AN ABSTRACT OF THE THESIS OF

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Title: Biomass Stock, Net Primary Productivity and Growth Efficiency of 11 Conifer Species Growing on a Gradient of Water Deficit in Western Oregon.

Abstract approved: ____

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To gain a better understanding of the growth potential of alternative timber species in the Pacific Northwest of the United States, a species comparison study was initiated in 1996 by Starker Forests Inc. in western Oregon at three locations with varying water deficits. Eleven species were evaluated at each site: *Abies grandis*, *Chamaecyparis lawsoniana*, *Cupressocyparis leylandii*, *Picea sitchensis* and a *Picea sitchensis* variety resistant to weevils, *Pinus ponderosa*, *Pinus monticola*, *Pseudotsuga menziesii*, *Sequoiadendron giganteum*, *Tsuga heterophyllum*, and *Thuja plicata*. An unplanted, naturally-regenerated plot was also included at each site. In this study, we assessed and compared the aboveground biomass stock and net primary productivity (ANPP) of planted stands of these eleven species at age 26 years. Aboveground biomass was determined using inventory data and reported biomass functions for each species. Additionally, understory, midstory, and forest floor biomass were also measured at each plot. Soil samples were also collected to characterize the organic matter content of the soil to a depth of 1 m. ANPP was calculated using data on aboveground biomass increment (using two years of tree inventory) and litterfall, which was determined using bimonthly litterfall measurements over the course of one year. In addition, leaf area index (LAI) was determined for each plot using a ceptometer. LAI and

ANPP data were utilized to calculate the growth efficiency of each species at each site. There was a site-by-species interaction for all measured characteristics.

In terms of biomass production of planted trees, in general, the wet site had a higher amount of biomass stock (averaging 235 Mg ha^{-1}) and several of the 11 species showed reduced productivity at the dry site (averaging 193 Mg ha^{-1}). For example, *Abies grandis* (376 Mg ha^{-1}), *Tsuga heterophylla* (350 Mg ha^{-1}), and *Sequoiadendron giganteum* (331 Mg ha^{-1}) thrived on the moister site and perished on the dry site (24, 30 and 52 Mg ha^{-1}, respectively), whereas *Pinus ponderosa* and *Pinus moniticala* exhibited the opposite response. In terms of ecosystem biomass stock (including overstory, midstory and forest floor), the wet site had the highest biomass accumulation, averaging 345 Mg ha^{-1}, followed by the intermediate site, averaged 269 Mg ha^{-1}, and the dry site, averaged 73 Mg ha^{-1}. The distribution of plant-derived biomass (over 85%) indicated that biomass stock was largely controlled by planted trees (overstory), except for the *Abies grandis* plot at the dry (Campbell) site due to the presence of trees of other species which had naturally regenerated.

When SOMC was included in the ecosystem biomass stock, belowground biomass was larger than aboveground biomass stock. The belowground biomass stock showed the same trend, decreasing from the wet (Huffman) site, averaging 515 Mg ha^{-1}, to the dry site, averaging 257 Mg ha^{-1}. While the unplanted, naturally-regenerated plot at the wet site showed high soil organic matter content, those plots showed the lowest percentage of aboveground biomass to belowground biomass, ranging between 2% and 5% across the three sites. In terms of dominant tree species for the unplanted, naturally-regenerated plots, while the wet site had mostly Douglas-fir, the dry site had mostly Oregon white oak.

Crop tree ANPP had a similar trend, decreasing from the wet (17 Mg ha^{-1} year^{-1}) to dry (8 Mg ha $^{-1}$ year^{-1}) site conditions. While the highest crop tree ANPP was observed for *Tsuga heterophylla* at the wet site (30 Mg ha^{-1} year^{-1}), the lowest crop tree ANPP was also observed for the same species at the dry site (4 Mg ha^{-1} year^{-1}) because of high mortality of planted trees.

In terms of growth efficiency, the dry site showed the highest ANPP growth efficiency, averaging 2.6 Mg m^{-2} year^{-1}, followed by the intermediate site, averaging 2.2 Mg m^{-2} year^{-1}, and the wet (Huffman) site averaging 1.7 Mg m^{-2} year^{-1} due to high leaf area index at the wet site. Across all species, *Sequoiadendron giganteum* and *Pseudotsuga menziesii* showed higher growth efficiency cross a range of LAI.

Biomass Stock, Net Primary Productivity and Growth Efficiency of 11 Conifer Species Growing on a Gradient of Water Deficit in Western Oregon

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Erkan Babat, Author

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Chapter 1 Literature Review: Evaluating Forest Carbon Storage and Sequestration Response to Climate Variability and Drought Conditions.

1.1 Introduction

Forests are an essential component of the world's biological carbon (C) cycle and can help to stabilize the climate by absorbing atmospheric C and storing it in soil and living and dead trees (Ryan et al., 2010). A better understanding of the spatial distribution of forest biomass across continents, regions, and landscapes is becoming increasingly important since there is greater interest in including forest C storage in forest management and climate change mitigation strategies (Krankina et al., 2014).

Forest biomass is the mass of the living tissue in a given area. Ecosystem biomass has been used for a variety of purposes, including the characterization of ecosystems (Ji 2012), the estimation of C stocks (Garcia 2010), the prediction of fire behavior (Gonzalez 2015), the assessment of ecological functioning and site productivity, the supply of food for wildlife (Garroutte 2016), the production of sustainable energy, and the replacement of species richness and composition of plant communities (Guevara et al., 2021). In terms of the size and longevity of individual trees as well as the accumulation of biomass in individual stands, the evergreen conifer forests in the Pacific Northwest (PNW) of the United States are unrivaled (Waring, 1979). However, climate change has an impact on plant growth and species distribution, and increasing thermal constraints and water deficits can have a detrimental impact on vegetation productivity in these areas. (Raymond et al., 2014). Accurate estimations of growth potential or dynamics would be helpful to improve our knowledge and understanding of how commercially and ecologically valuable species are sensitive to climate and water deficits. Therefore, it is necessary to investigate differences in growth patterns between species and sites. Additionally, variation in growth patterns, biomass production, and productivity must be evaluated in terms of establishment and yield potential. This chapter will provide a background on the forest, climate change, and the importance of quantifying forest biomass production, carbon sequestration, as well as characteristics of different commercially and ecologically valuable species in the PNW.

1.2 Literature Review

1.2.1 Forest of the Pacific Northwest and Climate Change

The PNW is the term used to describe the area of western North America that includes the states of Washington and Oregon as well as northern California and southern British Columbia. The forests of the PNW are regarded as some of the most productive in North America (Grier, 1979). In the PNW, the forest sector is one of the greater economic contributors with almost 50% of forestland having a wide variety of timber productivity levels, including both the less productive Ponderosa pine (*Pinus ponderosa*) forests east of the Cascade Mountains, and wetter, more productive forests dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) west of the Cascade Range (OFRI, 2019). Oregon is the leading lumber producer in the United States, accounting for 16% of total softwood lumber production for many years (OFRI, 2019).

CO_2 and water are converted by plants into energy-storing organic compounds that can be used for plant maintenance, growth, seed production, and conversion to plant defense chemicals. (Peterson et al., 2014). Temperature, soil moisture, light, and nutrients availability are all factors that influence CO_2 fixation and plant growth. These variables play a significant role in regulating photosynthesis and respiration rates, as well as water and nutrient intake from soils and biomass production. One of the most effective methods for preventing the increase in CO_2 concentrations around the world is the photosynthetic carbon capture by trees (Bastin et al., 2019).

However, atmospheric CO_2 concentrations have been rising consistently from 285 ppm in 1750 to 394 ppm in 2012 (Peterson et al., 2014). According to the IPCC Fifth Assessment Report, the effect of humans on climate has been the major cause of observed warming since the mid-20th century. The predicted warming trend is continuing from average warming of 2.1 °C by the 2040s to 3.8 °C by the 2080s; precipitation may be changeable, but the magnitude and direction remain unclear in the PNW (Raymond et al., 2014). Global and local factors, the El Niño-Southern Oscillation and mountain ranges, influence climate variability, and change in the PNW (Dalton et al., 2013). Both factors have a significant effect on plant species, distribution, and growth in the PNW.

Climate is an essential factor affecting the spatial distribution of fire regimes, influencing fire intensity, frequency, seasonality, and size (Krawchuk et al., 2009). Increased temperatures are expected to lengthen wildfire and growing seasons, increase evaporative demand, reduce soil and fuel moisture, increase the chance of large flames, and increase the amount of land burned by wildfires (Halofsky et al., 2020; Peterson et al., 2014). Climate is also an important element influencing insect and disease disturbance regimes, as well as the frequency of major disturbance occurrences. Temperature is the most important abiotic element impacting herbivorous insects since it influences their abundance, survival, and development (Bale et al., 2002). Climate change can also modify the degrees of physiological stress and C fixation in host plants, making them more or less vulnerable to insect attacks and plant diseases (Peterson et al., 2014). Insects and diseases play a role in tree mortality in reaction to drought stress because trees weakened by protracted drought stress have compromised defenses against disease, and insect attacks, which may ultimately kill the tree (McDowell et al., 2011). According to climate model projections, by 2100, due to increasing temperature, beech bark disease and several insect species and some fungus such as *Armillaria* spp. are likely to have stronger or more widespread effects on forest composition and structure in the PNW (Dukes et al., 2009).

Douglas-fir is a major tree species in the PNW and a globally important economic resource (Simmons, 2016). Periodic outbreaks of insects and pathogens have been shown to have widespread, disastrous effects on productivity and tree survival (Whitehead 2011). As a foliage disease, swiss needle cast is specific to Douglas-fir and is produced by the fungal pathogen *Nothophaeocryptopus gaeumannii*. Swiss needle cast causes Douglas-fir needles to become chlorotic and fall from the tree prematurely. As tree mortality is rare and occurs only after many years of defoliation, the major effect of Swiss needle cast infection is reflected in reduced diameter and height growth (Lan et al., 2019, Maguire et al. 2011; Shaw et al. 2011). The pathogen reduces gas exchange and blocks stomata, which results in lower C fixation and, hence, reduced growth (Manter et al., 2000).Root diseases such as Laminated root rot, or black stain root disease spreading from root to root and producing dying or dead trees in patches, are another importance disease affecting Douglas-fir productivity. Laminated root rot is produced by fungal pathogen *Phellinus weirii* and affects Douglas-fir, *Abies grandis* (grand fir) and other conifers in the PNW. Laminated root rot is the most destructive disease of young-growth Douglas-fir in the PNW (Miller et al., 2006), it has an impact on growth, chlorotic foliage, needle loss, and host mortality (Goheen et al., 1998), producing considerable reduction on forest productivity (Bogdanski et al., 2008).

1.2.2 Forest Biomass and Carbon Sequestration

The Intergovernmental Panel on Climate Change (IPCC) suggested in 2022 that an increase of 1 billion ha of forest lands will be necessary to limit global warming effect to 1.5°C by 2050. The biological carbon cycle is driven by photosynthesis in which a plant sequesters carbon to make glucose for the tree to grow and survive. Trees convert CO_2 into solid C, which is stored in the wood, and release oxygen as a byproduct. Global afforestation, and reforestation is the most effective strategy to mitigate climate change, due to the ability of the trees to capture photosynthesis C, (Bastin et al., 2019). Forests play a critical role in the U.S. and global C cycles, with C absorbed by forest growth and harvested wood products presently offsetting 12-19% of the U.S. fossil fuel emissions (Ryan et al., 2010). According to the Oregon Forest Resources Institute's report Carbon in Oregon's Managed Forests, the total C sequestered in Oregon by the state's forests and wood products is projected to be the equivalent 49.5 million metric tons of CO_2 equivalent every year (OFRI, 2021).

The stock-change technique is commonly used to estimate the amount of carbon sequestered in forests, in which the quantity is measured as the net change in C stocks over time (Pearson et al., 2007). The most accurate and precise methods to estimate tree C stocks include direct methods, such as a field inventory, where diameter and height of all trees in sample plots are measured. The most direct way to convert field measurements from forests to C is using allometric functions that can translate tree diameter and height tree biomass (kg), although its accuracy depends on those equations being available for a given species, and whether the equations predict only stem biomass, or total biomass which includes the components of the tree: foliage, bark, stem, branches, and, in some cases, roots.

Forest biomass stock (Mg ha^{-1}), net primary productivity (NPP, Mg ha^{-1} $year^{-1}$), and leaf area index (LAI, m^2 m^{-2}), individually or in combination, are significant metrics of forest productivity (Gholz et al., 1982). The quantity of C intake after deducting plant respiration from gross primary productivity (GPP, Mg ha^{-1} $year^{-1}$) is described as NPP, an important characteristic of terrestrial ecosystems and a key component of the global C cycle. (Lambers et al., 2008). Some studies show the impact factors of NPP, such as precipitation, temperature, and atmospheric CO_2

concentration and, have concluded that soil moisture is one of the most important factors controlling NPP (Yu and Chen, 2016). Aboveground net primary productivity (ANPP, Mg ha^{-1} $year^{-1}$) represents the net flux of C from the atmosphere into the above-ground components of plants (i.e branches foliage and stems). ANPP can be quantified by biomass accumulation in both wood (stem and branches) and foliage and loss through litterfall, herbivory, and volatilized or leached organic compounds.

Changes in climate and atmospheric chemistry (e.g., CO_2 concentration) may be causing ongoing changes in forest NPP and biomass accumulation because it influences on photosynthesis and respiration (Peterson 2014). Climate change and elevated CO_2 levels can impact plant growth by altering resource availability and environmental conditions. Although lower respiration rates in the PNW are frequently accompanied by higher NPP, water deficits and cold winter temperatures are the primary factors limiting NPP in this region (Grier and Running, 1977).

Light interception is a major factor in determining the productivity of forest ecosystems, as leaf area regulates productivity via its influence on canopy light interception and the subsequent photosynthesis and evapotranspiration (Jose 1997). Light use efficiency (LUE) is a key biophysical parameter characterizing the ability of plants to convert absorbed light to carbohydrates. LUE have transitioned from research instruments to practical methods for evaluating the silvicultural activities of individual forests and predicting global trends in forest productivity (Waring et al., 2016). The definition of the Growth Efficiency (GE) index is annual growth (of stemwood or total aboveground biomass) per unit of leaf area. The crown and canopy structure correlate with growth efficiency (Dean 2004). The ability to assess GE on individual trees enables estimations of tree susceptibility to pests and diseases, as well as the determination of which management practices can promote stand growth (Waring et al., 2016).

1.2.3 Species Introduction

Species introduction studies are important to understand that alternative production species or to increase the resilience of single species stands in a given area. This will be helpful for biodiversity conservation and reforestation efforts and silvicultural management of species introduction. While using native species has some benefits for plantations, choosing the wrong species or seed sources for reforestation can result in productivity loss or complete plantation failure (White et al., 2007).

To understand the growth potential of alternative timber species in the PNW, a study was started in 1996 by Starker Forests Inc. Three different sites were chosen spanning a gradient of water availability: Huffman (Coastal), Underhill (Central Coastal Range), and Campbell (Inland). On each site, 11 plots were laid out measuring approximately 51 m x 51 m each. Each plot was planted with a single tree conifer species. Eight species native to Oregon and three non-native species were planted at the three different sites. These species include Douglas-fir, giant sequoia, grand fir, Leyland cypress, Sitka spruce, Port Orford cedar, western hemlock, western red cedar, Willamette valley ponderosa pine, western white pine, and weevil resistant Sitka spruce.

Coastal Douglas-fir (*Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco) is found in mixed evergreen and mixed conifer forests in the PNW. Because of its great productivity and wood quality, coastal Douglas-fir (hereafter referred as Douglas-fir) is considered one of the most valuable timber species on the planet (Hermann and Lavender, 1999). It is used in the western U.S. for a variety of purposes, including dimensional lumber, telephone poles and railway ties, as well as for Christmas trees. Douglas-fir trees need excellent drainage. Douglas-fir also needs to have moderate summer water availability, depending on water holding capacity of the soil in the higher elevations of the western U.S. that receive snow, and in the lower foothills that have relatively cold winters and hot summers (USDA, nd). In terms of soil texture, Douglas-fir may grow in a wide range of soils, but it thrives in deep, moist, and well-drained clay loams, silty clay loams, and silt loams (USDA, nd). Douglas-fir is the leading species harvested in the PNW, accounting for 70% of the timber volume harvested (Simmons 2016).

Giant Sequoia (*Sequoiadendron giganteum* (Lindley) J. Buchholz) is a long-lived pioneer species endemic to California's western slope. Water availability is linked to the presence of giant sequoia groves and warming temperatures without a matching increase in precipitation may make the vulnerability of giant sequoia groves particularly during multiyear droughts (Cox et al., 2021). Giant sequoia grows in a humid climate with hot, dry summers. Deep, well-drained sandy loams are ideal for giant sequoia growth. In terms of volume, the giant sequoia is the largest tree in the world (Burns and Honkala 1990). The production of timber and the storage of C are two of the goals of a functioning landscape in forestry. Understanding the growth-density correlations for giant sequoia is important for planning future management for the species, given its potential for rapid growth (Cox et al., 2021).

