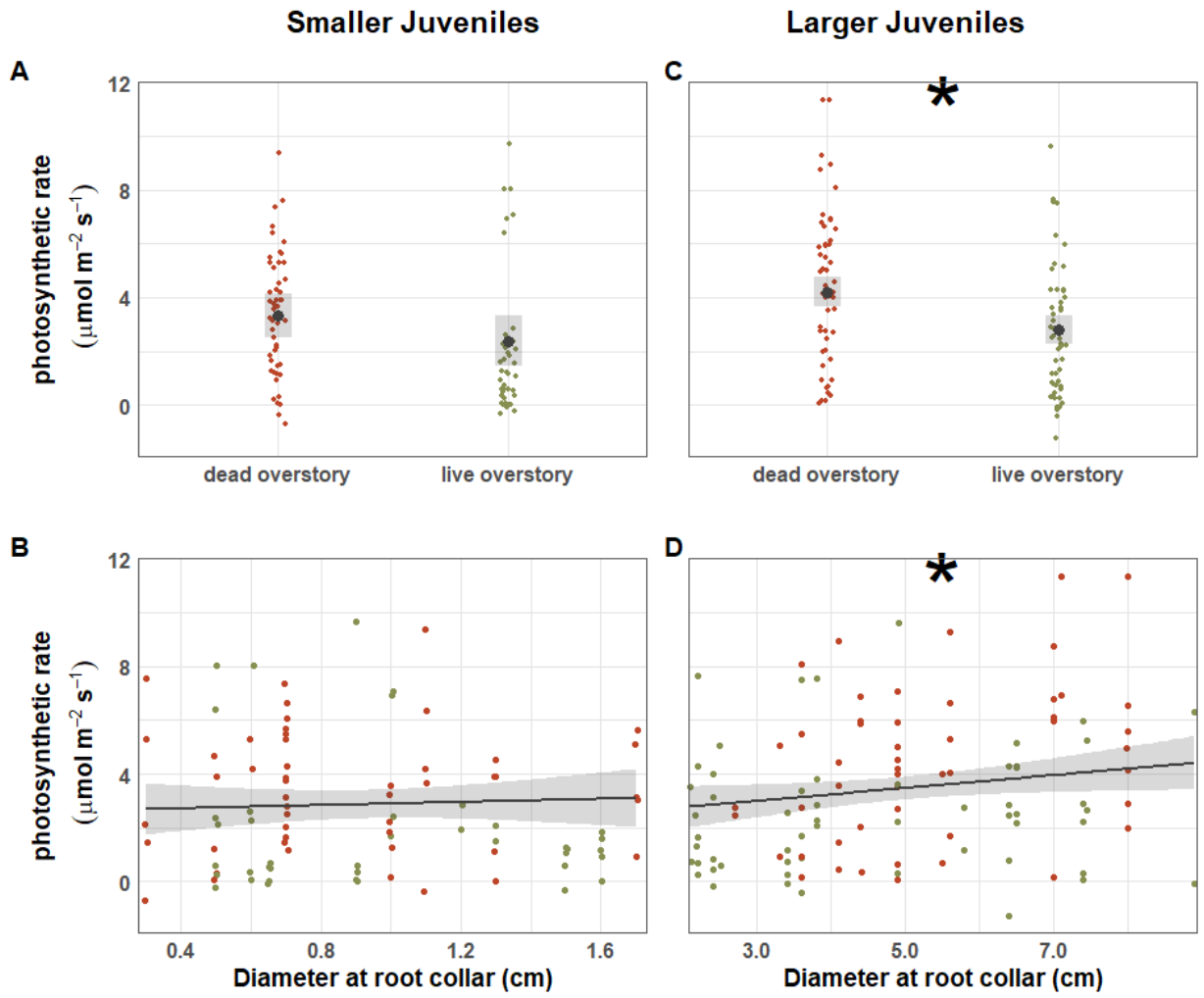

Figure 3.4. *Model results for smaller (<2 cm DRC) juvenile piñon (left column, A-B) and larger (>2 cm DRC) juvenile piñon (right column, C-D) photosynthetic rates in relation to a priori covariates of overstory plot type (live and dead, A and C; large circles show predicted mean response with shaded area showing mean prediction uncertainty), and juvenile tree size (DRC, B and D). Photosynthetic rates were significantly higher in dead overstory (orange) environments than in live overstory (green) for larger trees (C), but not for smaller trees (A). Similarly, photosynthetic rates increased significantly with individual juvenile tree size for larger trees (D), but no relationship was detected for smaller trees (B). Colors denote live (green) and dead (red) overstory environments. Asterisks indicate significant modeled relationships.*

For microclimate variables, both soil moisture and VPD had significant relationships with A_{net} for smaller and larger trees. For models of smaller and larger trees, average soil moisture positively affected A_{net}, and this effect was larger for smaller trees than larger trees (Figure 3.5A and C), suggesting smaller trees may be more sensitive to changes in soil moisture compared to

larger trees. No top models included an interaction for overstory plot type and soil moisture. Mean daily VPD was negatively related to smaller tree A_{net} (Figure 3.5B) and larger tree g_s (Appendix 2:Supplementary Table S3.1), and larger tree A_{net} was negatively associated with mean daily maximum VPD (Figure 3.5D). The effect of mean daily maximum VPD on larger tree vigor was nearly twice as strong as the effect of mean daily VPD on smaller tree vigor (Appendix 2:Supplementary Table S3.1). Additionally, our top models for larger juveniles showed support for an interaction between overstory plot type and VPD (maximum VPD for A_{net} and mean VPD for g_s). Neither of these interactions were significant, though the interaction of overstory and maximum VPD in the A_{net} model had a confidence interval that showed marginal overlap of zero, and inclusion in the selection of a top model suggests some support for the interaction.

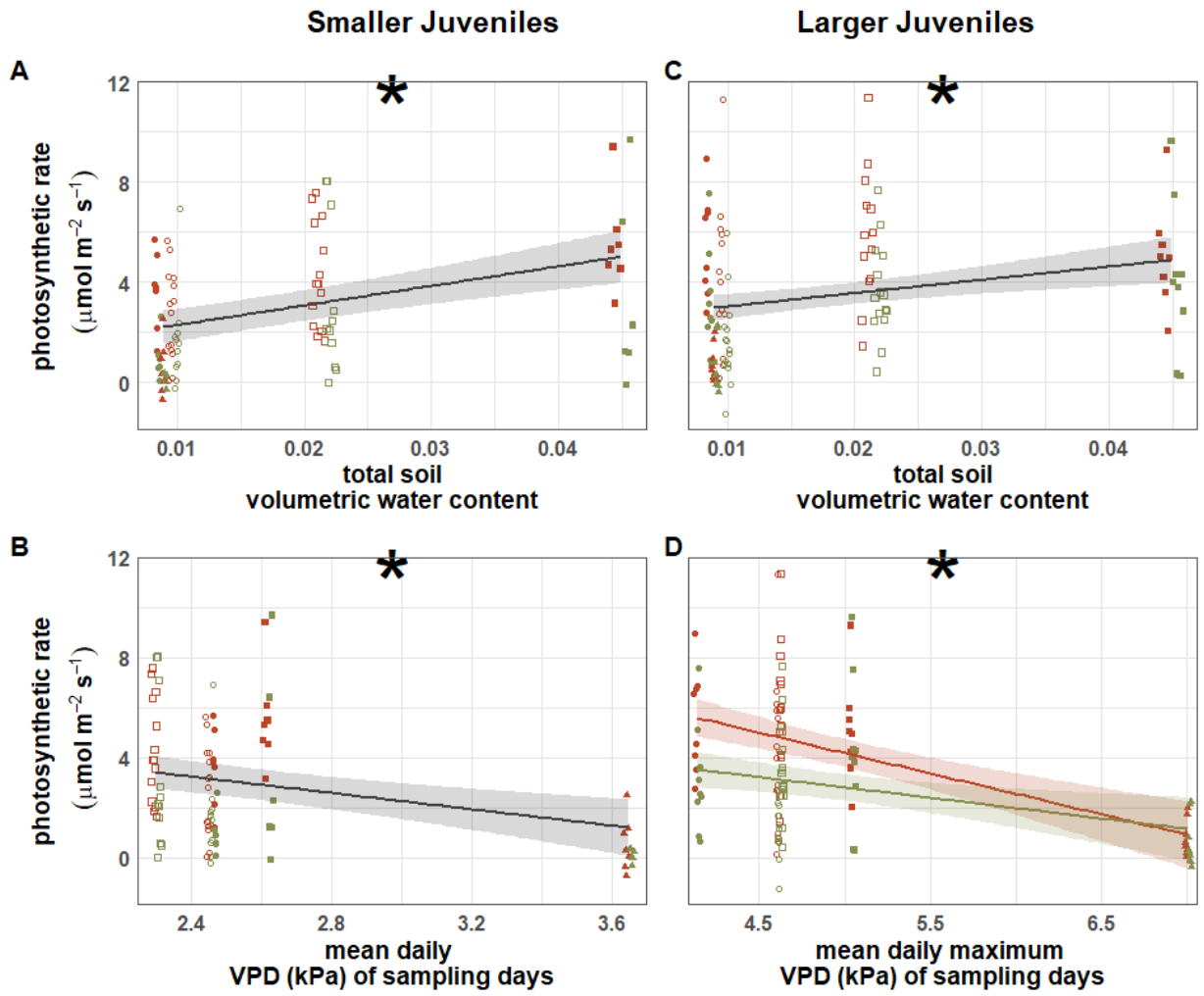

Figure 3.5. *Model results for smaller (<2 cm DRC) juvenile piñon (left column, A-B) and larger (>2 cm DRC) juvenile piñon (right column, C-D) photosynthetic rates in relation to soil moisture (VWC) (A-B) and vapor pressure deficit (VPD) microclimate conditions during days of sampling (B-D). For both smaller trees and larger trees, photosynthetic rates increased significantly with soil moisture conditions, and decreased significantly with increasing mean daily VPD on sampling days for smaller trees (B), and with mean daily maximum VPD on sampling days for larger trees (D). There was a marginally significant relationship for the interaction of overstory environment and mean daily maximum VPD on responses for larger trees (D). Colors denote live (green) and dead (red) overstory environments. Symbols denote different sampling periods, including June 2021 (closed circles), July 2021 (closed triangles), August 2021 (closed squares), June 2022 (open circles), and August 2022 (open squares). Asterisks indicate significant modeled relationships.*

DISCUSSION

Prior work on regeneration patterns after overstory tree die-off in piñon-juniper woodlands has established that advance regeneration, or juveniles which established prior to the

overstory die-off event, are less impacted by the die-off event than new regeneration, and likely provide the potential basis for woodland recovery (Redmond et al., 2015). Yet, potential mechanisms for these patterns and for variation in extant juvenile responses to die-off are largely unknown. Our results showed that, although juvenile A_{net} and g_s were highly variable among individual juvenile trees, both A_{net} and g_s were on average higher in dead overstory environments (Figure 3.4A and C), and significantly higher for larger juveniles in dead overstory compared to live overstory environments (Figure 3.4C). These results suggest a relative competitive release, or a (near-term) positive effect of overstory mortality on large juvenile tree photosynthetic and stomatal conductance rates. Importantly, A_{net} and g_s for trees of all sizes in both live and dead overstory environments was explained, in part, by microclimate conditions, with positive impacts of soil moisture and negative impacts of VPD (Figure 3.5). Given the absence of strong differences in juvenile responses to microclimate variables in live or dead overstory environments (i.e., lack of interactions and highly similar responses overall), higher A_{net} and g_s for larger juveniles in dead overstory environments suggests light availability as a likely source of competitive release for these juveniles. Yet, with greater exposure to direction radiation and associated elevated VPD in dead overstory environments (though not directly observed here), individuals will inevitably face fundamental physiological limitations, especially longer periods of inactivity with stomatal closure to reduce water loss and greater passive water loss at extreme VPDs even with stomatal closure (Grossiord et al., 2017; Morillas et al., 2017; Pangle et al., 2015). Consequently, the results of this study suggest opposing outcomes for juvenile trees following overstory mortality: additional resource availability, especially light, which can facilitate higher A_{net} and g_s when microclimates are not highly limiting and thus potentially greater long-term growth and competitive ability; yet, high VPD conditions may limit A_{net} and g_s

diurnally (reflected in instantaneous VPD relationships, discussed below, and see Figure 3.3) with implications for longer-term limitations to growth and viability (Adams et al., 2015). Ultimately, whether juvenile piñon pine responses indicate a pathway for woodland recovery following overstory mortality remains unresolved, though larger juveniles are most likely to outperform smaller juvenile counterparts in the near-term and may eventually provide the next reproductively mature overstory cohort.

Our results suggest that juvenile size (here, DRC), an approximation of physical and physiological maturity, explains some variation in juvenile A_{net} and g_s among larger juvenile sizes (~ 2 – 9 cm DRC), and likely relates to the positive relationships between tree size and capacity for resource acquisition. We observed a significant positive relationship of tree size with A_{net} and g_s responses in both live and dead overstory environments (Figure 3.4D), suggesting that among piñon juveniles, more generally, the largest juveniles are acquiring and using more resources than smaller juveniles, and are therefore likely to respond to resource changes more effectively (Ma et al., 2023). Larger individuals can have more developed root systems or greater capacity for new growth, both in depth of larger roots and spread of finer roots (Schwinning et al., 2020), which allows for greater water and nutrient uptake (Forrester et al., 2022) in support of leaf-level photosynthesis and stomatal conductance and, therefore, allows greater acquisition of light energy for photosynthesis and carbon gain (Peltier et al., 2021). While larger individuals also require more resources, especially soil water, to maintain their metabolic activity for which abiotic stresses can be especially limiting (Férriz et al., 2021), our results do not suggest that these individuals experienced any greater limitations of average microclimate conditions than any other individuals across sizes and overstory environments. Similarities in sensitivity to microclimate conditions across juvenile tree sizes and live and dead

overstory types (Figure 3.5A-D) suggests that the primary resource change in dead overstory environments leading to higher vigor of larger juveniles would likely be increased availability of photosynthetically active radiation (Borodkin, 2016; Ramage et al., 2023). While our larger juveniles in this study were typically not located directly beneath overstory trees (data not shown), the spreading crowns of live overstory piñon and juniper trees likely limit light to non-dominant or -codominant trees during most periods of sunlight with the likely exception of high-angle, midday sunlight when trees are less likely to be active (due to higher VPD conditions limiting openness of stomata and therefore gas exchange). Therefore, with the loss of live crown foliage of overstory tree cover, and especially following loss of needles from branches, newly available light may be the driving influence on increased vigor of larger juvenile trees which are able to best access this light. While marginally significant in this study, smaller trees also showed patterns of higher vigor in dead compared to live overstory environments (Figure 3.4A), which may be indicative of additional light availability occurring with loss of live overstory tree foliage. A weaker overall response, however, of these smaller trees may be attributed not only to smaller physical stature and less crown area for intercepting light as compared to larger juveniles, but also potentially to shading which may continue to occur, at least for smaller juveniles, from standing dead trees and other surrounding live juniper trees (or even larger juveniles) (Sprugel, 2002; Williams et al., 1999). Furthermore, because stomatal conductance also increased significantly with individual juvenile tree size among larger juveniles (~ 2-9 cm DRC), larger trees appear to dominate in overall resource acquisition (and subsequent use) compared to smaller trees, and therefore are physically capable of greater growth activity following resource release from overstory mortality.

All juveniles in this study, regardless of live or dead overstory conditions, were impacted by average soil moisture and VPD conditions in expected ways (Figure 3.5A-D), though the relative strength of influence of each variable differed with tree size. Lessons from these results of average microclimate are relevant especially in relation to expected climate changes in this region (Bradford et al., 2020; Costanza et al., 2023). The effects of average soil moisture availability and VPD conditions on A_{net} and g_s are well documented, and the sensitivity of juveniles to these microclimate conditions in this study emphasize how easily vigor of young trees will be impacted as climate warming exacerbates drought stress, and associated plant function and plant-plant interactions (Grossiord et al., 2018a, 2019, 2020; McDowell et al., 2019). Moreover, these effects occurred for juveniles in both live and dead overstory environments, indicating environmental limitations for juveniles regardless of the known facilitative benefits of live canopy cover in these woodlands (Breshears et al., 1997; Redmond and Barger, 2013). It is important to note that negative vigor relationships with VPD observed in this study were driven especially by the hottest and driest period in which we sampled (mid-July 2021), during which gas exchange activity was especially low and during which these trees, as generally isohydric strategists, already limit their growth activity through limited stomatal conductance (Limousin et al., 2013). We measured a fairly limited time-period, and so these (and likely higher) VPD conditions are likely present for these trees more generally at other periods during growing seasons (Kannenberg et al., 2024; Petrie and Savage, 2022). We expect these VPD conditions to become more prevalent as mean temperatures and temperature extremes increase in this area, and therefore our results remain an important indicator of limitations specifically for juvenile tree vigor and therefore woodland development. Furthermore, our plot-level microclimate data show that VPD conditions were consistently higher (hotter, drier air)

than our sitewide reference conditions across sampling periods (Appendix 2:Supplementary Figure S3.3). This indicates that forecasts of greater climate-driven limitations to tree viability in this region may underestimate abiotic limitations individual trees experience at the microclimate scale.

Yet, evidence from numerous previous studies in piñon-juniper woodlands in the southwestern U.S. suggest that precipitation and soil water patterns are as much or more limiting than the effects of atmospheric dryness in these systems (Adams et al., 2015; Grossiord et al., 2017, 2018a; Kannenberg et al., 2024). Years in which sampling occurred for this study included some high and low variation in precipitation but relatively average VPD conditions compared to long-term records (i.e., 1991-2020 climate normal). This is notable because the contrasting results of declines in tree performance demonstrated by the studies result from induced experimental or result from observed studies occurring with severe meteorological and soil drought. Indeed, these and other similar studies (e.g., Guérin et al., 2018) emphasize the relative favorability of weather conditions in which our study was conducted, and suggest that physiological and growth declines in piñon will occur with more substantial abiotic limitation. Additionally, these studies have often occurred in sites which experience more chronic climate stresses (e.g., longer seasonal drought, more reliance on monsoon precipitation pulses), potentially explaining variation with a similar (though broader) experiment in New Mexico (Morillas et al., 2017), and suggesting that our study site could be situated in a more isolated and favorable physiographic area (e.g., similar to McDowell et al., 2019). Therefore, while our results suggest some evidence of near-term benefit to A_{net} and g_s activity in dead overstory environments, our broader results of the relative microclimate across both live and dead

overstory environments underline the potential susceptibility of these juveniles to future severe abiotic stress.

The lack of strong interaction relationships for average microclimate conditions and overstory conditions (live vs. dead canopy, except marginally for VPD – see Figure 3.5D) is surprising given the presumptive degree of additional direct radiation exposure in dead compared to live overstory tree cover. While we analyzed average pooled microclimate conditions, it is also possible that raised crowns of larger overstory trees and the relatively open canopy of this woodland, resulting in high incident light and less buffer to drying effects of wind throughout the site, resulted in similar air temperature and humidity variation in live and dead overstory environments (Máliš et al., 2023). Yet, it is notable that we observed that maximum VPD conditions were more important than mean conditions in explaining larger juvenile tree vigor (specifically A_{net}, but not g_s) compared to mean VPD conditions for smaller juvenile tree vigor (Appendix 2:Supplementary Table 3.1). Consistent with their larger physical presence, it is possible that larger trees are more sensitive to extreme conditions as compared to smaller juveniles (Ma et al., 2023). Although not a significant effect, our top model selected for larger trees showed some support for a greater negative effect of maximum VPD on larger juvenile photosynthetic rates growing under dead overstory as compared to live overstory (Figure 3.5D). Potential differences in microclimate effects for smaller and larger trees is further emphasized by the larger impact of soil moisture (compared to VPD) on smaller juveniles, suggesting that smaller juveniles may experience a greater amount of continued facilitation from heat stress by dead overstory trees, or surrounding live juniper trees (as discussed above), but less so in relation to soil moisture (Urza et al., 2019).

It is a physical reality that in dead overstory environments, radiation is received at greater intensity, and will occur earlier within a typical, uncloudy day, than in live overstory environments (De Frenne et al., 2021). The consequences of this distinction in diurnal patterns of microclimate variation between dead and live overstory environments is that juveniles persisting in dead overstory environments will experience microclimate limitation to physiological activity sooner on a given day than may occur in more buffered, live overstory environments. We did not measure diurnal patterns of gas-exchange in this study, but our measurements of instantaneous VPD conditions concurrently with A_{net} and g_s measurements that spanned several hours each morning of sampling and can provide insight into when stomata may close in response to VPD. Though we scaled the data in our models to reduce the influence of instantaneous VPD on mean daily microclimate conditions, we observed that these instantaneous VPD data suggest a common threshold at which trees of all sizes and in all overstory conditions tend to "shut down" their growth activity (see Figure 3.3). Above approximately 4.1 kPa VPD, all of our sampled juveniles, across sampling periods, were inactive, suggesting limited stomatal opening, and transitions to conserving water for the remaining daylight hours in a given day. Consequently, although larger juveniles responded positively overall to dead overstory environments in this study in near-term responses, the physiological activity of these juveniles is likely to be more temporally limited on a diurnal timeframe than for trees in more buffered, live overstory environments. Therefore, the net outcome, and longer-term outcomes, of higher A_{net} likely driven by higher light availability, but potentially less active time, is unclear. It is possible that these larger trees, showing greater plasticity in response to resource changes following overstory mortality, may benefit enough from greater light availability to obtain and store necessary carbon for continued growth and survival, even with less available time for non-

limited (i.e., < 4.1 kPa) physiological activity in dead overstory environments. Indeed, prior work has concluded that individuals with higher growth plasticity during favorable abiotic periods are better competitors with counterparts during less favorable abiotic periods (Macalady and Bugmann, 2014; Pangle et al., 2015). Yet, it is also possible that greater extremes experienced in dead overstory environments will ultimately limit carbon gain over time and predispose these trees to carbon starvation, especially as drought conditions become more frequent and severe with climate warming, unless soil moisture remains adequate (Adams et al., 2015; Guérin et al., 2018). Therefore, while our results suggest that larger juveniles may benefit in the near-term from additional resources after overstory mortality, longer-term outcomes remain unresolved without additional related monitoring of physiological activity, carbon storage, and subsequent woodland development dynamics.

Ecological and Management Implications

Many prior investigations of the relationship between live overstory tree cover and regeneration patterns in piñon-juniper woodlands have involved discussions of the importance of facilitation for piñon germination, growth, and survival (Chambers, 1999; Redmond et al., 2018; Redmond and Barger, 2013; Urza et al., 2019). However, it has been demonstrated that (single-leaf) piñon juveniles rely less on facilitative cover from trees or nurse shrubs once they have reached a stage of growing adult needles (Urza et al., 2019). While our study was not designed to investigate competitive and facilitative mechanisms directly, the question of when and whether juveniles may be released from competition with overstory trees is inherent in our objectives. As discussed in preceding paragraphs, the clearest outcome of juveniles benefitting from competitive release from overstory trees was the increased A_{net} and g_s of larger juvenile

trees, in particular, which appears to be related most likely to increased available light. Collectively, the weaker relative influence of VPD conditions and general pattern of higher A_{net} in dead overstory for smaller trees suggests that, due to physical size in relation to their surroundings, smaller trees may still experience a greater degree of shading. However, it is not clear whether the lack of strong vigor relationships for smaller trees with overstory mortality is due to less capacity to capture newly available light (and other) resources (i.e., less leaf area, less developed root systems), or if they continue to benefit from what facilitative shade remains. While live overstory environments undeniably provide some essential protection from direct radiation-driven heat and evaporative stress (Breshears et al., 1997; Urza et al., 2019), smaller juveniles in live overstory environments in our study still showed relatively high sensitivity to soil moisture and VPD conditions but did not benefit from additional available light. Therefore, the nuances of facilitation and competition for these previously-established juveniles remain unresolved. Because these juveniles have adult foliage, it is possible that their A_{net} would increase if additional light became available (e.g., when standing dead trees fall), but their more limited access to water resources (i.e., lower observed stomatal conductance rates) may prevent them from withstanding additional stress induced by higher incident light. Lastly, our results are difficult to interpret in the broader discussions of competition and facilitation in that the spatial gradient of stress observed only occurred between nearly adjacent treed environments (live and dead) at the same site, rather than a broader gradient, such as across elevations (Martens et al., 2001; Redmond et al., 2015). Furthermore, as previously stated, our sampling periods were not abnormally hot and dry for this site, potentially minimizing the strength of facilitative or competitive responses of the juveniles we studied (Ploughe et al., 2019).

