Physiological Constraints of Assisted Migration of Coast Redwoods (*Sequoia Sempervirens)* to Washington's Western Cascade Region

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Abstract

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There is broad interest in moving the iconic *Sequoia sempervirens* (D. Don*)* Endl. to western Washington to assist in the climate pressured species' habitat shift northward as well as provide cultural, ecological, carbon, and timber value to PNW forests. This research investigates the ecophysiological constraints of young redwoods in comparison with native species, *Pseudotsuga menziesii* (Mirb.) Franco and *Thuja plicata* (Donn.) through testing of *S. sempervirens* genetic entries under controlled greenhouse drought conditions and across a soil moisture gradient in a field study outside of its native range. In the drought trial, measurement of photosynthetic efficiency (F_v/F_m) as a stress metric, water potential, growth investments and survival show that *S. sempervirens* had similar or better drought response than native *P. menziesii* and consistently better than *T. plicata*. *S. sempervirens* clones showed similar levels of drought response, surviving almost 2 months of drought conditions, though a select few clones had early stress and mortality in the drought. In field conditions, *S. sempervirens* had a lower mortality rate

(23% post establishment) than the native, but nursery stock affected, *P. menziesii* (27.97% post establishment). A majority (10/16) of *S. sempervirens* clone lines also showed similar levels of vigor as Douglas-fir, while the remaining 6/16 demonstrated significantly lower vigor 10 months after planting. *S. sempervirens* clone performance in the greenhouse and field trial differ enough to suggest that greenhouse drought tolerance is not a predictor of successful *S. sempervirens* clone selection in Washington field conditions (p = 0.342). While there is much left to understand about *S. sempervirens* ecophysiological limitations, assisted migration of *S. sempervirens* to western cascade region of Washington could be feasible given early coast redwood performance.

Table of Contents

Background

Douglas-fir-dominated Pacific Northwest (PNW) forests are facing rapidly changing conditions due to climate change; regional models predict temperatures to increase 1.5-3.2 °C by 2040 (Kliejunas, 2011). There has already been an increase in large scale fires, drought conditions, and warmer, wetter winters, which have contributed to increased drought stress, beetle outbreaks and fungal diseases (Agne et al., 2018). While climate change creates an unpredictable and varying future, some models predict 10-40% rotation age volume loss for some species and locations (Pedlar et al., 2012). Climate adaptation strategies, such as increased thinning, variable density harvesting, and moving away from monocultures, that minimize ecological and economic impacts of climate change to PNW forests are needed to maintain forest productivity (Puettman et al., 2011).

Assisted population migration and assisted species migration are tools to combat climate change. Assisted population migration keeps within the species' natural range, moving genetic stock, while species migration moves beyond a species' natural range (Figure 1). While proposed assisted migration has been controversial due to historically grounded concerns about invasive species and native species advocacy, it has been widely used in tree conservation and forestry given trees are long lived, sessile and cornerstone species (Hewitt et al. 2011). Assisted migration may ensure that forests that are planted under current conditions will be adapted to the temperatures predicted 40-100 years from now (Sáenz-Romero et al. 2014). This research addresses the potential of coast redwood to be moved to Washington for potential carbon, ecological, and wood production benefits, but does not explicitly address the ethical, social, or legal constraints of moving redwoods outside their native range, nor potential impacts to native forest ecosystems.

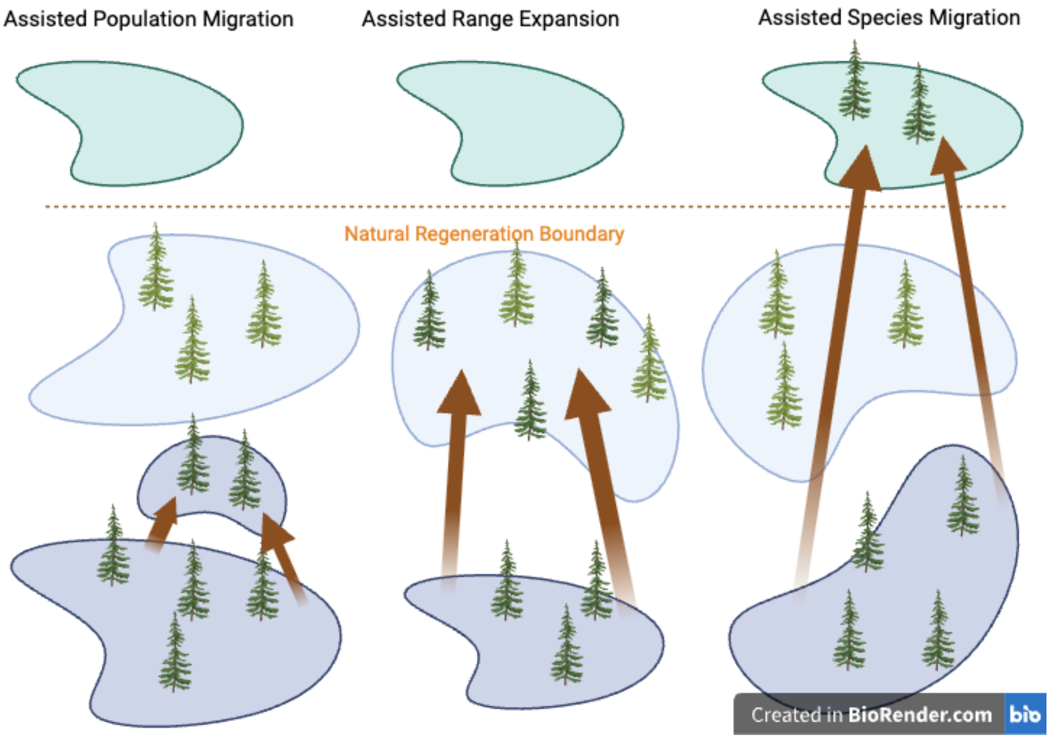


Figure 1 Illustration based on USDA Northwest Climate Hub's description of assisted migration, population, range and species migration (2021).

In the PNW, foresters have implemented assisted range expansion and population migration to promote specific species and create a more drought- and heat-tolerant forest (Figure 1). Projects like the Assisted Migration Adaptation Trials based in British Columbia, the U.S. Forest Service Experimental network of Assisted Migration and Establishment Silviculture (ENAMES) project, and the Open Redcedar Adaptation Network (ORAN) community science project have all begun the work of shifting seed stock north along the western coast (Sáenz-Romero et al., 2014, Woods, 2011, US Forest Service, 2024, Open Redcedar Adaptation Network). Forestry has begun investigating assisted range and species migration as a climate adaptation to preserve forest health, function, and diversity as well as preserving specific species in suitable future climates.

Sequoia sempervirens (coast redwoods) are an iconic and culturally important species, occupying a limited range close to the Pacific Ocean from central California to southern Oregon (Figure 2). These trees were once widely spread but are now limited to climatic refugia and are more recently threatened by logging and climate change (Jenkins & Jenkins, 2017). As with many species, climate change is predicted to cause drastic changes to their habitat. Redwood's native range is becoming hotter and drier, and there has been a 33% decrease in the fog frequency that is key to redwood ecology and drought tolerance in their native range (Johnstone & Dawson, 2009). While long-lived trees like redwoods have survived a wide variety of conditions over the course of their lives, they are unlikely to keep up with the rate of anthropogenic climate change (Fernández et al., 2015, Klápště et al., 2020). However, there is hope that with the loss of habitat to the south, the effects of which are already visible, there will be a compensatory gain of suitable habitat to the northern edge of their range, well into Oregon (Fernández et al., 2015). As a species with limited range, low seed dispersal (primarily basal resprout propagation), small population, and enormous cultural significance, it is a prime candidate for assisted species migration (Aitken et al., 2007, Lunt et al. 2013, Hewit et al., 2011).

Figure 2 Current range of coast redwoods spans coast range of California and Southern Oregon in green (Little, 1971). The extent of assisted species migration (orange arrow) attempted in this study to the study stie (yellow dot), Pack Forest, in the western cascade region of Washington state (~450km further than the northernmost extent of the coast redwood native range).

Assisted species migration of coast redwoods could be crucial for the species' survival and could provide ecological benefits to the receiving forests by increasing canopy height and structural complexity (Figure 1, Sillett et al., 2022). Coast redwoods are impervious to most pests, fungus, and fire due to thick bark (~1 ft) and decay resistant heartwood (Roy, 1996, Van

Pelt et al., 2016). Redwoods are also a fast-growing, large biomass species that close canopies in only a couple of decades, making them valuable for restoration sites and as habitat for species reliant on mature and old growth forests (Kerhoulas et al. 2020, Douglass, 1966). Their ability to resprout along the trunk and base makes redwoods an incredibly resilient species, increasing recovery in post fire, wind damage or post timber harvest (Roy, 1996, O'Hara et al., 2017). Redwoods are highly prized for their richly colored and high-quality wood, and can also store vast amounts of carbon, valuable in both timber and carbon markets (Van Pelt et al., 2016). One weakness is damage to bark by deer, elk and bears sometimes leading to extensive peeling and mortality.

Redwoods have been described as charismatic megaflora which increases the support and popularity of redwood stands in Washington (Jenkins et al., 2017). In fact, redwoods have been planted all over the world as part of botanical collections due to their aesthetic and cultural value. Redwoods have also already been planted as part of forestry initiatives in Germany, New Zealand, Portugal, Spain, and United Kingdom; demonstrating redwood's adaptability, as well as the enormous demand for this popular species (Kruser et al., 1995, Watt & Kimberly, 2023, Klápště et al., 2020). Redwood assisted migration has already begun to take place, with significant efforts to increase planting of redwoods throughout Oregon, and social support for species conservation, ecological and timber objectives (Jenkins & Jenkins, 2017). There have also been steps taken within the state of Washington, with groups like Propagation Nation pushing for planting coast redwoods across the state (Propagation Nation, 2024). Local landowners have already begun to include redwoods as part of their climate adaptation strategy for carbon sequestration, conservation, resilience, and restoration (De la Torre et al., 2021). Redwoods could increase species diversity in the Douglas-fir, western hemlock and Sitka spruce forests of Washington to create a more fire-, pest-, and disease-resistant forest and provide economic security to PNW forestry in the face of climate change.

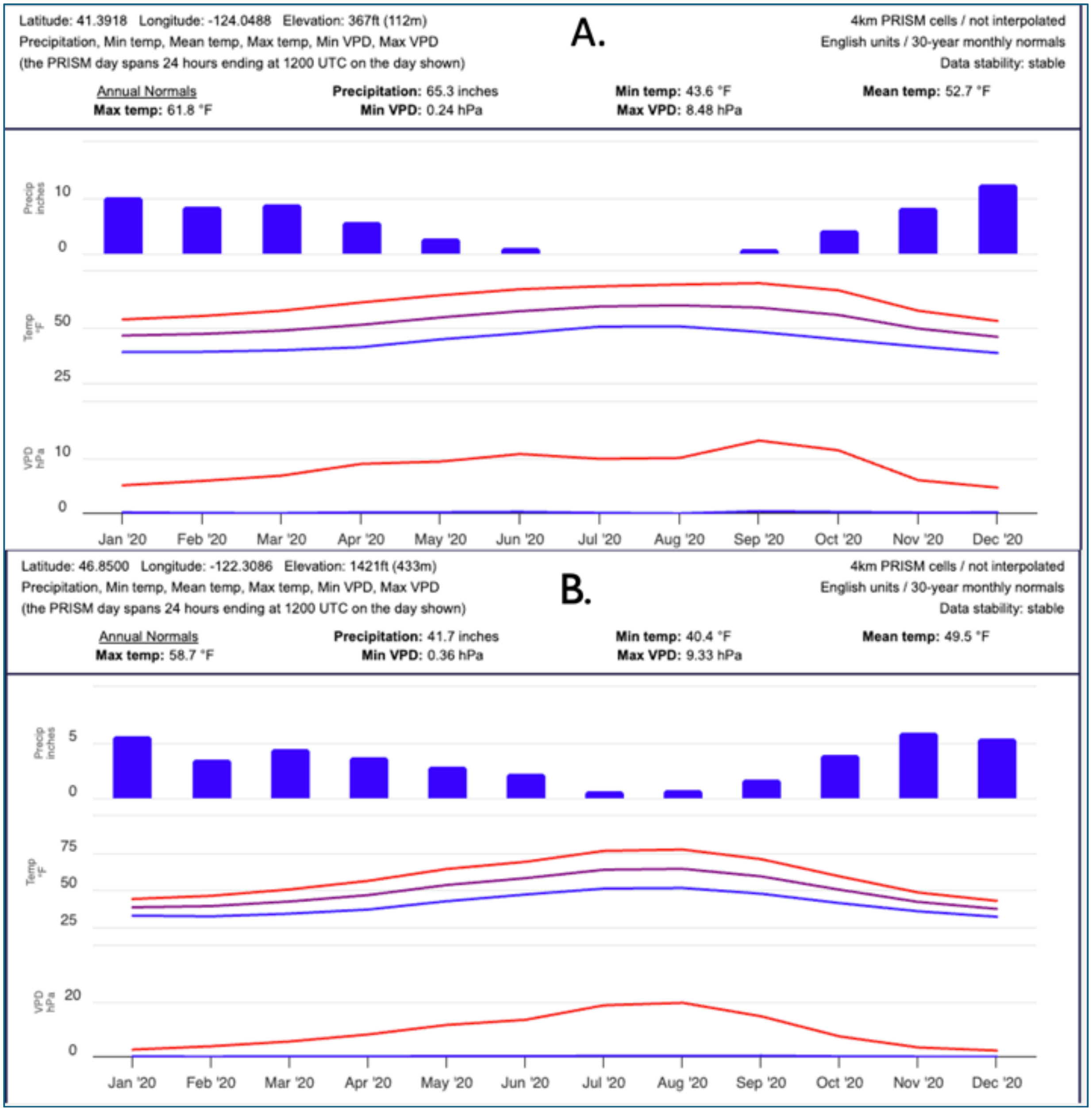


Figure 3 PRISM data indicating average precipitation (blue bars) per month, average monthly maximum (red line), average (purple line) and minimum (blue line) precipitation, VPD monthly maximum (red line) and minimum (blue line). Graphics pulled from PRISM profile of the Redwood National and State Park, stable temperatures and over 10 inches of monthly precipitation in winter months, consistently low vapor pressure deficit. B. PRISM profile of Pack Forest, the study site in western cascade region

However, enthusiasm for widespread movement of coast redwoods north of their existing range may exceed current knowledge of the species ecological limits, and media reports of efforts to move redwoods have both raised awareness of assisted migration efforts and brought criticism of those efforts from environmentalists (Jenkins & Jenkins, 2017, Velasques-Manoff, 2023). Additionally, redwood assisted migration into Washington is far ahead of the predicted habitat shift northward and is limited by physiological factors such as absence of fog moisture, lower temperatures and drought conditions (Jenkins et al, 2017, Fernández et al., 2015). Assisted migration for climate change requires species to be able to tolerate current environmental conditions and biological constraints, to thrive and propagate in the climate of the future (Saénz et al., 2016). This is especially crucial to long-lived redwoods, where delicate seedlings must survive current climate conditions well outside their native range in the hopes that mature forests will be established in a future climate. Moving redwoods north in latitude will expose them to novel conditions beyond their native foggy coastal California range including high-temperature summer droughts, with lower air moisture and precipitation (Litvak et al., 2011, Figures 2 & 3). However, research has shown that redwoods demonstrate a wide range of genotypic and phenotypic variety in their adaptability to new environments (Kruser 1995, De la Torre et al. 2022, Litvak et al., 2011, Klápště et al., 2020). Understanding the ecophysiological constraints of redwoods will help to determine feasibility of redwood assisted migration in large-scale, plantations. In this study we investigate the physiological limitations of coast redwoods in Washington state in response to drought and field conditions and evaluate redwood production clones to search for suitable stock and environment. We have partnered with the Redwood Tree Improvement Cooperative for redwood stock testing and will be sharing the results of this research with them as a collaborative effort to promote and improve redwood clonal lines for the PNW. Clonal stock was obtained from a broad geographic range extending from southern coastal Oregon to south of the San Francisco Bay area.

Chapter 1: Drought Stress Response of Coast Redwoods in Greenhouse

1.1 Introduction

Redwoods have long been known to depend on the heavy fog of their native coastal habitat, contributing up to 30% of its annual water input (Burgess & Dawson, 2004). Since high vapor pressure deficit is a rare and infrequent issue in their habitat, redwoods exhibit poor stomatal regulation (Johnstone & Dawson, 2010). It has been speculated that the fog-enabled-open-stomata is the key to redwoods impressive growth rate, maximizing photosynthesis and carbon accumulation (Johnstone & Dawson, 2010). Thus, climate change predictions about limited fog conditions in the future are assumed to limit redwood survival and their ability to grow (Fernández et al. 2015, Ambrose et al., 2015).

However, recent research has shown coast redwood's ability to adapt to more arid conditions and conserve water, despite a high rate of water use (Latvik et al, 2011). Redwoods exposed to high vapor pressure deficit while still receiving water through soil irrigation exhibited stomatal regulation and maintained elevated levels of leaf water potential (Ψ) and avoided excessive xylem cavitation (Latvik et al, 2011). Kerhoulas and Polda (2020), even demonstrated redwood seedlings outperforming native Douglas-fir in xeric inland California drought conditions, maintaining higher Ψ, growth rate, and lower mortality. However, questions remain about their ability to perform outside of their range in northern, fogless, and drought prone locations, and with differences in the timing of and severity of seasonal conditions of Washington. Data in Figure 3 indicate that redwoods will receive less precipitation (~24 inches less annually) in western cascades of Washington than in their foggy coastal native range (De La Torre et al., 2022, Kerhoulas and Polda, 2020, PRISM, 2024).

We measured plant stress via mortality, growth, fluorescence (Fv/Fm) as a metric of the stress of photosystem II, and branch water potential (Ψ_{branch}) of several redwood genetic entries and local species: *Pseudotsuga menziesii* (Douglas-fir), and *Thuja plicata* (western redcedar) (Woo et. al, 2008). We used this data to resolve the following questions and our corresponding hypothesis:

1) What are the differences between redwood and native species response to drought stress? We predict that species native to the western cascades are accustomed to local drier conditions and are likely to have higher drought tolerance than introduced coast redwoods (Cruickshank 2025).

2) What are the differences between redwood genetic entries' responses to drought stress? We predict differences in coast redwood genetic entries will result in significantly different drought stress responses (Klápště et al., 2020). Previous studies have found that coast redwoods demonstrate gradients of adaptation corresponding to their seed source such that coast redwoods from both hotter southern and drier inland origin will survive longer under drought conditions (Ambrose et al., 2015, Litvak et al., 2011).

3) What is the relationship between the explanatory variables of reduced soil volumetric water content and competition for limited water among genetic entries with the plant responses: Fv/Fm (i.e., dark adapted fluorescence--a measure the maximum photochemical efficiency of photosystem II), Ψ_{branch}, biomass investments in roots and shoots, mortality, and growth rate in drought conditions? We predict that volumetric water content is positively correlated with Fv/Fm, and $\Psi_{\text{branch.}}$ We predict that redwoods will have the largest difference between predawn

and midday $\Psi_{branch,}$ due to their poor stomatal regulation (Charrier et al., 2020, Johnstone & Dawson, 2010). Plants with the highest underground biomass investment will have the longest survival time, and plants will not be able to grow as much during drought conditions compared to their pre-drought growth rate. Finally, Zenes et al. (2020), demonstrated that seedlings change stomatal regulation strategy when in competition for water resources. Therefore, we predict that plants exposed to competition conditions when water is limited take a conservative water use approach and show signs of systemic stress later than plants grown solo in pots.

This study provides a deeper understanding of coast redwood drought stress response outside of its moist native range to assist in future decisions about the suitability of coast redwood production clone lines and site selection.

1.2 Methods

1.2.1 Experimental Design

A greenhouse experiment was conducted on *Sequoia sempervirens* (coast redwood), *Pseudotsuga menziesii* (Douglas-fir), and *Thuja plicata* (western redcedar) seedlings to explore differences in drought response. Coast redwood used in this trial: 18 clone lines of plug +1, 1 clone line plug +1.5 used only in the interspecies trial, and 1 true seedling plug +1.5. Clonal lines of coast redwood were grown at Sequoia Orchids and Green Diamond nurseries in California. The Douglas-fir and Western redcedar used in this experiment are plug +1 seedlings, Douglas-fir seedlings were bare-root, both seedlings grown at Silva Seed Nursery, Roy, WA. Plants were stored at 2 °C prior to starting the experiment, root length and height were measured and then immediately planted on March 30, 2024, in 1-gallon and 2-gallon pots depending on treatment. Pots contained 3-way mix of topsoil, sandy loam, and compost (Puyallup Bark Supply) and fertilized (Nutricote 13-13-13 plus micronutrient Controlled Release Fertilizer) April 11, 2024, with 8.5g of fertilizer per gallon (8.5g and 17g respective to pot size) to minimize nutritional limitation, then allowed to acclimate until July. Pots were planted with seedlings according to both trial and treatment which are described as an interspecies trial comparing coast redwood, Douglas-fir and western redcedar and a redwood-specific trial comparing coast redwood response among genetic entries of known stock—most clones selected for previously fast and straight growth forms.

Table 1 Treatment groups for Interspecies Trial, using coast redwood (CR-116 clone line plug + 1.5) in a total of 54 pots. Replicates are limited for Douglas-fir due to poor nursery stock. Even so, some of the planted Douglas-fir had early non drought related mortality. Surviving Douglas-fir entered drought conditions with existing levels of stress.

Treatment	Pot Size (gallon)	Plant	Number of replicates
Solo	1	Coast redwood	6
Solo	1	Douglas-fir	6
Solo	1	Western redcedar	3
Duplicate	2	Coast redwood Coast redwood	6
Duplicate	2	Douglas-fir Douglas-fir	3
Duplicate	2	Western redcedar Western redcedar	6
WRC_DF	2	Western redcedar Douglas-fir	3
CR_DF	2	Coast redwood Douglas-fir	3
CR_WRC	2	Coast redwood Western redcedar	6

The interspecies trial allows for a direct comparison of coast redwood drought tolerance with two native conifer species. The duplicate-planted pots test whether species have a different drought response when in competitive soil moisture environments. Mixed species pots allow for comparison of drought response in a competitive environment between native species and between coast redwoods and native species.

Table 2 Treatment groups for redwood trial where X is a different genetic entry, this is repeated 19 times for each one resulting in 300 pots. Benchmark_121 is planted with a seedling from California Seed Zone 95 (labeled CR-121. Benchmark_13 is planted with a coast redwood clone (labeled CR-13) from north of Rockport, CA that has performed well in previous trials.

Treatment	Pot Size (gallon)	Plant(s)	Number of replicates
Solo	1	CR-X	3
Duplicate	2	CR-X	3
		CR-X	
Benchmark_121	2	CR-X	3
		CR-121	
Benchmark_13	2	CR-X	3
		CR-13	

The coast redwood trial allows for the direct comparison among redwood clone drought response. Like the interspecies trial, the redwood trial contains treatments for single and duplicate pots to capture each genetic entry in both solo and competitive drought environments. However, rather than mixed pots, this trial relied on key reference genetic entries to examine the success of a redwood clone and is designed to identify candidate drought-resistant clones. The CR_13 clone line demonstrated good drought tolerance in a pilot greenhouse trial and was selected as a high point of redwood clone performance. The CR-121 is a seedling rather than a clone which serves as a benchmark for commercial seedling performance, a more affordable option to land managers interested in sourcing redwoods. The term genetic entry will be used to describe both seedlings and clone lines. Twelve pots in the redwood trial experienced at least one seedling mortality during the acclimatization period, likely due to shipping and planting stress.

The potted plants were grown at a greenhouse located on the grounds of University of Washington's Center for Sustainable Forestry. Once potted, pots were randomized on April 18 and continued to be randomized weekly until the end of the trial to control effects of greenhouse location, bench edge and position from sprinkler. The greenhouse was programed to extend shade covers once the internal temperature reaches 26.66 ºC, begin swamp coolers at 29.5 º C and begin heat pump cooling at 32.2 º C; thus, minimizing higher temperatures. During acclimatization and recovery periods, plants were watered every other day with 8.95L/m^2 using spray nozzles suspended over the potting benches. We used a 2-drought approach to assess drought response. The initial drought (Drought 1), July 1, 2024, until July 11, 2024, involved complete cessation of the watering schedule (Figure 4, PRISM, 2024). Drought 1 ended when one of the three species reached mean fluorescence of 0.5, western redcedar was the species with the most rapid response. A recovery period, from July 11 to 31, during which programmed watering schedule was resumed with additional hand watering to promote a complete recovery from drought conditions. Drought 2 began July 31st and continued until death of at least one plant per pot triggered destructive sampling for biomass measurements, ending on October 12th (Figure 4). The final days of Drought 1 had higher greenhouse temperatures and vapor pressure deficit than those experienced at any point during Drought 2 (Figure 4) despite the expectation that temperatures would be warmer in the second drought than the first, as August typically results in the highest temperatures in the region (Figure 4).

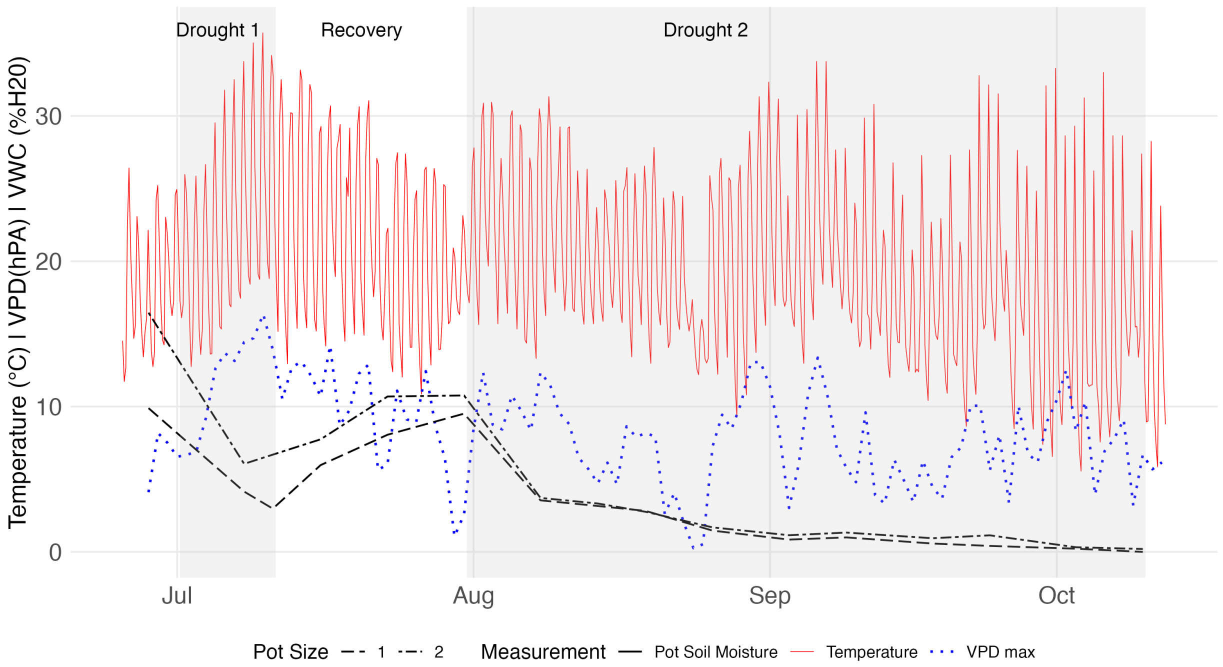


Figure 4 Environmental conditions during the experimental period. The temperature (red solid line) was measured by ibutton monitors placed on benches. Vapor pressure deficit was obtained from PRISM data for 46.8495, -122.3106 and adjusted based on internal temperature of the greenhouse (expressed as a positive value for shared y-axis, blue dotted line)). Mean volumetric water content was measured weekly and combined with pots of the same volume (black dash dot line). Soil moisture measured on weekly basis, averages for both pot sizes (# of gallons). Shading illustrates periods of drought conditions.

