

THESIS

INCREASED ARIDITY IS ASSOCIATED WITH STRONGER TRADEOFFS IN
PONDEROSA PINE VITAL FUNCTIONS

Submitted by

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ABSTRACT

INCREASED ARIDITY IS ASSOCIATED WITH STRONGER TRADEOFFS IN PONDEROSA PINE VITAL FUNCTIONS

Trees must allocate resources to core functions, like growth, defense, and reproduction, for populations to persist in the future. A changing climate is leading to more extreme droughts and hotter temperatures, and it is uncertain how trees will allocate resources to these functions under more extreme climatic conditions. Resource allocation patterns vary among individuals and in response to drought stress, limiting our understanding of how forests will respond to climate warming. Yet the impacts of drought on long term trends of reproductive investment have been seldom compared with growth or defensive traits simultaneously. We conducted a 21-year survey of growth, defense (resin duct area), and reproduction (cone production) in 80 ponderosa pine individuals spanning 8 populations along the Front Range of Colorado, USA. We used linear mixed models to describe tradeoffs among these vital functions and to characterize variability among individuals and within individuals over time. Within individual trees, we found a tradeoff over time between growth and reproduction and defense and reproduction, where growth and total resin duct area were lower in years of high cone production. Trees located at sites with hotter and drier climates showed stronger annual tradeoffs between annual reproduction and growth. In contrast, when comparing among trees, we found no evidence that trees with high long-term reproduction invested less in growth or defense. In our study, we found local drought conditions change the year-to-year tradeoffs in allocation between reproduction and growth. Our results support the environmental stress hypothesis of masting,

which predicts that greater interannual variation in tree functions (reproduction, growth, defense) is associated with more marginal environments, such as those that are prone to drought. With warming temperatures and increased exposure to drought stress, trees will be faced with stronger interannual tradeoffs, which could lead to further decreases in growth and defensive efforts, ultimately increasing mortality.

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CHAPTER 1: INCREASED ARIDITY IS ASSOCIATED WITH STRONGER TRADEOFFS IN PONDEROSA PINE VITAL FUNCTIONS

1.1 Introduction

Trees must acquire and store resources to maintain fitness and carry out core functions in order to survive. Extreme droughts and warming temperatures increase pressure on trees to adequately distribute resources (Allen et al., 2010; Ferrenberg et al., 2013; Enright et al., 2015; Lauder et al., 2019), making it difficult for trees to fulfill all their functions, and ultimately making them more susceptible to mortality or regeneration failure. Consequently, many studies of life history theory emphasize potential tradeoffs and synergies among functions (Linhart & Mitton, 1985; Bazzaz et al., 1987; Herms & Mattson, 1992; Barringer et al., 2012; Redmond et al., 2019). For instance, individuals who grow faster may curtail resources to defensive traits and be less defended to abiotic or biotic attacks (Herms & Mattson, 1992). The year-to-year investment in different functions within an individual tree is important in that it affects the dynamics of important processes in forests, such as seed production, growth, and carbon sequestration (Bazzaz et al., 1987; Pearse et al., 2016). However, we know far less about how tree functions trade off over time in contrast with how they trade off among individuals observed at the same time.

Understanding year-to-year variation in tree functions is especially important when species mast (i.e., produce variable and synchronous seed crops) because, in these species, reproduction is highly pulsed in certain years. Mast years (i.e., years of high seed production) use a significant amount of resources, likely resulting in resource tradeoffs as allocation patterns are curtailed from other physiological mechanisms to reproductive efforts (Kelly & Sork, 2002;

Pearse et al., 2016). This process may be explained by the resource-switching hypothesis, which postulates that trees allocate resources to reproduction one year and then away from reproduction in other years. This hypothesis is supported by several studies that have found a negative association between growth and seed production across a variety of masting species and populations (Linhart & Mitton, 1985; Koenig & Knops, 2000; Barringer et al., 2012). However, some studies have not found growth-reproduction tradeoffs, and instead found tradeoffs between defense and reproduction (Redmond et al., 2019). Although there is evidence of resource tradeoffs among growth and reproduction or defense and reproduction, studies seldom assess all three of these functions simultaneously (Tuller et al., 2018; Redmond et al., 2019). Differential investment of resources to growth and defense has been extensively investigated among and within pines (Ferrenberg et al., 2015), relative to pine reproduction (Redmond et al., 2019). This in part is due to the complex defensive system that pines have evolved, called oleoresin (hereafter referred to as ‘resin’), to protect against insect infestation, which remain visible in annual xylem growth rings in pine species. This makes long term observations of xylem growth and resin ducts more obtainable. In contrast, seed production in masting species is more difficult to observe due to the cycles high variability which often requires measurements over longer periods of time.

Resource allocation patterns may vary considerably across and within populations over environmental gradients. Populations located in more climatically stressful areas with more limited resources available may exhibit greater tradeoffs between growth, reproduction, and defense allocation. This in part could be due to climatic constraints causing smaller pools of resources that a plant has to allocate to functions, resulting in stronger prioritization of one trait over another as a plant tries to cope with performing multiple functions. Similarly, individuals

located in less stressful microenvironments or with genetic adaptations to better handle drought stress (e.g., greater water use efficiency [WUE]) may be better able to allocate resources to growth, defense, and reproduction simultaneously. Understanding whether tradeoffs in tree functions vary predictably among populations over a climatic gradient will help anticipate the impacts of climate change on tree functions. However, our understanding of the impact of climate and individual drought resistance on resource allocation patterns is poorly understood. Genetic differences in individual drought resistance have resulted in varying responses to resource limitations (Bazzaz et al., 1987; Livingston & Splittlehouse, 1993). Furthermore, there is evidence of acclimation to drought across individual and annual functions of trees (Bogdziewicz et al., 2020). These variations further complicate our understanding of climatic constraints and individual drought resistance on resource allocation patterns and warrants further attention.

This research focuses on the impacts of drought on resource allocation trends of defense, reproduction, and growth, in ponderosa pine. Ponderosa pine (*pinus ponderosa var. scopulorum*) is a widely distributed mast seeding species across much of the western U.S. that has been subjected to increasing pressures from fire (Rodman et al., 2020), bark beetle outbreaks (Kane & Kolb, 2010), and drought stress (Williams et al., 2013; Lauder, 2020). Increasing pressures along with ponderosa pine's expansive topographic and climatic range underscore the importance of understanding this species resource allocation patterns. This study utilizes a 21-year time span (2000-2020) of ponderosa pine annual xylem growth, resin duct production, and cone production across a broad climatic gradient to compare variability in resource allocation over time and among individuals. Our study addresses two objectives. First, we determine the relationship between resin duct production, xylem growth, and cone production and how that varies among

individuals and over time. Second, we assess whether resource allocation patterns vary in relation to long-term drought conditions at a site and a tree's individual water use efficiency. We hypothesized that high cone producing individuals or high cone years would drive tradeoffs among functions due to high resource demand during mast years. We also predicted that high drought resistance would lower growth and defensive efforts and result in stronger tradeoffs due to limited resource availability and increased stress from drought. Additionally, we hypothesized that individuals located in sites with high climatic water deficit and high drought stress would lead to tradeoffs among resin duct production and growth as individuals experiencing strong drought pressures would prioritize defense over biomass production.