The need for targeted, system-specific management approaches in piñon-juniper woodlands has become increasingly important due to both the relative lack of current frameworks for these systems, the wide range in types of piñon-juniper systems, and the present threats of climate change to piñon-juniper persistence, especially in the southwestern US. In other dry forested systems of this region, there is increasing interest in reducing tree density and the use of uneven-age silvicultural principles for maintaining structural diversity and to improve resistance and resilience to future drought (Andrews et al., 2020; Phillips et al., 2024; Redmond et al., 2023). Our results emphasize the importance of considering advance regeneration size classes as important sources of woodland composition when management decisions regarding tree removal or reforestation are concerned (Phillips et al., 2024). As has been suggested elsewhere, our results suggest that, although larger juveniles may outperform smaller juveniles, a diverse range of size and age classes are an important component of resilience, as the effects on their vigor are not equivalent (e.g., Ma et al., 2023). Our results suggest a potential pathway of woodland development following overstory mortality which relies especially on established larger juveniles near co-dominant and reproductive status, while smaller juveniles may continue to benefit from some degree of facilitative cover for further physical development.

CONCLUSIONS

Forest and woodland systems in which juvenile plants are distinctly dependent on facilitative effects of tree canopy cover for establishment are especially vulnerable to climate change-induced increases in disturbances to canopy trees. In piñon-juniper woodlands of the southwestern US, where new regeneration has been limited following prior occurrences of widespread drought-driven overstory mortality, potential recovery pathways appear to be

especially dependent on responses of surviving juvenile individuals. We show that among juvenile tree sizes ranging from very small to large saplings, photosynthetic and stomatal conductance rates increase with size, and larger juveniles show higher vigor in dead overstory compared to live overstory environments. Yet, as juveniles of all sizes in both live and dead overstory environments were similarly limited by microclimate soil moisture and vapor pressure deficit conditions, the longer-term results of these trends are unclear. The apparent sensitivity of these juveniles to microclimate conditions even during years of relatively average weather suggest that future increases in meteorological and soil drought may limit future survival, unless greater vigor of larger juveniles sufficiently supports their accession to reproductive maturity and the next overstory cohort. This study underscores the importance of considering current woodland structure and advance regeneration size classes in management decisions. While larger juveniles may drive woodland recovery in the near term, maintaining a diverse range of size and age classes is crucial for resilience. Future management strategies should account for the differential responses of juveniles to overstory mortality and the potential implications for woodland dynamics under changing climatic conditions.

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CHAPTER 4

EFFECTS OF OVERSTORY MORTALITY ON JUVENILE PIÑON PINE GROWTH DEPEND ON WEATHER AND SITE CONDITIONS ACROSS LOCAL AND REGIONAL ENVIRONMENTAL GRADIENTS

INTRODUCTION

Broader impacts of climate change on tree species distributions, such as decreasing viability at warmer and drier range margins, may be mediated in part by variation in adaptations of, or within, local populations to abiotic stress and climate variability (Brodribb et al., 2020; Gazol et al., 2023; Vasey et al., 2022). Adaptations of populations to local climate variability and chronic stressors may be especially crucial for the capacity of trees to resist and recover from extensive and severe disturbance, such as heatwaves and drought. Changing climate conditions in many regions, especially dryland ecosystems, includes more frequent occurrences of severe disturbances and also exacerbates abiotic stresses in post-disturbance environments in which recovery processes occur (Costanza et al., 2023). With rising temperatures and increasing atmospheric and soil drought (Bradford et al., 2020), dryland tree species face additional pressures in recovery and subsequent resilience to such severe, intense, and increasingly frequent disturbance events (Shriver et al., 2021). Understanding variation in population responses to post-disturbance environments is important for anticipating changes in local dryland forest and woodland communities as climate warming progresses, and can facilitate targeted management

toward sensitive or priority areas and populations, or away from areas of expected population extirpation (Noel et al., 2023).

For species which occupy broad ranges of environmental conditions, population adaptations to local environmental conditions are often described in relation to gradients of warmer and drier to cooler, wetter locales in which populations persist (Dixit et al., 2022; Gazol et al., 2023), often reflecting latitudinal and altitudinal distributions. Local populations which typically experience more chronic stresses like heat and seasonal drought may be better adapted to withstand post-disturbance environmental stress characterized by high incident light, temperatures, and evaporative demand (Camarero et al., 2024; Guérin et al., 2020). Alternatively, these populations may not possess the plasticity (e.g., morphological adjustments, like higher root densities or more water-conservative leaf structures, and physiological adjustments, like water-use efficiency) necessary to utilize available resources in post-disturbance environments to effectively persist through concurrent or subsequent periods of elevated stress (Dixit et al., 2022; McBranch et al., 2019). Similarly, local populations which typically experience lower mean temperatures or more consistent seasonal moisture availability may be more susceptible to suddenly elevated heat- or water demand-related stresses in post-disturbance environments (Candido-Ribeiro and Aitken, 2024). Yet, the extent to which differential post-disturbance responses exist across different local populations of a species is further mediated by covarying site conditions, such as density of competing vegetation, and especially interannual weather variation dictating pace and extent of growth as related to population-level trait variation (Candido-Ribeiro and Aitken, 2024; Gazol et al., 2023; Vasey et al., 2023, 2022).

Understanding patterns and mechanisms, and forecasting drought-related tree die-off globally has improved rapidly in recent years (Allen et al., 2015; Hammond et al., 2022; Xu et al., 2024), but major knowledge gaps remain for understanding the near-term outcomes for juvenile trees which are less susceptible to direct mortality and can persist after overstory tree die-off (Camarero, 2021; Ma et al., 2023; Redmond et al., 2015; Redmond and Barger, 2013). Climate change-driven alterations to disturbance patterns strongly impact demographic patterns by inducing mortality of older overstory cohorts, which may threaten the viability of new or surviving younger cohorts, especially juvenile trees which are typically less stress-resistant than their adult counterparts (Luu et al., 2024; Shriver et al., 2021). Juvenile sensitivity to climate change stressors is often interpreted from landscape-scale, niche-based (i.e., correlative) demographic patterns (e.g., Dobrowski, 2011), or from controlled experiments with imposed heat and drought stress (e.g., Rother et al., 2015). Relatively little is known about how juveniles respond *in situ* to stressors and rapid resource change associated with post-disturbance environments, which reflect underlying biophysical complexities of juvenile tree resource-use plasticity and site characteristics, rather than expression of adaptations to specific (often imposed) stressors (Gazol et al., 2023). Disturbances such as drought-driven overstory tree die-off can rapidly alter resource conditions for surviving juveniles, including greater extremes of temperatures and evaporative demand (De Frenne et al., 2021), but also higher light and potentially soil water and nutrient availability (Grossiord et al., 2018a). At the site level, juveniles present in relatively more productive sites with higher tree densities may experience continued light limitations from greater shading from dead or surviving trees, whereas warmer and drier sites may experience higher degrees of abiotic limitation with less residual dead tree cover (Phillips et al., 2024). Additionally, while local population adaptations may be informative

for assessing variation in post-disturbance responses of juveniles, juvenile responses are likely to vary based on size and age-related physical maturity. While larger juveniles likely possess physical capacities to better access available resources, these larger individuals may also be more limited by additional resource requirements associated with greater maintenance costs, whereas smaller juveniles require less resources but also may not possess sufficient resource access (or, alternatively, may continue to benefit from their smaller size being subject to more persistent shade) (Augustine and Reinhardt, 2019; Camarero et al., 2024; Forrester et al., 2022). It is overall unclear how juvenile tree strategies, especially at different stages of physical maturity (e.g., larger and smaller juvenile trees) respond to abiotic conditions across different populations to inform responses to disturbance and ultimately the potential for resilience to disturbance.

In piñon-juniper woodlands in the southwestern US, extensive drought-driven overstory mortality has caused demographic pressures in many woodlands (Shriver et al., 2021), as new piñon regeneration relies on seed availability and facilitation by overstory trees, or facilitation by nurse shrubs (Redmond et al., 2018, 2015; Redmond and Barger, 2013). Surviving juvenile trees following overstory die-off events represent a crucial reservoir for future woodland regeneration and development, and can provide the next cohort of reproductively mature overstory trees, therefore providing the basis for woodland resilience. While much research has focused on observations of spatial and environmental patterns of juvenile presence following overstory die-off, less is known about development and growth patterns of surviving juveniles which inform subsequent woodland development trajectories. Additionally, piñon-juniper woodlands span a wide range of environmental conditions, especially differentiated by temperatures and the relative influence of summer monsoon (vs winter-dominated) precipitation (Falco and Waring, 2020; Kannenberg et al., 2023; Romme et al., 2009; Samuels-Crow et al., 2023). While

juveniles will face more open and exposed conditions following overstory die-off events, weather patterns, general site conditions, and local population adaptations may interact to explain variation in growth responses of surviving juveniles across the range of piñon-juniper woodlands (Vasey et al., 2023, 2022). Understanding how local populations of piñon and juniper trees adapt to these changing conditions is imperative for predicting future ecosystem trajectories.

To assess the outcomes of overstory tree mortality on juvenile trees across different populations of piñon pine, we conducted an experiment to compare growth responses of juveniles spanning a range of sizes under live and dead overstory at different sites and over two years. Our objectives were to (1) assess growth of juvenile piñon trees in dead and live overstory environments to understand the influences of overstory condition, (2) to examine inter-population variation in growth in live and dead overstory environments across both regional (latitudinal) and local (elevational) gradients, (3) to assess the influence of juvenile size, or physical maturity, a proxy for resource acquisition and stress tolerance, on juvenile growth in live and dead overstory, and (4) to understand how growth of different populations and in live and dead overstory environments changes with interannual weather variation. Many prior studies have investigated the impacts of imposed abiotic limitations like heat and atmospheric and soil drought on growth of adult piñon trees, demonstrating strong influences of water limitations and, to a lesser degree, heat on shoot growth, needle emergence, and other related growth and physiological responses (Adams et al., 2015; Grossiord et al., 2017, 2017; Guérin et al., 2020, 2018; McBranch et al., 2019). Additionally, observational studies have established patterns of adult piñon growth sensitivities at different sites to climate variation, especially interactions of precipitation and growing season heat and atmospheric dryness (e.g., Redmond et al., 2017). Yet, little evidence exists for how juvenile growth is affected by overstory mortality,

especially if associated resource changes increase the risk of extreme abiotic stress, across regional and local environmental gradients, and by variation in weather. With this study, we aim to advance understanding of the outcomes of overstory disturbance on juvenile piñon pine and potential insights into population-level differences in these outcomes. Ultimately, this knowledge can inform proactive management strategies, such as seed sourcing for reforestation efforts and targeted assisted migration initiatives, to enhance the resilience of pinyon-juniper woodlands in the face of ongoing climate change and disturbance regimes.

METHODS

Descriptions of Study Locations and Sites

In this project, we investigated growth responses of juvenile piñon pine trees to mortality of overstory trees in piñon-juniper woodlands spanning regional (latitudinal) and local (elevational) environmental gradients (Figure 4.1). We chose 3 study locations across a latitudinal gradient within the geographic distribution of two-needle piñon pine (*Pinus edulis*) from northern Arizona to northern Colorado. The selection of these locations was based on differences in climate, especially differences in mean annual temperatures and differences in the relative strength of bimodal, monsoonal precipitation patterns (detailed below) which can strongly affect tree growth (Peltier and Ogle, 2019; Samuels-Crow et al., 2023). At these locations, we established study sites across an elevational gradient in which piñon pine was a dominant overstory tree species, spanning low-mid-high elevation piñon pine dominated stands, to capture local environmental gradients, such as temperature, precipitation, and vegetation density (Falco and Waring, 2020). Over the course of the initial two years of study, we dropped

high-elevation study sites from two study locations due to personnel safety concerns and wildfire which burned through one study site. Additionally, we excluded one low-elevation study site where we were unable to find sufficient piñon juveniles for sampling. As a result, our study included sites for the following: low- and mid-elevations at our southern location near Flagstaff, AZ ("AZL" and "AZM"); low-, mid-, and high-elevations at our middle study location near Cortez, CO ("SCOL", "SCOM", and "SCOH"); and, mid-elevation at our northern location near Dinosaur National Monument in northwestern CO "NCOM"). Therefore, our regional, latitudinal environmental gradient of study was represented by comparable mid-elevation sites (AZM, SCOM, and NCOM), and local environmental gradients were represented most fully within the SCO region (SCOL, SCOM, and SCOH), in addition to AZ (AZL and AZM). We describe general climate, soils, and vegetation characteristics of these sites below, with detailed information available in Table 4.1.

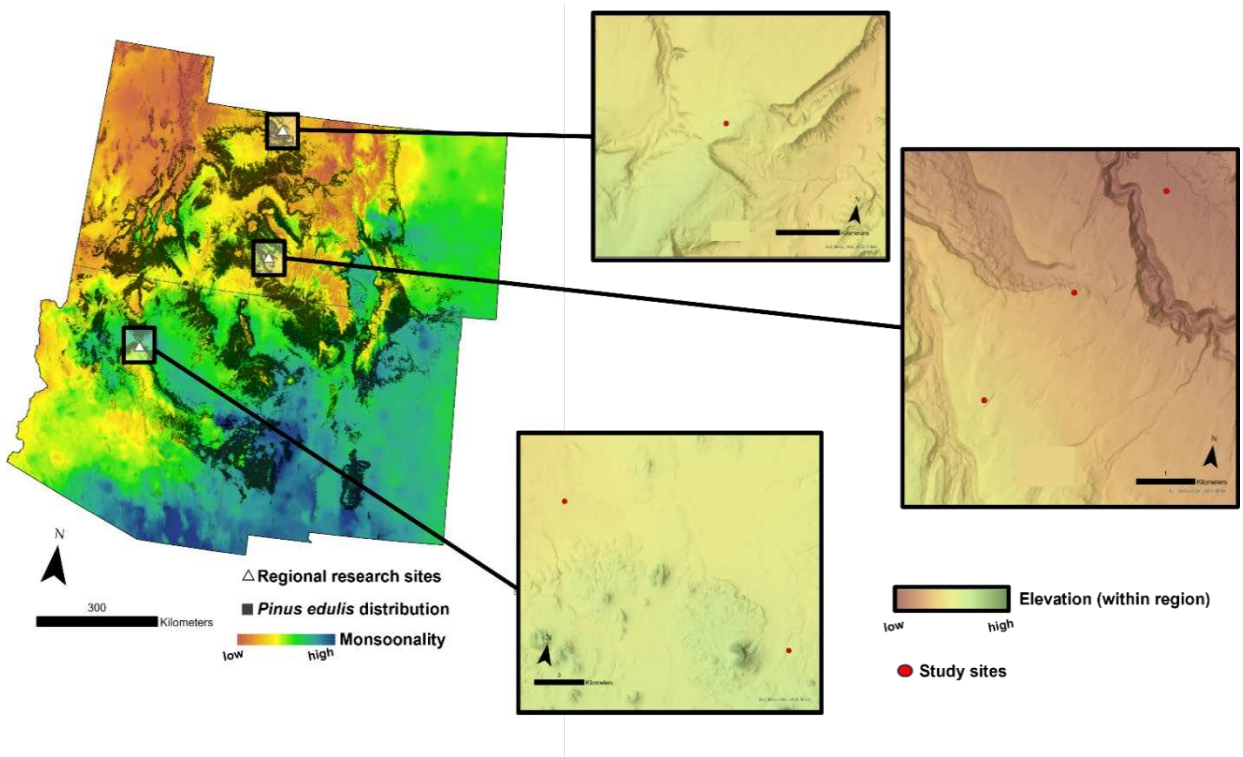

Figure 4.1. *Map of study extent. We established sites across a latitudinal regional gradient which reflected differences in climate, notably the prevalence of monsoon precipitation (full extent map). Regions included northern Arizona (AZ), southern Colorado (SCO), and northern Colorado (NCO). Within each region, we established study sites across elevational gradients to capture local environmental variation. However, several sites were dropped due to various concerns (see Methods), and resulting sites included low- and mid-elevations in AZ (AZL and AZM), low-mid-high elevations in SCO (SCOL, SCOM, SCOH), and a mid-elevation site in NCO (NCOM).*

Our southern study sites, AZL and AZM, represented piñon-juniper woodlands at the warm and dry extent of the distribution of *P. edulis* sites in our study, with a relatively strong bimodal, monsoonal precipitation regime on average (Table 4.1), and well-drained, volcanic-origin soils. Regarding general tree cover and structure, cover of piñon and juniper trees at AZL was patchy, with large spaces of unvegetated soil (with some biological soil crusts) in between individual or small patches of trees, with piñon and juniper trees at similar abundances. In contrast, treed patches at the AZM site are much closer in proximity, and inter-tree spaces generally are vegetated by herbaceous vegetation, with more minimal occurrences of bare soil.

At AZM, piñon was largely dominant, though juniper was also abundant and a few scattered ponderosa pine (*Pinus ponderosa*) were present.

Our mid-latitude study sites, SCOL and SCOM and SCOH, were representative of moderately warm and dry piñon-juniper woodlands at the core of *P. edulis* distribution, with moderate monsoonal precipitation patterns (Table 4.1), and very rocky, well-drained soils. Sites in this region reflected a wide range of biotic conditions as well: similar to AZL, the SCOL site was characterized by very patchy cover of single or few trees with wide inter-tree spaces; however, at SCOL, these interspaces were somewhat vegetated with both herbaceous and shrubby vegetation, as well as considerable areas of bare (or biological soil crust) soil and large and extensive rock cover. Tree cover of piñon and juniper was similar in terms of abundance of each species. The SCOM site contained a variety of inter-tree space sizes, though much smaller than those at SCOL, and these spaces were sparsely vegetated with herbaceous and shrubby vegetation, with very rocky soils. Trees at SCOM occurred mostly in patches of several trees, and piñon pine was more abundant than juniper. Conditions at SCOH were comparatively unique, in terms of tree and ground cover. Tree cover was considerably dense and largely continuous at SCOH, and only limited juniper was present. Inter-tree spaces were relatively small, and were often small patches of bare ground, or vegetated with herbaceous vegetation and cacti. Considerable cover of gambel oak (*Quercus gambelii*) in shrubby form was also present, as were other large shrubs such as serviceberry (*Amelanchier alnifolia*). Soils were also very rock at the SCOH site, though cover of large rocks was not as prevalent as downslope sites.

Our northern study site, NCOM, was near the northern extent of *P. edulis* distribution, representative of cooler but also dry piñon-juniper woodlands with more unimodal, snow-dominated precipitation regimes (Table 4.1) and well-drained rocky and sandy soils. Tree cover

at this site was relatively dense (greater than SCOM, less than SCOH), and while considerable juniper was present, piñon dominated overstory environments. Inter-tree spaces were often vegetated with herbaceous and shrub vegetation, but large surface rocks were also scattered throughout the site.

Table 4.1. *Characteristics of study sites, including latitude, elevation, basal area, and climate information. Regional areas chosen for site selection follow a distinct gradient of monsoonality (proportion total annual precipitation received in July-September), and some regions included multiple sites situated across a local elevation gradient. Climate information includes 30-year normal precipitation, vapor pressure deficit (VPD), climatic moisture deficit (CMD; Hargreaves), and monsoonality (all data obtained from ClimateNA, https://climatena.ca/). Additionally, for each climate variable we included yearly differences from 30-year normals for years included in our analyses (2020-2022) which illustrate relative weather-related stresses specific to each site. Site codes: AZL = low-elevation, northern Arizona; AZM = middle-elevation, northern Arizona; SCOL = low-elevation, southwestern Colorado; SCOM = middle-elevation, southwestern Colorado; SCOH = high-elevation, southwestern Colorado; NCOM = middle-elevation, northern Colorado.*

Site	**AZL**	**AZM**	**SCOL**	**SCOM**	**SCOH**	**NCOM**
Latitude	35.5	35.5	37.9	37.9	37.9	40.6
Elevation (m)	1910	2066	1934	2111	2291	2099
Basal area (m^2 ha^{-1})	57.5 (± 30.1)	78.2 (± 26)	37.4 (± 17.9)	72.4 (± 31.6)	97.2 (± 27.4)	187.8 (± 56.5)
Precipitation (mm)	315.7 (± 72.8)	450.7 (± 107.4)	351.4 (± 75.7)	405.7 (± 87.6)	472.2 (± 101.9)	362.8 (± 87.8)
VPD (kPa)	0.75 (± 0.04)	0.69 (± 0.04)	0.7 (± 0.04)	0.62 (± 0.03)	0.56 (± 0.03)	0.54 (± 0.03)
CMD (mm)	939.7 (± 94.5)	790.6 (± 109.4)	819.1 (± 92.8)	708 (± 98.2)	601.7 (± 105.5)	598.8 (± 96.6)
Monsoonality (proportion)	0.45 (± 0.15)	0.40 (± 0.15)	0.33 (± 0.09)	0.34 (± 0.09)	0.33 (± 0.09)	0.24 (± 0.08)
2020 Prec. Difference	-81.67	-101.70	-51.40	-53.70	-56.23	-80.80
2021 Prec. Difference	-39.67	-69.70	-0.40	4.30	15.77	-53.80
2022 Prec. Difference	18.33	-10.70	13.60	16.30	22.77	6.20

2020 VPD Difference	0.05	0.06	0.03	0.03	0.03	0.02
2021 VPD Difference	0.04	0.03	0.03	0.03	0.02	0.04
2022 VPD Difference	0.01	0.01	0.01	0.01	0.01	0.02
2020 CMD Difference	148.33	184.40	77.90	85.97	87.30	102.17
2021 CMD Difference	48.33	50.40	17.90	8.97	-10.70	67.17
2022 CMD Difference	3.33	10.40	-18.10	-23.03	-29.70	-0.83
2020 Mons. Difference	-0.24	-0.23	0.00	0.00	0.00	-0.12
2021 Mons. Difference	0.14	0.15	0.10	0.10	0.09	0.10
2022 Mons. Difference	0.11	0.12	0.03	0.03	0.03	-0.01

Experimental Design and Field Sampling

We designed an experiment to compare growth of piñon pine juveniles occurring beneath and adjacent to live overstory trees and juveniles occurring beneath and adjacent to dead overstory trees. To make more direct comparisons across these conditions, we established study plots under live overstory tree cover at the beginning of our study, and subsequently introduced a mortality treatment to half of these plots. In the summer of 2019, we established 30 plots under live overstory woodland cover at each study site. We selected plots first by identifying stands of healthy piñon-juniper woodland cover and searching for individual, dominant piñon trees on which to center our plots ("focal tree"). We selected these focal trees by identifying dominant, apparently healthy (≥ 90% live green foliage, no evidence of insect- or other damage which would indicate decline in health) piñon trees. Selected focal trees were at least 10 m apart to avoid obvious influence of one plot environment on another. Additionally, we selected against

trees on slopes greater than 15%. After establishing all plots, we randomly assigned each of our 30 overstory tree plots per site to a plot treatment type of live overstory or dead overstory (see below for details on mortality treatment implementation). To quantify overstory woodland structure around selected focal trees, we measured diameter at root collar (or, basal diameter; hereafter, "DRC") of all non-juvenile trees (≥ 9 cm DRC) within a distance of 7m of each focal tree stem, which was approximately 1.25 times the height of focal trees, on average.

In the winter of 2019-2020 (~late November-early March), we initiated a mortality treatment for half of our live overstory plots at each study elevation and location according to random treatment assignment previously described. Our objective with this treatment was to create an analogue to the biophysical outcomes of drought-induced mortality of overstory piñon trees, as has been seen in many regions throughout the range of piñon-juniper woodlands. As such, we sought to create dead overstory environments with standing dead trees, leaving as little physical disturbance to remaining live vegetation as possible. We created these dead overstory environments by girdling overstory piñon trees in each plot assigned to the mortality treatment. We girdled piñon pine because the majority of overstory tree mortality in these woodlands in the preceding years had occurred in piñon pine, and less so in juniper (various spp.). Girdling consisted of using a chainsaw to girdle approximately 0.5-2.5 inches deep into the sapwood (dependent on stem diameter and desire to maintain standing dead trees) and 3 inches vertically along the stem of all overstory trees (≥ 9 cm DRC) in a given plot. The pace of mortality and the extent to which overstory trees retained dead needles differed substantially across sites and years in which growth was studied. Consequently, we tracked the proportion of needle retention of overstory trees for both live and dead overstory plot types and across years in order to control for

this wide plot- and site-level variation in our analyses (see below description of analysis for additional detail).