1.2.2 Measurements

To capture growth, root collar diameter (RCD) was measured just above soil level with calipers and height measured from soil level to topmost living tissue. Size metrics were measured prior to Drought 1 as baseline, at the end of recovery period, 2 weeks into Drought 2, and upon destructive measurements for biomass (varied time depending on death).

Fv/Fm was measured weekly using a Chlorophyll Fluorometer OS30P+ (Opti Science, OS30P+, 2000) after 30 minutes of dark adjustment using clips on the greenest tissue of the plant. Soil VWC was measured weekly using Campbell’s Hydrosense II, zone 6, throughout both droughts and recovery period. Pots with any mortality were removed for destructive biomass sampling; the time from mortality to biomass destruction varied due to limited work force, possibly leading to more breakage or shrinkage on delayed samples.

Water potential was measured on five plants from each species (but not consistent genetic entry for redwood) for pre-dawn (Ψ_{PD}, ~4 am) and midday water potential (Ψ_{MD}, ~12 pm), to find maximum and minimum level of drought stress, using a 615D Pressure Chamber Instrument (PMS Instrument, 2019) at the beginning and end of Drought 1. New plants were chosen for each measurement date but used the same plant for both predawn and midday measurements. Only Ψ_{MD} was measured midway through the recovery period (July 18th). Both Ψ_{PD} and Ψ_{MD} were measured for the beginning of Drought 2 and 2 weeks into the drought trial to mirror the timeline of Drought 1. Drought measurement pots (July 11 and August 14) were randomly chosen from unsampled solo 1-gallon pots across the soil moisture gradient; samples were taken from 2-gallon pots when solo pots were not available. Samples were 60 mm long, selecting for branches with woody stems, some living leaves, and at least one set of branching. Leaves were removed from the branch to allow a clean seal around the branch when inserted into the pressure bomb.

Biomass sampling began August 14th for pots with at least one mortality. Plants were measured for final root collar and height, then clipped to separate stem from root tissue. Roots were manually cleaned to remove soil, rinsed and dried. Stem and roots were bagged separately. All tissue was dried at 80 °C until reaching constant mass, roots for 24 hrs. and stems for 96 hrs. Biomass investment ratio was calculated as Root (g)/ Shoot (g) for each plant. Plants with premature mortality (died before beginning of Drought 1) were not measured for biomass since sampling began over 1 month after their death and assumed additional loss of biomass.

Temperature data was collected on each half bench of the trial using Thermochron ibutton temperature monitors, to ensure that there were no obvious hot spots in the greenhouse (Ibutton Link Technology). Maximum VPD was sourced from PRISM data set for the Pack

Forest Location and duration of the drought (PRISM, 2024, Figure, 3). Maximum VPD for the greenhouse was calculated using this formula:

$$SVP(T) = 6.112\ x \exp\left(\frac{17.67\ x\ T}{T + 243.5}\right)$$

To find the saturation vapor pressure for both inside (ibutton) and outside (PRISM) temperatures. PRISM value for outside maximum VPD was then multiplied by the ratio between the outside and inside temperatures to determine inside maximum greenhouse VPD.

1.2.3 Statistical analysis

A generalized linear mixed model in the "glmmTMB" package in R with a beta distribution was used for determining strength of environmental parameters such as vapor pressure deficit (VPD), soil moisture, and time as well as factors such as genetic entry or species and treatment influencing fluorescence (Fv/Fm, a bounded response variable) of redwoods, using the following formula:

Fluorescence=β_0 + f_1(max greenhouse VPD) a+ f_2(VWC)+

f_3(Species/Genetic Entry) + f_4(Treatment)+ ε, (1|Plant)

Temperature was excluded as an environmental variable due to high (.83) correlation with max greenhouse VPD. Species is used in the model when comparing redwoods to native species in the Interspecies Trial. Genetic Entry is used in the redwood trial when comparing to reference seedling CR-121. Although dead plants have a Fv/Fm value equal to 0, 0.00001 was added to all fluorescence values to fit the beta distribution modeling assumptions. Individual plant repeat measurements were added as random effect.

For quantified analysis of decline in photosynthetic function, fluorescence values rather than binary mortality data were used in a non-parametric Kaplan Meier (KM)- estimator using the R package 'survival' to determine the probability of `time to event` (Cruickshank et al.

2025). Fluorescence was not measured to mortality for half of the plants in paired plots to avoid biomass loss from the first mortality per plot, thus, an alternative "event" was used. While the exact threshold at which mortality occurs is unknown for species and environmental conditions, in this greenhouse trial the lowest survivable Fv/Fm during Drought 1 and recovery period was measured as 0.59 for coast redwoods (Woo et al., 2008). All redwoods that reached a lower Fv/Fm did not recover even when water was reintroduced. Therefore, we used the conservative value of 0.5 Fv/Fm as the threshold to indicate damage to the photosynthetic system where the plant is unlikely to recover and accounts for some censorship of data in our experimental design. Survival was calculated using the following formula:

$$Probability\ of\ event(t) = \prod_{tj<t} 1 - \frac{(Count\ of\ fluorescence < 0.5)_j}{(Count\ of\ measurements)_j}$$

Where probability of a plant reaching a non-viable fluorescence is calculated for every t_j-measurement point until approaching t- when all plants have reached non-viable fluorescence. Log rank analysis was used for pairwise comparisons within treatment groups as well as for each genetic entry. While KM was originally developed for medical studies, there is a growing application in forest and ecophysiological sciences (Cruickshank et al. 2025, Maringer et al. 2020).

To calculate stem volume, RCD was converted from mm to cm, and the following formula was used to find the volume of a cone:

$$Stem\ Volume = \pi * \left(\frac{RCD}{2}\right)^2 * \left(\frac{Height}{3}\right)$$

Comparisons of biomass ratio and survival times between species and genetic entries were made using a non-parametric Kruskal Wallis and corresponding Dunn's test for pairwise comparison using the "FSA" package in R.

Paired t-test was used to evaluate difference in Ψ_{PD} and Ψ_{MD} and for each species, as well as for stem volume growth for each species and redwood genetic entry during control and drought periods.

Linear models in the “lme” package in R were used to determine the relationship between log transformed volumetric water content and absolute value of water potential.

A logistic function was used to determine the relationship between soil moisture and fluorescence using the “nlme” package in R. The point of inflection, the point where plants begin to steeply decrease Fv/Fm in response to soil moisture drops, was calculated as 95% to the point of the asymptote. Formula:

$$\frac{Fv}{Fm} = \frac{Asym}{1 + \exp\left((xmid - VWC)/scal\right)}$$

1.3 Results

The trials (Interspecies and Redwood) will be addressed in separate sections (A & B respectively) of the results since the first observes differences between species while the latter between redwood genetic entries. Methods remain the same.

1.3 Interspecies Trial-

1.3.1 A. Generalized Linear Mixed Model

In the interspecies trial, comparing a select redwood clone line (CR-116) with two other native species, a generalized linear mixed effect model showed significant overall differences in fluorescence were driven by changes in environmental elements, both VPD and VWC (Figure 5). VWC is significantly positive indicating lower soil moisture is correlated to a decrease in Fv/Fm; while VPD has a positive correlation, this is unexpected as higher VPD typically causes higher plant stress (lower Fv/Fm) but in this case the VPD was highest at the beginning of the drought—a high temperature event during drought the first drought (Figure 4). The VPD was lowest when the plants were under the most stress at the end of the drought. Additionally, both native species show a negative significant impact on fluorescence when compared to coast redwoods, meaning that both native species had lower fluorescence values when controlling for all other variables such as environmental factors and pot treatment. This captures the low fluorescence from seedlings that died prior to the beginning of the drought, which severely affected Douglas-fir (Figure S1). There was no significant treatment effect, planting trees in 1-gallon pots, in competition with a plant of the same or other species, had no effect on their fluorescence throughout the drought trial.

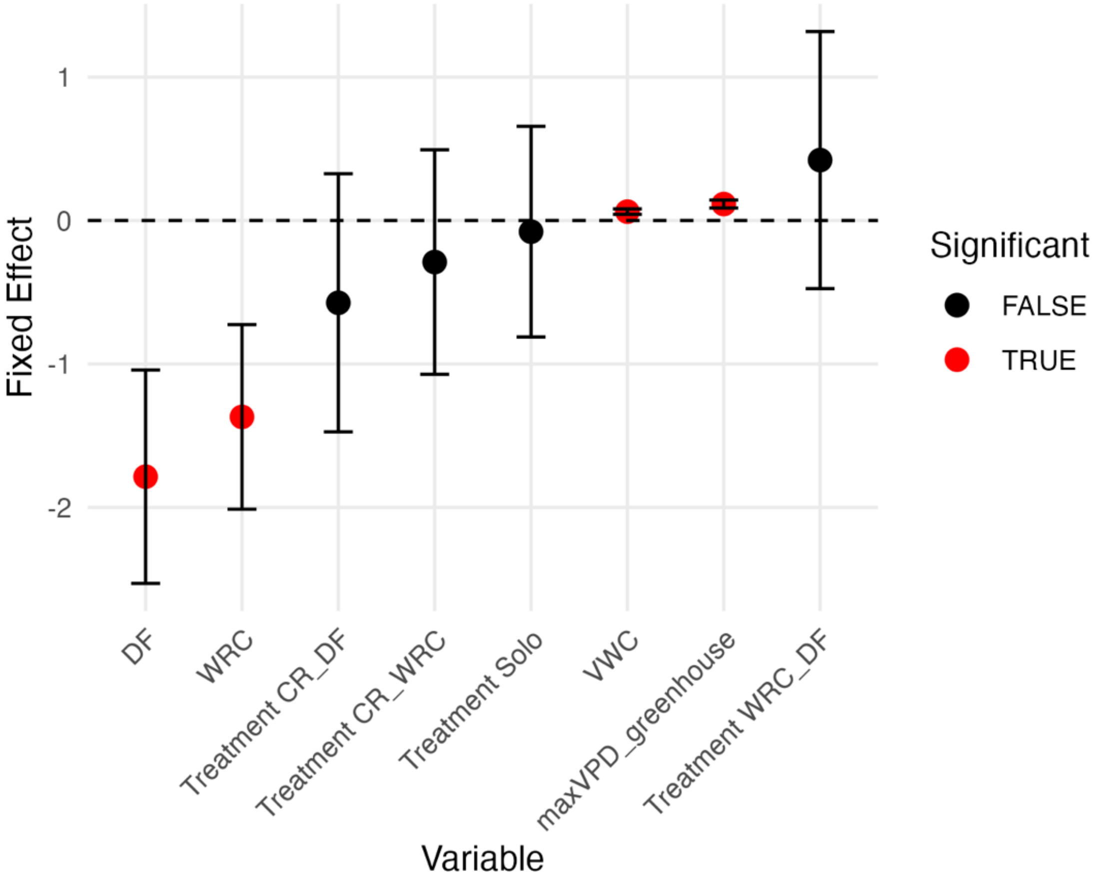


Figure 5 GLMM compares species (WRC-western redcedar, DF-Douglas-fir, CR-coast redwood), treatment groups (solo pots, duplicate pots, mixed pots- CR_DF, CR_WRC, WRC_DF) and environmental factors (Time, VWC, max VPD) and their impact on fluorescence (Fv/Fm). Categorical variables are compared for significance relative to reference for Species factor as Coastal Redwood (CR), and reference for Treatment factor using - "Duplicate" pot (i.e., two seedlings of the same species in one 2-gallon pot). Significance was set as $p < 0.05$.

1.3.2 A. Kaplan Meier Curves

The Kaplan Meir survival curve analysis reveals the exact conditions where species had an impact on fluorescence within treatment groups. There were significant differences (log rank pairwise, $p < 0.05$) between the species depending on the treatment (Table 3), despite limitations in sample size due to early mortality in Douglas-fir as well as western redcedar (Figure 6A). Solo pot treatment shows low Fv/Fm of western redcedar (log rank pairwise, $p < 0.05$) compared to coast redwood and Douglas-fir, while coast redwood and Douglas-fir have similar levels of survival (Figure 6A, Table 3).

Comparisons of treatments within species support the GLMM model that pot treatment has no significant (log rank pairwise, $p > 0.05$) effect on fluorescence for any of the species (Figure 6B).

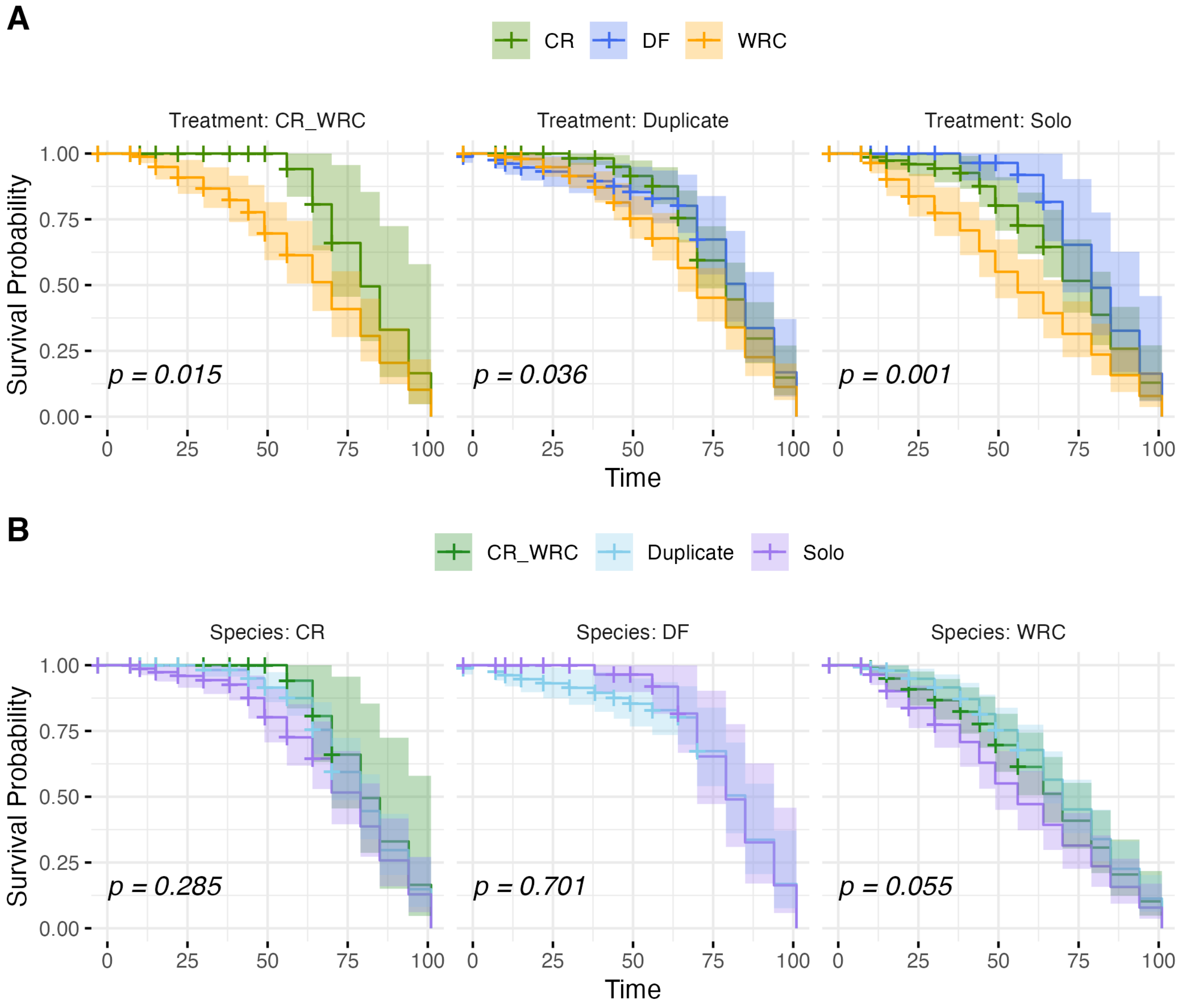


Figure 6 KM curves indicate probability of each species (WRC-western redcedar, DF-Douglas-fir, CR-coast redwood) reaching non recoverable Fv/Fm levels for each day of trial. P values indicate the log rank test measuring differences between the curves. A. Probability of Fv/Fm of each species staying about 0.05 throughout the course of the drought, organized by treatment group (solo pots, duplicate pots, mixed pots- CR_DF, CR_WRC, WRC_DF). Treatments of mixed pots "CR_DF" and "DF_WRC" have been removed due to small sample sizes driven by early mortality. B. Probability of Fv/Fm of each treatment group staying about 0.05 throughout the course of the drought, organized by species. P values indicate log rank test measuring differences between the curves indicating the lack of impact of treatment on each species fluorescence curves.

In duplicate planting pot treatment, those under competitive but not interspecies competition, there was overall differences in log rank curves (p =0.036), but pairwise analysis shows no significant differences.

Interspecies competition treatments were limited by Douglas-fir mortality, but the interspecies pots containing western redcedar and coast redwood result in coast redwood maintaining significantly (log rank, $p = 0.01$) higher Fv/Fm function throughout the drought period. This supports the model that coast redwood had similar to, or higher Fv/Fm than native species in every treatment group (Figure 6A).

*Table 3 Interspecies log rank pairwise comparison of species KM curve in each treatment group. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$.*

Treatment	group1	group2	P value	Significance
CR_WRC	WRC	CR	0.01	*
Duplicate	CR	DF	0.98	
Duplicate	WRC	DF	0.11	
Duplicate	WRC	CR	0.06	
Solo	CR	DF	0.22	
Solo	WRC	DF	0.004	**
Solo	WRC	CR	0.01	*

While early Douglas-fir mortality decreased average fluorescence and limited sample size, Figure 7 shows that Douglas-fir seedlings that survived initial planting shock (aka survived until Drought 1) were able to survive well into Drought 2 (DF mean days until death ~70). When focusing on only plants that survived into drought conditions (i.e., removing nursery stock issues), there is earlier drought mortality in western redcedar (WRC mean days until death ~43), significantly earlier than Douglas-fir ($p > 0.01$). Meanwhile coast redwood did not differ significantly from either native species on survival time during drought conditions (CR mean days until death ~64).

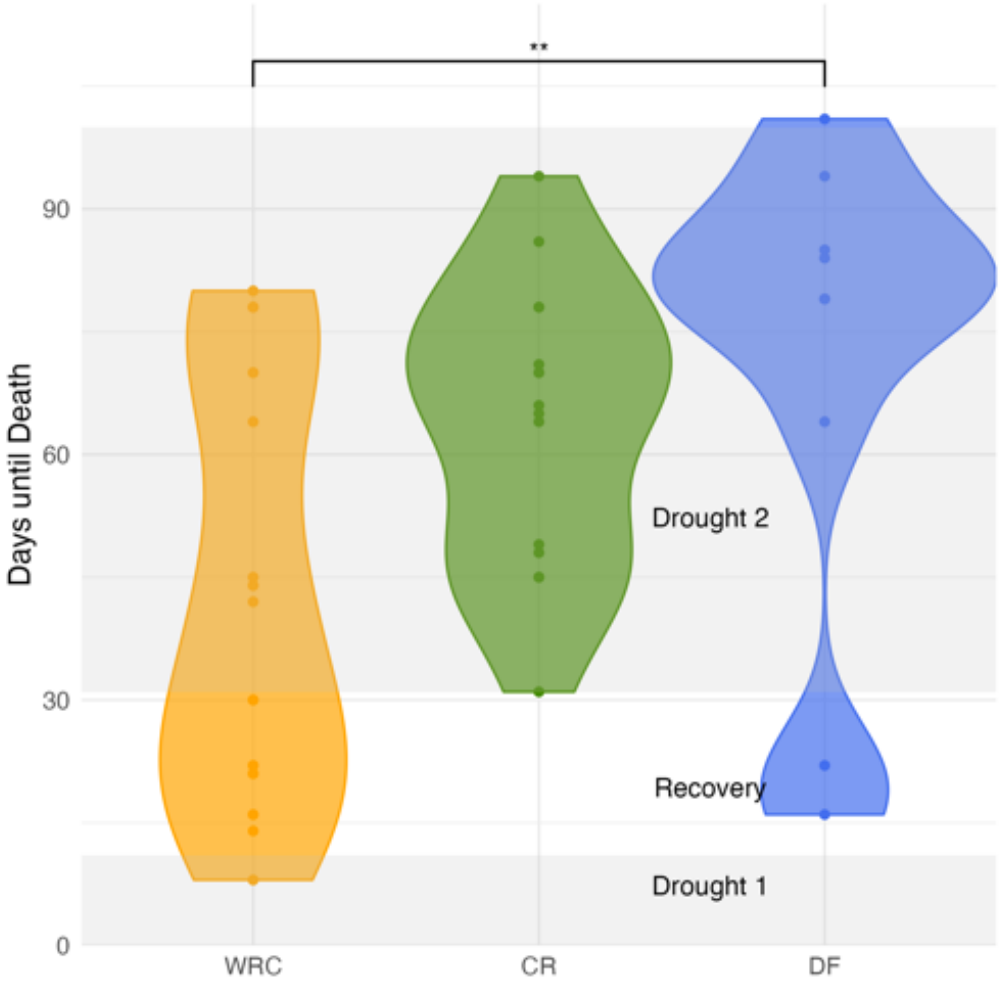


*Figure 7 Kruskal Wallis comparison of time until death (since onset of drought conditions July 1) for each species (WRC-western redcedar, DF-Douglas-fir, CR-coast redwood), excluding those that died prior to drought conditions, followed by Dunn's test to reveal significant difference between western redcedar and Douglas-fir time until death. Excludes death dates for premature mortality due to nursery stock issue, also excludes some of the later death dates because pots were destructively sampled for biomass upon first mortality; the 'survivor' of each 2-gallon pot do not have a time of death thus true mean survival times would be estimated to be longer. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$.*

1.3.4 A. Water Potential

Despite having the lowest mean Ψ_{PD}, VWC is not significantly correlated to Ψ_{PD} for coast redwood (lm, $p = 0.286$) (Figure 8A). However, coast redwood Ψ_{MD} is correlated with soil moisture and is there a significant difference between coast redwood Ψ_{PD} and Ψ_{MD} ($p < 0.01$) (Figure 8). Douglas-fir and western redcedar show a strong correlation between VWC and both Ψ_{PD} and Ψ_{MD} ($p < 0.001$, $p < 0.01$), while also showing a significant difference between Ψ_{PD} and

Ψ_{MD} ($p < 0.05$, $p < 0.01$). The three species fall along a gradient from anisohydric to isohydric with western redcedar showing the worst stomatal control, Douglas-fir the best, and coast redwood in the center (Figure 8B, Charrier et al., 2020). Western redcedar has the lowest (mean $\Psi_{MD} = -2.16$) Ψ_{MD} and significant difference between Ψ_{PD} and Ψ_{MD} (t-test, $p < 0.01$). Ψ_{PD} shows no significant differences between species (Kruskal Wallis, $p = 0.235$), while Ψ_{MD} is significantly different only between coast redwood which was significantly higher than western redcedar (Dunn's test, $p=0.011$).

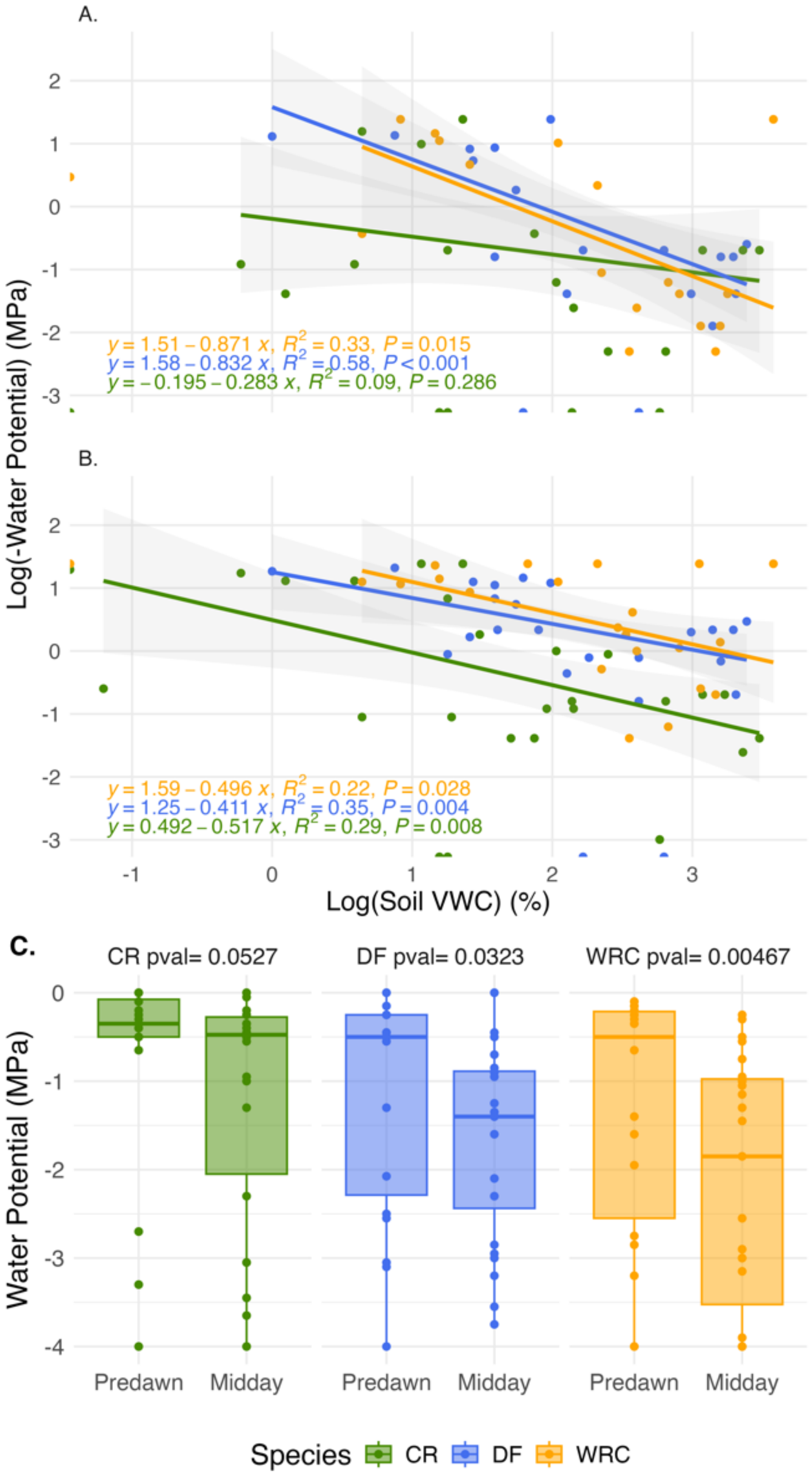


Figure 8 A. Linear regression between log of soil moisture and log of absolute value of branch water potential predawn (Ψ_{PD}) for each species (WRC-western redcedar, DF-Douglas-fir, CR-coast redwood. B. Linear correlation between log of soil moisture and log of absolute value of branch water potential mid-day (Ψ_{MD}) for each species. C. Paired t-test for each species comparing Ψ_{PD} and Ψ_{MD} measurements, where each measurement was linked to an individual plant on the same day ~8 hours apart

1.3.5 A. Soil Moisture

As seen in the generalized linear mixed model (Figure 5), soil moisture (mean VWC) had a significant impact on Fv/Fm for both redwoods and native species; logistic regression allows a comparison of the VWC and the 95% point of saturation (VWC_{95}) for Fv/Fm for each species. VWC_{95} differs for each species, indicating a soil moisture threshold may differ by species, although the nonlinear regressions explain only 27-68% of the relationship between VWC and Fv/Fm. Douglas-fir and western redcedar have lower plateau Fv/Fm values than coast redwood due to premature mortality (predrought) at higher soil moisture levels. However, Douglas-fir at lower soil moistures demonstrated an elevated level of drought tolerance in maintaining fluorescence until the low volumetric water content of 2.7%, despite the early mortality bringing down the plateaued fluorescence average. Western redcedar are the most sensitive species, indicating a drop in fluorescence with soil moisture as high as 4.04%. Coast redwoods have a lower inflection point (3.55%) for VWC, indicating they reach photosynthetic stress at soil moisture levels between the two native species. The logit model fit in Figure 9 shows coast redwoods maintaining higher fluorescence under similar conditions as observed in Figure 5, although the differences between species are small. Pots with premature mortality (prior to drought conditions on July 1) were removed for a better fit in the model and more accurate analysis of plant stress due to low VWC and not preexisting stress.