1.2 Materials and Methods

1.2.1 Study Area and Field Collection

We surveyed eight sites across the Colorado Front Range that spanned gradients of climate and elevation (Figure 1.1). At each site, we selected ten reproductively mature trees that had evidence of past reproduction. These trees appeared healthy and showed no evidence of severe dieback. We estimated traits related to cone production, xylem growth, resin duct production, and drought resistance by sampling diameter at breast height and neighborhood density of each tree measured. Diameter at breast height and local neighborhood density have been found to have meaningful impacts on the vital functions of interest (Krannitz & Duralia, 2004; Rodríguez-García et al., 2013; Flathers et al., 2016). Twenty-one years of historical cone counts were reconstructed using annual bud scale scars and the cone abscission scar method (Forcella, 1981b; Redmond et al., 2016). Five branches were randomly selected on each tree and annual cone counts (the year in which the cones were mature) were recorded from cone abscission scars on each annual branch segment using the annual bud scale scar dating method

(Forcella, 1981b; Redmond et al., 2016). The number of cone scars counted each year were averaged across the five branches and then multiplied by the total number of cone-bearing branches, which was obtained by visual count. This method has been found to be highly effective in reconstructing past cone production in *Pinus edulis* (Redmond et al., 2016) and has been widely used in other *Pinus sp.*, including ponderosa pine (Rodman et al., 2020; Wion et al., 2021). However, this method is unable to distinguish between aborted and fully mature cones and this method relies on sampling branches without significant scarring caused by other abiotic and biotic damage.

1.2.2 Dendrochronological and Resin Duct Methods

Each tree sampled had one intact 12mm and 5mm core taken as close to the ground as possible, at the same height (20-40 cm from the ground), and parallel to the slope (for trees located on slopes). The cores were dried, mounted, and sanded for resin duct and carbon isotope analysis. In the laboratory, all cores were progressively sanded following standard dendrochronological techniques (Stokes & Smiley, 1996). All cores were visually dated and cross dated using COFECHA. Tree cores that were weakly correlated (correlation below 0.20) were checked, redated, and manually verified using local ring width chronologies from ponderosa pine (Rodman et al., 2020; Veblen et al., 2000) and chronologies from the *International Tree-Ring Data Bank* (<https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>). Radial annual xylem growth measurements (mm) were taken for each 12mm core from the year 2000-2020 (n=76). For cores that were unable to be dated to 2000, cores were dated to earliest date of certainty (n=4).

All 12mm cores were scanned at 4800 dpi using an Epson Perfection V550 scanner. The scans were then used to measure and assign a calendar year to each vertical oleoresin duct

formed between 2000 and 2020. This was done manually using the ellipse tool in the program ImageJ (version 1.53e), similar to Redmond et al. (2019). Years with heavy scarring were not measured and assigned NA in the analyses. For our analyses, we used total duct area ($\text{mm}^2 \text{ year}^{-1}$) as our metric of defense for ponderosa pine. Total duct area (unstandardized) is the sum of duct area per annual ring. This metric has been found to be the best predictors of resin flow in pine, the first line of defense against bark beetle outbreaks (Hood & Sala, 2015).

1.2.3 Carbon Isotope Analysis Extraction Methods

Carbon isotope analysis ($\delta^{13}\text{C}$) was used to gauge an individual's drought resistance over the past 21-years. Carbon isotopes, often interpreted as carbon discrimination and water use efficiency, has been found to be correlated with transpiration in trees as well as a gauge of photosynthesis (Livingston & Splittlehouse, 1993; Lauteri et al., 1993; Farquhar, 1998). After all (5mm and 12mm) cores were cross-dated and measured for annual ring width and resin duct production, cores were dried in an oven at 100°C for two days. Each 5mm core was used to pool years 2000-2020 for carbon isotope analysis. 5mm cores that had damage or scarring from 2000-2020 were discarded and their respective 12mm core was used ($n=11$). The pooled years were ground to a fine powder using a wood file to 115 mesh (0.15mm [Borella et al. 1998]) to ensure the powder was homogenized. We attempted to provide equal amounts of material for each year pooled to prevent small growth years from being absent from the analysis or large years skewing the results. Early wood and late wood were not separated because our objective was to see how an individual allocates resources annually and on average, so seasonal differences were not of concern. Cellulose was not extracted before $\delta^{13}\text{C}$ measurements were taken due to numerous studies reporting non substantial variation in whole wood values and cellulose, and because of reports of a constant relationship between whole wood and cellulose in sapwood (Harlow et al.,

2006; Loader et al., 2003; Borella et al., 1998). Because we were only using the first 21 years, the impact of age on carbon discrimination was also not of concern.

The most recent 21-years for each 5mm core was collected as one sample to get an overall carbon discrimination measurement (found to be negatively correlated with water use efficiency). The ground samples (~1-2mg) were encapsulated in a small tin and sent to UC Davis for processing. Isotope ratios were obtained using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The sample's provisional isotope ratios were measured relative to a reference gas peak analyzed with each sample. The provisional values were finalized and corrected based on the known values of the included laboratory reference materials. The final delta values ($\delta^{13}C_{VPDB}$) were received from UC Davis and expressed relative to the international standards VPDB (Vienna Pee Dee Belemnite). The use of the term water use efficiency (WUE) in this study was defined by Farquhar (1989), as carbon isotope discrimination:

$$\Delta = \frac{(\delta^{13}C_a - \delta^{13}C_p)}{1 + \delta^{13}C_p/1000}$$

Where $\delta^{13}C_a$ is the atmospheric concentration of ^{13}C (assumed to be -8‰), and $\delta^{13}C_p$ as the plant concentration of ^{13}C (given by UC Davis in the form of $\delta^{13}C_{VPDB}$). Carbon discrimination is directly and negatively correlated to plant water use efficiency for structural carbon (Lauteri et al., 1993). As carbon discrimination decreases, water use efficiency increases and vice versa. The carbon discrimination values for each site were then centered in relation to the mean at each site to remove any potential impact that site has on carbon discrimination.

1.2.4 Climate and Weather Metrics

We calculated the mean 30-year cumulative climatic water deficit (CWD) at each site to assess average drought conditions using 800-meter resolution estimates of precipitation and temperature (PRISM Climate Group, 2020), heat load (calculated based on slope, aspect, and latitude), soil available water capacity (obtained from SSURGO at 150mm available water capacity depth), and day length. We quantified a 30-year average of CWD using a Thornthwaite-type water balance model following the equations provided in Lutz et al. (2010) using the Redmond (2022) CWD function in R. CWD is a biologically meaningful measure to assess the water balance at each site as it measures the amount of water by which potential evapotranspiration exceeds actual evapotranspiration (Stephenson 1990, 1998). Water balance has been found to be strongly correlated with vegetation distributions (Stephenson 1990, 1998). We also controlled for annual variability in weather that is known to impact tree growth and likely resin duct production by calculating the Forest Drought Severity Index (FDSI; Williams et al., 2013). FDSI is a combination of early summer vapor pressure deficit and winter–spring precipitation of the current year and late summer vapor pressure deficit of the prior year (see Williams et al., 2013 for details). FDSI is standardized so each site has a mean of 0 and a standard deviation of 1, with negative values indicating hotter and drier years.