Growth Sampling

To measure growth of juvenile piñon trees, we located piñon juveniles (defined as trees <9 cm DRC) in our plots across all sites that spanned a range of size classes (ranging from 0.3 – 8.9 cm; mean 3.1 cm ±2.5, median 2.3 cm) DRC which appeared healthy with no evident signs of stress or decline. This range of sizes provided a wide gradient on which to base our analysis of juvenile growth in relation to size in live and dead overstory environments, where smaller trees were among those for which we could reasonably distinguish interannual growth (see below) and the upper extent was the limit of our classification of juveniles in this study (approximately just below the tree size where reproductive maturity began to be evident). We selected similarly sized individuals from each of our live and dead overstory plot types to make measurements for comparisons across live and dead overstory environments and juvenile tree sizes. We sampled growth of individuals from measurements of lateral branches and needles, as we expected branch and needle growth to reflect relative resource availability (Magnin et al., 2017). For each individual juvenile tree, we randomly selected three branches to measure from the middle section of the crown area (Guérin et al., 2018; McBranch et al., 2019; Sprugel, 2002), though for smaller individuals we were sometimes limited to one or two branches for measurements. We measured annual growth using interannual bud scars, induced by the initiation of growing season phenology, as identifiers between years of growth (Adams et al., 2015). We also took corresponding needle length measurements (average of three needles) for each year of branch growth, when needles were present (Adams et al., 2015; Grossiord et al., 2017; Guérin et al., 2018). We measured growth up to 7 years prior to the sampling year,

resulting in growth records which spanned a maximum of 8 years (2015-2022). However, for smaller and younger trees, we measured as many years as were available on branches (typically record lengths of 4-5 years total among the smallest individuals). We also avoided sampling forked branches, as growth along these shoots would not have been proportionally representative of a primary growth axis; in these cases, some growth records ended prior to our 2015 target. Mean growth record length was 7.1 yrs (±1.4). We measured multiple branches on each individual in order to reduce some within-individual growth variation for subsequent analysis, and averaged growth measurements for each year across all sampled branches for each individual for analysis.

Analysis

Our study objectives included evaluating branch and needle growth of juvenile trees following overstory mortality, relative to differences across broad environmental gradients reflected in our site selections (population differences), assessing the influence of juvenile tree size on these patterns, and relative to post-treatment weather conditions. For both our branch and needle growth response variables, we calculated a growth ratio (branch growth ratio, BGR, and needle growth ratio, NGR) that reflected the relationship of post-overstory mortality growth relative to mean growth of years prior to overstory mortality. For each full year of growth following overstory mortality (2021 and 2022) we calculated our response variable as the growth of that year (averaged over the number of branches sampled on a given individual) over the mean growth of all measured years prior to overstory mortality (again, averaged over branches for an individual):

$$GR_{ij} = growth_{ijk} / growth_{pre\text{-}mortality}$$

Where GR_{ij} is the growth ratio (BGR or NGR) derived from the *growth* of individual tree *i* in post-mortality year *j* (*j* = 2, including 2021 and 2022) averaged over *k* branches relative to average *growth* of the same individual and *k* branches for the *pre-mortality* period measured. This follows similar approaches used in other studies (e.g., Cabon et al., 2023; Férriz et al., 2021; Kannenberg et al., 2022; Lloret et al., 2011) to assess growth responses after substantial changes in resource conditions (i.e., growth recovery following drought periods). Notably, we excluded 2020 growth measurements from our calculations of mean growth in pre-treatment periods. Because we induced mortality in overstory trees in the winter prior to the growing season of 2020, we expect that these trees were actively dying during 2020 and thus affecting resource conditions. As the progression of mortality was especially variable in the 2020 season, 2021 represented the first full season for most juveniles experiencing post-overstory mortality conditions. Additionally, for all models (described below), we separately modeled 2021 and 2022 ("first-" and "second-year" growth following overstory mortality) BGR and NGR, as we anticipated potential differences across these years due to progression of the post-mortality environments (potentially varying by site), different levels of overstory needle retention across sites (described previously), and weather variation across years. For all models, we included a fixed effect for the proportion of overstory tree needle retention at each plot (Figure 4.2) to control for variation in the timing of overstory mortality and loss of needles which would affect the plot microenvironment, including incoming solar radiation and associated temperatures, and precipitation throughfall. We also used a plot identifier as a random intercept term to account for spatial autocorrelation both for individuals in the same plot as well as plots within close distances at the same site. For modeling, we used the *lmer* function in the "lme4" package (Bates

et al., 2023) in the R statistical computing environment (R Core Team, 2020), using maximum likelihood-based estimates of model coefficients.

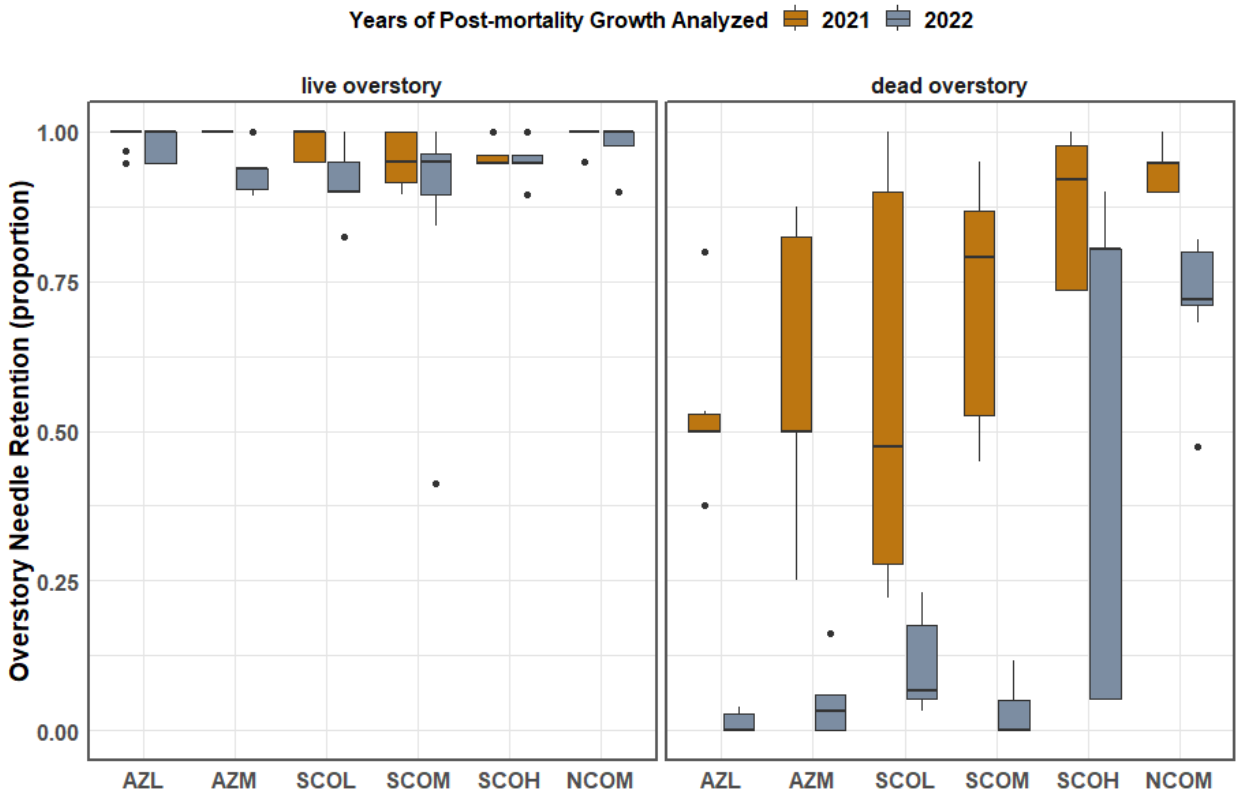

Figure 4.2. *Proportion of overstory needle retention summary data for each site, in both live and dead overstory environments. After inducing overstory mortality in our experiment, loss of dead needles from these trees, and circumstantial needle loss from live overstory plot types, was variable both across sites and years included in our growth analyses. We used these data as a fixed effect in all models to control for this variation.*

Our analysis consisted of modeling BGR and NGR, for first- and second-year growth periods, relative to: (a) all sites to examine overall patterns and differences within sites (populations); (b) comparable middle-elevation regional sites (AZM, SCOM, NCOM) to explicitly evaluate regional (AZ, SCO, NCO) differences in relation to monsoonality as an important distinguishing characteristic across regions (Samuels-Crow et al., 2023); (c) local

environmental gradients encompassed in elevational differences for the SCO region (low, middle, and higher elevations); and, (d) post-treatment interannual weather variability across all sites. For each model, we evaluated the effects of site-level variables interacting with overstory (treatment) environment (live and dead). For models across all sites (a), this interaction occurred for Site (factor) and overstory environment (factor). For models of growth in relation to regional climate differences (b), we modeled growth ratios in relation to mean (30-year normal of 1991-2020) monsoonality (derived from climate data obtained from ClimateNA, https://climatena.ca/, accessed on 3 January 2023; Wang et al., 2016), interacting with overstory environment. For models of growth in relation to local environmental gradients reflected in elevation for the SCO region (c), we modeled growth ratios relative to the elevation value for each site, interacting with overstory environment. Lastly, for models of growth in relation to post-treatment weather (d), we modeled growth ratios across sites in relation to yearly climatic moisture deficit (Hargreaves-based CMD; obtained from ClimateNA) for each site. We modeled growth ratios with seasonal and yearly variations of CMD as this variable captures ecologically relevant potential water deficit (Petrie and Savage, 2022), driven primarily by temperature, and this variable was simpler than testing combinations of precipitation and temperature or vapor pressure deficit variables together, given the increase in number of predictor variables and limited sample sizes. We calculated CMD differences ("dCMD") from the long-term (1991-2020) average to better assess the relative degree of abiotic stress in each year following treatment (Table 4.1). For each year of modeled growth, we included both the current year dCMD and the prior year dCMD, both interacting with overstory environment, since both current and lag-year effects have been shown to influence growth in semi-arid forests (e.g., Andrews et al., 2020; Guérin et al., 2018). In all models, to assess the influence of juvenile tree size, we included an interaction term for tree size

and overstory environment. We grouped trees into "smaller juveniles" (<= 2cm DRC) and "larger juveniles" (>2 cm DRC) based on physiological distinctions observed in prior work (see Chapter 2 of this Dissertation) and because juveniles in these systems have been divided into similar size classes in prior work on regeneration patterns in these systems (Redmond and Barger, 2013). This size division also was near to the median size of juvenile observed across all sites, and so resulted in nearly equally-sized juvenile groups on which our modeled effects and interpretations are based.

To evaluate model effects of live and dead overstory environments within each site in our model for growth ratios across all sites (a), we used comparisons of marginal mean model predictions for multi-level factor variables. We accomplished these comparisons using the emmeans function of the *emmeans* package (Lenth, 2023), using a false discovery rate *P*-value adjustment for multiple comparisons across sites, and setting our significance threshold at $\alpha = 0.10$. For all other effects, we evaluated confidence intervals to determine significance, where intervals which did not overlap zero indicated significance. We report on all effects and include all model results in our Appendix 3:Supplementary Materials (Table S4.1), regardless of significance determined by this evaluation, as all effects were considered in our models as core components of our study. Lastly, we calculated relative model fit by using root mean squared error for all models (Table S4.1).

RESULTS

Branch Growth Ratios (BGRs)

All sites models (a)

Juvenile piñon pine BGRs differed in dead and live overstory environments only within three different sites across 2 years of growth following overstory mortality, and these patterns

differed slightly between year 1 and year 2 (Figure 4.3). In the first year following overstory mortality, BGRs were greater in dead overstory environments compared to live overstory environments within both SCOM and SCOH sites. In these sites these differences also persisted in the second year of growth following overstory mortality. Additionally, in the second year of growth at the AZL site, BGRs were greater in dead overstory compared to live overstory environments. Notably, in the first year following overstory mortality, only BGRs in dead overstory environments at SCOM and SCOH were above 1 on average, suggesting that growth of juveniles at these sites was on average more than 100% of prior mean growth. However, in the second year of growth after overstory mortality, BGRs in dead overstory environments were nearly all, except at NCOM, greater than 1; similarly, nearly all BGRs in live overstory environments, except at SCOL, were below 1, on average. Importantly, there was no evidence of BGRs in dead overstory environments that were less than growth ratios in in live overstory environments within each site, over both years of post-mortality growth. Lastly, across years 1 and 2, both the interaction of juvenile tree size and overstory environment and the main effect of juvenile tree size were not significant. However, in the second year following overstory mortality, smaller juveniles (< 2 cm DRC) showed marginally greater growth than larger juveniles (> 2 cm DRC) in dead overstory environments (Figure 4.4).

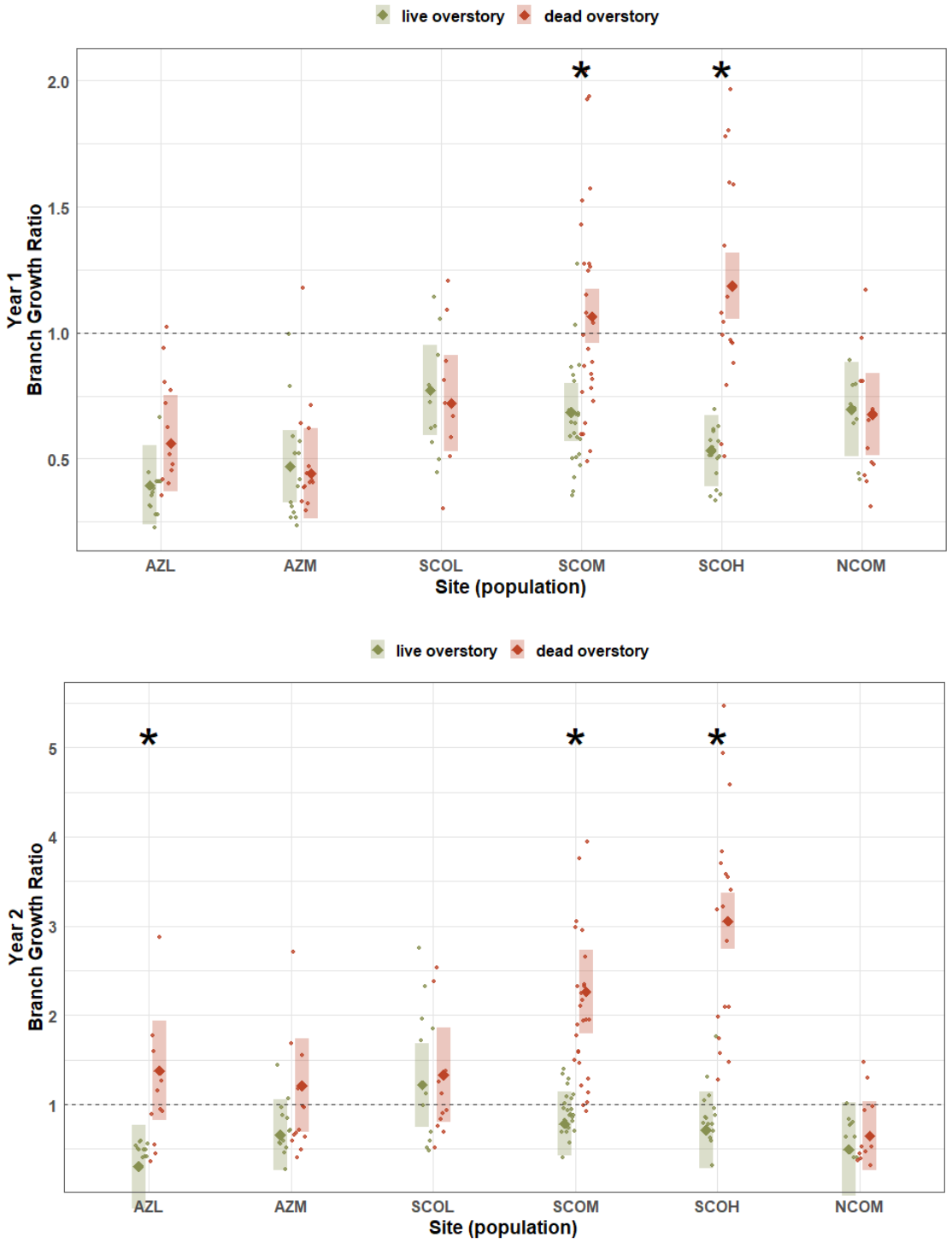

Figure 4.3. *Results of Branch Growth Ratio models for Year 1 (top panel) and Year 2 (bottom panel) of growth across all sites, showing model results for the interaction of Site and overstory environment (live and dead). Modeled effects are shown with means (large diamond symbols) and uncertainty of modeled estimates (shaded bars around large diamonds). Colors signify live (green) and dead (red) overstory environments. Significance of pairwise comparisons of branch growth ratios between dead and live overstory environments within each site are denoted with an asterisk. Marginally significant results are denoted with a period. The dashed horizontal line at 1.0 branch growth ratio indicates a reference*

branch growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.

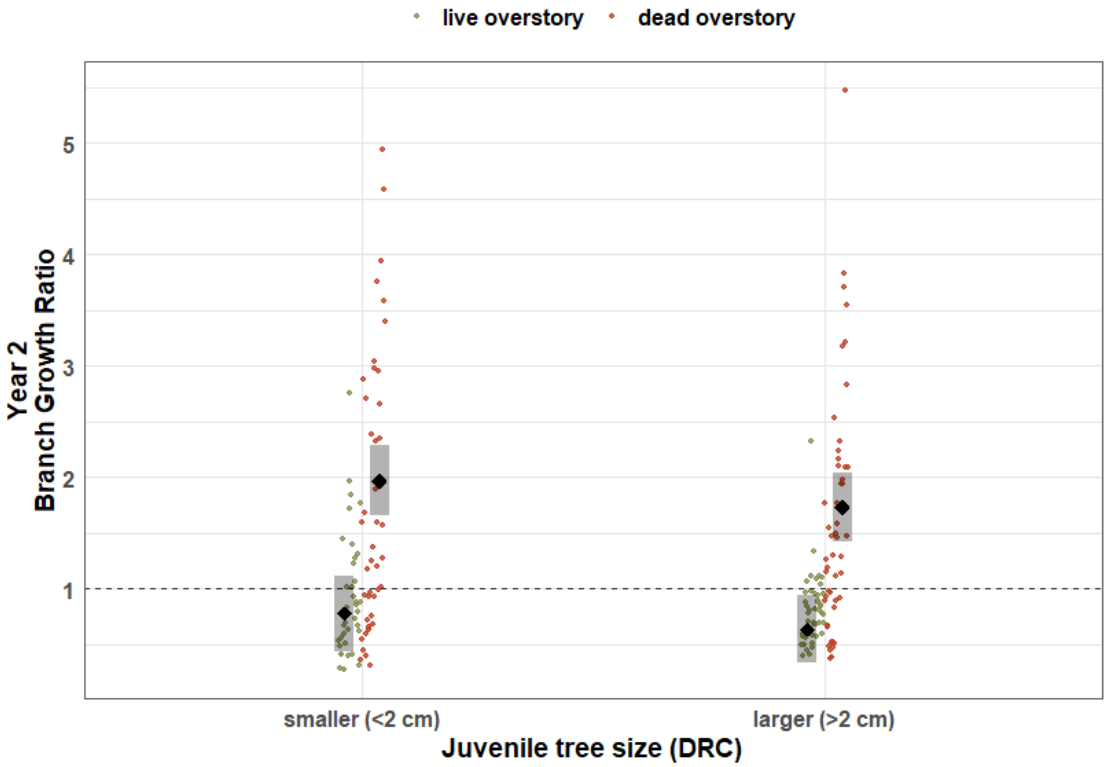

Figure 4.4. *Results of Branch Growth Ratio models for Year 2 of growth across all sites, showing marginally significant model results for the interaction of tree size (DRC, smaller and larger trees) and overstory environment (live and dead). Modeled effects are shown with means (large diamond symbols) and uncertainty of modeled estimates (shaded bars around large diamonds). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 branch growth ratio indicates a reference branch growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

Regional monsoonality gradient models (b)

For our models of BGR across the gradient of mean annual monsoon precipitation (proportion of total annual) encompassed in our comparable regional sites (AZM, SCOM, and NCOM), models for both years reflected significant interactions of monsoonality and overstory environment (Figure 4.5). Specifically, BGRs in dead overstory environments were strongly quadratic relative to monsoonality, reflecting the higher growth ratios which occurred at SCOM,

where monsoon precipitation is typically between that at AZM and NCOM. Furthermore, these models reflected similar BGRs which occurred in both dead and live overstory environments at both the lowest and highest monsoonality, or our NCOM and AZM sites, respectively. In contrast, in both years, BGRs in live overstory environments were mostly unchanged in relation to this regional monsoonality gradient. While no significant effects were observed for the interaction of overstory environment and juvenile tree size, there was marginal evidence for greater BGRs of smaller compared to larger trees in dead overstory environments, and only for the second year of growth following overstory mortality (Figure 4.6).

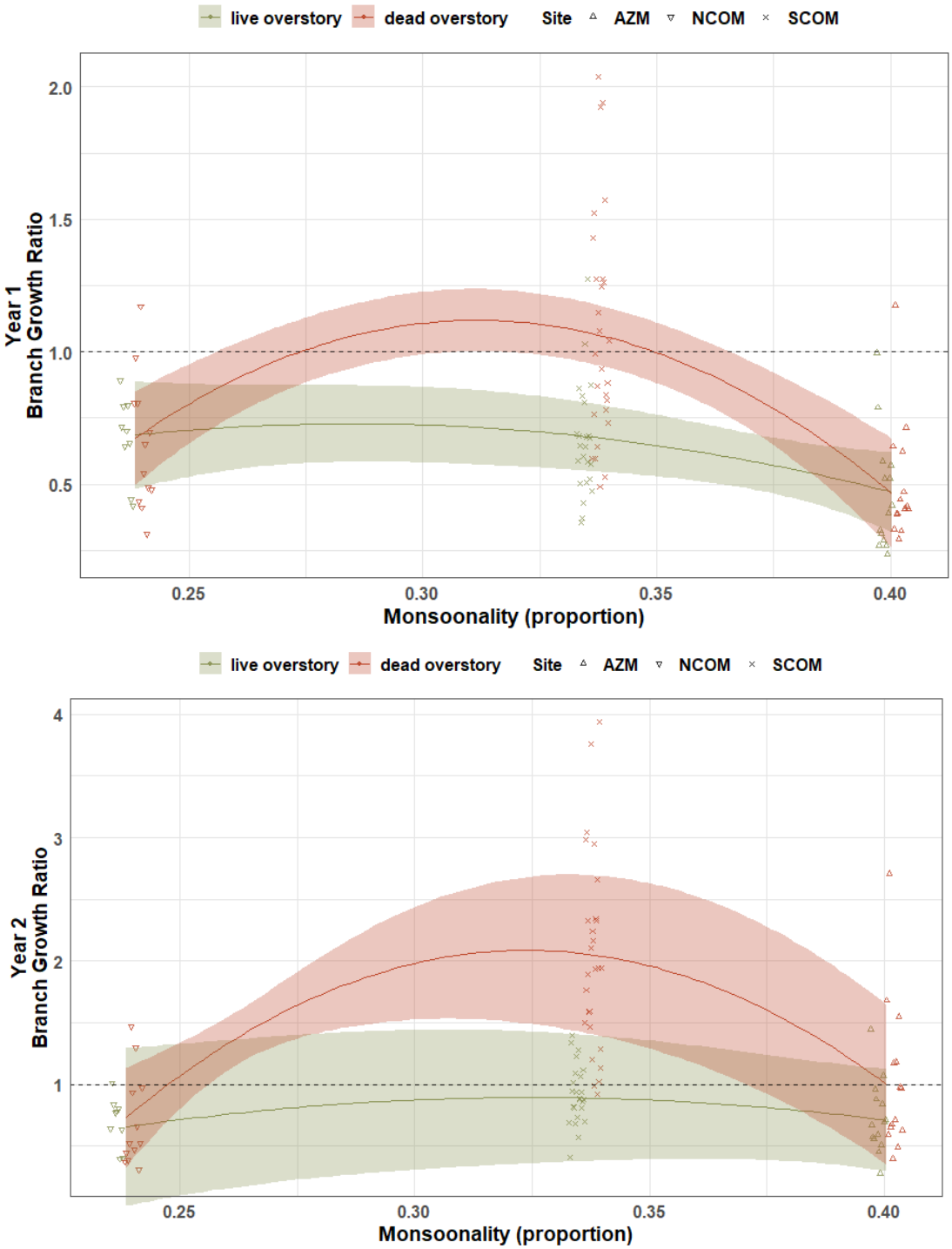

Figure 4.5. *Results of Branch Growth Ratio models for Year 1 (top panel) and Year 2 (bottom panel) of growth across a regional monsoonality gradient reflected in our comparable mid-elevation sites across regions (AZM = upward triangle, SCOM = x, and NCOM = downward triangle), showing model results for the interaction of monsoonality and overstory environment (live and dead). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 branch growth ratio indicates a reference branch growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

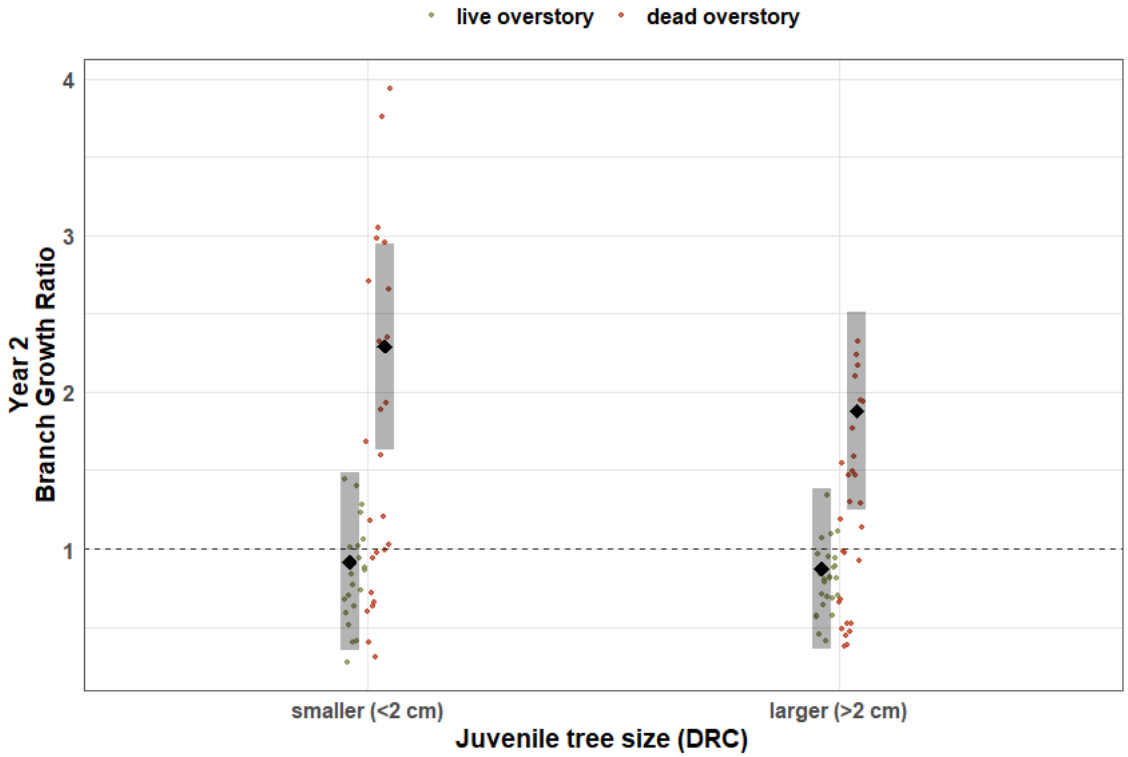

Figure 4.6. *Results of Branch Growth Ratio models for Year 2 of growth across a regional monsoonality gradient reflected in our comparable mid-elevation sites across regions (AZM, SCOM, and NCOM), showing marginally significant model results for the interaction of tree size (DRC, smaller and larger trees) and overstory environment (live and dead). Modeled effects are shown with means (large diamond symbols) and uncertainty of modeled estimates (shaded bars around large diamonds). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 branch growth ratio indicates a reference branch growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

Local elevational gradient models at SCO (c)

Our models of BGRs in relation to local elevational change in our SCO region showed strong relationships between BGRs and the interaction of elevation and overstory environment (Figure 4.7). In both 1- and 2-years following overstory mortality, BGRs in the SCO region in dead overstory environments increased significantly with elevation from lower to higher elevation sites. The relationship of BGRs in live overstory environments with elevation change was minimal but showed slight decreases with increased elevation. There was no evidence of

significant effects of juvenile tree size in either year, either interacting with overstory environment or as a main effect.