Grand fir (*Abies grandis* (Dougl.) Lindl.) is one of two true firs native to the northern Rocky Mountains and one of seven in the PNW. It tolerates shade, especially while it's young, although development is slowed in dense shadow. In some habitats, it is a dominant climax species (USDA, nd.). Grand fir grows well in soils derived from a variety of primary materials, including weathered lava (rock), sandstone, granite, and gneiss (Burns and Honkala 1990). It also grows well in rich alluvial soils along streams and valley bottoms, as well as damp soils with seepage, along the Pacific coast region to the Willamette Valley (Forester 1959).

Leyland cypress (*Cupressus leylandii*, Dallim. and A.B. Jackson.) is known a fast-growing coniferous evergreen tree. It is a hybrid of two new-world cypresses, specifically *C. nootkatensis* and *C. macrocarpa* (Greeg, nd). Deep, well-drained soils rich in calcium and magnesium, generated from parent materials of andesite, diorite, gabbro, or basalt, are ideal for Leyland cypress. It is an ecologically and commercially significant tree that has been appreciated and exploited as a material resource for generations. When compared to products that are in frequent contact with the soil, products created from its robust heartwood will endure longer when used above ground (Kelsey et al., 2015).

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is one of the most prominent trees along the PNW coast. This species' range extends from northern California to Alaska (Reeb et al., 2015). Sitka spruce grows in the hyper maritime to maritime cool mesothermal climates (Hurns and Honkala). Typically, Sitka spruce grows on damp, well-drained sites like marine terraces, alluvial floodplains (USDA, nd). This species prefers the full sun and is intolerant to shade and atmospheric pollution (USDA, nd). The Sitka spruce tip weevil (*Pissodes strobe*) (Coleoptera: Curculionidae) is the most prevalent insect parasite of Sitka spruce in forest plantations. (Hurns and Honkala). The weevil infests and destroys the tree's leader regularly, slowing growth and causing severe stem deformations. The attacked tree can recover in a few years, but in severe infestations, the tree will only grow into a shrubby form (Norman 2009).

Port Orford Cedar (*Chamaecyparis lawsoniana* (A.Murray bis) Parl.) is widely known and renowned for its horticultural purposes and the quality of its wood. In most of its range, Port Orford cedar can be found near stream sides, bogs, and other moist environments in southern Oregon and along the coast from Reedsport south. *Phytophthora lateralis*, a root disease introduced into wild stands in 1952, has resulted in considerable mortality of this plant across its range. *Phytophthora lateralis* spreads through both living spores in water and more resilient long-lasting spores in the soil.

Willamette valley ponderosa pine (*Pinus ponderosa var. willamettensis*, Douglas ex C.Lawson) is a shade-intolerant evergreen conifer. Upland prairies, riparian woodlands, and oak savanna are some of their natural habitats. This sub-species is only located in Oregon's Willamette valley. Full sun and moist places are best for growth, but they can also endure dry weather and poor soils. The Willamette valley ponderosa pine is a fire-adapted species, thanks to its thick bark, which allows it to withstand severe fires. The earliest settlers in the Willamette valley recognized this and took advantage of it, burning brush and other conifers to reduce vegetative competition (USDA,nd).

Western hemlock, (*Tsuga heterophylla* (Raf.) Sarg.) one of the most shade-tolerant tree species, is also often a dominant forest evergreen tree, Western hemlock can be found in humid places along the Pacific Coast and in the northern Rocky Mountains (Earle, nd). Mild, humid regions that experience frequent precipitation and fog throughout the growing season are optimal for plant growth (Burns and Honkala 1990). It is utilized to assist decrease stream bank erosion, maintaining aquatic ecosystems, improving wildlife, and increasing biodiversity in forest riparian buffers. Western hemlock wood is a well-known versatile raw resource and produces ideal pulpwoods for producing paper and paperboard (Lang, nd).

Western redcedar (*Thuja plicata* D. Don) is a native, long-lived evergreen tree that grows along the Pacific Coast from the southern part of the Alaska Panhandle through British Columbia (Tesky 1992). It prefers moist, acidic, well-drained soils, but has also been cultivated in the Midwest's heavy clays. Because of its lightness, attractive appearance, durability, and high insulating capabilities, western redcedar wood is widely utilized in roofing for shingles and shakes (USDA, nd).

Western white pine (*Pinus monticola* Douglas ex D. Don in Lambert 1832) grows on western mountain ranges in parts of British Columbia, Washington, Oregon, and California. The species may grow on a wide range of soil types, but it thrives in deep, well-drained soils with a medium to fine texture and excellent water holding capacity (Lowery, 1984). Western white pine is an important timber species, having the potential to keep producing biomass at age past 100 years (IFPC, 2019). With the right carpentry equipment, the wood of the western white pine can be easily shaped into window and door frames, paneling, shelving, and even some structural uses.

The PNW is known for its priceless, extraordinarily productive forested areas. However, it is anticipated that climate change would result in higher average temperatures, altered precipitation patterns, and more severe and pervasive disturbances. In the PNW, the increased evapotranspiration requirements and the reduced water availability during the growing season may be harmful to the development and survival of certain tree species. The management of species selection for reforestation can be influenced by knowledge of how sensitive commercially and ecologically significant species are to climate and water balance deficits in western Oregon. In addition, researchers can better understand the effects that environmental factors and management techniques can have on forest production and C sequestration by examining the primary productivity of 11 conifer species along the water deficit gradient in PNW.

1.3 Objectives and Hypothesis

This study aims to contribute to our understanding of how to predict the resilience of tree species to anticipated climate change and to inform species selection for reforestation efforts in the PNW. The main question for this study is how does the productivity of eleven native and non-native conifer species differ across a water deficit gradient in western Oregon? The main objective of this study is to measure and compare aboveground biomass stock, net primary productivity, and leaf area index of the eleven conifer species across a water deficit gradient in Western Oregon. The hypotheses include:

1. Ecosystem biomass stock and net primary productivity of eleven conifer species will be different across sites.
2. The ecosystem biomass stock and net primary productivity of some species will be largely affected, while other species will be unaffected by increased water deficit across sites.
3. Stand productivity and growth efficiency are different across species, and environmental factors affect each species differently.

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Chapter 2 Biomass Stock of 11 Conifer Species Across a Water Deficit Gradient in Western Oregon.

2.1 Introduction

The first, and maybe the most important, silvicultural decision is the selection of the species to use for reforestation. Silvicultural management decisions and an available crop tree species selection may have detrimental or positive effect on stand growth and condition for a long time when establishing a new stand. Understanding the effects of species selection on forest ecosystems as a whole can help forest managers develop strategies for diverse objectives, such as forest restoration, timber production, and carbon sequestration.

Plant biomass plays a significant role in maintaining the ecosystem and life of humans and the Earth, and with forests accounting for an estimated 80% of global biomass, they contribute significantly to the biosphere's carbon pool and are essential for the exchange of gases and energy between the atmosphere and the surface (USDA, n.d). Plant biomass is influenced by the growth characteristics of the trees, while the amount of growth can be affected by different environmental factors (Ali 2003). While there are differences in how different tree species distribute their biomass, the majority of species commit a sizeable amount of their biomass to the stem, which is what makes up the majority of the aboveground biomass in forests (Nunes et al., 2013). Some studies show that about 80-90% of biomass was calculated as stem biomass in 120-200 year old coniferous forests (Gholz et al., 1982).

The forests of the PNW are characterized by their high productivity, dominance by long-lived species, and potential for large biomass accumulation. (Waring and Franklin, 1979, Franklin et al., 2017). Forest biomass accumulation is a useful metric for determining forest productivity (Gholz et al., 1982). The study of biomass (or carbon) of forests growing in different site conditions can improve our understanding how climate affect forest health and productivity. Determining vegetation biomass is essential to estimate the carbon storage capacity of ecosystems. A large fraction of the carbon stored in forest ecosystems is found in overstory trees (Flamenco et al., 2019). Although overstory biomass contains a large fraction of stored carbon, other ecosystem components should be accounted for to estimate forest ecosystem biomass accurately. These include midstory vegetation, understory vegetation, forest floor, and soil organic matter.

Forest biomass is determined as the dry mass of organic matter per unit of land area. Each tree should be accounted for to estimate forest biomass. There are different methods to estimate total or component biomass stock, such as the harvest method, allometry, and multi-stage sampling. The first one is harvesting or direct methods. All trees in the sample areas are cut down and all fresh and dried weights of trees parts (bole, branch, leaves/needled, etc.) are weighed. Although this method is the most accurate for calculating biomass, it can be expensive and time-consuming to use across large regions. Even though there are significant drawbacks, this harvest approach is typically used to improve the most common allometry method (Navar, 2009). Many generalized biomass equations are available for numerous North American tree species (Ter-Mikealin et al. 1996, Chojnacky et al. 2014). Besides the tree, other components are also necessary for calculating ecosystem biomass, including understory vegetation biomass. (Guevara et al. 2021). Although there are many improved biomass equations, when locally developed species-specific biomass equations are used, total estimated biomass can be more accurate (Herman et al., 2018).

Changes in temperature and precipitation as a result of climate change are anticipated to affect soil water availability, which is related to plant physiological processes including productivity as well as tree growth and development (Peterson et al., 2014). Because of decreasing soil water availability, during the PNW growing seasons, trees may lose water, resulting in increased plant stress, or even close stomata, which can stop plant growth. Restaino et al. (2016), anticipates that water deficit-related stress will increase, leading to a decline in Douglas-fir growth across the United States.

In 1996, Starker Forests Inc. installed a species introduction study at three sites covering a water deficit gradient, testing 12 different conifer species, both native and non-native, at three sites in order to collect information about potential alternative timber species to Douglas-fir in the area. This study represents a unique opportunity to collect data that can help to understand how these conifer species respond to the climate variability across a water deficit gradient in western Oregon, informing species selection for reforestation efforts in the PNW, using estimates of aboveground vegetation biomass (including crop species, understory, midstory), forest floor and soil. Although the species used in this study have a long life-span, intensive forest management is reducing harvest age to 50 years (Briggs, 2007; Curtis et al., 2007), so our estimate at age 25-26 years represent an approximately half of the rotation length (Flamenco et al., 2019).

2.2 Methods

2.2.1 Sites Description

The species introduction study was tested in three sites owned by Starker Forests Inc., covering a gradient of water deficit throughout the company's properties from the center of the Coast Range to the fringe of the Willamette Valley in western Oregon. The sites are classified as wet (Huffman), intermediate (Underhill), and dry (Campbell) (Figure 2.1).

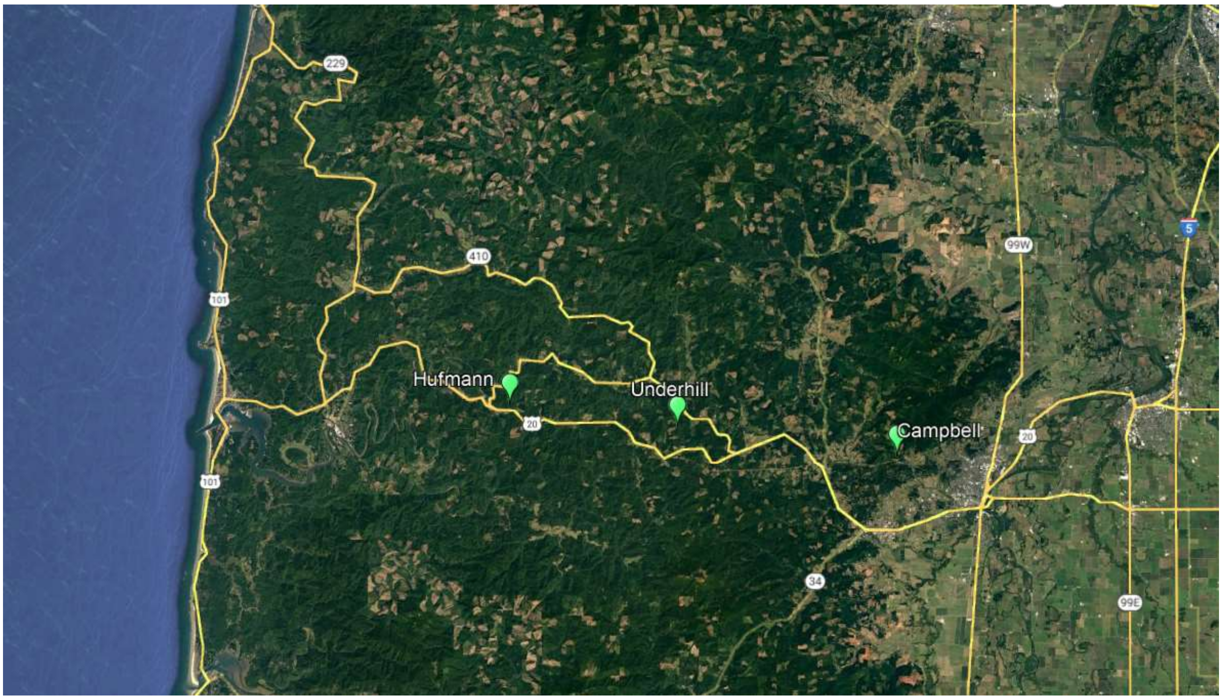

Figure 2.1. Locations of the wet (Huffman), Intermediate (Underhill), and Dry (Campbell) study sites in Western Oregon, USA (Google Earth).

The wettest site is situated at 44°37'58.0"N 123°45'17.3"W, in the central coastal range, close to Eddyville, OR. Based on historical PRISM data, the site has the lowest average annual potential evapotranspiration (800 mm) and the highest average annual rainfall (2,000 mm) of the three sites (PRISM Climate Group, n.d.). The area has well-drained and fine-loamy soils. The site property name is Huffman, so from here and after will be referred wet (Huffman) site.

The intermediate site is situated at 44°37'00.2"N 123°34'48.6"W, close to Blodgett, OR. Based on historical PRISM data, the site has the intermediate average annual precipitation of 1,700 mm and the intermediate average annual potential evapotranspiration of 850 mm. The area has well-drained, and silty-clay loam soil. The site property name is Underhill, so from here and after this study and will be referred to as the Underhill (intermediate) site.

The driest site is located closed to Corvallis, OR, at 44°35'42.6"N 123°21'07.3"W. Based on historical PRISM data, the site has the lowest average annual precipitation of 1,300 mm and highest average annual potential evapotranspiration of 940 mm among the three sites. The area has well-drained, and silty clay soils. The site property name is Campbell, so from here and after this study will be referred dry (Campbell) site.

2.2.2 Species and Stock Type

A species introduction study was established by Starker Forests Inc. in 1996, with the aim to compare the productivity of 12 tree species across a gradient water deficit in western Orgon (from the Coast Range to the western foothills of the Willamette Valley). The species include coastal Douglas-fir (DF), grand fir (GF), the giant sequoia (GS), Japanese larch, Leyland cypress (LC), Port-Orford-cedar (POC), Sitka spruce (SSP), western hemlock (WH), western redcedar (WRC), a weevil resistant variety of Sitka spruce (WRSP), Willamette Valley ponderosa pine (WVPP), and western white pine (WWP). The Japanese larch plots had nearly 100% mortality at all three sites and these plots were considered as control plots in order to compare differences between plots planted with crop species and unplanted (UP) plots with natural regeneration (Figure 2.2).

Figure 2.2. Plots layout at the wet (Huffman, left), intermediate (Underhill, center), and dry (Campbell, right) sites. Species description can be found in Table 2.1.

At each site, 12 plots were laid out measuring approximately 51 x 51 m each (Figure 2.2). Before planting, a winged sub-soiler was used to sub-soil the plots after clearing them of vegetation. During the first two years of growth, herbicide applications were done to manage competing vegetation. Each plot was planted at a 3 x 3 m spacing with a single tree species which was randomly assigned in 1996.

The trees were purchased on the open market from various nurseries around the region, including Champion, Georgia Pacific, Louisiana Pacific, Pelton and Sylvan Options nurseries (Table 2.1). All seedlings were grown as Styro-5 or 6 stock types. All of the newly planted seedlings were protected from animal browsing with vexar tubing. Because seedlings for all species were not available in sufficient quantities in 1996, four species were planted in 1997 and one species was planted 1998 (Table 2.1).

Table 2.1. List of species, including planting year and nursery that produced the seedlings.

Species	Species ID	Year Planted	Nursery
Douglas-fir	DF	1996	Georgia Pacific
Grand Fir	GF	1996	Champion
Giant Sequoia	GS	1997	Louisiana Pacific
Leland Cypress	LC	1997	Sylvan Options
Japanese larch	JL	1996	Georgia Pacific
Port Orford Cedar	POC	1997	Louisiana Pacific
Sitka Spruce	SSP	1997	Louisiana Pacific
Weevil Resistant Sitka Spruce	WRSS	1998	Pelton
Western hemlock	WH	1996	Microseed
Western redcedar	WRC	1996	Champion
Western White Pine (Blister Rust Resistant)	WWP	1996	Champion
Willamette Valley Ponderosa Pine	WVPP	1996	Qualitree

2.2.3 Weather Measurement

The weather station was installed in a clear place at each site to measure air temperature, solar radiation (CS301, Apogee Instruments), precipitation (TE525MM, Texas Electronics), and relative humidity (RH; HMP60, Vaisala). A datalogger took weather readings every 30 seconds and averaged them every 30 minutes (CR300, Campbell Scientific). Additionally, PRISM data (source) was used to get estimates of past daily and monthly averages of climate variables in a given area, such as mean and minimum precipitation, and maximum temperature, and minimum and maximum vapor pressure deficit (VPD, kPa). The on-site weather station was used to calibrate past Prism data through a linear regression approach, which allowed for more accurate data when completing missing weather readings and for historical data.