1.2.5 Statistical Analysis

1.2.5.1 Models among individuals

To assess resource allocation patterns among individuals between growth, defense, and reproduction, we modeled xylem growth, total resin area, and cone abundance at maturity using linear mixed models. We focused on cone abundance at maturity for analyses because trees put a substantial amount of resources into seeds during the year of cone maturation (Bazzaz et al.,

1987; Cone & Rapp, 2014, Han & Kabeya, 2017, Redmond et al., 2019), rather than cone initiation, which in ponderosa pine occurs two years prior to seed maturation (Krannitz & Duralia, 2004). In our models, sites were included as a random effect to account for variation across populations. Our response variables in our mixed effects models were mean (21-year) xylem growth and mean (21-year) total resin area, while mean (17- year) cone abundance at maturity was our predictor variable. An additional model was run to assess the association between xylem growth (predictor variable) and total resin area (response variable) among individuals. The linear mixed models used to assess relationships among individuals used 21-year averages of the data collected and included fixed effects that accounted for individual diameter at breast height (DBH), and local neighborhood density (BA). Site CWD and individual carbon discrimination were used separately as interactions for each model iteration. CWD was included as an interaction to test our hypothesis that site drought conditions impacted the relationship between growth, defense, and reproduction. Similarly, carbon discrimination was included in the model as an interactive effect to assess how individual drought resistance impacted the relationships measured.

1.2.5.2 *Models over time*

To assess the resource allocation patterns across years between growth, defense, and reproduction, we used a similar modeling approach to above. The linear mixed models used to assess changes to relationships over time used data over a 17-year period (2004-2020, n=1322) due to limited cone production data prior to 2004. All response variables and predictor variables in these models were the same as above, except we used annual cone, growth, and resin duct data rather than their averages. These annual models also included a fixed effect that accounted for annual FDSI, as FDSI has been found to strongly influence ponderosa pine growth and likely

resin duct production over time (Williams et al., 2013). Trees nested within sites were included as random effects to account for variation among individuals within each site.

Linear mixed models were run using the package *lme4* (Bates et al., 2015) in R (R Core Team 2022). All fixed effects were scaled, and all dependent variables were log transformed (natural log) to improve model fit. Data calculations and data merging were done using the R packages *dplyr* (Wickham et al., 2021) and *data.table* (Dowle et al., 2021). Modeling assumptions were verified using R package *sjPlot* (Lüdecke, 2021) to test for linearity, normality, and homogeneous variance. All plots made were plotted using R packages *sjPlot* (Lüdecke, 2021), *ggeffects* (Lüdecke, 2018), and *ggplot2* (Wickham, 2016). Some model results were back transformed for visualizations. All analyses were performed in R (R Core Team 2022).

1.3 Results

1.3.1 Tradeoffs in Reproduction, Growth and Defense Among Individuals

Among individuals, we observed a positive relationship between total resin area and radial xylem growth (Figure 1.2), such that individuals with higher xylem growth also tended to have higher resin duct production. We found no association between total resin area and cone abundance among individuals (Tables 1.1 & 1.2). Likewise, xylem growth was not associated with cone abundance among individuals (Tables 1.1 & 1.2). Climatic water deficit (CWD) varied substantially, from 2.3 to 252.4, among the eight sites. However, CWD did not significantly change the relationships among long-term average xylem growth, cone abundance, and total resin area among individuals. Likewise, carbon discrimination also did not affect the relationships among long-term average radial xylem growth, cone abundance, and total resin area among individuals. Carbon discrimination was positively associated with individual average total

resin area ($P=0.04$, Table 1.2 & Figure 1.3), indicating that trees experiencing greater drought stress (lower carbon discrimination) have higher total resin area. Of the covariates measured, we found that neighborhood density (BA) was negatively associated with xylem growth and total resin area (Tables 1.1 & 1.2), but this finding was inconsistent among the models ran for total resin area. Tree size (DBH) had no relationship with xylem growth or total resin area in any model tested (Tables 1.1 & 1.2).

1.3.2 Tradeoffs in Reproduction, Growth and Defense Among Years

We found that annual total resin area and annual radial growth were positively associated (Tables 1.3 & 1.4), such that in years of high annual radial growth there was also high total resin area (Figure 1.4). Annual resin duct production and xylem growth were both negatively associated with annual cone abundance (Figures 1.4 and 1.5). In years of high cone abundance, we found a lower production of resin ducts and lower growth rates, indicating a growth-reproduction and a defense-reproduction tradeoff. We found that CWD had a simple positive effect on growth and total resin area ($P=0.03$ and $P=0.02$, respectively; Table 1.3), such that sites with greater CWD (i.e. hotter and drier sites) tended to have higher annual growth and total resin duct area (Table 1.3). In our growth-cone model, there was also a significant negative interaction between site CWD and cone abundance. As CWD increased, we observed a more negative relationship between cone abundance and growth, indicating a greater tradeoff between these functions at sites with greater CWD. At the sites with the highest CWD, we observed a strong negative relationship between cone abundance and growth. Whereas, at sites with low CWD, we observed little or no tradeoff between cone abundance and growth (Figure 1.5). Carbon discrimination did not interact with any of the associations measured. Of the covariates measured, FDSI was positively associated with annual xylem growth and annual total resin area

in all models tested, indicating that trees had greater growth and resin duct production during cool and wet (high FDSI) years.

1.4 Discussion

Tradeoffs among vital functions have been widely documented in forests throughout the world (Redmond et al., 2019; Barringer et al., 2012; Vázquez-González, et al., 2020; Martín et al., 2015). However, very few studies have assessed tradeoffs between reproduction, growth, and defense simultaneously, either over long periods of time or large geographic areas. Additionally, the impacts of drought and individual drought resistance on these tradeoffs are poorly understood. In our study, we found that years of high annual cone abundance appeared to curtail both growth and total resin area, despite the potential risk of biotic invasion. A decrease in both total resin area and xylem growth may be necessary in order to develop a large enough seed crops to increase pollination efficiency or satiate predators (Pearse et al., 2016). The tradeoff between reproduction and growth and defense is consistent with the resource-switching hypothesis of masting that suggests that, in high seed production years, resources are allocated toward reproduction and shunted away from other functions (Pearse et al., 2016). Additionally, trees located in hotter and drier climates had greater year-to-year tradeoffs in allocation between reproduction and growth, suggesting that, with warming temperatures, trees will be faced with stronger interannual tradeoffs of fundamental functions.

Contrary to the defense-reproduction and growth-reproduction relationships, we found a positive association among growth and resin ducts within each individual (year-to-year variation) as well as among individuals. Our results add to the growing body of research that have examined these relationships and have found that more growth leads to an increase in resin duct production (i.e. total resin duct area) and mean resin duct size (Kane & Kolb, 2010; Hood &

Sala, 2015; Ferrenberg et al., 2014; Redmond et al., 2019). Total resin area has been shown to be the best correlate of resin flow, the primary defense against stem-boring insects (Hood & Sala, 2015). The positive association between total resin duct area and xylem growth in our study and others is logical in that larger annual xylem growth rings allows for greater area of resin ducts. Thus, the positive relationship between these two functions is likely due to developmental constraint. These results indicate that the factors that promote growth (available nutrients or water availability) would also lead to more resin duct production.

