AN ABSTRACT OF THE THESIS OF

Erin E. Baumgart for the degree of Master of Science in Sustainable Forest Management presented on December 16, 2021.

Title: Effect of Root and Shoot Manipulation on the Morphology and Physiology of Oregon White Oak (*Quercus garryana*) Seedlings in the Nursery and Following Outplanting.

Abstract approved: ____

Anthony S. Davis

Oregon white oak, or Garry oak (*Quercus garryana*), has been adversely affected by land-use conversion, landscape fragmentation, and anthropogenic fire suppression. Its historical range has contracted significantly to the point where an estimated 1-5% remains intact. Natural regeneration is difficult due to a lack of seed sources and the physiological characteristics of the seed. Because of this, artificial regeneration has become essential for helping to sustain current populations. However, seedlings can be difficult to establish due to high mortality from post-planting water stress. Nursery cultural practices can improve future field survival in reforestation projects by manipulating a seedling's morphology and physiology. The primary objective of this study was to evaluate the effect(s) of container size in combination with pruning treatments on Oregon white oak seedlings. The experiment began in the greenhouse and then transitioned to a field experiment and determined the effect of seedling morphology and physiology on growth, water stress and field survival after planting. Overall, seedlings cultivated in the three container sizes showed similar height (HT), shoot dry mass (SDM), root dry mass (RDM), root-to-shoot ratio (R:S) and root volume (R_V) but differed in root collar diameter (RCD) and root length (R_L) after one greenhouse growing season. Compared to seedlings cultivated in a D27 container, seedlings cultivated in both D40 and D60 containers had smaller RCD but greater R_L. Both container size and top pruning impacted net photosynthesis (A), transpiration (E), stomatal conductance (g_s), water use efficiency (WUE) and pre-dawn water potential (Ψ_{PD}) at various times throughout the field growing season. While end-of-season RCD and survival were not statistically significantly different among container size or between pruning treatments, end-of-season HT was impacted by both container size and pruning treatment. Seedling HT was greater for seedlings cultivated in D27 containers compared to seedlings cultivated in a D40 container, where D60 seedlings displayed an intermediate HT. Additionally, seedling HT was greater among unpruned seedlings compared to pruned seedlings. This study showed that nursery-based decisions such as container size and field treatments such as top pruning can impact Oregon white oak seedling morphology and physiology, which can aide in offsetting the stresses of low water availability in the field.

Effect of Root and Shoot Manipulation on the Morphology and Physiology of Oregon White Oak (*Quercus garryana*) Seedlings in the Nursery and Following Outplanting.

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Erin E. Baumgart, Author

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CONTRIBUTION OF AUTHORS

Erin E. Baumgart and Anthony S. Davis designed the study. Erin E. Baumgart collected the data and analyzed it. Erin E. Baumgart wrote the thesis with critical revisions by Anthony S. Davis.

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DEDICATION

This thesis is dedicated to my late aunt, Margaret Welke.

CHAPTER 1: General Introduction

Global State of Oak Regeneration

Oaks (*Quercus*) are classified in the Fagaceae, with more than 400 species found throughout five continents (Aldrich and Cavender-Bares 2011). Mexico, with 161 species, contains the greatest oak diversity (Valencia-A 2004). While oaks are found in an array of geographical locations, plant communities, and soil-types, they are generally considered a long-lived, and deeply rooted genus that is successful in xeric environments (Abrams 1990, Stone and Kalisz 1991, Aldrich and Cavender-Bares 2011). Oaks often thrive in areas with consistent disturbance regimes, and regenerate with open canopies (Agee 1996, Aldrich and Cavender-Bares 2011). They are used for wood and paper products, provide excellent habitat and food sources for animals, and host exceptionally biodiverse ecosystems (Aldrich and Cavender-Bares 2011). In the United States, *Quercus* is the largest genus of trees (Bonner 2008).

Globally, regeneration has proven to be difficult for many oak species and several suspected limiting variables have been investigated (Larsen and Johnson 1998, Fuchs 2001). Limiting factors are varied and include acorn predation (Fox 1982, Kikuzawa 1988, Herrera 1995, den Ouden et al. 2005), vegetative competition (Bielinis and Robakowski 2011), altered disturbance regimes (Agee 1996), and water availability (Nardini et al. 1999, Chirino et al. 2011), among others (Loftis and McGee 1993, Larsen and Johnson 1998). The quantity and scope of research on various oak species highlights their cultural and biological importance, as well as the need to overcome the limitations in regeneration to keep them in our ecosystems.

Oregon White Oak: Historical Habitat & Ecology

As a deciduous tree in a conifer-dominated landscape, Garry oak, or Oregon white oak (*Quercus garryana* Dougl. Ex Hook.), is a unique tree in the Pacific Northwest. Its range includes the western portion of Canada and the United States, from southwestern British Columbia to southern California (Stein 1990), spanning a wide precipitation gradient (Stein 1990) and elevations from sea level to 2290 m (Fuchs 2001). Although tolerant of high rates of precipitation and rich soils, the species is a weak competitor relative to other native tree species, which often constrains it to occupy more marginal sites (Silen 1958, Stein 1990). It is generally found on drier sites and south-facing aspects, often in gravelly soils with extended droughty summer conditions (Silen 1958, Stein 1990, Larsen and Johnson 1998).

Because Oregon white oak is the only native oak species in the state of Washington, it adds biodiversity to the landscape while providing critical habitat and forage for a wide range of wildlife (Stein

1990). The tree can reach 30 m in height (Columbia Gorge Audubon Society 1991), 246 cm in diameter (Stein 1990) and live for up to 400 years (Agee 1996). In Washington, over 321 species of birds and mammals depend on oak ecosystems (Columbia Gorge Audubon Society 1991), while in British Columbia, habitat provided by its direct and associated ecosystems can be linked to at least 694 species, subspecies, and varieties of plants (Fuchs 2001).

Oregon white oak has adapted to ecosystems with disturbances, specifically frequent and low intensity fires (Hanna and Dunn 1996, Agee 1996). Prior to European settlement in the 1800s, Indigenous people managed oak savannahs using fire on the landscape to promote the growth of primary food sources such as camas (*Camassia* spp.) (Agee 1996, Fuchs 2001, Thysell and Carey 2001). Older saplings and mature trees have corky bark that is resistant to fire damage (Silen 1958, Agee 1996). Younger seedlings are less fire resistant, and aboveground shoot can be damaged or die with high intensity fires (Dunn 1998, Voeks 2000). However, the root systems are very resilient, and remain intact if the fire is not hot or deep enough to damage the root system (Columbia Gorge Audubon Society 1991, Larsen and Johnson 1998). Oregon white oak has adventitious buds on its root collar, by which it can regenerate vegetatively if the shoot is damaged (Agee 1996, Fuchs 2001). In nature, several stems are typically produced during the seedling stage with a single stem taking dominance during the sapling stage (Hibbs and Yoder 1993). With vegetative growth, aboveground shoots can die back several times, while the underground root system continues to develop (Hibbs and Yoder 1993, Larsen and Johnson 1998). Additionally, oak populations depend on the microsites created by fire for regeneration from seed (Agee 1996, Dunn 1998).

Compared to pre-European settlement, the current habitat range has contracted where an estimated 1-5% remains (Crawford and Hall 1997, Fuchs 2001, Gucker 2007). While the literature fails to precisely estimate the current range, some areas have been inventoried at a more extensive scale than others. Habitat in British Columbia, Canada (Fuchs 2001), the South Puget Sound, Washington (Crawford and Hall 1997, Dunn 1998), and the Willamette Valley, Oregon (Christy and Alverson 2011) have been mapped, indicating estimated local populations and rates in change over time. However, larger regional surveys of current populations are lacking, due to a lack of parameters defining oak habitat since populations often slowly diminish because of encroaching and over-topping vegetation (Goldenberg 2021). This also poses problems when surveying habitat by aerial observation, since oak populations are less visible (Goldenberg 2021). Methods such as utilizing survey data from Global Land Office (GLO) maps define historical pre-settlement vegetation types and can be compared to current survey results. With survey records from 1851 and 1920 of the Willamette Valley, Oregon, white oak was noted as historically significant in regional forest and savannah vegetation classes, but the area has since declined (Christy and Alverson 2011). Furthermore, conservation has proven to be difficult as >83% of habitat falls under private ownership (Gucker 2007).

Oregon white oak has been negatively impacted by habitat fragmentation associated with urban and agricultural land-use conversion (Crawford and Hall 1997, Thysell and Carey 2001, Devine et al. 2007b). Additionally, the practice of fire suppression has increased the encroachment of native conifers, primarily Douglas-fir (*Pseudotsuga menziesii*) (Thysell and Carey 2001, Marsico et al. 2009), leading to a significant change in community plant ecology and structure (Agee 1996). Thus, Oregon white oak is often out-competed by more vigorous and shade-tolerant conifers as well as invasive non-native plant species, such as scotch broom (*Cytisus scoparius*) (Silen 1958, Stein 1990, Erickson 1996, Agee 1996, Dunn 1998, Thysell and Carey 2001). Due to the decrease in suitable habitat, many associated plants, insects, and animal species have declined to critical levels, including golden Indian paintbrush (*Castilleja levisecta*), mardon skipper (*Politer mardon*), smallflower wakerobin (*Trillium parviflorum*), western gray squirrel (*Sciurus griseus*), and the western pocket gopher (*Thomomys mazama*) (Thomas and Carey 1996, Thysell and Carey 2001). Additionally, several plant and animal species are considered locally extinct, including the Lewis woodpecker (*Melanerpes lewis*), racer snake (*Coluber constrictor*) and the rose checker-mallow (*Sidalcea malviflora* var*. virgata*) (Dunn 1998).

Regeneration Strategies and Range Contraction

The range of Oregon white oak is shrinking due to land use change and inadequate natural regeneration. Oregon white oak is monoecious and depends on both male and female springtime flowering to be synchronous to produce a successful seed crop (Stein 1990). Acorn production is irregular from year to year, especially under competitive or sub-optimal growing conditions (Stein 1990, Koenig et al. 1994, Devine et al. 2007a, Bonner 2008). However, little is known about the nuance of timing in the reproductive ecology of the species (Silen 1958, Koenig et al. 1994, Fuchs 1998). The fruit is a nut, often called an acorn, and ripens the same year as flowering (Bonner 2008). Variability in acorn production is considered to be an evolutionary strategy that facilitates improved rates of pollination and satiates seed predators in mast years (Vander Wall 1990, Koenig et al. 1994, Fuchs 2001). Insects, including the filbertworm (*Melissopus latiferreanus*) and the filbert weevil (*Curculio occidentalis*) (Silen 1958, Stein 1990), are primarily responsible for insect-related acorn predation, which occurs at higher rates during low mast years (Bonner 2008).

Acorn dispersal is heavily dependent on the hoarding behavior of rodents and birds who use the fruit as a long-term food source (Fuchs 2001) due to their decay-resistant characteristics (Vander Wall

1990). Animals and oak species have coevolved, where animals serve as both a partner in progeny dispersal as well as a predator (Fox 1982). In British Columbia, Steller's jays (*Cyanocitta stelleri*) are the primary mode of dispersal where transport distances can reach 1 km or more (Fuchs 1998). However, many acorns are consumed in the process (Silen 1958, Vander Wall 1990, Koenig et al. 1994, Fuchs 1998). Attempts at artificial regeneration originating from acorns is difficult due to predation (Silen 1958, Bell and Papanikolas 1997). Additionally, seeds have become increasingly scarce over the landscape because of the decrease in local oak populations (Devine et al. 2007a). Historically, long-distance acorn dispersal was made possible by native peoples (Stein 1990) who also used acorns as a food source (Columbia Gorge Audubon Society 1991). In nature, unless the microsite is ideal for germination and the radicle can penetrate the topmost layer of organic materials and soil, the acorn will not establish (Silen 1958).

Natural regeneration of Oregon white oak is further hindered by its physiology. Acorns are recalcitrant, requiring a high humidity environment to avoid desiccation (Stein 1990, Bonner 2008). In nature, high humidity is met through the presence of duff on the forest floor or burial by animals (Barrett 1931, Silen 1958, Stein 1990). If the acorns are not held to a critical moisture content of 25 to 35 percent, seed quality declines rapidly (Loftis and McGee 1993, Devine and Harrington 2010). Additionally, species in the white oak subgenus have very few dormancy requirements and germinate soon after maturation (Silen 1958, Stein 1990). While the radicle rapidly emerges in the autumn, the cotyledon emerges several weeks after the radicle has become established (Columbia Gorge Audubon Society 1991, Bonner 2008). Consequently, acorn storage is an atypical practice (Stein 1990, Bonner 2008) and direct sowing is most successful shortly after autumn collection (Bonner 2008).

In addition to propagation by seed, Oregon white oak is capable of vegetative reproduction from stumps and roots (Agee 1996), enabling a silvicultural practice known as coppicing. The root collar contains dormant buds that can resprout after a disturbance (Larsen and Johnson 1998), and has been noted to be the most reliable method of natural reproduction (Stein 1990) especially in more xeric conditions (Larsen and Johnson 1998). With this regeneration strategy, individuals can persist in-place for thousands of years (Columbia Gorge Audubon Society 1991) but limits the exploitation of new sites.

At the landscape-level, natural regeneration of Oregon white oak is largely constrained by distance from a parent tree (Silen 1958, Hanna and Dunn 1996), making population increases unlikely when left solely to ecological processes (Fuchs 1998). Due to the overall decline in suitable habitat as well as characteristics of both parent trees and their acorn progeny, intervention though restoration efforts are necessary in order to sustain and expand its range (Fuchs 1998, Harrington and Kallas 2002).

It is recognized that there is a global need for high quality seedlings to achieve large-scale reforestation efforts (Haase and Davis 2017). Nursery-grown seedlings are often required to help restore Oregon white oak populations throughout its native range (Hanna and Dunn 1996, Bell and Papanikolas 1997, Devine et al. 2007a). While artificial regeneration of Oregon white oak by planting seedlings may result in higher survival, the cost of nursery production and restoration efforts may be prohibitive (Bell and Papanikolas 1997).

Growing Quality Seedlings

To justify the cost of artificial regeneration efforts with seedlings, there is a need for quantitative standards for producing nursery-grown seedlings. Since 1990, a set of recommendations known as the Target Plant Concept has supported nursery and field managers in predicting seedling suitability to specific site conditions based on seedling attributes (Landis 2011, Dumroese et al. 2016, Grossnickle and MacDonald 2018, Davis and Pinto 2021). The Target Plant Concept outlines a framework for aligning seedling morphological and physiological metrics with resultant attributes that project a seedling's success in the field. While these guidelines have developed over time, current recommendations acknowledge the importance of measuring the functionality of both the root and shoot systems (Davis and Jacobs 2005). While each parameter defines a specific growth increment and mechanism at a point in time, the Target Plant Concept recommends measuring two or more of these variables to achieve a holistic picture of a seedling's future potential (Haase 2008, Landis 2011). These considerations will help us understand how timing and effort of seedling production in nursery culture will translate to field growth and survival (Grossnickle and Folk 1993, Mattsson 1996).

Chapter 2 describes an experiment to identify how container sizes and top pruning impact Oregon white oak seedling selected aspects of morphology, physiology, and field survival. Understanding the species-specific growth habits of Oregon white oak under specific nursery conditions can help define target seedling characteristics that are linked to future field success.

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CHAPTER 2: Effect of container size and field pruning on Oregon white oak (*Quercus garryana*) seedling morphology, physiology, and survival

INTRODUCTION

Post-Planting Water Stress

While there are numerous causes of seedling mortality post-planting, including both biotic and abiotic factors, one of the most important factors to address in the Pacific Northwest is moisture stress (Grossnickle 2005). Primary causes of seedling moisture stress include extreme temperatures and drought-related water stress (Burdett 1990, Grossnickle and Folk 1993, Hember et al. 2017). Environmental conditions in the region are predicted to become increasingly hot and droughty for longer periods in the future (Intergovernmental Panel on Climate Change 2007), suggesting that post-planting water stress will continue to limit reforestation and restoration success.

Water stress is a common problem directly after transplanting because seedling root systems are initially limited by small volume and poor soil contact, which creates deficits in meeting transpiration demands (Burdett 1990, Grossnickle and Folk 1993, Grossnickle 2005). To overcome this initial stress, nursery-grown seedlings need to be cultivated in such a way that their morphology (e.g., numerous root tips) and physiology (e.g., high water-use efficiency) support rapid root egress (Grossnickle and Folk 1993).

Water stress after outplanting is one of the primary causes of mortality in Oregon white oak (Bell and Papanikolas 1997, Fuchs 1998, Bakker et al. 2012). Compared to more mesic ecotypes, the less productive and well-draining soils found throughout its native range lead to lower water holding capacities and availability, making the species particularly at-risk to planting stress (Erickson 1996, Crawford and Hall 1997, Dunn 1998). This is especially concerning in a Mediterranean climate like the Pacific northwest, which has prolonged droughty conditions during the growing season (Dunn 1998, Voeks 2000). The time immediately after planting is one of the most critical survival periods (Bell and Papanikolas 1997), and 10-25% mortality is not uncommon during the first two growing seasons (Devine and Harrington 2010). In one experiment in British Columbia, 59-78% of Oregon white oak seedlings were killed by water stress in rocky soils (Fuchs 1998, Fuchs et al. 2000). Oregon white oak seedlings are typically planted in the fall or spring (Bell and Papanikolas 1997, Dunn 1998, Devine and Harrington 2010). Spring-planted seedlings in particular need to have the capacity to quickly expand their root systems to prepare for the droughty summer conditions after planting (Dunn 1998, Devine et al. 2007a).

While supplemental irrigation can help improve survival of seedlings post-planting, it is often unavailable on restoration sites (Bell and Papanikolas 1997, Devine and Harrington 2010).