Each site's monthly potential evapotranspiration (PET) values were determined using the temperature-based equation derived from Hamon (1963), which was then used to determine the monthly water deficit and water surplus. To calculate PET, this equation accounts for saturated water vapor concentration, mean temperature, and day length. The equation is as follows:

$$PET(mm) = 1.2 \times D \times 0.1651 \times (2 \times \frac{L}{86.400}) \times 216.7 \times \frac{6.108 \times e^{\frac{(17.26939 \times T)}{(T+237.3)}}}{(T + 237.3)}$$

where D represents the number of days in a given month; L represents the average day length (seconds) for a given month; T represents the average monthly air temperature (°C); and V represents the saturated vapor density at the daily mean air temperature T (g m^{-3}). The water deficit/surplus was calculated as the difference between monthly PET and rainfall. When rainfall exceeds PET, there is a surplus of water. When PET exceeds rainfall, there is a water deficit.

2.2.4 Tree Inventory

At the three sites, there had not been any silvicultural activities and nor any previous inventory measurements during the 26 years since they were planted. During the winter of 2021, a 30 x 30 m measurement plot was installed inside each planted plot. The square measurement plot consisted of 100 trees within 10 x 10 rows, which was surrounded by a 3-4 row buffer. The four corners of each measurement plot were marked with PVC pipes, marking the corner closest to the first measurement tree. Inside each measurement plot, tree diameter at 1.47 m height (DBH, cm) and total height (m) in the winter of 2021 and 2022 were measured. Tree DBH was measured on all trees using diameter tape. Heights were measured in 1/3 of the trees, across a range in the diameter distribution, using a Vertex IV ultrasonic hypsometer. Within each plot, a linear regression model was used to predict heights of the trees whose heights were not measured using the reciprocal of DBH and the natural log of height of measured trees (Arabatzis and Burkhart, 1992). Stem volume over-bark (m^3) was determined for each tree using region-specific volume equations with species-specific coefficients for each species at each site. These volume equations and species-specific coefficients were obtained from Gonzalez-Benecke et al. (2018), Wensel and Krumland (1983), Zhou and Hemstrom (2010), Zianis et al. (2005), Pillsbury et al. (1998), and Poudel et al. (2019). All equations are listed in Appendix (1).

2.2.5 Overstory (Crop Tree) Biomass

Using inventory data collected in winter 2021 and 2022, the aboveground biomass of the overstory crop trees (B_{CT}, Mg ha^{-1}) was determined by using species-specific (or genus-specific) biomass equations reported in the literature (Chojnacky et al., 2014; Poudel et al., 2019; Zhou et al., 2009 and 2010). In addition, root biomass was calculated using the equation was published by Chojnacky et al. (2014). Table 2.2 shows the total aboveground biomass equations used for each species. We checked a number of biomass equations reported (2-4 per species), selecting the function that showed the more reliable estimations. Appendix 2 shows the list of references from literature for biomass equations for each species.

Table 2.2. Total aboveground biomass equations used for each species.

Species	Biomass Equations	Reference
DF	$\mathrm{EXP}(-2.8246 + (1.6385 \times (\ln(D))) + 1.0474 \times (\ln(H))) \times 1.0274$	Poudel et al., (2019)
GF	$\mathrm{EXP}(-2.5384 + (2.4814 \times (\ln(D))))$	Zhou et al., (2009)
GS	$\mathrm{EXP}(-3.8735 + (2.1251 \times (\ln(D))) + 0.601 \times (\ln(H))) \times 1.0247$	Poudel et al., (2019)
LC	$\mathrm{EXP}(-3.8735 + (2.1251 \times (\ln(D))) + 0.601 \times (\ln(H))) \times 1.0247$	Chojnacky et al., (2014)
POC	$\mathrm{EXP}(-2.0336 + 2.2592 \times \ln(D))$	Zhou et al., (2009)
SSP	$\mathrm{EXP}(-2.5826 + (1.8196 \times (\ln(D))) + 0.7108 \times (\ln(H))) \times 1.0091$	Poudel et al., (2019)
WH	$\mathrm{EXP}(-2.5826 + (1.8196 \times (\ln(D))) + 0.7108 \times (\ln(H))) \times 1.0091$	Poudel et al., (2019)
WRC	$\mathrm{EXP}(-2.5443 + (1.5701 \times (\ln(D))) + 0.9162 \times (\ln(H))) \times 1.0151$	Poudel et al., (2019)
WRSP	$\mathrm{EXP}(-2.5826 + (1.8196 \times (\ln(D))) + 0.7108 \times (\ln(H))) \times 1.0091$	Poudel et al., (2019)
WVPP	$\mathrm{EXP}(-0.6616 + (0.8288 \times (\ln(D))) + (0.2127 \times (\ln(D^2)) + (0.4145 \times (\ln(H)))) \times 1.0246$	Poudel et al., (2019)
WWP	$\mathrm{EXP}(-2.5356 + 2.4349 \times \ln(D))$	Zhou et al., (2010)

D: DBH (cm); H: Height (m)

2.2.6 Midstory Biomass

All non-crop trees with a DBH of greater than 2.5 cm were considered to be part of the midstory in each plot. The DBH of all these trees was measured with a diameter tape, and the species were recorded using plant codes from the USDA Natural Resources Conservation Service plant database. Midstory inventories were measured in the summer of 2021 and 2022. Generalized biomass functions reported by Ter-Mikaelian and Korzukhin (1997), Ohmann et al. (1976), and Chojnacky et al. (2014) were used to estimate the total aboveground biomass for all midstory trees found at each plot (B_M, Mg ha^{-1}). Root biomass was estimated using the equation published by Chojnacky et al. (2014). Table 2.4 shows the list of midstory species found at the three study sites and the range of DBH measured across the sites in year 2022.

Table 2.3. List of midstory tree species found at the 3 study sites with their codes and range of diameter at breast height (DBH, cm) measured across the sites in year 2022.

Code	Species	DBH range
ABGR	Grand fir	2.1 - 6.3
ACMA	Bigleaf maple (*Acer macrophyllum* Pursh)	3.7 - 22.0
ALRU	Red alder (*Alnus rubra* Bong.)	2.3 - 18.6
ARME	Pacific madrone (*Arbutus menziesii*)	3.8 - 14.3
COCO	Beaked hazelnut (*Corylus cornuta* Marsh.)	2.1 - 9.3
CRDO	Hawthorns (*Crataegus douglasii*)	4.0 - 7.5
POTR	Poplar (*Populus* spp)	3.1 - 21.5
PREM	Bitter cherry (*Prunus emarginata* (Dougl. ex Hook.)	2.0 - 25.2
PSME	Douglas-fir (*Pseudotsuga menziesii)*	2.3 - 35.5
QUGA	Oregon White Oak (*Quercus garryana*)	2.8 - 26.0
RHPU	Cascara buckthorn (*Rhanmus purshiana* (D.C.) Cooper)	2.0 - 12.3
SANIN2	Elderberry (*Sambucus* spp.)	2.8 - 14.0

2.2.7 Understory Biomass

During the summers of 2021 and 2022, assessments of understory vegetation cover (%) and height (cm) by growth form (forbs, fern, graminoids, shrubs, and brambles) were carried out in five 1 x 1 m vegetation survey subplots per plot. Application of biomass equations for each growth form reported by Guevara et al. (2021) allowed for the estimation of understory vegetation biomass (B_U, Mg ha^{-1}) using cover or a combination of cover and height.

2.2.8 Forest Floor

Forest floor biomass of each plot (B_{FF}, Mg ha^{-1}) was estimated using five 23 x 23 cm subplots located randomly inside each plot. Raking and gathering the forest floor inside the frame was done until bare mineral soil was reached. The collected material from the five points was put in a labelled bag and placed in a cooler until lab processing. In the lab, samples of the forest floor were put in aluminum trays and dried at 75ºC for at least 72 h. After that time, the dry mass (g) of forest floor was weighed and a subsample was grounded and put in a glass vial and sent to A&L Western Agricultural lab for chemical analysis.

2.2.9 Soil Bulk Density and Organic Matter

Four soil cores at varying depths (0-15, 15-30, 30-50, and 50-100 cm) were taken at the center of each plot using an AMS soil core sampler in the winter of 2022. Samples collected were 4 cm in diameter and 15 cm in length. All soil samples were put separately in labelled bags and placed in a cooler until lab processing. At the lab, the soil samples were put in aluminum trays, and dried at 75°C for at least 72 h. After that time, the soil samples were sieved in a 2 mm sieve to remove fine roots and rocks, and dry weight (g) of soil (with rocks) and fine roots were determined. Bulk density (g cm^{-3}) was estimated using the dry mass of the soil (with rocks) and the volume of the soil core for each depth and plot. All sieved soil samples (without rocks) were sent to A&L Western Agricultural lab for soil organic matter percentage (SOM%) analysis. Soil organic matter content per ha (SOMC, Mg ha^{-1}) was then estimated for each soil depth as the product of SOM%, bulk density (g cm^{-3}), and the soil depth that the soil cores were extracted from.

2.2.10 Statistical Analysis

In the 2021and 2022 inventory data, there was no replication in the species combinations. Therefore, a formal statistical analysis could not be done and causal inferences about the connection between trees growth could not be made. However, an ANOVA test was used to test differences in overstory, midstory, understory, forest floor and SOMC across the sites, using the Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC). Sigma Plot version 14.0 (Systat Software, Inc. San Jose, CA) was used to create all figures.

2.3 Results

2.3.1 Weather

The wet (Huffman), intermediate (Underhill), and dry (Campbell) sites are located along a climate gradient from the mid-Coast Range to the Willamette Valley in western Oregon. Precipitation and temperature measurements are useful climate indicators, but they do not reflect the energy and water balance (Restaino et al., 2016). The primary climate variables of interest that differentiate the three sites are those that affect water deficit levels, such as rainfall, PET, and maximum VPD which are plant relevant variables (Table 2.4).

Table 2.4. Mean yearly total annual rainfall (mm), total PET (mm), maximum monthly VPD (kpa), maximum and minimum monthly temperature (°C), mean monthly relative humidity (%), and mean monthly radiation (MJ m^2 month^{-1}) between 2021 and 2022 for the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites.

Weather variable	Wet	Intermediate	Dry
Rainfall (mm)	1849	1574	1136
PET (mm)	847	904	993
Maximum VPD (kPa)	0.8	0.9	1.1
Maximum Temperature (°C)	16.3	16	16.9
Minimum Temperature (°C)	6.4	5.6	6.3
Relative Humidity (%)	85.1	84.8	78.6

Across years 2021 and 2022, the average maximum monthly VPD at the dry (Campbell) site was higher compared to the other sites, peaking in July at 2.5 kPa. The VPD of the Intermediate site peaked 1.92 kPa in July, while at the wet (Huffman) site, VPD peaked 1.68 kPa in August. The wet (Huffman) site showed the lower maximum VPD across both years. The intermediate (Campbell) site was, is general, in between the other sites. In addition, the differences in maximum VPD across sites was larger in summer, and smaller in winter (Figure 2.3).

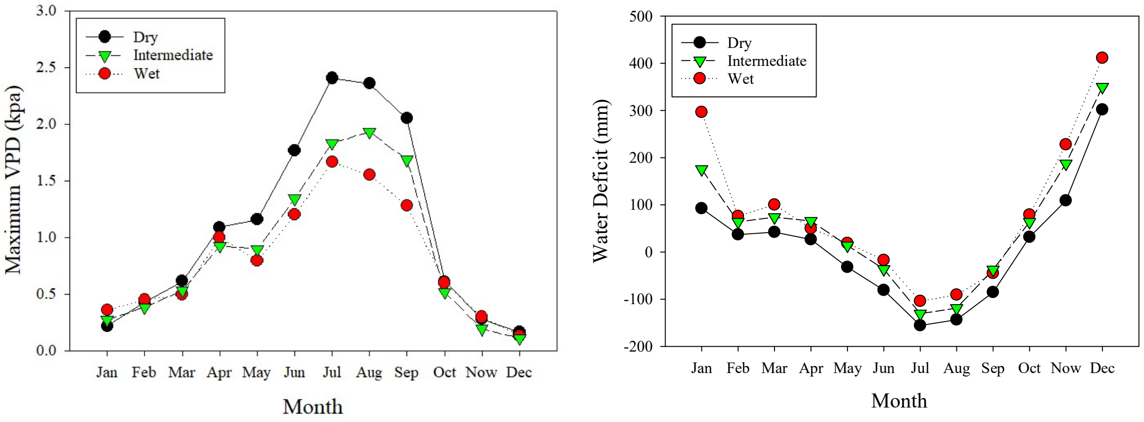

Figure 2.3. Average monthly a) maximum vapor pressure deficit (VPD, kPa) and water deficit (mm) for the dry (Campbell), intermediate (Underhill), and wet (Huffman) sites across years 2021 and 2022. Periods of water surplus are indicated by readings above the zero line, whereas water deficit is indicated by readings below the zero line.

The period of water deficit at the dry (Campbell) site began in early April and lasted until the end of September, which was the longest period of the three sites (Figure 2.3). While this site also had the highest peak water deficit in July with 155.6 mm, the lowest peak water surplus in December with 301.6 mm. The period of water deficit at both the intermediate (Underhill) and wet (Huffman) sites lasted from mid-May to mid-September. While the duration of the water deficit period was comparable between the two sites, the peak water deficit in July at the intermediate (Underhill) with 130.7 mm and wet (Huffman) with 104.4 mm. In addition, the wet (Huffman) site had the highest peak water surplus in December with 411 mm, whereas the intermediate (Underhill) site had a peak water surplus of 350 mm.

2.3.2 Crop Tree Inventory

Overall, the wet (Huffman) site tended to have larger trees and plots with larger stocking and productivity, and the dry (Campbell) site tended to have smaller trees and plots with reduced stocking and productivity (Table 2.5). Despite the fact that for most of the species productivity and survival declined dramatically at the dry (Campbell) site, some species, such as WRC and WVPP showed reduced productivity and survival at the wet (Huffman) site, indicating that site conditions effects on tree performance were species-dependent.

Table 2.5. Average diameter at 1.37 m height (DBH, cm), height (HT, m), basal area (BA, $m^2\ ha^{-1}$), stem volume over-bark (VOL, $m^3\ ha^{-1}$), trees per hectare (TPH, ha^{-1}) during 2022 for plots planted with 11 conifer species at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites. Current annual increment (CAI) in DBH (cm $year^{-1}$), height (m $year^{-1}$), BA ($m^2\ ha^{-1}\ year^{-1}$), VOL ($m^3\ ha^{-1}\ year^{-1}$) between years 2021 and 2022 and mean annual increment in VOL at year 2022 (MAI_{VOL}, $m^3\ ha^{-1}\ year^{-1}$) are also shown.

		Year 2022						CAI (2021-2022)				MAI_{VOL} $m^3\ ha^{-1}\ y^{-1}$
Site	Species	Age y	DBH cm	HT m	BA $m^2\ ha^{-1}$	VOL $m^3\ ha^{-1}$	TPH ha^{-1}	DBH cm y^{-1}	HT m y^{-1}	BA $m^2\ ha^{-1}\ y^{-1}$	VOL $m^3\ ha^{-1}\ y^{-1}$	
W	DF	25	23.6	21.4	43.2	375.8	947	0.3	1.2	1.2	29.9	14.5
	GF	25	27	22.3	59.7	517.8	980	0.4	0.4	1.9	27.4	19.9
	GS	24	38.7	21.3	97.5	617.8	786	0.5	1.8	2.4	64.4	24.7
	LC	24	24.3	20.1	36.8	308.6	764	0.5	0.7	1.0	16.3	12.3
	POC	24	24.2	14.6	51.1	344.1	1066	0.3	0.7	1.5	22.4	13.8
	SSP	24	23.6	12.8	49.7	215.6	1066	0.4	0.6	1.7	4.3	8.6
	WH	25	25.4	20.2	54.7	451.4	1012	0.9	0.4	3.3	44.4	17.4
	WRC	25	19.1	10.3	29.9	145.7	883	0.7	0.6	2.1	16.6	5.6
	WRSP	23	22.8	14.4	46.2	240.6	1055	0.5	0.9	2.2	27.3	10.0
	WVPP	25	21.5	13.5	21.2	116.2	549	0.3	0.2	0.8	6.8	4.5
	WWP	25	22.9	15.3	29.3	189.3	667	0.5	0.8	1.0	19.3	7.3
I	DF	25	24.4	20.6	43.7	363.5	893	0.6	0.8	2.1	29.9	14.0
	GF	25	24.7	18.5	44.1	358.2	840	0.6	0.5	1.7	21.7	13.8
	GS	24	30.9	15.7	81.8	384.4	1044	0.8	0.8	5.0	38.2	15.4
	LC	24	20.8	17.8	39.4	293.8	1119	0.3	0.4	1.2	13.6	11.8
	POC	24	23.9	15.5	49.0	349.3	1044	0.6	0.5	2.4	25.7	14.0
	SSP	24	21.9	10.2	31.5	105.9	807	0.8	0.4	2.1	3.8	4.2
	WH	25	24.5	17.5	43.2	308.6	850	0.7	0.4	2.4	24.9	11.9
	WRC	25	18.0	9.9	23.5	111.4	829	1.0	0.4	2.6	15.4	4.3
	WRSP	23	19.6	10.2	25.9	90.5	807	0.9	0.4	2.3	11.7	3.8
	WVPP	25	21.1	13.6	36.4	195.8	990	0.4	0.3	1.3	12.2	7.5
	WWP	25	23.6	15.9	34.8	231.3	753	0.6	0.5	1.9	17.4	8.9
D	DF	25	23.3	17.5	42.4	298.2	958	0.6	0.5	2.3	23.2	11.5
	GF	25	11.3	6.6	5.6	18.6	506	0.5	0.2	0.5	2.2	0.7
	GS	24	21.5	9.0	25.5	81.8	614	1.0	0.4	2.1	10.0	3.3
	LC	24	19.0	13.3	31.4	195.7	1033	0.4	0.6	1.3	13.9	7.8
	POC	24	18.6	8.7	7.4	34.7	258	0.9	0.1	0.4	2.2	1.4
	SSP	24	14.7	6.9	13.2	30.7	732	0.5	0.4	0.9	0.8	1.2
	WH	25	16.8	8.7	8.3	30.1	355	0.5	0.1	0.5	2.5	1.2
	WRC	25	20.5	11.5	35.0	175.3	1012	0.8	0.5	2.7	18.1	6.7
	WRSP	23	12.8	6.8	12.1	29.2	850	0.7	0.2	1.4	3.9	1.2
	WVPP	25	19.9	13.2	32.1	168.3	980	0.5	0.5	1.4	13.5	6.5
	WWP	25	20.2	11.7	21.0	100.4	624	0.8	0.2	1.7	8.7	3.9

W: Wet. I; Intermediate. D: Dry. Species description can be found in Table 2.1.