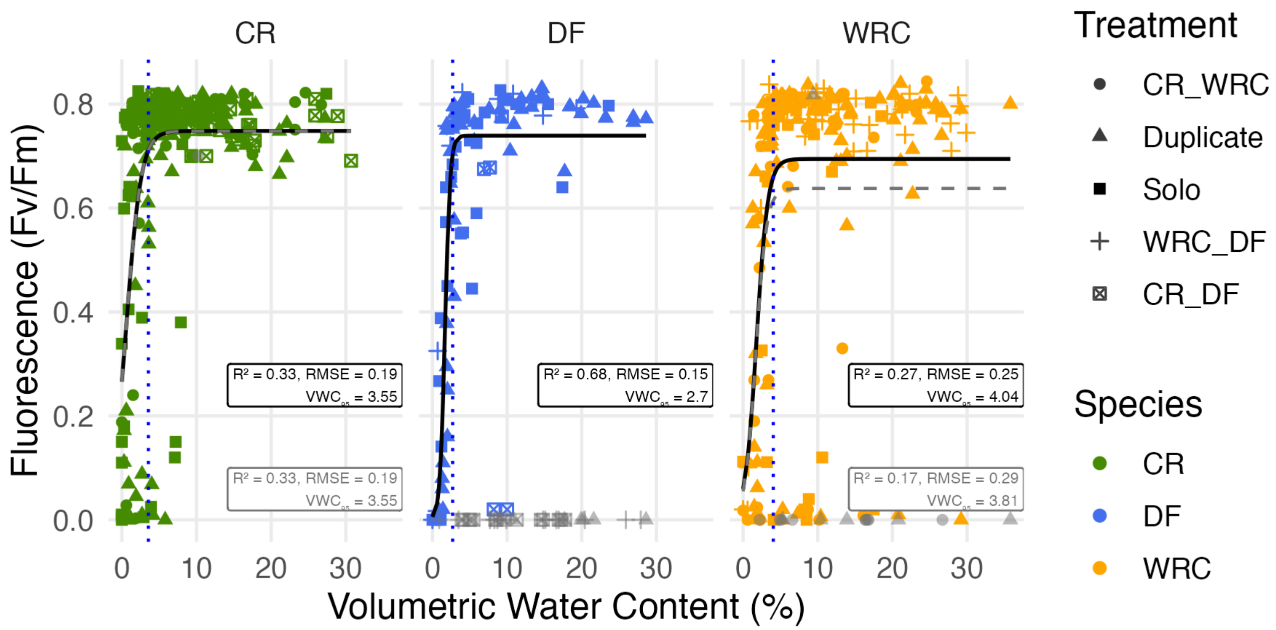


Figure 9 Logistic function describes the correlation between soil moisture and Fv/Fm over the course of the drought for each Species (WRC-western redcedar, DF-Douglas-fir, CR-coast redwood), original analysis with all data (grey) was not able to fit a curve on Douglas-fir. Premature (pre drought condition) mortality was removed, and curve was fit on drought induced data (black). VWC_{95} (blue dotted line) describes the inflection point where soil moisture begins to have a steep effect on plant stress. The curves are underfitting the asymptote describing healthy Fv/Fm measurements which are clustered along 0.8 Fv/Fm for all 3 species.

1.3.6 A. Biomass Ratio

Biomass investments described as root: shoot ratio for each species show that western redcedar has significantly lower root biomass in proportion to its stem than both coast redwoods (Dunn’s Test $p < 0.001$) and Douglas-fir ($p < 0.001$) (Figure 10A). Coast redwoods and Douglas-fir do not differ in their proportional biomass investment (Dunn’s Test $p = 0.1$). Biomass investments did not translate to longer survival time in drought conditions for coast redwoods or western redcedar (Figure 10B). There was significant correlation ($p < 0.01$) between biomass investment in roots and survival for Douglas-fir, though only upon removal of missing samples from nursery stock early fatality; in addition, many Douglas-fir had larger, lignified secondary roots which is likely related to lifting from nursery beds, resulting in high root/shoot ratios for Douglas-fir (Figure 10B).

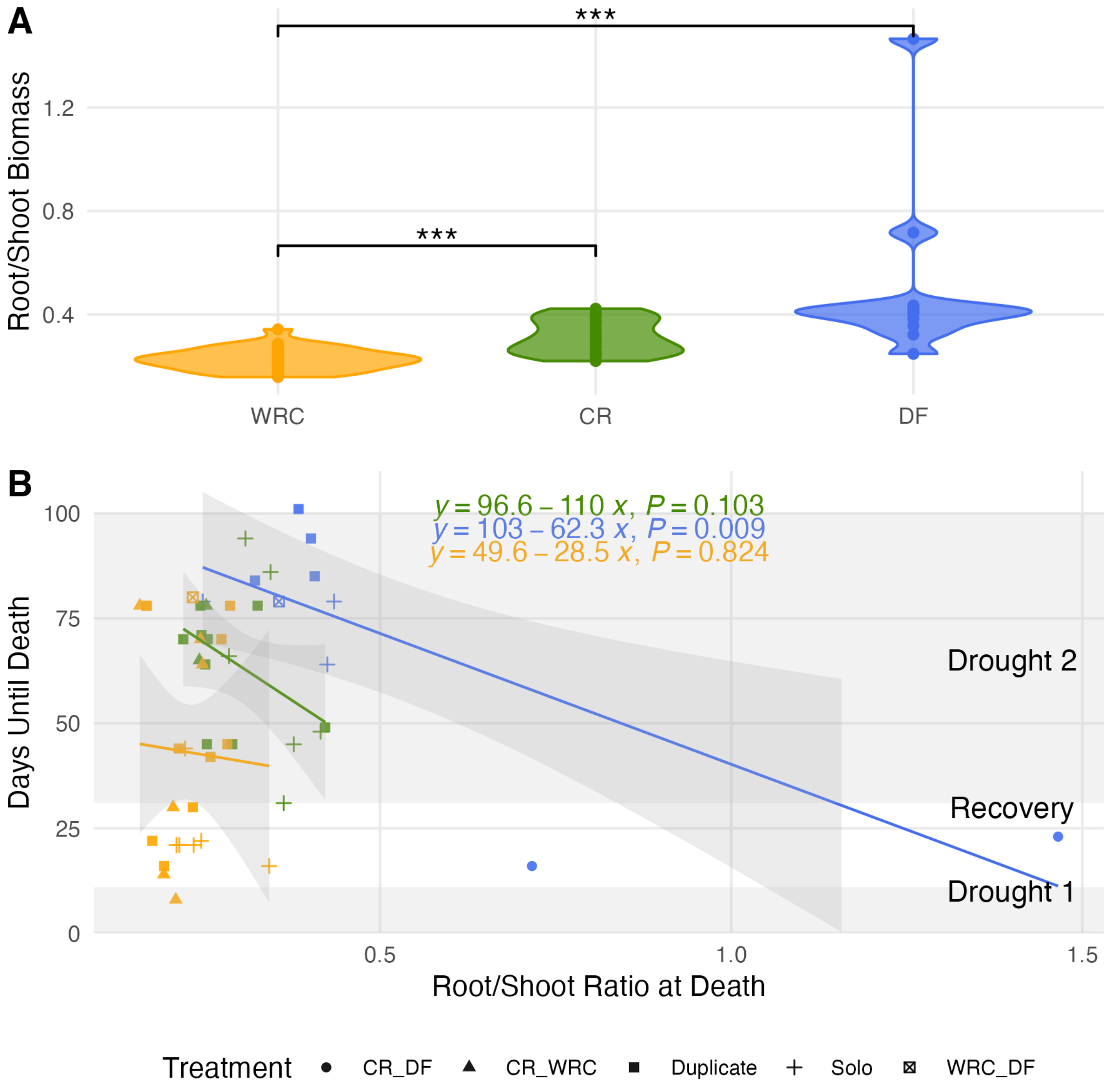


*Figure 10 A. Root/Shoot ratio of biomass for each species (WRC-western redcedar, DF-Douglas-fir, CR-coast redwood). Dunn's test determines significant differences between the species. B. Linear regression between root to shoot ratio and its impact on survival duration during drought conditions. Those which died prior to drought conditions were not sampled for biomass. Excludes death dates for premature mortality due to nursery stock issue, also excludes some of the later death dates because pots were destructively sampled for biomass upon first mortality. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$.*

1.3.7 A. Growth

The measurement of root collar diameter and height at planting, before the start of the drought, and at the end of the experiment allowed for comparison of growth during drought and non-drought periods. Western redcedar (t-test, $p < 0.001$) and coast redwood show a significant difference (t-test, $p < 0.001$) in its stem volume growth during control compared to the drought periods (Figure 11). Growth reductions can be attributable to a shrinking of root collar diameter with drought and/or a loss in stem height due to wilting and stem breakage. Douglas-fir shows no difference (t-test p = 0.1) in stem volume growth, though they had a reduction in stem volume during drought conditions, likely due to stem contraction. Post hoc test following a Kruskal Wallis test (p = 0.003) of pre-drought growth shows that western redcedar had significantly more stem volume growth than coast redwood or Douglas-fir (p = 0.01 and p = 0.02 respectively). However, Kruskal Wallis test comparing stem volume change during drought between species shows no significant difference (p = 0.1).

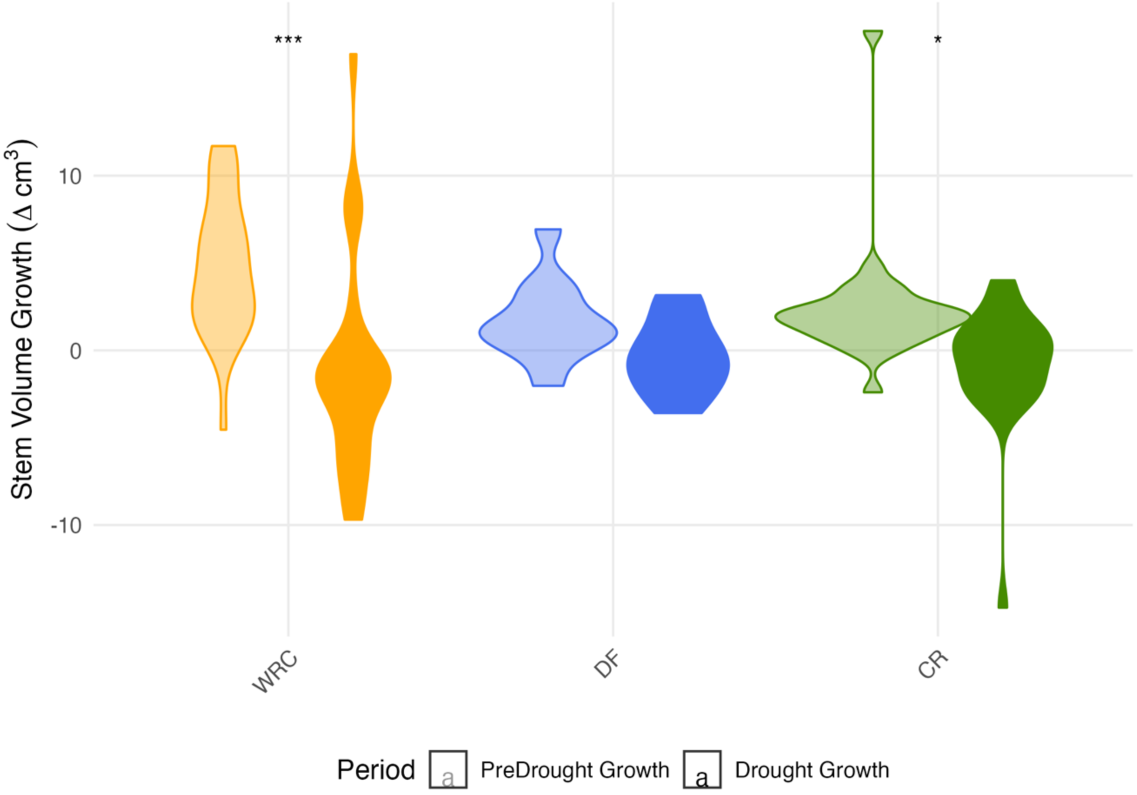


*Figure 11 Paired T-test between growth in stem volume during control (April -June) and drought periods (July-October) for each species (WRC-western redcedar, DF-Douglas-fir, CR-coast redwood). Negative change in volume indicates the shrinking of the stem with water loss. In order of decreasing control mean delta stem volume. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$.*

1.3 Redwood Trial-

1.3.1 B. Generalized Linear Mixed Model-

Similar to the GLMM results from the multiple species comparison, VWC and VPD had a strong effect on plant fluorescence in the redwood trial (Figure 12). As moisture decreases in drought conditions, fluorescence in plants was significantly lowered ($p < 0.001$). Meanwhile VPD was also unexpectedly positive, likely due to the hot dry period early in the drought but low VPD conditions later in the drought ($p < 0.001$) (Figure 4, Figure 12). Solo pot treatment was the only treatment group that had a significant negative impact on fluorescence ($p = 0.01$). And finally, only a small handful of clones had a negative impact on fluorescence compared to reference seedling CR-121. CR-3 had high mortality prior to drought conditions (7/15 plants) and surviving samples had variable survival during drought conditions and therefore had a very significant ($p < 0.01$) negative effect on fluorescence compared to the reference CR-121 (Figure 12, Figure S6). CR-5 had premature mortality (3/15) and though those that made it into the drought variable survival and lower fluorescence ($p = 0.01$; Figure 12, Figure S3 and 4). CR-6 had no premature mortality, but some replicates began dying immediately in response to drought conditions (3/15) and thus also significantly negatively impacted fluorescence ($p = 0.01$) (Figure S3 and S4). No clones had a significantly positive effect on fluorescence relative to the reference seedling, CR-121 nor benchmark CR-13 genetic entry (Figure 12).

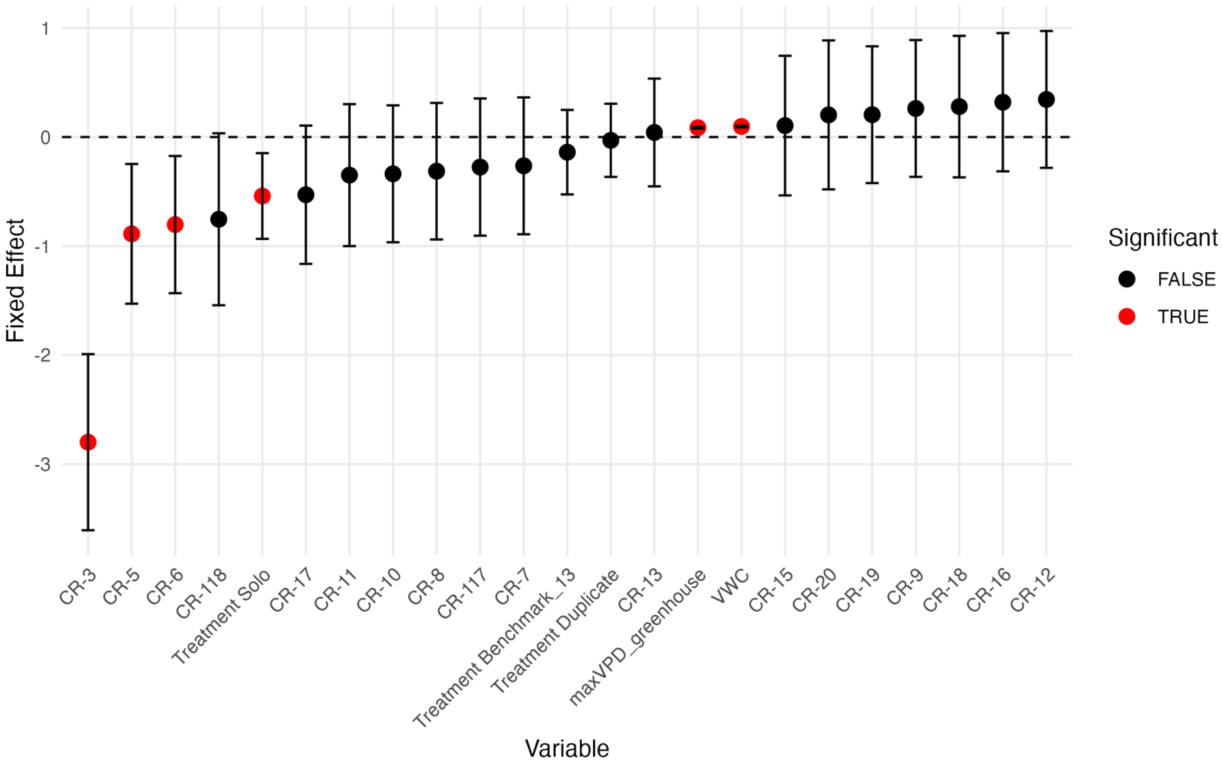


Figure 12 GLMM compares coast redwood genetic entries, treatment groups (solo pots, duplicate pots, benchmark_121 and benchmark_13) and environmental factors (Time, VWC, max VPD) and their impact on fluorescence (Fv/Fm). Categorical variables are compared for significance relative to reference seedling, CR-121, and reference for treatment using "Benchmark 121" pot (i.e., two plants of the same species in one 2-gallon pot). Significance was set as p < 0.05.

1.3.2 B. Kaplan Meier Curves-

While the generalized linear mixed model reflects the overall impact of genetic entry on fluorescence, KM curves predicting likelihood 'survival' (i.e., plant staying above .5 Fv/Fm at a given point in the trial), show more detail to these significant differences, in the context of treatment groups and pairwise analysis other than CR-121. Similarly to the model, CR-3 is significantly lower probability of 'survival' than every other genetic entry throughout the entire trial (Figure 13A, Figure S3, Table S5). CR-118, CR-17 and CR-5, rank worse than 6 other clone lines in log rank parwise assesments (Figure 13A, Table S5). CR-6 is significantly worse than 7 other clones in pairwise analysis. Conversely, CR-20 has signficiantly higher probability of avoiding Fv/Fm stress than 13 of the 19 clones (Figure 13A, Table S5).

Generalized Linear Mixed Model predicted that only the solo pot treatment had a signficantly negative effect on fluoresecence of redwood plants (Figure 12). By analyzing the effect of treatment on specific genetic entries, we can see that solo treatment is only significantly lower probability than other treatments for two clones CR-11 and CR-117 (Figure 13B).

Overall, treatments did not seem to have a significant difference in Fv/Fm levels throughout the droughts for many of the redwood genetic entries (log rank, $p < 0.05$ in 2/19 genetic entries). For both CR-11, and CR117, the solo pot treatment was significantly lower (log rank, $p < 0.05$ between solo pot and other treatments) than the other probability curves (Table S7). There were several clone lines that could not be analyzed for all 4 treatments due to early mortality of at least one plant in the pot, such as CR-11, CR-18, CR-15.

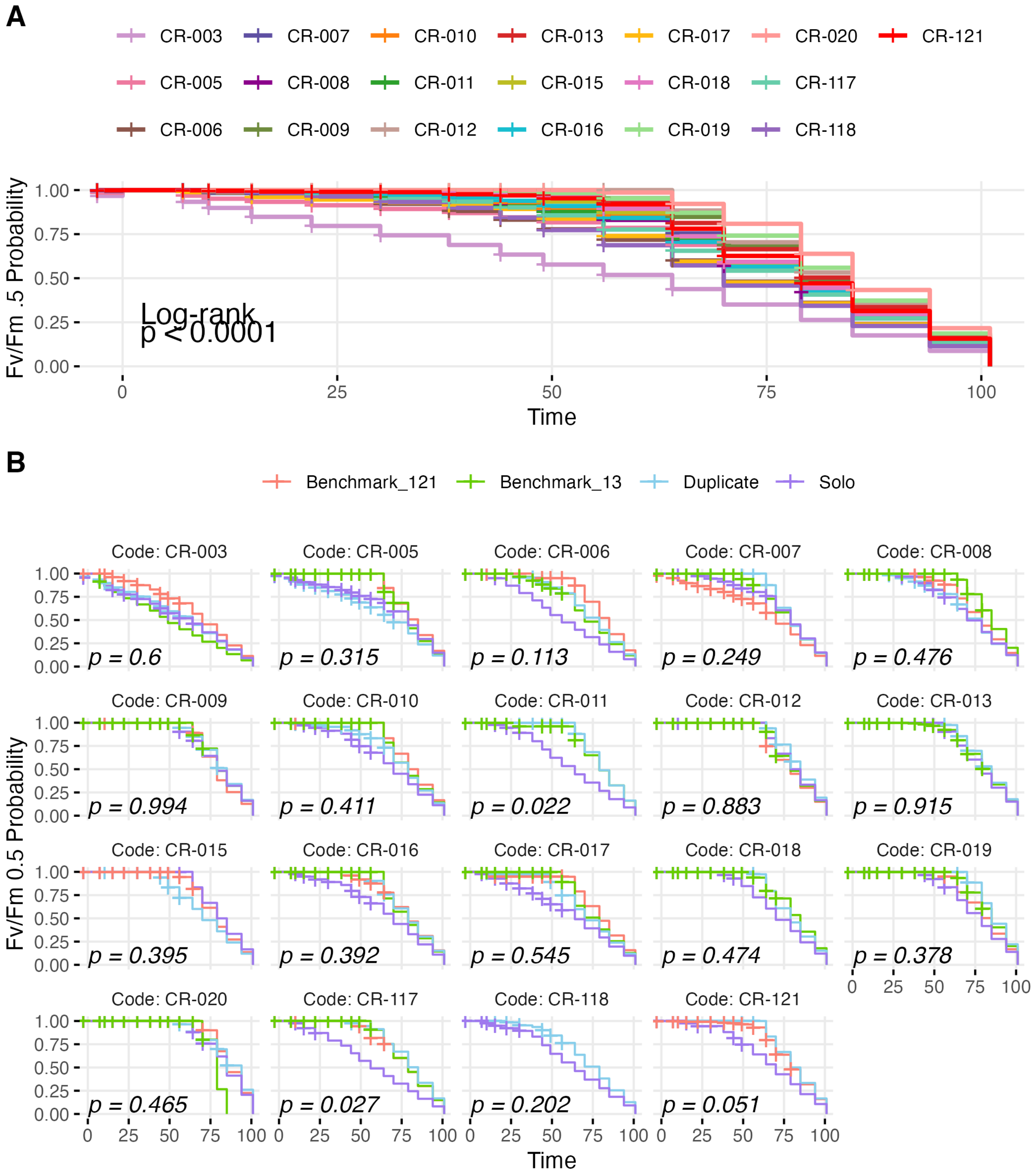


Figure 13 KM curves indicate probability of each genetic entry reaching non recoverable Fv/Fm levels for each day, Confidence intervals have been removed for visual clarity. A. p- value indicates log rank comparison for all genetic entry. B. Comparison of each treatment probability curve for each genetic entry. Note that the two benchmark genetic entries, CR-121, and CR-13, are reflecting their Fv/Fm probability when paired with all other clone lines in the benchmark treatment pots. CR-118 was not part of either benchmark treatments.

1.3.3 B. Soil Moisture

There is a consistent moderate to significant correlation between water content and fluorescence (most genetic entries ~$R^2 > 0.5$, RMSE > 0.1). Those with premature mortality (CR-3) or very early mortality (CR-6) had poor or no fit of the model ($R^2 < 0.02$) (Figure 14). VWC_{95} differs slightly for each genetic entry, indicating that the soil moisture threshold at which photosystem II begins to be impacted differs for each genetic entry, as well as providing a threshold for redwood function with VWC. Genetic entries that only begin to have a steep fall in Fv/Fm <2.5% are CR-117 and CR-121 which would indicate higher drought tolerance (Figure 14). Conversely, those that began to show drop in fluorescence at much higher VWC (3.5%) include CR-15, CR-16, CR-17, CR-20, and CR-8, interestingly none of which were marked as significant by the model (Figure 12). Note that most of the genetic entries in the redwood trial have an inflection point lower than the 3.55% VWC observed for coast redwood clone (CR-116) in the mixed species trial (Figure 9).

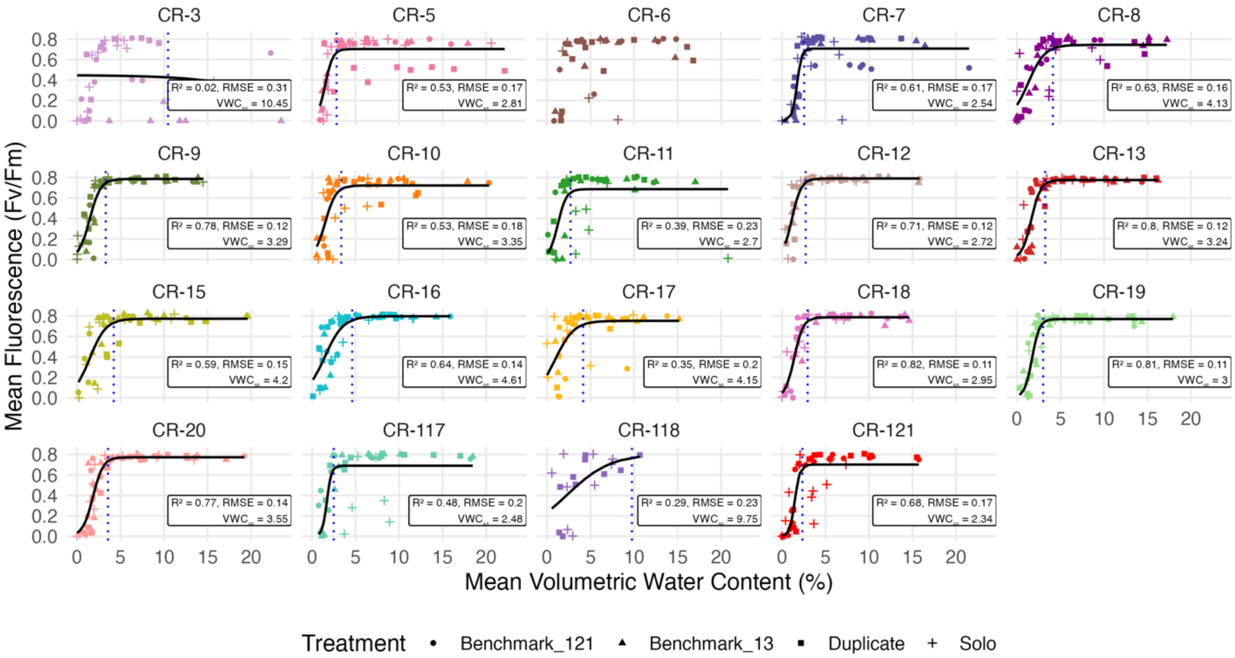


Figure 14 Logistic model of mean volumetric water content and plant fluorescence for all coast redwood summarized by genetic entry and treatment group for each time of measurement. VWC95 describes the inflection point where soil moisture begins to have a steep effect on plant stress. CR-118 has limited samples because it was only part of the solo and duplicate pot treatment groups. Mean for each treatment group at each date is represented by a point. Model was unable to fit logit function for CR-6). Full data points in Supplemental Figure S6.

