Mixing tree species and density management to reduce drought susceptibility in coastal plantation forests of British Columbia

by

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## **ABSTRACT**

The coastal forests of British Columbia have been experiencing longer and more intense droughts in recent years. To evaluate the effects of species composition and density on drought sensitivity, a study was conducted in a Douglas-fir:western redcedar plantation established in 1992, in the eastern variant of the Coastal Western Hemlock very dry maritime (CWHxm1) bio- geoclimatic subzone along the east side of Vancouver Island. This plantation consists of a 4x3 factorial design with four different species mixtures (Douglas-fir:western redcedar mixtures of 1:0, 1:1, 1:3, and 0:1) at three different planting densities (500, 1000, and 1500 stems/ha). In summer 2022, measurements were taken to evaluate soil moisture, drought tolerance and water use efficiency of these stands. Soil moisture decreased with increasing stand density except for pure Douglas-fir stands which had consistently low soil moisture at all densities. Drought indices calculated from tree core data showed that drought resistance, resilience and recovery increased with decreasing stand basal area. Wood carbon isotopic data indicated that western redcedar trees in their pure stands had higher water use efficiency at lower basal area and these trees were sensitive to drought compared to Douglas-fir trees. Douglas-fir benefitted when mixed with Western redcedar and showed higher water use efficiency in mixed stands compared to pure stands both during wet and dry years. In conclusion, reducing stand basal area, which can be achieved by mixing the two species and controlling stand density, can help reduce the drought susceptibility of these forests to long-term drought.

## **PREFACE**

This thesis incorporates data collected by Surabhi Lukose during the summer of 2022 and data obtained from British Columbia Ministry of Forests. The author of the thesis takes responsibility for the research design, data organization, data collection, data analysis, and manuscript writing. Dr. Bradley D. Pinno contributed to the research design, aided with data analysis, and edited the manuscript. Dr. Kwadwo Omari contributed to the research design and provided support with data analysis and manuscript edits as well.

The partial findings of this thesis, titled "Mixing tree species along with density management to reduce drought susceptibility in coastal plantation forests of British Columbia" were shared through a lightening talk at the 2023 Growth and Yield Innovation Conference held at Canmore, Alberta and 2024 ALES Graduate Research Symposium held at the University of Alberta. Additionally, the results were presented as a poster at the 89th and 90th Forest Industry Lecture Series, 2023 ALES Graduate Research Symposium and 2023 Bentley Lecture Series held at the University of Alberta, 2023 CIF Conference held at Nanaimo, British Columbia and 2023 SAF Conference held at Sacramento, California. It is important to note that none of the contents from the results of this thesis has been published elsewhere before.

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## **CHAPTER I: Literature Review**

## 1.1 Climate change and drought

With the increasing level of atmospheric carbon dioxide and other greenhouse gases, the earth's climate is expected to warm up by an average of  $1.4^{\circ}$  to  $5.8^{\circ}$  C by the end of this century (Houghton et al. 2001). As per Intergovernmental Panel on Climate Change's (IPCC) analysis, global carbon cycle has been affected and will be affected in the near future due to the adverse effects of climate change. These recent changes in climate has affected forest ecosystems across the globe (Khaine and Woo 2015). The warming climate has been altering the structure and demography of forests by affecting tree growth, resource availability, nutrient cycling and reproduction (Barrett et al. 2011).

With the advent of climate change, there has been an increase in the intensity and frequency of climactic events (Spinoni et al. 2019). Of these several climatic events, the one that has been greatly impacting forests are prolonged periods of reduced precipitation, known as drought which is often accompanied by increased heat stress (Daniels et al., 2011). Out of all the vegetation types, forests are considered potentially most susceptible to drought (Mcdowell and Allen 2015). This vulnerability arises from their dependence on efficient water transport systems, which can be compromised under drought conditions, ultimately influencing their health and resilience. Extreme droughts affects the vigor and structure, carbon storage and aboveground biomass of forests (Khaine and Woo 2015). Continuous water stress affects tree growth and reduces forests' ability to act as carbon sink (Brzostek et al. 2014). Drought significantly affects forest productivity, results in water deficiency, increases vulnerability to biotic disturbances and thereby increases subsequent mortality (Merlin et al. 2015). Due to the high average annual temperature (°C) and summer water deficit, trees growing in western Canada are more prone to serious and extensive droughts compared to trees growing in eastern Canada (Peng et al. 2011). Drought-stressed forests are likely to become more susceptible to damage by insects and diseases (Volney and Hirsch 2011).

## 1.2 Drought in British Columbia

Wide-spread droughts are considered one of the most expensive natural catastrophes in Canada and can cause serious impacts on a variety of industries, including forestry, agriculture, human health, recreation and aquatic ecosystems (Wang and Davies 2015). The projected variations in temperature and precipitation patterns may differ globally however, British Columbia is anticipated to experience more pronounced warming and precipitation changes compared to the global average, resulting in significant implications on its forests (Choat et al. 2018).

The northeastern and southern parts of the province are expected to experience significant warming over the next century, indicating the potential for an increased frequency and intensity of wildfires, droughts, and insect outbreaks (Vore et al. 2020). On Vancouver Island in British Columbia, the mean annual temperature is predicted to increase by 1.5°C, while summer precipitation is predicted to drop by 14% below pre-industrial levels by 2050 (Brooke 2022). Periods of drought on Vancouver Island are increasing in duration and intensity owing to their placement in the lee of major mountain ranges, which results in low precipitation with considerable unpredictability (Coulthard et al. 2016, Simms and Brandes 2016). Although, the temperate rainforests in the coast are considered water-rich, yet seasonal water scarcity often occur during summer when water storage is limited and when the water demand is highest (Stephens et al. 1992).

## 1.3 Mixing tree species to improve drought tolerance

Mixed forests, characterized by the coexistence of at least two tree species, represent more than two thirds of the total forested areas on Earth. Many studies have shown that mixed- species forests can be more productive than monocultures and some have also shown that they can be more resistant and resilient to climate extremes (Zhang et al. 2012, Lebourgeois et al. 2013, Pretzsch et al. 2013).