Overall, across all species, the wet (Huffman) site showed trees with larger DBH, averaging 24.8 cm (Table 2.5). The intermediate (Underhill) site showed trees with DBH 7.2% smaller than the wet site and the dry (Campbell) site had trees with the smallest DBH, averaging 27.2% lower than the wet site. GS trees at the wet (Huffman) site showed the largest DBH, averaging 38.7 cm (age 25 years), whereas GF trees at the dry (Campbell) site showed the smallest DBH, averaging of 11.3 cm (age 26 years). A similar trend was observed for tree height (HT), where, across all species, the wet (Huffman) site showed taller trees, averaging at 16.9 m (Table 2.5). The intermediate (Underhill) site showed trees with HT 1.9 m shorter than the wet site, and the dry (Campbell) site had trees with HT 6.6 m shorter than the wet site. GF at the wet (Huffman) site had the tallest trees, averaging of 22.3 m HT. Interestingly, GF growing at the dry (Campbell) site were the shortest across all species and sites, averaging 6.6 m HT (age 26 years).

Overall, across all species, the wet (Huffman) site showed the largest BA and VOL, averaging 47.2 m^2 ha^{-1} and 320 m^3 ha^{-1}, respectively (Table 2.5). The intermediate (Underhill) site showed BA and VOL about 12.7 and 20.7% lower than the wet (Huffman) site, while the dry (Campbell) site, had the lowest yield, averaging 54.9 and 67.0% lower than the wet (Huffman) site. While the highest BA was observed for GS at the wet (Huffman) site (97.5 m^2 ha^{-1} at age 25 years), the lowest BA was observed for GF at the dry (Campbell) site (5.6 m^2 ha^{-1} at age 26 years). Similarly, the largest VOL was observed for GS at the wet (Huffman) site (617.8 m^3 ha^{-1} at age 25 years), the lowest VOL was observed for GF at the dry (Campbell) site (18.2 m^3 ha^{-1} at age 26 years).

Across all species, similar survival was observed for the wet (Huffman) and the intermediate (Underhill) sites (965 trees ha^{-1}). On the other hand, the dry (Campbell) site showed reduced survival, averaging of 734 trees ha^{-1}. At the wet (Huffman) site, POC, SSP, WH and

WRSP showed more than 95% survival, while at the intermediate (Underhill) site, that level of high survival was observed only for LC and POC. At the dry (Campbell) site, only LC showed survival larger than 95%. On the other hand, survival lower than 60% was observed for WVPP at the wet (Huffman) site, and GF, GS, POC, WH and WWP at the dry (Campbell) site. Consistent survival across sites was observed for DF (86.4%), WRC (82.0%) and WWP (63.3%) (Table 2.5).

Overall, across all species, while the wet (Huffman) site showed the highest CAI for HT and VOL, averaging 0.7 (m year^{-1}) and 25.4 (m^3 ha^{-1} year^{-1}), respectively, the intermediate (Underhill) site had the highest CAI for DBH and BA, averaging 0.66 (cm year^{-1}) and 2.2 (m^2 ha^{-1}), respectively (Table 2.5). CAI for HT at the wet (Huffman) site was almost two times larger than at the dry (Campbell) site. The species with the largest CAI for HT and VOL was GS at the wet (Huffman) site (1.8 m year^{-1} and 64.4 m^3 ha^{-1} year^{-1}, respectively. When growing at the dry (Campbell) site, average CAI for HT and VOL was only 0.4 m year^{-1}, and 10.0 m^3 ha^{-1} year^{-1}, a 78 and 84% reduction, respectively. Similarly, MAI_{VOL} had a decreasing trend from average the wet (Huffman) site (12.6 m^3 ha^{-1} year^{-1}) to the dry (Campbell) site (4.1 m^3 ha^{-1} year^{-1}). Across sites, DF showed very stable productivity, having MAI_{VOL} of 14.5, 14.0 and 11.5 m^3 ha^{-1} year^{-1}, when growing at the wet, intermediate and dry sites, respectively. GS showed the largest MAI_{VOL} at the wet (Huffman) and intermediate (Underhill) sites, whereas DF showed the largest MAI_{VOL} at the dry site.

2.3.3 Overstory (Crop Tree) Biomass

Across all species, the wet (Huffman) site showed the largest B_{CT}, averaging 234.8 Mg ha^{-1}. The intermediate (Underhill) site showed the second-highest B_{CT}, averaging 193.0 Mg ha^{-1} (17.8 % less than the wet site), followed by the dry (Campbell) site, which averaged 68.2 Mg ha^{-1} (61.4 % less than the wet site). Across all sites, GF growing at the wet (Huffman) site showed the largest

B_{CT} (375.6 Mg ha^{-1}). Interestingly, the same species showed the lowest B_{CT} of all species and sites (24.3 Mg ha^{-1}) when growing at the dry (Campbell) site. The three species with largest B_{CT} at the wet (Huffman) site (GF, WH, and GS) showed a dramatic decrease in productivity when growing at the dry (Campbell) site, averaging only 35 Mg ha^{-1}. On the other hand, B_{CT} of WRC, WVPP, and WWP had an opposite trend, decreasing at the wet (Huffman) site, while DF showed relatively stable B_{CT}, averaging 300 Mg ha^{-1} across sites (Figure 2.4). In general, crop tree root biomass (B_R) averaged about 20% of B_{AG} across species and sites.

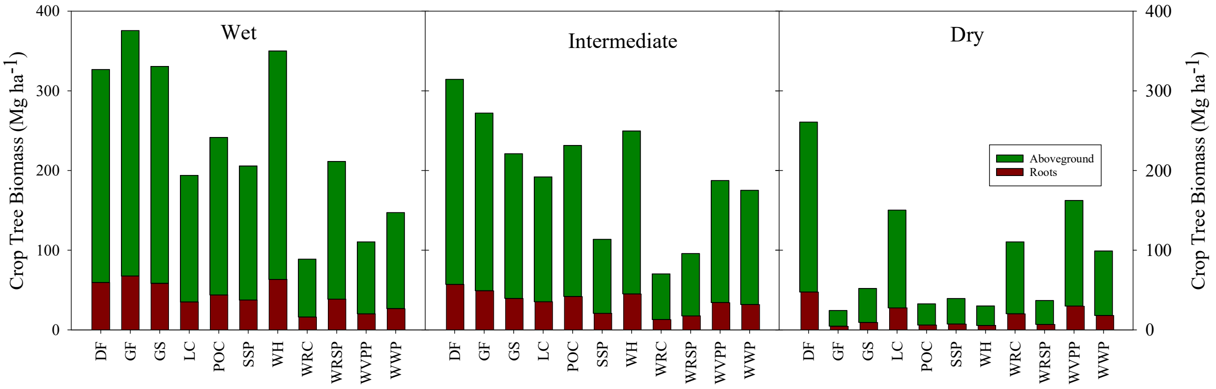

Figure 2.4. Overstory (crop tree) above-ground (grey bars) and roots (black bars) biomass stock (Mg ha^{-1}) of 11 species growing at wet (Huffman), intermediate (Underhill), and dry (Campbell) sites in central Oregon. Species description can be found in Table 2.1.

2.3.4 Midstory Biomass

Across all species, the dry (Campbell) site showed the largest B_M, averaging 5.7 Mg ha^{-1}. The intermediate (Underhill) and wet (Huffman) sites averaged 2.5 and 3.8 Mg ha^{-1}, respectively. While at the wet (Huffman) and intermediate (Underhill) site most plots did not have any volunteer trees, GF plot at the dry (Campbell) site showed the highest amount B_M (26.5 Mg ha^{-1}). The UP plot represents a naturally-regenerated stand, as it has no surviving planted trees at any site. At the wet (Huffman) and intermediate (Underhill) sites, the UP plot showed the largest B_M, averaging 20.2 and 17.2 Mg ha^{-1}, respectively, which was composed almost completely of naturally-regenerated Douglas-fir. At the dry site (Campbell), midstory biomass was composed only of Oregon white oak (12.4 Mg ha^{-1}). The composition of hardwood species growing in the midstory differed between sites and crop species planted (Figure 2.5). B_M included aboveground and roots components.

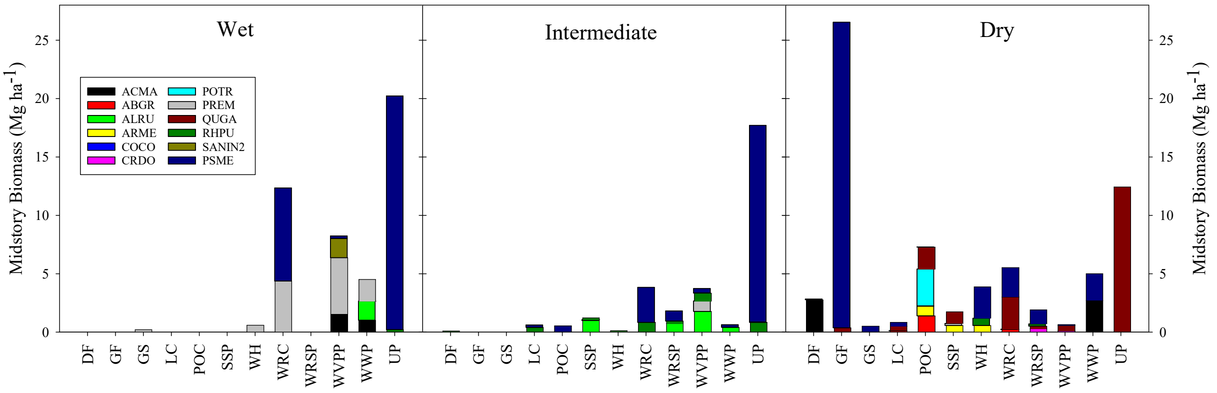

Figure 2.5. Midstory biomass stock including aboveground and roots biomass (Mg ha^{-1}) of plots planted with 11 conifer species, including a naturally regenerated unplanted (UP) plot, growing at wet (Huffman), intermediate (Underhill), and dry (Campbell) sites in central Oregon. Midstory vegetation includes all conifer and broadleaf species with DBH>2.5 cm identified by USDA species code (Table 2.3). Planted conifer species description can be found in Table 2.1.

2.3.5 Understory Biomass

Averaged across all species, the dry (Campbell) site had the greatest overall B_U averaging 2.9 Mg ha^{-1}, followed by the intermediate (Underhill) site (8.3% less) and the wet (Huffman) site (53.1% less). While some plots at the wet (Huffman) site did not have any understory vegetation (e.g. GF, POC, SSP and WRSP), at the dry site those plots showed a large abundance of understory. At the dry (Campbell), WH had the highest B_U (7.0 Mg ha^{-1}), which was mostly composed by ferns and brambles. At the wet (Huffman) site, there was a large abundance of ferns, while at the dry (Campbell) site, understory was dominated by graminoids (Figure 2.6). The naturally-regenerated UP plots showed high B_U, ranging between 4.1 and 5.7 Mg ha^{-1}. B_U included only aboveground components.

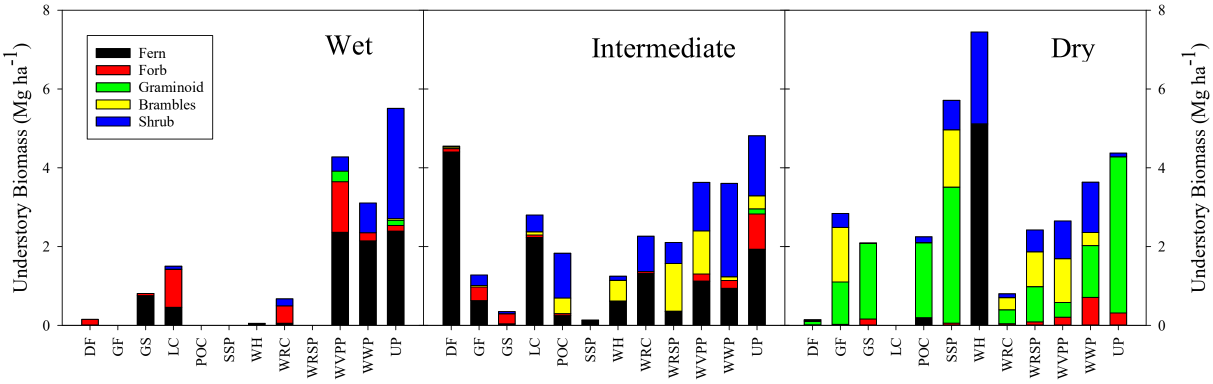

Figure 2.6. Understory biomass stock (Mg ha^{-1}) of plots planted with 11 conifer species, including a naturally regenerated unplanted (UP) plot, growing at wet (Huffman), intermediate (Underhill), and dry (Campbell) sites in central Oregon. Midstory vegetation includes forbs, ferns, graminoids, shrubs and brambles. Planted conifer species description can be found in Table 2.1.

2.3.6 Forest Floor Biomass

Overall, across all species, the wet (Huffman) site showed larger B_{FF} than the other sites, averaging 10.9 Mg ha^{-1}, while the intermediate (Underhill) and the dry (Campbell) sites, B_{FF} averaged 8.0 and 6.0 Mg ha^{-1}, respectively (Figure 2.7). Sitka Spruce plots (either SSP or WRSP) showed the largest B_{FF} at the wet (Huffman), averaging 17.5 Mg ha^{-1}. Interestingly, the same species showed the lowest B_{FF} when growing at the dry (Campbell) site (3.0 Mg ha^{-1}).

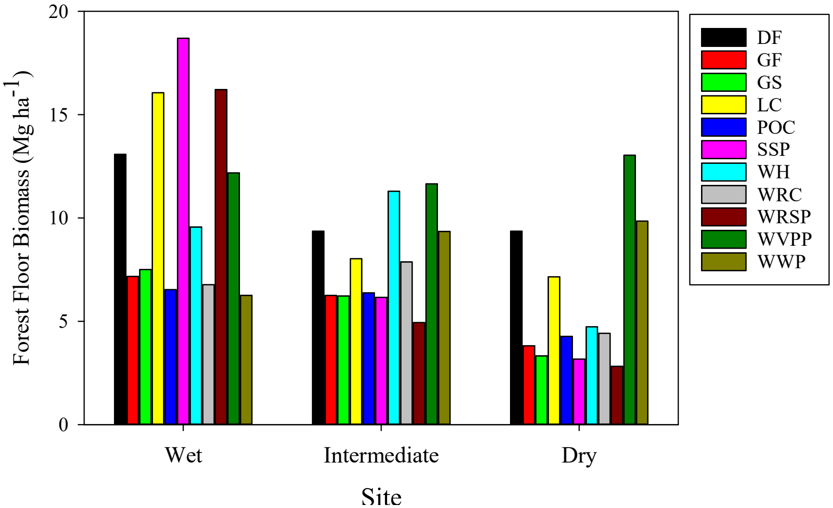

Figure 2.7. Forest floor biomass stock (Mg ha^{-1}) of plots planted with 11 conifer species growing at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites in central Oregon. Planted conifer species description can be found in Table 2.1.