Drought Tolerance and Drought Avoidance Strategies

Understanding plant strategies, such as drought avoidance and drought tolerance, is crucial in improving reforestation in dry environments (Farooq et al. 2013). Drought avoidance occurs when plants can maintain high tissue water content in water-limited environments (Blum 2005, Farooq et al. 2013). Some plant morphology strategies that increase access to water are the development of deep, dense, and vigorous root systems with an abundance of fine roots (Abrams 1990, Comas et al. 2013). They can also reduce water loss by decreasing photosynthetic activity through stomatal closure and by reducing leaf area (Blum 2005, Ryan 2011, Merz et al. 2017, Ramírez-Valiente and Cavender-Bares 2017), which shifts resources from the shoot to the root.

Drought tolerance occurs when individuals can endure lower tissue water content in water-limited environments (Farooq et al. 2013). Plants can control levels of organic and inorganic solutes to decrease water potential, called osmotic adjustment (Serraj and Sinclair 2002). This mechanism helps plants maintain leaf turgor, which manages stomatal activity (Kiani et al. 2007), while promoting increased water intake through the roots (Chimenti et al. 2006). Maintaining high turgor pressure is possible by cellular structure and elasticity (Farooq et al. 2013, Hahm et al. 2018). The point at which turgor pressure is lost in droughty conditions is turgor loss point (Ψ_{TLP}), or wilting point (Farooq et al. 2013). This value is an indicator of drought tolerance (Ramírez-Valiente and Cavender-Bares 2017). A plant with a more negative Ψ_{TLP} can maintain higher rates of net photosynthesis and stomatal conductance in lower soil water potential (Ramírez-Valiente and Cavender-Bares 2017). Species in xeric ecosystems generally show lower Ψ_{TLP} values than those in more mesic conditions (Ramírez-Valiente and Cavender-Bares 2017). While useful in droughty conditions, these strategies may come at the cost of growth (Farooq et al. 2013).

Oregon white oak has evolved strategies of both drought avoidance and drought tolerance (Abrams 1990). One method of drought avoidance is the development of deeply penetrating root systems with an abundance of fine roots (Abrams 1990, Stone and Kalisz 1991, Columbia Gorge Audubon Society 1991). This allows increased access to available water in deeper soil profiles (Abrams 1990, Aldrich and Cavender-Bares 2011, Hahm et al. 2018). Oregon white oaks prioritize early growth of the root over the shoot, where the biomass of the root system can be three times that of the shoot (Columbia Gorge Audubon Society 1991). Leaves are thick, leathery and hypostomatous (having stomata only on the underside), which reduces water loss associated with transpiration (Merz et al. 2017).

Oregon white oaks can become dormant in extreme drought conditions and drop leaves if necessary (Columbia Gorge Audubon Society 1991). Oaks have a xylem structure that is ring-porous (Abrams 1990, Hahm et al. 2018, Skelton et al. 2018, 2021). During conditions where water is readily available, water moves through larger diameter, early-wood vessels with minimal hydraulic resistance (Abrams 1990). However, when water becomes more scarce, it transitions to smaller diameter, late-wood vessels that reduce the risk of cavitation (Abrams 1990).

Manipulating Seedling Morphology and Physiology for Drought Resistance

There are several ways that nursery cultural practices can influence a seedling's ability to overcome drought stress by impacting morphological and physiological characteristics (Duryea 1984). The choice of growing media, seedling spacing and choice of growing location (i.e., nursery bed or greenhouse), irrigation (i.e., timing, frequency, and duration), fertilizer (i.e., timing and rate), and pruning (i.e., root-pruning and shoot-pruning) are significant drivers of seedling structure and health (Duryea 1984). During peak growth, seedlings can quickly accumulate biomass by taking advantage of available water, light and fertilizer (Duryea 1984). Watering events can impact a seedling's drought avoidance strategies, such as controlling moisture stress, increase favorable morphology characteristics (e.g., root-to-shoot ratio (R:S) and root collar diameter (RCD)), and change physiological characteristics, such as reducing transpiration (Grossnickle and South 2017, Schuster et al. 2017). Frequency of irrigation impacts the timing of budset as well as seedling dormancy (Duryea 1984).

During hardening, seedlings are exposed to reduced levels of resources. By withholding irrigation, seedlings can acclimate to low water conditions and experience moderate plant moisture stress (PMS) (Duryea 1984). This process is called drought hardening. *Quercus ilex* seedlings cultivated with the practice of drought hardening have improved drought tolerance through changes in physiology, specifically, reduced stomatal conductance, transpiration and adjusted osmotic potential (Villar-Salvador et al. 2004). This practice can increase drought resistance in seedlings, which may be beneficial in future field conditions (van den Driessche 1991, 1992, Grossnickle and South 2017, Valliere et al. 2019).

One approach to manipulating a nursery-grown seedling's morphology is through the choice of container. Container sizes vary in volume, depth, width and spacing (Funk 1971, Rose et al. 1997, Davis and Jacobs 2005, Pinto et al. 2011). Root physiology and growth potential can also be successful indicators of a seedling's ability to avoid drought stress by supporting rapid root egress (Stone 1955, Rose et al. 1997, Davis and Jacobs 2005, Grossnickle 2005). In comparison to bareroot seedlings, container-grown seedlings ar easier to manage in nursery and field activities such as packing, shipping and outplanting, since root systems remain intact and in contact with growing media (Davis and Jacobs

2005, Dumroese et al. 2016) and transplant shock can be minimized (Miller 1999, Davis and Jacobs 2005). Container-grown seedlings also have the advantage of higher water potentials during their first growing season, due to the intact root system and increased number of fine roots (Davis and Jacobs 2005). A study of *Quercus rubra* found that container-grown seedlings had larger and more fibrous root structures, higher field survival, and increased biomass through the first growing season compared to bareroot seedlings (Wilson et al. 2007).

Root and shoot pruning can impact a seedling's structure and function. In bareroot nurseries mechanical methods such as undercutting, wrenching and lateral pruning are used to stimulate root growth, change the structure of the root system, or decrease the seedling R:S by removing biomass (Duryea 1984). In container-grown seedlings, top pruning can also be used to impact the shoot biomass and balance the demands of transpiration (Landis 2005, Grossnickle and South 2017). Top pruning can increase survival of a seedling in a droughty transplanting site (Kaczmarek and Pope 1993, South 1998, 2016, Landis 2005). The reduction in shoot biomass creates an unbalanced seedling favoring the root system, with reduced transpiration requirements (Larson 1975, South 1998). It can also maintain seedling health during critical periods of handling in the nursery and field (Mexal and Landis 1990). While top pruning initially reduces the biomass of the shoot, research suggests that there is no difference in subsequent growth between top pruned and non-pruned seedlings (Larson 1975, Kaczmarek and Pope 1993, South 1998). The impacts of top pruning Oregon white oak seedlings on field response and survival are relatively unstudied.

Assessing Seeding Quality

There are several morphological and physiological measurements commonly used to evaluate nursery-grown seedling quality (Thompson 1985, Haase 2008). Morphological measurements are commonly used to assess seedlings, as they are external qualities that can be measured quickly and visually (Mexal and Landis 1990, Dumroese et al. 2005, Haase 2008). Root collar diameter (RCD) is considered the most important morphological characteristic in predicting future field potential (Mexal and Landis 1990, Johnson and Cline 1991). RCD is also positively correlated with the size of the root system and overall growth potential (Grossnickle 2012). The larger the root system, the greater the ability for a plant to absorb necessary water and nutrients from the soil, which reduces water stress (Mexal and Landis 1990). While seedling height may not be an adequate singular indicator of seedling quality, when assessed alongside other characteristics, it becomes a more useful parameter because height is often correlated with other morphological characteristics yet easy to assess quickly (Johnson and Cline 1991). Seedling root-to-shoot ratio (R:S) is defined as the total plant root system mass or volume divided by the total shoot system mass or volume. R:S is a proxy indicator of the balance between the transpiration demands of the shoot and the absorptive capabilities of the root (Thompson 1985, Haase 2008). Root length is important due to the increased potential of roots to uptake water and nutrients (Davis and Jacobs 2005) and can be controlled by the shape of container (Burdett 1990). Larger root volumes have also been shown to reduce water stress in seedlings after planting (Haase and Rose 1993).

Measurements pertaining to seedling physiology are useful in assessing seedling quality and future field potential and reflect the internal processes of a seedling (Grossnickle and Folk 1993, Haase 2008). Transpiration is the passive flow of water from the root to the shoot and is managed by the guard cells which open and close the stomata (Hetherington 1998, Bond and Kavanagh 1999). When the stomata are closed, transpiration and photosynthesis are reduced while water potential is increased (Ditmarová et al. 2009, Buckley 2019). This is done to reduce water loss during times of water stress, and subsequently reduces turgor (Hetherington 1998). Instantaneous water use efficiency (WUE) is the ratio of the net photosynthesis rate (A) and transpiration rate (E) (Blum 2005). An increased WUE indicates a plant's ability to continue increasing its ratio of carbon assimilation through photosynthesis while experiencing water stress (Blum 2005). Greater net photosynthesis equates to greater growth capacity (Burdett 1990).

Goals and Objectives

The goal of my research is to provide new knowledge regarding seedling production of Oregon white oak in support of planting-based restoration practices in its historic native range.

Overall, the objectives of this study were to evaluate the singular and combined effect(s) of container size and pruning treatment on Oregon white oak (*Quercus garryana*) seedlings after one nursery and one field growing season. This was evaluated through the measurement of Oregon white oak seedling physiology and morphology both in the nursery cultivation period as well as in the early field establishment period.

Rationale and Significance

There is a need to restore former Oregon white oak savannah habitat, as the species holds specific ecological and cultural importance in our region. An estimated 1-5% of historic habitat remains intact (Crawford and Hall 1997, Fuchs 2001, Gucker 2007). This research will help us understand how nursery cultural practices can impact seedling morphology and physiology and assess whether specific seedling metrics can predict future field performance. This is especially important given the high financial costs, and critical ecological implications, of restoration efforts.

Research Questions

Two general research questions framed this project:

1. How does container size affect seedling morphology?
    - Where seedling morphology is described by: height (HT, cm), root collar diameter (RCD, mm), shoot dry mass (SDM, g), root dry mass (RDM, g), root-to-shoot ratio (R:S), root length (R_L, cm), root volume (R_V, cm^3)
2. What effects do container size, field pruning, and their interaction have on seedling physiology, morphology, and survival?
    - Where seedling physiology is described by: net photosynthesis rate (A, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$), transpiration (E, $\mu mol\ H_2O\ m^{-2} s^{-1}$), stomatal conductance (g_s, $mol\ H_2O\ m^{-2} s^{-1}$), instantaneous water use efficiency (WUE), and pre-dawn leaf water potential (Ψ_{PD}, MPa)
    - Where seedling morphology is described by: end of growing season height (HT, cm) and root collar diameter (RCD, mm)
    - Where seedling survival is defined by: end of growing season presence or absence of living seedling

Hypotheses

From these reseach questions, I hypothesized that:

- Seedling RCD, R_L, R_V, RDM, and R:S would increase with increasing container size but HT and SDM would not differ among container sizes after one greenhouse growing season
- Seedling A, E, g_s, WUE and Ψ_{PD} would increase with increasing container after one field growing season
- Pruned seedlings would experience increased A, E, g_s, WUE and Ψ_{PD} compared to unpruned seedlings after one field growing season
- Seedling HT and RCD would increase with increasing container size after one field growing season
- Pruned seedlings would experience decreased HT and RCD compared to unpruned seedlings after one field growing season
- Seedlings in larger container sizes would experience lower mortality relative to seedlings grown in smaller container sizes

- Pruned seedlings would experience lower mortality relative to unpruned seedlings after one field growing season

MATERIALS AND METHODS

Seed Collection and Storage

Seeds were sourced from a single Oregon white oak (*Quercus garryana* Douglas ex Hook.) stand located in Tenino, Washington (46°49'42.7"N 122°57'47.2"W). Acorns were collected in September 2019 and stored in a standard residential refrigerator at a temperature of 3-4°C through November 2019.

Acorns were transferred to the Oak Creek Building located at Oregon State University in Corvallis, Oregon (44°33'27.7"N 123°17'10.8"W) in December 2019. They were stored for five days in a cold room at a temperature of 1°C. They were then sorted by quality by using a float test (Bonner 2008) which uses density to roughly quantify the number of seeds with healthy, intact embryos. In this test, buoyant acorns are set aside for sowing and acorns that sink are discarded. Acorns were not sorted using any other method prior to planting.

Sowing in the Greenhouse

Acorns were sown from 8-10 December 2019 in the Oak Creek greenhouse (Figure 2.1). Each acorn was randomly assigned to one of three container factor-levels and one of five blocks (Figure 2.2). At time of sowing, some acorns were already germinating and had visible radicle growth. The greenhouse materials align with current commercial nursery standards. The growing media used was Sunshine Metro Mix 840PC RSi (Sungro Horticulture, Agawam, MA, USA). Seedling containers included D27L, D40L and D60L held in D20T Deepot trays (Stuewe & Sons, Inc., Tangent, OR, USA). Container dimensions and volumes are provided in Table 2.1.

During planting, each D20T Deepot tray was covered by a D20COVS stainless steel cover (Stuewe & Sons, Inc., Tangent, OR, USA) to minimize loss of growing media as containers were filled. Growing media filled each container completely, flush with the top. The tray was then lifted and tapped down on the greenhouse bench three times for compaction. Growing media was again filled level to the top of the container.

Acorns were sown at a density of one per container. The acorns were placed in the growing media radicle-end downward at a 45-degree angle. This angle provides conditions where both the radicle and cotyledon are free-to-grow. For acorns that had already germinated, the radicle was gently twisted though the growing media in a downward motion to minimize potential damage. Growing media was kept moist during the germination stage via light misting of overhead irrigation every other day. A total of 1122 acorns were sown equally among the three container sizes.

Germination rate was assessed at Week 18 (n = 510 germinants for a rate of 45.5%) and Week 21 (n = 534 germinants for a rate of 47.6%). After this time, germination rate plateaued and the remaining ungerminated acorns were culled from the experiment.

On Week 22, fertilizer and grit were applied to the top of each container (Figure 2.1). Each container was top-dressed with 4.15 g of slow-release fertilizer (Osmocote® Smart Release 8-9 Month Fertilizer 19-5-8 (N-P-K), The Scotts Company, Maryville, OH, USA). This quantity of fertilizer is the container nursery recommended medium application rate based on the volume of the D40 container. Each container also received ~0.6-cm layer of forestry grit (Target Products Ltd., Burnaby, British Columbia, Canada) on top of the fertilizer to minimize ideal growing conditions for greenhouse pests. Acorns that sprouted multiple shoots were clipped to a single dominant stem.

Watering to Target Container Capacity

Each tray was watered to container capacity, allowed to drain freely for one hour, and weighed. An average weight at container capacity was defined for each of the container sizes (D27, D40 and D60). Using the scientist technique defined in Dumroese et al. (2015), the target weight for irrigation was set at 85% of the weight at container capacity. Prior to a potential watering event, each tray was weighed individually and if the value was at or below the 85% target it was watered to container capacity. Tray locations post-watering were re-randomized within each block to account for natural environmental greenhouse gradients (Figure 2.2). The 85% target was held from Weeks 22 to 37. Average weight at container capacity was recalculated once (on Week 31) to account for changes in weight over time. The target weight was reduced to 70% of the weight at container capacity from Weeks 38 to 45 using methods previously described.

Due to circumstances surrounding COVID-19, the seedlings were moved to the Oxbow Farm and Conservation Center in Carnation, Washington (47°41'34.8"N 121°58'38.7"W) on Week 26 (8 June 2020). Once in the greenhouse, trays were randomly placed in their previously assigned blocks on the bench (Figure 2.2).

Greenhouse Measurements

Morphological measurements were taken after the greenhouse growing season, starting on Week 48 (11 November 2020). Height (HT, cm) and root collar diameter (RCD, mm) were measured for all seedlings (n = 450). HT was defined as the height from the media surface to the tip of the highest bud. RCD was defined as the transition point of the seedling from root to shoot, just above the growing media.

A 30% destructive random sampling was taken from each replicate (n = 135). Growing media was carefully washed from the seedling's root system (Figure 2.1). Root length (R_L, cm) and root volume (R_V, cm^3) were determined using the WinRHIZO Image Analysis software (Regents Instruments Inc., Quebec, QC, Canada). The root and shoot portions of each seedling were separated and dried at 60°C for 48 hours. After which, shoot dry mass (SDM, g) and root dry mass (RDM, g) weights were collected. The root-to shoot ratio (R:S) was calculated using the RDM and SDM measurements.

Field Site Description

Seedlings over-wintered in ambient conditions at the Oxbow Farm and Conservation Center Native Plant Nursery in Carnation, WA (47°41'34.8"N 121°58'38.7"W). The field site is in King County, WA, in the Snoqualmie Valley and approximately 300 meters east of the Snoqualmie River. The Snoqualmie River is found at the center of the Snoqualmie Valley and flows 130 km from south to north and in the Pacific Northwest Ecoregion and within the Snoqualmie River Watershed (17110010) (King County 2008, United States Geological Survey 2020). The land is recognized as the ancestral home of the Snoqualmie Indian Tribe (Oxbow Farm & Conservation Center 2021, Snoqualmie Indian Tribe 2021).

The area within the Snoqualmie Valley holds important ecological value in the region. The primary soil type is Nooksack silt loam with slopes < 2% (United States Department of Agriculture 2021). King County is home to 69 species of mammals, 220 species of birds, 12 species of amphibians, 8 species of reptiles, 50 species of native freshwater fish, over 200 species of saltwater fish, and 1,249 species of vascular plants (King County 2008). Historic overstory riparian habitat trees included red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), red cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), and black cottonwood (*Populus balsamifera*) (King County 2008).

The valley has been significantly altered from its historic ecological state. Land conversion has been primarily from forested floodplain to agricultural use and has changed the fluctuations in the watershed, as well as flooding severity and frequency (King County 2008). The bull trout (*Salvelinus confluentus)* is a threatened species whose habitat includes the Snoqualmie River (U.S. Fish & Wildlife Service 2021). There are no other listed threatened or endangered species in the area, although invasive species have flourished in the Snoqualmie River's frequently changing riverbanks (King County 2008).