The benefit of species mixing is often higher on resource poor compared to rich sites and during growth periods with limited rather than ample resource supply

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(Pretzsch et al. 2013, Lebourgeois et al. 2013). The functional processes that contribute to this increased drought tolerance in mixed stands include alterations in resource partitioning, which helps in improved use of resources leading to greater growth, differential rooting strategies as it helps complement root space and hydraulic redistribution and variations in stomatal closure as it controls stomatal conductance and transpiration (Kelty 1992, Prieto et al. 2012, Calama et al. 2013). These processes are influenced by both environmental conditions and individual tree characteristics (Mitchell et al. 2008, Mayoral et al. 2016). On the basis of stomatal conductance regulation, trees can be classified as isohydric and anisohydric (Fu and Meinzer 2019, Choat et al. 2012). Trees with higher isohydric characteristics reduce xylem cavitation by maintaining their water potential within a limited range (Choat et al. 2012). This approach results in trees closing their stomata, thereby diminishing their capacity to absorb carbon. Anisohydric trees, on the other hand keep their stomata open, thus reducing water potential during a drought event. This approach enables them sustain carbon assimilation rates while keeping their stomata open, although it increases the risk of hydraulic failure (McDowell et al. 2008). These differential responses to drought are supposed to allow complementarity among species, therefore facilitating the co-existence of species under stressful environmental conditions (Mayoral et al. 2015). The impact of mixing species on tree growth under drought conditions, compared to their performance in a monospecific environment is essential for understanding, forecasting and for the management of mixed species stands.

## 1.4 Density management for drought tolerance

Recent years have seen a broader shift in forest management objectives from just timber production to focusing more towards improving ecosystem resilience to future climate conditions (Franklin and Johnson 2012). Stand density influences tree growth and drought resistance within a forest ecosystem (Bradford and Bell 2017). Competition among trees is a matter of concern and may be even more important in coming decades as climate change and enhanced climate variability creates an imbalance between forest structure and moisture availability (Jump et al. 2017).

The management of stand density, such as thinning has a potential to enhance the drought resistance of individual trees over an extended period of time (20-30 years). Additionally, this approach may reduce the trees' vulnerability to secondary pathogens and insect infestations (Dobbertin et al. 2007).

Reducing stand density improves growth of individual trees by increasing availability of resources to remaining trees (Aussenac 2000). It can also be seen as an approach to restoring ecosystem resilience and reducing wildfire risk (Allen et al. 2002). Moderating competitive intensity by reducing density can help reduce drought induced tree growth declines (Bottero et al. 2017). Reducing stand density may also increase tree's resistance to drought by reducing competition for water (Giuggiola et al. 2013). This could also be considered as an interesting management option to help mitigate the increasing water stress risk and subsequent tree mortality resulting from climate change (Kerhoulas et al. 2013).

### 1.5 Species studied

#### 1.5.1 Coastal Douglas-fir:

Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) is a highly productive species widely distributed along the Pacific Coast of North America. The forests of the Pacific Northwest, which are often dominated by Douglas-fir, have total (i.e. above- and belowground) carbon densities higher than any other terrestrial ecosystem (Smithwick et al. 2002). The massive root system, abundant leaf waxes, effective stomatal control mechanism, and its high resistance to cavitation are some of the characteristics that help Douglas-fir survive drought. When Douglas-fir trees are under water/drought stress for a significant period of time, there can be a lag time in which photosynthetic capacity is reduced and the production of reserve carbohydrates is diminished, potentially resulting in a loss of vigour and the ability to withstand other environmental pressures (Bréda et al. 2006). Thinning improved drought resistance and resilience of Douglas-fir trees in Western Oregon, however these effects were seen to diminish over time (Vejpustková 2019). In Central Europe mixing Douglas-fir with European beech improved its drought resistance compared to that of its pure stands (Thurm et al. 2017). Therefore, it is plausible that combining these approaches could have an additive or even synergistic effect on Douglas-fir's drought tolerance. However, further research is needed to confirm this and understand the long-term implications of such combined management strategies.

## 1.5.2 Western redcedar:

Western redcedar (*Thuja plicata* Donn ex D. Don in Lamb.) is a coniferous evergreen tree that is prevalent along the northwest coast of North Americ (Antos et al. 2016). Unlike many conifers, it is capable of withstanding nutrient-deficient environments (Antos et al. 2016). It can also survive within a wide range of harsh biotic and abiotic environment, and is therefore classified as a "stress tolerant species" (Antos et al. 2016). Its shade tolerance and slow growth rate confines it to a subordinate position in mixed stands (Klinka & Brisco 2009). Redcedar occurs in mixture with a variety of tree species such as western hemlock, Douglas-fir, bigleaf maple and grand fir. Although redcedar withstands certain environmental stresses, its drought tolerance varies from moderate to low (Mathys et al. 2014).

## 1.6 Studying drought response by determining soil moisture

Drought and high-temperature reduces soil water availability and increases evaporative demand. This has been associated with widespread events of droughtinduced mortality in forests even in environments not considered to be water limited (Choat et al. 2018). Soil moisture serves as a reliable indicator of drought, reflecting recent precipitation, preceding conditions, and potential water storage (Keyantash and Dracup 2002). The soil column serves as a filter between incoming precipitation and throughfall (direct precipitation plus canopy drainage) and processes that remove water from the hydrologic system, i.e., evapotranspiration and subsurface drainage (Entekhabi et al. 1996). A deficit in soil moisture weakens trees by disrupting water availability and increases various risks like insect and pest damage (Lindner et al. 2010). Low soil moisture resulting from drought stress inhibits regeneration success and tree growth. During the growing season, tree growth is greatly influenced by water availability in the soil, and in some forested areas this can be the most important growth-limiting factor (Armson 1979). Water available to trees is that held in the soil at water potentials between field capacity and the permanent wilting point and variation in water availability is determined by the amount of precipitation, solar radiation, soil texture, competing vegetation, drainage, and other factors (Armson 1979).

Stand density impacts the distribution and infiltration of rainfall and influences tree's soil water consumption (Zhang et al. 2019), which in turn influences the soil water conditions beneath the forest. Dense stands with high canopy have high water interception compared to low density stands, which makes them vulnerable to environmental stresses. A piece of research on lodgepole pine in British Columbia found that optimizing stand structure and root water absorption through thinning and replanting leads to enhanced soil permeability and increased soil water content in the stands while maintaining appropriate stand density (Wang et al. 2019). Reducing stand density, increases water availability to the remaining trees (Aussenac 2000) by reducing stand transpiration and interception.