A tradeoff between reproduction and defense could have implications for the management of insect outbreaks in ponderosa pine forests, because it suggests that trees may be more susceptible to pest outbreaks during years of high cone production due to low resin duct production. Resin duct production is the first line of defense for pine species that are subjected to bouts of bark beetle outbreaks and individuals with higher total resin area are more likely to survive bark beetle outbreaks (Kane & Kolb, 2010). However, this apparently risky tradeoff may not be as much of a risk for individuals who generally produce more resins annually. A prior study found that the total percent resin duct area over a 10- and 20-year period was an important difference between live and dead ponderosa pine post bark beetle outbreaks, where ponderosa with more resin duct area were more likely to survive (Kane & Kolb, 2010). This means that some individuals may still have some form of protection from years prior to a mast year, suggesting that reduced resin duct allocation during mast years may not strongly limit immediate defensive capabilities. Though, individuals who produce large and frequent cone crops as well as individuals who produce less resin ducts overall are still at an increased risk from stem-boring herbivores during mast years.

The severity of growth-reproduction year-to-year tradeoffs was found to be impacted by broad climatic differences in water availability at each site and not by intra-site variability in water use efficiency (WUE). Hotter and drier site conditions (high CWD) led to strong annual tradeoffs between xylem growth and reproduction, while cooler and wetter site conditions had less severe annual tradeoffs between the two functions. The impact of site CWD on the growth-reproduction relationship is consistent with the environmental stress hypothesis of masting, which predicts that greater interannual variation in tree functions (reproduction, growth, defense) is associated with more marginal environments, like those that are prone to drought (Pearse et al., 2017). These results are similar to a rainfall exclusion experiment that found that individuals exposed to drought maintained tree fecundity by shifting resources from growth to reproductive efforts (Bogdziewicz et al., 2020). Likewise, ponderosa pine individuals who were located in hotter and drier sites showed similar allocation patterns in order to allocate resources to the high demand of large seed crops during cone maturation.

In our study, individual carbon discrimination did not interact with these associations, suggesting that by intra-site variability in water use efficiency is not playing a role in allocation patterns in ponderosa pine. Several studies have associated a strong positive correlation between carbon discrimination and annual xylem growth (Livingston & Spittlehouse, 1993; McDowell et al., 2003), as well as higher carbon discrimination resulting in higher reproductive yields (Hall et al., 1993). However, these studies seldom pooled carbon isotopes and utilized annual measurements of radial growth or leaf matter. Nevertheless, we did find a significant negative relationship between average total resin duct area and carbon discrimination. These results suggest that genetic variation in drought resistance can impact individual average allocation to total resin area, in that individuals who have higher water use efficiency (lower carbon

discrimination) produce higher total resin area on average. This finding indicates that individuals who may be experiencing higher drought stress allocate more resources on average, to total resin area. To the best of our knowledge, this is the first study that has tested or found such a relationship utilizing carbon isotopes in tree rings.

Our results indicate that trees can resist changes in tree fecundity during drought events by curtailing resources from other functions. Individuals located in drought-prone sites maintained reproductive efforts by curtailing growth, implying that drought may not have immediate effects on fecundity. The ability to maintain fecundity during drought conditions has also been seen in other studies (Bogdziewicz et al., 2020; Barringer et al., 2012), where individuals that experienced higher local drought stress had more severe tradeoffs among reproduction and other core functions. However, our study was done on relatively short-time scale compared to the long-life span of ponderosa pine (commonly found between 300-500 years old [Huckaby et al., 2003]). Continued increases in acclimation and resistance to drought could have adverse effects on long term forest reproductive efforts. There has already been evidence of decreased reproduction in pine species (Redmond et al., 2012), and a reduction in post-fire pine regeneration (Rodman et al., 2020); which has been attributed to warming across the western USA. As aridity increases across the west, stronger annual tradeoffs during mast events may indirectly affect future fecundity by modifying resource investment in reproduction and further decreasing growth and defensive efforts, ultimately increasing rates of tree mortality.

This study provides support for year-to-year tradeoffs between defense and growth and reproduction within individuals but did not detect the same tradeoffs across individuals. The lack of these tradeoffs may be due to the limitations of an observational study design. As a result, we were unable to control for resource or water availability across trees. Another key limitation is

the cone abscission scar method used to reconstruct historic cone production. Although this method is highly effective at reconstructing cone production (Redmond et al., 2016; Rodman et al., 2020; Wion et al., 2021), it is unable to distinguish between aborted or fully mature cones, and we are unable to quantify the variation of seeds produced in each fully mature cone. Another limitation of this methodology is that we were unable to sample heavily damaged branches or fast-growing shoots that had no visible cone markers, further limiting the branches that were able to be sampled. As a result, there could be noise in our model that reduced our ability to detect tradeoffs among individuals. However, our results are consistent with the resource switching and environmental stress hypothesis in masting species, as well as consistent with several studies that have assessed tradeoffs in pines.

1.5 Conclusion

Long term drought can negatively impact forest succession by constraining resource availability and modifying resource investment patterns. Individuals located in drought-prone areas exhibited strong tradeoffs between reproduction and growth. Furthermore, years of high cone abundance had lower total resin area, potentially leaving individuals vulnerable to biotic attacks. As climate warms and drought conditions become more common and severe in the coming century, we may expect greater tradeoffs between the core functions of growth and reproduction. This could lead to further periodic decreases in growth and defensive efforts, ultimately increasing mortality. Our results shed light on the impacts that drought can have on individual fitness in a widespread species located in drought-prone areas.

1.6 Tables

Table 1.1. Results of models used to assess tradeoffs in reproduction, growth, and defense among individuals with CWD as an interaction. Numbers show the standardized coefficients +/- 1 SE and coefficients in bold were statistically significant ($P < 0.05$). Marginal R^2 provides the variance explained by the fixed effects and conditional R^2 provides the variance explained by the entire model.

Defense ~ Growth Models (Response: Mean Total Resin Duct Area)				
	β	SE	T value	P value
Growth	0.11	0.01	10.82	<0.001
CWD	0.02	0.01	1.34	0.18
BA	-0.00	0.01	-0.01	0.99
DBH	0.01	0.01	1.50	0.14
Growth*CWD	0.02	0.01	1.12	0.27
Marginal R^2 /Conditional $R^2 = 0.77/0.78$, DF= 72				
Defense ~ Cone Models (Response: Mean Total Resin Duct Area, log transformed)				
	β	SE	T value	P value
Cones	-0.03	0.08	-0.38	0.71
CWD	0.17	0.13	1.27	0.21
DBH	-0.03	0.08	-0.43	0.67
BA	-0.14	0.07	-1.94	0.06
Cones*CWD	-0.01	0.04	-0.29	0.77
Marginal R^2 /Conditional $R^2 = 0.17/0.44$, DF= 72				
Growth~Cones Model (Response: Mean Xylem Growth, log transformed)				
	β	SE	T value	P value
Cones	0.00	0.09	0.01	0.99
CWD	0.13	0.18	0.75	0.46
DBH	-0.12	0.09	-1.34	0.18
BA	-0.20	0.08	-2.47	0.02
Cones*CWD	-0.03	0.05	-0.85	0.52
Marginal R^2 /Conditional $R^2 = 0.14/0.54$, DF= 72				

Table 1.2. Results of models used to assess tradeoffs in reproduction, growth, and defense among individuals with carbon discrimination ($\Delta^{13}\text{C}$) as an interaction. Numbers show the standardized coefficients +/- 1 SE and coefficients in bold were statistically significant ($P < 0.05$). Marginal R^2 provides the variance explained by the fixed effects and conditional R^2 provides the variance explained by the entire model.