Planting Seedlings

The field site was outlined and mowed prior to planting (12 February 2021, Figure 2.3). Seedlings remained in the same block assignment as in the greenhouse (Figure 2.4). Each tray was randomized and planted in a block-column, where seedlings were also randomized (n = 315). Holes were drilled using a gas-powered auger fitted with a six-inch diameter drill bit in a grid at $2m^2$ spacing. Seedlings were planted on 27-28 February 2021. Each seedling was outfitted with a 5” x 30” Rigid Seedling Protector Tube and VisPore® Tree Mat (Forestry Suppliers, Jackson, MI, USA) secured with landscape staples. The field was mowed again on 30 May 2021 and 30 July 2021 to reduce shading from surrounding vegetation as well as discourage wildlife browsing habits that might lead to seedling damage. Seedlings received no supplemental irrigation after they were planted.

One ZL6 cellular data logger was placed in each block on 7 March 2021 (METER Group, Inc., Pullman, WA). Each logger hosted three TEROS 11 soil moisture and temperature sensors (METER Group, Inc., Pullman, WA). Sensors were placed at a depth in the soil profile of 17.8 cm, the depth of a D27 container (Table 2.1). The sensors were arranged in each block diagonally on a southeasterly transect, with equidistant spacing. Data was logged every 6 hours. Sensors remained in the ground from 7 March 2021 – 30 July 2021. On 30 July 2021 sensors were rearranged so one of three sensors in each block were placed at a depth corresponding to each of the three container depths (Table 2.1). The sensors were placed in a central location in each block. Data was averaged at each depth among blocks from 7 March 2021 – 10 November 2021 (Figure 2.5).

From January through October 2021, a nearby weather station approximately 1,770 m away reported a minimum air temperature of -4.4°C, a maximum air temperature of 40.3°C, a mean air temperature of 11.9°C and total precipitation of 95.61 cm (Figure 2.5) (Weather Underground 2021).

Pruning Treatments

Within each block the container sizes were replicated three times (Figure 2.4). On 21 & 27 March 2021, seedlings in two of the three replicates in each block were pruned to 2-cm height. Seedlings in the third replicate were left unpruned, as a control.

Field Measurements

To inform timing of data collection, budbreak was assessed on 21 April 2021 (at which time n = 133 seedlings (42%) had broken bud) and again on 19 May (at which time n = 307 seedlings (97%) had broken bud) (Table 2.2, Figure 2.6). Net photosynthesis (A, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$), transpiration (E, $\mu mol\ H_2O\ m^{-2}s^{-1}$), and stomatal conductance (g_s, $mol\ H_2O\ m^{-2}s^{-1}$) were measured three times over the course of the summer (early-season: 18-20 June 2021, mid-season: 20-21 July 2021 and late-season: 28-29 August 2021), five weeks apart, using a LI-6400xt with a broad leaf chamber (Li-COR Inc., Lincoln, NE, USA). Three seedlings were randomly selected from each row (n = 135) and measurements were taken between 10 am and 2 pm. Variables were set at the following: 20°C block temperature, a PAR value of

1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, reference CO_2 concentration of 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and a relative humidity between 55-65%. Data was logged once the chamber displayed a 3/3 steady state. The leaf selected for measurement was chosen as representative of the remaining leaves on the seedling. If the measured leaf did not encompass the full 6-cm^2 chamber area, a photo of the leaf was taken, and area was adjusted to correct for area measured in the chamber using FIJI (ImageJ, National Institute of Health, (Schindelin et al. 2012)). Water use efficiency (WUE) was calculated as A/E.

Water potential (Ψ_{PD}) data was collected using a PMS pressure chamber (PMS Instruments, Albany, OR, USA). Measurements were taken twice over the course of the summer (mid-season: 4 July 2021 and late-season: 20 August 2021), six weeks apart. Three seedlings were randomly selected from each row (n = 135) and measurements were taken beginning at 2 am until 30 minutes prior to sunrise. The leaf selected for measurement was chosen as representative of the remaining leaves on the seedling and was destructively sampled. Seedlings were substituted for another randomly chosen seedling if it contained fewer than five total leaves.

Survival and seedling growth were assessed in the field at the end of the growing season, on 23-24 October 2021. Seedling height (HT, cm) and root collar diameter (RCD, mm) were measured for all seedlings (n = 315). HT was defined as the height from the soil surface to the tip of the highest bud. RCD was defined as the transition point of the seedling from root to shoot, just above the soil surface. Seedling survival was assessed as presence or absence of living seedlings.

ANALYSIS

Greenhouse Measurements

The experimental design is a completely randomized design, consisting of five blocks, each of which contained nine trays of seedlings (with each tray containing ten seedlings). Three of the nine trays in each block represented a container factor-level (Figure 2.2). Seedlings were equally spaced within each tray to occupy ten of the twenty slots, high grading such that only the most vigorous seedlings of similar height (~4 cm) remained in each block (n = 450). Each tray was treated as a single experimental replicate (n = 45), and seedlings were considered the individual observation-level unit.

All analyses were completed using RStudio (version 4.0.3). A linear mixed model (LMM) was used to define each response variable pertaining to seedling morphology (HT, RCD, SDM, RDM, R:S, R_L and R_V), with a three-level container size treatment (D27, D40 and D60) as the fixed effect, and a five-level factor block as a random effect. The assumption of independence of errors was met based on the experimental design, while all other assumptions were checked graphically using the residuals of errors. The assumption of normality was met in all the models. However, the assumption of constant variance was relaxed in models where the assumption was not met. All pairwise comparisons were adjusted using a Tukey correction for a family of three comparisons ($\alpha = 0.05$).

Field Measurements

A full factorial design was used, with a two-level factor for pruning treatment (pruned or unpruned), a three-level factor for container size (D27, D40 and D60), and five blocks. Block-columns are the replicate and seedlings are the observation-level unit. To measure A, E, g_s, WUE, and Ψ_{PD}, three of the seven seedlings in the block-column were randomly sampled and used to calculate replicate means ($n = 45$). For HT, RCD, and survival, all seven seedlings in the block-column were sampled and used to calculate replicate means.

A linear mixed model (LMM) was used to define each response variable pertaining to seedling physiology (A, E, g_s, WUE, and Ψ_{PD}), and morphology (HT and RCD), with a three-level container size (D27, D40 and D60) and two-level pruning treatment (pruned or unpruned) as the main effects, and a five-level factor block as a random effect. I was interested in both main effects as well as their interaction. Assumptions were met by the standards described above. All pairwise comparisons were adjusted using a Tukey correction for a family of fifteen comparisons ($\alpha = 0.05$).

RESULTS

Greenhouse Measurements

Morphology (HT, RCD, SDM, RDM, R:S, R_L, and R_V)

There is no evidence that *Q. garryana* seedling HT ($p = 0.3854$), SDM ($p = 0.3236$), RDM ($p = 0.3678$), R:S ($p = 0.2388$), or R_V ($p = 0.2819$) were statistically different across container sizes (Table 2.3 and Figure 2.7). However, there is evidence that seedling RCD ($p = < 0.0001$) and R_L ($p = 0.0003$) were statistically different across container sizes (Table 2.3 and Figure 2.7). Compared to those in a D27 container, D40 seedlings had 10% smaller RCD and 28% longer roots, and D60 seedlings had a 13% smaller RCD and 42% longer roots (Figure 2.7, Appendix Table A.1, and Table A.2). Neither RCD ($p = 0.3587$) nor R_L ($p = 0.5265$) differed between seedlings grown in D40 and D60 containers (Figure 2.7, Appendix Table A.1, and Table A.2).

Field Measurements

Physiology (A, E, g_s, WUE and Ψ_{PD})

There was evidence that early-season A differed between pruned and unpruned seedlings (p = 0.0129) but not among seedlings grown in different container sizes (p = 0.4010) and the main effects did not interact (p = 0.3678) (Table 2.4 and Figure 2.8). Thus, regardless of container size, pruning had a significant effect on early-season A such that rates were 11% greater among pruned seedlings compared to unpruned seedlings (Figure 2.8, Appendix Table A.3, and Table A.4). Additionally, there was no evidence that mid- or late-season A differed among seedlings grown in different container sizes (p = 0.9162, p = 0.2637, respectively) or between pruned and unpruned seedlings (p = 0.8017, p = 0.2364, respectively), and the two main effects did not interact (p = 0.9588, p = 0.8064, respectively) (Table 2.4 and Figure 2.8).

There was evidence that early-season E differed between pruned and unpruned seedlings (p = < 0.0001), but not among seedlings grown in different container sizes (p = 0.3143), and the main effects did not interact (p = 0.8009) (Table 2.4 and Figure 2.8). Pruning had a significant effect on early-season E such that rates were 22% greater among pruned seedling compared to unpruned seedlings (Figure 2.8, Appendix Table A.3, and Table A.4). There was evidence that mid-season E differed among seedlings grown in different container sizes (p = 0.0416), but not between pruned and unpruned seedlings (p = 0.5929), and the main effects did not interact (p = 0.6079) (Table 2.4 and Figure 2.8). Thus, regardless of pruning treatment, mid-season E was 13% greater for seedlings cultivated in D60 containers compared to those grown in D40 containers (Figure 2.8, Appendix Table A.3, and Table A.4). Additionally, there was no evidence that late-season E differed among seedlings grown in different container sizes (p = 0.3469) or between pruned and unpruned seedlings (p = 0.1382), and the two main effects did not interact (p = 0.3477) (Table 2.4 and Figure 2.8).

There was evidence that early-season g_s differed between pruned and unpruned seedlings (p = 0.0001), and among seedlings grown in different container sizes (p = 0.0244) but the main effects did not interact (p = 0.0529) (Table 2.4 and Figure 2.8). Pruning had a significant effect early-season g_s such that rates were 29% greater among pruned seedlings compared to unpruned seedlings. Additionally, early-season g_s was 18% and 17% greater for seedlings cultivated in D27 and D60 containers, respectively, compared to those growth in D40 containers (Figure 2.8, Appendix Table A.3, and Table A.4). There was evidence that mid-season g_s differed among seedlings grown in different container sizes (p = 0.0346), but not between pruned and unpruned seedlings (p = 0.5485), and the main effects did not interact (p = 0.7748) (Table 2.4 and Figure 2.8). Thus, regardless of pruning treatment, mid-season g_s

was 18% greater for seedlings cultivated in D60 containers compared to those grown in D40 containers (Figure 2.8, Appendix Table A.3, and Table A.4). There was evidence that late-season g_s differed among seedlings grown in different container sizes ($p = 0.0017$), but not between pruned and unpruned seedlings ($p = 0.8737$), and the main effects did not interact ($p = 0.0854$) (Table 2.4 and Figure 2.8). Thus, regardless of pruning treatment, late-season g_s was 30% and 18% greater for seedlings cultivated in D60 containers compared to those growth in D40 and D27 containers, respectively (Figure 2.8, Appendix Table A.3, and Table A.4).

There was evidence that early-season WUE differed between pruned and unpruned seedlings ($p = 0.0308$) but not among seedlings grown in different container sizes ($p = 0.8958$), and the main effects did not interact ($p = 0.2014$) (Table 2.4 and Figure 2.8). Thus, regardless of container size, pruning had a significant effect on early-season WUE such that rates were 8% greater among unpruned seedlings compared to pruned seedlings. There was evidence that mid-season WUE differed between pruned and unpruned seedlings ($p = 0.0006$), among seedlings grown in different container sizes ($p = < 0.0001$), and the main effects did interact ($p = 0.0034$) (Figure 2.8, Appendix Table A.3, and Table A.4). Mid-season WUE was greater among pruned seedlings compared to unpruned seedlings only when cultivated in D27 containers; there was not a difference in mid-season WUE between pruned and unpruned seedlings when cultivated in either D40 or D60 containers. When pruned, mid-season WUE was greater for both D27 and D40 seedlings relative to D60 seedlings but when unpruned, mid-season WUE was greater for D40 seedlings relative to D27 seedlings. There was no evidence that late-season WUE differed between pruned and unpruned seedlings ($p = 0.5874$) or among seedlings grown in different container sizes ($p = 0.4160$) (Table 2.4 and Figure 2.8). Although there was evidence that the main effects did interact ($p = 0.0129$), there was no evidence that mean late-season WUE was statistically significantly different for any pruning treatment and container combinations.

There was no evidence that mid-season Ψ_{PD} differed among seedlings grown in different container sizes ($p = 0.0767$) or between pruned and unpruned seedlings ($p = 0.2609$) and the two main effects did not interact ($p = 0.4252$) (Table 2.4 and Figure 2.8). While there was no evidence that late-season Ψ_{PD} differed among seedlings grown in different container sizes ($p = 0.1051$), there was evidence that it differed between pruned and unpruned seedling ($p = < 0.0001$), and the interaction between pruning and container size was significant ($p = 0.0030$) (Table 2.4 and Figure 2.8). Specifically, late-season Ψ_{PD} was significantly lower among unpruned seedlings relative to pruned seedlings when grown in D27 and D60 containers but did not differ between unpruned and pruned seedlings when grown in D40 containers (Figure 2.8, Appendix Table A.3, and Table A.4).

Morphology (RCD and HT)

After one field growing season, there was no evidence that end-of-season RCD differed among seedlings grown in different container sizes (p = 0.2471) or between pruned and unpruned seedlings (p = 0.2691) and the two main effects did not interact (p = 0.7569) (Table 2.5 and Figure 2.9).

There was evidence that end-of-season HT differed among seedlings grown in different container sizes (p = 0.0441) and between pruned and unpruned seedlings (p = 0.015), and the two main effects did not interact (p = 0.4111) (Table 2.5 and Figure 2.9). End-of-season seedling HT was 25% greater among unpruned seedlings compared to pruned seedlings. Additionally, end-of-season HT was 23% and 8% greater for seedlings cultivated in D27 containers compared to those grown in D40 and D60 containers, respectively, and 14% greater for seedlings cultivated in D60 containers compared to those grown in D40 containers (Figure 2.9, Appendix Table A.5, and Table A.6).

Survival

End-of-season survival was 98% (n = 309) (Table 2.6). Mortality (n = 6 seedlings) occurred early in the growing season, prior to budbreak (Table 2.2). Although low, all mortality occurred within the pruned treatment. However, the high level of survival suggests no effect of pruning or container treatments and indicates that seedlings were grown well enough to survive field conditions.

DISCUSSION

How does container size affect seedling morphology?

Seedlings cultivated in the three container types showed similar HT, SDM, RDM, R:S and R_V at the end of one greenhouse growing season. Despite the difference in each container's volume, seedlings in all three container sizes allocated similar proportions of biomass to root and shoot, with no statistically significant difference in R:S. Evidence of similar patterns of biomass allocation exist for *Quercus suber* as reported in Chirino et al. (2008). In this study, R:S was greater than was found in other studies for *Quercus ilex* and *Quercus suber* (Ramírez-Valiente et al. 2018). This difference could be attributed to difference in growth habits between the species, environmental conditions, or cultural practices in the nursery. The study's results suggest that Oregon white oak seedling allometry is conservative for shoot biomass relative to root biomass. This idea is supported by growth patterns in other *Quercus* spp. (Rundel 1979, Long and Jones 1996, Jacobs et al. 2005). Under resource-limited environments container-grown *Quercus rubra* seedlings directed carbon allocation to their roots, suggesting that its growth strategy is adapted to resource-limited environments (Kolb et al. 1990, Canham et al. 1996).

In this study, container effect was evident for RCD where seedlings grown in D27 containers had larger RCD relative to D40 and D60 seedlings. RCD is considered the most important morphological parameter in predicting future field potential (Mexal and Landis 1990, Johnson and Cline 1991) and may be especially important in xeric planting sites (Tsakaldimi et al. 2005). In general, RCD is considered a successful predictor of field performance because it is positively correlated to root volume and structure (Jacobs et al. 2005). Larger RCD also indicates greater nutritional status (Tsakaldimi et al. 2013). These results are similar to those reported for *Quercus ilex* and *Quercus coccifera* in relation to RCD (Tsakaldimi et al. 2013). These results suggest that seedlings in smaller containers may shift their allometry to favor shoot growth, where larger container sizes provide seedlings greater root growth opportunities through larger container size volumes.

A container effect was also evident in D40 and D60 seedlings where R_L was larger relative to D27 seedlings. Root structure is an important morphological consideration for Oregon white oak, especially retaining the fine roots and the natural structure of the taproot (Devine et al. 2009, Gould and Harrington 2009). Larger root systems allow seedlings greater access to water and nutrients (Davis and Jacobs 2005). *Quercus suber* seedlings allocated more biomass to the roots in larger containers relative to smaller containers (Chirino et al. 2008). While seedling RDM was equal across all three container sizes, the length of roots was greater in D40 and D60 seedlings relative to D27 seedlings. From this, it could be concluded that the D40 and D60 roots were comprised of lighter weight fine roots. This was evident in a similar study of *Quercus suber*, where the larger container size had greater biomass allocated to fine roots (Chirino et al. 2008).

What effects do container size, field pruning, and their interaction have on seedling physiology, morphology, and survival?