2.3.7 Soil Organic Matter Content

Soil organic matter content (SOMC, Mg ha^{-1}) was calculated using the soil organic matter (OM, %) and bulk density (g cm^{-3}) determined at each plot (Appendix 3). Overall, across all species, the wet (Huffman) site showed larger SOMC than the other sites, averaging 471.8 Mg ha^{-1} for the whole 0-100 cm profile, while the intermediate (Underhill) and the dry (Campbell) site averaged 308.7 and 246.7 Mg ha^{-1} for the whole 0-100 cm profile, respectively (Table 2.6). The top 15 cm soil layer accounted for 15-40% of total SOMC, while the bottom 50 cm soil layer (50-100 cm) accounted for 25-53% of total SOMC. Interestingly, the largest SOMC was observed at the plot planted with UP at the wet (Huffman) site (794 Mg ha^{-1}), followed by the WH at the wet site (778 Mg ha^{-1}), while the lowest SOMC was observed also at the plot planted with WH, but at the dry (Campbell) site (148 Mg ha^{-1}).

Table 2.6. Soil organic matter content (Mg ha^{-1}) at 0-15, 15-30, 30-50 and 50-100 cm depth, on plots planted with 11 conifer species, including a naturally regenerated unplanted (UP) plot, at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 2.1.

	Wet				Intermediate				Dry			
Species	0 - 15	15 - 30	30 - 50	50 - 100	0 - 15	15 - 30	30 – 50	50 - 100	0 - 15	15 - 30	30 - 50	50 - 100
DF	153.8	83.6	63.7	109.4	103.7	43.7	55.4	83.3	67.9	28.9	40.0	111.8
GF	97.3	56.1	175.7	225.2	104.9	64.8	71.7	154.5	50.7	37.3	28.1	59.2
GS	50.6	47.6	60.1	115.6	141.4	84.1	31.2	102.9	82.8	49.1	45.8	111.2
LC	106.2	81.3	64.9	143.0	138.4	52.4	61.1	98.7	85.7	91.8	56.4	168.7
POC	121.9	56.3	40.4	81.2	119.7	75.2	47.0	91.7	58.0	44.1	37.5	95.8
SSP	108.7	83.2	37.7	166.6	70.7	43.9	36.9	83.4	35.2	35.9	32.5	118.7
WH	147.7	161.1	180.9	289.0	66.1	73.3	63.0	134.7	47.1	56.6	6.1	38.9
WRC	136.8	59.8	70.8	96.9	76.1	65.1	82.5	108.9	48.7	36.7	42.5	105.5
WRSP	97.9	79.1	64.2	179.9	67.2	39.8	40.9	100.0	51.2	62.0	30.4	82.8
WVPP	117.9	123.8	106.9	165.2	28.3	38.8	35.0	48.0	51.6	48.7	58.2	105.3
WWP	93.5	75.4	98.3	193.0	76.7	66.6	52.7	133.9	65.2	39.5	48.0	122.0
UP	122.3	117.1	147.1	407.6	134.2	77.1	45.8	90.1	49.2	34.9	44.3	113.1

2.3.8 Ecosystem Biomass

When all vegetation derived biomass was included (overstory, midstory, understory and forest floor), total vegetation biomass (B_V, Mg ha^{-1}) was larger for DF, GF, GS and WH growing at the wet (Huffman) site, which averaged 293 Mg ha^{-1} (Figure 2.8). Across all species, the wet (Huffman) site showed larger B_{AG} than the other sites, averaging 190 Mg ha^{-1}, while the intermediate (Underhill) and the dry (Campbell) site averaged 156 and 81 Mg ha^{-1}, respectively (Figure 2.8). The UP (naturally-regenerated) showed the lowest B_{AG} across all sites and species, having 21.9, 19.1 and 14.4 Mg ha^{-1} at the wet (Huffman), intermediate (Underhill) and dry (Campbell) sites, respectively.

Belowground biomass (B_{BG}) was separated into roots (B_R) and SOMC (Mg ha^{-1}). The wet (Huffman) site showed larger SOMC than the other sites, averaging 471 Mg ha^{-1} for the whole 0-100 cm profile, while the intermediate (Underhill) and the dry (Campbell) site averaged 308 and 246 Mg ha^{-1} for the whole 0-100 cm profile, respectively (Table 2.8). A similar trend was observed for B_R, decreasing from 39.7 (Mg ha^{-1}) at the wet (Huffman) site, to 16.4 (Mg ha^{-1}) at the dry (Campbell) site.

Overall, across all species, total ecosystem biomass ($B_E = B_{AG} + B_{BG}$, Mg ha^{-1}) was larger at the wet (Huffman) site, averaging 345.5 Mg ha^{-1}, while the intermediate (Underhill) and the dry (Campbell) site averaged 269 and 73 Mg ha^{-1}, respectively (Figure 2.8). The largest B_E was observed at the WH plot at the wet (Huffman) site (averaging 569 Mg ha^{-1}), and the lowest was observed at the WH plot at the dry (Campbell) site (averaged 94 Mg ha^{-1}). Interestingly, the UP (naturally-regenerated) showed the third largest B_E at the wet (Huffman) site (averaged 436 Mg ha^{-1}). DF plots showed the second largest B_E at each site, having averaged 375, 303, and 241 Mg ha^{-1} at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites, respectively.

Acoss all sites and species, B_{AG} corresponded to 38% of B_{BG}. The percent of B_{AG} to B_{BG} was larger at the intermediate (Underhill) site, averaging 47%, while the wet (Huffman) and the dry (Campbell) site averaged 40 and 28%, respectively (Figure 2.8). When growing at the dry (Campbell) site, B_{AG} of GS corresponded to 16% of B_{BG} (including roots and SOMC) while at the wet (Huffman) site, B_{AG} of GS corresponded to 84% of B_{BG} (including roots and SOMC). The UP (naturally-regenerated) plots showed the lowest percent of B_{AG} to B_{BG}, ranging between 2 and 5% across the three sites (Figure 2.8).

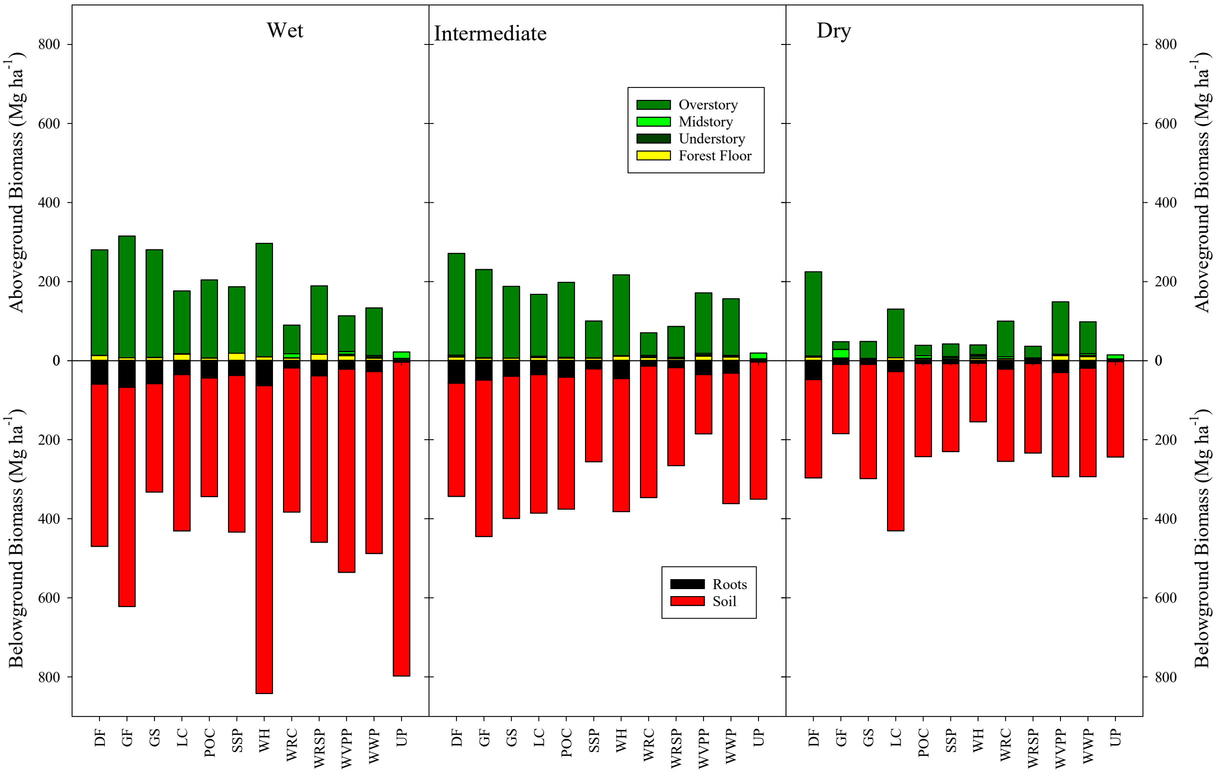

Figure 2.8. Ecosystem biomass stock (including aboveground and belowground biomass components; Mg ha^{-1}) of plots planted with 11 conifer species, including a naturally regenerated unplanted (UP) plot, growing at wet (Huffman), intermediate (Underhill), and dry (Campbell) sites in central Oregon. Aboveground components include overstory (crop trees), midstory, understory and forest floor. Belowground components include root biomass (overstory and midstory) and soil organic matter content from 0 to 100 cm soil depth. Species description can be found in Table 2.1.

2.3.9 Relationships between BA and SOMC, with Biomass Stock

The relationships between overstory BA and B_{CT}, B_M and B_U, and between SOMC and B_{AG}, are shown in Figures 2.9 (BA) and 2.10 (SOMC). Table 2.7 shows the parameter estimates of the significant relationships shown in Figure 2.9. There was no significant relationship between BA and B_{FF} ($P=0.095$; Figure 29), but a significant relationship between BA and B_{CT}, B_M and B_U ($P<0.0001$; Figure 2.9). As those relationships were not different across sites ($P > 0.40$), a single model was fitted for each case but the relationship between BA and B_{CT} was fitted two models for two group of species. Because the relationship BA and B_{CT} for GS had a different trend compare the other species. The positive relationship between BA and B_{CT} was better described by a sigmoidal model, while the negative relationship between BA and B_M and B_U, was better described by an exponential decline model. Overall, a steep decrease in B_M and B_U was observed for overstory BA between 10 and 40 m^2 ha^{-1} (reduction in B_M and B_U of about 0.4 and 0.1 Mg ha^{-1} per 1 m^2 ha^{-1} BA increment). When BA was larger than about 40 m^2 ha^{-1}, B_M and B_U were negligible. When the BA increased between 20 and 60 m^2 ha^{-1}, B_{CT} increased about 6.2 Mg ha^{-1} per each m^2 ha^{-1} BA increment. When BA was larger than 60 m^2 ha^{-1}, little increment in B_{CT} was observed.

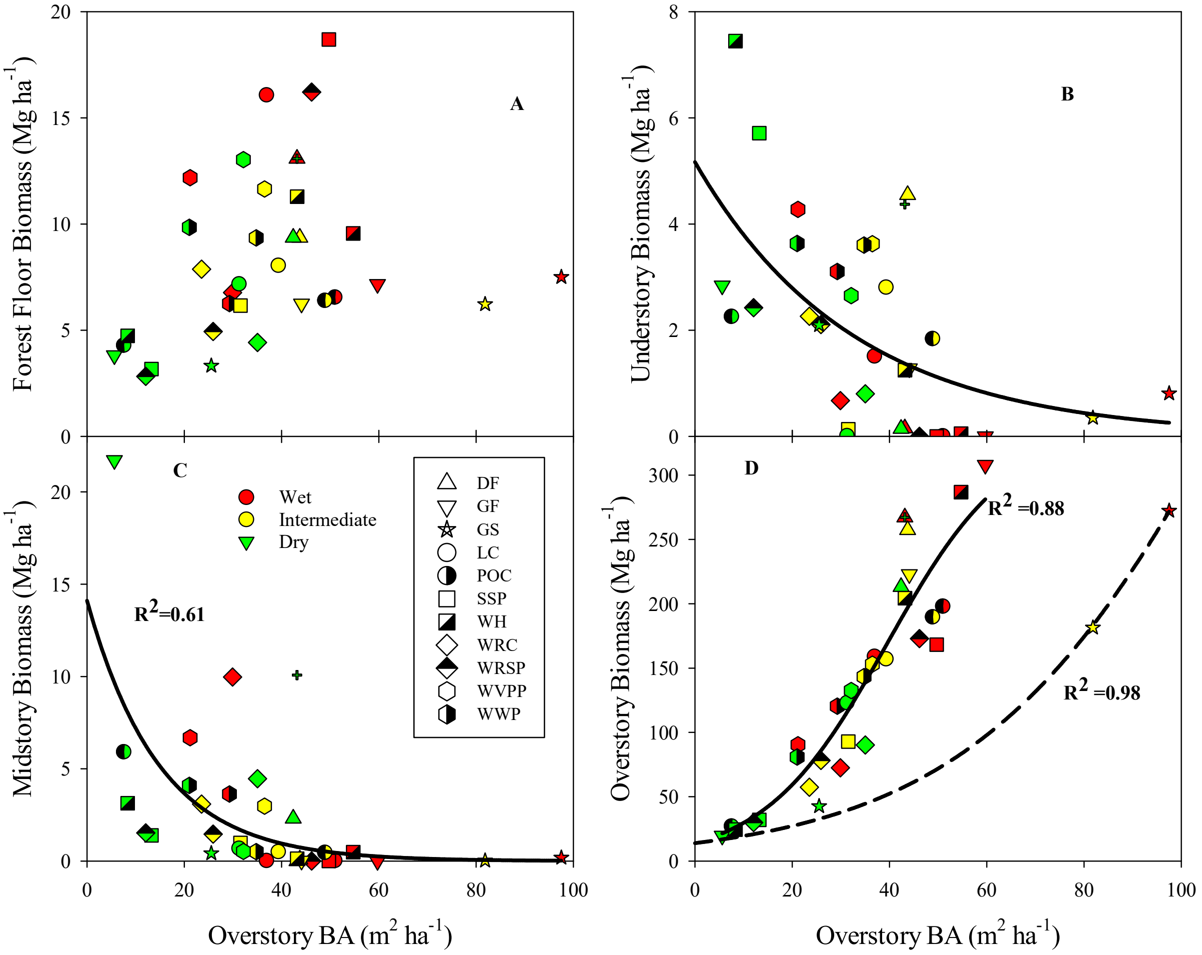

Figure 2.9. Relationships between overstory basal area (BA, m^2 ha^{-1}) and aboveground biomass stock (Mg ha^{-1}) including forest floor (A, B_{FF}), midstory (B, B_M), understory (C, B_U), overstory (crop tree)_ (D, B_{CT}) of plots planted with 11 conifer species, growing at wet (Huffman), intermediate (Underhill), and dry (Campbell) sites in central Oregon. For the relationship BA and BCT dash line for just GS, and black line for rest of all species.

A weak relationship was observed between B_{AG} and SOMC at 0-15 (P=0.032; R^2=0.13) and at 0-100 (P=0.026; R^2=0.14) cm depth (Figure 2.10). When UP (naturally-regenerated) plots (crosses in Figure 2.10) were not included, the relationship was improved (P=0.0009 and R^2=0.30 for SOMC at 0-15 cm; P=0.004 and R^2=0.24 for SOMC at 0-100 cm).

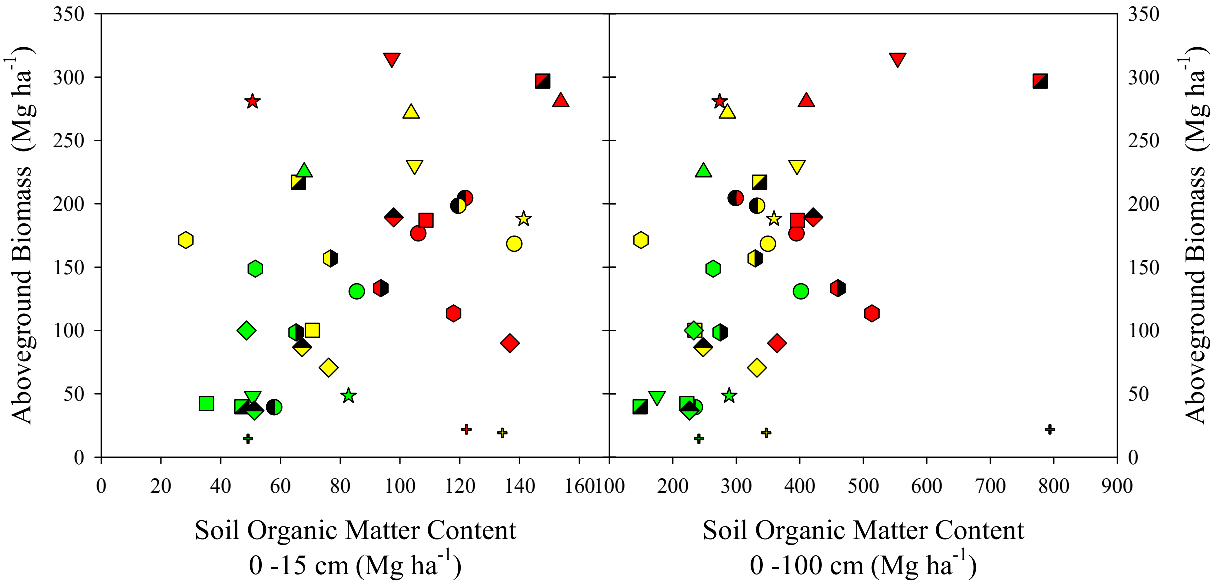

Figure 2.10. Relationships between total aboveground biomass (B_{AG}, Mg ha^{-1}) and SOMC at a) 0-15 cm and b) 0-100 cm depth of plots planted with 11 conifer species, including a naturally regenerated unplanted (UP) plot, growing at wet (Huffman), intermediate (Underhill), and dry (Campbell) sites in central Oregon.. Symbols and colors description can be found in Figure 2.9 legend (in addition, UP plots were included in this figure as crosses). Species description can be found in Table 2.1.