Defense ~ Growth Models (Response: Mean Total Resin Duct Area)				
	β	SE	T value	P value
Growth	0.11	0.01	10.82	<0.001
$\Delta^{13}\text{C}$	-0.00	0.01	-0.12	0.90
BA	0.00	0.01	0.04	0.97
DBH	0.01	0.01	1.26	0.21
Growth* $\Delta^{13}\text{C}$	0.01	0.01	1.45	0.15
Marginal R^2 /Conditional $R^2 = 0.69/0.77$, DF= 72				
Defense ~ Cone Models (Response: Mean Total Resin Duct Area, log transformed)				
	β	SE	T value	P value
Cones	-0.03	0.07	-0.48	0.63
$\Delta^{13}\text{C}$	-0.11	0.05	-2.08	0.04
DBH	-0.04	0.08	-0.51	0.61
BA	-0.16	0.07	-2.26	0.03
Cones* $\Delta^{13}\text{C}$	0.00	0.04	0.08	0.94
Marginal R^2 /Conditional $R^2 = 0.10/0.43$, DF= 72				
Growth~Cones Model (Response: Mean Xylem Growth, log transformed)				
	β	SE	T value	P value
Cones	-0.02	0.08	-0.30	0.76
$\Delta^{13}\text{C}$	-0.08	0.06	-1.50	0.14
DBH	-0.11	0.08	-1.24	0.22
BA	-0.21	0.08	-2.65	0.01
Cones* $\Delta^{13}\text{C}$	0.01	0.05	0.27	0.79
Marginal R^2 /Conditional $R^2 = 0.10/0.50$, DF= 72				

Table 1.3. Results of models used to assess tradeoffs in reproduction, growth, and defense year-to-year variation within individuals with CWD as an interaction. Numbers show the standardized coefficients +/- 1 SE and coefficients in bold were statistically significant (P < 0.05). Marginal R² provides the variance explained by the fixed effects and conditional R² provides the variance explained by the entire model.

Defense ~ Growth Models (Response: Annual Total Resin Duct Area, log transformed +1)				
	β	SE	T value	P value
Growth	0.10	0.00	27.90	<0.001
CWD	0.03	0.01	2.25	0.02
FDSI	0.02	0.00	4.93	<0.001
Growth*CWD	-0.00	0.00	-1.08	0.28
Marginal R ² /Conditional R ² = 0.54/0.66, DF= 1314				
Defense ~ Cone Models (Response: Annual Total Resin Duct Area, log transformed +1)				
	β	SE	T value	P value
Cones	-0.02	0.00	-4.94	<0.001
CWD	0.07	0.03	2.4	0.02
FDSI	0.05	0.00	10.03	<0.001
Cones*CWD	-0.00	0.00	-1.40	0.16
Marginal R ² /Conditional R ² = 0.12/0.56, DF= 1314				
Growth~Cones Model (Response: Mean Xylem Growth, log transformed)				
	β	SE	T value	P value
Cones	-0.03	0.01	-3.44	0.001
CWD	0.18	0.08	2.16	0.03
FDSI	0.13	0.01	11.72	<0.001
Cones*CWD	-0.02	0.01	-3.23	0.001
Marginal R ² /Conditional R ² = 0.15/0.65, DF= 1314				

Table 1.4. Results of models used to assess tradeoffs in reproduction, growth, and defense year-to-year variation within individuals with carbon discrimination ($\Delta^{13}\text{C}$) as an interaction. Numbers show the standardized coefficients +/- 1 SE and coefficients in bold were statistically significant ($P < 0.05$). Marginal R^2 provides the variance explained by the fixed effects and conditional R^2 provides the variance explained by the entire model.

Defense ~ Growth Models (Response: Annual Total Resin Duct Area, log transformed +1)				
	β	SE	T value	P value
Growth	0.10	0.00	28.30	<0.001
$\Delta^{13}\text{C}$	-0.00	0.01	-0.97	0.33
FDSI	0.02	0.00	4.75	<0.001
Growth* $\Delta^{13}\text{C}$	-0.00	0.00	-0.35	0.73
Marginal R^2 /Conditional $R^2 = 0.50/0.65$, DF= 1314				
Defense ~ Cone Models (Response: Annual Total Resin Duct Area, log transformed +1)				
	β	SE	T value	P value
Cones	-0.02	0.00	-5.06	<0.001
$\Delta^{13}\text{C}$	-0.01	0.01	-1.43	0.15
FDSI	0.05	0.00	9.88	<0.001
Cones* $\Delta^{13}\text{C}$	-0.00	0.00	-0.37	0.71
Marginal R^2 /Conditional $R^2 = 0.09/0.62$, DF= 1314				
Growth~Cones Model (Response: Mean Xylem Growth, log transformed)				
	β	SE	T value	P value
Cones	-0.03	0.01	-3.67	<0.001
$\Delta^{13}\text{C}$	-0.03	0.03	-1.22	0.22
FDSI	0.12	0.01	11.51	<0.001
Cones* $\Delta^{13}\text{C}$	0.00	0.01	0.06	0.95
Marginal R^2 /Conditional $R^2 = 0.09/0.72$, DF= 1314				