Considering tree size, larger trees require more resources to survive making them more susceptible to the impacts of precipitation. (Chhin et al. 2008, Meyer and Bräker 2001). Inorder to withstand a more negative gravitational water potential and to meet their water requirements, taller trees requires greater amount of water to be transported to its different parts. (Woodruff et al. 2004). Conversely, compared to smaller trees, large trees possess much extensive root systems enabling them to absorb soil moisture from deeper soil strata. (Brassard et al. 2009). Hence, tree response to growth greatly depends on soil water availability and belowground water absorption strategy (Brassard et al. 2009).

# 1.7 <u>Studying drought response using tree rings: focus on stand and tree level</u> characteristics

Analysing tree rings help understand the response of trees to drought stress over decades. Trees in temperate forests generate two distinct type of wood known as earlywood and latewood. Earlywood consisting of large diameter cells and thin cell walls is distinguished by its light colour and is formed during spring and early summer (Fritts 2012). Latewood characterized by thick cell walls and thin cells are dark in colour. These are produced towards later phase of summer. Due to the contrasting colours, the annual growth rings are clearly visible in the stem of a tree's cross section. The chemical and physical traits of the wood cells formed during each year reflect the environmental conditions that affected the tree's growth during that year and can be used to study the climatic factors such as precipitation, temperature, fire events etc. that influenced the tree's growth during the past years. Due to the annual and seasonal data that tree rings provide and the consistent occurrence of negative ring-width anomalies associated with drought, they are an exceptionally excellent proxy for drought. Drought impacts can be observed by the presence of narrow rings produced during years of low moisture availability (Douglass 1914, Stickel 1933, Lyon 1936). Tree rings can be used to determine the three drought indices: resistance, recovery, and resilience of trees to arid stress. These indices are highly dependent on species type, competitive status of a tree within the stand, tree size, and site conditions. (Lloret et al. 2011).

Stand-level properties are likely to affect tree's response to drought particularly because of competition effects (Linares et al. 2010). Consistent with this, high site basal area and tree density have been associated with reduced individual growth (Vilà-Cabrera et al. 2011) and high drought- induced mortality (Floyd et al. 2009, Galiano et al. 2010). Reducing stand density helps forests to cope up with climate change (Sohn et al. 2016). From a silviculture point of view, reducing stand basal area consistently improves drought tolerance of trees, particularly in drier sites without altering the climatic drivers of tree growth (Zhang et al. 2019)

Considering tree level characteristics, tree height is an important trait that affects drought tolerance. For instance, in a study on *Pinus sylvestris* in northeast Iberian Peninsula, trees with faster height growth were less resistant to drought than slow-growing trees, but showed faster drought recovery (Serra-Maluquer et al. 2018). Smaller trees benefit from their position in the stand, with reduced exposure to temperature or solar radiation, conditions that may become favorable during drought episodes (Aussenac 2000). Nonetheless, other studies showed the opposite pattern (Galiano et al. 2010) and argued that large-size trees may be better competitors for water resources due to their large root systems. Studies have reported positive relation between tree size and vulnerability to drought (Bennett et al. 2015). The reason why larger trees are less resistant and resilient during extreme drought events may be related to their position in the stand (micro-environmental effects) and to inherent physiological constraints. Taller trees can be exposed to elevated atmospheric water demands and present longer hydraulic path lengths, both of which exacerbate drought stress (Ryan and Yoder 1997). A deeper understanding of the effect of tree size on drought could help predict long-term forest health under drier conditions.

## 1.8 Studying drought response using stable carbon isotopes

Stable isotopes have similar chemical properties, however the difference in the number of neutrons, makes one element heavier than the other. This difference finds utility in various fields including environmental and paleoclimatological investigations (Peterson and Fry 2003). Carbon-12 and Carbon-13, each with six protons but with six and seven neutrons, respectively are the two stable isotopes of carbon. Carbon isotopes found in trees are used for studying the physiological response of trees to environmental stressors such as drought (Saurer et al. 1997, Treydte et al. 2007). Stable carbon isotope ratios ( $\delta^{13}$ C) are used as a proxy for understanding the changing climatic conditions over time (McCarrol and Loader 2004). Stomatal closure and reduced water availability can cause a potential increase in the  $\delta^{13}$ C of trees. (Leavitt and Long 1989, Voelker et al. 2014).

During normal conditions, when stomata are fully opened and intercellular concentration of carbon dioxide is high, there is more discrimination between the isotopes and trees preferentially fix Carbon-12 relative to Carbon-13, as the lighter isotope diffuses through stomata more rapidly and reacts with RuBisCO more readily. When a tree is drought stressed the rate of stomatal conductance to photosynthesis is low, which reduces the flow and internal concentration of CO<sub>2</sub> (McCarroll & Loader 2004). A drop in the intercellular concentration of CO<sub>2</sub> (relative to ambient concentrations outside the leaf), affects the ratio of Carbon-13 to Carbon-12 (known as  $\delta^{13}$ C) being fixed by RuBisCO (Farquhar et al. 1982), resulting in a greater proportion of Carbon-13 being fixed and thereby an increase in the  $\delta^{13}C$  of photosynthates. Higher (less negative) values of  $\delta^{13}C$  indicate less discrimination against Carbon-13, which can be primarily attributed to stomatal closure. Furthermore, a lesser discrimination between the isotopes indicates a higher water-use efficiency (WUE), the ratio of the photosynthesis to stomatal conductance. (McCarroll and Loader 2004). As a result,  $\delta^{13}$ C reflects plant water status at the time of carbon fixation, and analyzing the isotopic composition of wood in tree rings will help us better understand the effect of past drought events (Warren et al. 2001). Wood carbon isotope composition ( $\delta^{13}$ C) provides information about stomatal control and water-use efficiency of tree species with a less negative  $\delta^{13}C$ value indicating higher WUE (Farquhar et al. 1989).

Several factors such as species type, tree's growth stage, tree morphology and drought characteristics affect the WUE of a tree in response to drought. The overall effect on stand growth and ecosystem water balances depends on the amount of increases in water use and water use efficiency of trees in the stand (Falkenmark and Rockstrom 2006). Reducing stand basal area can improve WUE at the individual tree level. This occurs due to the reduced competition for resources in low basal area stands, which allows individual trees to experience less stress and utilize available water more efficiently for growth and other biological processes. In addition, reduced competition helps individual trees to develop more extensive root systems, which allows them access a wider range of soil water resources. However, it's crucial to note that the effects of stand basal area on WUE can vary significantly depending on several factors like climate, temperature, soil characteristics, species composition, stand structure and age.