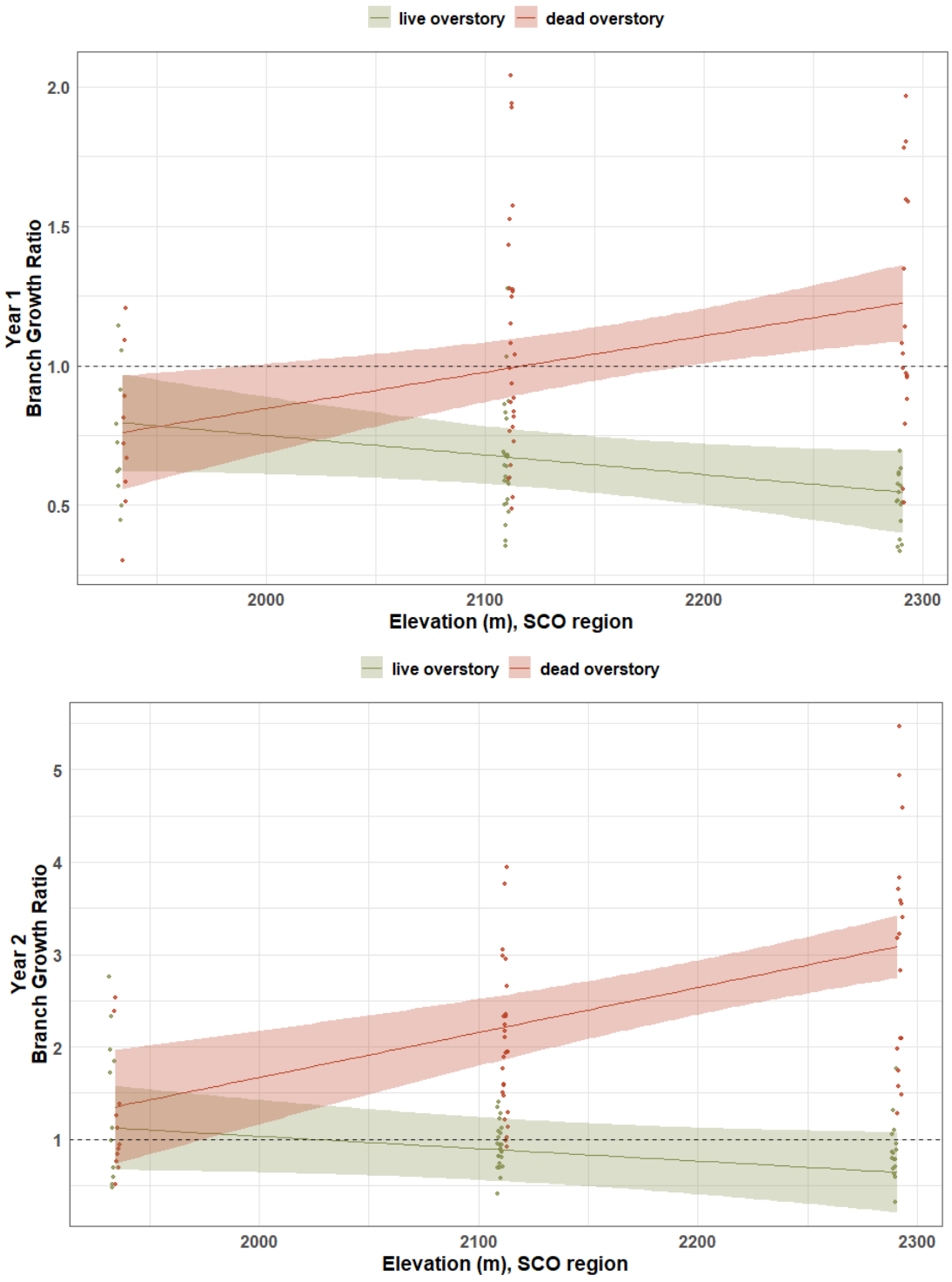

Figure 4.7. *Results of Branch Growth Ratio models for Year 1 (top panel) and Year 2 (bottom panel) of growth across the local elevational gradient encompassed in our southwest Colorado sites (SCOL, SCOM, and SCOH), showing model results for the interaction of elevation (m) and overstory environment (live and dead). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 branch growth ratio indicates a reference branch growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

Post-mortality weather models across sites (d)

Our models of BGRs in relation to weather variation following overstory mortality showed mixed importance of overstory environments interacting with climatic moisture stress across different years, though BGRs predominantly had a negative relationship with higher differences of CMD from normal climate conditions. In the first year following overstory mortality (Figure 4.8), BGRs had a negative relationship with higher dCMD in the year prior to growth, without a significant interaction with overstory environments. This relationship reflected higher BGRs which occurred at SCO region sites and low dCMD compared to low BGRs across other sites. dCMD in this year prior to the first year of growth were especially high at AZ sites, though only moderately greater at NCOM than SCO sites (though growth ratios remained low at NCOM). Additionally, first year BGRs were negatively related to dCMD in the year of growth, and this relationship was very strong with dead overstory environments and minimally related to live overstory environments. This relationship showed strong differences in growth between dead and live overstory environments for low dCMD at SCO sites, but little to no differences for higher dCMD, which were similar at AZ sites and NCOM, though the greatest dCMD occurred at NCOM.

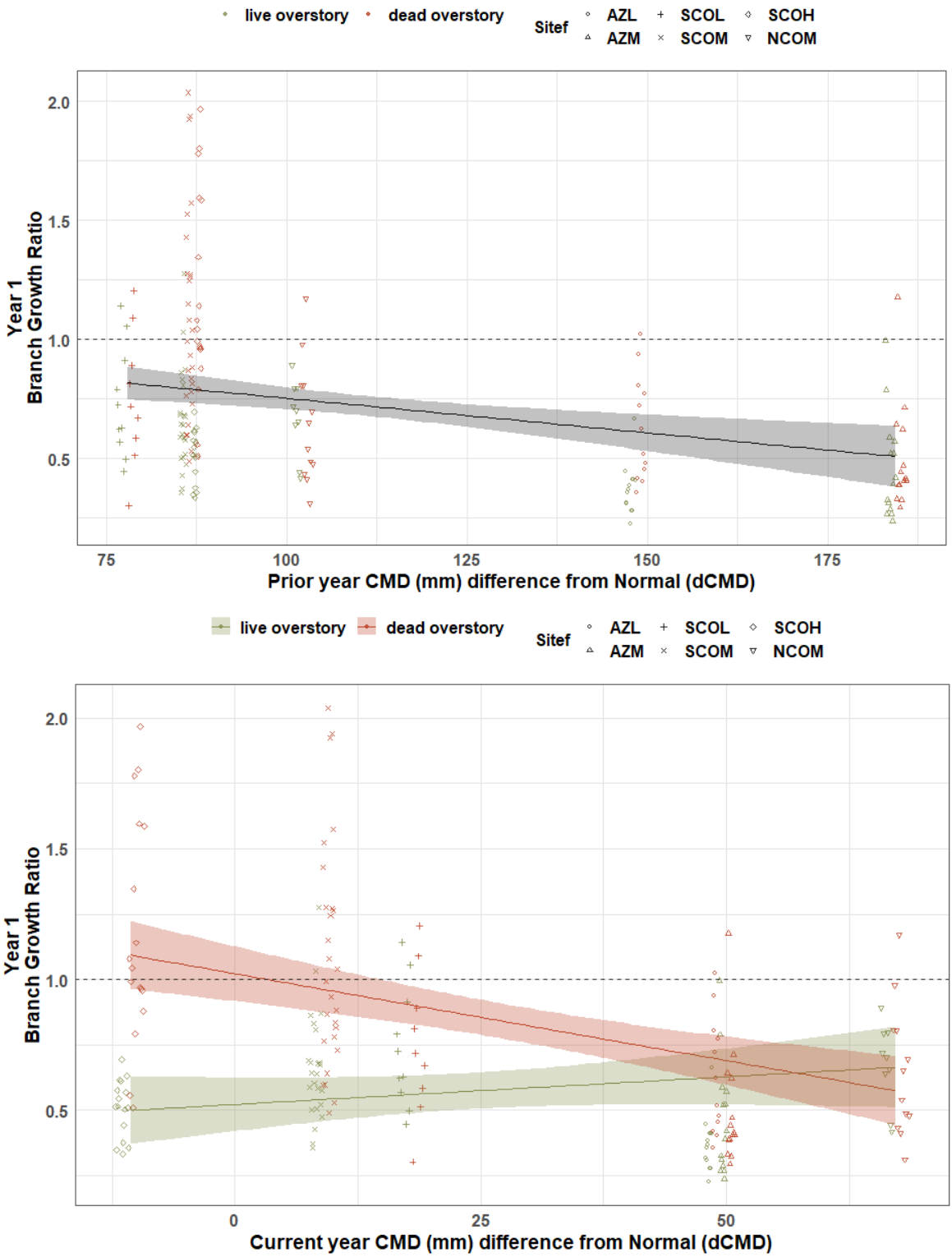

Figure 4.8. *Results of Branch Growth Ratio models for Year 1 of growth in relation to post-mortality weather effects across sites. The top panel shows Year 1 branch growth ratios in relation to prior year CMD differences from normal (dCMD) for which an interaction with overstory environment was not significant. The bottom panel shows Year 1 branch growth ratios in relation to current year dCMD,*

including a significant interaction with overstory environment. Colors signify live (green) and dead (red) overstory environments. Shapes denote sites: AZL = circle; AZM = upward triangle; SCOL = plus sign; SCOM = x; SCOH = diamond; NCOM = downward triangle. The dashed horizontal line at 1.0 branch growth ratio indicates a reference branch growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.

In the second year of growth following overstory mortality (Figure 4.9), there was a significant interaction between overstory environment and dCMD from normal for the year prior to growth, and an insignificant relationship between BGRs and dCMD in the year of growth. This first relationship between BGRs and dCMD in the year prior to growth reflected a lag effect of prior year conditions on the second year of growth, which was the same year of year 1 growth following overstory mortality (2021). The interaction between overstory environments and dCMD in this prior year for the second year of growth showed a strong negative relationship between BGRs in dead overstory environments and dCMD. As with the effects of this same year of CMD on the first year of growth, differences between dead and live overstory growth ratios were large for SCO sites, but minimal to none for AZ and NCOM sites which experienced similarly high dCMD from normal. Interestingly, despite negative dCMD from normal (much less climatic moisture deficit than normal) during the year of growth in the second year for SCO sites, and low differences from normal for other sites, there was no significant relationship detected with BGRs, with or without the interaction of overstory environments.

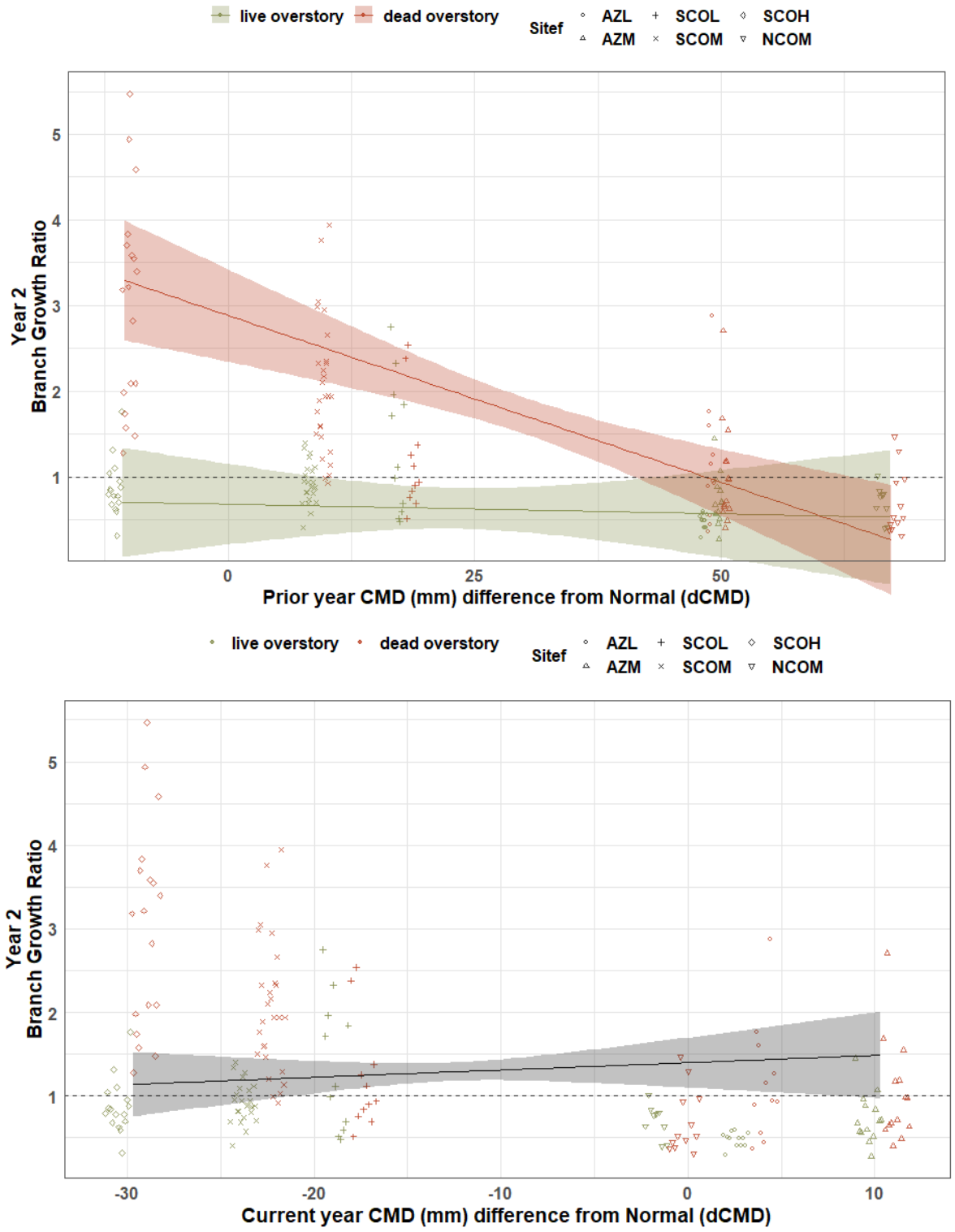

Figure 4.9. *Results of Branch Growth Ratio models for Year 2 of growth in relation to post-mortality weather effects across sites. The top panel shows Year 2 branch growth ratios in relation to prior year CMD differences from normal (dCMD), including a significant interaction with overstory environment. The bottom panel shows Year 2 branch growth ratios in relation to current year dCMD for which an interaction with overstory environment was not significant. Colors signify live (green) and dead (red)*

overstory environments. Shapes denote sites: AZL = circle; AZM = upward triangle; SCOL = plus sign; SCOM = x; SCOH = diamond; NCOM = downward triangle. The dashed horizontal line at 1.0 branch growth ratio indicates a reference branch growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.

Needle Growth Ratios (NGRs)

All sites models (a)

Models of NGRs overall showed largely similar patterns to BGRs within and across sites (Figure 4.10). In the first year after overstory mortality, NGRs were higher in dead overstory compared to live overstory environments at both SCOH and SCOM. NGRs at other sites were lower and were not different between dead and live overstory environments. In year 2 of growth following overstory mortality, NGRs were much more similar across sites. NGRs remained higher in dead overstory compared to live overstory environments at SCOH and SCOM sites, but no differences were evident at SCOL and NCOM. At AZL and AZM sites, NGRs in dead overstory environments were marginally greater than those in live overstory environments. Notably, between the first and second years of growth after overstory mortality, as a general trend, NGRs increased in the second year in dead overstory environments in particular, with all NGRs in dead overstory environments above 1 on average in the second year. Importantly, as with BGR, there was no evidence of NGRs in dead overstory environments being less than corresponding live environments within the same site, for both years, reflecting generally similar, and sometimes greater growth in dead overstory environments, as described above. Regarding the effects of juvenile tree size, the model of first year NGRs showed marginally greater growth among smaller juveniles compared to larger juveniles in dead overstory environments (Figure 4.11), and no differences in the second year.

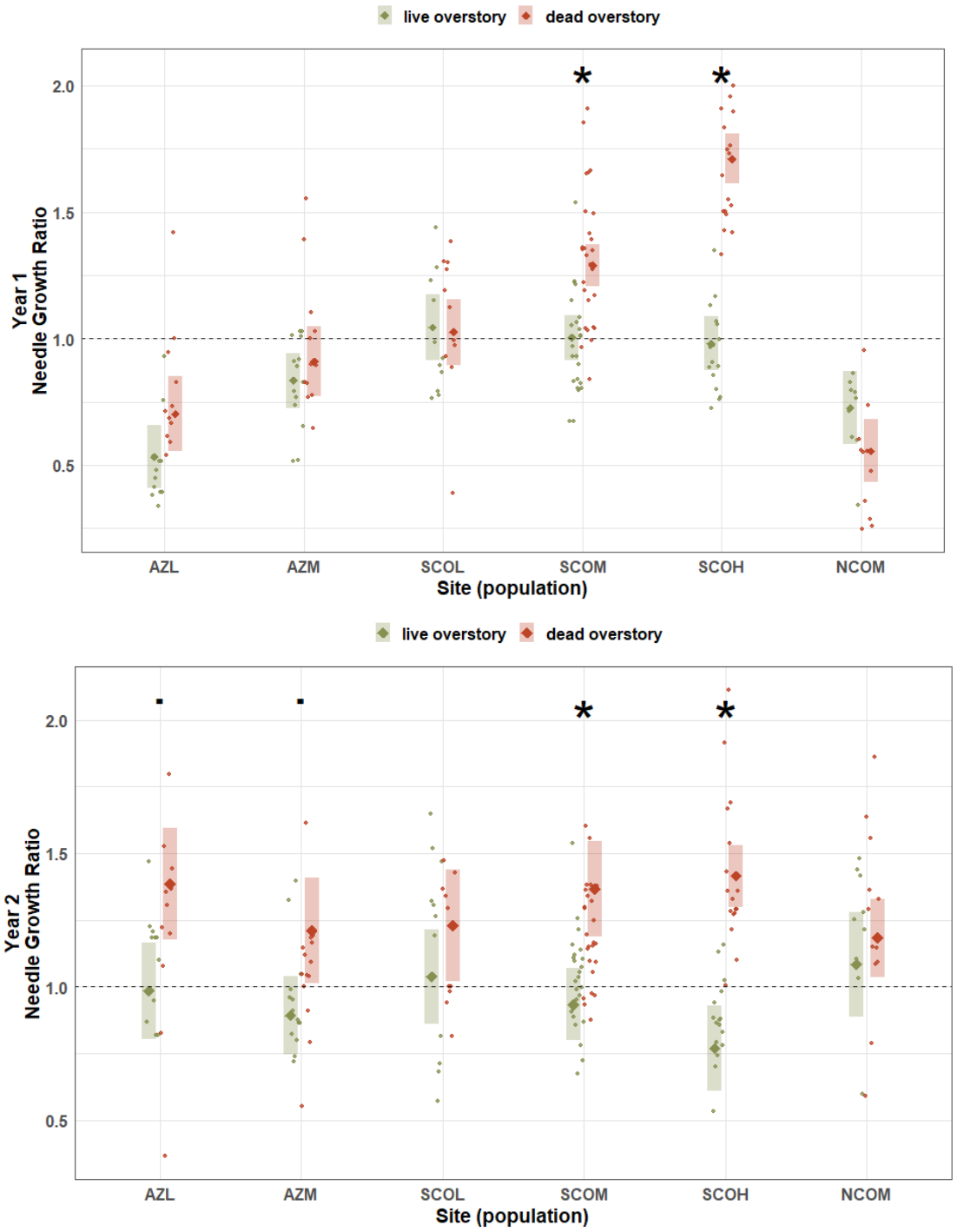

Figure 4.10. *Results of Needle Growth Ratio models for Year 1 (top panel) and Year 2 (bottom panel) of growth across all sites, showing model results for the interaction of Site and overstory environment (live and dead). Modeled effects are shown with means (large diamond symbols) and uncertainty of modeled estimates (shaded bars around large diamonds). Colors signify live (green) and dead (red) overstory environments. Significance of pairwise comparisons of needle growth ratios between dead and live overstory environments within each site are denoted with an asterisk. Marginally significant results are denoted with a period. The dashed horizontal line at 1.0 needle growth ratio indicates a reference needle growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

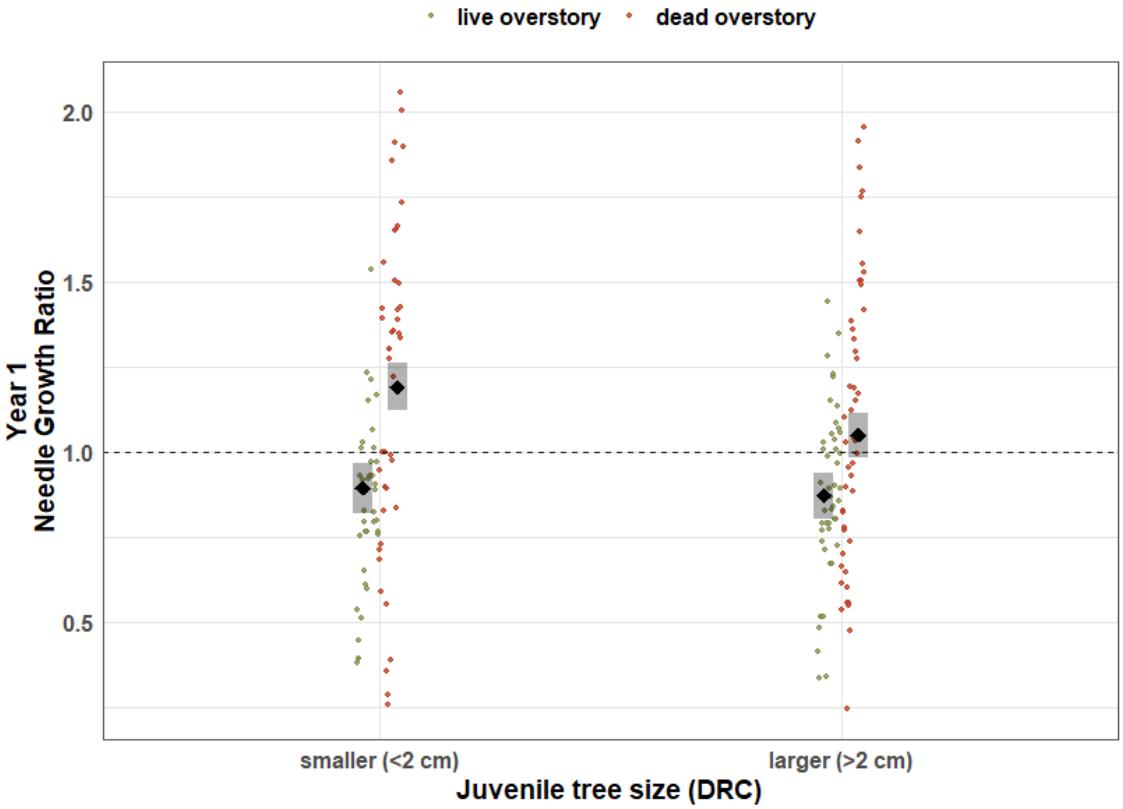

Figure 4.11. *Results of Needle Growth Ratio models for Year 2 of growth across all sites, showing marginally significant model results for the interaction of tree size (DRC, smaller and larger trees) and overstory environment (live and dead). Modeled effects are shown with means (large diamond symbols) and uncertainty of modeled estimates (shaded bars around large diamonds). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 needle growth ratio indicates a reference needle growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

Regional monsoonality gradient models (b)

Our model of NGRs in relation to the regional monsoonality gradient differed across year 1 and year 2 after overstory mortality (Figure 4.12). In the first year following overstory mortality, NGRs were related to the interaction of monsoonality and overstory environment. NGRs in dead overstory environments showed a quadratic relationship with monsoonality, where NGRs peaked at intermediate monsoonality, reflecting higher NGRs in our SCO region compared to the other regions. However, NGRs in dead overstory environments at the lowest

and highest monsoonality (NCOM and AZM, respectively) were lower and similar to live overstory environments. In contrast, NGRs in live overstory environments showed little relationship with monsoonality. Additionally in this first year of growth following overstory mortality, smaller trees showed marginally greater growth than larger juvenile trees in dead overstory environments, though this relationship was marginally significant (Figure 4.13). In the second year of growth following overstory mortality, NGRs were more linearly related to monsoonality across our comparative regional sites, and there was no evidence of a significant interaction with overstory environment. As such, NGRs were highest at the lowest monsoonality (our NCOM site) and declined linearly with increasing monsoonality (across SCOM and AZM).