1.7 Figure

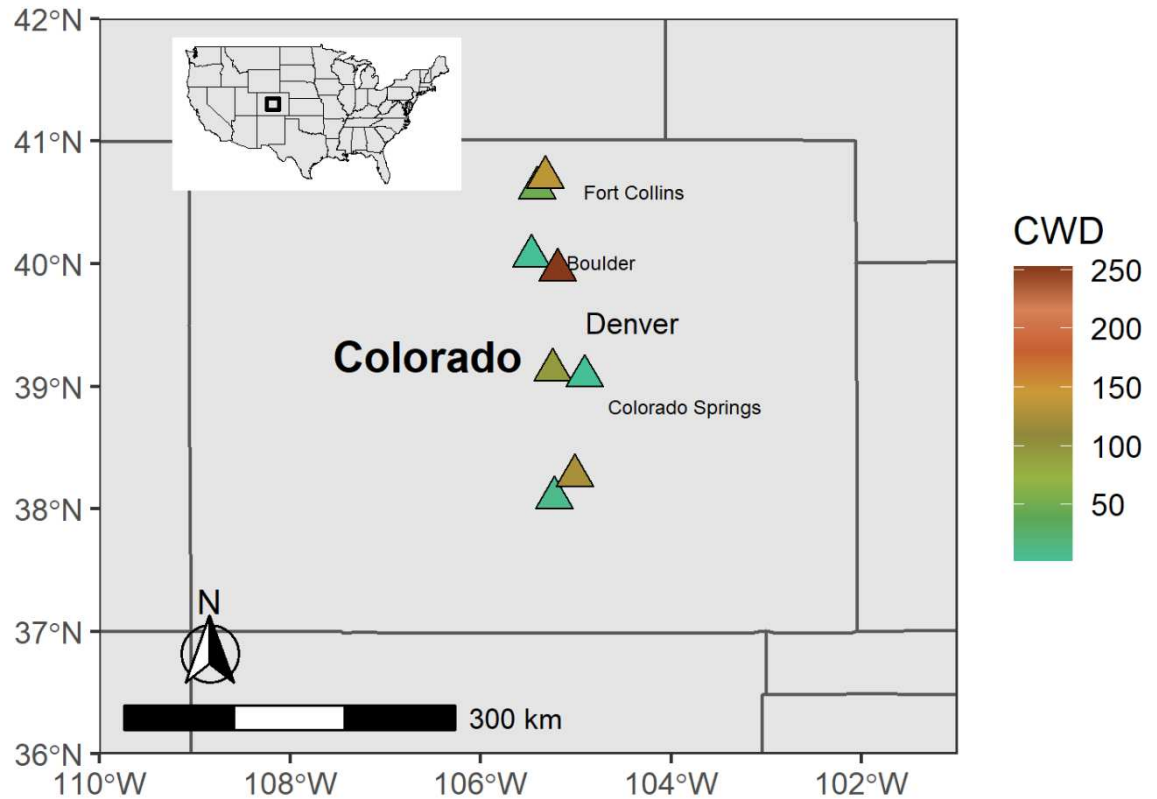


Figure 1.1. Locations of the eight study sites sampled across the Colorado Front Range to assess impacts the drought on resource allocation to growth, defense, and reproduction. Sites spanned a climatic water deficit gradient (CWD [2.28-252.43]) and elevation gradient (1747-2843 meters) along the Front Range. Site acronyms are listed adjacent to plot marker.

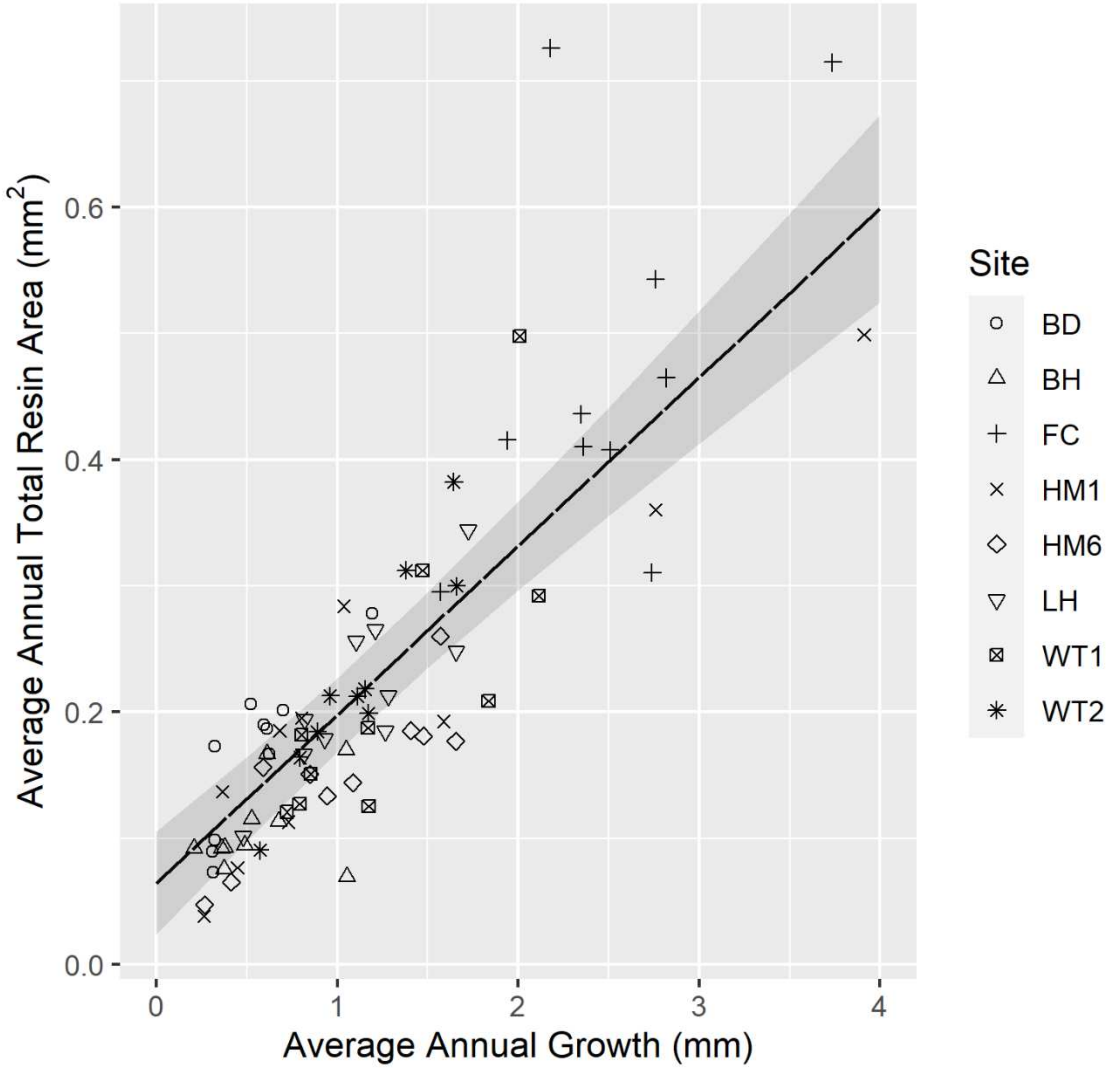


Figure 1.2. The linear relationship between the individual 21-year average growth and total resin area among individuals, when accounting for stand density and individual diameter at breast height ($P < 0.001$). Each data shape represents each individual nested within each site. Shaded areas represent the 95% confidence interval.