## Study Objective

The main objective of this study is to compare and contrast the efficiency of a Douglas-fir: Western redcedar plantation in moderating the effects of drought across different combinations of densities and mixtures. With the increasing droughts in British Columbia, this study will help us understand the ways of managing a Douglas-fir: Western redcedar mixed plantation to increase its long term adaptability to droughts. For that, we looked at the effect of planting density and species composition on i) soil moisture ii) drought resistance, resilience and recovery at both stand level and tree level iii) water use efficiency of the individual tree species during wet and dry years.

Chapter 2 will discuss the methodology and results of the study and chapter 3 will give a conclusion of the thesis.

## <u>CHAPTER II: Mixing tree species and density management to</u> reduce drought susceptibility in coastal plantation forests of <u>British Columbia</u>

## **2.1 INTRODUCTION**

Prolonged droughts with its severe impact on forests, agriculture and human health is considered as an important natural disaster across Canada. The response of forests to decreased water availability from postulated increases in future drought conditions is considered a key issue in the current climate change scenario (Wigley et al. 1984). Drought-stressed forests are thereby likely to become more susceptible to damage by insects and diseases, especially those whose life cycles are favored by warmer temperatures (Volney and Hirsch 2005). With the increasing severity of summer droughts in the watersheds on Vancouver Island of British Columbia, by 2050, it's expected that mean annual temperature on Vancouver Island will rise by 1.5°C with an expected 14% decrease in summer precipitation (Farmer and Lauren 2020). Vancouver Island's location exposes it to unique challenges regarding drought. Situated in the downwind shadow of the mountain ranges, the island receives limited and unpredictable precipitation, which increases the frequency and intensity of water scarcity. (Coulthard et al. 2016, Simms and Brandes 2016). To better cope up with drought and alleviate its impacts, it is essential to understand how silvicultural techniques can be thoughtfully implemented in order to help forests adapt to a changing climate and ensure their continued health and ecological value. However, as the exact impacts of climate change remain unclear, it's crucial to assess a diverse set of current and innovative forest management practices in order to identify solutions that can bolster ecological resilience and ensure the continued delivery of ecosystem services, products, and benefits even as environmental conditions shift.

Drought resistant tree selection can be considered as a long-term solution for creating low- maintenance forests that can thrive with minimal intervention. Such a selection involves considering trees where the leaves use water efficiently and continue to grow and photosynthesize at relatively low water concentrations. Such trees may also exhibit characteristics like extensive root systems, thick leaf wax and bark, good stomatal control, and the capacity for leaf cells to function at low water concentration (Coder and Warnell 1999). Careful selection and growing trees exhibiting such drought resistant characteristics in mixtures can be considered as a valuable silvicultural strategy and a promising long-term option to cope up with the increasing threat of climate change (Brang et al. 2014).

Planting of species mixtures help reduce severity of drought impact on forests by offering protection from pests and diseases, resistance to wind damage and biotic disturbances, enhancing nutrient cycling, improving soil fertility and tree nutrition and conserving native plant and animal species. (Forrester et al. 2004, Jactel and Brockerhoff 2007, Montagnini 2000) The benefit of species mixing is often higher on resource poor compared to rich sites and during growth periods with limited rather than ample resource supply (Lebourgeois et al. 2013). During a drought condition, water availability becomes the primary limiting resource for trees. This creates a competitive environment in monocultures as individual trees compete for the same limited water resources. In contrast, mixed stands have trees with diverse water use strategies and root structures, allowing them to access water from different soil depths and utilize water more efficiently, thus reducing overall competition within the stand. To persist and thrive into the future, most trees will need to survive multiple drought or heat events (McDowell et al. 2022). Hence developing stands with long-term climate change adaptation strategies requires a stronger understanding about the ecological functioning of these mixed stands.

Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and Western redcedar (*Thuja plicata* Donn ex D. Don in Lamb) are a species mix with good ecological combining ability. Douglas-fir, one of Canada's most highly valued trees, is a potential species because of its high growth rate, good wood quality and adaptability to various site conditions (Kleinschmit and Bastien 1992). The deep rooting system, waxy needle coating and efficient stomatal balance help Douglas-fir trees thrive during dry conditions while Western redcedar is a stress-tolerant generalist that can persist under adverse conditions for long periods and can eventually grow to be a very large tree on a wide variety of sites. (Antos et al. 2016).

Its high stomatal sensitivity to water scarcity, shallow, fibrous root system, which allows efficient moisture absorption from near-surface soil, shade tolerance and slow growth helps the tree endure drought. However, extended or severe droughts can overwhelm the coping mechanisms of these species, leading to stress, crown dieback, and potentially death. Hence, to ensure the survival of a Douglas-fir: Western redcedar mixed forest under drought, its necessary to examine the characteristics that aid drought tolerance at both stand level and at individual tree level.

Regulating stand basal area is used as a mechanism for moderating the effects of drought- induced stress by increasing average resource availability to individual trees (Ammer 2017). Reducing stand basal area helps moderate competitive intensity within a stand (Steckel et al. 2020), which regulates water loss in the ecosystem by reducing stand leaf area index and thus evapotranspiration. As a consequence, the decrease in soil water content is slower and sufficient soil water availability is maintained for the trees during water stress events (Pretzsch et al. 2013). Changes in soil water content can help predict the onset and severity of future droughts.

Tree rings characterize the relation between growth response and climatic conditions of a site. Dendrochronological studies use tree rings to calculate drought resistance, recovery and resilience of different species in order to assess their growth performance before, during and after periods of stress. Resistance is defined as the capacity of a species to remain basically unchanged when it is subjected to a disturbance. Recovery is the capacity to regain growth or any other characteristic negatively affected after a disturbance and resilience is the ability to recover predisturbance structures and functions after a disturbance. Stable carbon isotopic ratios in tree rings record the balance between stomatal conductance and photosynthetic rate (Farquhar et al. 1982, Francey and Farquhar 1982), providing information about physiological responses to environmental conditions (McCarroll and Loader 2004). During photosynthesis, ribulose-1,5-biphosphate carboxylase/oxygenase discriminates against the heavier Carbon-13 in favor of Carbon-12 contributing to a lower Carbon-13 to Carbon-12 ratio ( $\delta^{13}$ C) in the leaves and wood of trees than in the atmosphere (Farquhar et al. 1982). When drought

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stressed, trees limit water loss from transpiration by closing stomata, which also limits the atmospheric CO<sub>2</sub> available for photosynthesis, forcing increased assimilation of Carbon-13 during carboxylation and leading to greater water-use efficiency (WUE). Carbohydrates produced under drought stress conditions have a higher  $\delta^{13}$ C value reflecting less Carbon-13 discrimination and higher WUE and this drought stress signature is preserved within the annual growth rings of trees.