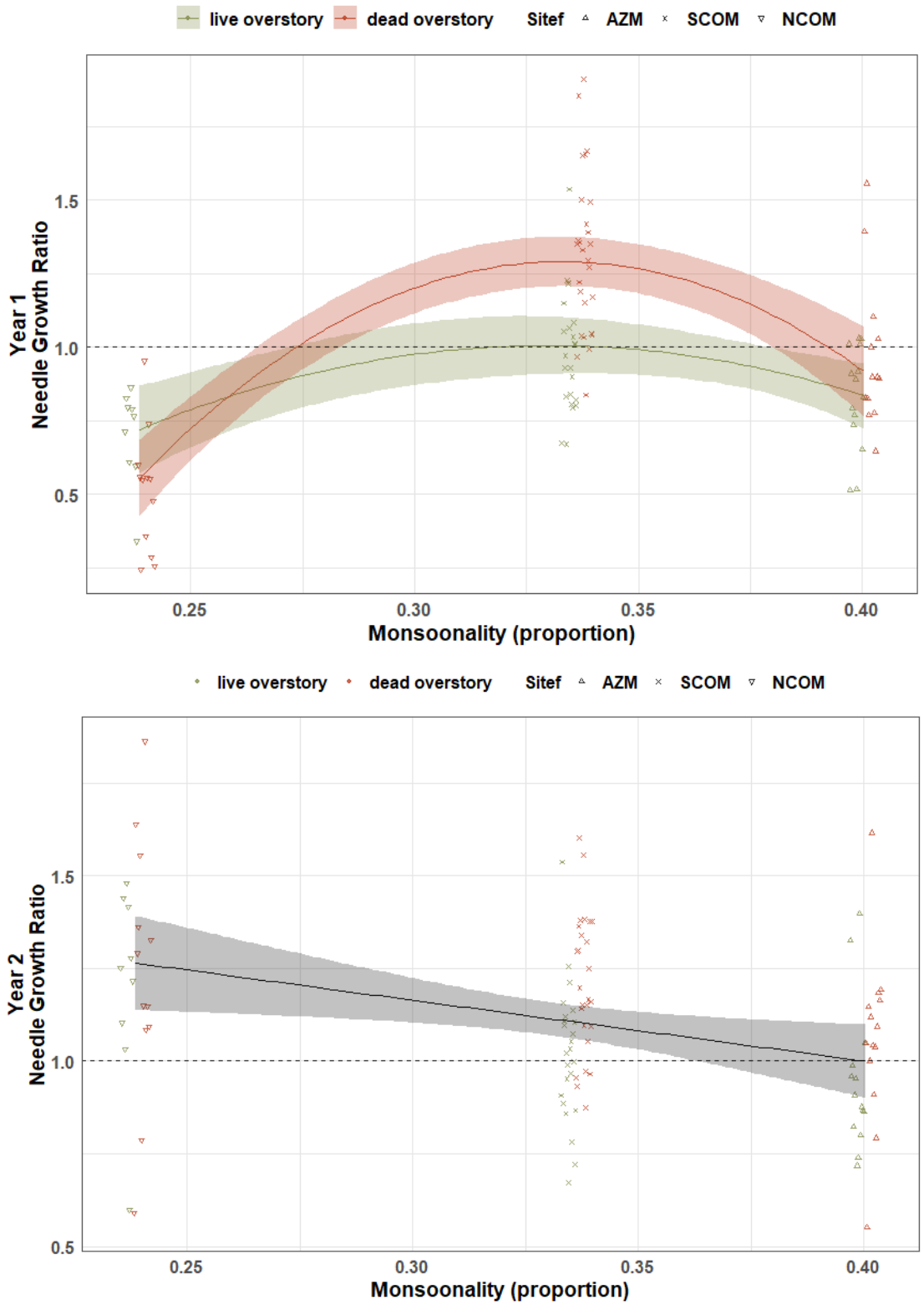

Figure 4.12. *Results of Needle Growth Ratio models for Year 1 (top panel) and Year 2 (bottom panel) of growth across a regional monsoonality gradient reflected in our comparable mid-elevation sites across regions (AZM = upward triangle, SCOM = x, and NCOM = downward triangle), showing model results*

for the interaction of monsoonality and overstory environment (live and dead). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 needle growth ratio indicates a reference needle growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.

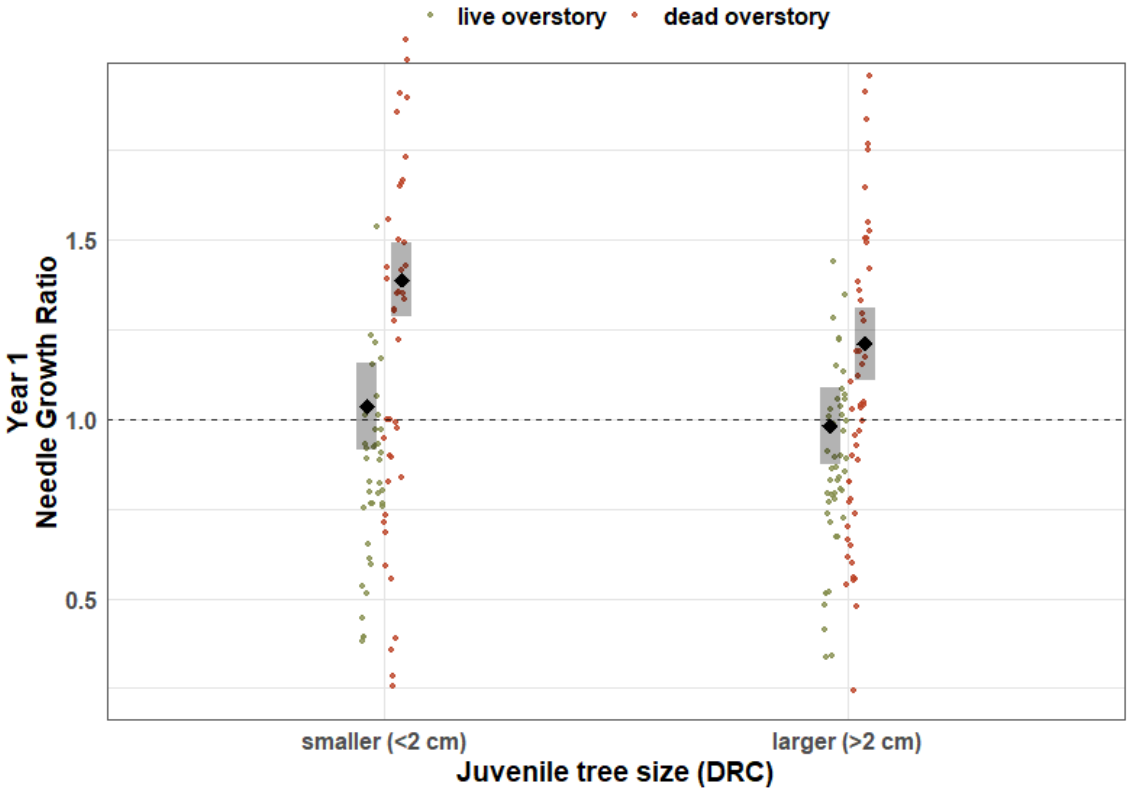

Figure 4.13. *Results of Needle Growth Ratio models for Year 2 of growth across a regional monsoonality gradient reflected in our comparable mid-elevation sites across regions (AZM, SCOM, and NCOM), showing marginally significant model results for the interaction of tree size (DRC, smaller and larger trees) and overstory environment (live and dead). Modeled effects are shown with means (large diamond symbols) and uncertainty of modeled estimates (shaded bars around large diamonds). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 needle growth ratio indicates a reference needle growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

Local elevational gradient models at SCO (c)

NGRs across our elevational site gradient in the SCO region were related to local elevation and juvenile tree size in both years of growth following overstory mortality (Figure 4.14). In the first year following overstory mortality, there was a significant effect of the

interaction of elevation and overstory environments, where NGRs increased significantly with elevation in dead overstory environments, but changed little with elevation in live overstory environments. In this year of growth, smaller trees also had greater NGRs on average than larger trees (not shown). However, in the second year following overstory mortality, there was not a significant interaction between elevation and overstory environment, though each effect was individually significant. NGRs in dead overstory were greater than live overstory, and there was an overall decrease in NGRs with increasing elevation, though this pattern was stronger (but not significantly related) for live overstory environments.

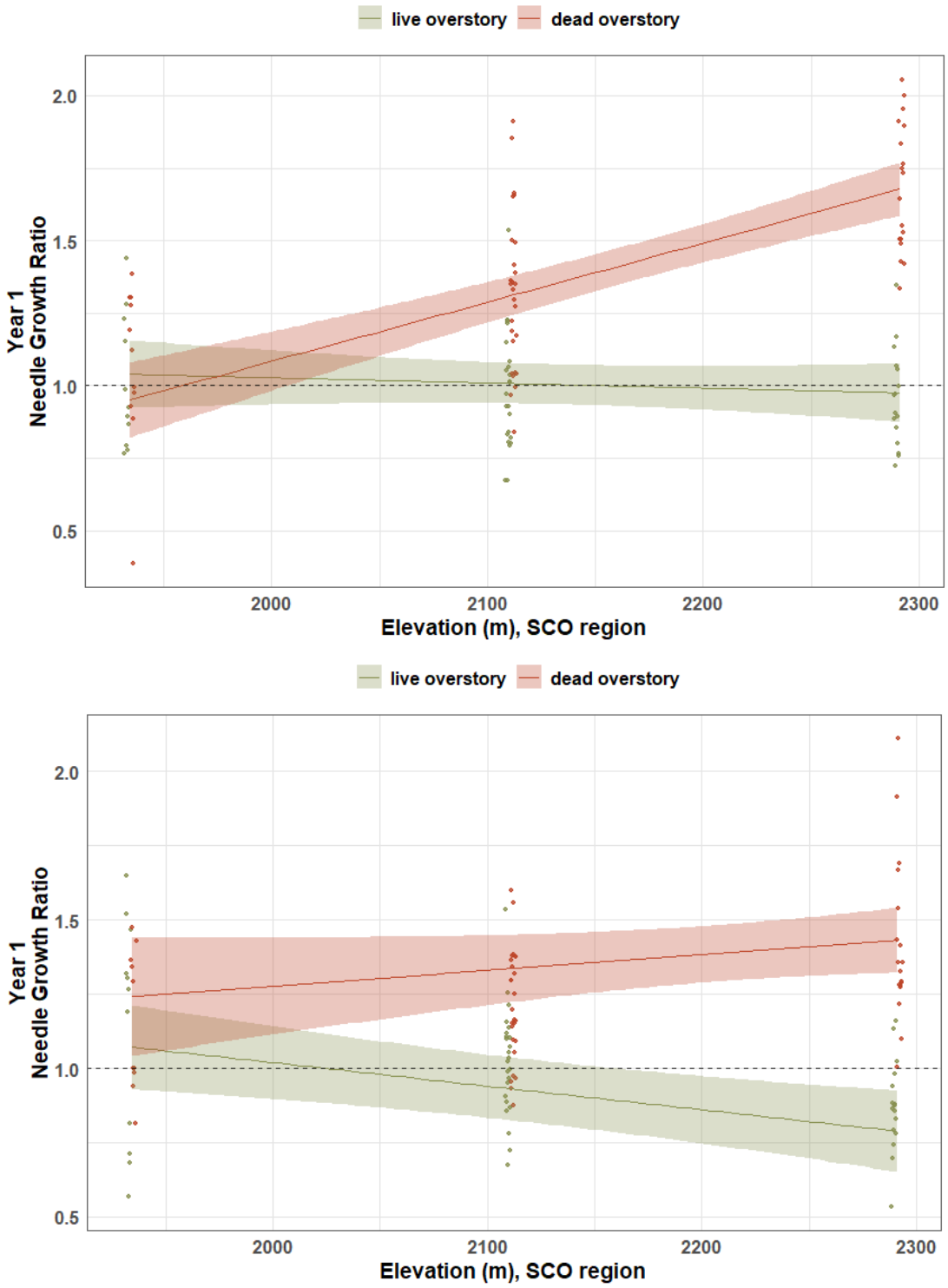

Figure 4.14. *Results of Needle Growth Ratio models for Year 1 (top panel) and Year 2 (bottom panel) of growth across the local elevational gradient encompassed in our southwest Colorado sites (SCOL, SCOM, and SCOH), showing model results for the interaction of elevation (m) and overstory environment (live and dead). Colors signify live (green) and dead (red) overstory environments. The dashed horizontal line at 1.0 needle growth ratio indicates a reference needle growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.*

Post-mortality weather models across sites (d)

NGRs modeled with yearly dCMD across sites showed significant interactions with dCMD and overstory environments in general, but with differing directions of relationships for conditions in years prior to growth (lag effects) and conditions in years during growth. Because patterns of current year weather relationships are consistent with expected relationships relative to results of branches and prior work on piñon needle length, while apparent prior year effects are not (Grossiord et al., 2017; Guérin et al., 2018), we only present results for current year weather relationships here (Figure 4.15). In both live and dead overstory environments, first-year NGRs were negatively related to increasing dCMD values in the year during growth, and this relationship was especially strong for dead overstory environments. This result reflects lower growth which occurred at sites with higher dCMD, including AZL, AZM, and NCOM, and higher growth occurring at SCO sites. NGRs in the second year following overstory mortality were negatively related to dCMD during the year of growth, but this relationship did not significantly vary with overstory environment. NGRs in this second year were more similar across sites, and increases occurred in AZ and NCOM in particular.

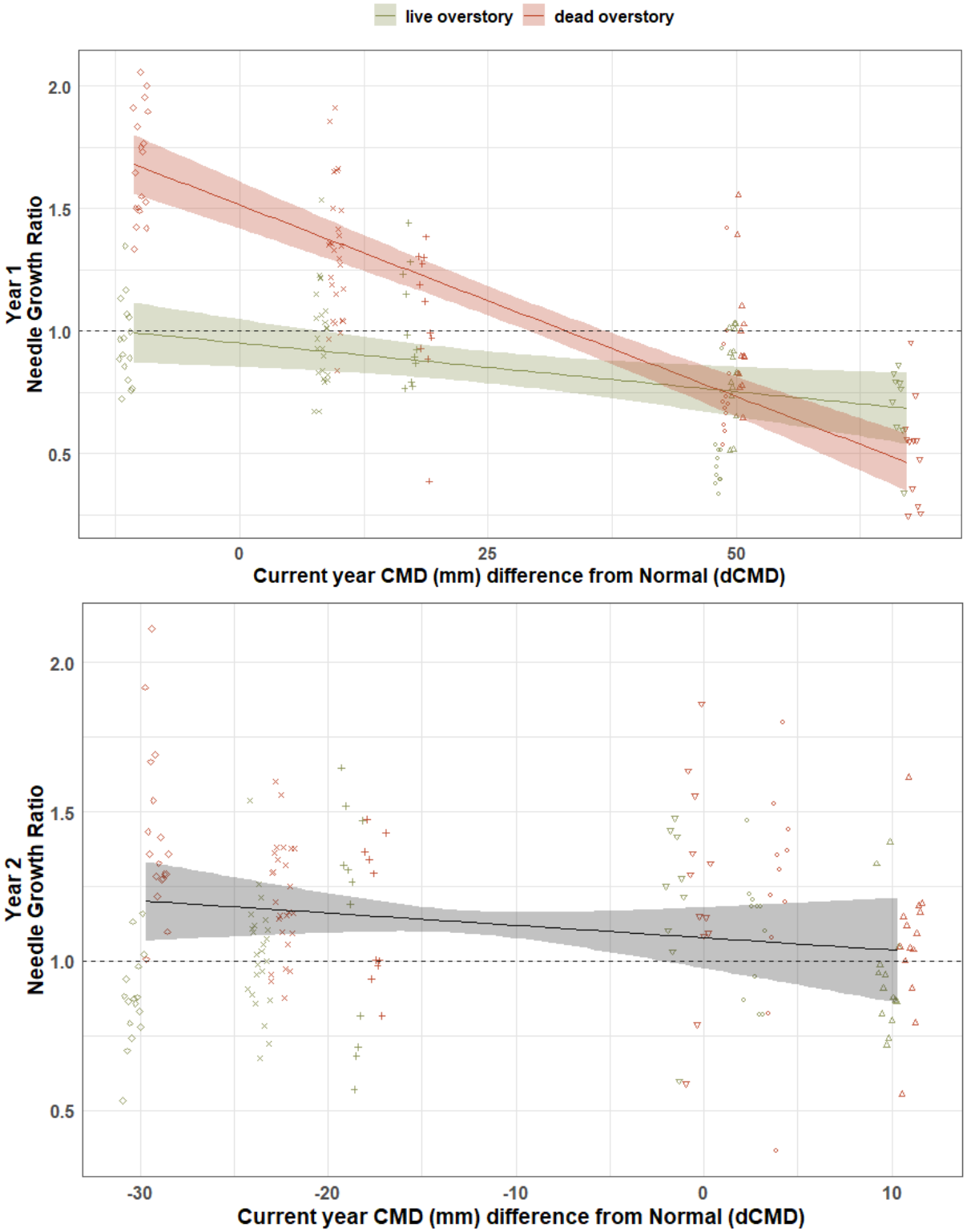

Figure 4.15. *Results of Needle Growth Ratio models for Year 1 (top panel) and Year 2 (bottom panel) of growth in relation to post-mortality weather effects across sites. The top panel shows Year 1 needle growth ratios in relation to current year CMD differences from normal (dCMD), including a significant interaction with overstory environment. The bottom panel shows Year 2 needle growth ratios in relation*

to current year dCMD for which an interaction with overstory environment was not significant. Colors signify live (green) and dead (red) overstory environments. Shapes denote sites: AZL = circle; AZM = upward triangle; SCOL = plus sign; SCOM = x; SCOH = diamond; NCOM = downward triangle. The dashed horizontal line at 1.0 needle growth ratio indicates a reference needle growth ratio value which would equate to post-mortality growth that is equal to the mean of prior growth.

DISCUSSION

In this study, we observed three primary patterns of juvenile piñon branch and needle growth in years following overstory mortality, relative to growth in years preceding overstory mortality: (1) growth ratios in dead overstory environments at SCOM and SCOH were generally highest among all sites, and greater than corresponding within-site growth ratios in live overstory environments in both year 1 and year 2 of growth following overstory mortality; (2) broadly, growth ratios across sites and overstory conditions increased from year 1 to year 2 following overstory mortality and were generally equivalent to or greater than mean growth prior to overstory mortality (i.e., near or greater than 1); these increases were especially evident for needles at NCOM, and for AZL and AZM resulted in at least marginally greater growth ratios in dead compared to live overstory environments; (3) across sites and two years of near-term growth responses following overstory mortality, we did not observe any indications of decline in growth ratios of juvenile trees in dead overstory relative to live overstory environments in each site. These overarching patterns appear to be the result primarily of post-overstory mortality weather variation across the sites and across years of post-mortality growth, in combination with greater light resources in dead overstory environments. Additionally, consistently high growth across two years at the highest elevation site in our study, SCOH, may reflect distinctly beneficial combinations of post-mortality biophysical conditions related to favorable growing conditions and light availability, mediated by relatively dense overstory structure. Lastly, our results may reflect some degree of population- and tree-level differences in growth strategies in

response to weather variation, especially related to differences in monsoonality between the southernmost (AZ) and northernmost (NCO) regions. Notably, we did not observe consistent relationships of growth ratio variation with tree size either generally or within live and dead overstory environments, though some marginal evidence showed greater growth of smaller compared to larger trees in dead overstory environments. Overall, these results appear to suggest that growth responses of juveniles across a wide range of environmental conditions generally favor increased light available after overstory mortality, supported especially by more favorable weather in some sites, and mediated in part by the pace of overstory mortality, and the potential differences in capacity or pace at which trees in different sites are able to leverage improved resource conditions for (secondary) growth. Ultimately, the outcomes of piñon pine resilience, and the subsequent development trajectories of these woodlands, in the face of drought-driven structural and resource change occurring with overstory mortality may be determined especially by the interplay of local weather and prior overstory structure, in addition to the extent and pace of overstory mortality (Gazol et al., 2023; Ramage et al., 2023). In this study, our results suggest that across our observed populations of juvenile trees, growth responses were at least resistant (or neutral) to, and in some cases responded favorably to acute resource change which occurs with mortality of dominant trees, and may serve as future reproductive overstory cohorts (Facciano et al., 2023). However, as we did not observe any occurrences of severe drought during post-mortality growth periods, we are unable to determine how these patterns would persist under more extreme conditions.

The most striking result in this study was the observed growth responses of juvenile trees in dead overstory environments at our SCOM and SCOH sites which were consistently greater than those in live overstory environments within each of the sites, and reflected consistently

higher growth than mean growth prior to overstory mortality (Figure 4.3 and 4.10). From our models of post-mortality growth ratios and weather relationships, it is evident that the SCO region generally experienced weather conditions following overstory mortality that were not substantially different from the normal range of variability for that region (e.g., Figure 4.8 and 4.9). These results contrast strongly with those from our other regions in which growth was much lower and weather conditions were substantially different from normal (i.e., higher climatic moisture deficits compared to normal). Consequently, it is likely, particularly in relation to other sites, that these patterns of relatively favorable weather across multiple years in the SCO region were supportive of strong growth responses of juvenile piñon in dead overstory environments, consistent with higher growth responses which occur during even brief periods of favorable conditions water-limited woodlands (Andrews et al., 2020; Grossiord et al., 2017; Kannenberg et al., 2023; Vasey et al., 2023, 2022). Moreover, it is evident from differences in growth ratios between dead and live overstory environments, where growth in live overstory environments was relatively unsensitive to weather variation (e.g., Figure 4.8 and 4.9), that growth at SCOM and SCOH was strongly influenced by mortality of overstory trees and resulting increases light availability for photosynthesis and growth. While mortality of overstory trees may also facilitate an increase in precipitation which reaches the soil surface and becomes available for uptake by surviving juveniles, in addition to facilitating warmth which enhances metabolic activity whole-tree growth responses, our results support a suite of resource changes which relate to elevated growth patterns in dead overstory environments (Facciano et al., 2023; Ramage et al., 2023). Indeed, other work at the same middle-elevation site in the SCO region as this study (SCOM, see Chapter 2 of this Dissertation) demonstrated juvenile vigor responses as likely primarily dependent on changes in light, given no evidence for live and dead overstory

environment tree vigor differences relative to sub-canopy microclimate conditions. Similarly, in an analysis of growth of residual trees following thinning in piñon-juniper stands, growth differences were not attributable to precipitation or soil moisture but rather likely to differences in light environments (Borodkin, 2016). Yet, is equally notable that these observed growth responses of juvenile piñon in dead overstory environments at the SCOM and SCOH sites occurred with weather conditions within a normal range of variation, and not with exceptionally cooler or wetter than normal conditions. While considerable work in piñon-juniper systems, both experimental and observational, has demonstrated the negative effects of atmospheric and soil droughts on (adult) tree growth (e.g., Adams et al., 2015; Grossiord et al., 2017; Guérin et al., 2018; Redmond et al., 2017), few studies have explicitly discussed growth in relation to normal weather conditions (but see Redmond et al., 2017 for longer-term growth-climate relationships). Our results from SCOM and SCOH demonstrate that juvenile growth following overstory mortality can respond favorably to resulting resource conditions when weather conditions are normal.