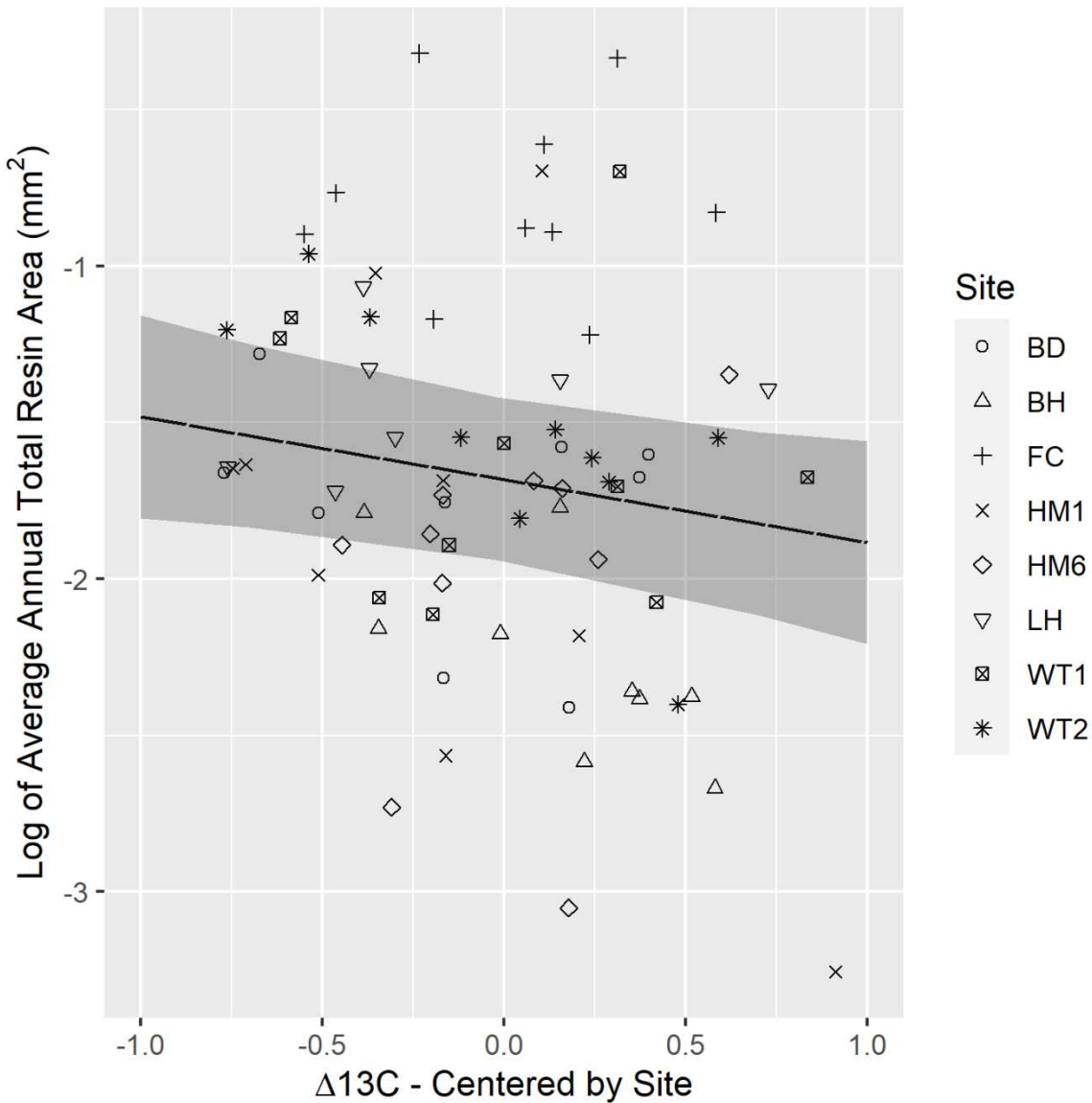


Figure 1.3. The linear relationship between the individual 21-year average total resin duct area and average individual carbon discrimination among individuals, when accounting for stand density and individual diameter at breast height ($P=0.04$). Individuals with higher carbon discrimination had a lower average total resin duct area over the past twenty years. Individuals who have lower drought stress have higher carbon discrimination and show less prioritization of resin duct production than individuals who are under higher drought stress (lower carbon discrimination). Shaded areas represent the 95% confidence interval. Each data shape represents each individual nested within each site. Shaded areas represent the 95% confidence interval.

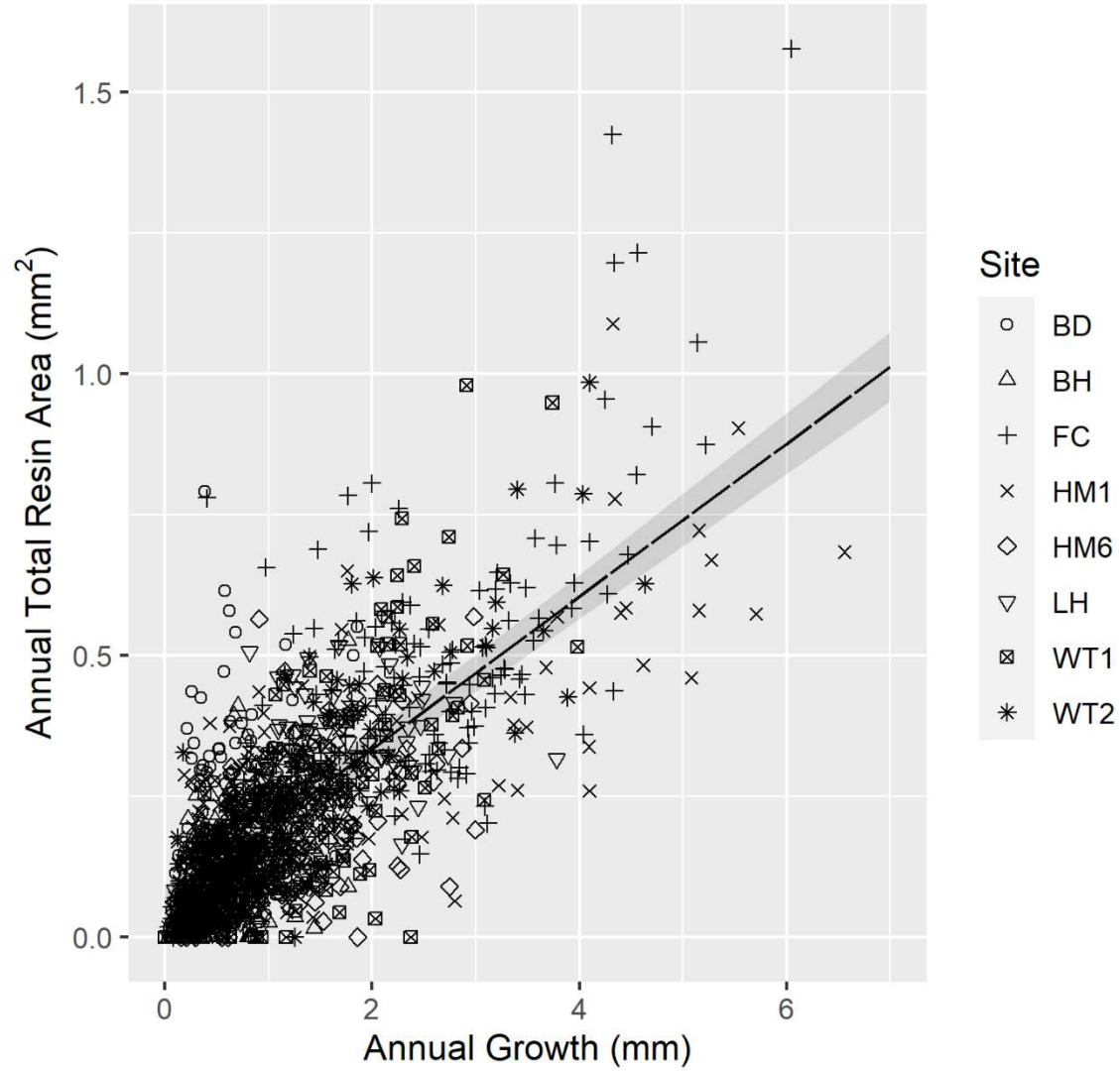


Figure 1.4. The relationship between annual total resin area and annual xylem growth among individuals when accounting for annual FDSI. Each shape represents one year of data nested within each individual and nested within each site, and the shaded area represents 95% confidence intervals.