In the Maritime and Submaritime biogeoclimatic subzones of the southern Coastal Western Hemlock zone in British Columbia, Canada, coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and Western redcedar (*Thuja plicata* (Donn ex D. Don in Lamb.), are two important economic species that are highly recommended for planting (Green et al. 1994).

Both species naturally occur in this biogeoclimatic zone (Meidinger and Pojar 1991) and exhibit different growth characteristics, with Douglas-fir being a fast growing pioneer species and Western redcedar being a slow growing, climax species. In this study, we compared the drought response of coastal Douglas-fir and Western redcedar trees growing in four mixture proportions and three planting densities in a dry maritime forest on eastern Vancouver Island. Our objective was to ascertain how species composition and stand density affected soil moisture, drought indices (resistance, resilience and recovery) and water use efficiency. In particular, the goal was to determine if stand level characteristics (stand basal area) or tree level characteristics (tree height) played a more significant role in enhancing drought tolerance. Understanding these factors is crucial for developing effective management strategies to protect British Columbia's Douglas-fir and Western redcedar forests from the growing threat of long-term drought.

## **2.2 METHODS**

## Study site

The study was conducted in a Douglas-fir–Western redcedar mixed plantation established in the early spring of 1992 at MacDonald Lake near Sooke, British Columbia (48°30'35"N, 123°43'51"W, elevation 325 m) (Figure1) in the eastern variant of the Coastal Western Hemlock very dry maritime (CWHxm1) biogeoclimatic subzone (Meidinger and Pojar 1991). The CWHxm1 sub-zone is found at lower elevations along the east side of Vancouver Island and has warm, dry summers and moist, mild winters with relatively little snowfall (Green et al. 1994). The mean annual precipitation and temperature are 1425 mm and 9.4 °C, respectively (Klinka et al. 1991). The soil moisture regime was mostly fresh with some moist areas and the soil nutrient regime was medium and rich (Green et al. 1994).

The study consisted of a 4x3 factorial design, with four combinations of Douglas-fir and Western redcedar mixtures (1:0, 1:1, 1:3, and 0:1) and three levels of density (500, 1000, and 1500 stems/ha), corresponding to tree spacing of 4.47 m, 3.16 m, and 2.58 m respectively. There were 12 treatments with 2 replicates for each. Variability in moisture regime among the study sites influenced the experimental layout, resulting in a factorial design replicated in two blocks. Due to limited space, two plots from one block were established in another block, creating an unbalanced design of 10 plots in one block and 14 plots in the other. The plot sizes for densities of 500, 1000, and 1500 stems/ha were 40.23 m x 40.23 m, 28.44 m x 28.44 m and 23.22 m x 23.22 m, respectively. The plots were enclosed with fences to prevent deer browsing. All trees were 2 years old at the time of planting. (Omari et al. 2021)

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Hitzerlan Budson Erlope Brwart Hitzerlan Hitzerlan Hitzerlan		Treatment	Density (sph)	Mixture
USGAA SmithRis		1	1500	Fd100%
COLUMBIA		2	1500	Fd50%Cw50%
Burns Lake Prince George Gra Praser Lake		3	1500	Fd75%Cw25%
10 M		4	1500	Cw100%
A CARLER AND A CARL		5	1000	Fd100%
"Belaticoola		6	1000	Fd50%Cw50%
	the family of a	7	1000	Fd75%Cw25%
PoltHardy	Ed	8	1000	Cw100%
A Montelling	- they be	9	500	Fd100%
Vancouvery	Come La	10	500	Fd50%Cw50%
Island Vancouver	Pres -	11	500	Fd75%Cw25%
The second second		12	500	Cw100%
	- ei			

Figure1: Location of experimental site. The point in red shows the exact location of the study site

## Standardized Precipitation Evapotranspiration Index

Standardized Precipitation Evapotranspiration Index (SPEI, unitless) was used to identify the drought years (Vicente-Serrano et al. 2010). SPEI is a multiscalar index based on precipitation and temperature data, and it is suitable to detect, monitor, compare and analyse different drought types and impacts in the context of global warming. The SPEI reflects both water surplus (positive values) and water deficit (negative values) as standardized deviations from the average monthly climatic water balance (Vicente-Serrano et al. 2010). The index uses a climate water balance approach, i.e., precipitation minus evapotranspiration, where potential evapotranspiration is calculated using the Thornthwaite equation and therefore includes the influence of temperature on drought conditions. The time scale is represented by a figure for the number of months, e.g. SPEI-6 stands for the past six months. An year with an SPEI value of less than -0.5 is considered as a drought year. SPEI-6 from April to September was calculated using R software (R.4.3.0). 2015 and 2016 were considered as drought years while 2019 and 2020 were considered as wet years for this study. (Figure 2)



Figure 2: Standard Precipitation Evapotranspiration index values for 6 months calculated over the growing season using R software

## Field Data Collection

Soil moisture measurements were taken using Fieldscout TDR 350 Soil Moisture meter. Each plot was divided into 9 subplots and 5 soil moisture readings were taken at each subplot with one at the centre and four along each cardinal direction. The data points within the subplots were averaged to obtain one soil moisture value per plot. Moisture measurements were taken at a depth of 12cm. The measurements were taken during 5 consecutive (and non-rainy) days to ensure uniform moisture conditions.

Tree cores were collected by randomly selecting six dominant and codominant trees per species in monocultures as well as mixed-species plots. Tree height and diameter at breast height (DBH) were recorded for each tree using a laser hypsometer and diameter tape respectively. Two tree cores per tree was taken in perpendicular direction at breast height. One of the tree core was used for ring width analysis and the other tree core was used for carbon isotope analysis. DBH measurements collected in 2019 by the British Columbia Ministry of Forests was used to calculate stand basal area.