1.3.5 B. Biomass Ratio

Biomass investments are highly variable in redwoods (Kruskal Wallis, p <0.001). CR-121, the coast redwood seedling benchmark had significantly higher root to shoot ratios than the other genetic entries which are all clones (Figure 15A). The other benchmark, CR-13, was only significantly different from CR- 20 with the lowest root to shoot ratio. Biomass investments did not translate to longer survival times in drought conditions (lm, p = 0.955) (Figure 15B).

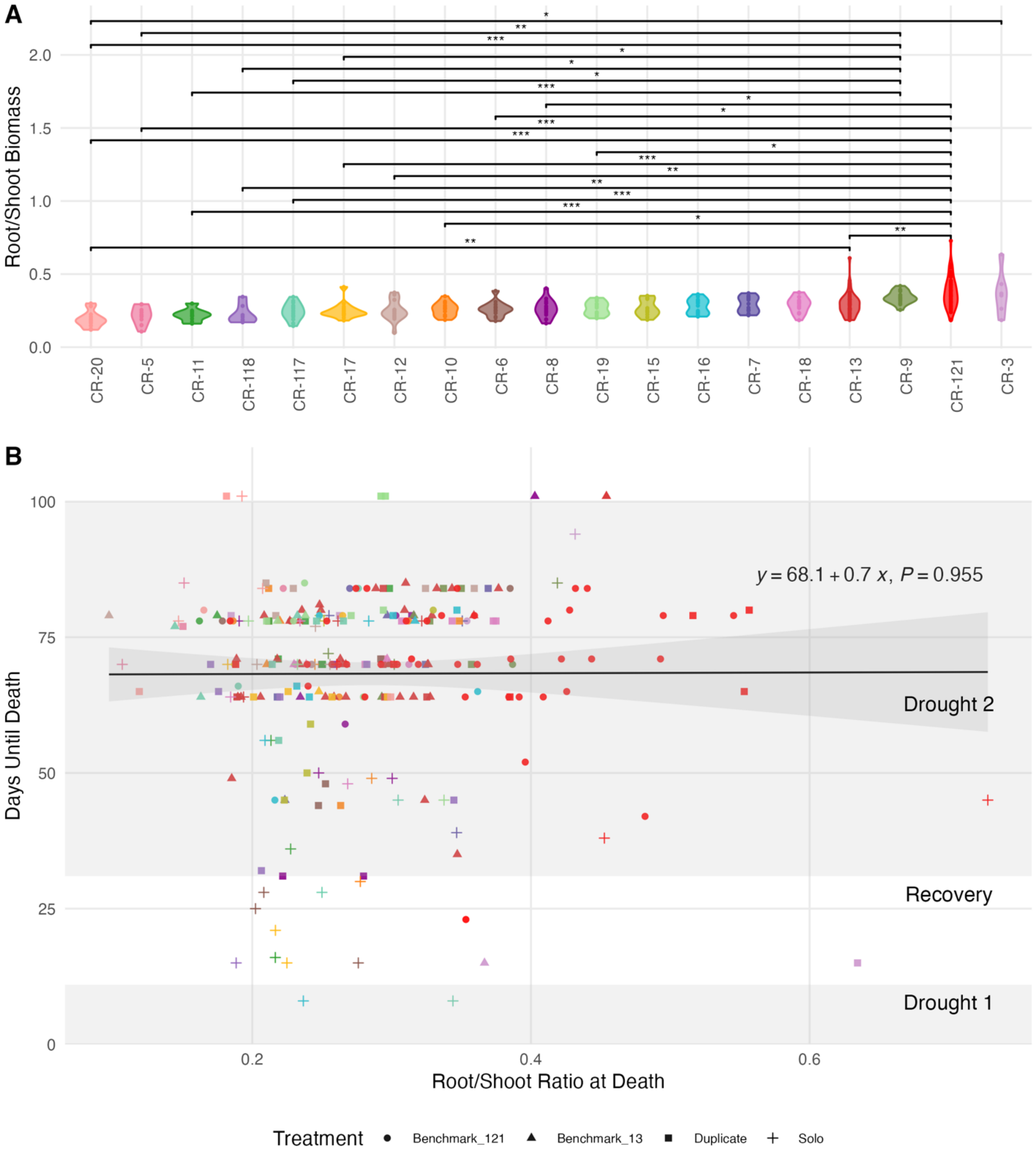


*Figure 15 A. Root/Shoot ratio of biomass between redwood genetic entries ordered from left to right based on mean ratio. Dunn's test determines significant differences between the species. Data from Chloe Fuller's Capstone. B. Linear regression of biomass ratio with survival time during drought conditions. Days until death only available for those that died within the drought and recovery period, and only captures plants that died prior to destructive biomass sampling of their pot. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$.*

1.3.6 B. Growth

Eleven of the nineteen genetic entries have significant differences in stem volume change between their own pre-drought and drought periods (Figure 16). Variability in CR-121 stem volume likely comes from higher genetic variability between individuals, and/or higher rates of forking leading to low accuracy in RCD measurements and inconsistency on which stem was measured for height. Loss of stem volume during drought conditions could be attributable to loss of water from stem tissue. CR-6 did not have a correlation between soil moisture and fluorescence that fit within the model and also experienced the greatest shrinking during drought (Figure 14 and 16). Predrought growth rates are significantly different (Kruskal Wallis, p= 2.162e-05). The pairwise differences are between CR-10 and CR- 11, CR-121, CR-13 and CR-20, as well as between CR-20 and CR-6. While a comparison of drought stem volume change between genetic entries was significant (Kruskal Wallis, p = 0.01), a Dunn's test revealed no individual pairings had a significant difference.

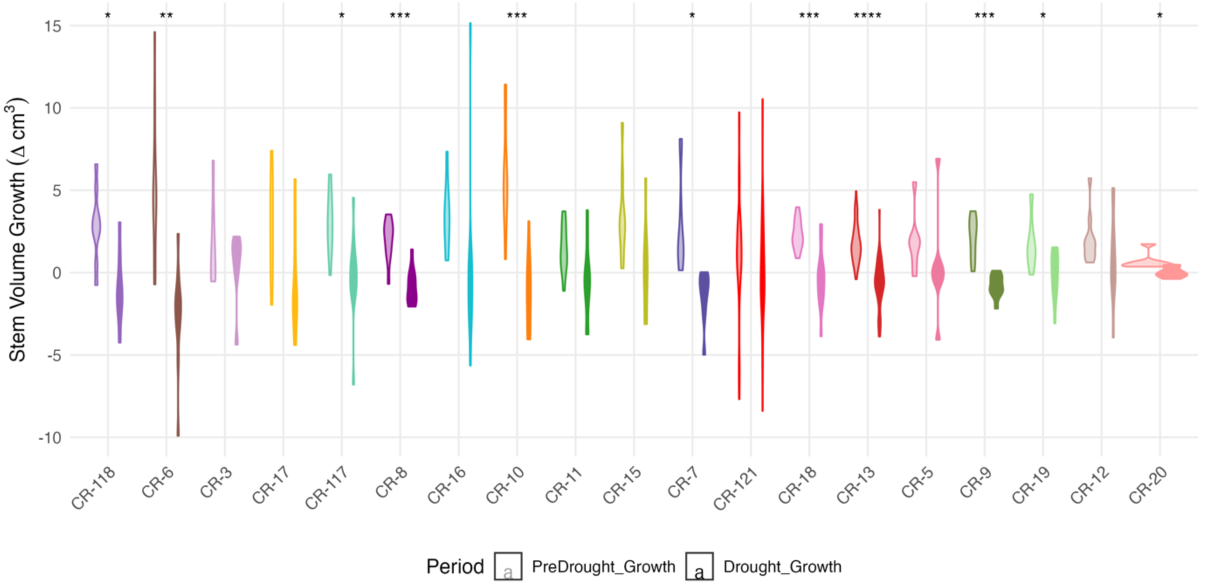


*Figure 16 Paired T-test between growth in stem volume during control (April -June) and drought periods (July-October) for each coast redwood. Negative change in volume indicates the shrinking of the stem with water loss. *** significance at p < 0.001, ** significance at p < 0.01, * significance at p < 0.05.*

1.4 Discussion

Impact of Species

Results of the interspecies trial were clearly impacted by Douglas-fir nursery stock quality. In analysis that included metrics of Douglas-fir that died prior to the drought conditions beginning, Douglas-fir performed worse than both coast redwood and western redcedar (Figure 5). However, when samples were limited to those that died as a result of drought conditions (after onset of drought conditions July 1st), Douglas-fir had longer survival times than western redcedar or coast redwood (Figure 7). Nonetheless, this trial found that coast redwoods performed just as well if not better than Douglas-fir and consistently better than western redcedar. In fact, western redcedar is a candidate for range shifts further north through assisted migration precisely because of its drought intolerance; the results are promising indicators that coast redwoods might be able to be planted in areas that are now too dry for western redcedar (Open Redcedar Adaptation Network). Douglas-fir, a drought tolerant native species, serves as a good metric on whether coast redwoods can survive in the colder winter, and summer drought environment of Washington (Cruickshank et al, 2024). We found that coast redwoods maintained similar levels of fluorescence, similar levels of Ψ_{branch}, biomass allocations, and some redwoods' fluorescence inflection point was at a lower level of soil moisture than Douglas-fir. Though affected by Douglas-fir nursery stock, our results are consistent with Kerhoulas and Polda (2020), where coast redwoods demonstrated higher Ψ_{branch}, larger above ground biomass allocations, growth and survivorship than native Douglas-fir in xeric inland habitat.

Impact of Genetic Entry

There is a growing interest in coast redwood drought tolerance, not only in the context of assisted migration but in their own native range as well (Fernández et al., 2015). Phenotypic traits of different redwood genetic entries have been associated with higher drought tolerance such as resistance to xylem cavitation (De la Torre et al., 2020). Previous provenance studies have attempted to match these phenotypic traits with source location but have failed to do so (Kruser et al., 1995, Klapste et al., 2020). Cruickshank et al. (2025) found that while source location did not influence survival in drought, initial condition of the plant, and root to shoot ratio had considerable influence. Our findings found that while the root to shoot ratio did not correlate with redwood survival in drought conditions, initial condition did impact some clone lines (CR-3, CR-5), and premature mortality also indicated low drought tolerance. A possible explanation of limited impact of biomass ratio is the severity of the drought limiting growth, and size of pot, limiting more roots from finding new sources of water at lower soil levels. Although, post-experiment excavation of roots showed no signs of roots being bound by pots.

Impact of Competition

The experimental design provided a unique opportunity to compare redwood drought stress in multiple conditions to see if competition (inter- and intra-species clones) changed its water efficiency and decreased level of drought stress (Zenes et al., 2020). However, our study showed that there was no significant effect of treatment on redwood fluorescence except for in solo treatment group in the redwood trial only (Figure 12, 13B). While this supports the original hypothesis, one possible explanation for this distinction can be seen in Figure 4, where the average solo pot (1-gallon) VWC shows a much lower (~6% less) initial soil moisture than 2-gallon pots (duplicate and benchmark treatment pots). This could have been caused by the smaller pot position on the bench in relation to sprinklers as well as relative lower surface area of smaller pots. During the recovery period, hand watering was implemented to regain soil saturation as fast as possible, and 1-gallon pots more closely approached 2-gal pots level of VWC. Both pot sizes show a similar decrease in VWC during Drought 2 (Figure 4).

Environmental Impacts

Redwood response to abiotic stressors, not simply their relative performance is crucial to assess assisted migration feasibility. The drought trial lasted about 100 days, with a 20-day recovery period after an 11-day initial drought, meant to replicate a typical PNW summer. Redwoods on average survived 67 days of drought conditions (data censoring due to biomass sampling, decreased this average), with the last 47 of those being consecutive days with zero water (Figure S5). Only 16 of the 266 plants in the redwood trial died as a result of Drought 1 (Death date during Drought 1 or Recovery period), indicating most redwoods can withstand or recover from 11 days of no water. Except for a single clone line (CR-118), all the coast redwoods showed limited impact to photosystem II (drop in Fv/Fm) until soil moisture dropped below 5% (Figure 9, 14).

However, as predicted, coast redwoods had significant difference between their predawn and midday water potential, anisohydricity (Figure 8A, Charrier et al., 2020). A small negative predawn water potential indicates that the plant is under low stress from soil moisture, but large negative midday water potential indicates high VPD and poor stomatal regulation (Charrier, 2020, Johnstone & Dawson, 2010). Burgess and Dawson (2004) demonstrated that this poor stomatal regulation allows redwoods to uptake air moisture in their foggy native range, key factors in its growth but also suggest a mechanism for coast redwood range limitation. In this study, coast redwoods showed good daily recovery from water stress, presumably in the absence of higher air moisture as would be associated with fog.

Our hypothesis that higher root to shoot ratio would increase survival in the drought was, that a plant's ability to invest in roots to extract soil moisture increases their drought tolerance, was not supported (Cruickshank et al., 2025). Additionally, this study found that, stem volume did not increase for redwoods overall (-0.04 cm^3 volume lost on average during the drought), while multiple studies have found that redwoods are able to increase above ground biomass than other species in similar drought conditions (Kerhoulas and Polda, 2020, Ambrose et al, 2015). It is possible that the limitation of deeper soil moisture due to pot size and severity of the drought conditions did not support redwood root growth, and increased root size did not increase soil moisture uptake in a limited volume.

Limitations and Future Analysis

One clear limitation to this study was premature mortality due to Douglas-fir and some coast redwood clone lines (CR-3 and 5, and to a lesser extent CR-7 and 20 which lost one sample each) which obscured differences in stress from drought or nursery stock quality. Analysis was difficult due to limited sample size upon exclusion of premature mortality samples and altered results when included. Sample size was also a limiting factor due to the number of genetic entries and treatments, especially for CR-118 which was excluded from benchmark competition treatments due to plant number limitations. Additionally, limitations in workforce and the extended survival of so many plants resulted in early biomass sampling, causing a loss of data for the 'survivors' in 2-gallon pots with a single mortality decline in fluorescence and concrete death dates. Finally, while Woo et al., (2008) encourages the use of Fv/Fm as a metric for plant stress in droughts since it is fast, nondestructive and highly sensitive to change; photosystems are one of the last things to be affected by plant stress (Trueba et al., 2019). Hydraulic function and stomatal conductance are all affected in earlier stages of plant stress and could be better metrics of early drought stress, however, Fv/Fm continues to be a good metric of plant viability and low probability of recovery in the case of water reintroduction (Woo et al., 2008, Trueba et al., 2019).

Since no effect of treatment was found, future studies could focus on greater replication samples for each genetic entry and measurements of plants until death, and improved Douglas-fir stock. Biomass sampling prior to drought conditions could also help differentiate between root-to-shoot ratio being a helpful trait in drought conditions, or a response to drought conditions. Further study of redwood stomatal control, vapor pressure deficit and growth could help clarify redwoods' ability to survive and gain its signature heights without its native fog environment.

Forest managers should consider these as promising results for assisted migration as coast redwoods had similar if not better outcomes in droughts than native species. One surprising result was that seedling stock (i.e., CR-121 used as a benchmark) was not significantly outperformed by any of the clone lines previously selected for high growth performance; it is unclear if this result only reflects growth under drought stress. Furthermore, early tree growth in a greenhouse may not be an indication of later stages of stand development. While genetic entry selection and nursery quality should continue to be refined for drought tolerance, coast redwoods assisted migration to inland western Washington would not appear to be limited by summer drought.

Chapter 2: Field Trial of Coast Redwoods in West Cascades

2.1 Introduction

Inland western Washington differs from coast redwood's native range in more ways than simply rainfall and fog (Figure 3). Field trials allow for study of environmental factors that differ from their native range such as freezing temperatures, summer heat, lack of fog, soil drainage and nutrition differences (Canham & Murphey et al., 2017). Redwood hexaploidy allows greater genetic diversity and has been speculated to improve adaptation to a wide variety of sites and climates (Dagley et al., 2017, Kruser, 1995).

Determining if site quality or other factors are limiting redwood survival and vigor is crucial for understanding the potential of coast redwood assisted migration to Washington. Additionally, provenance studies for redwoods have shown that the source location of coast redwoods could be matched to the target environment to increase likelihood of survival: matching seeds from throughout the native range to conditions in Southern Carolina, France, and United Kingdom (Kruser et al., 1995). Inland western Washington conditions will be a test of fitness for this species, especially considering the study site is much farther north than the native range, with the previous, northern but coastal, limit being Vancouver, BC (January mean T = 2 ºCelsius) (Kruser et al., 1995).

Coast redwood's native range is quite narrow, limited to the coastal range of California and Southern Oregon. These sites are mostly foggy with limited temperature range, with soils mostly characterized by depth, moderately to very acid, and vary in textures: loam, sandy loam, fine sandy loam, silt loam, to clay loam (Borchert et al., 1988; Douglass, 1966). We planted redwoods across 4 sites with different soil series (Wilkeson and Barneston) in the University of Washington's Experimental Pack Forest varying aspect, slope, and relative drainage of parent material to see if these factors affect redwood survival and different varieties suitability to these conditions.

While coast redwoods have already been planted in western Washington, in Pack Forest itself (including successful trials from 1930), there has not been a comprehensive study of large-scale plantation style coast redwoods. The objective of the field trial is to expose redwoods to a variety of site qualities and environmental conditions in the western Washington Cascades and determine suitable and potentially champion clone lines for those conditions. Through measurement of mortality and vigor, along a soil gradient of conditions, we hope to determine the environmental limitations of coast redwoods in this novel environment.

This research addresses the following questions: 1) How does redwood mortality and vigor compare to the native species Douglas-fir? We predicted that redwoods would have lower survival than native Douglas-fir. 2) Are there redwood genetic entries that are better suited to western Washington conditions? We predicted that in the genotype variation, there will be some genetic entries that are more and less suitable in western cascade conditions. 3) Does site quality affect redwood survival and vigor? We predicted that site quality (e.g., soil drainage) will have a very strong effect on redwood survival. 4) Does the redwood's genetic entry greenhouse drought tolerance from a drought until death study, predict survival in field conditions? We predicted that genetic entries that performed best in the greenhouse drought conditions (Chapter 1) will also perform well in field conditions, in particular on drier sites.

2.2 Methods

This experiment was conducted at Pack Forest, University of Washington Center for Sustainable Forestry (46˚50’N; 122˚16’W), encompassing four field planted study sites. Four sites with replicated plots were planted in spring of 2024. The sites follow a gradient of site soil quality to test the environmental limits of redwood growing conditions (National Cooperative Soil Survey, 2025).

Sites were planted in March of 2024 with 5 rows x 6 columns plots with 8 foot spacing (Figure 17). The plots are composed of 22 redwood clones and 8 Douglas-fir seedlings; seedlings were randomly planted on the grids. Seventeen of the redwood clones and seedling correspond with those in the greenhouse trial, data presented here is limited to those (Chapter 1). All genetic entries were grouped together, 17 for coast redwood, and 8 for Douglas-fir, for species comparisons. Benchmark clone line CR-13, greenhouse interspecies trial CR-116, and clone line CR-118 are all absent from field plots (Chapter 1). Plants were tagged and measured over the summer (~3 months after planting), and again in November (~10 months after planting), after the growing season of 2024. Sites are named by descriptors of the soil type.

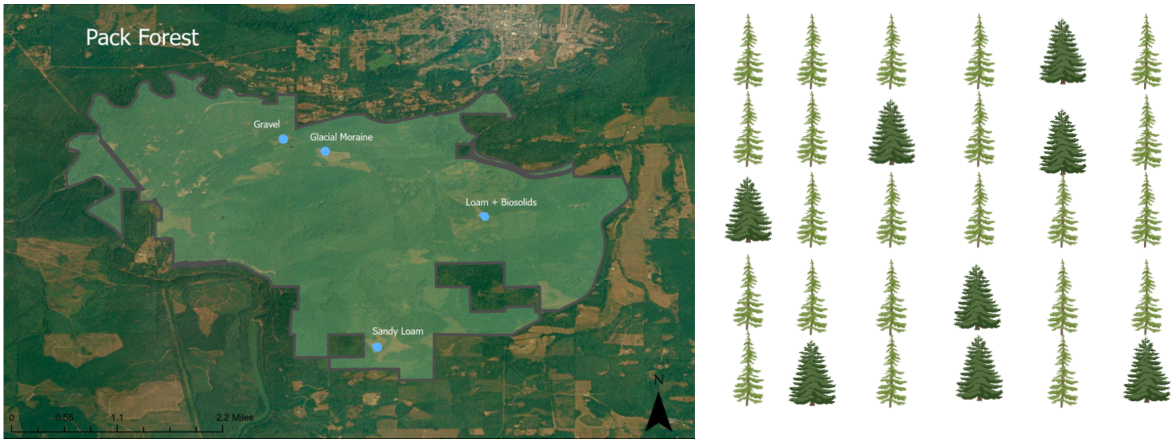


Figure 17 A. Study sites locations within Pack Forest boundary, B. Example of individual plot composition in 5x6 plots that make up each site, 8 Douglas-fir, and 22 coast redwood.

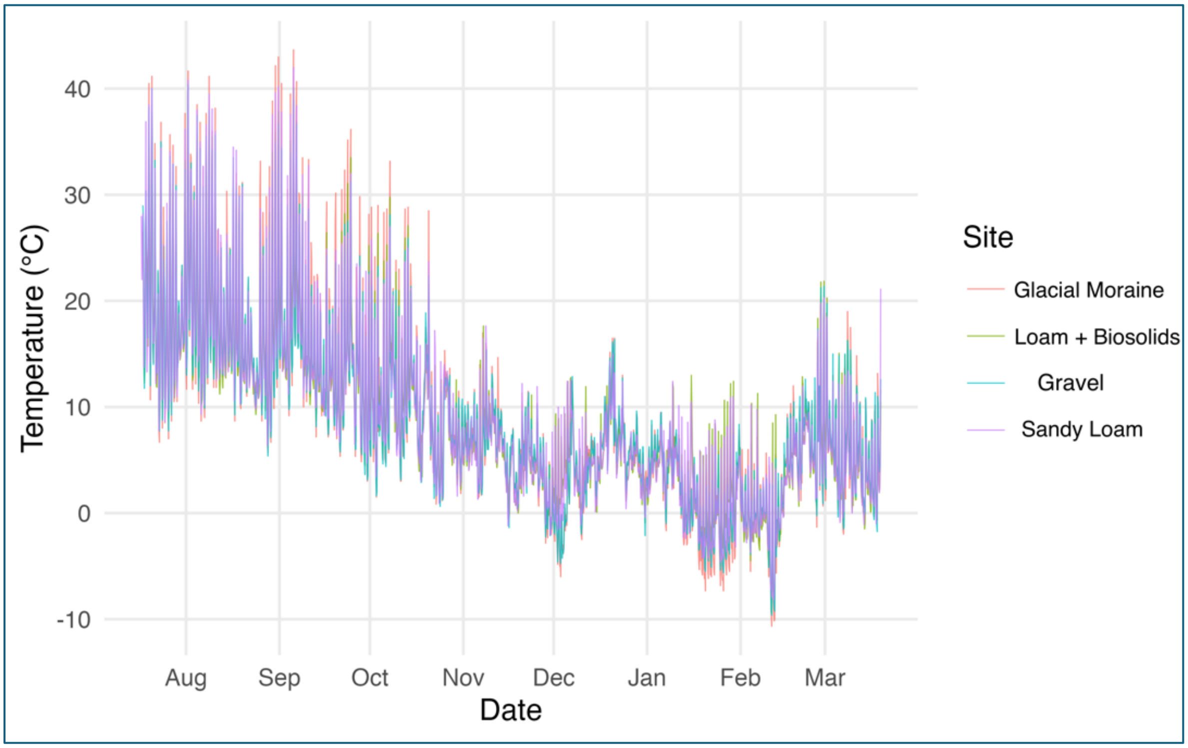


Figure 18 Mean temperature for each site as measured at multiple points, every 4 hours, throughout sites beginning 4 months (July 2024) after planting to up until April 2025, almost 1 year after planting and past the measurement period. Kruskal Wallis test determines no significant difference in temperature between sites (P = 0.16). January mean T = 2℃ among all the sites.

2.2.1 Study Sites

Figure 17 shows location of the 4 sites within Pack Forest as well as diagram of a plot.

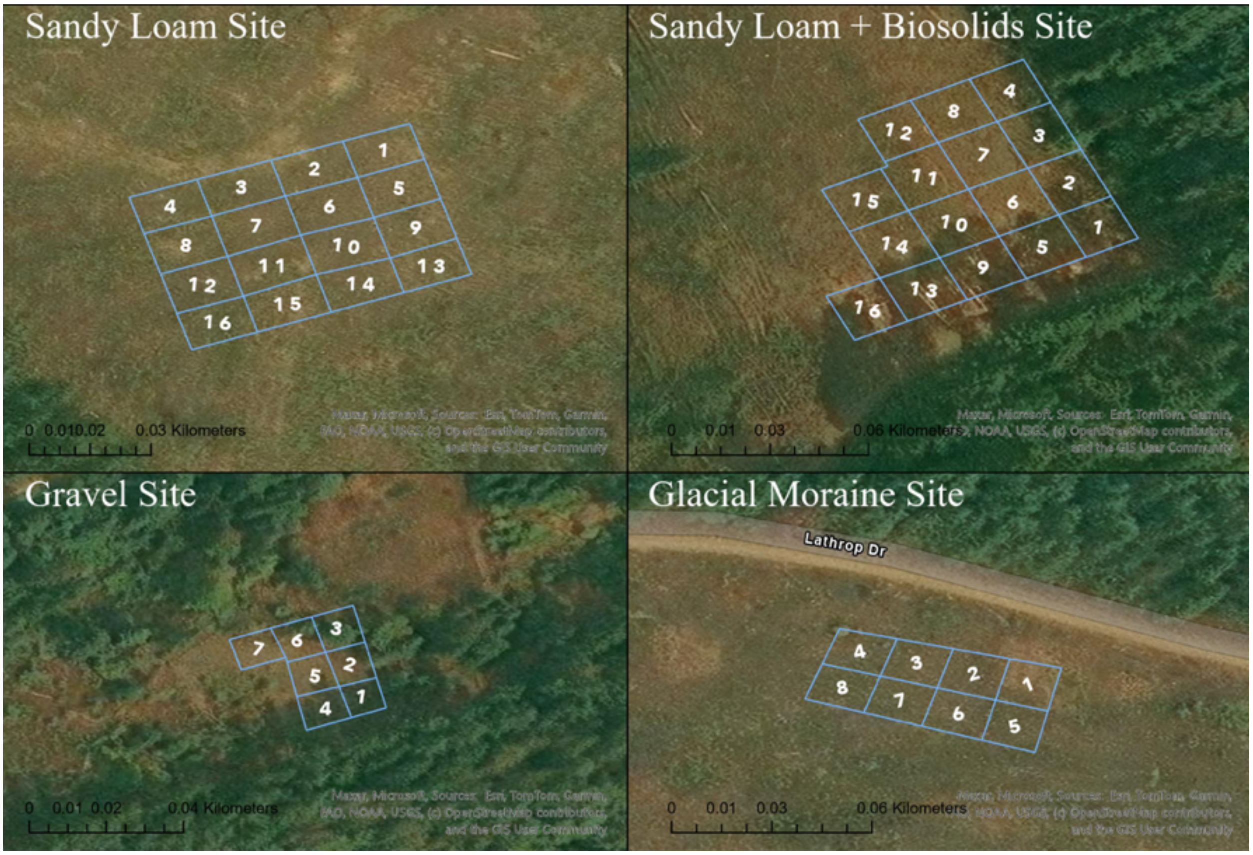
Figure 19 shows number of plots and orientation of each site.