Parameter estimates and fit statistics for the regression of understory, midstory and overstory biomass on BA are shown in Table 2.7.

Table 2.7. Parameter estimates and fit statistics of the equations for predicting understory, midstory and overstory crop tree biomass (Mg ha^{-1}) from overstory basal area (BA) for stands planted with conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Group1 (*) includes DF, GF, GS, LC, POC, WH, WRC, WRSP, WVPP and WWP. Group 2 (**) includes just GS.

Model	Parameter	Parameter Estimate	SE	R2	RMSE
$B_M = a * \exp(-b * BA)$	a	14.1041	1.6812	0.63	2.21
	b	0.0674	0.0132		
$B_U = a * \exp(-b * BA)$	a	5.1696	0.65	0.48	2.891
	b	0.0307	0.0062		
$^{*}B_{CT} = \frac{a}{(1+\exp(-\frac{(BA-c)}{b}))}$	a	255.6531	13.5774	0.86	31.66
	b	8.5438	1.6015		
	c	32.8304	1.9553		
$^{**}B_{CT} = \frac{a}{(1+\exp(-\frac{(BA-c)}{b}))}$	a	848.2002	1368.618	0.98	5.82
	b	29.2028	11.67		
	c	119.4902	76.3163		

2.4 Discussion

The tree size and survival data were collected from the 2021 inventory when most trees were 25 years old. In general, most of species had higher survival rate and most productivity under conditions of higher water availability but some of them show a slight decline in survival and tree size from wet to dry site except for WWP and WVPP had a opposite trend which is more drought tolerant species. The amount of survival was larger than 60% for most of species at wet (Huffman), and intermediate (Underhill) site except WVPP and WWP had 52% and 62% at the wet site respectively. At the dry site the amount of survival of GF, GS, POC, WH is less than 60%. Especieally, POC at the dry had mostly standing death trees with lower survival rate (32 %) which may be affected by Phytophthora pathogen. While WH had 95% survival rate at the wet site, it had the lowest survival rate with 24% at the dry site which showed less drought tolerance species and may be affected drought in few years old seedlings (Guevara et al. 2022). Under this circumstances, the amount total biomass stock at each plot may be affected by the survival rate. In general, large differences in biomass stock across species were found on the three tested sites. Overall, larger B_{CT} was observed at the wet (Huffman) site, followed by the intermediate (Underhill) and the dry (Campbell) site. Stands growing under larger water availability averaged 60% more B_{CT} accumulation than the dry site.

A similar trend in B_{CT} across sites was observed for GF, GS, WH, POC, WRSP, and SSP: these species had much larger biomass accumulation in the wet (Huffman) and intermediate (Underhill) site than the dry (Campbell). While GF, GS, POC are humid-adapted trees, WH thrives in humid Pacific Northwest regions (Burns, and Honkala, 1990). Although the B_{CT} of GF, GS, and WH was greater than all other species at the wet (Huffman) and intermediate (Underhill) sites, they showed a sharp decline when growing at the dry (Campbell), a site characterized by higher

VPD, PET and water deficit. This result suggests a very low drought tolerance of these three species. Moreover, McCulloh et al. (2014) reported higher vulnerability to cavitation of GF and WH, when compared to DF. In the same direction, Emmingham (2005) classified GF as medium-low drought tolerant species. SSP and WRSP showed a similar response of sharp decrease in B_{CT} when growing at the site with large water deficit, but storing half the biomass compared to GF, GS and WH. Abundant moisture availability and the absence of a severe summer drought are necessary for the development of SSP (Wilbur et al., 1979).

While GF, GS, POC, WH, WRSP, and SSP showed largest B_{CT} at the wet (Huffman) site, WVPP, and WWP showed larger B_{CT} at the intermediate (Underhill) site, with small differences with the dry (Campbell) site. Moreover, WVPP showed larger B_{CT} at the dry (Campbell) site. Concurrent with our findings, Emmingham (2005) classified WVPP as highly drought tolerant species. WWP showed similar survival across sites, while WVPP showed increased mortality at the wet site (Huffman), indicating that the species may be more susceptible to an excess of water.

A different trend was observed for DF, LC, and WRC. These species showed relatively stable B_{CT} across sites, although the magnitude was different for each species, with DF being the species with larger B_{CT}. This response shows that these species can grow in a wide range of climatic conditions. When comparing biomass stock of DF and WRC across sites, Flamenco et al., (2019) reported large differences in aboveground biomass stock between the species, but reduced differences between sites (Oregon's central Coast Range to Oregon's Cascade foothills).

Similar to B_{CT}, there was a general trend that lower B_{AG} was observed at the site with reduced water availability. Ecosystem biomass was largely controlled by planted trees except for the GF plot at the dry (Campbell) site, which had a large proportion of volunteer/midstory trees, and the UP (naturally regenerated) plots at all sites, where understory vegetation and a midstory of hardwoods and conifer volunteer trees accounted for most of the aboveground biomass stock across the three sites. When comparing B_{AG} between UP (naturally regenerated) and all planted plots, the biomass of UP (naturally regenerated) plots corresponded to 7-24% at the wet (Huffman) site, 7-27% at the intermediate (Underhill) site, and 6-39% at the dry (Campbell) site. The composition of the UP (naturally regenerated) plots also differed across sites, while at the wet (Huffman) and intermediate (Underhill) sites the UP plots were dominated by naturally-regenerated Douglas-fir (see Figure 2.5), at the dry (Campbell) site it was dominated by Oregon white oak trees, a species well adapted to hot, dry conditions, commonly found close to the Willamette Valley. The positive relationship between overstory BA and B_{AG} was shared by all species and sites, more biomass stock where trees are larger (Balderos 2013) with the exception of GS, where for the same BA, GS stands showed reduced biomass than the other species. This response is an effect of low wood density of GS (Piirto 1986), high bark thickness with low bark density (Bauer et al. 2010; Bold et al. 2020).

Although most of the plots showed little B_M, averaging to 1-2% of B_{AG} at the wet (Huffman) and intermediate (Underhill) sites, it accounted for 8% of B_{AG} at the dry (Campbell). Moreover, B_M represented 15 and 45% of B_{AG} for POC and GF. Reduced growth and larger mortality promoted the presence of midstory at the dry (Campbell) site. The negative exponential relationship between overstory BA and B_M summarizes that effect. For BA>40 m^2 ha^{-1}, negligible B_M was observed. A similar trend was reported by Flamenco et al. (2019).

It is expected that increased light availability, due to lower overstory leaf area and more opened canopies, should favor the presence of understory. At the wet (Huffman) site, B_U accounted for less than 1% of B_{AG}, and the GF, POC, SSP and WRSP plots did not have any understory. That fractional biomass increased to 1.4 and 5.6% at the intermediate (Underhill) and the dry

(Campbell) sites, respectively. The largest B_U, that accounted for 19% of B_{AG}, was observed at WH growing at the dry (Campbell) site, a site where WH showed a high mortality and reduced growth. The negative exponential relationship between overstory BA and B_U reflects that effect. For BA>40 m^2 ha^{-1}, negligible understory biomass was observed.

The species composition of the understory also changed across sites. At the wet (Huffman) and intermediate (Underhill) sites, the understory (if any) was dominated by ferns and brambles, while at the dry (Campbell) site, the understory was dominated by graminoids, and in a lesser extent, brambles. It is worth noting that the understory at the WH plot at the dry (Campbell) site (the plot with largest B_U), was largely dominated by ferns and brambles. It is possible that interactions occur between the overstory and the understory, which may allow the presence of certain species to germinate and grow depending on the growth dynamics and canopy structure of the overstory (Smith 2011). Further research is needed in this area.

Even though the wet (Huffman) site had larger B_{FF} (10.9 Mg ha^{-1} across all species), while the intermediate (Underhill) and dry (Campbell) sites was lower forest floor biomass (8 and 6 Mg ha^{-1}, respectively), there was no relationship between overstory BA and B_{FF}. Nevertheless, our results are agreement with Edmonds (1991), who reported the highest forest floor accumulation in productive, cooler, and wetter coastal regions, and the lowest accumulations in less productive, warmer, and drier inland regions. While most of the species showed decreased B_{FF} with increasing water deficit, WWP and WVPP showed a different trend, with no reduction, or even increasing, B_{FF} with increasing water deficit. WVPP showed the largest B_{FF} at both, the intermediate (Underhill) and dry (Campbell) sites, while SSP and WRSP showed the largest B_{FF} at the wet (Huffman) site. Differences in foliage production and turnover (Hikosaka 2005), and needle chemistry, which affects foliage decay (Chae et al., 2019), may help to explain the results observed.

The soil contained a large amount of biomass as soil organic matter (Flamenco et al., 2019). In this study, the ratio of root biomass is 22 % of tree component each plot across the sites that has been reported to account for 10-40% of total tree biomass (Santantonio et al., 1977), and root to aboveground biomass ratios is 22% (Chojnacky et al., 2014). In our study, SOMC accounted for more the 40% of B_E (the sum of B_{AG} and SOMC). Results from our study agree with estimates from U.S. Forest Service's Forest Inventory and Analysis (FIA) Program, which concluded that about half of Oregon's stored forest carbon is found belowground in soil. Soil organic matter range is between 46% and 94% of B_E at each plot across the sites. Nevertheless, the lack of relationship between SOMC and B_E across the sites implies that no effect (detrimental or incremental) exists between planted conifer forests and soil organic matter content. Additional research is needed to better understand site and species interactions in that relationship. Overall, across the sites, the wet (Huffman) site had the highest B_E and SOMC, followed by the intermediate (Underhill) and dry (Campbell) site (Figure 2.10). Our findings are agreement with other reports that concluded that as mean annual precipitation increase, soil organic matter levels increase, and increasing soil moisture result in greater biomass accumulation (Bot and Benites 2005). In terms of soil depth distribution, depth of 0-15 cm had higher concentration and amount of soil organic matter comparing the other depths across the sites, which may be affected by the contribution of leaf dropping and roots on the surface (Foth 1978).

2.5 Conclusions

Whole ecosystem tree biomass stock of 11 species varies by species and site by site. While the amount of biomass stock of WH, GF, GS, WRSP, and SSP declined with decreasing water availability from wet to dry sites, WVPP and WWP had an opposite trend. The amount of DF, LC, WRC biomass was the most stable across the three sites. In terms of ecosystem biomass stock, the wet site had highest biomass accumulation, followed by the intermediate and dry sites. The distribution of plant-derived biomass indicated that biomass stock was largely controlled by planted trees. When SOMC was included into the ecosystem biomass stock, belowground biomass was larger than aboveground biomass stock.

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Chapter 3 Net Primary Productivity and Growth Efficiency of 11 Conifer Species across a Gradient Water Deficit in Western Oregon.

3.1 Introduction

Oregon, which has some of the most productive forests in the world, has the highest forest carbon sequestration among western states and one the highest in the country (OFRI, n.d). Net primary production (NPP) represents the amount of biomass fixed by plants through photosynthesis each year. As NPP plays a significant role in the global carbon budget and carbon sequestration, developing a better understanding of the relationship between forest species and ecosystems' leaf area index and NPP is crucial (Clark et al., 2001). Estimates of NPP can provide valuable information for land management, conservation planning, and natural resource management decisions, as they help identify regions where ecosystem productivity is high and where interventions may be needed to improve productivity.

Evergreen forests exhibit high biomass accumulation, which is attributed to their significantly higher annual aboveground net primary productivity (ANPP) relative to broadleaf forests (Waring, 1979). ANPP has been shown to be strongly influenced by the amount of foliage in a given ecosystem. This is because the interception of light by photosynthetic material, which is largely concentrated in the foliage, is the fundamental means of dry matter production in most plants. It's important to note, however, that ANPP is also influenced by a wide range of other factors, such as temperature, water availability, nutrient availability, the activity of decomposers, and the intrinsic capacity of different tree species to transform the amount of light intercepted into biomass, which is a function of the amount of foliage and the efficiency to fix carbon per unit light intercepted by the canopy of the trees. Therefore, to fully understand ANPP in a given ecosystem, it's important to consider all of the factors that may be influencing it. Furthermore, in analyzing ANPP of forests, it is important to consider the contributions of all ecosystem components, not just the overstory trees. For example, understory vegetation such as shrubs and herbaceous plants, as well midstory vegetation which includes naturally regenerated tress that grow under the canopy of the overstory, can significantly contribute to the overall ANPP of the whole forest ecosystem.

Evidence from multiple studies suggest that ongoing changes in ANPP can be attributed, at least in part, to climate change (Gholz, 1982; Restaino 2016; Yuan et al., 2021). Climate change can impact forest productivity in several ways, including alterations in temperature, precipitation patterns, and extreme weather events. For example, increased temperatures may lead to higher rates of evapotranspiration, which can decrease water availability for plants and ultimately reduce ANPP. On the other hand, increased precipitation may stimulate ANPP in some regions. Additionally, climate change can also cause shifts in the timing of seasonal events, such as budburst and leaf senescence, which can impact the duration of the growing season and ultimately affect productivity (Von Blon 2022). Changes in the frequency and intensity of disturbances such as fires, droughts, and insect outbreaks, can also have significant impacts on forest ANPP.

The estimation of ANPP is important for the assessment of carbon balance and for gaining a better understanding of the response of economically and ecologically valuable species to water deficit gradients in ecosystem production, both on a global and regional scale. Accurately quantifying ANPP allows us to assess the capacity of ecosystems to remove CO_2 from the atmosphere through photosynthesis and to better understand the carbon cycle, which is critical for informing climate change mitigation strategies. Additionally, understanding how water availability affects ANPP is important for predicting the impacts of climate change on ecosystem productivity and identifying regions that may be particularly vulnerable to future water stress.

Leaf area index (LAI, m^2 m^{-2}), the projected green leaf area per unit ground area, is a crucial measurement for describing and comparing the composition and productivity of plant and forest ecosystems (Kram, 1998; Thomas and Winner, 2000). Leaf area is the surface over which photosynthesis and transpiration occur, making LAI a critical measurement for characterizing NPP, transpiration, water use, and stem wood growth. As such, LAI is a valuable metric for ecophysiologists, modelers, and natural resource managers (Gholz, 1982; Waring, 1983). Even in drier zones in western Oregon, the LAI of conifer forests is significant (Grier, and Running, 1977). Studies show that LAI may be affected by annual precipitation changes, climatic differences, the amount of light, and species variation (Jose et al., 1997). Furthermore, growth efficiency (GE), defined as the ratio of NPP to projected leaf area, is a useful metric for describing forest vigor and growth processes (Waring et al. 1980 and 2016). Some researchers have investigated the growth efficiency of individual trees for various species and stand conditions (Stancioiu, 2006). Climate, soil quality, species composition, and management practices all have an impact on growth efficiency. When nitrogen and phosphorus fertilizers were applied annually to a Norway spruce plantation, growth efficiency increased (Waring 1983).

This chapter compares carbon sequestration (using ANPP) of 11 conifer species across a gradient of water deficit in three sites in western Oregon. The study also compares estimates of LAI and GE across species and sites, with the aim to evaluate their sensitivity to climate variability. This information would help in predicting the response of forests to climate change and in making more informed management decisions in order to improve health, productivity and sustainability of PNW forests.

3.2 Method

3.2.1 Site Descriptions

The species introduction study was tested in three sites owned by Starker Forests Inc., covering a gradient of water deficit throughout the company's properties from the center of the Coast Range to the fringe of the Willamette Valley in western Oregon. The sites are classified as wet (Huffman), intermediate (Underhill), and dry (Campbell) (Figure 3.1).