### Lab Analyses

Tree cores were oven dried at 70°C for 72 hours and then mounted on boards made of 1.3 cm thick plywood with 5 slots precisely 5.5 mm wide and 3 mm deep. The cores were then progressively sanded using a fine belt sander with 120-300 grit paper until the rings were clearly visible and then scanned at 1200 dpi to obtain high resolution images. The scanned images were used to measure ring widths using the C.Dendro and CooReader software. The Ring Width Series of each of the cores were measured to the nearest 0.001 mm. The dataset was extracted to an Excel spreadsheet.

Radius of tree= Diameter at breast height/2

Radius corresponding to each year was calculated using the formula below where R = radius, RW = ring width, n=2022, n-1 = years prior to 2022  $R_n = Radius$  of tree – Bark Thickness  $R_{n-1} = R_n - RW_n$ 

Once the radius was obtained, Basal area (BA) was calculated using the formula  $\pi^*$ Radius<sup>2</sup>. Further, basal area was used to calculate the Basal area increment (BAI) using the formula below where n=2022, n-1 = years prior to 2022:

#### $BAI_n = BA_n - BA_{n-1}$

BAI was used to calculate the drought indices, resistance, recovery and resilience using the below formulas to describe tree growth response to drought (Lloret et al. 2011):

Resistance = BAID/BAIpreD Recovery = BAIpostD/BAID Resilience = BAI<sub>postD</sub>/BAI<sub>preD</sub> where  $BAI_D$  is the average BAI of the 2 years (2015 and 2016) corresponding to the drought period,  $BAI_{preD}$  is the average BAI for the 2 years (2013 and 2014) preceding the drought event and  $BAI_{postD}$  is the average BAI for the 2 years (2017 and 2018) following the drought event.

The tree cores to be used for isotope analysis were air dried for six months. The dried cores were dipped in distilled water for a second to ensure that the rings were clearly visible and tree rings corresponding to a series of dry (2015-2016) and wet years (2019-2020) as calculated by SPEI index, were separated manually from the cores using a scalpel and placed in a scintillation vial. The extracted core portion was then ground and put back into the corresponding scintillation vials. The extracted core portion was then ground and put back into the corresponding scintillation vials, and sent to the Ján Veizer – Stable Isotope Laboratory, University of Ottawa to determine their  $\delta^{13}$ C values.

The samples were weighed (0.6mg) into tin capsules and the isotopic composition of organic carbon was determined by the analysis of CO<sub>2</sub> produced by combustion on an Elementar VarioEL Cube Elemental Analyser followed by "trap and purge" separation and on-line analysis by continuous-flow with a DeltaPlus Advantage isotope ratio mass spectrometer coupled with a ConFlo III interface (Ján Veizer – Stable Isotope Laboratory, University of Ottawa).

Values of  $\delta^{13}$ C were determined in parts per mil (‰) relative to the standard Vienna Pee Dee belemnite (VPDB) based on the following equation (Farquhar et al. 1982, McCarroll and Loader 2004):

$$\delta^{13}C = \left(\frac{\text{Rsample}}{\text{Rstandard}} - 1\right)1000$$

where Rsample and Rstandard represents the ratio of  ${}^{13}C/{}^{12}C$  of samples and standard respectively.  $\delta^{13}C$  was used as a proxy for intrinsic water-use efficiency as a less negative  $\delta^{13}C$  value denotes a higher WUE. (Farquhar et al. 1989).

#### Data Analysis

Linear mixed models with a random effect at block level was used to study the interactive effect of mixture and density combinations on different response variables such as soil moisture, drought indices (resistance, resilience and recovery) and carbon isotopic concentration (during wet and dry years). lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) packages were used for this analysis. Further, Tukey pairwise comparison was performed using pair emmeans function, whenever treatment effects were considered significant. Two sample t-test was used to analyse the difference between two species across their mixtures. Stand basal area  $(m^2/ha)$ for each plot was calculated using MS Excel. Multiple linear regression model was used to test the relationship of stand basal area and tree height to drought resistance, resilience and recovery as well as the relation between stand basal area and  $\delta 13C$  of the two tree species. The results were considered significant at 95% confidence intervals and at alpha = 0.05. Overlapping confidence intervals represent nosignificant difference. All statistical analysis were performed using R software (R.4.3.0) (R Development Core Team, 2019) with packages *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al., 2017)

## **2.3 RESULTS**

Soil moisture decreased with increasing stand density (p=0.001) except for pure Douglasfir stands, (Fig. 3) which had least moisture (p=0.002) among all mixtures with soil moisture not varying across densities. For all other mixtures, soil moisture was highest for trees planted at 500 stems/ha (p<0.001).



Figure 3: Average soil moisture measured as volumetric water content (VWC) at three different densities (stems/ha) and four different mixtures of Douglas-fir (Fd): Western redcedar (Cw) at 12cm depth. The error bars indicate standard error

Drought resistance (p=0.034, p=0.039), resilience (p=0.005, p=0.007) and recovery (p=0.049, p=0.042) decreased with increasing stand basal area for Douglas-fir and Western red cedar respectively (Fig 4a, 4b, 4c). Due to low stand basal area, Western redcedar trees in their pure stands had higher drought resistance (p=0.030), resilience (p=0.010) and recovery (p=0.024) compared to Douglas-fir trees in their pure stands. (Fig. A1: 4g, 4h, 4i). Western redcedar trees in their pure stands at 1000 stems/ha showed maximum drought resistance.

Drought resistance of Douglas-fir trees increased on mixing with Western redcedar due to a reduction in stand basal area (Fig. 4g). For example, the stand basal area decreased from 29.5 m<sup>2</sup>/ha in Fd100% to 25.5 m<sup>2</sup>/ha in Fd50%Cw50%. In addition, drought recovery (p=0.07) of Western redcedar decreased (Fig. 4h,41) in both Fd25% Cw75% (0.09) and Fd50% Cw 50% mixtures (p=0.007) compared to the pure stands as basal area increased from 14.03 m<sup>2</sup>/ha in pure stands to 25.9 m<sup>2</sup>/ha in Fd25% Cw75% and 25. m<sup>2</sup>/ha in Fd50% Cw50%. Drought resilience (0.02) for Western redcedar also decreased in Fd50%Cw 50% mixtures (p=0.029) as mixing with Douglas-fir increased stand basal area (Table 1). The overlapping confidence intervals showed that there is no significant difference between the decrease of drought resistance and drought resilience with increasing stand basal area for Douglas-fir and Western redcedar. However, Western red cedar had higher drought recovery than Douglas-fir at lower basal areas as shown by the non-overlapping confidence intervals.