Sandy Loam site: sixteen plots- southeast aspect, elevation is 469.3 meters (1539 feet) with ~25% slope, last harvested in 2022, cleared of downed wood and herbicide treated in 2023. High quality, Wilkeson soil described as “well drained; medium to rapid runoff; moderate permeability” (National Cooperative Soil Survey, Wilkeson). Site index for this site using previous Douglas-fir harvest is 120 at 50 years. (Pack Forest Stand Database, 2025).

Sandy Loam + Biosolids site: sixteen plots- northwest aspect, elevation is 505 meters (1656 feet), and 8-25% slope last harvested 2023. This site also has Wilkeson soil, well drained, but with variable rocky content and a history of biosolid application in the 1990s, creating both higher water availability and drainage (National Cooperative Soil Survey, Wilkeson). Site index for this site using previous Douglas-fir harvest is 120 at 50 years (Pack Forest Stand Database, 2025).

Gravel site: seven plots- northwest aspect, elevation is 278 meters (917 feet), with 0-10% slope, last harvested in 2013. This site has Barneston soil, described as “somewhat excessively drained; Saturated hydraulic conductivity is moderately high in the upper 50 cm and very high below” due to large rock and sandy composition, glacial outwash (National Cooperative Soil Survey, Barneston). Site has a history of Douglas-fir laminated root rot and has failed as a Douglas-fir plantation in the past. Site index for this site using previous Douglas-fir harvest is 105 at 50 years (Pack Forest Stand Database, 2025).

Glacial Moraine site: eight plots- north aspect, elevation is 308.54 meters (1012 feet), with 1-10 % slope, last harvested in 2021. This site has harsh conditions, Barneston soil, even more rocky as a glacial terminal moraine with limited soil with a history of high mortality of Douglas-fir, (National Cooperative Soil Survey, Barneston). Site index for this site using previous Douglas-fir harvest is 95 at 50 years (Pack Forest Stand Database, 2025).



Sandy Loam Site

Sandy Loam + Biosolids Site

Gravel Site

Glacial Moraine Site

Maxar, Microsoft, Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, (c) OpenStreetMap contributors, and the GIS User Community

Figure 19 Pack Forest Study sites, subdivided into plots of 30 plants each. Aerial view of sites provided by Imagery Hybrid; base layer of ArcGIS pro-2025.

2.2.2 Measurements

Vigor (Table 4), height (cm, soil to tallest point), root collar diameter (RCD, mm, diameter 1cm above soil) was measured in a 3-week window in summer (June and July) approximately 3 months after planting and again in November 2024, 10 months after planting. Measurements also included notes about microsites for each plant, including vegetative competition, coverage from slash or planting in a depression.

Table 4 Visual assessment of plant vigor based on health of visible plant structures.

Vigor	Description
0	Dead, there is no remaining visible living tissue.
1	Close to death, most needles are brown and dry with some needles remaining green growth or minimal new resprout at the base.
2	Struggling to survive but has some healthy structures (green, straight, and soft needles), considerable damage but pulling through.
3	Fairly healthy; seedlings have some damage or dead limbs, but overall, most branches have green, healthy tissue.
4	Healthy, some needle curling or minimal brown tips but not dried or dead branch tips.
5	Extremely healthy, no sign of leaf curling, leaf drying, etc.

To calculate stem volume for living trees only, RCD (Root Collar Diameter) was converted from mm to cm, and the following formula was used to find the volume of a cone:

$$Stem\ Volume = \pi * \left(\frac{RCD}{2}\right)^2 * \left(\frac{Height}{3}\right)$$

2.2.3 Statistical analysis

Rather than using species specific clone lines to compare coast redwoods with Douglas-fir, all genetic entries were grouped when making interspecies comparisons. Interspecies comparison of vigor at each site was made using Wilcox's nonparametric test. Comparisons between redwood genetic entries root-to-shoot ratio and mean vigor, and stem volume change as well as sites' mean vigor were made using a non-parametric Kruskal Wallis and corresponding Dunn's test for pairwise comparison using the "FSA" package in R.

Linear mixed models using the "lmer" package in R were used to determine differences in November vigor and the possible effect of genetic entry and site while plot was held as a random effect.

Linear models were used to correlate time to mortality in the greenhouse with mortality rate in the field, as well as initial root/shoot ratio of the redwood genetic entries with field survival. Chi-squared tests were used to test for differences in mortality between species and sites, using Yates' correction. A generalized linear mixed model with the "ordinal" package in R using greenhouse vigor data (Chapter 1) was used to provide additional context for the field trial results of the genetic entries.

2.3 Results

2.3.1 Interspecies Comparison

In a linear model considering both species and site as a factor, Douglas fir had a negative impact on vigor in November 2024 in comparison with coast redwood (Figure 20). Douglas-fir for the field trial was of the same nursery stock as those used in the greenhouse (Chapter 1) and faced high mortality in field conditions as well. Sites also had negative effects on plant vigor relative to the reference Sandy Loam site, following the gradient predicted by site quality. Glacial moraine has a substantial and significantly negative effect on the vigor of plants, with high mortality for both species (Figure 20).

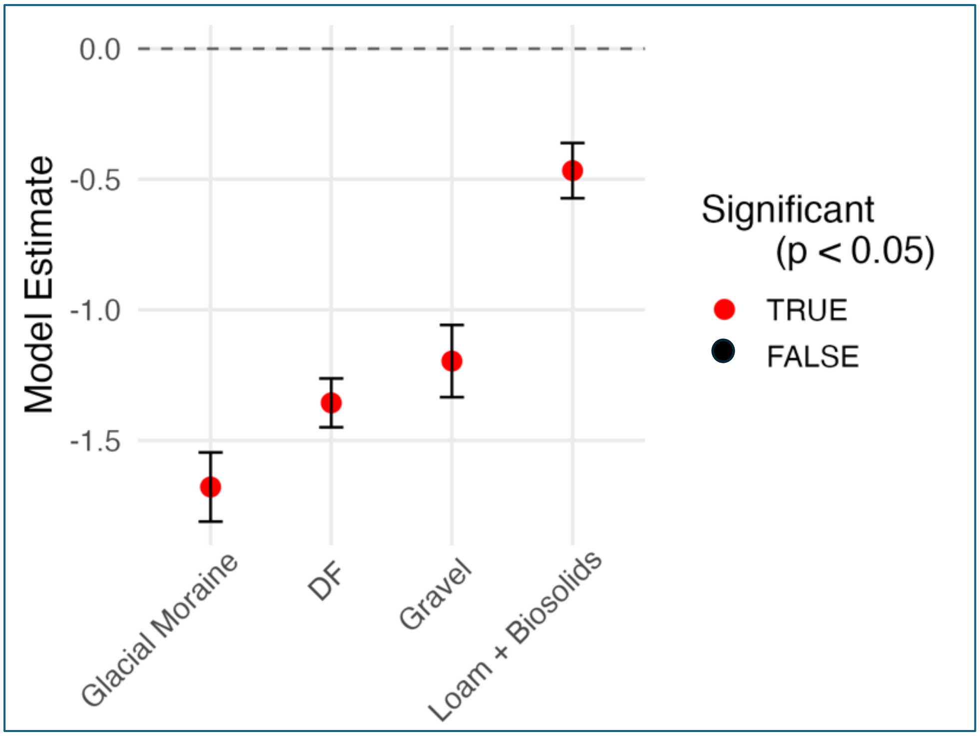


Figure 20 Linear Mixed Model testing the effect of species (DF- Douglas-fir relative to Coast Redwood) and site (Loam + Biosolids, Glacial Moraine, and Gravel, relative to Sandy Loam,) on November 2024 vigor. Negative model estimates in red all had significantly lower vigor than the reference.

Douglas-fir outcomes were clearly affected by nursery stock issues, of the 354 seedlings planted only 74 Douglas-fir remained alive (79% mortality) 10 months after planting (Table 5). However, coast redwoods also reached >30% mortality (259/759) in their first 10 months after planting. Chi-squared test indicated that overall morality was significantly different between species (p< 2.2e-16). This is supported by the Wilcoxon's test for each individual site which indicates significant ($p < 0.001$ for each site) differences in vigor for each species, which includes mortality but also health of living plants (Table 4).

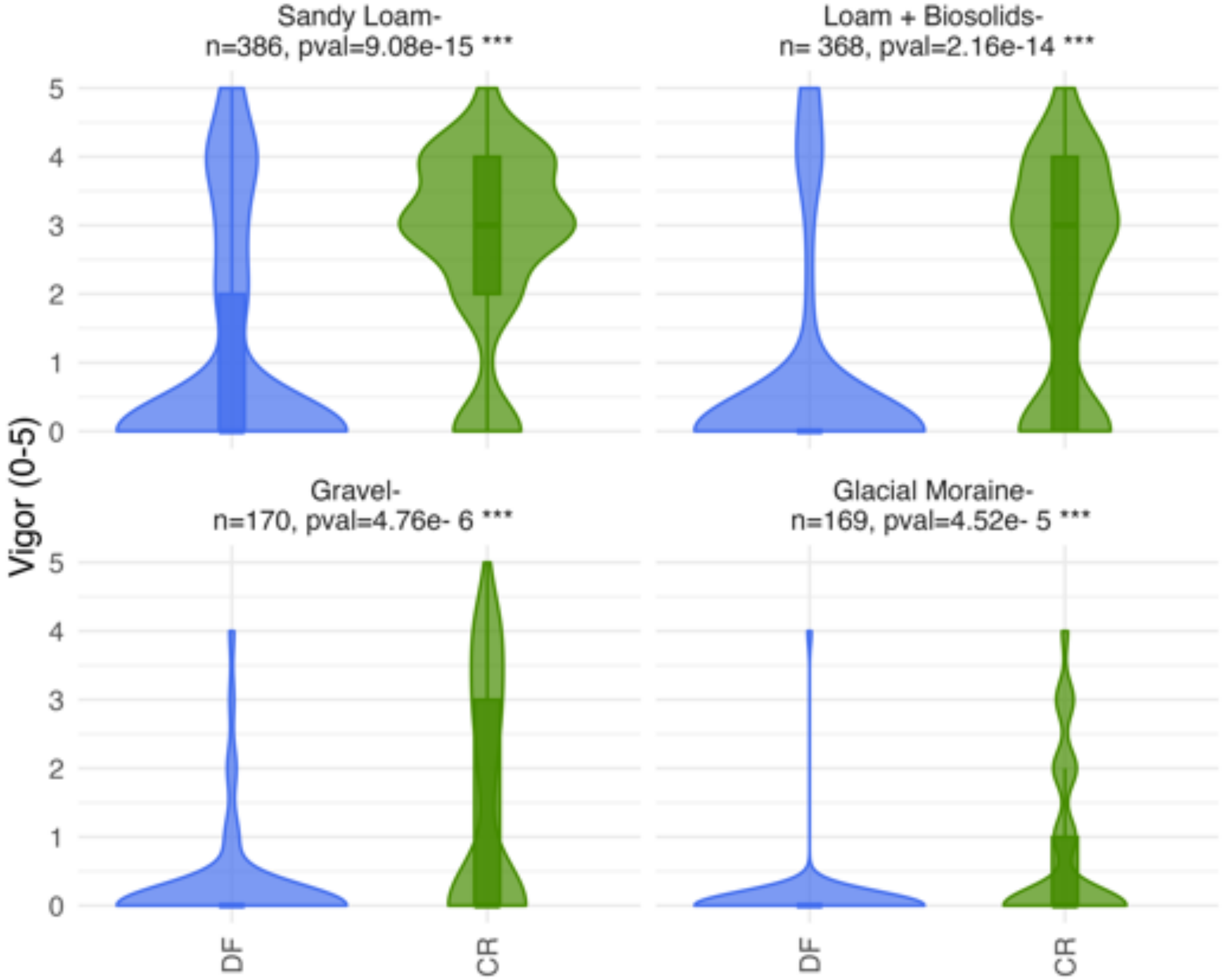


*Figure 21 Wilcoxon test comparing November 2024 vigor, 10 months after planting between coast redwood (CR) and Douglas-fir (DF) at each site. Coast redwood seedlings (CR, green) had significantly greater survival than Douglas-fir (DF, blue) on all sites, P < 0.001=***.*

Table 5 Summary table of establishment mortality (from planting in March to July first measurement) total mortality, vigor, root collar diameter (RCD), and height for each species (all genotypes combined) per site November 2024. Bottom two lines include the values for all the sites combined.

Species	Site	Count	Establishment Mortality	Establishment % Mortality	Total Mortality	Total % Mortality	Mean Vigor	St dev Vigor	Mean RCD	Mean Height
CR	Sandy Loam	262	30	11.45	40	15.27	2.73	1.38	5.37	36.28
CR	Loam + Biosolids	253	21	8.30	72	28.46	2.24	1.62	4.47	34.91
CR	Gravel	113	7	6.19	63	55.75	1.40	1.68	4.39	35.69
CR	Glacial Moraine	131	19	14.50	84	64.12	0.76	1.16	3.86	33.97
DF	Sandy Loam	124	75	60.48	81	65.32	1.14	1.71	6.61	29.74
DF	Loam + Biosolids	115	54	46.96	92	80.00	0.70	1.53	5.85	30.65
DF	Gravel	56	20	35.71	49	87.50	0.25	0.77	6.06	21.64
DF	Glacial Moraine	59	32	54.24	58	98.31	0.07	0.52	5.40	46.00
CR	Total	759	77	10.14	259	34.12	2.03	1.64	4.66	35.50
DF	Total	354	181	51.13	280	79.10	0.68	1.44	6.07	29.50

2.3.2 Redwood Comparison

Overall, many of the coast redwood genetic entries had similar levels of survival from March 2024 planting to November 2024, one full growing season and cold temperatures since planting (Figure 18). A Dunn’s test shows that two clone lines (CR-3 and CR-20) differ significantly from at least 3 other high vigor clone lines. CR-3, which also had early mortality in the greenhouse trial (Chapter 1), had significantly lower vigor overall than 6 other clones (Figure 22 A) and the highest mortality rate- 67% (Table 6). Only the effect of the poor sites, glacial moraine and gravel, was stronger than the negative effect of CR-3 on vigor (Figure 22). The glacial moraine and gravel site had a more extreme effect than the next six clone lines which all still had negative effects on November vigor when compared to the reference seedling CR-121.

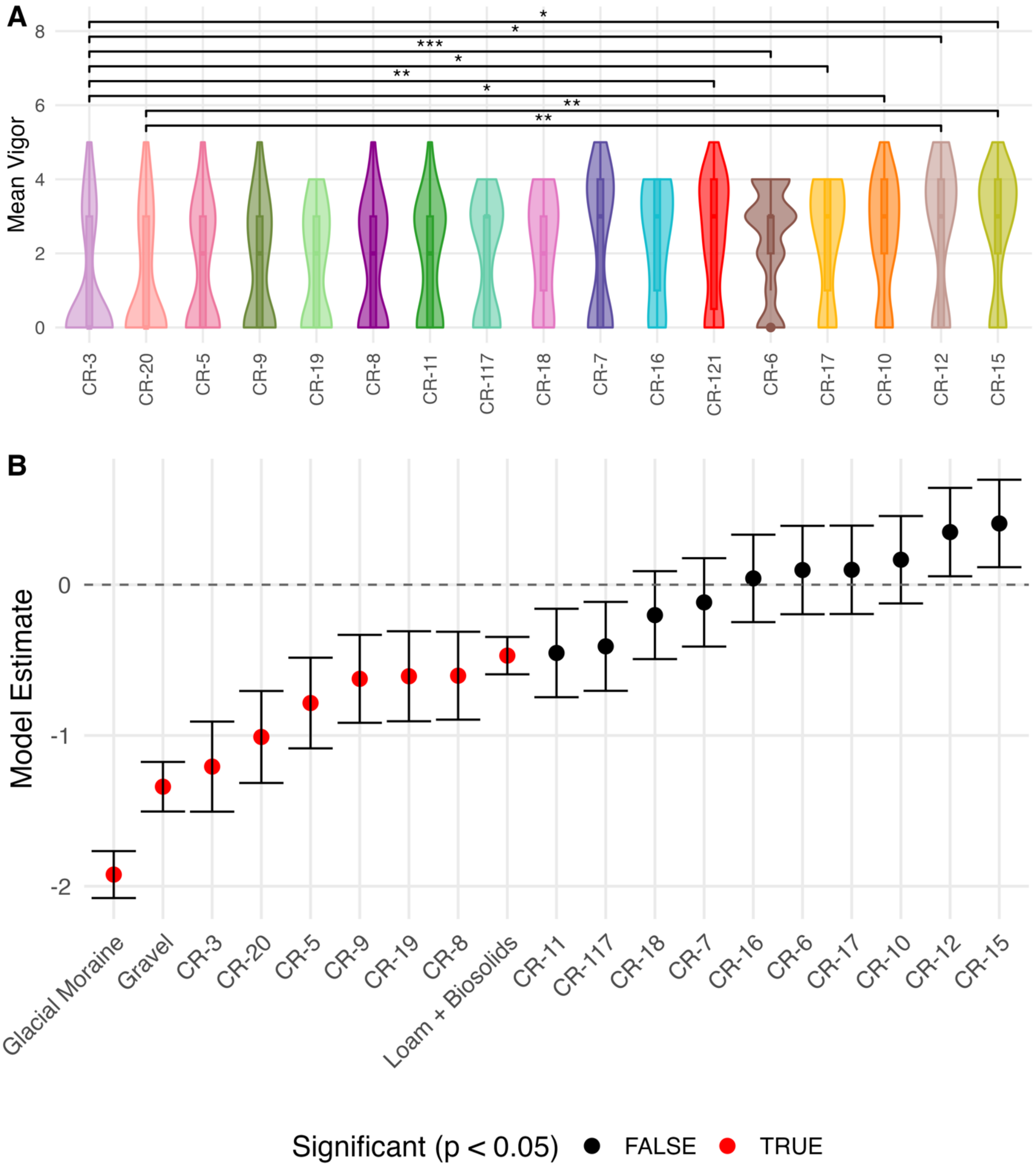


*Figure 22 A. Kruskal Wallis ($p < 0.05$) post hoc comparison Dunn's Test shows significant differences in vigor for CR-20 and CR-3 as significantly lower vigor. B. Linear mixed model to predict the influence of factors, genetic entry and site on plant vigor. Plot included as random variable. Categorical variables compared to CR-121 for genetic entry and Sandy Loam for sites. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$.*

While analysis focuses on vigor and mortality as of November 2024, it is important to distinguish early establishment mortality. The early summer (Establishment Mortality) measurements show a group of genetic entries with higher mortality (CR-3, CR-20, CR-5, and CR-19), and 4 with no mortality (CR-121—the reference seedling, CR-6, CR-10, and CR-18). Table 6 indicates that the majority of the mortality took place between measurements in June/July and November. These post establishment months experienced the highest temperatures and likely the highest VPD (Figure 18). Plants measured in November had yet to experience a freeze (Figure 18).

Table 6 Summary of genetic entry count, establishment mortality (planting in March to first measurement in July), total mortality), vigor, RCD and height across all sites as measured in November 2024.

Code	Count	Establishment Mortality	Establishment % Mortality	Total Mortality	Total % Mortality	Mean Vigor	St dev Vigor	Mean RCD	Mean Height
CR-3	42	24	57.14	28	66.67	1.07	1.63	2.87	29.25
CR-5	41	12	29.27	20	48.78	1.54	1.61	3.64	29.05
CR-6	45	0	0	8	17.78	2.4	1.4	6.4	54.04
CR-7	45	3	6.67	18	40	2.16	1.89	4.5	24.8
CR-8	46	3	6.52	19	41.3	1.72	1.57	3.97	29.67
CR-9	46	2	4.35	20	43.48	1.63	1.6	3.6	23.92
CR-10	47	0	0	10	21.28	2.45	1.54	5.8	40.86
CR-11	45	3	6.67	15	33.33	1.87	1.53	5.05	37.47
CR-12	45	1	2.22	13	28.89	2.64	1.82	4.51	28.08
CR-15	47	1	2.13	10	21.28	2.7	1.6	5.08	40.43
CR-16	47	0	0	9	19.15	2.34	1.48	5.28	45.58
CR-17	45	3	6.67	10	22.22	2.4	1.51	5.89	46.37
CR-18	46	0	0	11	23.91	2.09	1.47	5.64	37.01
CR-19	42	6	14.29	17	40.48	1.67	1.52	3.75	26.4
CR-20	39	17	43.59	23	58.97	1.23	1.63	3.04	18.63
CR-117	44	2	4.55	16	36.36	1.89	1.57	4.34	33.39
CR-121	47	0	0	12	25.53	2.36	1.62	4.62	30.53

Growth, measured by stem volume change (from summer to November 2024) was not significantly different in a Kruskal Wallis test ($p>0.05$). Decreases in stem volume can occur through death of leader, wilting, or even death of most of the plant but where a small resprout remains. A linear mixed model shows that the genetic entries had different impact on predicted growth amount between June/July and November 2024. Reference seedling CR-121 had the lowest stem volume change (Figure 23 A), and no clone lines had a significant negative impact on stem volume growth compared to the reference (Figure 23 B). The clone lines that had significant positive impact on growth CR-10, and 17, also had positive impact on vigor but were not significant (Figure 22 B, Figure 23 B). All sites had a negative impact on stem volume change relative to the reference site Sandy Loam. This may be affected by stem volume change only capturing growth on living plants.

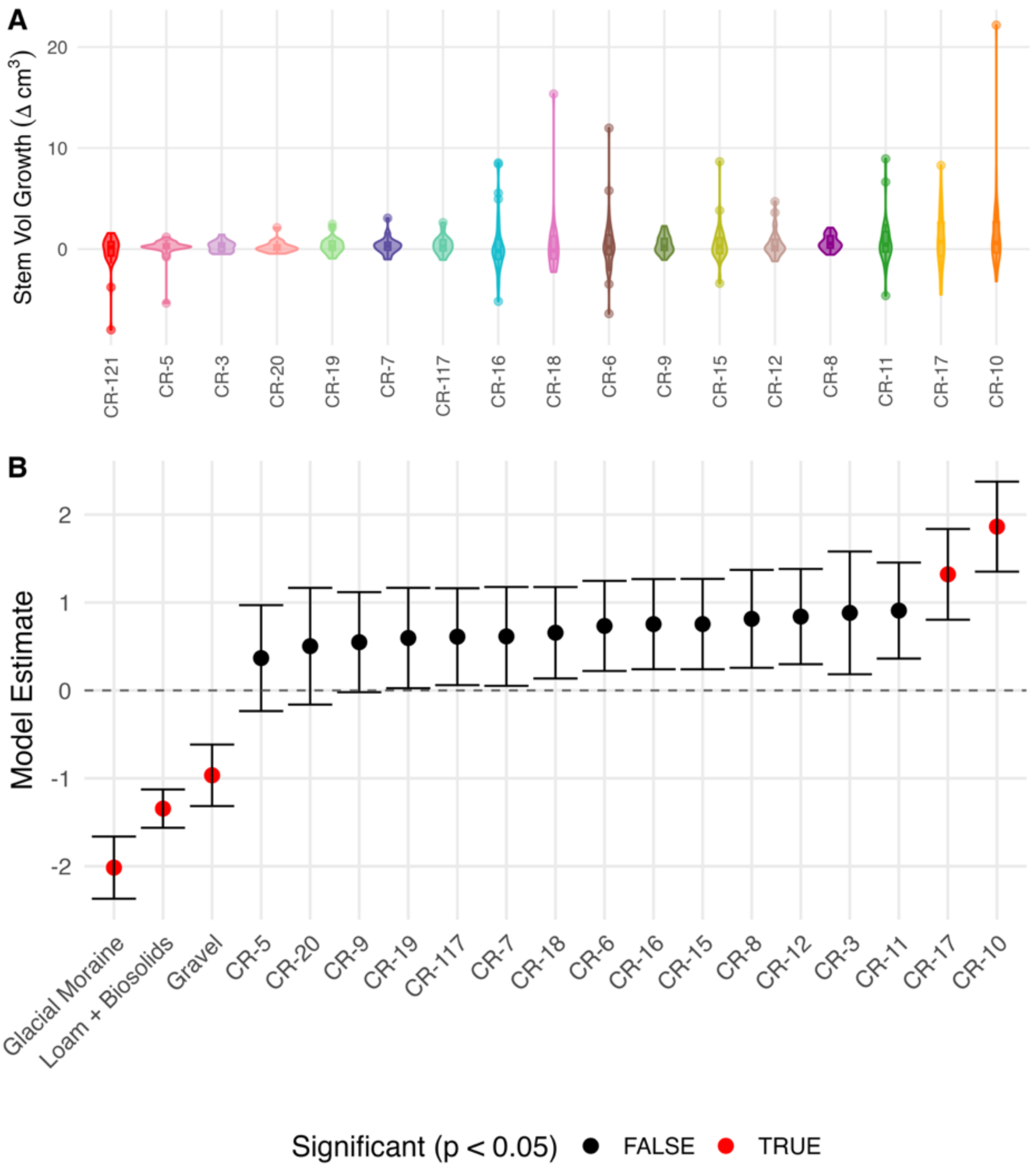


*Figure 23 A. Kruskal Wallis ($p = 0.62$) shows no significant differences between stem volume growth for redwood genetic entries between June/July 2024 and November 2024, listed in order of mean stem volume change. B. Linear mixed model to predict the influence of genetic entry (reference CR-121) and site (reference Sandy Loam) on plant stem volume growth. Plot included as random variable. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$*

2.3.3 Site Quality Comparison

Average vigor for coast redwoods increases with the predicted site quality index, related to soil drainage but also possibly nutrient availability. As referenced in Figure 22, the glacial moraine had the strongest negative impact on plant vigor and the highest mortality (~64%). The sandy loam site has maintained a mean measurement of ~3 vigor, meaning most of the plants were still alive (~15% mortality) and the remaining plants are mostly healthy (Table 7). This site is the highest soil quality but on the higher end of elevation (469.3 m).