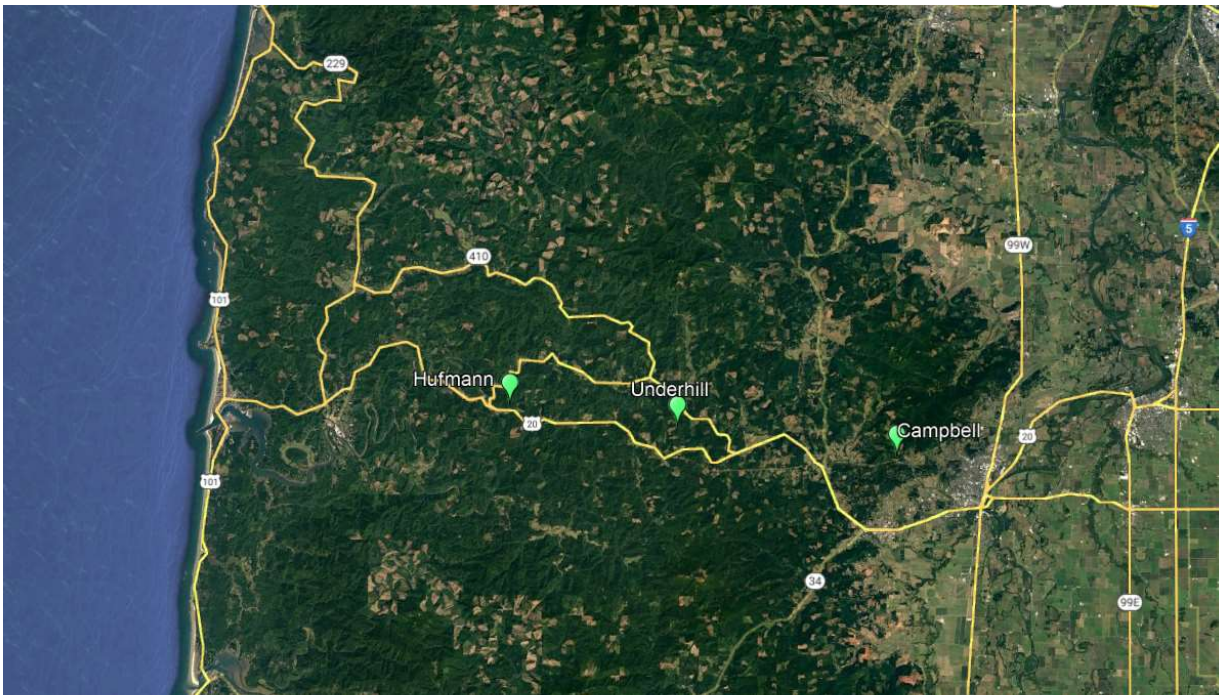

Figure 3.1. Locations of the wet (Huffman), Intermediate (Underhill), and Dry (Campbell) study sites in Western Oregon, USA (Google Earth).

The wettest site is situated at 44°37'58.0"N 123°45'17.3"W, in the central coastal range, close to Eddyville, OR. Based on historical PRISM data, the site has the lowest average annual potential evapotranspiration (800 mm) and the highest average annual rainfall (2,000 mm) of the three sites (PRISM Climate Group, n.d.). The area has well-drained and fine-loamy soils. The site property name is Huffman, so from here and after will be referred wet (Huffman) site.

The intermediate is situated at 44°37'00.2"N 123°34'48.6"W, close to Blodgett, OR. Based on historical PRISM data, the site has the intermediate average annual precipitation of 1,700 mm and the intermediate average annual potential evapotranspiration of 850 mm. The area has well-drained, and silty-clay loam soil. The site property name is Underhill, so from here and after this study and will be referred to as the Underhill (intermediate) site.

The driest site is located closed to Corvallis, OR, at 44°35'42.6"N 123°21'07.3"W. Based on historical PRISM data, the site has the lowest average annual precipitation of 1,300 mm and highest average annual potential evapotranspiration of 940 mm among the three sites. The area has well-drained, and silty clay soils. The site property name is Campbell, so from here and after this study will be referred dry (Campbell) site.

3.2.2 Species and stock type

A species introduction study was established by Starker Forests Inc. in 1996, with the aim to compare the productivity of 12 tree species across a gradient water deficit in western Orgon (from the Coast Range to the western foothills of the Willamette Valley). The species include coastal Douglas-fir (DF), grand fir (GF), the giant sequoia (GS), Japanese larch, Leyland cypress (LC), Port-Orford-cedar (POC), Sitka spruce (SSP), western hemlock (WH), western redcedar (WRC), a weevil resistant variety of Sitka spruce (WRSP), Willamette Valley ponderosa pine (WVPP), and western white pine (WWP). The Japanese larch (UP) plots had nearly 100% mortality at all three sites and it was excluded from this study (Figure 3.2).

Figure 3.2. Plots layout at the wet (Huffman, left), intermediate (Underhill, center), and dry (Campbell, right) sites. Species description can be found in Table 2.1.

At each site, 12 plots were laid out measuring approximately 51 x 51 m each (Figure 3.2). Before planting, a winged sub-soiler was used to sub-soil the plots after clearing them of vegetation. During the first two years of growth, herbicide applications were done to manage competing vegetation. Each plot was planted at a 3 x 3 m spacing with a single tree species which was randomly assigned in 1996.

The trees were purchased on the open market from various nurseries around the region, including Champion, Georgia Pacific, Louisiana Pacific, Pelton and Sylvan Options nurseries (Table 2.1). All seedlings were grown as Styro-5 or 6 stock type. All of the newly planted seedlings were protected from animal browsing with vexar tubing. Because seedlings for all species were not available in sufficient quantities in 1996, four species were planted in 1997 and one species was planted 1998 (Table 3.1).

Table 3.1. List of species, including planting year and nursery that produced the seedlings.

Species	Species ID	Year Planted	Nursery
Douglas-fir	DF	1996	Georgia Pacific
Grand Fir	GF	1996	Champion
Giant Sequoia	GS	1997	Louisiana Pacific
Leland Cypress	LC	1997	Sylvan Options
Japanese larch	JL	1996	Georgia Pacific
Port Orford Cedar	POC	1997	Louisiana Pacific
Sitka Spruce	SSP	1997	Louisiana Pacific
Weevil Resistant Sitka Spruce	WRSS	1998	Pelton
Western hemlock	WH	1996	Microseed
Western redcedar	WRC	1996	Champion
Western White Pine (Blister Rust Resistant)	WWP	1996	Champion
Willamette Valley Ponderosa Pine	WVPP	1996	Qualitree

3.2.3 Weather measurement

The weather station was installed in a clear place at each site to measure air temperature, solar radiation (CS301, Apogee Instruments), precipitation (TE525MM, Texas Electronics), and relative humidity (RH; HMP60, Vaisala). A datalogger took weather readings every 30 seconds and averaged them every 30 minutes (CR300, Campbell Scientific). Additionally, PRISM data (source) was used to get estimates of past daily and monthly averages of climate variables in a given area, such as mean and minimum precipitation, and maximum temperature, and minimum maximum vapor pressure deficit. The on-site weather station was used to calibrate past Prism data through a linear regression approach, which allowed for more accurate data when completing missing weather readings and for historical data.

3.2.4 Litterfall

At each study plot, five 0.5 m^2 circular litterfall traps were randomly installed in March 2021 using plastic tubing and mesh net. Litterfall was collected every two months between March 2021 and March 2022, and dried at 74°C for a minimum of 72 hours in a drying oven. After that, dry litter material was divided into four categories: needles from crop species (NF_{CT}), foliage from all other vegetation (including midstory and understory) (LF_V), woody material from all species, plus miscellaneous (LF_M). An OHAUS NV4101(g) scale was used to determine the dry mass of each litterfall component.

3.2.5 Leaf Area Index

Measurements of LAI were collected during the period of peak leaf area in late July and early September 2021 using a Ceptometer (LP-80, Decagon Devices). Measurements were taken within two hours of solar noon on cloudless days. Above canopy photosynthetically active radiation (PAR) was measured with a PAR sensor (SQ-521, Apogee Instruments) connected to datalogger (H21-USB, ONSET Computer Corporation, Bourne, MA), which was placed in a nearby clearcut approximately 100-300 m from the study site boundary at a height of 1-2 m and programmed to collect PAR data every 10 seconds. The below canopy measurements were taken at breast height with the Ceptometer pointed towards the plot center. Prior to sampling each plot, the time (Hour: Minute: Second) was recorded using a wristwatch that was calibrated with the above canopy datalogger. A total of 90 measurements were collected in a series of nine line transects inside each study plot. The best effort was made to collect subsamples evenly and randomly, without any discrimination. After the last measurement, the subsamples were averaged in the field using the Ceptometer's internal processor and recorded, along with a timestamp indicating the end of plot subsampling. The same procedure was used over all study plots in all three sites.

Back at the lab, above canopy PAR data was downloaded from the datalogger and matched with below canopy data based on the below canopy timestamp. LAI was calculated using an inversion of Monsi and Saeki's Beers - Lambert equation expressed below:

$$LAI = \frac{-\ln\left(\frac{I}{Io}\right)}{0.52}$$

where LAI (m^2 m^{-2}) is the effective plot projected leaf area index, I is below canopy PAR (µmol m^{-2} s^{-1}), Io is above canopy PAR (µmol m^{-2} s^{-1}) and 0.52 is the recommended light extinction coefficient (*k*) value (Pierce and Running, 1988).

3.2.6 Crop Tree Aboveground Net Primary Productivity ($ANPP_{CT}$)

In winter 2021 and 2022, each study plot was inventoried. Diameter at breast height (DBH, mm) and height (m) of all living trees were measured with metric diameter tapes and Haglof Vertex IV, respectively. Total aboveground biomass (kg) of each tree was estimated using species-specific (or genius specific) biomass equations reported in literature (see Chapter 2, Table 2.3). ANPP of crop trees ($ANPP_{CT}$; Mg ha^{-1} $year^{-1}$) was computed as the change in stand-level biomass between 2022 and 2021 plus the sum of LF_{F-CT} in litterfall traps between March 2021 and March 2022.

3.2.7 Midstory Aboveground Net Primary Productivity ($ANPP_M$)

All non-crop trees with a DBH of greater than 2.5 cm, were considered to be a volunteer trees or part of the midstory of each plot. Midstory inventory measurement was measured in July of 2021 and 2022. Total aboveground biomass of each midstory/volunteer tree (kg) was estimated using species-specific biomass equations reported in the literature (see Chapter 2). ANPP of midstory/volunteer trees ($ANPP_M$; Mg ha^{-1} year^{-1}) was computed as the change in stand-level biomass of all midstory/volunteer between 2022 and 2021 plus the sum of $LF_{F\text{-}V}$ in litterfall traps between March 2021 and March 2022.

3.2.8 Understory Aboveground Net Primary Productivity ($ANPP_U$)

During summer of years 2021 and 2022 assessments of understory vegetation cover (%) and height (cm) by growth form (forbs, fern, graminoids, shrubs, and brambles) were carried out in five 1 x 1 m vegetation survey subplots per plot. Application of biomass equations for each growth form reported by Guevara et al. (2021) allowed for the estimation of understory vegetation biomass (Mg ha^{-1}) for each study plot, using cover or a combination of cover and height. ANPP of understory vegetation ($ANPP_U$; Mg ha^{-1} year^{-1}) was computed as the change in biomass of the understory between 2022 and 2021.

3.2.9 Ecosystem Aboveground Net Primary Productivity ($ANPP_E$)

Ecosystem ANNP ($ANNP_E$, Mg ha^{-1} year^{-1}) was determined as the sum of Crop tree ANPP, midstory ANPP, and understory ANPP: $ANPP_E = ANPP_{CT} + ANPP_M + ANPP_U$.

3.2.10 Growth Efficiency

Growth efficiency (GE; Mg m^{-2} year^{-1}) was computed as the ratio of $ANPP_{CT}$ (Mg ha^{-1} year^{-1}) to projected leaf area (m^2 ha^{-1}).

3.3 Statistical Analysis

As the study plots for each species are not replicated within each site, a formal statistical analysis could not be done to test differences in ANPP between tested species. However, an ANOVA test was used to test differences in $ANPP_E$, $ANPP_{CT}$, $ANPP_M$ and $ANPP_U$ across the sites, using the Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC). Linear and non-linear model fitting was used to analyze the relationships between BA and LAI with ANPP. Sigma Plot version 14.0 (Systat Software, Inc. San Jose, CA) was used to create all figures.

3.4 Results

3.4.1 Litterfall

Total litterfall (LF, Mg ha^{-1} year^{-1}) was composed of crop tree needlefall (NF_{CT}, Mg ha^{-1} year^{-1}), litterfall of other vegetation (LF_V, Mg ha^{-1} year^{-1}) and miscellaneous litterfall ((LF_M, Mg ha^{-1} year^{-1}). Across all species, the wet (Huffman) site showed the largest NF_{CT}, averaging 4.9 Mg ha^{-1} year^{-1}. The intermediate (Underhill) site showed the second-highest NF_{CT}, averaging 4.4 Mg ha^{-1} year^{-1} (10.2% less than the wet site), followed by the dry (Campbell) site, which was 48.6% lower than the wet site (Figure 3.3). Across all sites, LC growing at the wet (Huffman) site showed the largest NF_{CT} (7.19 Mg ha^{-1} year^{-1}), while WRSP growing at the dry (Campbell) site showed the lowest average annual NF_{CT} (0.9 Mg ha^{-1} year^{-1}). Although the amount of LF of most species has a decreasing trend from wet to dry sites, the annual LF of WWP had the opposite trend.

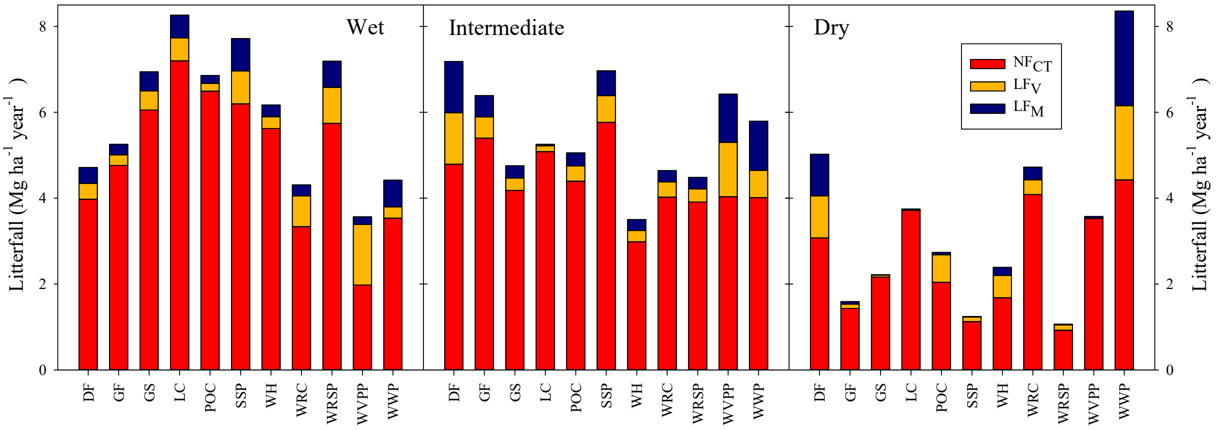

Figure 3.3. Annual litterfall (Mg ha^{-1} year^{-1}) between March 2021 and March 2022 for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites, including crop tree needles (NF_{CT}), other vegetation foliage (LF_V), and miscellaneous (LF_M). Species description can be found in Table 3.1.

When looking at the seasonal dynamics of monthly NF_{CT}, there was not a unique pattern across all species and sites (Figure 3.4). Some species, as WH, peaked in late summer (August), while other species, as WRC, peaked late fall (Oct-Dec). Interestingly, SSP and WRSP peaked in early spring (Mar-Apr) at the wet (Huffman) and dry (Campbell) sites. A shift in NF_{CT} timing was observed for LC, WWP, and DF, which peaked between Aug-Oct at the wet (Huffman) and intermediate (Underhill) sites, but in late summer at the dry (Campbell) site.

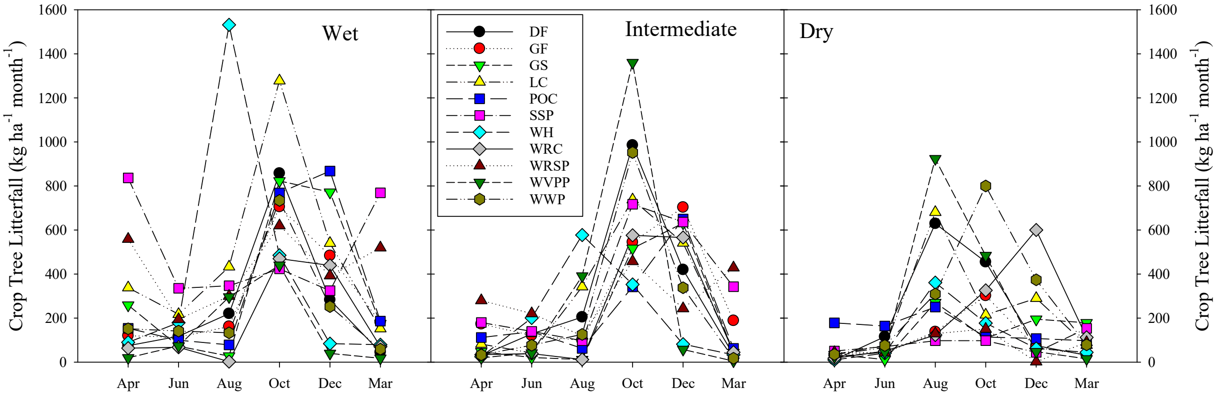

Figure 3.4. Monthly crop tree needlefall (kg ha^{-1} month^{-1}) between March 2021 and March 2022 for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 3.1.

3.4.2 Leaf Area Index

Across all species, the wet (Huffman) site showed the largest projected LAI, averaging 10.3 m^2 m^{-2}. The intermediate (Underhill) site showed the second-highest LAI, averaging 7.3 m^2 m^{-2} (29.1% less than the wet site), followed by the dry (Campbell) site that averaged 3.2 m^2 m^{-2} (69 % less than the wet site) (Figure 3.5). Across all sites, GF, POC, SSP and WRSP growing at the wet (Huffman) site showed the greatest LAI (over 14 m^2 m^{-2}), while GF, POC, SSP and WRSP growing at the dry (Campbell) site showed the lowest, averaging less than 3 m^2 m^{-2}. Although the amount of LAI of most species had a decreasing trend from wet to dry sites, the average LAI of LC was relatively stable across the sites.