Yet, our results from lower-middle-higher elevations in the SCO region also demonstrate the mediating influences of overstory structure on growth responses relative to overstory mortality and post-mortality weather conditions. While results of growth responses in relation to weather variation across all sites show comparatively normal weather conditions in the SCO region generally (Figure 4.8 and 4.9), our models of growth ratios across elevation differences of SCOL, SCOM, and SCOH show increased growth ratios in dead overstory environments with increasing elevation, with low growth ratios and no differences between overstory environments at SCOL (Figure 4.7 and 4.14). Therefore, while weather variation across all sites can inform broad regional differences, local gradients of site productivity inform some within-region

differences (Dixit et al., 2022, 2021; Vasey et al., 2022). While the lower elevation SCOL site is among the hotter and drier sites of all sites in our study, the higher elevation SCOH site experiences some of the coolest and wettest conditions on average (Table 4.1). These results exemplify the role of elevation gradients and the wide range of conditions which piñon-juniper woodlands occupy, and demonstrate how average weather conditions in a region may result in highly divergent levels of abiotic stress for trees based on elevation change (Peet, 1981). Yet, while these results themselves are unsurprising given the foundational effects of abiotic suitability for growth, what is notable especially are site-related differences of overstory tree density and the varying degrees of needle retention across our years of study for this region (Figure 4.2). In particular, it is somewhat surprising that the highest growth responses occurred at the high elevation site (SCOH) where tree density was highest and needle retention remained much higher than other SCO region sites (Figure 4.2), potentially indicating light limitations, especially relative to SCOM where prior work (Chapter 2 of this Dissertation) indicated the importance of light as a driving component of post-mortality vigor responses of juveniles. These results suggest that the interplay of favorable growing conditions and light availability are not uniformly interactive in supporting the growth responses observed across SCO region sites. Instead, results from this region may suggest a mediating balance created both by increased light availability after overstory mortality and both a higher density of remaining dead trees and higher levels of needle retention, providing additional facilitative shade at the SCOH site. This balance of light and shade may be especially important for buffering heat-related stresses during diurnal (afternoon) and seasonal (dry periods, like mid-summer) periods of tree inactivity (stomatal closure, water conservation) (Limousin et al., 2013; Urza et al., 2019). These results may also be similar to those found for the effects of moderate, but not severe thinning intensities

in piñon-juniper woodlands for supporting new regeneration (Phillips et al., 2024). Moreover, elevated growth ratios at SCOH could reflect a greater degree of competitive release, given higher tree densities at that site, combined with favorable temperature and precipitation conditions, given the role of neighborhood tree structure in semi-arid conifer forests for influencing soil water, competitive interactions, and tree growth and reproduction (Andrews et al., 2020; Belmonte et al., 2022; Flake and Weisberg, 2019; Petrie and Savage, 2022; Ramage et al., 2023; Shriver et al., 2021). In comparison, growth ratios in live and dead overstory environments at the low elevation site (SCOL) remained highly similar in both years following overstory mortality (Figure 4.7 and 4.14), despite this region experiencing generally more favorable weather which appeared to be a component of growth responses at higher elevations. At this site, temperatures and atmospheric water demand are likely to be more limiting, especially for juvenile trees (Shriver et al., 2021). And, while speculative, together these results might suggest that growth ratios in dead overstory environments at the SCOM site could have been greater with additional overstory density to provide additional shade, perhaps in dense patches of overstory trees. Ultimately, our results for the SCO region highlight the interplay of both regional and local gradients of climate differences, weather variation, and resource change mediated by site differences in biotic conditions like overstory structure, indicating some balance or optimum for observed differences in responses.

Interestingly, when comparing branch growth ratios across regional middle-elevation sites, growth responses of juveniles in dead overstory at SCOM remained higher than AZM and NCOM, despite favorable changes in weather which occurred at AZM and NCOM sites during the second year of growth (Figure 4.5 and 4.12). These results are also primarily driven by differences in weather conditions following overstory mortality as discussed above (Figure 4.8

and 4.9), where climatic moisture deficits at SCOM were below normal (but still within normal variation) and AZM and NCOM sites were slightly above normal during the second year of growth. Presumably, SCOM benefitted from compounded years of supportive growth environments which facilitated relatively high growth ratios in dead overstory environments, especially if gains in first-year growth of branches and needles elevated the capacity of trees at the site to acquire more light energy for subsequent growth (Kannenberg et al., 2022; Macalady and Bugmann, 2014; Peltier et al., 2021). However, as we assessed growth ratios and not raw growth, it remains notable that growth responses, relative to prior growth, in other regions did not show as strong of responses as those in SCOM to resource change in combination with normal weather conditions at those sites. These regional comparisons could suggest potential differences in population-level tree growth strategies which have been demonstrated similarly for other conifer species in relation to environmental gradients (Camarero et al., 2024; Dixit et al., 2022; Vasey et al., 2023). Local populations which persist in climates with chronic heat- and water limitation-related stresses (Table 4.1) (marginal conditions relative to a range of conditions, as observed in this study) may typically display growth strategies which are overall slower or sensitive to seasonal pulses of favorable weather conditions (Dixit et al., 2022; Grossiord et al., 2018b; Vasey et al., 2023, 2022). For populations distinctly dependent on monsoon precipitation for instance, such as our AZ region where 40-45% of precipitation is received in a monsoon seasonal period (Table 4.1), these individuals may possess growth strategies especially reliant on such pulses of resources associated with monsoon precipitation (Peltier and Ogle, 2019; Samuels-Crow et al., 2023). For populations which persist in climates more consistent with winter-dominated precipitation and longer dry growing season periods, such as our NCO region, growth strategies may be deliberately slow so as to conserve limited

resources over longer potential periods of resource limitations (Vasey et al., 2022). In our study, it is possible that these more marginal populations were both limited by higher climatic water deficits in the first year of growth, and also did not experience large enough resource pulses associated with their normal growth strategies which would have otherwise facilitated stronger growth responses to overstory mortality (and, more generally, in live overstory environments)(Guérin et al., 2018; McBranch et al., 2019). Though we did not study traits related to the different populations we observed in this study, nor did we test growth strategies explicitly, the results from our modeled relationships among regional middle-elevation sites in part suggest a higher degree of growth plasticity at the SCOM site across growth years in this study (Candido-Ribeiro and Aitken, 2024; Grossiord et al., 2017; McDowell et al., 2019), or at least plasticity in response to resource pulses (Kannenberg et al., 2023; Vasey et al., 2023). While typically applied to analyses of data informing species distribution relationships with climate (e.g., frequency and abundance), these growth results broadly mirror the concept of a climatic optimum wherein the occurrence and vigor of individuals can be highest, on average (especially in these systems mostly dominated by only two species) (Martin and Canham, 2020). While these relationships are possible and consistent with some evidence of population-level differences in growth strategies at marginal and interior (or core) sites within a wide gradient of piñon distribution, it is at least clear from our results that post-mortality weather variation is a major source which defines observed responses in secondary growth of juvenile piñon. Indeed, the broad similarities in patterns of both branch and needle growth across sites seemingly underlines the predominant role of weather variation in driving observed responses for each site.

While general trends of greater growth ratios in the second year occurred across nearly all sites and overstory conditions (Figure 4.3 and 4.10), increases in growth ratios for AZL and

AZM illustrate resilience of juveniles in the AZ region to both acute resource change from overstory mortality and variation weather ranging from hot and dry to comparatively normal conditions. Branch growth ratios modeled in relation to weather conditions across all sites suggested influences of prior-year weather on current-year growth (Figure 4.8 and 4.9). Compared to branch growth ratios in the SCO region (including lower growth at SCOL), branch growth ratios in year 1 at AZL and AZM were low and overall well below mean growth prior to mortality. While weather conditions during the first year of growth were within a normal range of variation for all sites, climatic moisture deficits at AZL and AZM were far above average, and well over one standard deviation of the mean climatic moisture deficit condition for each site (Table 4.1). As such, branch growth appeared to be influenced in part by prior-year weather (Guérin et al., 2018). In contrast, needle growth ratios appeared to be primarily influenced by current year weather conditions, given comparable patterns with current but not prior year weather (e.g., changes were not as large year-year, and NCOM needle growth displayed the largest year-year change concurrent with the largest year-year weather change) (see results note, and Guérin et al., 2018). Nonetheless, branch and needle growth ratios in year 2 following overstory mortality increased from year 1 and increased in dead overstory environments more than in live overstory environments on average (Figure 4.3 and 4.10). Consequently, the rebound in growth responses which occurred at AZ sites, especially in dead overstory environments where resource change was most acute, seems to suggest a substantial level of resilience to highly limiting weather conditions one-year prior to the first year of post-mortality growth (Camarero et al., 2024; Facciano et al., 2023). Piñon trees in this region, which experiences the hottest and driest conditions among our studied sites on average (Table 4.1), likely have structural traits, such as xylem with high resistance to embolism (Guérin et al., 2020) and smaller

and thicker needles which aid conservative water use (Guérin et al., 2018), which allow them to resist periods of acute abiotic stress, namely drought. Yet, these traits may also result in slower growth strategies overall, as these xylem characteristics may also limit the efficiency with which water can be moved through the tree when available. Yet, our results demonstrate that such traits, which likely existing to some degree in these populations, can provide a foundation for resilience to acute resource change resulting from both overstory mortality and high variation in weather stresses like climatic moisture deficits (Camarero et al., 2024). Additionally, increases in growth ratios in the second year following overstory mortality in the AZ region, as well as more broadly in our study, could partially reflect soil biogeochemistry changes occurring with the progression of overstory mortality over time, especially the deposition of dead plant material, decomposition, and subsequent pulses of nitrogen availability for tree growth and maintenance (Grossiord et al., 2018a). It is inevitably unclear, but likely that more extended periods of adverse weather may have limited subsequent growth responses among these populations given relatively conservative resource use and growth strategies (e.g., Pangle et al., 2015), but the apparent resilience of these juveniles to short (~season-year) periods of high climatic moisture deficits in combination with overstory mortality is notable. Similarly, that juveniles demonstrated this apparent growth resilience with normal, rather than abnormally cool or wet weather, highlights the capacity for juveniles in these populations to respond to relatively small improvements in abiotic conditions underlying physiological activity.

Across all sites in this study, we did not find any declines in growth of juveniles, on average, in dead overstory environments relative to live overstory environments and relative to average growth of individuals prior to the occurrence of overstory mortality (Figure 4.3 and 4.10). This result is particularly important given limiting weather conditions which were evident

for the AZ region in the year prior to year 1 of growth, and in the NCO region during year 1 of growth (which was also the prior year for year 2 of growth) (Table 4.1). Many studies on piñon pine have demonstrated detrimental effects of experimental and natural abiotic stresses, namely atmospheric and soil droughts, on growth of (mostly adult) piñon pine. Heat and drought have been shown to limit short-term physiological responses (Grossiord et al., 2017; Morillas et al., 2017), phenological development of needles (Adams et al., 2015), needle length and shoot growth (Grossiord et al., 2017; Guérin et al., 2018), with implications for long-term carbon storage and potential resistance to subsequent periods of severe abiotic stress. Additionally, reduced growth has been associated with limiting climate periods (Redmond et al., 2017), and periods of low radial growth have been associated with higher susceptibility to mortality during severe drought (Cabon et al., 2023). In our study, we did not impose specifically limiting heat- or water limitation-related growing conditions, and so comparison with results of these studies primarily rests on the distinction of apparently supportive, largely normal weather conditions by year 2 of this study and severely limiting periods of abiotic stress in comparison studies. But our analyses are important in demonstrating resistant (or, neutral; i.e., growth ratios ~ 1) and resilient (i.e., growth ratios > 1) growth of juvenile trees, across a range of sizes (Figure 4.3 and 4.10), to acute resource change associated with mortality of overstory trees, including greater exposure to direct radiation and heat, as well as temperature-driven evaporative demand on plant and soil surfaces. Yet, in our study, our growth ratio also relies on prior growth patterns, for which previous occurrences of severely limiting conditions (e.g., 2018; see Appendix 3:Supplementary Figure S4.1) may contribute to higher relative growth observed for post-mortality periods in our experiment (Guérin et al., 2018). Broadly similar responses across populations suggest that potential trait-related variation contributing to the capacity for acclimation to resource change in

different environmental conditions would be attributable to individual-or microenvironmental-level differences (Candido-Ribeiro and Aitken, 2024; Gazol et al., 2023; Vasey et al., 2022) (additionally, see below discussion). Longer-term monitoring of juveniles in post-mortality environments and evaluating tree-level microclimates may help resolve some level of mechanisms driving our observed growth response results, especially if multi-year periods of elevated (above normal) abiotic stress are studied (Guérin et al., 2018; McBranch et al., 2019).

Although we designed this study to assess the influence of juvenile tree size on growth in live and dead overstory environments, we found only marginal evidence for differences in growth ratios based on tree size. Specifically, we found some evidence that smaller trees (< 2 cm DRC) had higher growth ratios in dead overstory environments than larger trees (> 2 cm DRC). This result is initially counter to the expectation that larger trees tend to have greater physical access to light and soil resources supporting physiological activity and growth. Yet, several explanations might exist in part for the marginal difference in smaller and larger trees, and the general variation observed across tree sizes. It has been illustrated elsewhere that young trees, in particular first-year seedlings, are frequently carbon limited and therefore prioritize aboveground growth for improved light capture (e.g., Augustine and Reinhardt, 2019; Pirtel et al., 2021). In this way, smaller trees in our study, even existing in dead overstory environments, may still face some level of shade which larger juveniles do not, thus promoting growth of photosynthetic structures, when abiotic conditions are not overly limiting (Magnin et al., 2017). In contrast, larger trees which potentially experience a wider range of abiotic conditions, including heat and evaporative demand from direct radiation, may display relatively more conservative growth strategies, even if they are capable of generally higher photosynthetic rates (see Chapter 2 of this Dissertation)(Grossiord et al., 2017). Alternatively, smaller and larger trees could face different

microenvironmental limitations which can result in different degrees of partitioning growth in photosynthetic system structures relative to belowground structures, especially when water is not the primary limiting factor (Magnin et al., 2017). Similarly, it is possible that larger trees in dead overstory environments may have greater apical control and partition growth to greater crown area, such as higher numbers of branches or more leaves per branch (Williams et al 1999). Yet, a more straightforward, though less informative, explanation results from a high likelihood of individual-level variation in both performance and morphology. For instance, branches of small, understory piñon juveniles we measured frequently were indistinguishable from any main shoot. While we based our branch selection on apparently secondary axes for these young trees, it is unclear whether these branched axes were functionally different from the apparent primary axis, potentially leading to higher observed relative growth, as compared to distal branches of larger individuals. Moreover, a limitation of our results includes the inability to appropriately characterize individual microenvironments which could partially explain some observed growth variation, especially across sizes. Microenvironmental variation in light (Sprugel, 2002), driven by surrounding trees, including remaining live juniper, shrubs, or other juvenile trees, as well as microtopographic variation, which can strongly affect water collection in these systems, are among potential sources of individual variation (Williams et al., 2018). Ultimately, some of these potentially distinguishing features may be leveraged by future work to help explain some observed variation in growth both within and across sites.

CONCLUSION

This study exemplifies how the outcomes of disturbance, especially after mortality of overstory trees, on recovery trajectories of piñon-juniper woodland systems are strongly

dependent on both weather variation and overstory structural conditions before and after mortality. While we are unable to show longer-term results on growth and trajectories of surviving juveniles, or determine the role of greater abiotic limitations on growth responses, our results provide important evidence of broad growth resilience of juvenile piñon pine following overstory mortality. Our results demonstrate that weather conditions which are within a normal range of variation can strongly support positive growth responses of juveniles in combination with increased light availability across multiple populations, from northern Arizona, to southern Colorado, to northern Colorado. However, growth responses of juveniles at our highest elevation site demonstrated that, even with high variability in overstory needle retention (and thus light environments) following mortality, juvenile growth could highly exceed prior mean growth. These results demonstrate the role of overstory structure in mediating responses, and potentially the beneficial role of moderately open light environments for juvenile tree growth, and thus the role of facilitating shade even in the most productive, least hot and dry site among those studied here. Notably, growth responses at the most southern sites in AZ, which typically experience the hottest temperatures, and very seasonally dependent (monsoon) precipitation showed resilience to high climatic moisture deficits even only 1 year prior to the first year of growth following overstory mortality. Our findings suggest that while tree size may influence growth to some extent, the observed differences were marginal, with smaller trees showing slightly higher growth ratios in dead overstory environments. This underscores the importance of considering individual-level variation and microenvironmental factors in understanding growth patterns in piñon-juniper woodlands. Overall, our study provides valuable insights into the resilience and adaptive capacity of juvenile piñon trees in response to overstory mortality and varying environmental conditions. Ecological forest management can leverage population-level

information for sourcing seed collections, informing reforestation, and for assisted migration efforts to help mitigate overall impacts of climate change on forest and woodland cover and longevity. However, these efforts may be equally impacted by individual and population differences which are mostly expressed in relation to interannual weather variation. These findings contribute to our understanding of forest dynamics and inform future research efforts aimed at mitigating the impacts of climate change on woodland ecosystems.

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CONCLUSION

Tree recruitment is the basis of species viability and the persistence of forest and woodland communities. Yet, tree recruitment involves the accumulation of survival and growth of juveniles over time as individuals progress from newly germinated seedlings to saplings. Because juveniles, especially younger, smaller individuals, typically require a narrower range of abiotic conditions for survival and growth over time relative to mature, overstory trees, these juveniles are more susceptible to greater climate-driven stresses as climate warming progresses. In this dissertation work, I sought to better understand the survival, growth, and physiology of juvenile trees of differing stages of physical maturity in relation to variation in overstory tree structure and mortality, and related conditions of temperature and humidity (or vapor pressure deficit), soil moisture, and light. Moreover, I sought to elucidate how interannual variation in weather (i.e., across multiple growing seasons), and consequently microclimates, impacted juvenile survival and growth, given the complex interplay of temperature, moisture, and light-related resource limitations for juvenile trees. I investigated survival and growth outcomes of juveniles in two different semi-arid, dryland systems, including a ponderosa pine/Douglas-fir dry mixed conifer forest and six piñon-juniper woodland sites spanning a regional climate gradient and local elevation gradients in the southwestern U.S. I used primarily field-based experimental approaches to evaluate juvenile responses to fine-scale variation in tree structure and associated microclimate conditions, and to resource differences associated with live and dead overstory cover. I evaluated juvenile responses from the perspective of individual survival, physiology (including photosynthetic and stomatal conductance rates), and growth (including diameter, branches, and needles).

In Chapter 1 of this dissertation, I found that young juveniles of both ponderosa pine and Douglas-fir respond in similar ways to overstory structure and microclimate conditions, with primary differences being the magnitude of survival and growth, which was much lower for Douglas-fir. For both species, microsites which resulted in the highest survival and growth included the intersection of warmer and drier spring conditions and above-average canopy openness (light) conditions, and below-average warm and dry later season conditions. Across three years of study, establishment of both newly germinated seedlings and older, larger seedlings occurred in these conditions, which was seemingly related to the cooler and more humid spring weather conditions in which this study began. These results mirror prior research on regeneration pulses and thresholds for these species in dry mixed conifer forests, illustrating the spatially and temporally narrow niches for successful recruitment of juveniles of these species, which can be mediated by variation in overstory structure and microclimates at fine spatial scales. These results have important implications for the design and monitoring of longevity of dry forest restoration treatments, which produce overstory structural heterogeneity at fine spatial scales, demonstrating how associated management decisions can affect regeneration trajectories for these dominant species.

In Chapters 2 and 3 of this dissertation, I found evidence of near-term benefits to photosynthetic and stomatal conductance rates, and branch and needle growth of juvenile piñon pine following overstory mortality, but these benefits were limited to a subset of sampled juveniles and at only two of six sites. The results of these studies also demonstrated the sensitivity and susceptibility of juvenile piñon trees to adverse abiotic conditions, such as hot and dry microclimates, which can result from the loss of live overstory cover. In Chapter 2, the largest juveniles in dead overstory environments had higher photosynthetic and stomatal

conductance rates than juveniles in live overstory environments and smaller juveniles in both live and dead overstory environments. Because juvenile responses to microclimate temperature and humidity and soil moisture conditions were similar across sizes and in both live and dead overstory environments, the higher photosynthetic and stomatal conductance rates of larger juveniles in dead overstory environments likely resulted from other resource change, such as light availability. Yet, responses to microclimate conditions also suggested a general sensitivity of these juveniles to abiotic limitations, and a potential threshold of physiological activity in hot and dry conditions suggests particular limitations for juveniles in dead overstory environments which can accumulate over time and potentially result in carbon starvation, decline, and mortality. In Chapter 3, I found that only juveniles at middle- and high-elevation piñon-juniper in the southwestern Colorado region had consistently greater growth in dead overstory environments in years following overstory mortality, as compared to mean growth prior to overstory mortality (i.e., "growth ratios"). These results, in comparison with those from southern and northern latitude sites (northern Arizona, and northern Colorado, respectively), were more likely due to favorable weather conditions in the southwestern Colorado region in the first year following overstory mortality. Additionally, juveniles at sites which experience hotter and drier climate conditions on average, such as lower elevations and more southern latitudes, may have slower growth strategies more dependent on resource pulses (e.g., monsoon precipitation), which potentially limited their near-term growth responses as observed in this study. Moreover, growth responses across elevational gradients exemplify the role of elevation in site productivity (e.g., more moderate temperatures on average) in mountainous regions, and also likely reflect a greater degree of competitive release (e.g., of light) for juveniles in dead overstory environments occurring at the highest elevation site where overstory tree density was

highest. Limited growth responses at other sites during relatively normal weather years, in addition to reflecting different growth strategies, underline the susceptibility of these juveniles to increased hot and dry conditions (e.g., drought) projected for these woodlands, especially at southern latitudes and lower elevation sites.

Across the work presented in this dissertation, the importance of overstory-mediated microclimates was dependent on year-year weather conditions and demonstrated dynamic relationships between juvenile development and covariance among temperature, moisture, and light. For ponderosa pine and Douglas-fir juveniles, moderately-high canopy openness, or above-average light conditions, were important components of survival and growth. However, these influences appeared to be dependent in part on weather conditions including temperature and humidity conditions below average climate normals, and average precipitation. This contrasted with the effects of a warm and dry year during the study which resulted in newly germinated seedling survival benefitting from lower-light, higher-overstory cover microenvironments. For piñon pine juveniles, the outcomes of overstory mortality on juvenile physiology and growth were dependent on microclimate conditions, weather in the first year following overstory mortality, and broad differences across regional climatic and local elevational gradients. For the largest juveniles in a middle-elevation, mid-latitude site, overstory mortality was related to higher photosynthetic and stomatal conductance rates compared to juveniles in live overstory environments. At this site and an upslope higher-elevation woodland site in the same region, branch and needle growth ratios were consistently higher in dead compared to live overstory environments following overstory mortality. Among possible drivers of these responses were the favorable weather conditions in years following mortality at these sites, and the release from competition with surrounding trees, especially at the denser higher

elevation site, likely due to increased light availability. In contrast, at other sites which did not experience as favorable weather conditions, few growth differences between live and dead overstory environments were evident, suggesting changes in light with overstory mortality were less impactful relative to temperature and moisture conditions. Moreover, the sensitivity of all juveniles to hotter and drier microclimates and weather conditions across sites suggests susceptibility to hotter and drier conditions as expected in these woodlands, and as known limitations to physiology and growth in this species. In this way, the potential for increased light availability following overstory mortality is unlikely to provide substantial benefits to these juveniles as climate warming progresses, possibly with the exception of higher-elevation and wetter sites, emphasizing the importance of intact woodland structures for future resilience of these systems.