The physiological impacts of top pruning Oregon white oak seedlings are not well known. However, there is evidence that photosynthetic activity increases after top pruning, which can increase seedling growth in other species (Basave Villalobos et al. 2015). In the present study, pruning resulted in higher early-season net photosynthesis and transpiration. Additionally, these seedlings did not suffer a significant reduction in carbon input despite being in droughty conditions during the late summer growing season. Photosynthesis is a trade-off of CO_2 assimilation at the cost of water lost through transpiration, where initial root growth depends on photosynthesis (Burdett 1990). Therefore, transpiration is a key indicator of the internal water balance (Wuenscher and Kozlowski 1971). The measured rates of net photosynthesis are similar to both evergreen and deciduous Mediterranean oaks (Epron and Dreyer 1993, Tretiach 1993) and California oaks (Hollinger 1992). However, Tretiach (1993) noted that both net photosynthesis and transpiration decreased significantly during the month of July for both evergreen *Q. ilex* and deciduous *Q. pubescens*, which does not align with the results from the present study. Additionally, Tretiach (1993) found that evergreen *Q. ilex* recorded its highest rate of photosynthesis in October, highlighting the drought avoidance strategies between evergreen and deciduous oaks in their leaf structure. Transpiration rates of 3.8 µmol H_2O $m^{-2}s^{-1}$ were recorded in mature *Quercus petraea* trees during droughty conditions at the beginning of the growing season (Breda et al. 1993), which is similar to the values we recorded for Oregon white oak in the field. The differences in rates could be attributed to the differences in age, drought tolerance strategies among species, or environmental conditions such as severity of drought conditions.

While WUE was initially lower among pruned seedlings, it was greater with pruning for D27 seedlings mid-season. WUE indicates the ability to minimize water loss compared to carbon gained (WUE = A/E). Despite greater A among pruned seedlings, the higher WUE among unpruned seedlings was driven by much greater E among pruned seedlings relative to unpruned seedlings. Similar values of WUE were noted in other *Quercus* spp., where greater WUE occurred in more drought tolerant species native to xeric environments compared to those native to mesic environments (Wuenscher and Kozlowski 1971). WUE is a good indicator of seedling water status, therefore, pruning had a positive impact on WUE in both early- and mid-season conditions.

Stomatal conductance is an important indicator of early drought stress (Flexas and Medrano 2002). *Quercus* is known to maintain higher values of stomatal conductance and net photosynthesis while experiencing droughty conditions compared to other co-occurring species (Abrams 1990) but the sensitivity of response depends on the species (Damesin and Rambal 1995). Deciduous *Quercus pubescens* and *Quercus robur* close stomata when relative leaf water content falls below 90%, where evergreen *Q. ilex* responds when values fall to 85% (Rundel 1979). Closing of stomata reduces water loss through transpiration (Rundel 1979) but which comes at a loss of carbon assimilation (Méthy 1996). In the present study, pruned seedlings had a higher rate of stomatal conductance than unpruned seedlings. D60 and D27 seedlings maintained a higher early-season stomatal conductance relative to D40 seedlings. D60 seedlings continued to maintain a higher mid- and late-season stomatal conductance relative to D27 and D40 seedlings. Values < 0.1 mol H_2O $m^{-2}s^{-1}$ indicate levels of severe stress (Flexas and Medrano 2002). Recorded values during late-season for our Oregon white oak seedlings ranged from 0.28 to 0.38 among the main effects, indicating that conditions were well above severe drought even during the driest portion of the growing season. Similar values of stomal conductance were found in Oregon white oak (Davis 2005) and *Quercus suber* (Chirino et al. 2008). Our results suggest that Oregon white oak was experiencing some stress and responded with decreasing stomatal conductance. This strategy reflects drought tolerance within the species through conservative water use (Breda et al. 1993, Damesin and Rambal 1995).

Late-season water potential was higher with pruning for both D27 and D60 seedlings. More specifically, seedlings cultivated in D27 and D60 containers were under less moisture stress when pruned compared to when unpruned. Top pruning is known to reduce moisture stress in container-grown oak seedlings (Kaczmarek and Pope 1993). Pemán et al. (2006) notes that *Q. ilex* grown in larger containers had the most efficient water uptake. Our study indicates a lower Ψ_{PD} than has been recorded in other species (Rundel 1979, Damesin and Rambal 1995, Méthy 1996) but similar to other values recorded of Oregon white oak (Davis 2005). While we did not determine the turgor loss point (Ψ_{TLP}), it has been recorded in other oak species ranging from -2.6 to 2.95 MPa (Rundel 1979, Damesin and Rambal 1995, Nardini et al. 1999). Our lowest recorded value during the late-season measurement was -0.90 Mpa.

Neither pruning nor container size had a statistically significant effect on seedling RCD after one growing season in the field. However, pruning resulted in reduced HT. Seedings grown in a D27 container were tallest, and D60 seedlings were intermediary. Studies have conflicting information whether pruned seedlings will be able to catch-up to their unpruned counterparts in subsequent growing years. Although, longer-term growth impacts of top pruning Oregon white oak could be considerable by increased growth for both root and shoot biomass, as well as field survival. Kaczmarek & Pope (1993) noted that pruned *Q. rubra* seedlings had equal or greater height growth compared to unpruned seedlings after five field growing seasons. While our study does not address overall root growth after one field season, additional studies investigating root growth and structure differences among the container size and pruning treatments may be informative.

Seedling survival (98% or above for all treatments) was not influenced by either pruning container size after one growing season in the field. Oregon white oak mortality varies dramatically both east and west of the Cascades (Bell and Papanikolas 1997, Devine and Harrington 2008, Bakker et al. 2012). Our results are similar to those reported for *Q. ilex* and *Q. coccifera* in relation to field survival (Tsakaldimi et al. 2013).

The slow-release fertilizer application was applied in the greenhouse at the same rate for all container sizes in the greenhouse, so D27 seedlings received a greater rate of fertilizer and D60 seedlings received a lower rate of fertilizer relative to D40 seedlings. This could have been a confounding variable and impacted the overall growth among the container sizes. Seedlings cultivated in the D27 container size had the most conservative R_L but greatest RCD. Although, if D27 seedlings had the greatest field potential because of higher fertilizer rates in the nursery, we would expect D60 seedlings to be shortest. However, D60 seedlings were intermediate in height and greater than D40 seedlings.

In summary, this study found that morphological differences in Oregon white oak seedlings occur in RCD and R_L among container sizes. These results align with similar results of *Q. rubra* seedlings where larger RCD and root system has the greatest field potential and can successfully compete with vegetation, and where RCD was a stronger indicator of field growth relative to root structure (Dey and Parker 1997, Wilson et al. 2007). Additionally, A, E, g_s, WUE and Ψ_{PD} were impacted by both container size and pruning treatments at various times during the growing season. This study suggest that Oregon white oak displays both drought avoidance and drought tolerant strategies. Given the high demand for container-grown seedlings in reforestation, and future predictions of a changing climate, developing quantifiable parameters in the nursery that effectively characterize Oregon white oak seedling quality and improve reliability and prediction of field survival will benefit restoration and reforestation programs.

CONCLUSION

Post-planting water stress is one of the primary causes of mortality in nursery-grown seedlings. Nursery cultural practices can positively impact future field survival in restoration projects by manipulating a seedling’s morphology and physiology. This is especially critical in Mediterranean *Quercus* species, that quickly develop a deep-reaching taproot to mitigate droughty summer conditions, and where bareroot and shallow nursery containers may not be sufficient stocktypes.

This study showed that nursery-based decisions such as container size and top pruning can impact an Oregon white oak seedling’s morphology and physiology, which can offset the stresses of low water availability in the field. After one growing season in the greenhouse, seedling container size impacted seedling morphology characteristics RCD and R_L. These morphological features are well-documented predictors of field growth and survival in many species. After one growing season in the field, we observed little relative impact on water stress due to container size. Seedlings cultivated in D60 containers performed best, likely due to the initial depth of the root system. However, seedlings cultivated in the D27 containers performed better than expected relative to seedlings cultivated in D40 and D60 containers. These results contradict previous studies for other *Quercus* spp. where larger seedlings significantly improved field performance.

Top pruning Oregon white oak seedlings also impacted their physiology and morphology after one field growing season. Pruning did not result in any negative impacts to the seedlings. Physiological variables were particularly impacted during early-season measurements. Seedlings that were top pruned resulted in an anticipated smaller end-of-season HT, however, seedling height is not an especially valuable morphological characteristic as it is often overused and overstated as a singular variable. While pruned seedlings were shorter after the field growing season, they displayed exceptional resiliency in terms of height recovery. Overall, pruned seedlings experienced less seasonal water stress relative to unpruned seedlings.

Neither pruning nor container size had a statistically significant effect on seedling survival after one growing season in the field. The Oregon white oak seedlings in our study proved to be extremely resilient to seasonal field conditions. This is especially poignant given the field season in which this study was conducted. Approximately four months after planting an anomalous heat event exposed the seedlings to uncharacteristically high temperatures. Despite this, there was no mortality seen in the study, offering evidence that Oregon white oak is resilient to high temperatures soon after planting.

This study provides evidence that decision-making in the nursery can significantly impact growth and survival for Oregon white oak seedlings, however, future studies could help refine guidelines for nursery managers and field practitioners. Our study outlines the biological growth strategies of Oregon white oak seedlings in the nursery and post-planting. In this study, seedlings were grown in ambient field conditions. However, future research investigating withholding water and increasing water stress to determine seedlings responses in more extreme field conditions would be insightful. Additionally, Seedlings cultivated in the D60 containers resulted in more fragile plugs relative to the D27 and D40 container sizes. This was especially apparent during planting. Holding the seedlings cultivated in the D60 containers in the greenhouse for a second growing season could result in a plug with greater root and soil stability at the time of planting. Furthermore, it would be beneficial to expand the range of planting sites by planting in a greater variety of locations. This could offer future evidence as to the reslilency of Oregon white oak in greater varieties of soil types and environmental conditions. Our study did not destructively sample the seedlings after the field growing season to explore the differences in root growth and expansion among treatments due to time and logistical constraints. However, this could provide useful evidence and allow us to further understand the root growth capabilities of the seedling in the field. Finally, investigating the impacts of reoccurring top pruning seedlings in subsequent years could be useful in more xeric field conditions. Longer-term studies are meaningful because mortality only increases with a greater timescale.

Evidence from this study helps inform future management decisions, both in the nursery and in the field, based on individual circumstances and capacity. All three container sizes proved to be successful, however, there were differences among them. Seedlings cultivated in a D60 container likely result in greater costs in the nursery relative to seedlings cultivated in D27 and D40 containers, however, may be more successful in the field in the longer-term and in more xeric conditions. Seedlings cultivated in the D27 containers were unexpectedly successful in the field but could be especially useful in restoration projects where fall planting is possible, providing more time for the root system to establish prior to limiting summer growing conditions. This study provides the information for programs to make informed decisions based on economic-tradoff.

In summary, Oregon white oak is a species that displays a strong tolerance to droughty field conditions. This study provides evidence that Oregon white oak can be successful in restoration projects with limiting environmental conditions. In light of this, methods to decrease water stress during reforestation planning processes could be beneficial, due to the recurring summer drought conditions in the Pacific Northwest. From the morphological and physiological results of this study, the use of container size and top pruning could improve seedling growth and survival rates in its native range in western Washington and demonstrates the potential for future restoration success with Oregon white oak seedlings. Overall, this study provides baseline information that can be used as an asset for nursery and field managers in their decision-making, allowing them to make more informed choices tailored to their programs.

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TABLES & FIGURES

Table 2.1

Deepot container size specifications.

Container size	Cell Diameter*		Cell Depth		Cell Volume	
	inch	cm	inch	cm	inch	cm
D27L	2.7	6.9	7.0	17.8	27.1	444.0
D40L	2.7	6.9	10.0	25.4	40.0	656.0
D60L	2.7	6.9	14.0	35.6	60.0	983.0

*diameter measurement for top diameter only as the container is tapered

Table 2.2

Average spring budbreak percentages over time by container size and pruning treatment.

	April 21	May 19
D27	41 %	98 %
D40	39 %	96 %
D60	48 %	99 %
pruned	48 %	96 %
unpruned	32 %	99 %

Table 2.3

Results from a linear mixed model (LMM) via ANOVA of the effect of container sizes on morphological variables of *Quercus garryana* seedlings after one season in the greenhouse, presented with F-statistics with associated P-values. Starred items indicate statistical significance (α = 0.05).

Variable	Container Size			
	df	F-statistic		p-value
HT (cm)	$_{2,38}$	0.9778		0.3854
RCD (mm)	$_{2,38}$	8.4210	*	< 0.0001
SDM (g)	$_{2,38}$	1.1626		0.3236
RDM (g)	$_{2,38}$	1.0270		0.3678
R:S	$_{2,38}$	1.4877		0.2388
R_L (cm)	$_{2,38}$	9.9176	*	0.0003
R_V (cm^3)	$_{2,38}$	1.3095		0.2819

Table 2.4

Results from a linear mixed model (LMM) via ANOVA of two main effects, container size and pruning treatment, as well as their interaction on physiological variables of field-planted *Quercus garryana* seedlings, presented with F-statistics with associated P-values. Different numbers indicate early-, mid-, and late-season measurements. Starred items indicate statistical significance (α = 0.05).

Variable	Main Effects	df	F-statistic		p-value
1) A (μmol CO_2 m^{-2} s^{-1})	container	2, 35	0.9382		0.4010
	pruning	1, 35	6.8753	*	0.0129
	interaction	2, 35	1.0295		0.3678
2) A (μmol CO_2 m^{-2} s^{-1})	container	2, 35	0.0878		0.9162
	pruning	1, 35	0.0640		0.8017
	interaction	2, 35	0.0421		0.9588
3) A (μmol CO_2 m^{-2} s^{-1})	container	2, 35	1.3851		0.2637
	pruning	1, 35	1.4511		0.2364
	interaction	2, 35	0.2165		0.8064
1) E (μmol H_20 $m^{-2}s^{-1}$)	container	2, 35	1.1964		0.3143
	pruning	1, 35	25.5211	*	< 0.0001
	interaction	2, 35	0.2235		0.8009
2) E (μmol H_20 $m^{-2}s^{-1}$)	container	2, 35	3.4881	*	0.0416
	pruning	1, 35	0.2912		0.5929
	interaction	2, 35	0.5049		0.6079
3) E (μmol H_20 $m^{-2}s^{-1}$)	container	2, 35	1.0913		0.3469
	pruning	1, 35	2.3018		0.1382
	interaction	2, 35	1.089		0.3477
1) g_s (mol H_20 $m^{-2}s^{-1}$)	container	2, 35	4.1352	*	0.0244
	pruning	1, 35	19.1978	*	0.0001
	interaction	2, 35	3.2010		0.0529
2) g_s (mol H_20 $m^{-2}s^{-1}$)	container	2, 35	3.7084	*	0.0346
	pruning	1, 35	0.3670		0.5485
	interaction	2, 35	0.2570		0.7748
3) g_s (mol H_20 $m^{-2}s^{-1}$)	container	2, 35	7.7192	*	0.0017
	pruning	1, 35	0.0256		0.8737
	interaction	2, 35	2.6416		0.0854
1) WUE	container	2, 35	0.11034		0.8958
	pruning	1, 35	5.06731	*	0.0308
	interaction	2, 35	1.67786		0.2014

2) WUE	container	$_{2, 35}$	18.2376	*	< 0.0001
	pruning	$_{1, 35}$	14.0702	*	0.0006
	interaction	$_{2, 35}$	6.7043	*	0.0034
3) WUE	container	$_{2, 35}$	0.8995		0.4160
	pruning	$_{1, 35}$	0.2999		0.5874
	interaction	$_{2, 35}$	4.9353	*	0.0129
1) Ψ_{PD} (MPa)	container	$_{2, 35}$	2.7658		0.0767
	pruning	$_{1, 35}$	1.3057		0.2609
	interaction	$_{2, 35}$	0.8764		0.4252
2) Ψ_{PD} (MPa)	container	$_{2, 35}$	2.4045		0.1051
	pruning	$_{1, 35}$	24.3117	*	< 0.0001
	interaction	$_{2, 35}$	6.8959	*	0.0030

Table 2.5

Results from a linear mixed model (LMM) via ANOVA of two main effects, container size and pruning treatment, as well as their interaction on morphological variables of *Quercus garryana* seedlings, presented with F-statistics with associated P-values. Starred items indicate statistical significance (α = 0.05).

Variable	Main Effects	df	F-statistic		p-value
RCD (mm)	container	2, 35	1.4555		0.2471
	pruning	1, 35	1.2610		0.2691
	interaction	2, 35	0.2807		0.7569
HT (cm)	container	1, 35	3.4167	*	0.0441
	pruning	1, 35	11.8474	*	0.0015
	interaction	1, 35	0.9119		0.4111

Table 2.6

End-of-season mortality (n = 6) for *Quercus garryana* seedlings (n = 315) after one growing season in the field.

Block	Row	Container	Pruning	Seedling	Survival
2	2	D40	pruned	2	dead
2	9	D60	pruned	5	dead
3	7	D40	pruned	4	dead
4	2	D27	pruned	7	dead
5	6	D27	pruned	1	dead
5	8	D60	pruned	7	dead

Figure 2.1

From top to bottom and left to right: sowing acorns in the Oak Creek greenhouse (8 December 2019), cotyledons emerging from acorns (4 March 2020), size and volume differences in Deepot container sizes (28 April 2020), D60 seedling (28 May 2020), seedlings in the Oxbow Farm and Conservation Center's Native Plant Nursery (6 July 2020), and washing growing media off of seedlings for destructive sampling of root and shoot characteristics (1 December 2020).