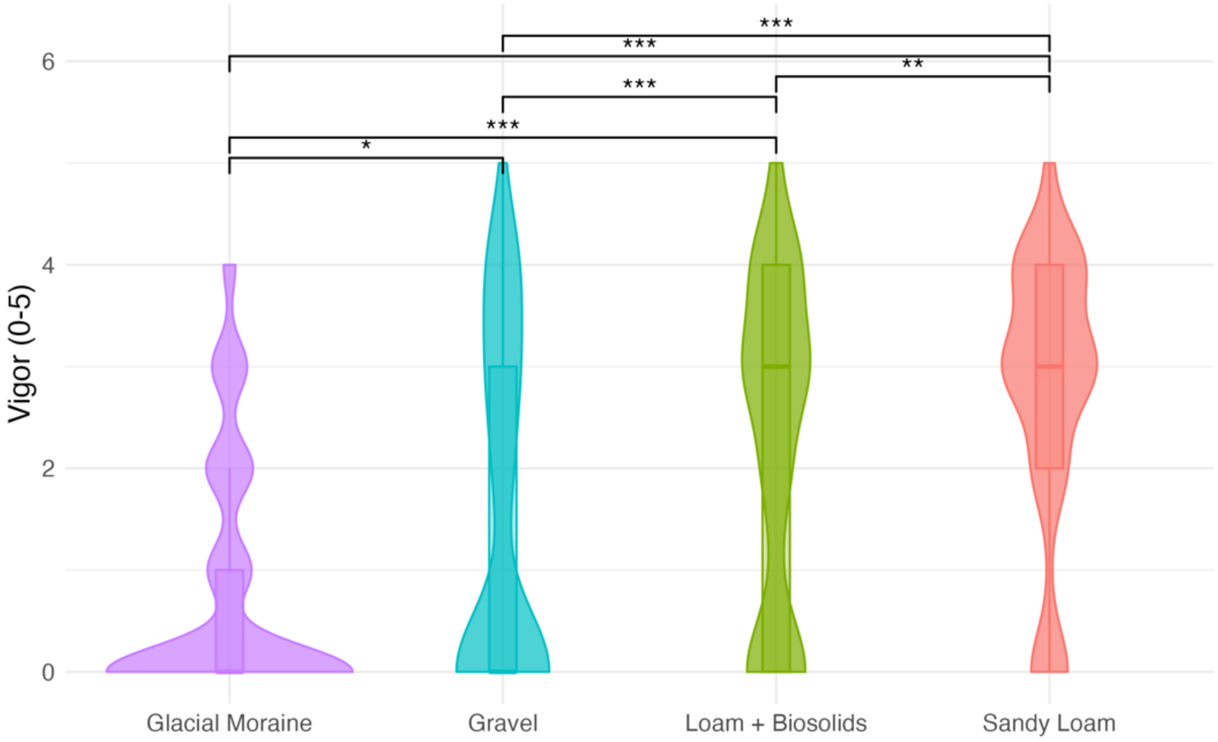


*Figure 24 Kruskal Wallis test for difference in vigor of redwoods at planted sites ($p < 0.05$), post-hoc Dunn's test shows levels of pairwise significance ($p < 0.05$) between sites. *** significance at $p < 0.001$, ** significance at $p < 0.01$, * significance at $p < 0.05$.*

Table 7 Site summaries for redwood only establishment mortality (planting in March to first measurement in July), total mortality, vigor, RCD and height.

Site	Count	Total Mortality	Total % Mortality	Mean Vigor	Std Dev Vigor	Mean RCD	Mean Height
Sandy Loam	262	40	15.27	2.73	1.38	5.37	36.28
Loam + Biosolids	253	72	28.46	2.24	1.62	4.47	34.91
Gravel	113	63	55.75	1.40	1.68	4.39	35.69
Glacial Moraine	131	84	64.12	0.76	1.16	3.86	33.97

2.3.4 Field Survival in Drought Tolerance Context

To determine possible factors in determining redwood success in field plots, investigating root-to-shoot ratio could contribute to redwoods' ability to establish in a site and lead to higher survival. We used initial root and shoot length measurements of the genetic entries matching those in the field, prior to being planted in the greenhouse. There is a significant positive correlation between root-to-shoot ratio and mortality, surprisingly, higher root length investments did not lead to increased survival, but rather the opposite ($p < 0.05$). It is possible that cultivars able to have the largest amount of healthy above ground tissue were able to establish earlier than annual weeds, or perhaps had better early carbon gain while soil moisture was not limiting.

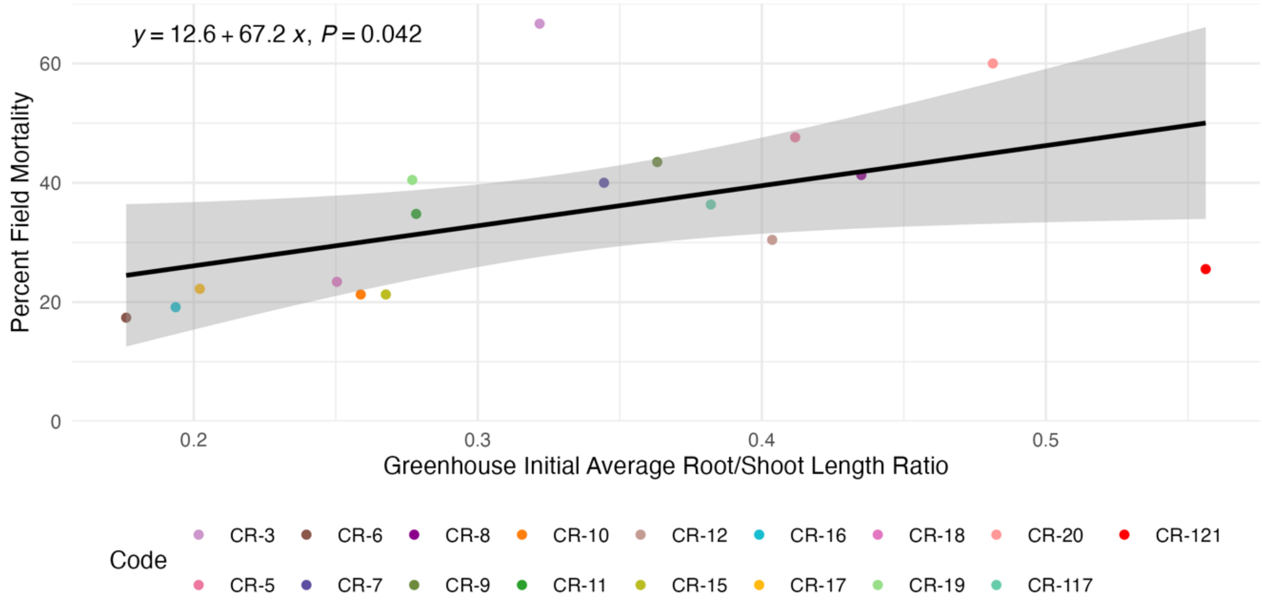


Figure 25 Linear regression of initial root to shoot length ratio per genetic entries planted in the greenhouse (Chapter 1, same nursery stock as planted in the field, measured prior to experiencing drought stress) positively correlated (p=0.042) to percent field mortality as measured in November 2024, 10 months after planting.

Drought tolerance in the greenhouse drought trial (Chapter 1) also did not translate to higher survival in inland western Washington field conditions. Average survival time in the greenhouse had no significant correlation with percent field mortality per genetic entry (Figure 25). Clone lines with the highest mortality, CR-3 (67%) and CR-20 (60%) in the field had opposite performance in the drought trial (Figure 26, Table 6). One of the clone lines with the lowest mortality in the field CR-6 (17%), had one of the fastest mean times to death in drought conditions (Table 6).

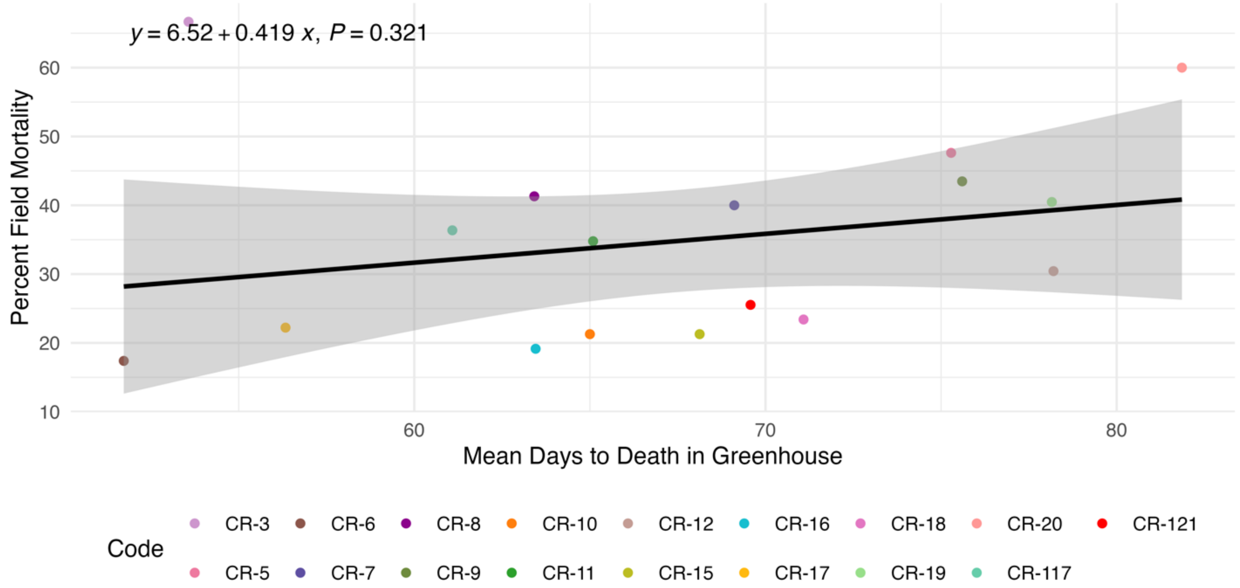


Figure 26 Linear regression of the average time to death for each genetic entry in the greenhouse drought conditions (Chapter 1, July 1- October 10, 2024) and percent mortality in the as measured in November 2024 field plots.

2.4 Discussion

Impacts of Species

Opposite to the original hypothesis that Douglas-fir would perform better than coast redwood, coast redwood had higher survival and vigor than the native species Douglas-fir. However, these results should be understood within the context of the nursery stocking issue. Douglas-fir mortality in this field trial reached 80% in only 10 months in the ground, compared to expected mortality ~20% within five years for trees planted in western Washington (Trobaugh, 2012). Redwood mortality across all sites (34%), is already above the expected value for Washington but compares to 31% mortality in Kerhoulas and Polda’s 2020 study planting redwoods in xeric, inland California in variable retention treatment groups, where redwoods also outlived native Douglas fir (41%). However, it is important to note that the impacts of species differences had less of an effect on plant vigor than the effect of growing in the worse site, glacial moraine (Figure 20). The lowest coast redwood mortality was found on a south facing aspect, sandy loam soil (15%, Table 5), suggesting coast redwood plantations might be easier to establish on better soils.

Impacts of Genetic Entry

As part of this study, we hoped to find redwood clone lines best suited to western Washington conditions. Coast redwoods are a hexaploid and thus have wide genetic diversity which could translate to specific genotypic matching to environmental conditions (Kapste et al., 2020; Kruser et al. 1995). While many of the clone lines performed roughly the same, and comparable to the seedling, there were a number that had significantly lower vigor (6/16 clones). In contrast, no redwood clone (selected from a group of commonly used for plantations in CA) performed significantly better than the seedling stock in vigor but 2 with significantly greater growth. Previous studies have found that redwoods exhibit provenance genotypic differences commensurate with the small latitude range of their native habitat and thus may have limited optimization to target locations (Kruser et al., 1995, Dagley et. al, 2017). It is important to note that results presented here represent the first-year establishment and may not be indicative of longer-term survival nor growth.

Drought tolerance in a greenhouse setting and length of relative root: shoot investments did not positively correlate with survival in the field (respectively $p = .342$, and $p = 0.034$ negative correlation). This result was unexpected. It is possible that other environmental factors (e.g., soil temperatures, vegetation cover, depth to suitable mineral soil, nutrient availability), not soil moisture, drove differences in vigor at each site. Other research has demonstrated redwoods' ability to survive and adapt to xeric inland conditions (Kerhoulas and Polda's 2020; De la Torre et al., 2021). One limitation is that relative biomass investment was only sampled at the end of the greenhouse drought trial; initial biomass is unknown for each redwood clone line, and length of roots is a poorer reflection of root investment.

When comparing the ranking of redwoods in both greenhouse drought and field conditions using the same response variable of Vigor, only 2 genetic entries showed similar responses (Figure 22 A, Figure 27). CR-3 is consistently low vigor in both field and greenhouse. CR-12 has a significant positive impact on vigor in the greenhouse and similarly positive but not significant impact on vigor in the field trial (Figure 22 A). CR-6, low vigor in the greenhouse has quite a positive effect on vigor in the field. Conversely, CR-11 and 16 have significant positive impact on vigor predictions compared to the reference in the greenhouse but fair unremarkably in the field.

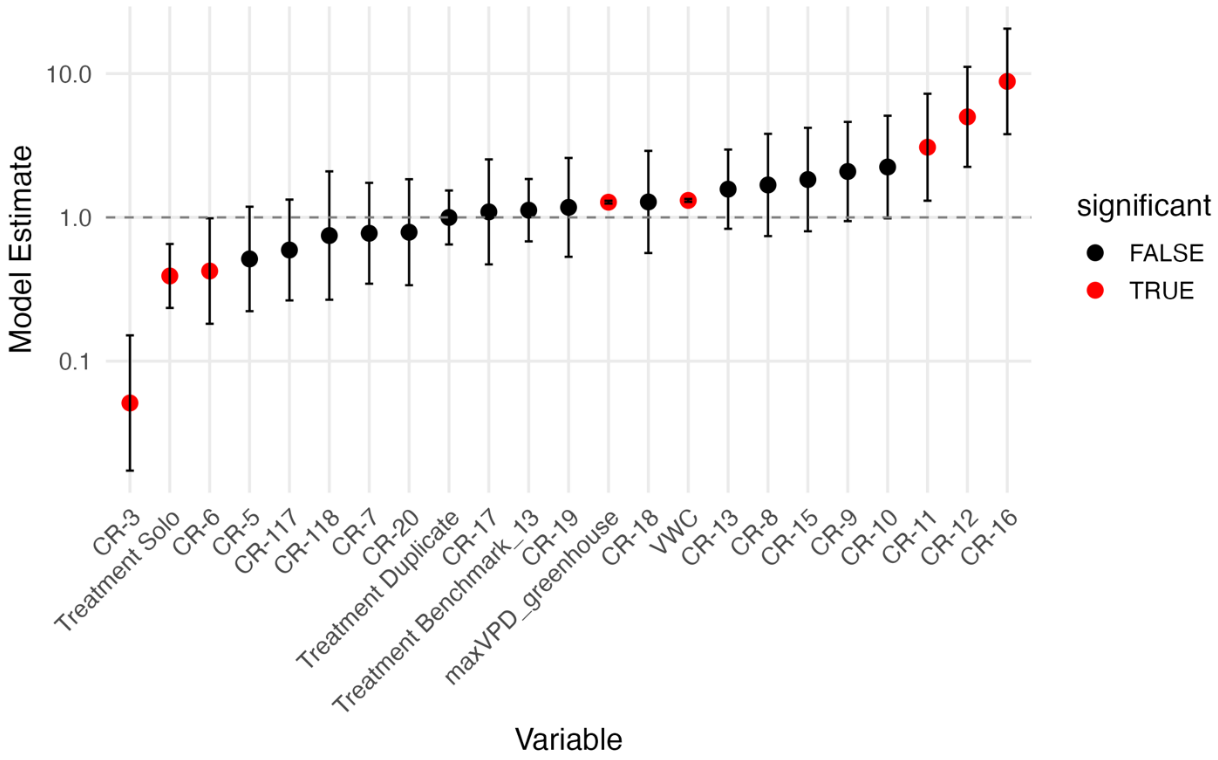


Figure 27 GLMM compares coast redwood genetic entries, treatment groups (solo pots, duplicate pots, benchmark_121 and benchmark_13) and environmental factors (Time, VWC, max VPD) as recorded in Chapter 1 and their impact on vigor collected weekly throughout drought periods. Categorical variables are compared for significance relative to reference seedling, CR-121, and reference for treatment using "Benchmark 121" pot (i.e., two plants of the same species in one 2-gallon pot). Significance was set as $p < 0.05$.

Impacts of Site

Concordant with the hypothesis the performance would change with site quality, site differences had a strong effect on mortality which followed the site quality gradient that had been previously determined for Douglas-fir. Coast redwood native soils are mostly on the gravelly loam Gamboa soil series, and all the other minor soil types also consist of a well-drained gravely sandy loam (Borchert et al., 1988). All four sites at Pack Forest have well drained soils, but Wilkeson is a sandy loam with organic matter, able to hold on to high levels of soil moisture (National Cooperative Soil Survey, Wilkeson). The two Barneston soil sites have

>50% mortality (Table 7) and may be lacking enough loamy soil and organic matter for the coast redwoods to find enough nutrients and soil moisture for their extensive early growth (National Cooperative Soil Survey, Barneston). Both sites have a history of lower site index (105 and 95), on previous stands of Douglas-fir at those sites (Pack Forest Stand Database). This suggests that coast redwoods will struggle to survive, much less put on their characteristic height and carbon storage on excessively drained sites with lower ranking site index.

Further research could test for differences in soil moisture, nutrient availability and within site variability-microsite factors such as vegetative shading, abiotic coverage, in a depression, duff, clay or other factors that may be contributing to the differences between site vigor.

Limitations and Future Analysis

One obvious limitation in the study was the Douglas-fir nursery stock mortality rate created difficulty in comparing coast redwood and Douglas-fir. The field sites will be infilled with new Douglas-fir stock to allow future comparisons to be made in the same site conditions. Additionally, use of the growth data will become more useful through time, and multiple growing season measurements may highlight differences in site quality for both species.

All sites are far from not only coast redwood's current native range, but also outside of its immediate predicted future range (Figure 2, Fernández et al., 2015). Coast redwoods were exposed to the cold end of previously proven coast redwood range (January mean T = 2 °C, winter of 2024/25) with several freeze incidents, thus, future measurements will capture post winter mortality (Figure 18). With no significant differences in temperature between sites, it is unlikely to be a contributing factor in the differences in mortality between sites as of November 2024 (Figure 18). Future analysis could delve into the sites' location at the proven temperature range limitation of redwoods. Cold testing at different points throughout winter as well as tracking mortality following frost events could help understand the onset of cold hardening of redwoods and the extent of temperature as a limiting factor.

While there is much left to determine, coast redwood assisted migration has promising feasibility given the first 10-month survival rate. However, site and genetic entry selection were key factors in determining vigor during the first year.

Acknowledgements

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Supplemental Material

Chapter 1. Supplemental

Table S1. Interspecies Fixed Effects Generalized Linear Mixed Model, refers to Figure 12.

effect	term	estimate	std.error	statistic	p.value	conf.low	conf.high	significant
fixed	maxVPD greenhouse	0.11	0.01	8.17	3.07E-16	0.09	0.14	TRUE
fixed	VWC	0.06	0.01	6.51	7.38E-11	0.04	0.08	TRUE
fixed	DF	-1.79	0.38	-4.70	2.55E-06	-2.53	-1.04	TRUE
fixed	WRC	-1.37	0.33	-4.17	3.05E-05	-2.01	-0.73	TRUE
fixed	Treatment CR_DF	-0.57	0.46	-1.25	0.21	-1.47	0.33	FALSE
fixed	Treatment CR_WRC	-0.29	0.40	-0.73	0.47	-1.07	0.49	FALSE
fixed	Treatment Solo	-0.08	0.37	-0.21	0.84	-0.81	0.66	FALSE
fixed	Treatment WRC_DF	0.42	0.46	0.92	0.36	-0.47	1.32	FALSE

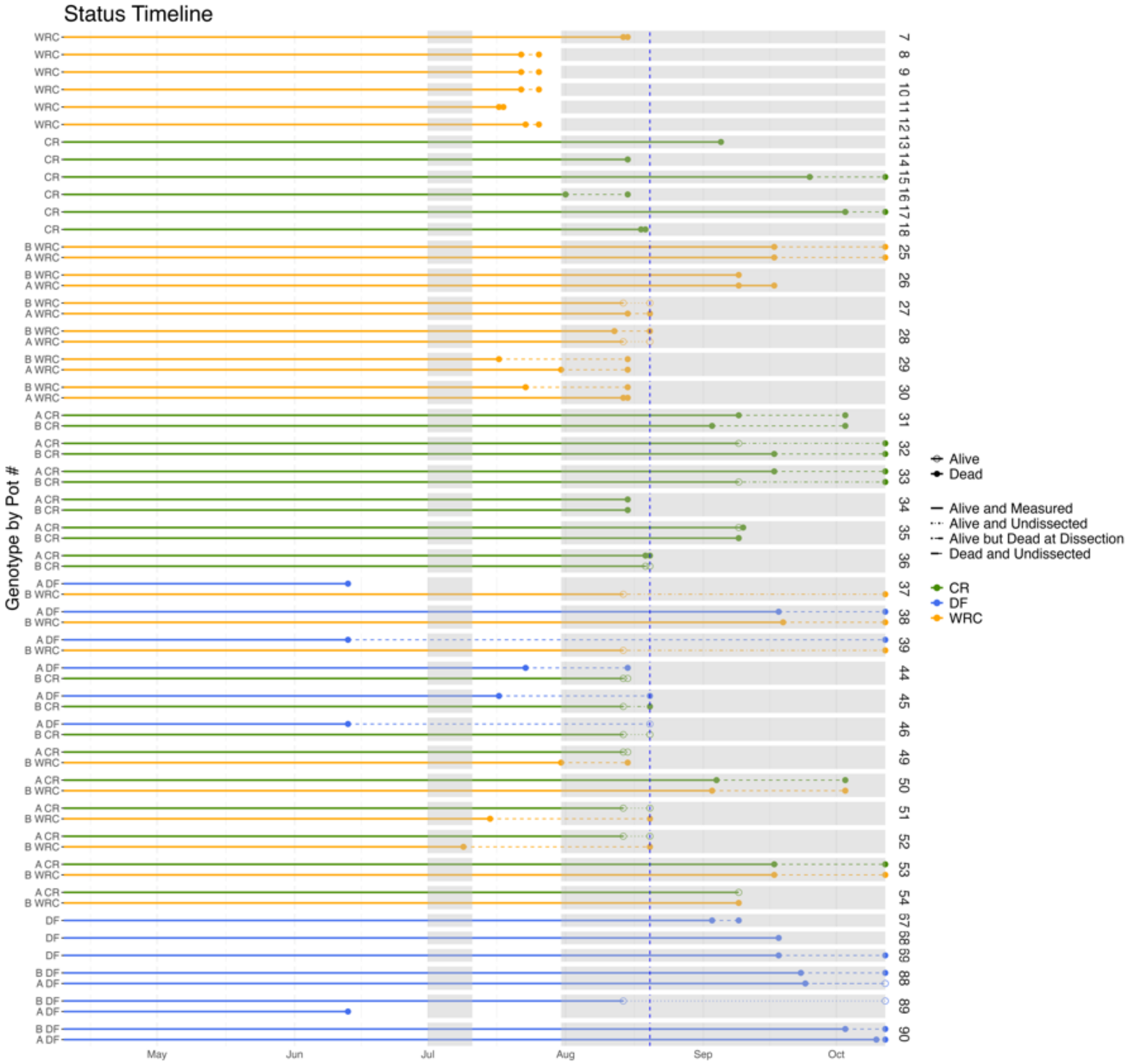


Figure S1. Interspecies Pot Flow Chart. This figure provides a graphical representation of each potted unit used in the study. Western redcedar (WRC, yellow lines), coast redwood (CR, green lines), and Douglas-fir (DF, blue lines) only labels with a single line represent a single seedling of each species respectively growing in a 1-gallon pot. Duplicate planted pots indicate pots where two of the same species were planted (i.e. duplicate A-CR, B-CR, etc.) or mixed-species pots (A-DF, B-CR). The length of the lines represents the survival of individuals in each pot.

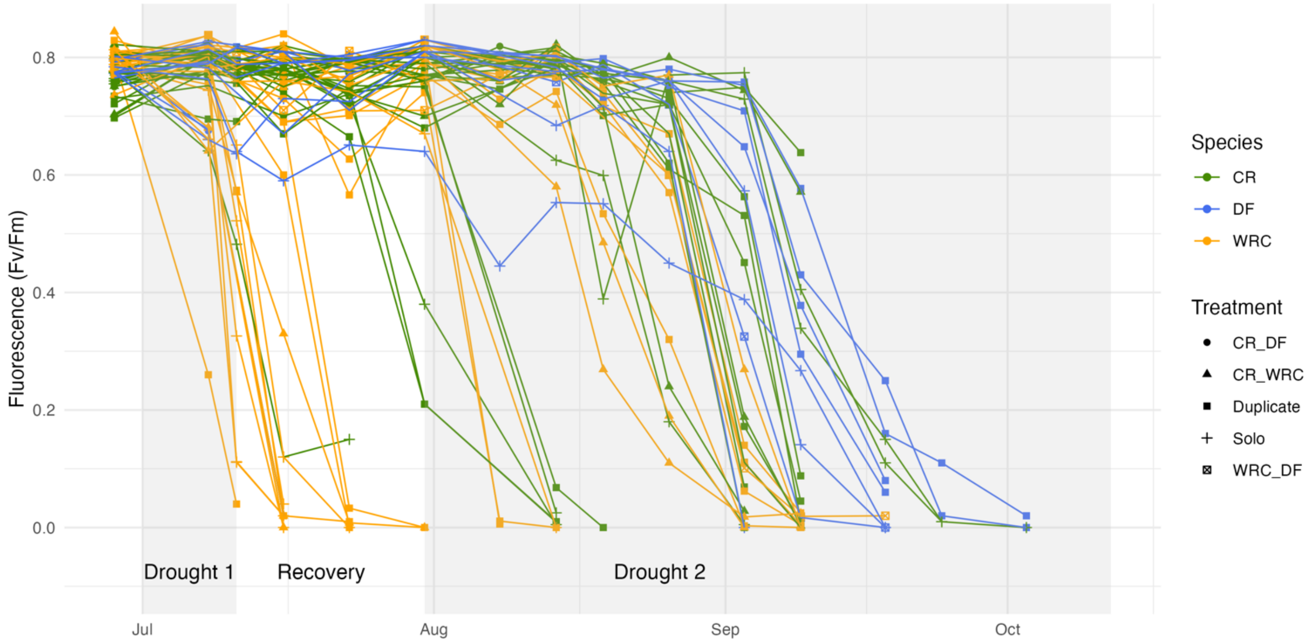


Figure S2. Fv/Fm of individual plants throughout the drought. Individuals are indicated by both species (color) and treatment groups (shape). Predrought mortality of Douglas-fir has been removed. Early mortality of western redcedar and one coast redwood are clearly visible during Drought 1 and Recovery. Surviving Douglas-fir do not have any mortality until far into Drought 2.

Table S2 Interspecies KM probabilities relating to Figure 6.