Tree height did not show any significant relation with drought resistance (p=0.210, p=0.259), resilience (p=0.007, p=0.173) and recovery (p=0.104, p=0.620) for Douglas-fir and Western redcedar respectively. This indicates that drought tolerance for both these species were dependent on stand level characteristic (stand basal area) and not on tree level characteristic (tree height). (Fig. 4d, 4e, 4f)

Density	Mixture	Tree	Tree height(m)	Stand basal
(sph)		height(m)	Western redcedar	area (m²/ha)
		Douglas-fir		
500	Cw100%		13.9±3.2	20.5±12
500	Fd100%	23.3±0.9		27.4±1.0
500	Fd25%Cw75%	21.4±1.2	$14.9 \pm 0.5$	14.3±0.2
500	Fd50%Cw50%	22.5±2.0	14.3±2.1	$18.9 \pm 5.3$
1000	Cw100%		11.0±2.6	$10.2\pm6.4$
1000	Fd100%	$19.8 \pm 5.1$		$20.3 \pm 7.6$
1000	Fd25%Cw75%	24.5±1.2	16.8±1.6	31.9±11.2
1000	Fd50%Cw50%	23.8±1.0	13.9±0.5	29.9±1.8
1500	Cw100%		11.0±2.9	11.4±7.2
1500	Fd100%	23.7±1.4		$40.8 \pm 6.0$
1500	Fd25%Cw75%	23.5±0.7	$14.9 \pm 1.4$	31.5±0.7
1500	Fd50%Cw50%	22.6±1.0	12.0±0.4	27.7±4.2

Table 1: Table showing tree height and stand basal area for different combination of density and mixtures



Figure 4: Trends in drought resistance (4a, 4d), resilience (4b, 4e) recovery (4c, 4f) in relation to stand basal area and tree height respectively for both Douglas-fir and Western redcedar. Corresponding  $r^2$ , p values and 95% confidence intervals (shaded areas) are given for each relationship

Due to the low basal area of western red cedar monocultures, trees in these stands had higher WUE (represented by lower  $\delta^{13}$ C values), compared to Douglas-fir trees in their pure stands both during wet (mean  $\delta^{13}$ Cvpdb = -24.9 ‰, p=0.011) and dry years (mean  $\delta^{13}$ Cvpdb =-24.71‰, p=0.01). WUE for Western redcedar trees decreased in mixtures compared to pure stands (Fig. 5a, 5b), due to an increase in stand basal area (Fig. A2).



Figure 5:  $\delta^{13}$ C concentration of Douglas-fir (5a) and Western redcedar (5b) across different mixtures during dry and wet years. A less negative  $\delta^{13}$ C value represents higher water use efficiency

## **2.4 DISCUSSION**

Soil moisture increased with decreasing stand density except for pure Douglas-fir stands which had consistently low soil moisture at all densities. Drought resistance, resilience and recovery decreased with increasing stand basal area for both species. In comparison to Douglas-fir, Western redcedar behaved as a highly sensitive species with greater difference in water use efficiency between dry and wet years across the different mixtures. Our results indicate that in this particular forest type, stand structure controls drought response more than individual tree characteristics.

A decrease in stand density leads to decreases in stand leaf area. Lower leaf area decreases the overall transpiration rate, which increases the soil water availability. During a drought, when water availability is limited, reduced transpiration rates in the low density stands conserve water and help trees use water more effectively. The consistently low soil moisture of pure Douglas-fir stands compared to all other mixtures is due to the high water demand of these fast growing trees. These align with the results from the productivity studies conducted by Omari et al. 2021 at the same experimental site, which states that pure Douglas-fir stands were most productive among all mixtures. It also indicates the high interspecific competition in these stands. In addition, at lower densities, mixed stands of Douglas-fir will be better able to withstand drought when grown in mixtures.

The vulnerability of tree growth to drought can be measured with indices of resistance, resilience and recovery (Lloret et al. 2011). Our results clearly demonstrate that stands with low basal area had higher drought resistance, resilience and recovery. Lower basal area stands show less demand for water and avoids strong competition, which can be advocated as a management strategy to impart higher drought resistance, resilience and recovery (Bottero et al. 2017, Sohn et al. 2016). The reduced resistance in greater basal area stands might increase vulnerability to disease and insect induced mortality due to high competition (Mcdowell et al. 2008, Anderegg et al. 2015) as well as reduce resilience to

disturbance (Johnstone et al. 2010) relative to trees in low basal area stands. Western redcedar shows lower drought resistance, resilience and recovery in mixed stands due to increase in stand basal area in the mixtures compared to its monocultures. Douglas-fir trees show better drought resistance and resilience in mixed stands than in its pure stands due to lower stand basal area. This shows that Douglas-fir benefits from the mixture at the expense of western red cedar due to increased resource availability in mixed stands. The low drought recovery of Douglas-fir in mixed stands is because of its anisohydric behavior. Anisohydric species continues to transpire and grow despite drought stress until the water runs out. (Pretzsch et al. 2013) Therefore, they slump less in growth, but risk morphological changes or losses of fine roots and leaves due to previous cavitation of water conducting pipes due to drought stress. This means a slower recovery after the drought stress, as growth can only be accelerated again after cavitation of xylem tissue and organ losses are overcome (Leuschner 1998). Isohydric species on the other hand reduce water consumption and growth already in the early phase of drought stress through stomata closure. Using such a preventive strategy might leave resources to neighbouring other species.

Competition and tree dominance have been shown to influence water use efficiency of trees (Barnard et al. 2012). As per our results, Douglas-fir trees in their pure stands showed least water use efficiency due to the high growth rate of these trees. Faster-growing trees have higher resource utilization and higher carbon assimilation necessary for growth. This increases their water use and lowers their water-use efficiency compared to slow growing species. A positive effect of mixing was seen on Douglas-fir trees as these trees showed an improved water use efficiency in mixtures compared to their monocultures. This is because of the differential use of water resources by species in these stands (Kelty 2006) and the higher resourceusing strategy of Douglas-fir trees. At species level, fast growth is associated with a competitive strategy, which trades off against stress tolerance (Ouédraogo et al. 2013). Fast-growing species often use resources at a high rate, giving them a competitive edge in environments where these resources are available. Slowgrowing species, on the other hand, are adapted to less productive environments and are better able to cope with resource shortages, such as droughts. The WUE of Western redcedar trees decreased in mixtures compared to their monocultures due to the high basal area in these stands, which increases transpiration rate leading to higher overall water loss.