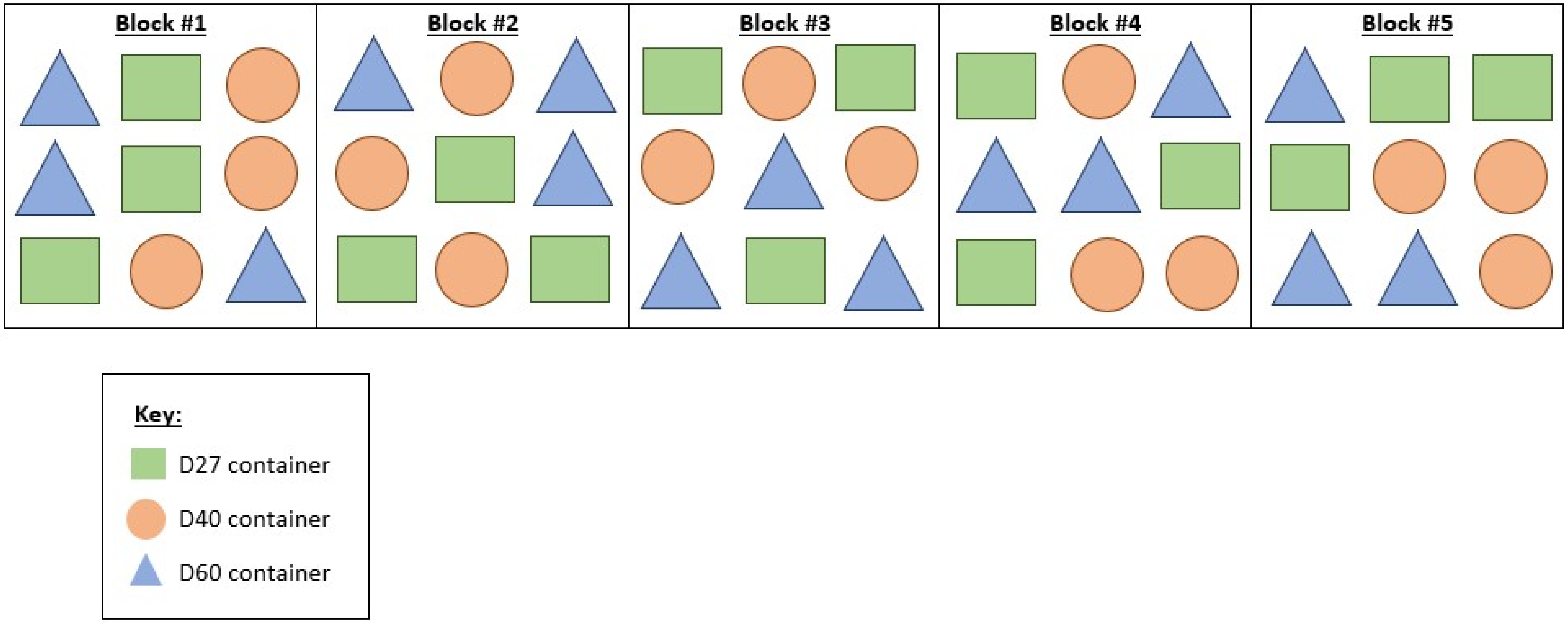

Figure 2.2

Greenhouse arrangement of trays in blocks. There are 10 seedlings in each tray, and nine trays in each block. Each block contains three trays of each factor-level of container sizes. Seedlings are the observation-level unit (n = 450), and trays are the experimental replicate (n = 45). All trays remain in their assigned block throughout the growing season but are randomly arranged within their block after watering.

Figure 2.3
From top to bottom and left to right: Mowing field site, layout of planting grid and flagging seedling planting spots, organizing trays for block-column planting arrangement, laying out Rigid Seedling Protector Tube and VisPore® Tree Mat at planting spots, planting seedlings and securing protective materials with bamboo and landscape staples, and final layout of field site. All photos taken February 2021.

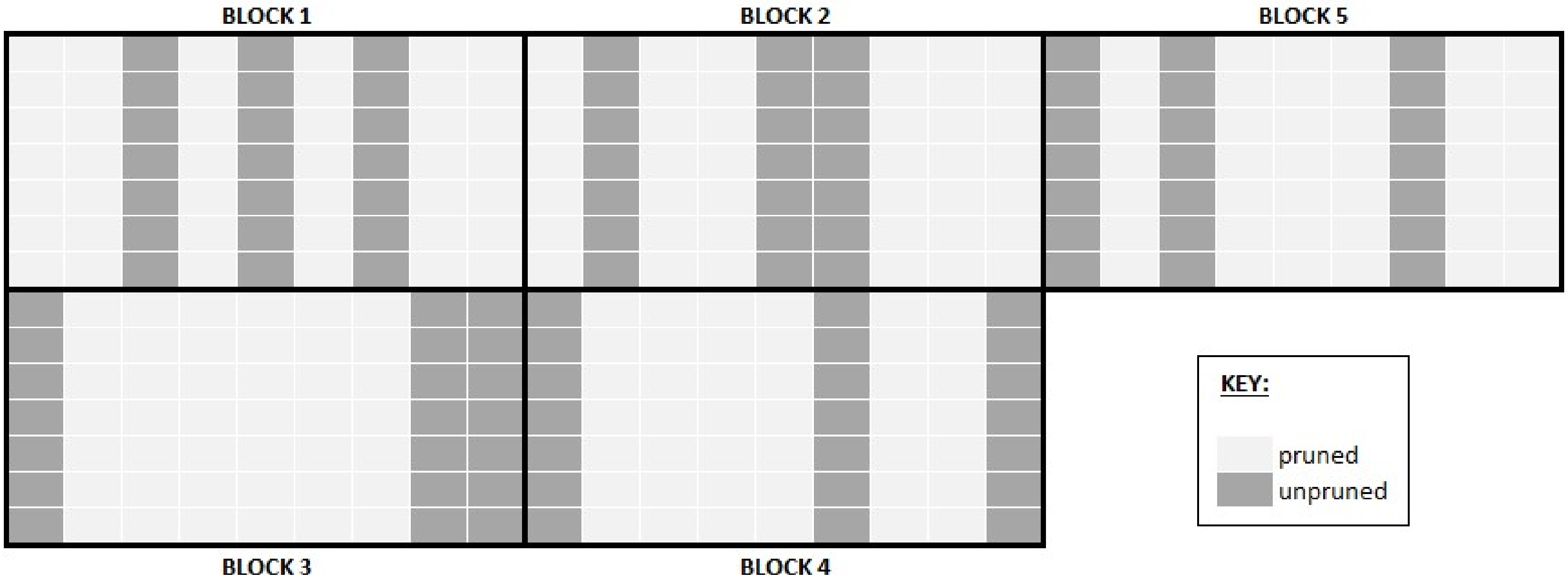

Figure 2.4
Field arrangement of seedlings. Each block, which corresponds to a greenhouse tray, consists of nine columns of seven seedlings. Seedlings are the observational-level unit (n = 315), and columns are experimental replicates (n = 45). Due to the factorial experimental design, each block contains three columns of each container size, where two rows are pruned (light gray), and one is unpruned (dark gray)

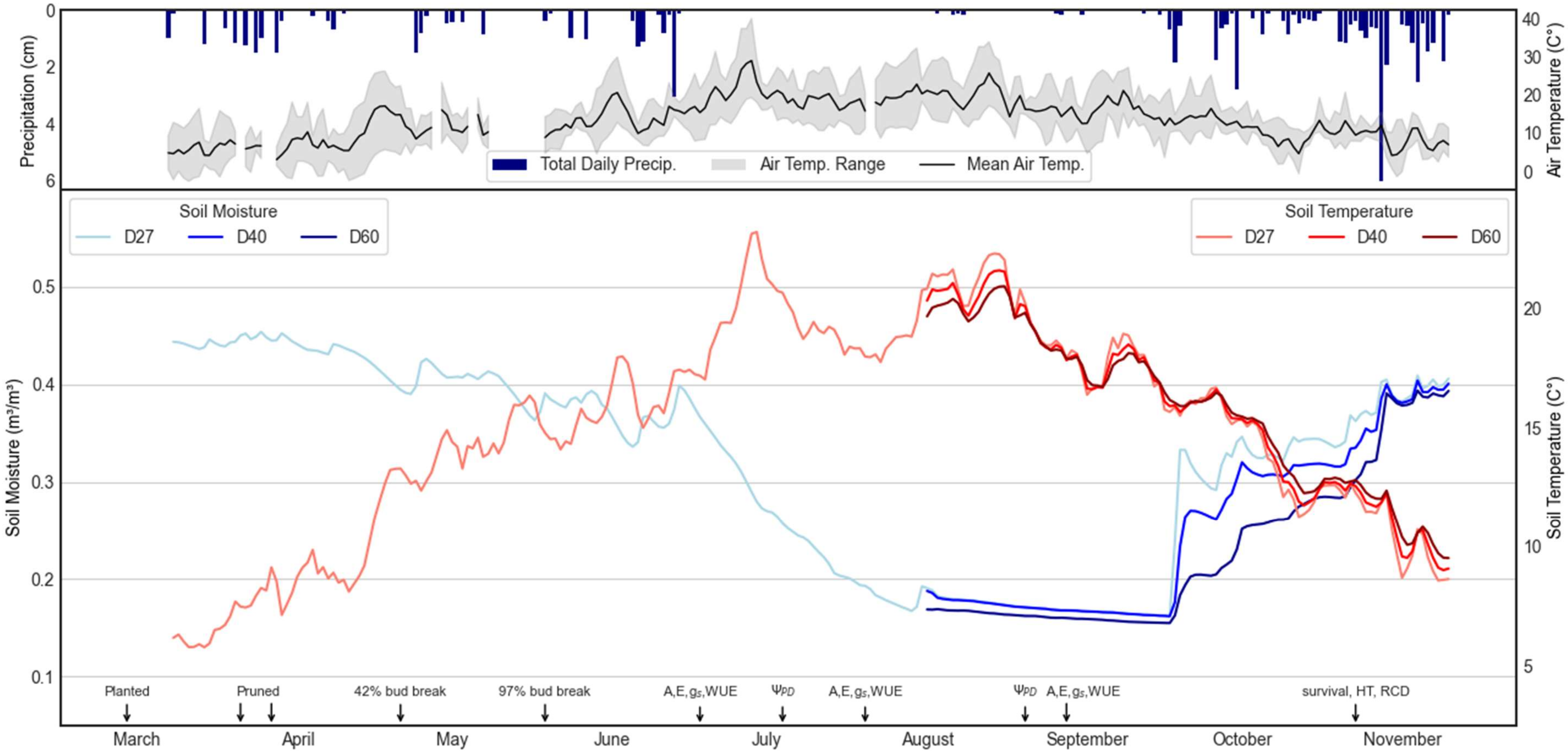

Figure 2.5

On-site soil moisture and soil temperature, and daily minimum air temperature, daily maximum air temperature, daily mean air temperature, and daily total precipitation (Weather Underground 2021) from 7 March 2021 – 10 November 2021. Soil moisture and temperature displayed soil conditions for D27 containers from 7 March – 30 July. Soil moisture and temperature displayed soil conditions for D27, D40 and D60 containers from 30 July – 10 November. Inset text displays important dates and sampling events. The Pacific Northwest heat dome was an anomalous heat wave that impacted the region from 26-28 June 2021 (Bhatia et al. 2021). Gaps in air temperature are due to unavailable data.

Figure 2.6

From top to bottom and left to right: Pruned seedling with swelling adventitious buds (22 April 2021), pruned seedling breaking bud (22 April 2021), unpruned seedling with swelling buds (22 April 2021), pruned seedling with multiple stems (19 May 2021), unpruned seedling (19 June 2021), and unpruned seedling displaying end-of-season budset (27 October 2021).

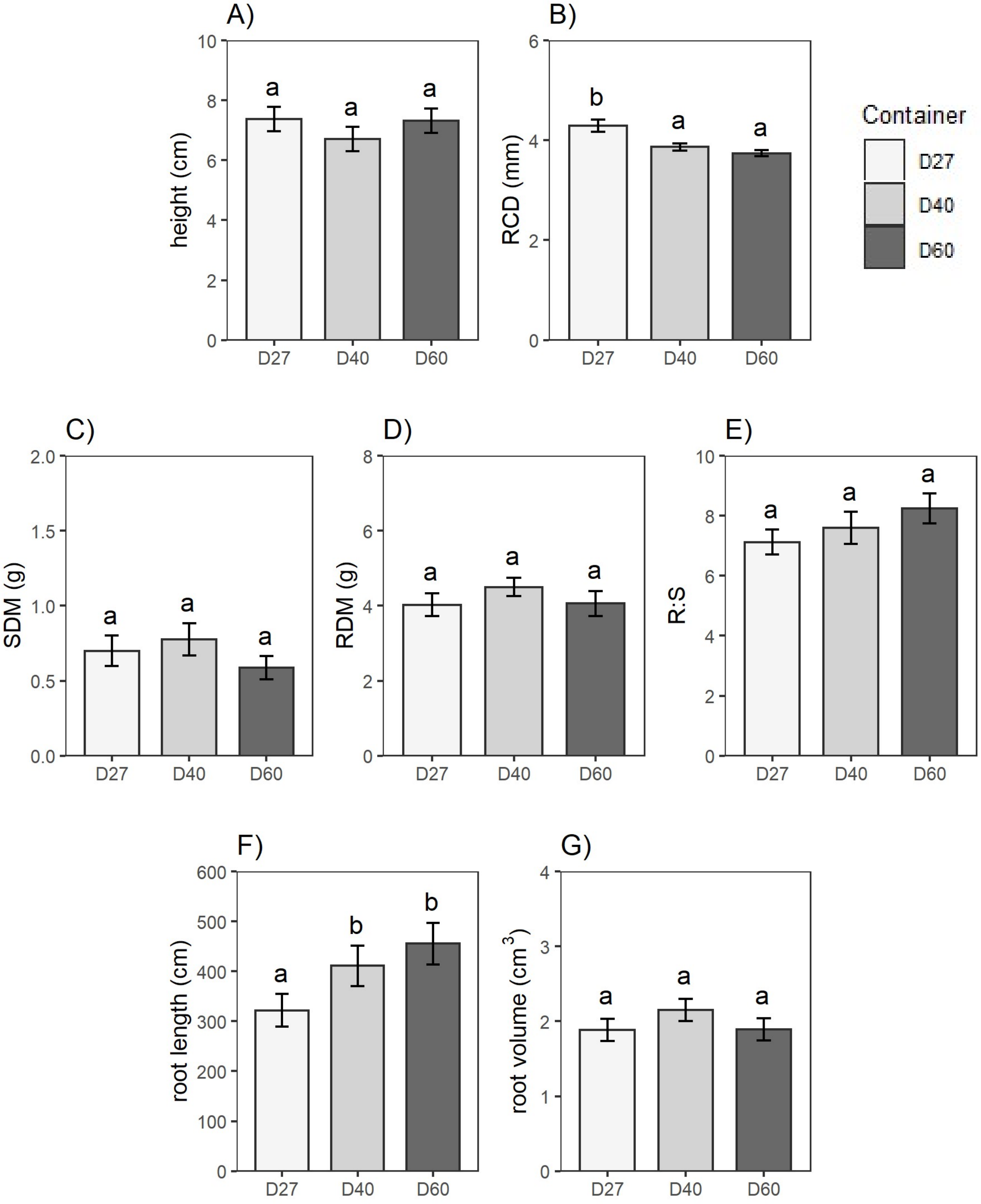

Figure 2.7

Mean (± SE) *Quercus garryana* seedling (A) HT (cm), (B) RCD (mm), (C) SDM (g), (D) RDM (g), (E) R:S, (F) R_L (cm), and (G) R_V (cm^3) after one growing season in the greenhouse. Different lowercase letters indicate statistically significant differences ($\alpha = 0.05$). Means are the result of fifteen replicated samples (n = 15).

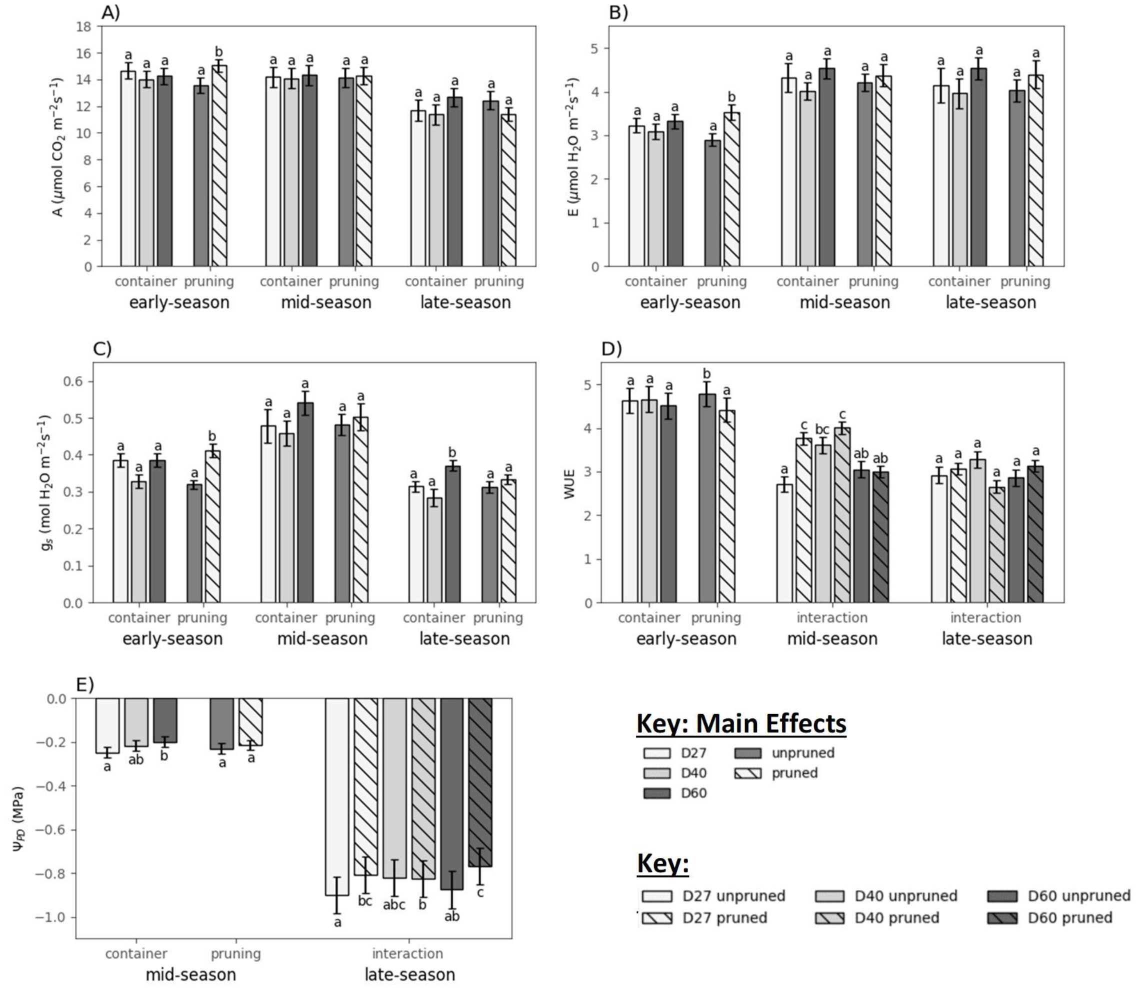

Figure 2.8

Mean (± SE) *Quercus garryana* seedling A) A (μmol CO_2 m^{-2} s^{-1}), B) E^1 (μmol H_2O m^{-2} s^{-1}), C) $g_s{}^1$ (mol H_2O m^{-2} s^{-1}), D) WUE^1, and E) $\Psi_{PD}{}^2$(MPa) for early-season, mid-season, and late-season sampling events. Different letters within sampling events indicate statistically significant differences (α = 0.05). Means are the result of fifteen replicated samples (n = 15). Interactions between main effects container size and pruning treatment were included when significant. Due to sampling design, statistical inference cannot be made among sampling events.