Treatment	Species	records	n.max	n.start	events	rmean	se(rmean)	median	0.95LCL	0.95UCL
CR_WRC	CR	61	61	61	13	81.41	3.67	79	70	NA
CR_WRC	WRC	92	92	92	62	65.53	3.02	70	64	79
Duplicate	DF	83	83	83	35	76.45	3.31	85	79	94
Duplicate	CR	163	163	163	65	78.15	1.95	79	70	85
Duplicate	WRC	164	164	164	95	68.98	2.22	70	64	79
Solo	DF	45	45	45	19	80.50	3.37	79	70	94
Solo	CR	89	89	89	50	72.38	2.88	79	70	85
Solo	WRC	95	95	95	77	57.61	3.06	56	49	70

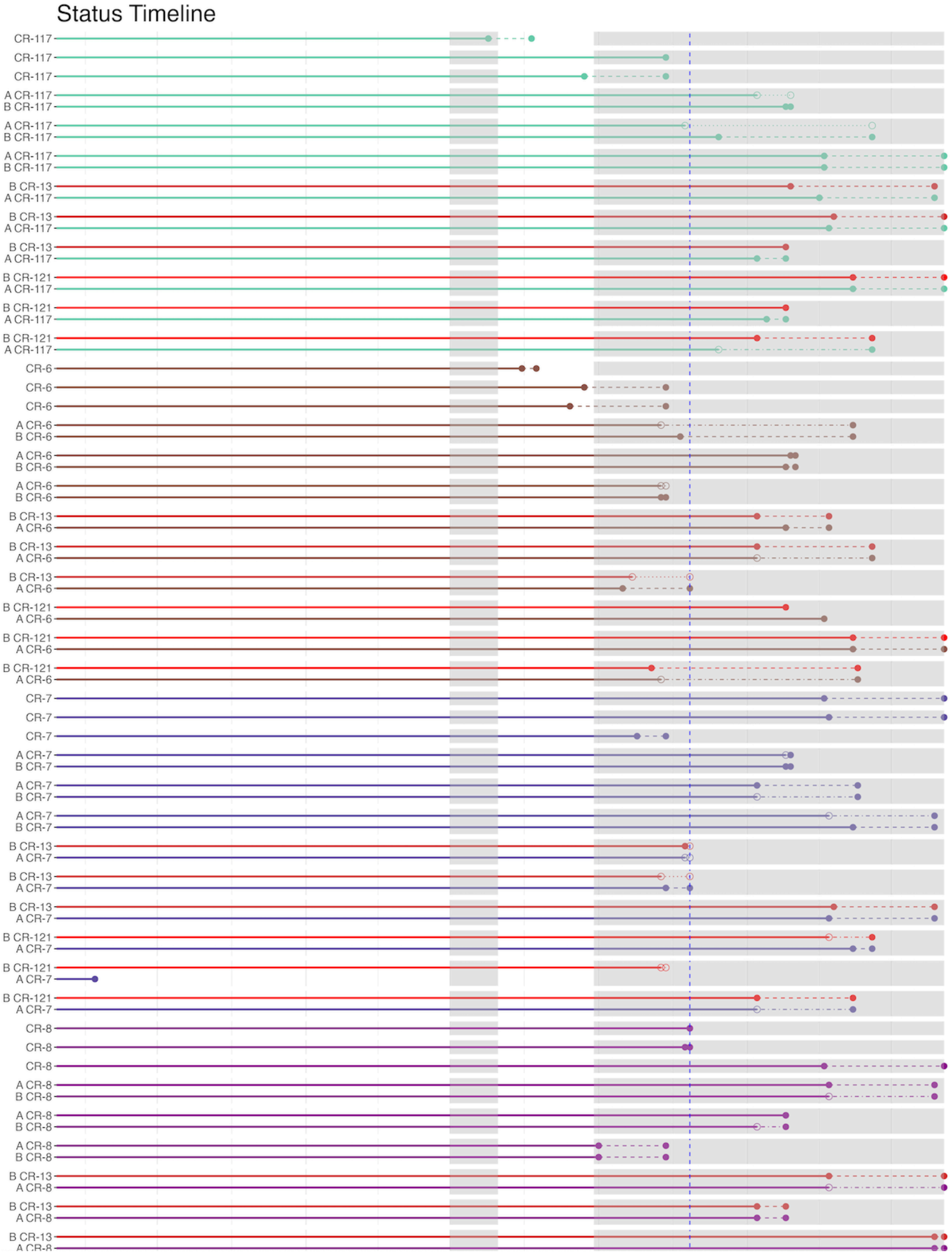
Table S3. Interspecies log rank comparison of KM curves for each treatment group within each Species, relating to Figure 6B.

Species	group1	group2	P Value	Significance
DF	Solo	Duplicate	0.70	
CR	Duplicate	CR_WRC	0.54	
CR	Solo	CR_WRC	0.34	
CR	Solo	Duplicate	0.34	
WRC	Duplicate	CR_WRC	0.49	
WRC	Solo	CR_WRC	0.22	
WRC	Solo	Duplicate	0.05	

Results Redwood Trial-

Table S3. Redwood Generalized Linear Mixed Model analysis relating to Figure 12.

effect	term	estimate	std.error	statistic	p.value	Conf low	Conf high	Sig
fixed	maxVPD greenhouse	0.09	0.00	21.47	2.73E-102	0.08	0.09	TRUE
fixed	VWC	0.10	0.00	24.50	1.39E-132	0.09	0.10	TRUE
fixed	CR-10	-0.34	0.32	-1.05	0.29	-0.96	0.29	FALSE
fixed	CR-11	-0.35	0.33	-1.05	0.29	-1.00	0.30	FALSE
fixed	CR-117	-0.28	0.32	-0.86	0.39	-0.90	0.35	FALSE
fixed	CR-118	-0.75	0.40	-1.87	0.06	-1.54	0.03	FALSE
fixed	CR-12	0.35	0.32	1.08	0.28	-0.28	0.97	FALSE
fixed	CR-13	0.04	0.25	0.17	0.87	-0.45	0.54	FALSE
fixed	CR-15	0.11	0.33	0.32	0.75	-0.53	0.75	FALSE
fixed	CR-16	0.32	0.32	0.99	0.32	-0.31	0.95	FALSE
fixed	CR-17	-0.53	0.32	-1.64	0.10	-1.16	0.11	FALSE
fixed	CR-18	0.28	0.33	0.84	0.40	-0.37	0.93	FALSE
fixed	CR-19	0.21	0.32	0.64	0.52	-0.42	0.83	FALSE
fixed	CR-20	0.20	0.35	0.58	0.56	-0.48	0.89	FALSE
fixed	CR-3	-2.80	0.41	-6.79	1.12E-11	-3.61	-1.99	TRUE
fixed	CR-5	-0.89	0.33	-2.72	0.01	-1.53	-0.25	TRUE
fixed	CR-6	-0.80	0.32	-2.50	0.01	-1.43	-0.17	TRUE
fixed	CR-7	-0.26	0.32	-0.82	0.41	-0.89	0.36	FALSE
fixed	CR-8	-0.31	0.32	-0.98	0.33	-0.94	0.31	FALSE
fixed	CR-9	0.26	0.32	0.82	0.41	-0.37	0.89	FALSE
fixed	Treatment Benchmark 13	-0.14	0.20	-0.70	0.48	-0.53	0.25	FALSE
fixed	Treatment Duplicate	-0.03	0.17	-0.17	0.86	-0.37	0.31	FALSE
fixed	Treatment Solo	-0.54	0.20	-2.69	0.01	-0.93	-0.15	TRUE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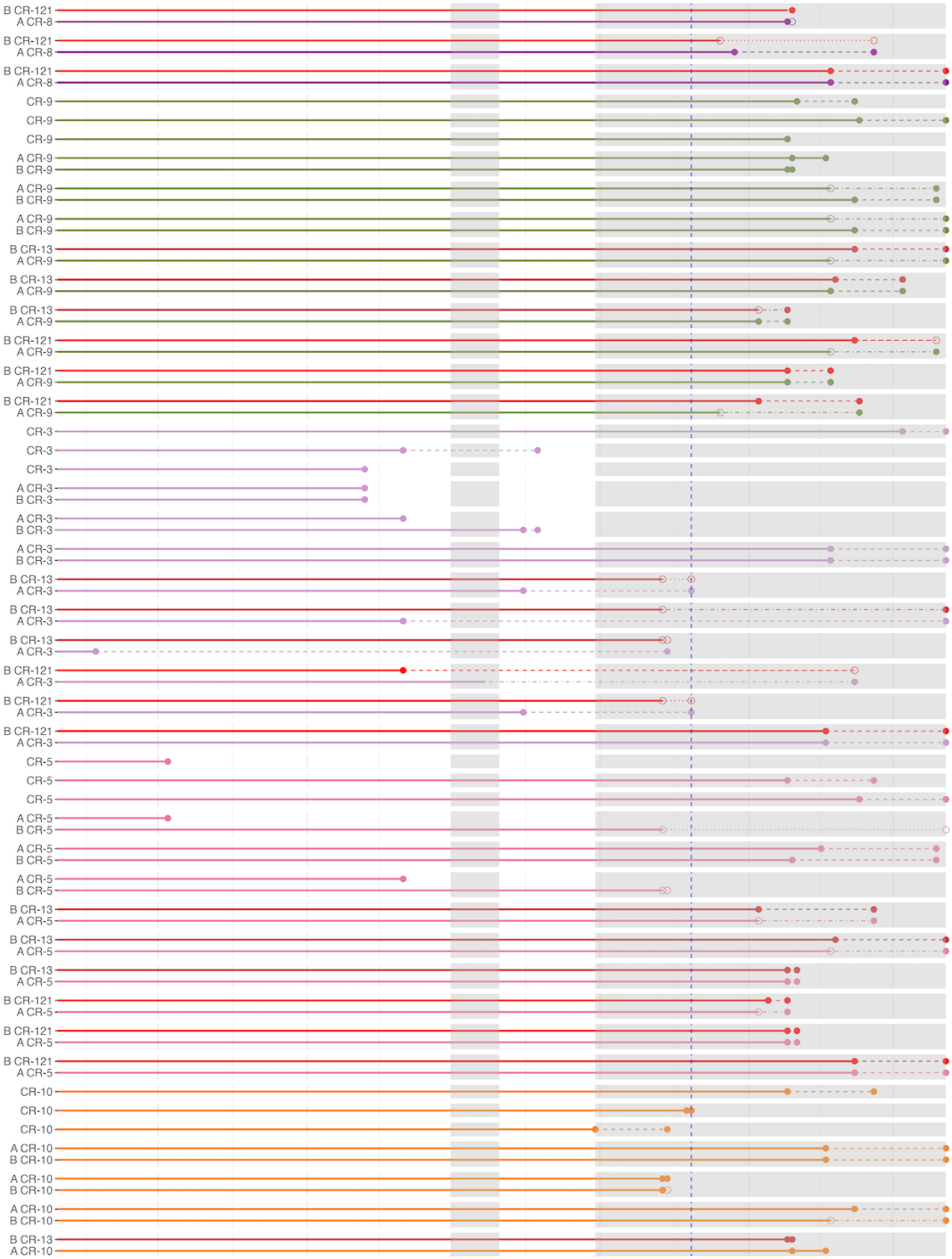
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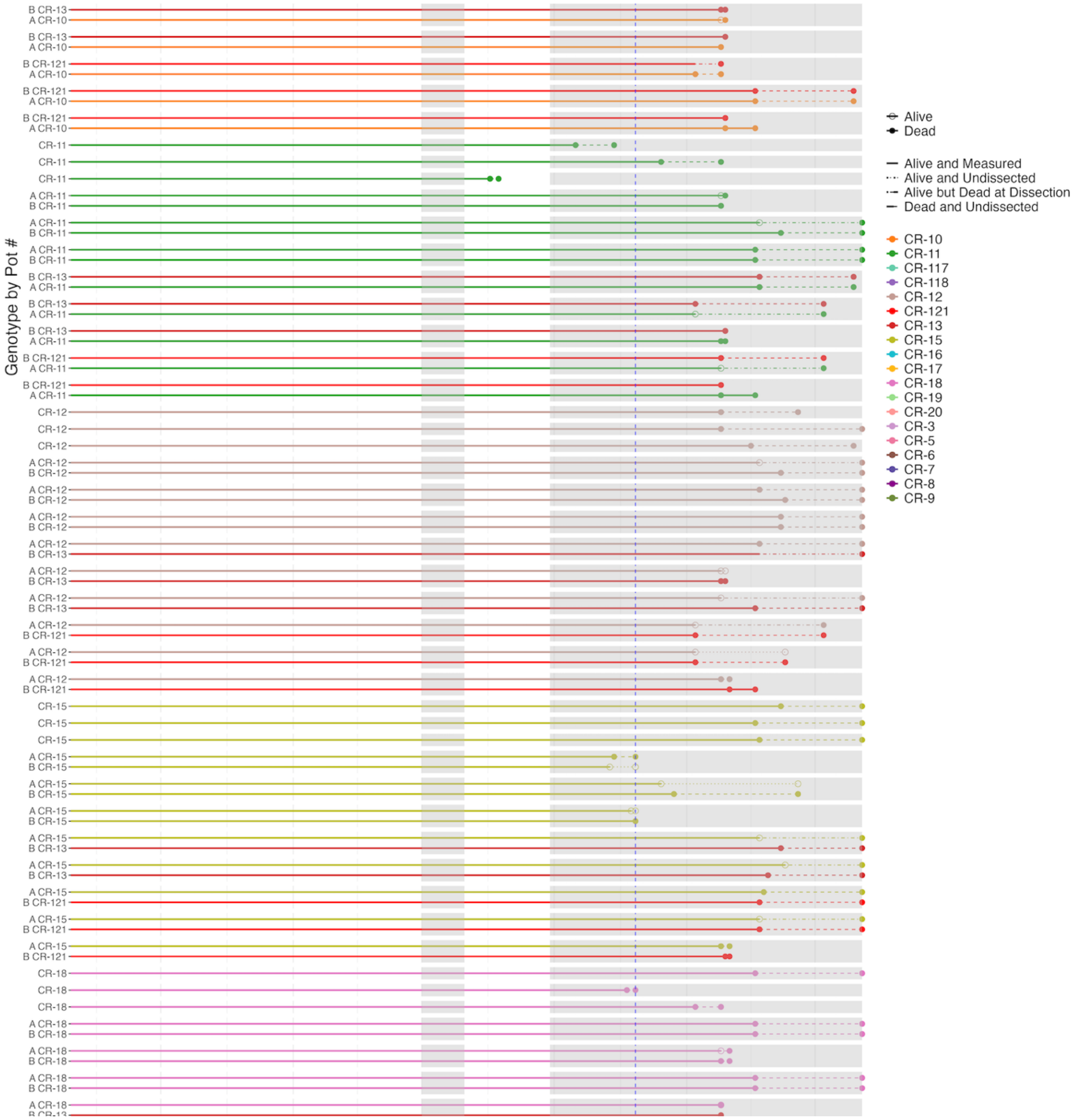
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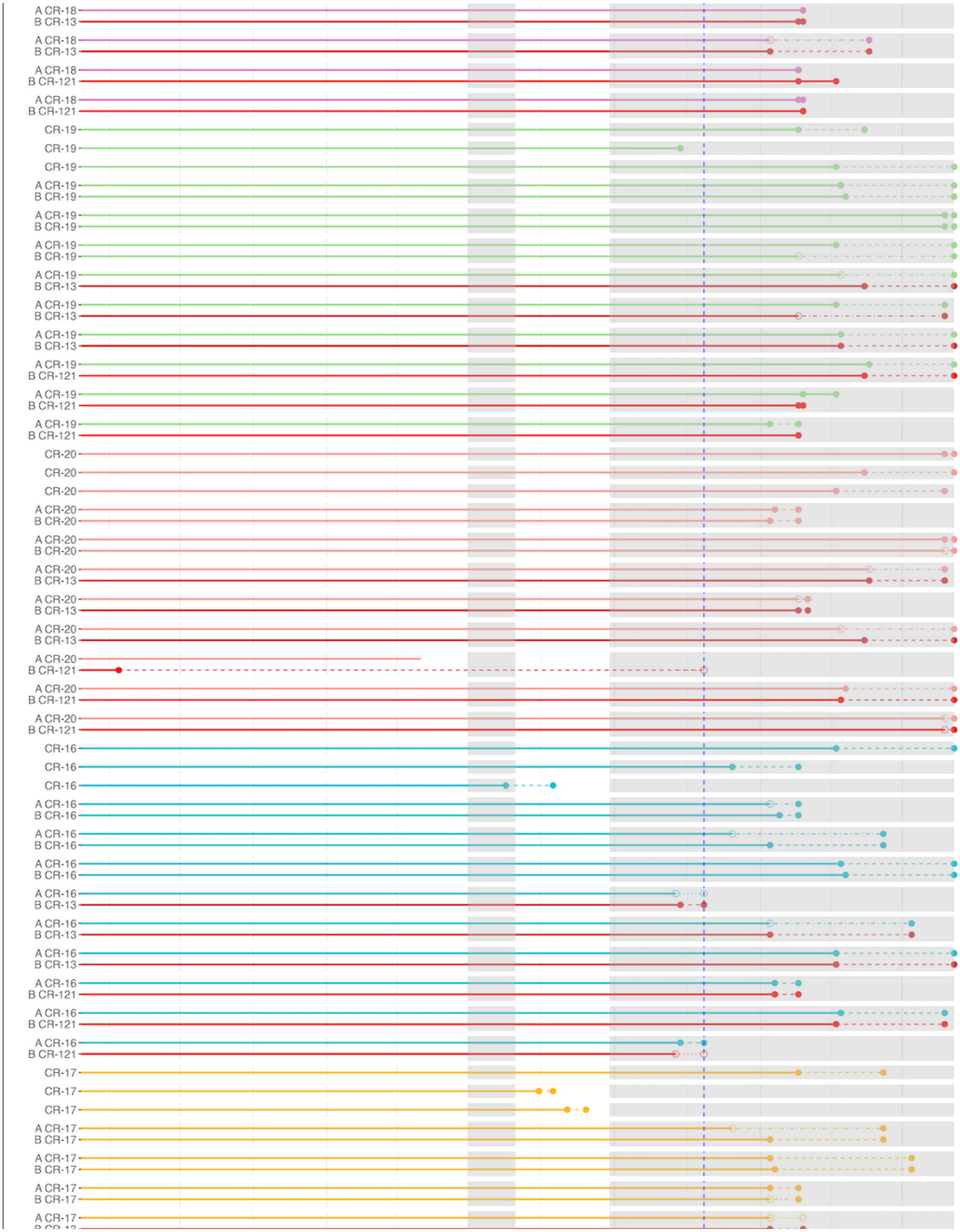
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A CR-20
B CR-20
A CR-20
B CR-13
A CR-20
B CR-13
A CR-20
B CR-13
A CR-20
B CR-121
A CR-20
B CR-121
A CR-20
B CR-121
CR-16
CR-16
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B CR-13
A CR-16
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A CR-17
B CR-17
A CR-17

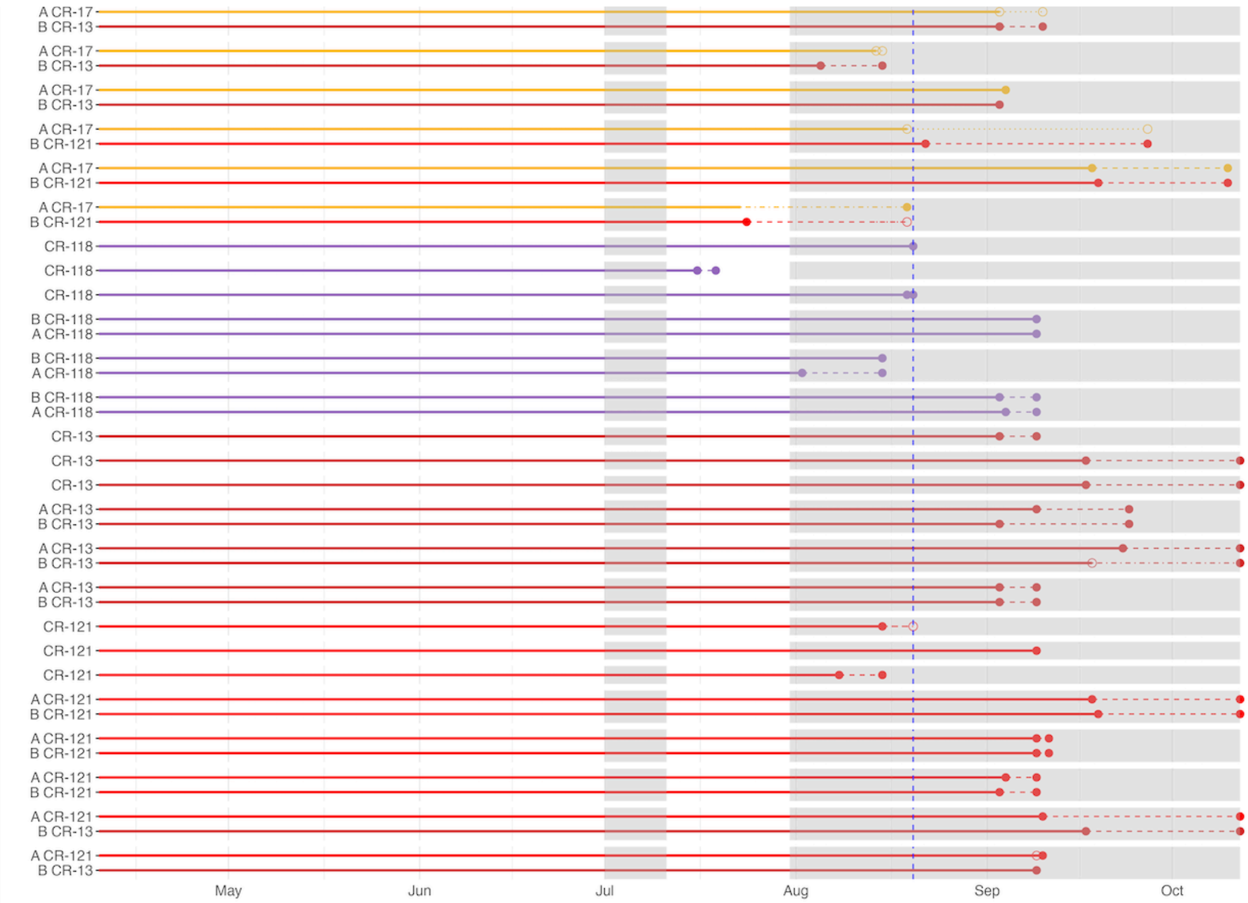

Figure S4. Redwood Pot Flow Chart indicating status of plants and timeline to biomass breakdown. Blue line indicates decision point where living plants were broken down once their pot partner died. Death dates for half of plants were lost for double pots after this date.

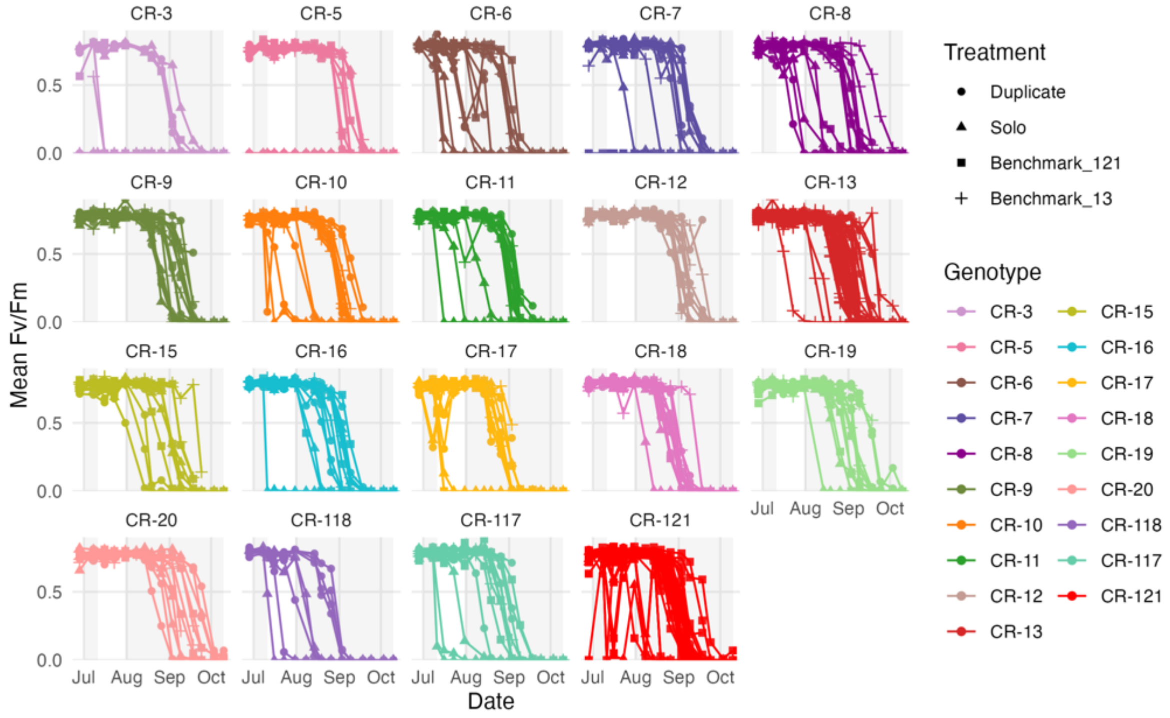

Figure S5. Fv/Fm value of individual plants grouped and colored by genetic entry and shapes indicate treatment group of data. Genetic entries CR-13 and CR-121 have larger sample sizes due to being planted in each pot for their corresponding benchmark treatment group.

Table S4. Redwood Kaplan Meir probabilities, simple Curves, relating to Figure 13A.

Code	records	N max	N start	events	R mean	Se	median	0.95LCL	0.95UCL
CR-3	213	213	213	174	27.27	2.20	34	26	40
CR-5	197	197	197	87	42.44	2.26	49	40	55
CR-6	197	197	197	100	40.77	2.06	40	40	49
CR-7	199	199	199	79	46.19	1.96	49	40	55
CR-8	210	210	210	94	46.35	1.75	49	40	55
CR-9	202	202	202	66	51.84	1.56	49	49	55
CR-10	215	215	215	100	46.30	1.72	49	40	55
CR-11	172	172	172	78	45.97	1.98	49	40	55
CR-12	202	202	202	59	53.27	1.58	55	49	64
CR-13	764	764	764	289	51.14	0.83	55	49	55
CR-15	153	153	153	59	48.09	1.97	49	40	55
CR-16	196	196	196	83	46.45	1.87	49	40	55
CR-17	182	182	182	83	41.32	2.18	40	34	49
CR-18	170	170	170	70	48.85	1.79	49	40	55
CR-19	212	212	212	74	53.38	1.48	55	49	64
CR-20	165	165	165	46	55.95	1.65	55	55	64
CR-118	136	136	136	82	40.01	2.33	40	34	49
CR-117	205	205	205	96	44.18	1.93	49	40	55
CR-121	806	806	806	333	49.53	0.83	49	49	55

Table S5. Redwood Pairwise Log Rank KM curve comparison by Genetic Entry, relating to figure 13A.