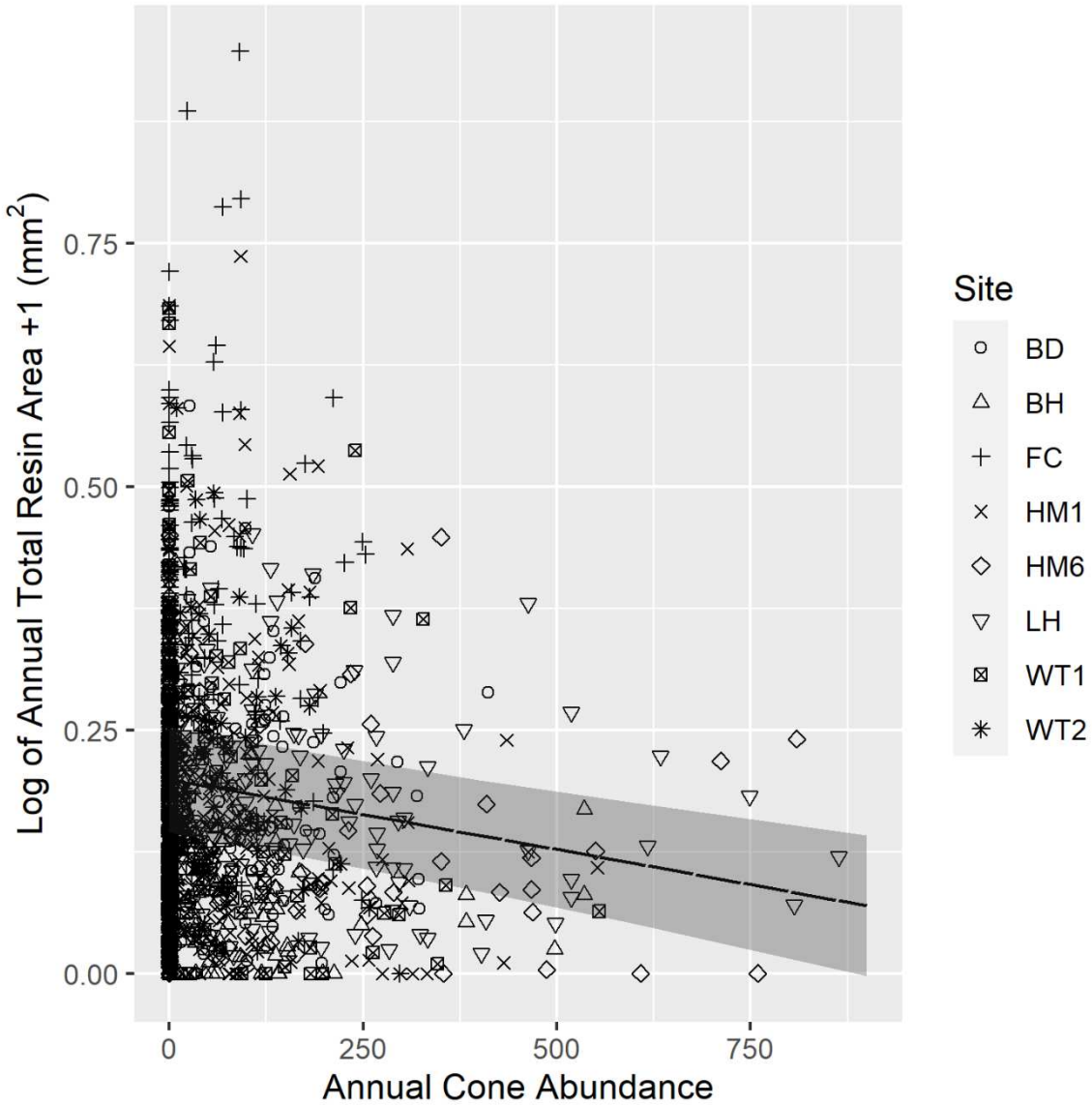


Figure 1.5. The relationship between annual cone abundance and annual total resin area within individuals when accounting for annual FDSI. Each shape represents one year of data nested within each individual and nested within each site, and the shaded area represents 95% confidence intervals.

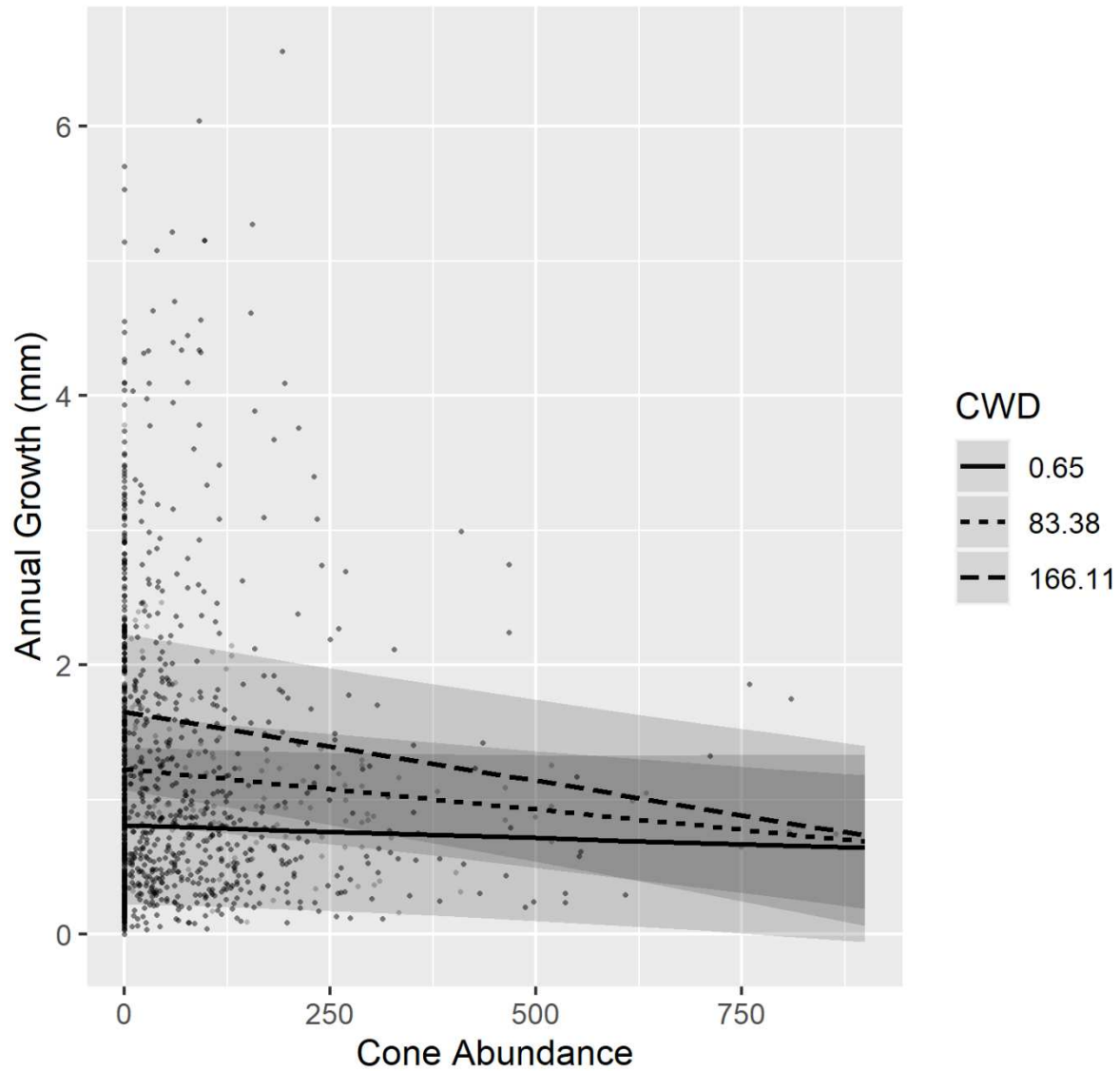


Figure 1.6. The relationship between annual xylem growth and annual total resin area when accounting for FDSI. The impact of site CWD is plotted with the three values representing ± 1 standard deviation away from the mean. Each dot represents annual measurements taken of each individual across the eight sites sampled.

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