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[1] Differences in mean average response variables are calculated with a Tukey-Kramer adjustment for a family of 15 comparisons. The compact letter display (CLD) on the bar graph indicates no statistically significant difference in means among groups for early-season g_s, mid-season E and g_s for main effect container, and late-season WUE for interaction, although there was evidence that the effect of pruning depended on container size (overall F test for interaction, p = 0.0244, p= 0.0416, p = 0.0346, p = 0.0129, respectively). Due to the adjustment for multiple comparisons, p-values for comparisons are more conservative than the overall test of the interaction. Note that the effect of pruning is estimated to reverse for D40 container size compared to D27 and D60 containers, which matches with the results of the test for the interaction.

[2] The CLD on the bar graph indicates a statistically significant difference in means among groups for mid-season Ψ_{PD} for main effect container, although there was no evidence that the effect of container was significant (p = 0.0767). Due to the Tukey-Kramer adjustment for multiple comparisons and the definition of (α = 0.05) in relation to the proximity of the main effect p-value, the CLD is incorrectly labeled.

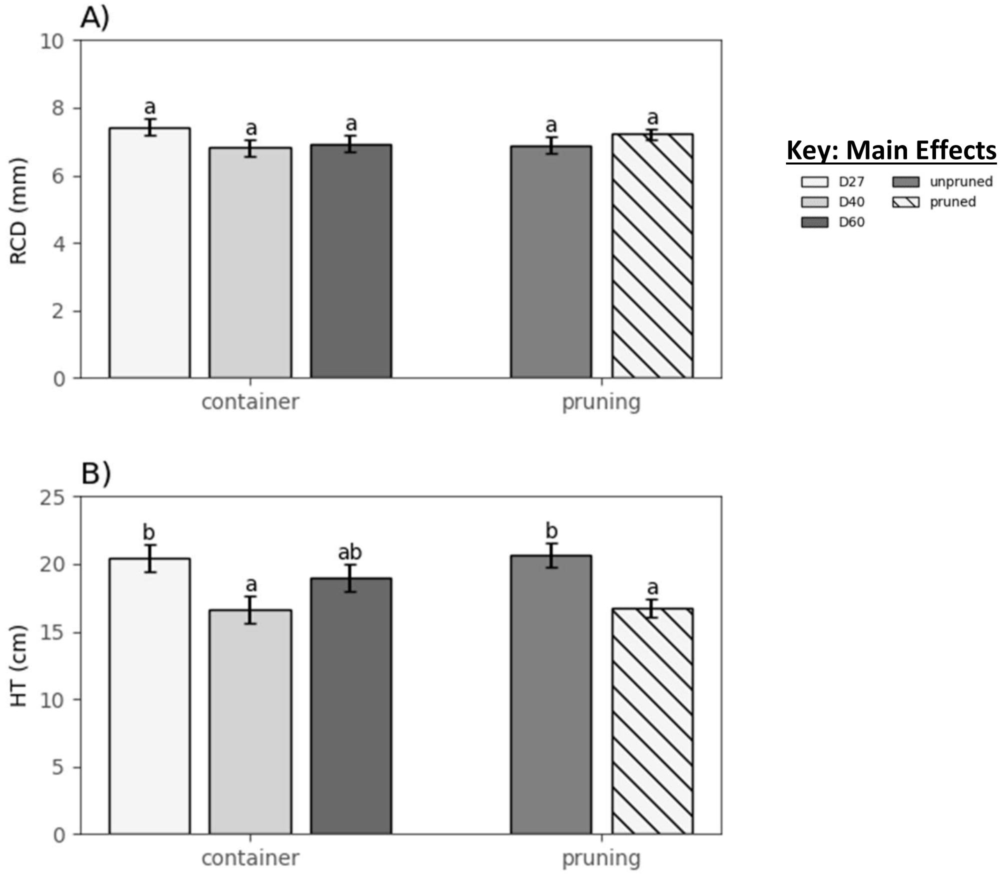

Figure 2.9

Mean (± SE) *Quercus garryana* seedling A) RCD (mm) main effects, and B) HT (cm) main effects after one field growing season. Different lowercase letters indicate statistically significant differences (α = 0.05). Means are the result of fifteen replicated samples (n = 15). Interactions between container size and pruning treatment were included when significant.

CHAPTER 3: General Conclusion

Oaks (*Quercus*) are an important genus of plants. Globally, regeneration has proven difficult and many reasons inhibiting their reforestation have been investigated. While oaks are known to possess qualities of both drought avoidance and drought tolerance, future predictions of climate change will make reforestation more difficult. However, nursery cultural practices can have a significant impact on the growth and survival of artificial reforestation efforts.

In the Pacific Northwest, Oregon white oak is a culturally and ecologically critical species. The species has a significantly depleted range; where habitat fragmentation, land-use conversion, and vegetative competition due to cultural practices of fire suppression have been detrimental. Natural regeneration is difficult due to lack of local populations in ideal historic habitat, as well as physiological characteristics of the acorn. Due to these issues, artificial regeneration is necessary to address the contraction in its range.

Nursery-grown seedlings can be cost-prohibitive. Container-grown seedlings can be especially labor-intensive but generally offer greater initial field success due to their intact root system post-planting. To justify the costs of artificial regeneration through nursery-grown seedlings, standards for producing and qualifying seedlings needs to be defined. Since 1990, a set of recommendations for nurseries known as the Target Plant Concept have been widely used. This set of recommendations focuses on growing seedlings defined by specific morphological and physiological parameters based on field conditions.

The goal of this thesis is to assess how nursery-based decisions such as container size and top pruning can impact an Oregon white oak seedling's morphology and physiology, and whether this can offset the stresses of low water availability in the field. The project described in Chapter 2 found that container size impacted RCD and R_L but did not impact HT, SDM, RDM, R:S, and R_V after one greenhouse growing season. Both container size and top pruning impacted A, E, g_s, WUE, and Ψ_{PD} at various times through the first field growing season. While end-of-season RCD and survival were not statistically different among container sizes, HT was impacted by both container size and top pruning. Our results suggest seedling container size and top pruning can alleviate post-planting water stress after the first field growing season.

There is a growing need for quality seedlings for global reforestation where seedlings should be grown based on the limitations of the field site. This project emphasizes the need for building species-specific knowledge which transcends the borders between the nursery and the field. This study and others promote collaborative efforts that capture a seedling’s entire ecological potential and reduces high nursery and environmental costs due to a lack of field establishment. The container size and pruning treatments explored in this study provide a globally scalable template for restoration of other *Quercus* spp. This is especially important where water scarcity is a significant limitation in both the greenhouse and field. The use of seedlings in reforestation is going to become even more important in the fight against climate change, so exceptional seedlings need to be grown in order to justify the cost of growing and establishment.

APPENDIX

Table A.1

Effects of container size on seedling morphology of *Quercus garryana* after one season in the greenhouse. Means (± SE and ± CI) are presented within each factor-level. Means are the result of fifteen replicated samples (n = 15). Different lowercase letters in the same column for each variable indicates a difference in statistical significance (α = 0.05).

Variable	Container	Mean		SE	CI		
HT (cm)	D27	7.4	a	0.4	6.2	,	8.5
	D40	6.7	a	0.4	5.6	,	7.8
	D60	7.3	a	0.4	6.2	,	8.5
RCD (mm)	D27	4.29	b	0.12	3.96	,	4.62
	D40	3.87	a	0.07	3.67	,	4.06
	D60	3.74	a	0.06	3.57	,	3.90
SDM (g)	D27	0.6984	a	0.1021	0.4149	,	0.9819
	D40	0.7767	a	0.1078	0.4776	,	1.0759
	D60	0.5866	a	0.0784	0.3689	,	0.8042
RDM (g)	D27	4.0267	a	0.3094	3.1678	,	4.8857
	D40	4.5002	a	0.2493	3.8081	,	5.1923
	D60	4.0571	a	0.3332	3.1320	,	4.9822
R:S	D27	7.1240	a	0.4158	5.9697	,	8.2784
	D40	7.5970	a	0.5341	6.1141	,	9.0800
	D60	8.2405	a	0.4961	6.8631	,	9.6178
R_L (cm)	D27	321.6220	a	32.7541	230.6819	,	412.5621
	D40	410.8393	b	40.5062	298.3760	,	523.3026
	D60	455.6135	b	41.5898	340.1417	,	571.0853
R_V (cm^3)	D27	1.885	a	0.147	1.478	,	2.291
	D40	2.152	a	0.147	1.745	,	2.559
	D60	1.890	a	0.147	1.483	,	2.297

Table A.2

Differences in mean average response variable between container sizes, with Tukey-Kramer adjustment for each family of three comparisons. Starred items indicate statistical significance (α = 0.05).

Variable	Comparison	Difference in mean	Tukey-adjusted CI				p-value
HT (cm)	D27 minus D40	0.7	-0.6	,	2.0		0.4277
	D27 minus D60	0.1	-1.2	,	1.3		0.9947
	D40 minus D60	-0.6	-1.9	,	0.7		0.4846
RCD (mm)	D27 minus D40	0.42	0.08	,	0.76	*	0.0119
	D27 minus D60	0.55	0.22	,	0.88	*	0.0006
	D40 minus D60	0.13	-0.10	,	0.35	*	0.3587
SDM (g)	D27 minus D40	-0.0784	-0.4321	,	0.2754		0.8521
	D27 minus D60	0.1118	-0.1925	,	0.4162		0.6460
	D40 minus D60	0.1902	-0.1255	,	0.5059		0.3169
RDM (g)	D27 minus D40	-0.4735	-1.3986	,	0.4516		0.4328
	D27 minus D60	-0.0304	-1.1012	,	1.0404		0.9974
	D40 minus D60	0.4431	-0.5300	,	1.4162		0.5136
R:S	D27 minus D40	-0.4730	-2.1238	,	1.1777		0.7656
	D27 minus D60	-1.1164	-2.6951	,	0.4622		0.2092
	D40 minus D60	-0.6434	-2.4213	,	1.1344		0.6544
R_L (cm)	D27 minus D40	-89.2172	-167.6032	,	-10.8313	*	0.0226
	D27 minus D60	-133.9914	-215.6827	,	-52.3001	*	0.0008
	D40 minus D60	-44.7742	-145.0308	,	55.4824	*	0.5265
R_V (cm^3)	D27 minus D40	-0.268	-0.729	,	0.194		0.3435
	D27 minus D60	-0.005	-0.466	,	0.456		0.9996
	D40 minus D60	0.262	-0.199	,	0.724		0.3573

Table A.3

Effects of container size and field pruning on seedling physiology of *Quercus garryana* after one season in the field. Means (± SE and ± CI) are presented within each factor-level for both main effects as well as their interaction. Means are the result of fifteen replicate samples (n = 15). Different numbers in the same column for each variable indicates a statistically significant difference in (α = 0.05). Different uppercase letters indicate early-, mid-, and late-season measurements.

Variable	Container	Pruning	Mean		SE	CI		
1) A (µmol CO$_2$ m^{-2} s^{-1})	D27	pruned	15.47817	a	0.66810	13.62322	,	17.33311
	D27	unpruned	13.87249	a	0.87069	11.45507	,	16.28992
	D40	pruned	14.21593	a	0.66810	12.36098	,	16.07087
	D40	unpruned	13.79628	a	0.87069	11.37886	,	16.21370
	D60	pruned	15.44431	a	0.66810	13.58937	,	17.29926
	D60	unpruned	13.07762	a	0.87069	10.66019	,	15.49504
2) A (µmol CO$_2$ m^{-2} s^{-1})	D27	pruned	14.37858	a	0.81356	12.11976	,	16.63740
	D27	unpruned	14.02262	a	1.01188	11.21318	,	16.83205
	D40	pruned	14.04880	a	0.81356	11.78998	,	16.30762
	D40	unpruned	14.11936	a	1.01188	11.30992	,	16.92879
	D60	pruned	14.41602	a	0.81356	12.15720	,	16.67484
	D60	unpruned	14.24471	a	1.01188	11.43527	,	17.05414
3) A (µmol CO$_2$ m^{-2} s^{-1})	D27	pruned	11.28109	a	0.89261	8.80279	,	13.75938
	D27	unpruned	12.05639	a	1.25414	8.57435	,	15.53843
	D40	pruned	10.46869	a	0.89077	7.99551	,	12.94187
	D40	unpruned	12.29160	a	1.25151	8.81684	,	15.76636
	D60	pruned	12.38055	a	0.74982	10.29872	,	14.46238

	D60	unpruned	12.94009	a	1.05061	10.02311	,	15.85706
1) E (µmol H$_2$0 m^{-2}s^{-1})	D27	pruned	3.49792	bc	0.22936	2.86112	,	4.13472
	D27	unpruned	2.95160	ab	0.16735	2.48697	,	3.41623
	D40	pruned	3.39637	abc	0.22936	2.75956	,	4.03317
	D40	unpruned	2.78499	a	0.16735	2.32036	,	3.24962
	D60	pruned	3.69405	c	0.22936	3.05725	,	4.33085
	D60	unpruned	2.94600	ab	0.16735	2.48137	,	3.41063
2) E (µmol H$_2$0 m^{-2}s^{-1})	D27	pruned	4.10216	a	0.37764	3.05367	,	5.15064
	D27	unpruned	4.54439	a	0.51921	3.10283	,	5.98595
	D40	pruned	3.90078	a	0.20996	3.31783	,	4.48372
	D40	unpruned	4.12273	a	0.26931	3.37500	,	4.87046
	D60	pruned	4.61481	a	0.24647	3.93050	,	5.29913
	D60	unpruned	4.44615	a	0.32536	3.54281	,	5.34949
3) E (µmol H$_2$0 m^{-2}s^{-1})	D27	pruned	3.77442	a	0.45123	2.52161	,	5.02722
	D27	unpruned	4.50642	a	0.61578	2.79675	,	6.21609
	D40	pruned	4.11273	a	0.37516	3.07111	,	5.15435
	D40	unpruned	3.80863	a	0.50345	2.41083	,	5.20644
	D60	pruned	4.20072	a	0.27413	3.43961	,	4.96183
	D60	unpruned	4.87213	a	0.34966	3.90131	,	5.84296
1) g$_s$ (mol H$_2$0 m^{-2}s^{-1})	D27	pruned	0.40221	bc	0.03032	0.31803	,	0.48638
	D27	unpruned	0.36964	abc	0.02023	0.31346	,	0.42582
	D40	pruned	0.36868	abc	0.03032	0.28451	,	0.45286
	D40	unpruned	0.28648	a	0.02023	0.23030	,	0.34266

	D60	pruned	0.46545	c	0.03032	0.38127	,	0.54962
	D60	unpruned	0.30361	ab	0.02023	0.24743	,	0.35979
2) g_s (mol H_20 $m^{-2}s^{-1}$)	D27	pruned	0.46684	a	0.04964	0.32903	,	0.60466
	D27	unpruned	0.48913	a	0.06685	0.30352	,	0.67473
	D40	pruned	0.43509	a	0.03719	0.33183	,	0.53835
	D40	unpruned	0.48183	a	0.04804	0.34846	,	0.61521
	D60	pruned	0.54320	a	0.03588	0.44359	,	0.64281
	D60	unpruned	0.53801	a	0.04600	0.41030	,	0.66571
3) g_s (mol H_20 $m^{-2}s^{-1}$)	D27	pruned	0.32377	abc	0.01584	0.27978	,	0.36776
	D27	unpruned	0.30610	ab	0.02030	0.24975	,	0.36245
	D40	pruned	0.31924	abc	0.02572	0.24783	,	0.39066
	D40	unpruned	0.24948	a	0.03421	0.15449	,	0.34448
	D60	pruned	0.36035	bc	0.01527	0.31796	,	0.40274
	D60	unpruned	0.38147	c	0.01827	0.33073	,	0.43220
1) WUE	D27	pruned	4.50273	a	0.30222	3.66362	,	5.34183
	D27	unpruned	4.75283	a	0.34420	3.79717	,	5.70849
	D40	pruned	4.26751	a	0.30222	3.42840	,	5.10661
	D40	unpruned	5.05317	a	0.34420	4.09751	,	6.00882
	D60	pruned	4.47238	a	0.30222	3.63327	,	5.31148
	D60	unpruned	4.54906	a	0.34420	3.59341	,	5.50472
2) WUE	D27	pruned	3.75854	c	0.13976	3.37050	,	4.14659
	D27	unpruned	2.71333	a	0.18625	2.19621	,	3.23045
	D40	pruned	4.00720	c	0.13976	3.61915	,	4.39524

	D40	unpruned	3.61452	bc	0.18625	3.09740	,	4.13164
	D60	pruned	3.00134	ab	0.13976	2.61330	,	3.38939
	D60	unpruned	3.05386	ab	0.18625	2.53674	,	3.57098
3) WUE	D27	pruned	3.06853	a	0.17122	2.59316	,	3.54391
	D27	unpruned	2.92121	a	0.21294	2.33000	,	3.51242
	D40	pruned	2.65385	a	0.17122	2.17847	,	3.12922
	D40	unpruned	3.28105	a	0.21294	2.68984	,	3.87226
	D60	pruned	3.13407	a	0.17122	2.65870	,	3.60945
	D60	unpruned	2.86219	a	0.21294	2.27098	,	3.45341
1) Ψ_{PD} (MPa)	D27	pruned	-0.23	a	0.03	-0.30	,	-0.16
	D27	unpruned	-0.27	a	0.03	-0.35	,	-0.18
	D40	pruned	-0.20	a	0.03	-0.28	,	-0.13
	D40	unpruned	-0.23	a	0.03	-0.31	,	-0.15
	D60	pruned	-0.21	a	0.03	-0.28	,	-0.13
	D60	unpruned	-0.19	a	0.03	-0.28	,	-0.11
2) Ψ_{PD} (MPa)	D27	pruned	-0.81	bc	0.08	-1.04	,	-0.57
	D27	unpruned	-0.90	a	0.08	-1.14	,	-0.67
	D40	pruned	-0.83	b	0.08	-1.06	,	-0.59
	D40	unpruned	-0.82	abc	0.08	-1.06	,	-0.59
	D60	pruned	-0.77	c	0.08	-1.00	,	-0.54
	D60	unpruned	-0.88	ab	0.08	-1.11	,	-0.64

Table A.4

Differences in mean average response variable between container sizes, with Tukey-Kramer adjustment for each family of fifteen comparisons. Starred items indicate statistical significance (α = 0.05).