	CR-3	CR-5	CR-6	CR-7	CR-8	CR-9	CR-10	CR-11	CR-12	CR-13	CR-15	CR-16	CR-17	CR-18	CR-19	CR-20	CR-118	CR-117
CR-5	0.0005																	
CR-6	0.0059	0.6044																
CR-7	0.0000	0.5239	0.2081															
CR-8	0.0000	0.5648	0.2105	0.9706														
CR-9	0.0000	0.0491	0.0072	0.1978	0.1855													
CR-10	0.0000	0.5690	0.2105	0.9706	0.9996	0.1844												
CR-11	0.0001	0.6219	0.2623	0.9458	0.9706	0.1855	0.9706											
CR-12	0.0000	0.0115	0.0015	0.0778	0.0682	0.6710	0.0680	0.0697										
CR-13	0.0000	0.0100	0.0005	0.1267	0.1012	0.9252	0.0976	0.1109	0.5162									
CR-15	0.0000	0.3837	0.1636	0.8031	0.7923	0.3653	0.7898	0.7522	0.1863	0.3233								
CR-16	0.0000	0.5386	0.2105	0.9996	0.9717	0.2066	0.9706	0.9510	0.0828	0.1381	0.8143							
CR-17	0.0046	0.6877	0.9458	0.2623	0.2623	0.0103	0.2623	0.3280	0.0026	0.0012	0.1926	0.2623						
CR-18	0.0000	0.2623	0.0853	0.6465	0.6219	0.4819	0.6213	0.6035	0.2430	0.4531	0.8722	0.6465	0.1109					
CR-19	0.0000	0.0100	0.0011	0.0680	0.0561	0.6213	0.0534	0.0579	0.9706	0.4496	0.1625	0.0682	0.0018	0.2081				
CR-20	0.0000	0.0017	0.0002	0.0115	0.0094	0.2105	0.0088	0.0100	0.4496	0.1139	0.0397	0.0117	0.0003	0.0562	0.4748			
CR-118	0.0319	0.4735	0.8722	0.1840	0.1861	0.0070	0.1861	0.2172	0.0015	0.0008	0.1389	0.1863	0.8031	0.0747	0.0011	0.0002		
CR-117	0.0002	0.8722	0.4556	0.6465	0.6710	0.0700	0.6710	0.7478	0.0206	0.0218	0.5030	0.6516	0.5389	0.3441	0.0153G	0.0026	0.3693	
CR-121	0.0000	0.0562	0.0045	0.3284	0.2830	0.5389	0.2757	0.2830	0.2320	0.4496	0.6219	0.3422	0.0088	0.7964	0.1931	0.0400	0.0054	0.0976

Table S6. Redwood Kaplan Meir probabilities, by Treatment, relating to Figure 13B.

Code	Treatment	records	N max	N start	events	R mean	Se (R mean)	median	0.95LCL	0.95UCL
CR-3	Duplicate	91	91	91	73	28.06	3.37	34	19	40
CR-3	Solo	46	46	46	37	26.77	4.92	34	14	49
CR-3	Benchmark_121	30	30	30	19	37.9	5.3	40	34	64
CR-3	Benchmark_13	46	46	46	45	20.52	4.54	19	8	40
CR-5	Duplicate	74	74	74	42	34.56	4	40	34	55
CR-5	Solo	46	46	46	25	40.38	4.8	49	40	64
CR-5	Benchmark_121	40	40	40	12	52.45	3.64	55	40	NA
CR-5	Benchmark_13	37	37	37	8	50.87	4.2	49	40	NA
CR-6	Duplicate	74	74	74	32	44.51	3.21	49	40	55
CR-6	Solo	47	47	47	38	28.64	4.19	26	14	49
CR-6	Benchmark_121	36	36	36	12	51.68	4.1	55	40	NA
CR-6	Benchmark_13	40	40	40	18	42.99	4.27	40	34	64
CR-7	Duplicate	76	76	76	21	51.21	2.66	49	40	64
CR-7	Solo	46	46	46	22	45.96	3.97	49	40	64
CR-7	Benchmark_121	41	41	41	22	35.82	5.18	40	34	64
CR-7	Benchmark_13	36	36	36	14	48.46	4.07	49	40	NA
CR-8	Duplicate	82	82	82	37	43.18	3.02	49	40	55
CR-8	Solo	45	45	45	25	43.27	3.73	40	34	55
CR-8	Benchmark_121	44	44	44	21	48.27	3.4	49	40	64
CR-8	Benchmark_13	39	39	39	11	55.27	3.35	55	49	NA
CR-9	Duplicate	84	84	84	26	52.36	2.47	55	49	64
CR-9	Solo	43	43	43	19	50.77	3.22	49	40	64
CR-9	Benchmark_121	35	35	35	8	50.51	4.12	49	40	NA
CR-9	Benchmark_13	40	40	40	13	52.6	3.29	49	49	NA
CR-10	Duplicate	87	87	87	40	45.74	2.78	49	40	55
CR-10	Solo	44	44	44	28	38.99	4.14	40	34	55
CR-10	Benchmark_121	44	44	44	18	52.17	3.03	52	40	64
CR-10	Benchmark_13	40	40	40	14	50	3.49	49	40	NA
CR-11	Duplicate	87	87	87	31	52.42	2.21	49	49	64
CR-11	Solo	46	46	46	34	33.21	4.02	34	19	49
CR-11	Benchmark_13	39	39	39	13	50.35	4.06	49	40	NA
CR-12	Duplicate	87	87	87	27	54.88	2.2	55	49	64
CR-12	Solo	44	44	44	18	52.17	3.03	52	40	64
CR-12	Benchmark_121	35	35	35	7	50.35	4.95	49	40	NA

CR-12	Benchmark_13	36	36	36	7	52.1	4.49	49	40	NA
CR-13	Duplicate	85	85	85	30	52.83	2.3	55	49	64
CR-13	Solo	44	44	44	20	49.67	3.21	49	40	64
CR-13	Benchmark_13	635	635	635	239	51.02	0.92	55	49	55
CR-15	Duplicate	67	67	67	26	43.41	3.44	40	34	55
CR-15	Solo	44	44	44	18	52.17	3.03	52	40	64
CR-15	Benchmark_121	42	42	42	15	49.86	3.36	49	40	64
CR-16	Duplicate	77	77	77	27	49.77	2.73	49	40	64
CR-16	Solo	45	45	45	29	37.48	4.3	40	34	55
CR-16	Benchmark_121	42	42	42	20	48.94	3.56	49	40	64
CR-16	Benchmark_13	32	32	32	7	49.57	5.1	49	34	NA
CR-17	Duplicate	79	79	79	35	43.17	3.05	40	34	55
CR-17	Solo	45	45	45	33	32.98	4.43	34	26	55
CR-17	Benchmark_121	26	26	26	7	48.63	6.04	49	40	NA
CR-17	Benchmark_13	32	32	32	8	46.95	5.16	49	34	NA
CR-18	Duplicate	86	86	86	33	50.56	2.33	49	40	64
CR-18	Solo	44	44	44	25	43.34	3.64	40	34	55
CR-18	Benchmark_13	40	40	40	12	52.36	3.82	55	49	NA
CR-19	Duplicate	83	83	83	23	57.47	2.07	55	49	64
CR-19	Solo	44	44	44	22	47.12	3.44	49	40	64
CR-19	Benchmark_121	44	44	44	18	51.54	3.24	55	40	64
CR-19	Benchmark_13	41	41	41	11	55.27	3.35	55	49	NA
CR-20	Duplicate	58	58	58	18	56.88	2.77	64	55	NA
CR-20	Solo	43	43	43	15	54.97	3.13	55	49	NA
CR-20	Benchmark_121	30	30	30	9	57.78	3.27	55	49	NA
CR-20	Benchmark_13	34	34	34	4	48.8	2.36	49	49	NA
CR-117	Duplicate	76	76	76	25	50.56	2.94	55	49	64
CR-117	Solo	46	46	46	37	29.12	4.31	26	19	49
CR-117	Benchmark_121	39	39	39	14	48.52	4.12	49	40	NA
CR-117	Benchmark_13	44	44	44	20	49.67	3.21	49	40	64
CR-118	Duplicate	91	91	91	49	43.52	2.71	49	40	55
CR-118	Solo	45	45	45	33	33.77	4.16	34	26	49
CR-121	Duplicate	88	88	88	36	52.17	2.14	52	49	64
CR-121	Solo	45	45	45	29	38.31	4.02	40	26	55
CR-121	Benchmark_121	673	673	673	268	50.06	0.9	49	49	55

Table S7. Redwood Pairwise Log Rank Assessment- by Treatment related to Figure 13B.

Code	Group 1t	Group 2	P-value	Sig
CR-3	Solo	Duplicate	0.93902449	
CR-3	Benchmark_121	Duplicate	0.4174294	
CR-3	Benchmark_13	Duplicate	0.4174294	
CR-3	Benchmark_121	Solo	0.4174294	
CR-3	Benchmark_13	Solo	0.4174294	
CR-3	Benchmark_13	Benchmark_121	0.40636973	
CR-5	Solo	Duplicate	0.47668409	
CR-5	Benchmark_121	Duplicate	0.13424686	
CR-5	Benchmark_13	Duplicate	0.13424686	
CR-5	Benchmark_121	Solo	0.35842625	
CR-5	Benchmark_13	Solo	0.35842625	
CR-5	Benchmark_13	Benchmark_121	0.78186169	
CR-6	Solo	Duplicate	0.06389125	.
CR-6	Benchmark_121	Duplicate	0.36627612	
CR-6	Benchmark_13	Duplicate	0.80210386	
CR-6	Benchmark_121	Solo	0.0414777	*
CR-6	Benchmark_13	Solo	0.14935842	
CR-6	Benchmark_13	Benchmark_121	0.36627612	
CR-7	Solo	Duplicate	0.70562214	
CR-7	Benchmark_121	Duplicate	0.15196849	
CR-7	Benchmark_13	Duplicate	0.83014404	
CR-7	Benchmark_121	Solo	0.44302205	
CR-7	Benchmark_13	Solo	0.83779441	
CR-7	Benchmark_13	Benchmark_121	0.44302205	
CR-8	Solo	Duplicate	0.99641462	
CR-8	Benchmark_121	Duplicate	0.57687359	
CR-8	Benchmark_13	Duplicate	0.22073663	
CR-8	Benchmark_121	Solo	0.57687359	
CR-8	Benchmark_13	Solo	0.22073663	
CR-8	Benchmark_13	Benchmark_121	0.514402	
CR-9	Solo	Duplicate	1	
CR-9	Benchmark_121	Duplicate	1	
CR-9	Benchmark_13	Duplicate	1	
CR-9	Benchmark_121	Solo	1	
CR-9	Benchmark_13	Solo	1	
CR-9	Benchmark_13	Benchmark_121	1	
CR-10	Solo	Duplicate	0.46054407	
CR-10	Benchmark_121	Duplicate	0.46054407	
CR-10	Benchmark_13	Duplicate	0.64932896	

CR-10	Benchmark_121	Solo	0.46054407	
CR-10	Benchmark_13	Solo	0.46054407	
CR-10	Benchmark_13	Benchmark_121	0.70495723	
CR-11	Solo	Duplicate	0.00352203	**
CR-11	Benchmark_13	Duplicate	0.78171776	
CR-11	Benchmark_13	Solo	0.03892868	*
CR-12	Solo	Duplicate	0.95187063	
CR-12	Benchmark_121	Duplicate	0.95187063	
CR-12	Benchmark_13	Duplicate	0.95187063	
CR-12	Benchmark_121	Solo	0.95187063	
CR-12	Benchmark_13	Solo	0.99140272	
CR-12	Benchmark_13	Benchmark_121	0.95187063	
CR-13	Solo	Duplicate	0.70163391	
CR-13	Benchmark_13	Duplicate	0.70163391	
CR-13	Benchmark_13	Solo	0.70163391	
CR-15	Solo	Duplicate	0.50323389	
CR-15	Benchmark_121	Duplicate	0.5274703	
CR-15	Benchmark_121	Solo	0.65084897	
CR-16	Solo	Duplicate	0.34265126	
CR-16	Benchmark_121	Duplicate	0.99479418	
CR-16	Benchmark_13	Duplicate	0.99479418	
CR-16	Benchmark_121	Solo	0.34265126	
CR-16	Benchmark_13	Solo	0.34265126	
CR-16	Benchmark_13	Benchmark_121	0.99479418	
CR-17	Solo	Duplicate	0.32770534	
CR-17	Benchmark_121	Duplicate	0.7377193	
CR-17	Benchmark_13	Duplicate	0.7377193	
CR-17	Benchmark_121	Solo	0.32770534	
CR-17	Benchmark_13	Solo	0.32770534	
CR-17	Benchmark_13	Benchmark_121	0.87761334	
CR-18	Solo	Duplicate	0.32663032	
CR-18	Benchmark_13	Duplicate	0.72550231	
CR-18	Benchmark_13	Solo	0.32663032	
CR-19	Solo	Duplicate	0.2300098	
CR-19	Benchmark_121	Duplicate	0.45671125	
CR-19	Benchmark_13	Duplicate	0.64729349	
CR-19	Benchmark_121	Solo	0.63545582	
CR-19	Benchmark_13	Solo	0.45671125	
CR-19	Benchmark_13	Benchmark_121	0.63545582	
CR-20	Solo	Duplicate	0.81908499	
CR-20	Benchmark_121	Duplicate	1	

CR-20	Benchmark_13	Duplicate	0.57847625	
CR-20	Benchmark_121	Solo	0.81908499	
CR-20	Benchmark_13	Solo	0.62533813	
CR-20	Benchmark_13	Benchmark_121	0.57847625	
CR-118	Solo	Duplicate	0.12600401	
CR-117	Solo	Duplicate	0.00654268	**
CR-117	Benchmark_121	Duplicate	0.89628274	
CR-117	Benchmark_13	Duplicate	0.89628274	
CR-117	Benchmark_121	Solo	0.04064365	*
CR-117	Benchmark_13	Solo	0.02740848	*
CR-117	Benchmark_13	Benchmark_121	0.89628274	
CR-121	Solo	Duplicate	0.02805784	*
CR-121	Benchmark_121	Duplicate	0.59363985	
CR-121	Benchmark_121	Solo	0.02805784	*

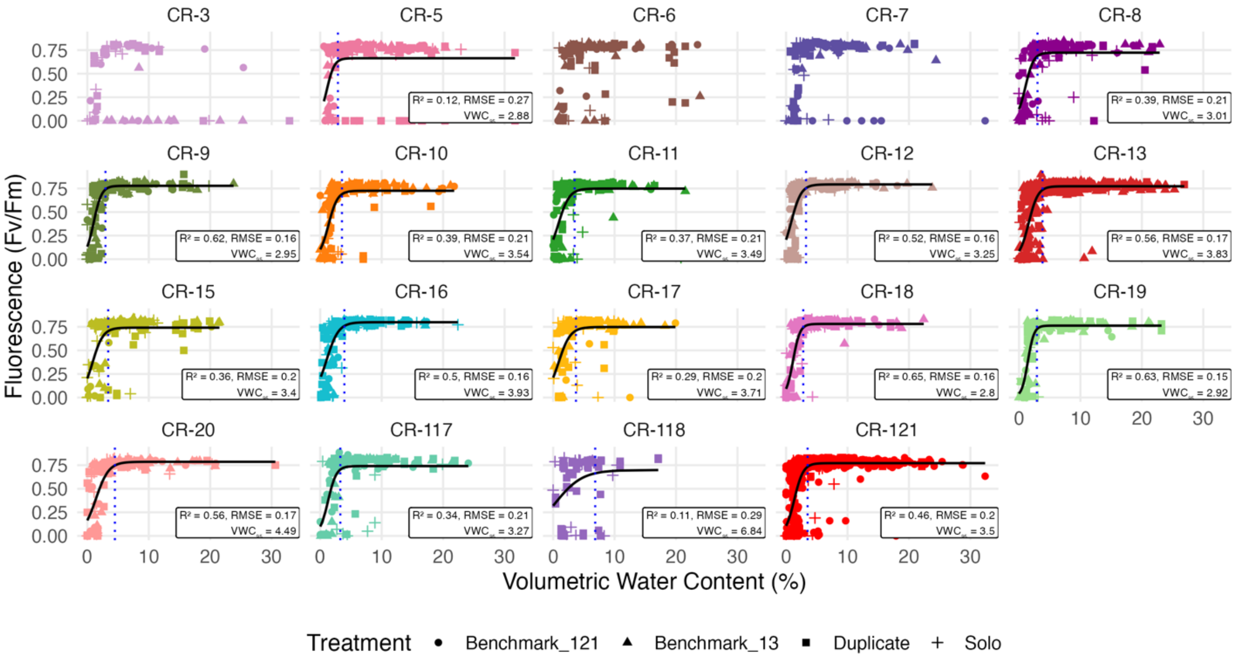

Figure S6. Raw data logit curve model fit to Volumetric Water Content and Fv/Fm for redwood genetic entry over duration of drought conditions. Summarized by treatment groups in Figure 14.

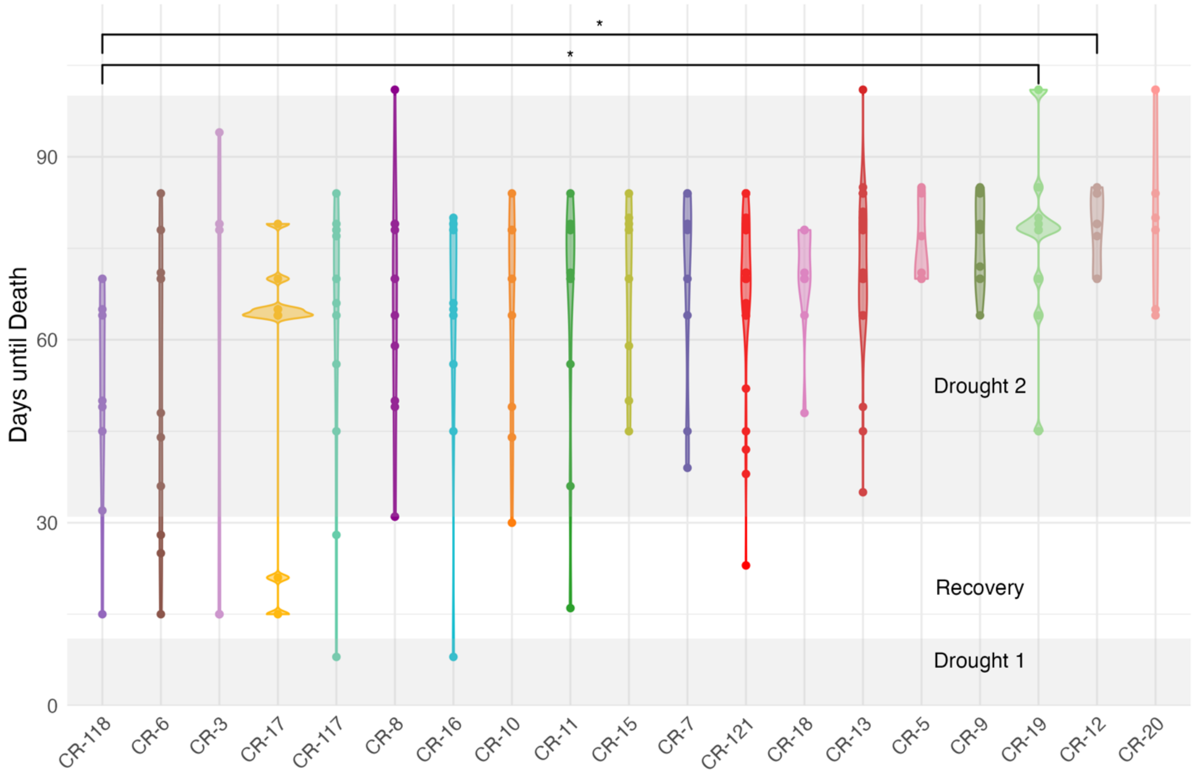

Figure S7. Violin plot of time until mortality for each genetic entry. Kruskal Wallis test shows sig difference ($p = 0.002314$), and Dunn's test shows difference between CR-118 and two other clone lines CR-19 and CR-12 ($p = 0.040$ and $p = 0.028$ respectively). Only considering death dates after drought conditions begin.

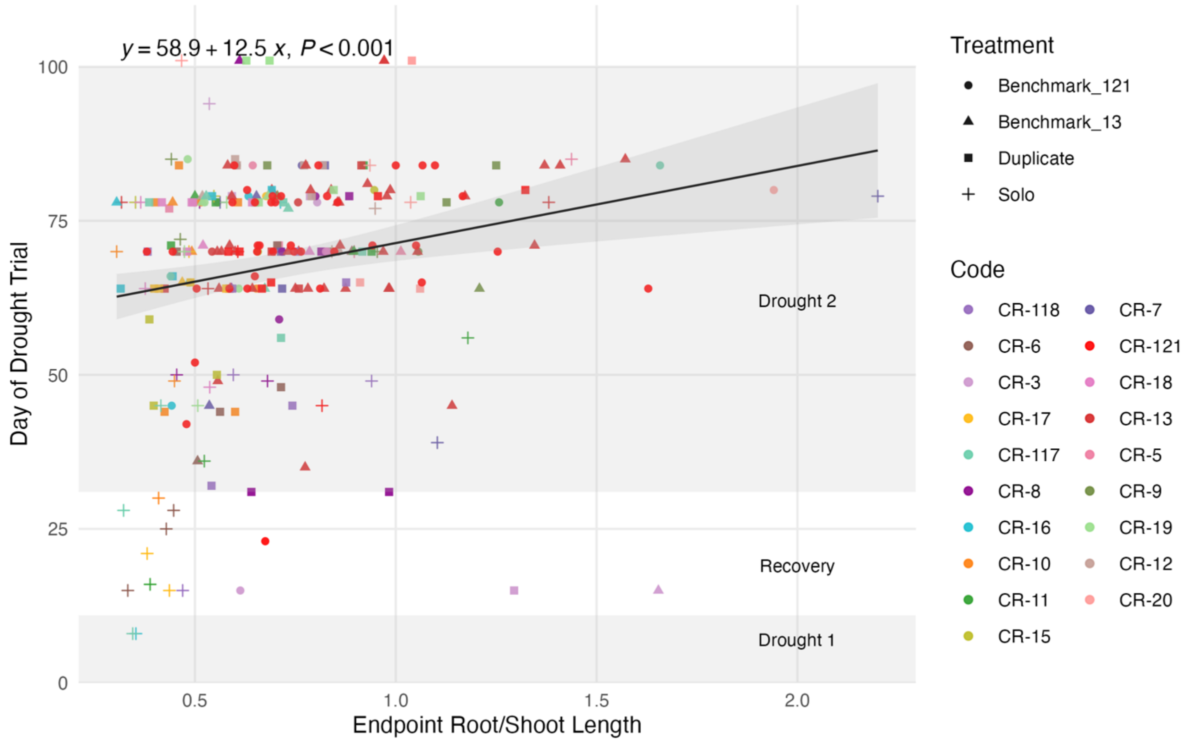

Figure S8. Scatterplot of endpoint Root: Shoot Ratio of length measurements vs Time until death in drought conditions. Significant positive correlation indicates that length investment rather than biomass investment may have a stronger impact on survival in drought conditions. Compares to Figure 15 which measures biomass ratio.

Chapter 2. Supplemental

Table S1. Linear Mixed Model for Vigor by Species and Site, related to Figure 20.

effect	term	estimate	Std error	statistic	df	P value	sig
fixed	DF	-1.36	0.09	-14.50	1093.41	1.02E-43	***
fixed	Loam + Biosolids	-0.47	0.11	-4.41	1090.96	1.12E-05	***
fixed	Gravel	-1.20	0.14	-8.65	719.56	3.26E-17	***
fixed	Glacial Moraine	-1.68	0.13	-12.69	774.63	1.21E-33	***

Table S2. Wilcox test between species at each site related to Figure 21.

Site Condition	Response	group1	group2	n1	n2	statistic	p	P adj	P adj signif
Sandy Loam	Winter Vigor	CR	DF	262	124	24080.5	2.27E-15	9.08E-15	****
Loam + Biosolids	Winter Vigor	CR	DF	253	115	21547	5.39E-15	2.16E-14	****
Gravel	Winter Vigor	CR	DF	131	59	5164	1.19E-06	4.76E-06	****
Glacial Moraine	Winter Vigor	CR	DF	113	56	4268.5	1.13E-05	4.52E-05	****

Table S3. Linear Mixed Model for Vigor by Genetic Entry and Site, related to Figure 22 B.

effect	**term**	**estimate**	**Std error**	**statistic**	**df**	**P value**	**sig**
fixed	CR-11	-0.62	0.29	-2.11	725.05	0.04	*
fixed	CR-117	-0.57	0.29	-1.95	724.18	0.05	
fixed	CR-12	0.18	0.29	0.63	724.14	0.53	
fixed	CR-121	-0.17	0.29	-0.57	726.06	0.57	
fixed	CR-15	0.24	0.29	0.83	724.40	0.41	
fixed	CR-16	-0.12	0.29	-0.43	723.98	0.67	
fixed	CR-17	-0.07	0.29	-0.23	724.05	0.82	
fixed	CR-18	-0.37	0.29	-1.26	723.74	0.21	
fixed	CR-19	-0.77	0.30	-2.59	724.10	0.01	**
fixed	CR-20	-1.18	0.30	-3.86	726.93	0.00	***
fixed	CR-3	-1.37	0.30	-4.60	724.60	5.01E-06	***
fixed	CR-5	-0.95	0.30	-3.16	726.32	0.00	***
fixed	CR-6	-0.07	0.29	-0.23	724.04	0.82	
fixed	CR-7	-0.28	0.29	-0.97	723.83	0.33	
fixed	CR-8	-0.77	0.29	-2.64	723.98	0.01	**
fixed	CR-9	-0.79	0.29	-2.71	724.13	0.01	**
fixed	Loam + Biosolids	-0.47	0.12	-3.79	724.98	0.00	***
fixed	Gravel	-1.92	0.16	-12.35	648.35	1.25E-31	***
fixed	Glacial Moraine	-1.34	0.16	-8.15	631.30	1.93E-15	***

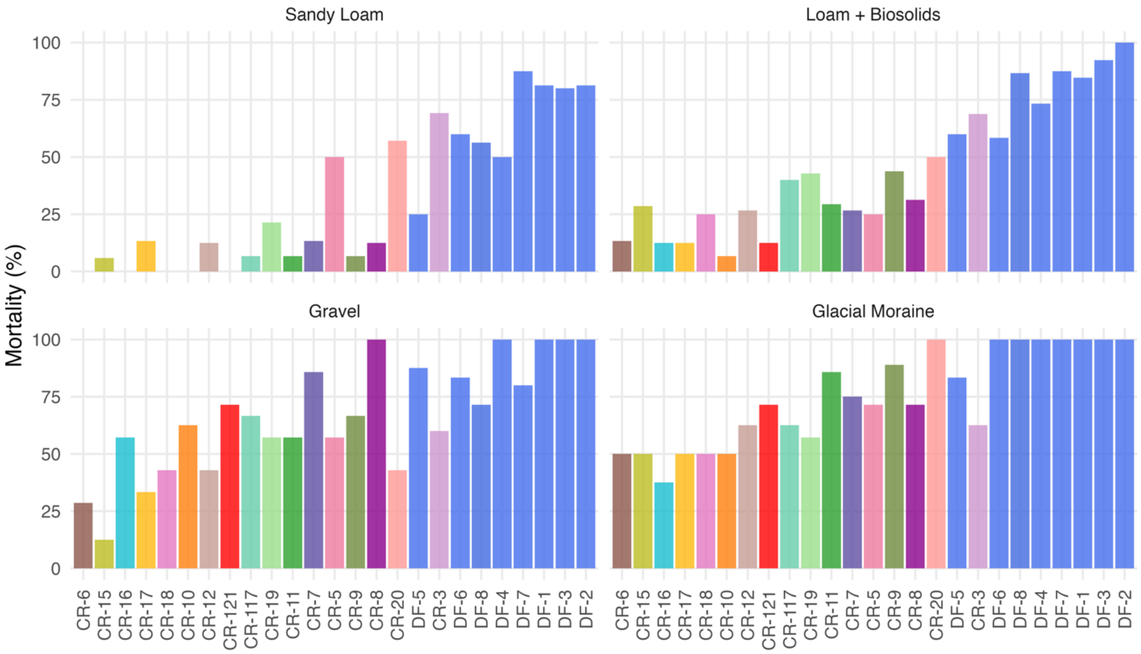

Figure S1. Percent mortality per genetic entry both redwood and Douglas-fir at each site as of November 2024.