WUE for Western redcedar in monocultures and mixtures was greater during drought years compared to wet years, meaning that they use less water per biomass during drought conditions. (Sinacore et al. 2019) There was a greater variation in the WUE for Western redcedar trees between wet and dry years indicating the high sensitivity of Western redcedar to climate extremes compared to Douglas-fir. Highly sensitive species have the ability to quickly adapt to changing environmental conditions, including drought as they have better stomatic control, osmotic regulation, can quickly adjust their water use and potentially even change their life cycle strategies to ensure their survival. (Yi, Koong et al. 2017)

Reducing stand basal area by fostering mixtures help improve tolerance of forests to future droughts (Bauhus et al 2017). Type of mixture and tree species identity greatly modulate the beneficial effects of mixtures regarding drought tolerance, which thus cannot be generalized (Pardos et al. 2021). Therefore, a combination of tree species with complimentary traits is considered as a beneficial mixture. It should be noted that mixtures do not always provide universally higher resistance or resilience during a disturbances compared to its monocultures. In most cases, it depends largely on the attributes of the species in mixture in relation to the specific disturbances. (Bauhus et al. 2017). It was observed that mixtures showed more stability in drought indices compared to pure stands and ecosystem stability is essential during an environmental stress (Huang et al 2019). No effect of tree size (tree height) was found on drought indices indicating that the drought tolerance of these forests were more dependent on stand level characteristics and not on tree level characteristics

## **CHAPTER III: Conclusion and Operational Implications**

Results from the study showed that low-density stands had higher soil moisture and trees growing in lower basal area stands showed better drought tolerance and water use efficiency. In summary, basal area mediated the influence of climate on drought tolerance of these stands. Altering stand basal area does not change the climate drivers of tree growth but significantly modulates the tree's capacity to cope with extreme drought. The two primary ways of achieving lower basal area stands include controlling planting density and strategically mixing tree species. These are two techniques currently being considered to face climate change.

Planting trees at lower densities, limits their interaction by increasing distance between the trees, thus reducing competition (Forrester and Tang, 2016). With decreasing competition, there is more space, water and nutrients available for trees to grow healthy. It helps improve carbon sequestration of individual trees. This approach further ensures that trees receive sufficient resources to thrive during stress events such as drought. Thinning is being widely employed as a density reduction treatment in high density stands. Thinning removes some trees, providing more space to the remaining ones. However regular monitoring of thinning treatments are essential to ensure proper density management in forests.

Appropriate selection of tree species and mixing trees with different growth pattern, complementary water-use strategies, stomatal control and nutrient needs can promote the overall health of forests. Mixed forests with their diverse range of adaptation can withstand extreme climatic conditions. Unlike trees in monocultures competing for the same resources, mixed stands provide resource partitioning and facilitation between tree species. This helps making them more tolerant to long-term effects of climate change. While creating mixed stands, care must be taken to select tree species with complimentary traits in order to experience the maximum benefit of facilitation during a stress event.

The findings from this study demonstrates that planting fast growing Douglas-fir together with slow growing Western redcedar at lower densities can help the coastal forests in British Columbia to minimize the impacts of drought and promote the sustained growth of these forests by making them more adapted to future drought conditions



Figure 6: Ways of creating drought tolerant stands of Douglas-fir and Western redcedar

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## **APPENDIX**



Figure A1: Drought indices across various mixtures 4g) drought resistance, 4h) drought resilience, 4i) drought recovery



Figure A2: Relation between and stand basal area for Douglas-fir and Western redcedar

Table A1: Statistical output for soil moisture, drought resistance, drought resilience, drought recovery and  $\delta$ 13C for species as well as density and mixture treatments.

## ANOVA TABLE

Model term	soil moisture (VWC%)	drought resistance	drought resilience	drought recovery	$\delta^{I3}C$ (‰) (dry years)	$\delta^{13}$ C (‰) (wet years)
		p-values				
density	0.001 **	0.364	0.464	0.505	0.607	0.740
mixture	0.002 **	0.231	0.034 *	0.027*	0.024*	< 0.001***
species		0.129	0.464	0.085	0.920	0.141
density*mixture	0.162					
density*mixture*species		0.031 *	0.209	0.910	0.037*	0.358

Table A2: ANOVA table for soil moisture

	NumDF	DenDF	F value	Pr(>F)
density	2	23.018	8.2616	0.001975 **
mixture	3	23.085	6.5899	0.002225 **
density:mixture	6	23.023	1.7164	0.162180

Table A3: ANOVA table for drought resistance

	NumDF	DenDF	F value	Pr(>F)
density	2	18	1.0673	0.36473
mixture	3	18	1.5693	0.23146
species	1	18	2.5188	0.12991
density:mixture	6	18	1.8610	0.14341
density:species	2	18	1.4035	0.27138
mixture:species	1	18	0.3807	0.54495
density:mixture:species	2	18	4.2317	0.3116 *

Table A4: ANOVA table for drought resilience

	NumDF	DenDF	F value	<b>Pr(&gt;F)</b>
density	2	17.330	0.8018	0.46449
mixture	3	17.476	3.5945	0.03473 *
species	1	17.002	0.5599	0.46452
density:mixture	6	17.279	1.2663	0.32280
density:species	2	17.002	0.9765	0.39678
mixture:species	1	17.002	1.5530	0.22959
density:mixture:species	2	17.002	1.7161	0.20947

Table A5: ANOVA table for drought recovery

	NumDF	DenDF	F value	Pr(>F)
density	2	17.222	0.7110	0.50502
mixture	3	17.537	3.8590	0.02765 *
species	1	17.000	3.3387	0.08528.
density:mixture	6	17.194	1.0335	0.43749
density:species	2	17.000	0.2441	0.78608
mixture:species	1	17.000	1.7929	0.19820
density:mixture:species	2	17.000	0.0941	0.91064

Table A6: ANOVA table for  $\delta^{13}C$  (‰) during dry years

	NumDF	DenDF	F value	Pr(>F)
density	2	7.6412	0.5329	0.607232
mixture	3	9.1037	5.0766	0.024629*
species	1	8.2659	0.0106	0.920599
density:mixture	6	8.9679	1.3345	0.334693
density:species	2	8.2659	10.4958	0.005386**
mixture:species	1	8.2659	1.6347	0.235780
density:mixture:species	2	8.2659	5.0205	0.037393*