Variable	Comparison	Difference in mean	SE	df	CI			t.ratio		p-value
1) A (μmol CO_2 m^{-2} s^{-1})	D27 Pruned minus D27 Unpruned	-1.60567	0.96707	35	-3.56893	,	0.35759	-1.66034		0.1058
	D27 Pruned minus D40 Pruned	0.07621	1.11668	35	-2.19076	,	2.34319	0.06825		0.9460
	D27 Pruned minus D40 Unpruned	-0.34343	0.96707	35	-2.30669	,	1.61983	-0.35512		0.7246
	D27 Pruned minus D60 Pruned	0.79488	1.11668	35	-1.47210	,	3.06186	0.71182		0.4813
	D27 Pruned minus D60 Unpruned	-1.57182	0.96707	35	-3.53508	,	0.39144	-1.62534		0.1131
	D27 Unpruned minus D40 Pruned	1.68189	0.96707	35	-0.28138	,	3.64515	1.73915		0.0908
	D27 Unpruned minus D40 Unpruned	1.26224	0.78961	35	-0.34075	,	2.86524	1.59856		0.1189
	D27 Unpruned minus D60 Pruned	2.40055	0.96707	35	0.43729	,	4.36381	2.48229	*	0.0180
	D27 Unpruned minus D60 Unpruned	0.03385	0.78961	35	-1.56914	,	1.63685	0.04287		0.9660
	D40 Pruned minus D40 Unpruned	-0.41964	0.96707	35	-2.38290	,	1.54362	-0.43393		0.6670
	D40 Pruned minus D60 Pruned	0.71867	1.11668	35	-1.54831	,	2.98564	0.64357		0.5240
	D40 Pruned minus D60 Unpruned	-1.64803	0.96707	35	-3.61129	,	0.31523	-1.70415		0.0972
	D40 Unpruned minus D60 Pruned	1.13831	0.96707	35	-0.82495	,	3.10157	1.17707		0.2471
	D40 Unpruned minus D60 Unpruned	-1.22839	0.78961	35	-2.83138	,	0.37461	-1.55569		0.1288
	D60 Pruned minus D60 Unpruned	-2.36670	0.96707	35	-4.32996	,	-0.40344	-2.44728	*	0.0196
	D27 Pruned minus D27 Unpruned	-0.35596	1.04214	35	-2.47161	,	1.75969	-0.34157		0.7347
	D27 Pruned minus D40 Pruned	-0.09674	1.20336	35	-2.53969	,	2.34621	-0.08039		0.9364
	D27 Pruned minus D40 Unpruned	-0.02618	1.04214	35	-2.14184	,	2.08947	-0.02512		0.9801

2) A (μmol CO_2 m^{-2} s^{-1})	D27 Pruned minus D60 Pruned	-0.22209	1.20336	35	-2.66503	,	2.22086	-0.18456	0.8546
	D27 Pruned minus D60 Unpruned	-0.39340	1.04214	35	-2.50906	,	1.72225	-0.37749	0.7081
	D27 Unpruned minus D40 Pruned	0.25922	1.04214	35	-1.85643	,	2.37488	0.24874	0.8050
	D27 Unpruned minus D40 Unpruned	0.32978	0.85090	35	-1.39765	,	2.05720	0.38756	0.7007
	D27 Unpruned minus D60 Pruned	0.13387	1.04214	35	-1.98178	,	2.24953	0.12846	0.8985
	D27 Unpruned minus D60 Unpruned	-0.03744	0.85090	35	-1.76486	,	1.68998	-0.04400	0.9652
	D40 Pruned minus D40 Unpruned	0.07056	1.04214	35	-2.04510	,	2.18621	0.06770	0.9464
	D40 Pruned minus D60 Pruned	-0.12535	1.20336	35	-2.56829	,	2.31760	-0.10416	0.9176
	D40 Pruned minus D60 Unpruned	-0.29666	1.04214	35	-2.41232	,	1.81899	-0.28467	0.7776
	D40 Unpruned minus D60 Pruned	-0.19590	1.04214	35	-2.31156	,	1.91975	-0.18798	0.8520
	D40 Unpruned minus D60 Unpruned	-0.36722	0.85090	35	-2.09464	,	1.36020	-0.43156	0.6687
	D60 Pruned minus D60 Unpruned	-0.17132	1.04214	35	-2.28697	,	1.94434	-0.16439	0.8704
3) A (μmol CO_2 m^{-2} s^{-1})	D27 Pruned minus D27 Unpruned	0.77530	1.52588	35	-2.32239	,	3.87300	0.50810	0.6146
	D27 Pruned minus D40 Pruned	-0.23521	1.76006	35	-3.80833	,	3.33791	-0.13364	0.8945
	D27 Pruned minus D40 Unpruned	1.58770	1.52480	35	-1.50781	,	4.68320	1.04125	0.3049
	D27 Pruned minus D60 Pruned	-0.88370	1.62337	35	-4.17932	,	2.41192	-0.54436	0.5896
	D27 Pruned minus D60 Unpruned	-0.32416	1.44698	35	-3.26170	,	2.61337	-0.22403	0.8240
	D27 Unpruned minus D40 Pruned	-1.01051	1.52372	35	-4.10383	,	2.08281	-0.66319	0.5116
	D27 Unpruned minus D40 Unpruned	0.81239	1.24455	35	-1.71418	,	3.33897	0.65276	0.5182
	D27 Unpruned minus D60 Pruned	-1.65900	1.36354	35	-4.42713	,	1.10912	-1.21669	0.2319
	D27 Unpruned minus D60 Unpruned	-1.09946	1.14790	35	-3.42982	,	1.23089	-0.95781	0.3447
	D40 Pruned minus D40 Unpruned	1.82291	1.52264	35	-1.26822	,	4.91403	1.19720	0.2393
	D40 Pruned minus D60 Pruned	-0.64849	1.62134	35	-3.93999	,	2.64301	-0.39997	0.6916

	D40 Pruned minus D60 Unpruned	-0.08895	1.44471	35	-3.02187	,	2.84397	-0.06157		0.9513
	D40 Unpruned minus D60 Pruned	-2.47140	1.36233	35	-5.23707	,	0.29428	-1.81410		0.0782
	D40 Unpruned minus D60 Unpruned	-1.91186	1.14646	35	-4.23930	,	0.41559	-1.66761		0.1043
	D60 Pruned minus D60 Unpruned	0.55954	1.27464	35	-2.02811	,	3.14719	0.43898		0.6634
1) E (µmol H$_2$0 m^{-2}s^{-1})	D27 Pruned minus D27 Unpruned	-0.54632	0.21780	35	-0.98847	,	-0.10416	-2.50837	*	0.0169
	D27 Pruned minus D40 Pruned	0.16661	0.15111	35	-0.14017	,	0.47339	1.10256		0.2777
	D27 Pruned minus D40 Unpruned	-0.44476	0.21780	35	-0.88692	,	-0.00261	-2.04208	*	0.0487
	D27 Pruned minus D60 Pruned	0.00560	0.15111	35	-0.30118	,	0.31238	0.03707		0.9706
	D27 Pruned minus D60 Unpruned	-0.74245	0.21780	35	-1.18460	,	-0.30030	-3.40889	*	0.0017
	D27 Unpruned minus D40 Pruned	0.71293	0.21780	35	0.27078	,	1.15508	3.27336	*	0.0024
	D27 Unpruned minus D40 Unpruned	0.10156	0.26840	35	-0.44332	,	0.64643	0.37838		0.7074
	D27 Unpruned minus D60 Pruned	0.55192	0.21780	35	0.10977	,	0.99407	2.53409	*	0.0159
	D27 Unpruned minus D60 Unpruned	-0.19613	0.26840	35	-0.74100	,	0.34874	-0.73076		0.4698
	D40 Pruned minus D40 Unpruned	-0.61138	0.21780	35	-1.05353	,	-0.16922	-2.80707	*	0.0081
	D40 Pruned minus D60 Pruned	-0.16101	0.15111	35	-0.46779	,	0.14577	-1.06549		0.2939
	D40 Pruned minus D60 Unpruned	-0.90906	0.21780	35	-1.35122	,	-0.46691	-4.17388	*	0.0002
	D40 Unpruned minus D60 Pruned	0.45036	0.21780	35	0.00821	,	0.89252	2.06780	*	0.0461
	D40 Unpruned minus D60 Unpruned	-0.29769	0.26840	35	-0.84256	,	0.24718	-1.10914		0.2749
	D60 Pruned minus D60 Unpruned	-0.74805	0.21780	35	-1.19021	,	-0.30590	-3.43461	*	0.0015
2) E (µmol H$_2$0 m^{-2}s^{-1})	D27 Pruned minus D27 Unpruned	0.44223	0.61718	35	-0.81071	,	1.69517	0.71654		0.4784
	D27 Pruned minus D40 Pruned	0.42166	0.55752	35	-0.71017	,	1.55349	0.75631		0.4545
	D27 Pruned minus D40 Unpruned	0.64361	0.53140	35	-0.43518	,	1.72241	1.21117		0.2339
	D27 Pruned minus D60 Pruned	0.09824	0.58665	35	-1.09272	,	1.28921	0.16746		0.8680

	D27 Pruned minus D60 Unpruned	-0.07042	0.54685	35	-1.18060	,	1.03975	-0.12878		0.8983
	D27 Unpruned minus D40 Pruned	-0.02057	0.42879	35	-0.89106	,	0.84992	-0.04798		0.9620
	D27 Unpruned minus D40 Unpruned	0.20138	0.39423	35	-0.59894	,	1.00170	0.51082		0.6127
	D27 Unpruned minus D60 Pruned	-0.34399	0.46604	35	-1.29009	,	0.60211	-0.73812		0.4654
	D27 Unpruned minus D60 Unpruned	-0.51266	0.41483	35	-1.35480	,	0.32948	-1.23584		0.2247
	D40 Pruned minus D40 Unpruned	0.22195	0.29212	35	-0.37108	,	0.81499	0.75980		0.4525
	D40 Pruned minus D60 Pruned	-0.32342	0.38355	35	-1.10206	,	0.45523	-0.84323		0.4048
	D40 Pruned minus D60 Unpruned	-0.49208	0.31937	35	-1.14045	,	0.15628	-1.54078		0.1324
	D40 Unpruned minus D60 Pruned	-0.54537	0.34448	35	-1.24470	,	0.15395	-1.58319		0.1224
	D40 Unpruned minus D60 Unpruned	-0.71404	0.27121	35	-1.26462	,	-0.16345	-2.63279	*	0.0125
	D60 Pruned minus D60 Unpruned	-0.16867	0.36787	35	-0.91548	,	0.57815	-0.45849		0.6494
3) E (μmol $H_2$0 m^{-2}s^{-1})	D27 Pruned minus D27 Unpruned	0.73201	0.72576	35	-0.74137	,	2.20538	1.00861		0.3201
	D27 Pruned minus D40 Pruned	0.69779	0.75933	35	-0.84374	,	2.23931	0.91895		0.3644
	D27 Pruned minus D40 Unpruned	0.39369	0.68108	35	-0.98897	,	1.77635	0.57804		0.5669
	D27 Pruned minus D60 Pruned	-0.36571	0.66737	35	-1.72055	,	0.98913	-0.54799		0.5872
	D27 Pruned minus D60 Unpruned	0.30570	0.63109	35	-0.97548	,	1.58687	0.48440		0.6311
	D27 Unpruned minus D40 Pruned	-0.03422	0.63325	35	-1.31979	,	1.25135	-0.05404		0.9572
	D27 Unpruned minus D40 Unpruned	-0.33832	0.53693	35	-1.42834	,	0.75171	-0.63009		0.5327
	D27 Unpruned minus D60 Pruned	-1.09772	0.51943	35	-2.15222	,	-0.04321	-2.11330	*	0.0418
	D27 Unpruned minus D60 Unpruned	-0.42631	0.47190	35	-1.38432	,	0.53171	-0.90338		0.3725
	D40 Pruned minus D40 Unpruned	-0.30410	0.58151	35	-1.48462	,	0.87643	-0.52295		0.6043
	D40 Pruned minus D60 Pruned	-1.06350	0.56539	35	-2.21131	,	0.08431	-1.88099		0.0683
	D40 Pruned minus D60 Unpruned	-0.39209	0.52207	35	-1.45194	,	0.66776	-0.75103		0.4577
	D40 Unpruned minus D60 Pruned	-0.75940	0.45492	35	-1.68294	,	0.16414	-1.66931		0.1040
	D40 Unpruned minus D60 Unpruned	-0.08799	0.39979	35	-0.89962	,	0.72363	-0.22009		0.8271
	D60 Pruned minus D60 Unpruned	0.67141	0.37597	35	-0.09185	,	1.43467	1.78580		0.0828

1) g_s (mol H_20 $m^{-2}s^{-1}$)	D27 Pruned minus D27 Unpruned	-0.03257	0.03645	35	-0.10656 , 0.04143	-0.89355		0.3777
	D27 Pruned minus D40 Pruned	0.08316	0.02862	35	0.02507 , 0.14125	2.90611	*	0.0063
	D27 Pruned minus D40 Unpruned	0.00095	0.03645	35	-0.07304 , 0.07495	0.02616		0.9793
	D27 Pruned minus D60 Pruned	0.06603	0.02862	35	0.00794 , 0.12412	2.30746	*	0.0271
	D27 Pruned minus D60 Unpruned	-0.09581	0.03645	35	-0.16980 , -0.02181	-2.62857	*	0.0126
	D27 Unpruned minus D40 Pruned	0.11573	0.03645	35	0.04173 , 0.18972	3.17508	*	0.0031
	D27 Unpruned minus D40 Unpruned	0.03352	0.04287	35	-0.05352 , 0.12056	0.78187		0.4395
	D27 Unpruned minus D60 Pruned	0.09860	0.03645	35	0.02460 , 0.17259	2.70510	*	0.0105
	D27 Unpruned minus D60 Unpruned	-0.06324	0.04287	35	-0.15028 , 0.02380	-1.47500		0.1492
	D40 Pruned minus D40 Unpruned	-0.08221	0.03645	35	-0.15620 , -0.00821	-2.25537	*	0.0305
	D40 Pruned minus D60 Pruned	-0.01713	0.02862	35	-0.07522 , 0.04096	-0.59864		0.5533
	D40 Pruned minus D60 Unpruned	-0.17897	0.03645	35	-0.25296 , -0.10497	-4.91010	*	< 0.0001
	D40 Unpruned minus D60 Pruned	0.06508	0.03645	35	-0.00892 , 0.13907	1.78539		0.0829
	D40 Unpruned minus D60 Unpruned	-0.09676	0.04287	35	-0.18380 , -0.00972	-2.25687	*	0.0304
	D60 Pruned minus D60 Unpruned	-0.16184	0.03645	35	-0.23583 , -0.08784	-4.44012	*	0.0001
2) g_s (mol H_20 $m^{-2}s$-^{1})	D27 Pruned minus D27 Unpruned	0.02229	0.07756	35	-0.13517 , 0.17974	0.28733		0.7756
	D27 Pruned minus D40 Pruned	0.00730	0.07655	35	-0.14810 , 0.16269	0.09531		0.9246
	D27 Pruned minus D40 Unpruned	0.05404	0.07025	35	-0.08857 , 0.19665	0.76923		0.4469
	D27 Pruned minus D60 Pruned	-0.04888	0.07528	35	-0.20171 , 0.10395	-0.64929		0.5204
	D27 Pruned minus D60 Unpruned	-0.05407	0.06956	35	-0.19529 , 0.08714	-0.77736		0.4422
	D27 Unpruned minus D40 Pruned	-0.01499	0.06208	35	-0.14102 , 0.11104	-0.24145		0.8106
	D27 Unpruned minus D40 Unpruned	0.03175	0.05413	35	-0.07813 , 0.14163	0.58663		0.5612
	D27 Unpruned minus D60 Pruned	-0.07116	0.06051	35	-0.19402 , 0.05169	-1.17598		0.2475
	D27 Unpruned minus D60 Unpruned	-0.07636	0.05323	35	-0.18442 , 0.03171	-1.43447		0.1603
	D40 Pruned minus D40 Unpruned	0.04674	0.05267	35	-0.06017 , 0.15366	0.88752		0.3809
	D40 Pruned minus D60 Pruned	-0.05617	0.05921	35	-0.17638 , 0.06403	-0.94870		0.3493