The results of these studies carry contrasting implications for density management, which has received much focus as a climate-adaptation tool to improve resilience in these dryland forest and woodland systems. Density reduction in ponderosa pine-dominated dry mixed-conifer forests may have the benefit of facilitating forest resilience by providing suitable microenvironments for regeneration and survival of dominant species, ponderosa pine and Douglas-fir. However, in piñon-juniper woodlands, implications for density management are likely to be highly dependent on site. Marginal sites, with hotter and drier climate conditions on average, are likely more dependent on retaining live overstory to ameliorate adverse abiotic conditions for juvenile trees. In contrast, where normal climate conditions are less limiting, such as in higher-elevation woodland sites, density reduction may facilitate woodland resilience by providing opportunities for resource release to extant juvenile trees. Yet, while shorter-term results from the studies presented here can facilitate more immediate concerns of adaptive

decision making, it is important to consider both the relatively normal weather in which the results of these studies were obtained, and the potential for longer-term responses to be affected by years of greater abiotic stress, such as severe drought. Opportunities for longer-term evaluation of juveniles progressing from younger, smaller individuals to older, larger individuals are needed to resolve the outcomes of trajectories initiated by individual survival and growth as observed here. Further study would help to understand especially the extent to which shorter periods of normal or more favorable microclimate and weather conditions can facilitate longer-term resilience of individuals and communities, and alternatively the extent to which short periods of limitations accumulate over time leading to individual and community decline.

APPENDICES

APPENDIX 1

SUPPLEMENTARY MATERIAL FOR CHAPTER 2:

CANOPY-MEDIATED MICROCLIMATE REFUGIA DO NOT MATCH NARROW REGENERATION NICHES IN A MANAGED DRY CONIFER FOREST

METHODS

Site Description: restoration treatment details and non-tree vegetation cover

Our study site was situated in a forest restoration treatment which was completed on ~ 61 ha of lower montane, dry mixed-conifer forest in 2018. Broad treatment objectives included reducing canopy cover and basal area, increasing gap size and irregularity, and reducing the risk of high severity fire. Treatment methods included mechanical thinning and mastication, with large trees removed from the site and smaller trees masticated or left on site via lop and scatter. Treatment resulted in a decrease of basal area and canopy cover from 19.0 m^2 ha^{-1} (±2.3) to 5.7 m^2 ha^{-1} (±1.4) and 43.6% (±5.5) to 13.7% (±3.5), respectively. Large ponderosa pine were prioritized in tree retention, with percentage of ponderosa pine basal area nearly doubling after treatment and quadratic mean diameter of all trees increasing from 17.7 cm ±2.0 to 29.2 cm ±2.3, while Rocky Mountain juniper was nearly entirely removed. Additionally, the mean area of tree groupings was decreased from 0.04 ha to 0.02 (with proportions of tree groups containing 1, 2-4, 4-9, and >9 trees made broadly even), and mean area of gap sizes increased from 0.22 ha to 1.55 ha, with gap size range also increasing from 0.03-1.40 ha to 0.02-16.60 ha. All treatment data are taken from Slack et al. (2021).

In this study we sought to limit the influence of competing vegetation on observed tree

regeneration outcomes in order to better evaluate the effects of overstory tree structure and microclimates on tree regeneration. Consequently, we chose to scarify all plots prior to planting in the first year of study (2019; as described in Methods: Juvenile life-stages, survival, and growth (Objective 2).). However, to account for any subsequent non-tree vegetation regeneration effects on our planted tree seeds and seedlings, in the second study year (2020, when a non-tree vegetation regeneration response was observed) we estimated percent cover of all non-tree vegetation (forbs, graminoids, shrubs, mosses/lichens) and percent cover of no vegetation (i.e., bare ground and litter). These data showed very little non tree vegetation cover overall, and that which occurred was limited to a few plots: forb cover was 3.4% ±4.3, graminoid cover was 0.9% ±1.5, moss/lichen cover was 1.2% ±6.1, shrub cover was 0.1% ±0.3, and cover with no vegetation (i.e. bare ground and litter) was 96.1% ±4.6. Of all plots, 74% had less than 5% non-tree vegetation cover, and 30% of all plots had zero vegetation cover. Lastly, soils at the study site are generally characterized as very gravelly sandy loams, indicating high drainage and relatively low vegetation productivity (data retrieved from Natural Resources Conservation Service, United States Department of Agriculture, Web Soil Survey, accessed at http://websoilsurvey.sc.egov.usda.gov/, on 01/03/2022).

Experimental design and field sampling: stratified random sampling

For strata of overstory tree density, we calculated basal area in a 3 m grid across the stand including all trees within a 15 m radius at each location, based on previously modeled light availability on a similar site (Cannon et al., 2019). Resulting basal area values ranged from 0 to 31 m^2ha^{-1}. For solar radiation exposure strata, we calculated the expected annual solar radiation using the method of Fu and Rich (2002. A geometric solar radiation model with applications in agriculture and forestry. *Computers and Electronics in Agriculture* 37, 25–35.

https://doi.org/10.1016/S0168-1699(02)00115-1) implemented in ArcGIS 10.4. Solar radiation within the site ranged from 1210-1638 $kWhm^{-2}$, with a median of 1429 $kWhm^{-2}$. We classified the upper 50th percentile of solar radiation as "exposed" and the lower 50th percentile as "sheltered" topographic positions.

Structure, topography, and microclimates (Objective 1): soil moisture lab calibration process

With a lab calibration process, we used soil cores to calibrate soil capacitance values to moisture readings by recording soil capacitance values and gravimetric soil moisture (full core weight minus instrument components) every 5 seconds until readings stabilized at zero apparent moisture remaining. Calibration equations were applied to capacitance values recorded from field measurements to convert readings to soil volumetric water content (VWC). Three separate calibrations were run on three randomly located soil cores, and the average VWC value from the three calibration equations was used for each corresponding field measurement for subsequent analysis (e.g., summarizing and modeling).

Juvenile life-stages, survival, and growth (Objective 2): *treatment of seeds*

Seeds of both species were treated only as directed by personal communication (21 January 2019) from the USFS Bessey Nursery manager, Richard Gilbert. These directions indicated no cold stratification was required. Seeds were soaked in room temperature water for 24 hours prior to planting, in both years seed planting occurred (2019 and 2020), as directed.

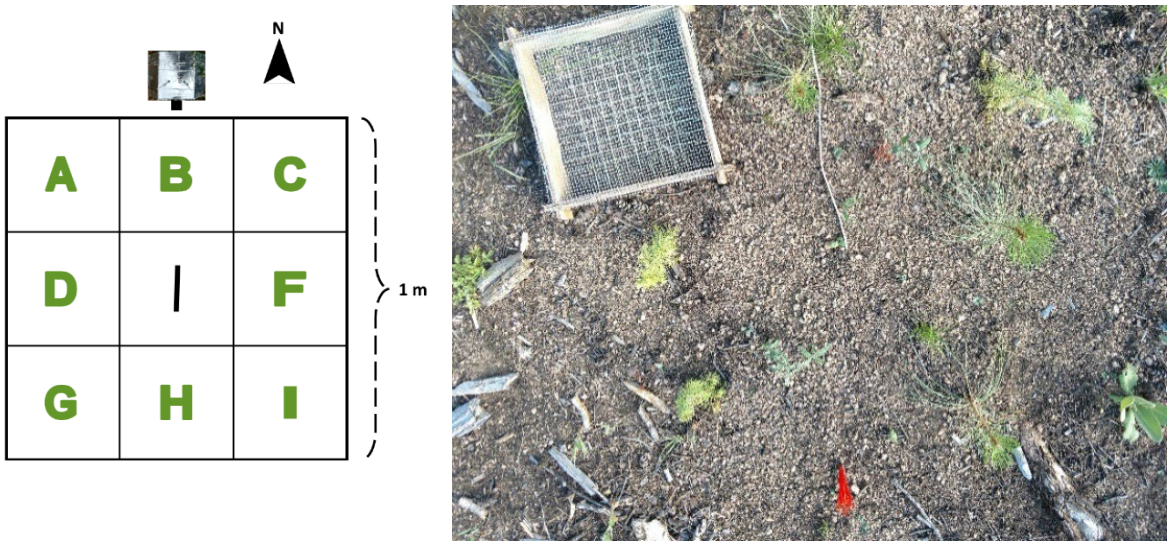

Figure S2.1. *Individual plot layout showing a diagrammatic representation of plot planting and sensor placements, and a photographic example of the layout implemented in the study. Locations of planted older seedlings and seeds (within a microgrid situated in a rodent exclosure, as seen in the wooden and wire material in the photo example) were randomized among positions A-I for each plot. The center cell of each plot layout was reserved for sampling soil moisture. Air temperature and humidity sensors were located at the north side of each plot (not shown in photo).*

RESULTS

Table S2.1. *Summary statistics (mean ± sd) of all variables considered in structure-topography and microclimate survival and growth models across species and life-stages in this study. Soil moisture and temperature sampling did not occur in June and August 2021.*

Variable	2019					2020					2021					Over-all
	May	June	July	Aug.	Sept.	May	June	July	Aug.	Sept.	May	June	July	Aug.	Sept.	
Vapor pressure deficit (VPD) (kPa)	0.5 (± 0.0)	1.0 (± 0.1)	1.4 (± 0.1)	1.5 (± 0.1)	1.3 (± 0.1)	1.0 (± 0.1)	1.5 (± 0.1)	1.6 (± 0.1)	1.8 (± 0.1)	1.2 (± 0.1)	0.6 (± 0.1)	1.4 (± 0.1)	1.3 (± 0.2)	1.4 (± 0.1)	1.2 (± 0.1)	1.2 (± 0.3)
Maximum VPD (kPa)	1.5 (± 0.2)	3.0 (± 0.3)	4.1 (± 0.5)	4.1 (± 0.5)	3.7 (± 0.5)	2.5 (± 0.2)	3.7 (± 0.3)	4.1 (± 0.4)	4.6 (± 0.6)	3.2 (± 0.4)	1.7 (± 0.3)	3.7 (± 0.6)	3.7 (± 0.7)	3.9 (± 0.8)	3.4 (± 0.8)	3.4 (± 0.9)
Soil volumetric water content (VWC) (%)	26.7 (± 16.3)	29.1 (± 18.6)	29.5 (± 19.5)	25.9 (± 16.9)	17.8 (± 12.8)	19.9 (± 13.8)	14.5 (± 11.3)	8.6 (± 8.7)	9.9 (± 10.8)	26.0 (± 14.6)	21.2 (± 12.6)	NA	9.8 (± 9.2)	NA	10.4 (± 9.6)	19.2 (± 7.9)
Soil temperature (°C)	11.4 (± 2.5)	16.1 (± 3.1)	23.4 (± 3.6)	22.8 (± 4.0)	18.0 (± 2.5)	25.0 (± 5.0)	27.9 (± 3.3)	32.9 (± 8.6)	33.7 (± 5.8)	30.4 (± 6.2)	17.9 (± 3.1)	NA	27.9 (± 5.2)	NA	19.0 (± 8.6)	23.6 (± 6.9)
Canopy openness (%)																47.5 (± 14.9)
5m basal area (m2)																0.1 (± 0.1)

Heat load index (HLI)																0.9 (± 0.1)

Table S2.2. *Summary statistics for survival and growth of across species and life-stages over the 3-year study (2019-2021). Statistics include mean and standard deviation and sample size. Blank entries indicate no applicable statistics for the corresponding life-stage and year entry.*

Species		**Life-stage**	**2019**		**2020**		**2021**	
			mean (± sd)	***n***	**mean (± sd)**	***n***	**mean (± sd)**	***n***
Ponderosa pine	**Survival**	2019 first-year new germinant seedlings	0.05 (± 0.17)	266	0.69 (± 0.38)	18	0.92 (± 0.14)	10
		2020 first-year new germinant seedlings			0.04 (± 0.15)	51	0.00 (± 0.00)	0
		older seedlings	0.83 (± 0.38)	162	0.83 (± 0.38)	134	0.93 (± 0.26)	111
	Growth	basal diameter (at planting)	0.47 (± 0.09)	162				
		proportional growth					0.29 (± 0.35)	103
Douglas-fir	**Survival**	2019 first-year new germinant seedlings	0.02 (± 0.07)	322	0.46 (± 0.29)	7	1 (± 0)	3
		2020 first-year new germinant seedlings			0.04 (± 0.11)	142	0.00 (± 0.00)	0
		older seedlings	0.48 (± 0.5)	161	0.73 (± 0.45)	77	0.93 (± 0.26)	56
	Growth	basal diameter (at planting)	0.35 (± 0.07)	161				
		proportional growth					0.12 (± 0.2)	52

Table S2.3. *Model estimates and uncertainty (coefficient ± standard error) for all model types across species, life-stages, and growth. Survival models included models for each individual year of survival data as applicable for each life-stage (2019 and 2020 for first-year new germinant seedlings cohorts; 2019-2021 for older seedlings), and integrated survival models for both life-stages. Growth models were done only for older seedlings. Model types included structure-topography models and microclimate models. Both model types for older seedlings included basal diameter (at planting) fixed effects; estimates and uncertainty shown are averaged from results of the two model types, per model year (2019-2021 and integrated models). Results for ponderosa pine are shown above those for Douglas-fir, as indicated by the species labels at the far left. Bolded model results indicate significance, based on 95% confidence interval overlap of zero for a given model estimate (no overlap was interpreted as significant).*

Species and Model and Variable Types			First-year new germinant seedlings			Older Seedlings				Growth (proportional)
			2019	*2020*	*Integrated*	*2019*	*2020*	*2021*	*Integrated*	*2019-2021*
PONDEROSA PINE	**Structure-topography**	***Canopy Openness (SKY)***	**1.1 (± 0.5) -1.1 (± 0.6)**	-1.7 (± 1.6)	**1.0 (± 0.3)**	**-1.3 (± 0.4)**	0.0 (± 0.3)	0.1 (± 0.5)	**-0.4 (± 0.2)**	**0.2 (± 0.0)**
		5m Basal Area (5m BA)	0.5 (± 0.4)	-0.2 (± 0.6)	**1.3 (± 0.4) -0.7 (± 0.3)**	-0.4 (± 0.4)	-0.2 (± 0.3)	-0.4 (± 0.4)	-0.2 (± 0.2)	0.0 (± 0.0)
		Topographic HLI	-0.1 (± 0.3)	-0.5 (± 0.8)	-0.3 (± 0.3)	0.0 (± 0.3)	0.4 (± 0.2)	0.0 (± 0.4)	0.3 (± 0.2)	**0.1 (± 0.0)**
		Structure * HLI (SKY or 5m BA * HLI)	NA	NA	NA	**-0.9 (± 0.3) (5m BA * HLI)**	NA	NA	**-0.4 (± 0.2) (5m BA * HLI)**	0.1 (± 0.0) (SKY * HLI)
	AIC_c		59.64	22.40	81.67	84.89	85.84	55.16	232.13	10.87
	AUC (survival) R^2 (growth)		0.95	0.93	0.95	0.82	0.81	0.81	0.77	0.33
	Basal diameter (at planting)		NA	NA	NA	**2.7 (± 0.6)**	**0.7 (± 0.4)**	0.5 (± 0.6)	**1.4 (± 0.3)**	NA
	Microclimate	***Vapor pressure deficit (VPD and MaxVPD)***	**0.6 (± 0.4) -1.2 (± 0.5) (May)**	-0.5 (± 1.7) (Sep)	**0.6 (± 0.4) -1.2 (± 0.5) (May)**	**-0.9 (± 0.3) (Sep)**	-0.2 (± 0.3) (Sep)	1.2 (± 0.7) (July)	**-0.4 (± 0.2) (Sep)**	0.1 (± 0.0) (Aug 2020 MaxVPD)

		Soil moisture (VWC)	0.1 (± 0.3) (May)	0.9 (± 1.1) (July)	0.2 (± 0.3) (Sep)	0.3 (± 0.3) (Sep)	-0.4 (± 0.3) (May)	**1.5 (± 0.8) (June 2020)**	0.1 (± 0.2) (Sep)	-0.1 (± 0.0) (July 2020)
		Soil temperature	NA	NA	-0.4 (± 0.3) (Sep)	NA	NA	0.9 (± 0.6) (May 2019)	-0.1 (± 0.2) (Sep)	**0.2 (± 0.0) (May 2019) -0.1 (± 0.0) (Aug 2020)**
	AIC_c		63.08	21.31	84.74	95.76	81.53	44.10	233.98	-1.16
	AUC (survival) R^2 (growth)		0.95	0.89	0.95	0.74	0.89	0.75	0.71	0.47
DOUGLAS-FIR	**Structure-topography**	***Canopy Openness (SKY)***	**2.9 (± 2.4) -4.1 (± 2.3)**	-0.8 (± 0.7)	0.4 (± 0.3)	0.2 (± 0.2)	-0.1 (± 0.3)	0.1 (± 0.6)	0.1 (± 0.2)	**0.1 (± 0.0)**
		5m Basal Area (5m BA)	-0.8 (± 0.6)	0.3 (± 0.4)	0.3 (± 0.3)	**0.3 (± 0.3) -0.4 (± 0.2)**	0.0 (± 0.4)	0.8 (± 0.9)	**0.2 (± 0.2) -0.5 (± 0.2)**	0.0 (± 0.0)
		Topographic HLI	0.1 (± 0.7)	**-1.1 (± 0.7)**	**-0.8 (± 0.3)**	0.3 (± 0.2)	0.5 (± 0.3)	NA	0.3 (± 0.2)	**0.1 (± 0.0)**
		Structure * HLI (SKY or 5m BA * HLI)	NA	NA	NA	**-1.0 (± 0.3) (5m BA * HLI)**	NA	NA	**-0.8 (± 0.2) (5m BA * HLI)**	**0.1 (± 0.0) (SKY * HLI)**
	AIC_c		35.24	36.83	84.70	127.19	76.81	32.92	226.78	-49.91
	AUC (survival) R^2 (growth)		0.93	0.94	0.97	0.82	0.66	0.78	0.75	0.27
	Basal diameter (at planting)		NA	NA	NA	**1.8 (± 0.3)**	**1.0 (± 0.4)**	0.2 (± 0.7)	**1.7 (± 0.3)**	NA

	Microclimate	***Vapor pressure deficit (VPD and MaxVPD)***	**1.0 (± 0.4) (Sep MaxVPD)**	0.8 (± 0.8) (Sep)	**-1.4 (± 0.5) (Sep VPD) 2.5 (± 0.7) -2.2 (± 0.6) (May MaxVPD)**	-0.2 (± 0.2) (June)	-0.3 (± 0.4) (May-Sep)	-0.6 (± 0.6) (Sep 2019)	**-0.5 (± 0.2) (Sep)**	-0.1 (± 0.0) (Sep 2021)
		Soil moisture (VWC)	-0.5 (± 0.5) (July)	**1.4 (± 0.7) (Sep)**	**0.6 (± 0.3) (Sep)**	-0.3 (± 0.2) (May)	0.5 (± 0.3) (August)	-1.0 (± 0.6) (May-Sep)	**-0.4 (± 0.2) (May)**	0.0 (± 0.0) (July 2020)
		Soil temperature	NA	**-3.3 (± 1.5) (Aug)**	-0.2 (± 0.5) (May)	NA	NA	NA	0.3 (± 0.2) (Sep)	**0.1 (± 0.0) (May 2019) -0.1 (± 0.0) (Aug 2020)**
	AIC_c		43.15	35.06	65.47	132.35	73.26	27.19	229.30	-51.97
	AUC (survival) R^2 (growth)		0.90	0.95	0.97	0.76	0.67	0.87	0.76	0.39

APPENDIX 2

SUPPLEMENTARY MATERIAL FOR CHAPTER 3:

JUVENILE PIÑON PINE VIGOR FOLLOWING OVERSTORY TREE DIE-OFF IS HIGHEST FOR LARGER JUVENILES AND LIMITED BY MICROCLIMATE CONDITIONS

METHODS

Weather anomalies during study period

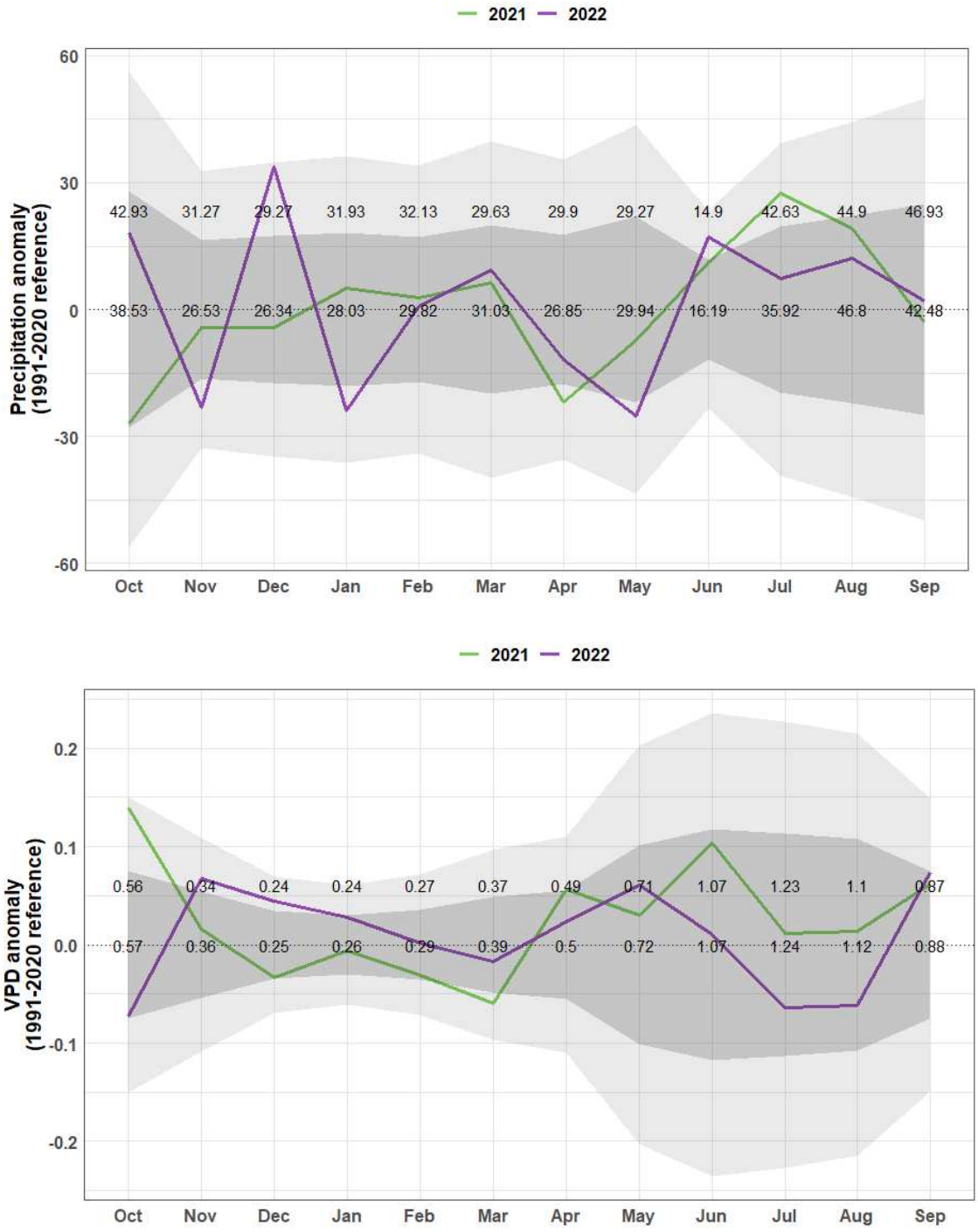

Figure S3.1. *Precipitation (top panel) and vapor pressure deficit (VPD, bottom panel) weather anomalies during years of sampling for this study (2021-2022) relative to long-term site climate normals (1991-2020). While some precipitation anomalies were evident during growing seasons of the study*

years (~May-September), VPD was largely within a normal range of variability. Climate data are displayed relative to the hydrological water year which spans October (previous year) - September (current year). Climate data were obtained from ClimateNA (https://climatena.ca/).