	D40 Pruned minus D60 Unpruned	-0.06137	0.05175	35	-0.16642	,	0.04368	-1.18599		0.2436
	D40 Unpruned minus D60 Pruned	-0.10292	0.05081	35	-0.20606	,	0.00023	-2.02557		0.0505
	D40 Unpruned minus D60 Unpruned	-0.10811	0.04187	35	-0.19311	,	-0.02311	-2.58212	*	0.0142
	D60 Pruned minus D60 Unpruned	-0.00520	0.04985	35	-0.10640	,	0.09601	-0.10421		0.9176
3) g_s (mol H_20 $m^{-2}s^{-1}$)	D27 Pruned minus D27 Unpruned	0.02229	0.07756	35	-0.13517	,	0.17974	0.28733		0.7756
	D27 Pruned minus D40 Pruned	0.00730	0.07655	35	-0.14810	,	0.16269	0.09531		0.9246
	D27 Pruned minus D40 Unpruned	0.05404	0.07025	35	-0.08857	,	0.19665	0.76923		0.4469
	D27 Pruned minus D60 Pruned	-0.04888	0.07528	35	-0.20171	,	0.10395	-0.64929		0.5204
	D27 Pruned minus D60 Unpruned	-0.05407	0.06956	35	-0.19529	,	0.08714	-0.77736		0.4422
	D27 Unpruned minus D40 Pruned	-0.01499	0.06208	35	-0.14102	,	0.11104	-0.24145		0.8106
	D27 Unpruned minus D40 Unpruned	0.03175	0.05413	35	-0.07813	,	0.14163	0.58663		0.5612
	D27 Unpruned minus D60 Pruned	-0.07116	0.06051	35	-0.19402	,	0.05169	-1.17598		0.2475
	D27 Unpruned minus D60 Unpruned	-0.07636	0.05323	35	-0.18442	,	0.03171	-1.43447		0.1603
	D40 Pruned minus D40 Unpruned	0.04674	0.05267	35	-0.06017	,	0.15366	0.88752		0.3809
	D40 Pruned minus D60 Pruned	-0.05617	0.05921	35	-0.17638	,	0.06403	-0.94870		0.3493
	D40 Pruned minus D60 Unpruned	-0.06137	0.05175	35	-0.16642	,	0.04368	-1.18599		0.2436
	D40 Unpruned minus D60 Pruned	-0.10292	0.05081	35	-0.20606	,	0.00023	-2.02557		0.0505
	D40 Unpruned minus D60 Unpruned	-0.10811	0.04187	35	-0.19311	,	-0.02311	-2.58212	*	0.0142
	D60 Pruned minus D60 Unpruned	-0.00520	0.04985	35	-0.10640	,	0.09601	-0.10421		0.9176
1) WUE	D27 Pruned minus D27 Unpruned	-1.60567	0.96707	35	-3.56893	,	0.35759	-1.66034		0.1058
	D27 Pruned minus D40 Pruned	0.07621	1.11668	35	-2.19076	,	2.34319	0.06825		0.9460
	D27 Pruned minus D40 Unpruned	-0.34343	0.96707	35	-2.30669	,	1.61983	-0.35512		0.7246
	D27 Pruned minus D60 Pruned	0.79488	1.11668	35	-1.47210	,	3.06186	0.71182		0.4813
	D27 Pruned minus D60 Unpruned	-1.57182	0.96707	35	-3.53508	,	0.39144	-1.62534		0.1131
	D27 Unpruned minus D40 Pruned	1.68189	0.96707	35	-0.28138	,	3.64515	1.73915		0.0908
	D27 Unpruned minus D40 Unpruned	1.26224	0.78961	35	-0.34075	,	2.86524	1.59856		0.1189

	D27 Unpruned minus D60 Pruned	2.40055	0.96707	35	0.43729	,	4.36381	2.48229	*	0.0180
	D27 Unpruned minus D60 Unpruned	0.03385	0.78961	35	-1.56914	,	1.63685	0.04287		0.9660
	D40 Pruned minus D40 Unpruned	-0.41964	0.96707	35	-2.38290	,	1.54362	-0.43393		0.6670
	D40 Pruned minus D60 Pruned	0.71867	1.11668	35	-1.54831	,	2.98564	0.64357		0.5240
	D40 Pruned minus D60 Unpruned	-1.64803	0.96707	35	-3.61129	,	0.31523	-1.70415		0.0972
	D40 Unpruned minus D60 Pruned	1.13831	0.96707	35	-0.82495	,	3.10157	1.17707		0.2471
	D40 Unpruned minus D60 Unpruned	-1.22839	0.78961	35	-2.83138	,	0.37461	-1.55569		0.1288
	D60 Pruned minus D60 Unpruned	-2.36670	0.96707	35	-4.32996	,	-0.40344	-2.44728	*	0.0196
2) WUE	D27 Pruned minus D27 Unpruned	-1.04521	0.21323	35	-1.47810	,	-0.61233	-4.90173	*	< 0.0001
	D27 Pruned minus D40 Pruned	-0.90119	0.24622	35	-1.40105	,	-0.40134	-3.66010	*	0.0008
	D27 Pruned minus D40 Unpruned	-1.29387	0.21323	35	-1.72675	,	-0.86098	-6.06784	*	< 0.0001
	D27 Pruned minus D60 Pruned	-0.34053	0.24622	35	-0.84039	,	0.15932	-1.38303		0.1754
	D27 Pruned minus D60 Unpruned	-0.28802	0.21323	35	-0.72090	,	0.14487	-1.35071		0.1855
	D27 Unpruned minus D40 Pruned	0.14402	0.21323	35	-0.28887	,	0.57691	0.67541		0.5039
	D27 Unpruned minus D40 Unpruned	-0.24865	0.17410	35	-0.60210	,	0.10480	-1.42819		0.1621
	D27 Unpruned minus D60 Pruned	0.70468	0.21323	35	0.27180	,	1.13757	3.30475	*	0.0022
	D27 Unpruned minus D60 Unpruned	0.75720	0.17410	35	0.40375	,	1.11065	4.34909	*	0.0001
	D40 Pruned minus D40 Unpruned	-0.39267	0.21323	35	-0.82556	,	0.04021	-1.84152		0.0740
	D40 Pruned minus D60 Pruned	0.56066	0.24622	35	0.06081	,	1.06052	2.27708	*	0.0290
	D40 Pruned minus D60 Unpruned	0.61318	0.21323	35	0.18029	,	1.04606	2.87562	*	0.0068
	D40 Unpruned minus D60 Pruned	0.95334	0.21323	35	0.52045	,	1.38622	4.47086	*	0.0001
	D40 Unpruned minus D60 Unpruned	1.00585	0.17410	35	0.65240	,	1.35930	5.77728	*	< 0.0001
	D60 Pruned minus D60 Unpruned	0.05251	0.21323	35	-0.38037	,	0.48540	0.24627		0.8069
3) WUE	D27 Pruned minus D27 Unpruned	-0.14732	0.21927	35	-0.59247	,	0.29783	-0.67187		0.5061
	D27 Pruned minus D40 Pruned	-0.35984	0.25320	35	-0.87386	,	0.15418	-1.42119		0.1641
	D27 Pruned minus D40 Unpruned	0.26736	0.21927	35	-0.17779	,	0.71252	1.21931		0.2309

	D27 Pruned minus D60 Pruned	0.05902	0.25320	35	-0.45500	,	0.57303	0.23308		0.8171
	D27 Pruned minus D60 Unpruned	-0.21286	0.21927	35	-0.65802	,	0.23229	-0.97077		0.3383
	D27 Unpruned minus D40 Pruned	-0.21252	0.21927	35	-0.65767	,	0.23263	-0.96918		0.3391
	D27 Unpruned minus D40 Unpruned	0.41469	0.17904	35	0.05122	,	0.77815	2.31622	*	0.0265
	D27 Unpruned minus D60 Pruned	0.20634	0.21927	35	-0.23881	,	0.65149	0.94101		0.3532
	D27 Unpruned minus D60 Unpruned	-0.06554	0.17904	35	-0.42900	,	0.29792	-0.36607		0.7165
	D40 Pruned minus D40 Unpruned	0.62720	0.21927	35	0.18205	,	1.07236	2.86037	*	0.0071
	D40 Pruned minus D60 Pruned	0.41886	0.25320	35	-0.09516	,	0.93287	1.65427		0.1070
	D40 Pruned minus D60 Unpruned	0.14698	0.21927	35	-0.29818	,	0.59213	0.67028		0.5071
	D40 Unpruned minus D60 Pruned	-0.20835	0.21927	35	-0.65350	,	0.23680	-0.95018		0.3485
	D40 Unpruned minus D60 Unpruned	-0.48023	0.17904	35	-0.84369	,	-0.11677	-2.68229	*	0.0111
	D60 Pruned minus D60 Unpruned	-0.27188	0.21927	35	-0.71703	,	0.17327	-1.23991		0.2233
1) Ψ_{PD} (MPa)	D27 Pruned minus D27 Unpruned	0.04	0.03	35	-0.02	,	0.09	1.40		0.1715
	D27 Pruned minus D40 Pruned	-0.03	0.02	35	-0.07	,	0.02	-1.18		0.2465
	D27 Pruned minus D40 Unpruned	0.00	0.03	35	-0.05	,	0.05	0.01		0.9883
	D27 Pruned minus D60 Pruned	-0.02	0.02	35	-0.07	,	0.02	-1.13		0.2673
	D27 Pruned minus D60 Unpruned	-0.04	0.03	35	-0.09	,	0.02	-1.31		0.1973
	D27 Unpruned minus D40 Pruned	-0.06	0.03	35	-0.12	,	-0.01	-2.36	*	0.0241
	D27 Unpruned minus D40 Unpruned	-0.04	0.03	35	-0.10	,	0.03	-1.20		0.2397
	D27 Unpruned minus D60 Pruned	-0.06	0.03	35	-0.12	,	-0.01	-2.32	*	0.0265
	D27 Unpruned minus D60 Unpruned	-0.07	0.03	35	-0.14	,	-0.01	-2.35	*	0.0247
	D40 Pruned minus D40 Unpruned	0.03	0.03	35	-0.03	,	0.08	0.98		0.3353
	D40 Pruned minus D60 Pruned	0.00	0.02	35	-0.04	,	0.05	0.05		0.9593
	D40 Pruned minus D60 Unpruned	-0.01	0.03	35	-0.06	,	0.05	-0.35		0.7270
	D40 Unpruned minus D60 Pruned	-0.03	0.03	35	-0.08	,	0.03	-0.94		0.3561
	D40 Unpruned minus D60 Unpruned	-0.04	0.03	35	-0.10	,	0.03	-1.15		0.2576

	D60 Pruned minus D60 Unpruned	-0.01	0.03	35	-0.07	,	0.04	-0.39		0.6961
2) Ψ_{PD} (MPa)	D27 Pruned minus D27 Unpruned	0.09	0.02	35	0.05	,	0.14	4.08	*	0.0002
	D27 Pruned minus D40 Pruned	0.02	0.02	35	-0.02	,	0.06	1.02		0.3134
	D27 Pruned minus D40 Unpruned	0.02	0.02	35	-0.03	,	0.06	0.67		0.5096
	D27 Pruned minus D60 Pruned	-0.04	0.02	35	-0.08	,	0.00	-2.00		0.0530
	D27 Pruned minus D60 Unpruned	0.07	0.02	35	0.02	,	0.12	2.99	*	0.0050
	D27 Unpruned minus D40 Pruned	-0.08	0.02	35	-0.12	,	-0.03	-3.24	*	0.0026
	D27 Unpruned minus D40 Unpruned	-0.08	0.03	35	-0.13	,	-0.02	-2.96	*	0.0055
	D27 Unpruned minus D60 Pruned	-0.13	0.02	35	-0.18	,	-0.09	-5.72	*	< 0.0001
	D27 Unpruned minus D60 Unpruned	-0.03	0.03	35	-0.08	,	0.03	-0.94		0.3535
	D40 Pruned minus D40 Unpruned	0.00	0.02	35	-0.05	,	0.04	-0.17		0.8669
	D40 Pruned minus D60 Pruned	-0.06	0.02	35	-0.10	,	-0.02	-3.03	*	0.0046
	D40 Pruned minus D60 Unpruned	0.05	0.02	35	0.00	,	0.10	2.16	*	0.0378
	D40 Unpruned minus D60 Pruned	-0.05	0.02	35	-0.10	,	-0.01	-2.30	*	0.0274
	D40 Unpruned minus D60 Unpruned	0.05	0.03	35	0.00	,	0.11	2.02		0.0516
	D60 Pruned minus D60 Unpruned	0.11	0.02	35	0.06	,	0.15	4.63	*	< 0.0001

Table A.5

Effects of container size and field pruning on seedling morphology of *Quercus garryana* after one season in the field. Means (± SE and ± CI) are presented within each factor-level for both main effects as well as their interaction. Means are the result of fifteen replicate samples (n = 15). Different lowercase letters in the same column for each variable indicates a statistically significant difference in (α = 0.05).

Variable	**Container**	**Pruning**	**Mean**		**SE**	**CI**
RCD (mm)	D27	pruned	7.44	a	0.29	6.64 , 8.23
	D27	unpruned	7.41	a	0.40	6.29 , 8.53
	D40	pruned	7.07	a	0.29	6.27 , 7.86
	D40	unpruned	6.55	a	0.40	5.43 , 7.67
	D60	pruned	7.15	a	0.29	6.36 , 7.94
	D60	unpruned	6.72	a	0.40	5.60 , 7.84
HT (cm)	D27	pruned	17.39	a	1.15	14.18 , 20.59
	D27	unpruned	23.45	b	1.63	18.92 , 27.98
	D40	pruned	14.89	a	1.15	11.68 , 18.09
	D40	unpruned	18.42	ab	1.63	13.88 , 22.95
	D60	pruned	17.81	ab	1.15	14.61 , 21.02
	D60	unpruned	20.14	ab	1.63	15.61 , 24.67

Table A.6

Differences in mean average response variable between container sizes, with Tukey-Kramer adjustment for each family of fifteen comparisons. Starred items indicate statistical significance (α = 0.05).

Variable	Comparison	Difference in mean	SE	df	CI	t.ratio		p-value
RCD (mm)	D27 Pruned minus D27 Unpruned	0.02	0.49	35	-0.98 , 1.03	0.05		0.9642
	D27 Pruned minus D40 Pruned	0.37	0.40	35	-0.45 , 1.19	0.92		0.3663
	D27 Pruned minus D40 Unpruned	0.88	0.49	35	-0.12 , 1.89	1.79		0.0828
	D27 Pruned minus D60 Pruned	0.29	0.40	35	-0.53 , 1.11	0.71		0.4820
	D27 Pruned minus D60 Unpruned	0.71	0.49	35	-0.29 , 1.71	1.44		0.1584
	D27 Unpruned minus D40 Pruned	0.35	0.49	35	-0.66 , 1.35	0.70		0.4873
	D27 Unpruned minus D40 Unpruned	0.86	0.57	35	-0.30 , 2.02	1.51		0.1406
	D27 Unpruned minus D60 Pruned	0.26	0.49	35	-0.74 , 1.27	0.54		0.5960
	D27 Unpruned minus D60 Unpruned	0.69	0.57	35	-0.47 , 1.85	1.21		0.2347
	D40 Pruned minus D40 Unpruned	0.51	0.49	35	-0.49 , 1.52	1.04		0.3060
	D40 Pruned minus D60 Pruned	-0.08	0.40	35	-0.90 , 0.74	-0.20		0.8391
	D40 Pruned minus D60 Unpruned	0.34	0.49	35	-0.66 , 1.35	0.69		0.4923
	D40 Unpruned minus D60 Pruned	-0.60	0.49	35	-1.60 , 0.41	-1.21		0.2360
	D40 Unpruned minus D60 Unpruned	-0.17	0.57	35	-1.33 , 0.99	-0.30		0.7670
	D60 Pruned minus D60 Unpruned	0.43	0.49	35	-0.58 , 1.43	0.86		0.3951
	D27 Pruned minus D27 Unpruned	-6.1	2.0	35	-10.1 , -2.0	-3.0	*	0.0045
	D27 Pruned minus D40 Pruned	2.5	1.6	35	-0.8 , 5.8	1.5		0.1352
	D27 Pruned minus D40 Unpruned	-1.0	2.0	35	-5.1 , 3.0	-0.5		0.6092

HT (cm)	D27 Pruned minus D60 Pruned	-0.4	1.6	35	-3.7	,	2.9	-0.3		0.7946
	D27 Pruned minus D60 Unpruned	-2.8	2.0	35	-6.8	,	1.3	-1.4		0.1771
	D27 Unpruned minus D40 Pruned	8.6	2.0	35	4.5	,	12.6	4.3	*	0.0001
	D27 Unpruned minus D40 Unpruned	5.0	2.3	35	0.3	,	9.7	2.2	*	0.0360
	D27 Unpruned minus D60 Pruned	5.6	2.0	35	1.6	,	9.7	2.8	*	0.0079
	D27 Unpruned minus D60 Unpruned	3.3	2.3	35	-1.4	,	8.0	1.4		0.1603
	D40 Pruned minus D40 Unpruned	-3.5	2.0	35	-7.6	,	0.5	-1.8		0.0864
	D40 Pruned minus D60 Pruned	-2.9	1.6	35	-6.2	,	0.4	-1.8		0.0819
	D40 Pruned minus D60 Unpruned	-5.3	2.0	35	-9.3	,	-1.2	-2.6	*	0.0127
	D40 Unpruned minus D60 Pruned	0.6	2.0	35	-3.5	,	4.7	0.3		0.7647
	D40 Unpruned minus D60 Unpruned	-1.7	2.3	35	-6.4	,	3.0	-0.7		0.4605
	D60 Pruned minus D60 Unpruned	-2.3	2.0	35	-6.4	,	1.7	-1.2		0.2525