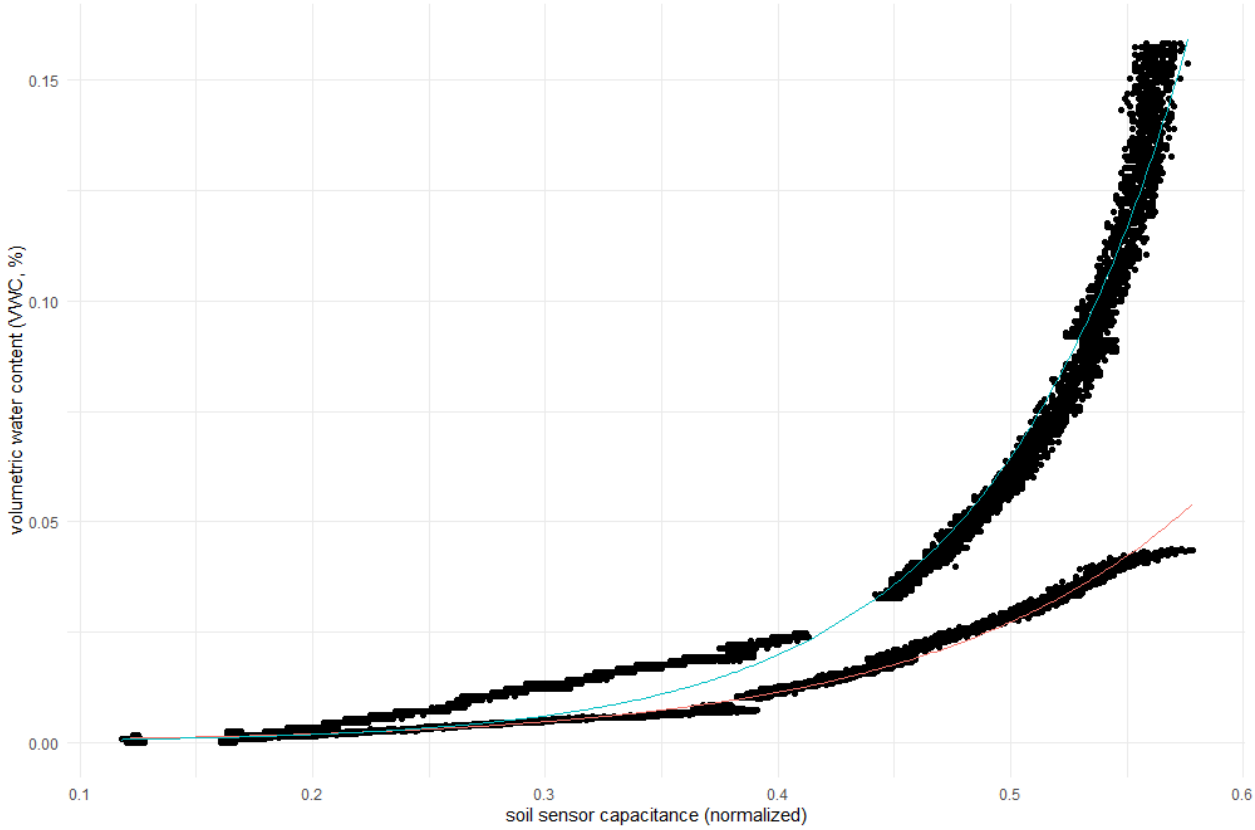

Figure S3.2. *Results for calibration of soil sensor capacitance values with volumetric water content. Soil cores of known volume and bulk density were calibrated in a laboratory through continuous drying and weighing of cores concurrent with soil capacitance measurements. Soil sensor capacitance values were normalized to the range of possible sensor values. Non-linear fits were determined for each soil core used for calibration (distinguished by color in the plot), and parameters of each regression were averaged for a common calibration equation used to convert all field-derived sensor capacitance values to volumetric water content (%).*

RESULTS

All model results

Table S3.1. *Results for all models of photosynthetic rates and stomatal conductance rates for both smaller and larger trees. Model details include predictor variables selected in top models, estimates for each predictor effect, 95% confidence interval limits, significance of estimates based on evaluation of confidence intervals, AIC_c values, and root mean squared error (RMSE) model fit values.*

Resp. Variable	Juvenile Size	Predictor Variable	Estimate	95% CI (low, high)	Significance	AICc	RMSE
Photosynthetic rate	Small (< 2 cm DRC)	Overstory (live)	-0.36	-0.784, 0.004	MARG	206.37	0.63
		Juvenile size	0.27	-0.959, 1.474	N	206.37	0.63
		Soil moisture (shallow-deep average)	0.37	0.228, 0.507	Y	206.37	0.63
		Vapor pressure deficit (mean daily, sampling days)	-0.28	-0.436, -0.141	Y	206.37	0.63
		Photosynthetic efficiency (quantum yield)	-0.26	-0.466, -0.017	Y	206.37	0.63
		Instantaneous VPD (scaled for ea. sampling day)	-0.24	-0.39, -0.087	Y	206.37	0.63
	Large (> 2 cm DRC)	Overstory (live)	-0.53	-0.802, -0.238	Y	261.66	0.74
		Juvenile size	0.23	0.046, 0.439	Y	261.66	0.74
		Soil moisture (shallow-deep average)	0.25	0.112, 0.408	Y	261.66	0.74
		Vapor pressure deficit (mean daily max, sampling days)	-0.56	-0.766, -0.366	Y	261.66	0.74
		Interaction: Overstory * VPD	0.27	-0.002, 0.562	MARG	261.66	0.74
		Photosynthetic efficiency (quantum yield)	-0.18	-0.304, -0.047	Y	261.66	0.74

		Instantaneous VPD (scaled for ea. sampling day)	-0.22	-0.37, -0.076	N	261.66	0.74
Stomatal conductance rate	Small (< 2 cm DRC)	Overstory (live)	-0.26	-0.731, 0.179	N	234.41	0.77
		Juvenile size	-0.35	-1.556, 0.882	N	234.41	0.77
		Soil moisture (shallow-deep average)	0.35	0.167, 0.512	Y	234.41	0.77
		Vapor pressure deficit (mean daily, sampling days)	-0.30	-0.485, -0.127	Y	234.41	0.77
		Instantaneous VPD (scaled for ea. sampling day)	-0.24	-0.431, -0.073	Y	234.41	0.77
	Large (> 2 cm DRC)	Overstory (live)	-0.62	-0.955, -0.323	Y	265.55	0.75
		Juvenile size	0.28	0.081, 0.477	Y	265.55	0.75
		Soil moisture (shallow-deep average)	0.23	0.07, 0.365	Y	265.55	0.75
		Vapor pressure deficit (mean daily, sampling days)	-0.49	-0.681, -0.265	Y	265.55	0.75
		Interaction: Overstory * VPD	0.26	-0.048, 0.539	N	265.55	0.75
		Instantaneous VPD (scaled for ea. sampling day)	-0.11	-0.243, 0.038	N	265.55	0.75

Comparison of microclimate, sitewide weather station, and downscaled point-based climate data

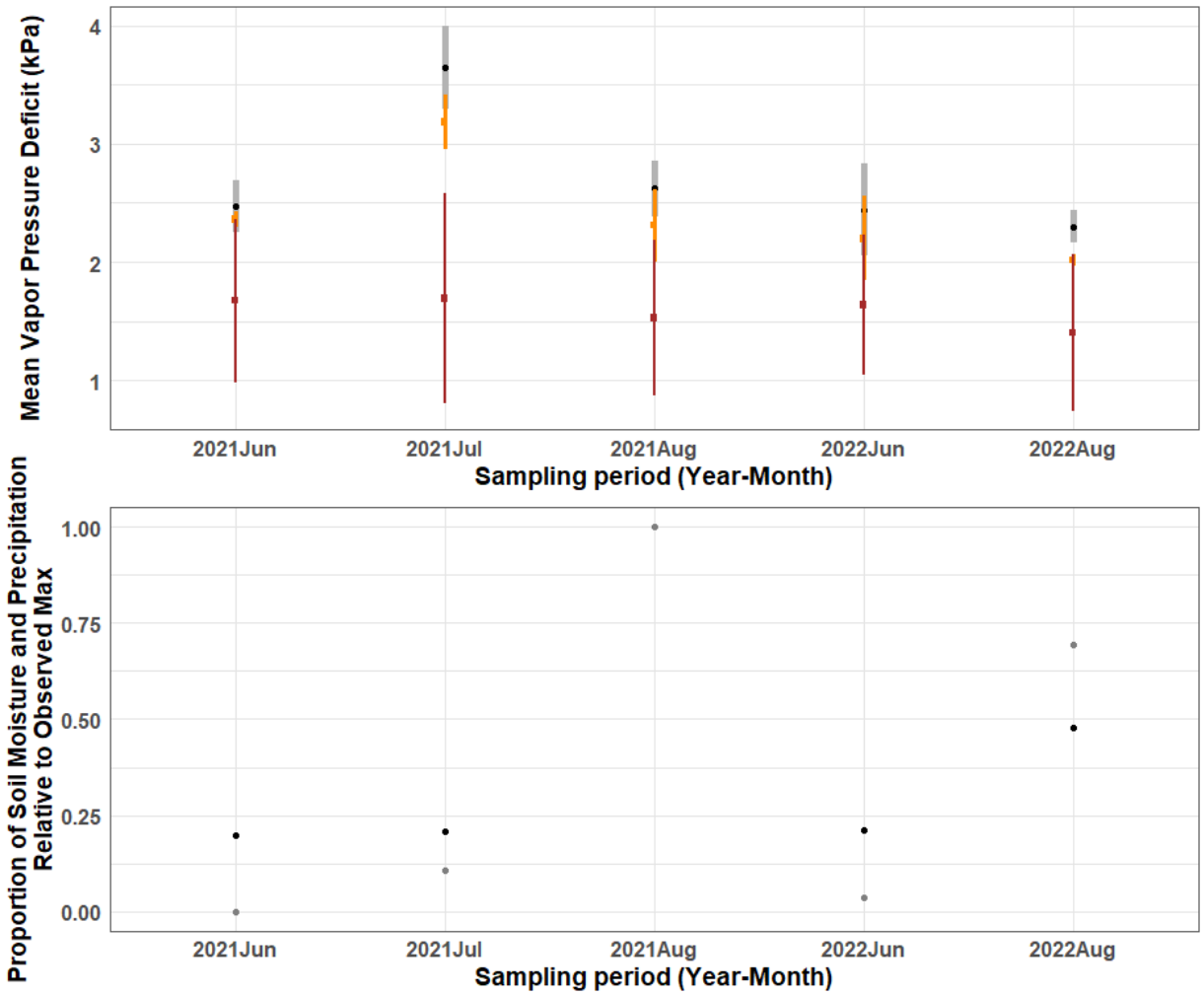

Figure S3.3. *Comparisons across data sources for values of mean vapor pressure deficit conditions (top panel) and soil moisture and precipitation (bottom panel) across different sampling periods in this study. Colors represent different data sources, where black circles are values from microclimate sensors used in this study, orange squares (VPD only) represent our sitewide reference weather station source, red squares (VPD only) are taken from downscaled point-based climate data for this site, and grey circles (bottom panel) represent precipitation conditions from downscaled point-based climate data. In the bottom panel, soil moisture and precipitation for each period are shown as proportions of the corresponding observed maximum across sampling periods, in order to show soil moisture and precipitation variation on the same scale. Generally, microclimate data reflected much higher VPD conditions, and soil moisture was more consistent than precipitation. Precipitation values are based on weekly sums of precipitation received prior to the corresponding sampling period (described in Methods).*

APPENDIX 3:

SUPPLEMENTARY MATERIAL FOR CHAPTER 4:

EFFECTS OF OVERSTORY MORTALITY ON JUVENILE PIÑON PINE GROWTH DEPEND ON WEATHER AND SITE CONDITIONS ACROSS LOCAL AND REGIONAL ENVIRONMENTAL GRADIENTS

RESULTS

Model Results

Table S4.1. *Model results for all models described in analysis. Table information includes model type (a-d, described in Analysis), year of growth modeled (2021 and 2022), and covariates included in each model for Branch Growth Ratios (BGR) and Needle Growth Ratios (NGR). Model information includes coefficient estimates ("Est.") for each model covariate, in addition to standard errors ("SE") of each estimate, model degrees of freedom ("DF"), 95% bounds of confidence interval estimates ("CI low" and "CI high"), and model root mean squared error ("RMSE").*

Model Type	Model Growth Year	Covariate	Branch Growth Ratios (BGR)						Needle Growth Ratios (NGR)					
			Est.	*SE*	*DF*	*CI low*	*CI high*	*RMSE*	*Est.*	*SE*	*DF*	*CI low*	*CI high*	*RMSE*
All sites (a)	Growth Year 1 (2021)	AZM	0.20	0.29	160	-0.37	0.78	0.73	0.77	0.21	161	0.38	1.23	0.53
		SCOL	1.01	0.31	160	0.48	1.61		1.31	0.22	161	0.88	1.80	
		SCOM	0.77	0.25	160	0.26	1.31		1.21	0.19	161	0.81	1.60	
		SCOH	0.37	0.27	160	-0.20	0.93		1.15	0.20	161	0.75	1.56	
		NCOM	0.80	0.32	160	0.19	1.40		0.50	0.24	161	0.05	0.97	
		dead OS	0.40	0.38	160	-0.36	1.20		0.60	0.28	161	0.07	1.14	
		DRC >2	-0.14	0.16	160	-0.45	0.17		-0.06	0.12	161	-0.28	0.17	
		OS needle ret.	-0.10	0.09	160	-0.30	0.08		-0.10	0.07	161	-0.24	0.05	
		AZM:dead OS	-0.52	0.41	160	-1.38	0.27		-0.24	0.30	161	-0.84	0.31	
		SCOL:dead OS	-0.58	0.45	160	-1.45	0.23		-0.48	0.32	161	-1.08	0.10	
		SCOM:dead OS	0.58	0.38	160	-0.21	1.33		0.30	0.28	161	-0.21	0.83	
		SCOH:dead OS	1.31	0.43	160	0.45	2.08		1.43	0.32	161	0.73	2.00	
		NCOM:dead OS	-0.50	0.49	160	-1.49	0.44		-0.87	0.36	161	-1.62	-0.18	

		dead OS:DRC >2	0.08	0.22	160	-0.37	0.52		-0.30	0.16	161	-0.59	0.02	
	Growth Year 2 (2022)	AZM	0.37	0.28	159	-0.18	0.88		-0.32	0.36	156	-1.08	0.36	
		SCOL	0.95	0.28	159	0.44	1.56		0.19	0.37	156	-0.52	0.89	
		SCOM	0.50	0.24	159	-0.04	0.99		-0.18	0.31	156	-0.85	0.39	
		SCOH	0.43	0.26	159	-0.09	0.98		-0.76	0.34	156	-1.43	-0.16	
		NCOM	0.20	0.30	159	-0.33	0.79		0.35	0.39	156	-0.41	1.16	
		dead OS	1.17	0.47	159	0.21	2.14		1.22	0.61	156	-0.12	2.40	
		DRC >2	-0.14	0.14	159	-0.40	0.15		-0.09	0.18	156	-0.48	0.27	
		OS needle ret.	0.19	0.16	159	-0.14	0.49	0.59	0.41	0.21	156	-0.02	0.80	0.81
		AZM:dead OS	-0.54	0.39	159	-1.27	0.22		-0.29	0.50	156	-1.26	0.82	
		SCOL:dead OS	-1.00	0.40	159	-1.83	-0.15		-0.73	0.54	156	-1.67	0.35	
		SCOM:dead OS	0.42	0.33	159	-0.21	1.10		0.11	0.44	156	-0.65	1.13	
		SCOH:dead OS	1.31	0.43	159	0.41	2.21		0.86	0.55	156	-0.22	1.90	

		NCOM:dead OS	-0.96	0.49	159	-1.96	-0.01		-1.06	0.64	156	-2.35	0.29	
		dead OS:DRC >2	-0.11	0.19	159	-0.51	0.28		0.33	0.26	156	-0.20	0.88	
Regional monsoonality (b)	Growth Year 1 (2021)	Mons	-0.38	0.17	89	-0.69	-0.09	0.76	-0.19	0.12	87	-0.43	0.05	0.53
		I(Mons^2)	-0.17	0.12	89	-0.41	0.05		-0.29	0.08	87	-0.46	-0.11	
		dead OS	0.99	0.31	89	0.38	1.60		0.88	0.22	87	0.44	1.36	
		DRC >2	-0.15	0.22	89	-0.60	0.23		-0.14	0.16	87	-0.45	0.15	
		OS needle ret.	-0.06	0.13	89	-0.32	0.20		-0.09	0.09	87	-0.27	0.08	
		Mons:dead OS	-0.57	0.24	89	-1.05	-0.12		-0.19	0.17	87	-0.53	0.14	
		I(Mons^2):dead OS	-0.56	0.16	89	-0.86	-0.26		-0.40	0.11	87	-0.63	-0.18	
		dead OS:DRC >2	-0.07	0.31	89	-0.66	0.53		-0.32	0.22	87	-0.74	0.17	
	Growth Year 2 (2022)	Mons	-0.09	0.12	88	-0.34	0.16	0.50	-0.35	0.13	89	-0.62	-0.11	0.78
		I(Mons^2)	-0.11	0.08	88	-0.25	0.04		NA	NA	NA	NA	NA	
		dead OS	1.34	0.62	88	0.06	2.69		0.07	0.53	89	-1.00	1.24	

		DRC >2	-0.05	0.15	88	-0.37	0.26		-0.02	0.23	89	-0.45	0.42	
		OS needle ret.	0.04	0.27	88	-0.54	0.63		-0.19	0.25	89	-0.70	0.31	
		Mons:dead OS	-0.46	0.16	88	-0.75	-0.16		0.03	0.20	89	-0.38	0.43	
		I(Mons^2):dead OS	-0.52	0.16	88	-0.86	-0.22		NA	NA	NA	NA	NA	
		dead OS:DRC >2	-0.38	0.21	88	-0.85	0.05		0.19	0.32	89	-0.53	0.89	
Local elevation in SCO region (c)	Growth Year 1 (2021)	elevn	-0.23	0.12	94	-0.47	0.00	0.85	-0.06	0.07	97	-0.21	0.09	0.55
		dead OS	0.84	0.30	94	0.32	1.37		0.90	0.19	97	0.55	1.33	
		DRC >2	-0.09	0.24	94	-0.61	0.43		-0.01	0.16	97	-0.31	0.33	
		OS needle ret.	-0.16	0.14	94	-0.43	0.09		-0.14	0.09	97	-0.31	0.04	
		elevn:dead OS	0.66	0.18	94	0.32	1.01		0.70	0.11	97	0.47	0.92	
		dead OS:DRC >2	-0.19	0.34	94	-0.85	0.44		-0.46	0.22	97	-0.91	-0.03	
	Growth Year 2	elevn	-0.17	0.10	96	-0.38	0.04	0.68	1.01	0.41	94	0.18	1.82	0.67
		dead OS	1.27	0.38	96	0.50	2.02		-0.34	0.21	94	-0.74	0.05	

		DRC >2	-0.26	0.20	96	-0.65	0.12		-0.34	0.11	94	-0.54	-0.13	
		OS needle ret.	0.18	0.16	96	-0.15	0.52		0.36	0.17	94	0.03	0.70	
		elevn:dead OS	0.79	0.16	96	0.48	1.15		0.54	0.29	94	-0.05	1.12	
		dead OS:DRC >2	-0.08	0.29	96	-0.65	0.45		0.57	0.18	94	0.23	0.91	
Post-mortality weather (d)	Growth Year 1 (2021)	dead OS	0.73	0.20	166	0.35	1.14	0.76	0.88	0.16	167	0.57	1.22	0.50
		DRC >2	-0.10	0.17	166	-0.43	0.23		0.02	0.12	167	-0.23	0.26	
		OS needle ret.	-0.02	0.08	166	-0.20	0.15		-0.02	0.07	167	-0.15	0.12	
		dCMD_2020	-0.34	0.11	166	-0.57	-0.11		-0.10	0.10	167	-0.33	0.10	
		dCMD_2021	0.15	0.11	166	-0.08	0.38		-0.27	0.10	167	-0.47	-0.06	
		dead OS:DRC >2	0.05	0.23	166	-0.40	0.49		-0.32	0.17	167	-0.66	-0.01	
		dead OS:dCMD_2020	0.09	0.16	166	-0.23	0.37		0.36	0.14	167	0.10	0.69	
		dead OS:dCMD_2021	-0.62	0.15	166	-0.92	-0.31		-0.79	0.14	167	-1.07	-0.51	

	Growth Year 2 (2022)	dead OS	1.40	0.25	165	0.93	1.89	0.58	1.13	0.30	162	0.54	1.75	0.82
		DRC >2	-0.09	0.14	165	-0.36	0.19		-0.06	0.19	162	-0.42	0.27	
		OS needle ret.	0.30	0.11	165	0.09	0.52		0.38	0.13	162	0.12	0.64	
		dCMD_2022	-0.08	0.24	165	-0.55	0.42		-0.51	0.27	162	-0.98	0.05	
		dCMD_2021	-0.06	0.24	165	-0.53	0.39		0.70	0.27	162	0.16	1.24	
		dead OS:DRC >2	-0.11	0.20	165	-0.51	0.23		0.31	0.26	162	-0.19	0.84	
		dead OS:dCMD_2022	0.43	0.33	165	-0.22	1.02		0.57	0.38	162	-0.16	1.29	
		dead OS:dCMD_2021	-1.01	0.32	165	-1.62	-0.37		-0.99	0.37	162	-1.68	-0.25	

DISCUSSION

Raw growth data by year

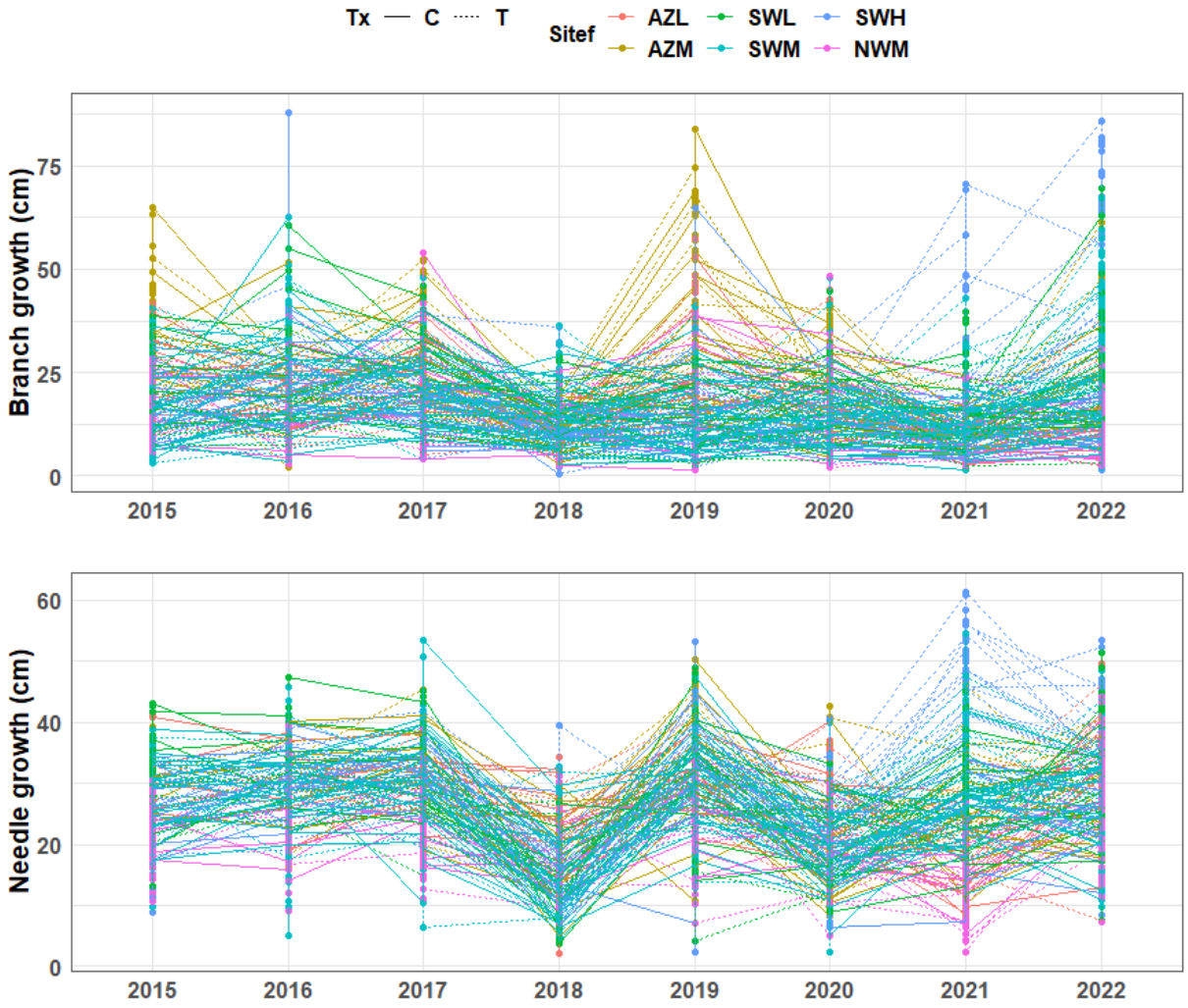

Figure S4.1. *Raw growth data for branches (top panel) and needles (bottom panel) across all sites and overstory environments (C = live overstory, T = dead overstory). General patterns of pre-mortality growth are evident and which impact the derivation of growth ratios for post-mortality growth analyses.*