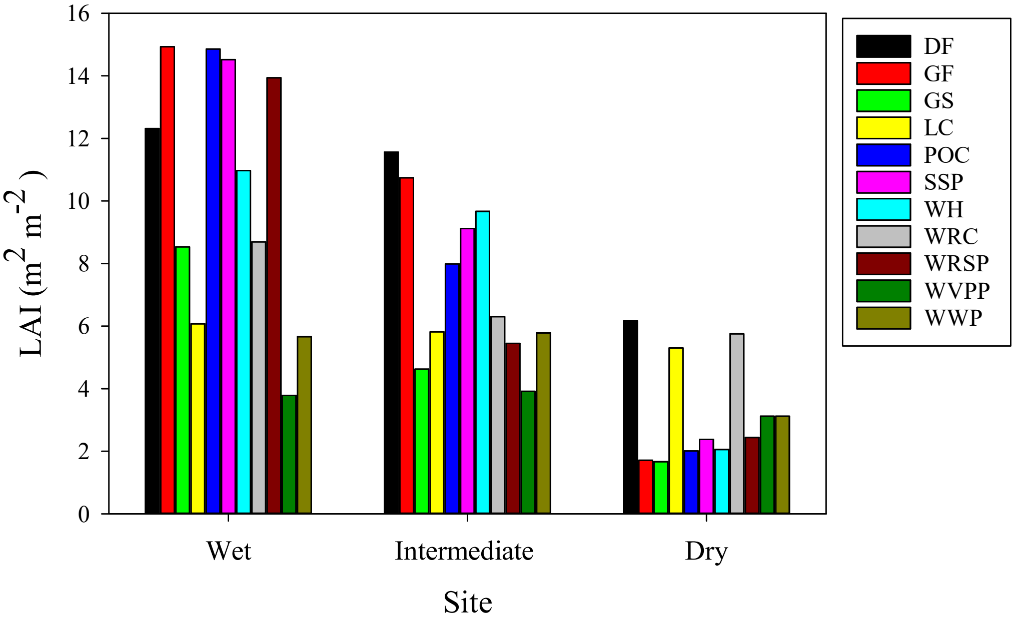

Figure 3.5. Projected Leaf Area Index (LAI, m^2 m^{-2}) between June and August 2022 for stands planted with different conifer species across the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 3.1.

3.4.3 Crop Tree Aboveground Net Primary Productivity

Across all species, the wet (Huffman) site showed the largest $ANPP_{CT}$, averaging 17.2 Mg ha^{-1} $year^{-1}$. The intermediate (Underhill) site showed the second-highest $ANPP_{CT}$, averaging 15.3 Mg ha^{-1} $year^{-1}$ (10.9 % lower than the wet site), followed by the dry (Campbell) site that averaged 8.4 Mg ha^{-1} $year^{-1}$ (51.2% less than the wet site) (Figure 3.6). When observing $ANPP_{CT}$ of each species across sites, the highest $ANPP_{CT}$ was observed for WH at the wet (Huffman) site (30.2 Mg ha^{-1} $year^{-1}$). When growing at the dry (Campbell) site, the same species showed a drastic decrease in $ANPP_{CT}$, having only 10.6% of what was observed at the wet (Huffman) site. Other species (GF, GS, SSP, WRSP, and POC) also showed a reduction in $ANPP_{CT}$ from wet to dry sites, but this reduction was less drastic than WH. Nevertheless, $ANPP_{CT}$ of WVPP and WWP showed a different trend, increasing from the wet to dry site by 85% and 35%, respectively. DF, LC, WRC, on the other hand, showed a relatively stable $ANPP_{CT}$ across sites.

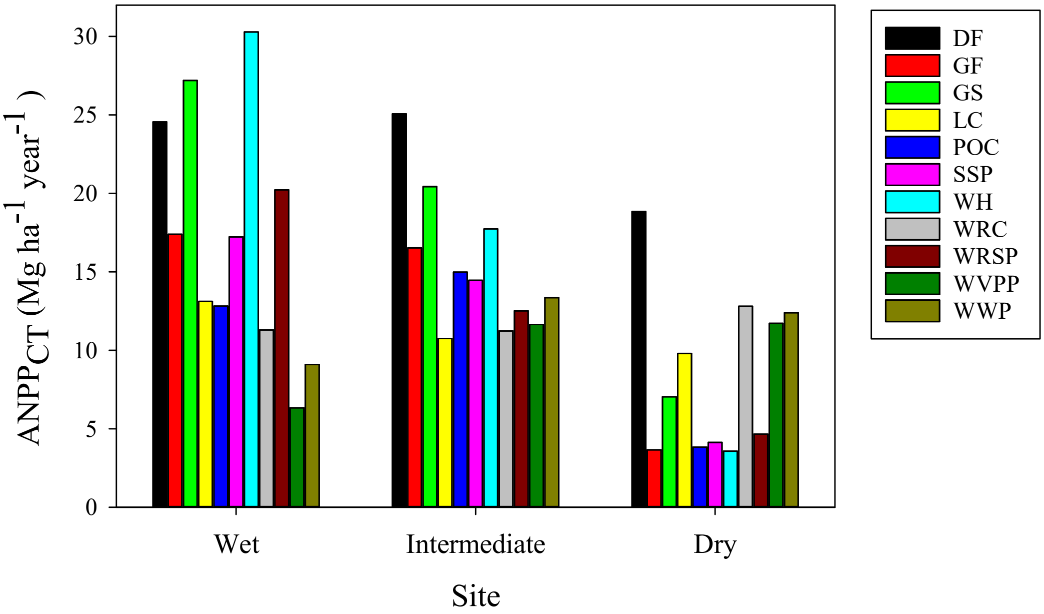

Figure 3.6. Crop tree net primary productivity ($ANNP_{CT}$; Mg ha^{-1} year^{-1}) between 2021 and 2022 for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 3.1.

3.4.4 Midstory Aboveground Net Primary Productivity

Across all species, the dry (Campbell) site showed the largest $ANPP_M$, averaging 6.1 Mg ha^{-1} year^{-1}. The wet (Huffman) site showed the second-highest $ANPP_M$, averaging 4.5 Mg ha^{-1} year^{-1} (27.2 % lower than the dry site), followed by the intermediate (Underhill) site that averaged 0.2 Mg ha^{-1} year^{-1}, (55.5% less than the dry site) (Figure 3.7). When observing $ANPP_M$ of each species across sites, the highest $ANPP_M$ was observed for GF at the dry (Campbell) site (2.5 Mg ha^{-1} year^{-1}), followed by WVPP at wet (Huffman) site (2.0 Mg ha^{-1}year^{-1}). It is important to remark that even though most plots had some midstory and volunteer trees inside, there were no such type of vegetation in DF, GF, GS, LC, and POC plots at the wet (Huffman) site. In addition, even though most plots had positive $ANPP_M$, negative $ANPP_M$ was observed for WRC at the dry (Campbell) site (-0.4 Mg ha^{-1} year^{-1}). The distribition of $ANPP_M$ for each species in each plot was shown appendix 8.

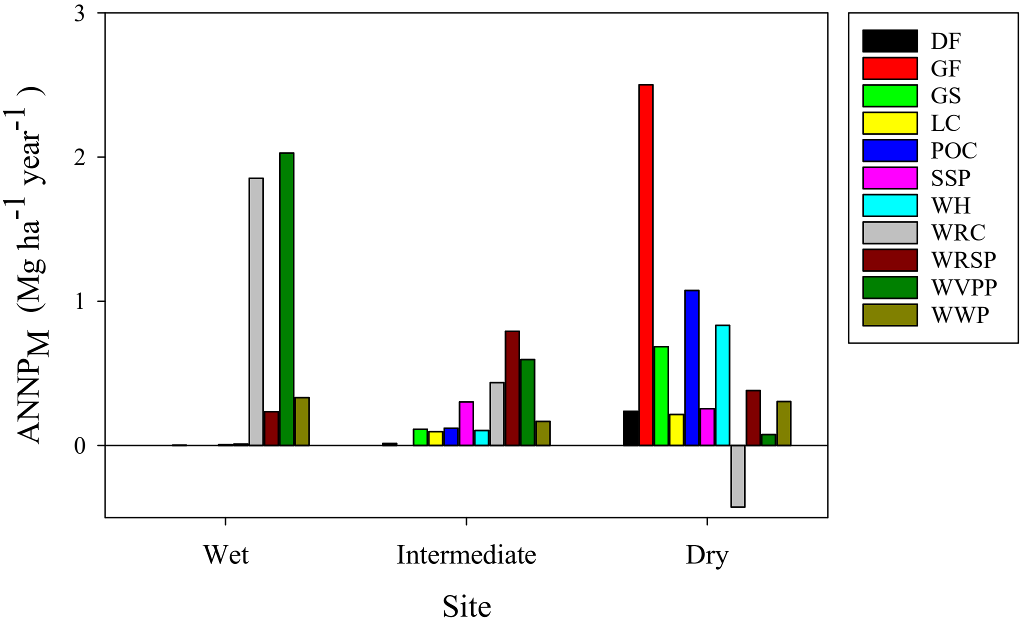

Figure 3.7. Midstory net primary productivity ($ANPP_M$; Mg ha^{-1} year^{-1}) between 2021 and 2022 for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 3.1.

3.4.5 Understory Aboveground Net Primary Productivity

Across all species, the dry (Campbell) site showed the largest $ANPP_U$, averaging 0.46 Mg ha^{-1} year^{-1}. The intermediate (Underhill) site showed the second-highest $ANPP_U$, averaging 0.31 Mg ha^{-1} year^{-1} (32.6 % lower than the dry site), followed by the wet (Huffman) site with -1.1 Mg ha^{-1} year^{-1} (Figure 3.8). When observing $ANPP_U$ of each species across sites, the highest $ANPP_U$ was observed for SSP at the dry (Campbell) site (3.8 Mg ha^{-1} year^{-1}), and the lowest $ANPP_U$ was observed for WVPP at the wet (Huffman) site (-4.6 Mg ha^{-1} year^{-1}). WRC, WVPP, and WWP groving at the wet (Huffman) ste had negative $ANPP_U$ (-0.3, -4.6,-2.17 Mg ha^{-1} year^{-1}), they had positive ANPP$_U$ at the dry (Campbell) site (0.4, 0.5,2.3 Mg ha^{-1} year^{-1}, respectively). It is important to remark that there was no understory vegetation in SSP and WRSP plots at the wet (Huffman) site. The distribition of ANPP$_u$ in terms of each grow habit in each plot was shown appendix 7.

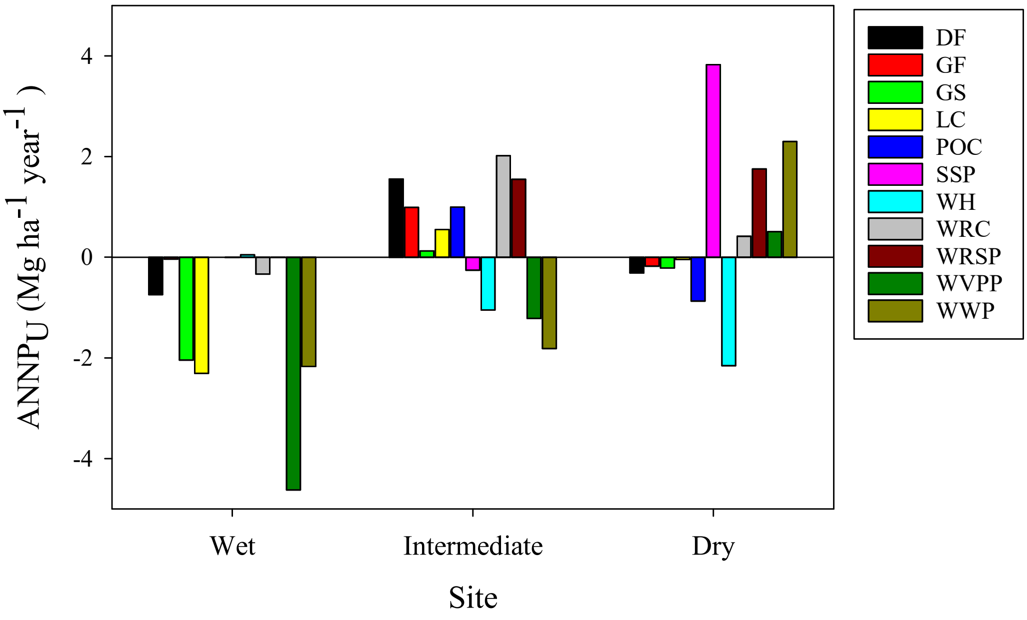

Figure 3.8. Understory net primary productivity (ANPP$_U$; Mg ha^{-1} year^{-1}) between 2021 and 2022 for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 3.1.

3.4.6 Ecosystem Aboveground Net Primary Productivity

Across all species, the wet (Huffman) site showed the largest ANPP$_E$, averaging 16.5 Mg ha^{-1} year^{-1}. The intermediate (Underhill) site showed the second-highest ANPP$_E$, averaging 15.8 Mg ha^{-1} year^{-1} (4.1 % lower than the wet site), followed by the dry (Campbell) site that averaged 9.4 Mg ha^{-1} year^{-1} (43.0 % less than the wet site) (Figure 3.9). Even though ANPP$_{CT}$ accounted for most of ANNP$_E$, understory and midstory accounted negatively for about 69% of ANPP$_E$ at the WVVP plot at the wet (Huffman) site, and by about 58% of ANPP$_E$ at the WH plot at the dry

(Campbell) site. The majority of plots showed neutral or negative ANPP$_U$, ranging from -5 to 3 Mg ha^{-1} year^{-1}.

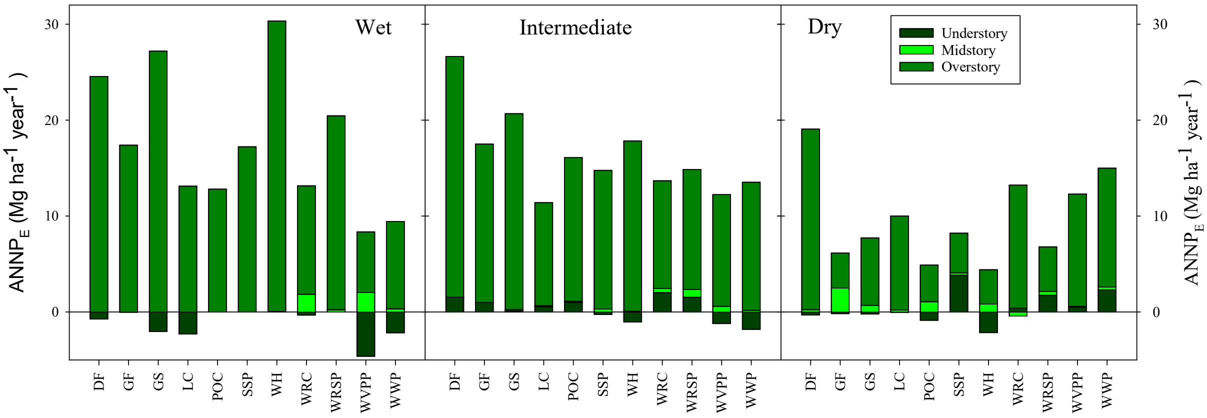

Figure 3.9. Average ANPP of all ecosystem components (ANPP$_E$, Mg ha^{-1} year^{-1}), including understory, midstory, overstory, for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 3.1.

3.4.7 Relationships between LAI, BA, and ANPP

The relationships between overstory BA and LAI (measured in year 2022), and ANPP$_T$ and ANPP$_M$ (measured between years 2021 and 2022) are shown in Figure 3.10. As the slope of the relationships between BA/LAI and ANPP$_T$/ANPP$_M$ were not different across the sites (P > 0.4), a single model was fitted for each case (Figure 3.11; Table 3.2). A sigmoidal model was fit for BA/LAI and ANPP$_{CT}$, and a power model was fit for BA or LAI and ANPP$_M$. Overall, a steep increase in ANPP$_{CT}$ was observed for BA between 20 and 50 m^2 ha^{-1} (about 0.4 Mg ha^{-1} year^{-1} ANPP$_{CT}$ increment per 1 m^2 ha^{-1} BA increment). On the other hand, for BA>60 m^2 ha^{-1}, only a small increment in ANPP$_{CT}$ was observed, which peaked at about 24 Mg ha^{-1} year^{-1}. A similar trend was observed for LAI, with a steep increase in ANPP$_{CT}$ for LAI between 4 and 8 m^2 m^{-2} (about 0.24 Mg ha-1 year^{-1} ANPP$_{CT}$ increment per 1 m^2 m^{-2} LAI increment). Conversely, a steep decrease in ANPP$_M$ was observed for BA between 10 and 40 m^2 ha^{-1} (about 0.035 Mg ha^{-1} year^{-1}

$ANPP_M$ reduction per 1 m^2 ha^{-1} BA increment). For the relationship between LAI and $ANPP_M$, there is a sharp decrease between 1 and 3 m^2 m^{-2} (about 0.002 Mg ha^{-1} $year^{-1}$ reduction per 1 m^2 m^{-2} increment), in general increasing LAI larger than about 4 m^2 m^{-2} is negligible. There was no relationship between BA or LAI and $ANNP_U$ (P= 0.4 and 0.6) respectively.

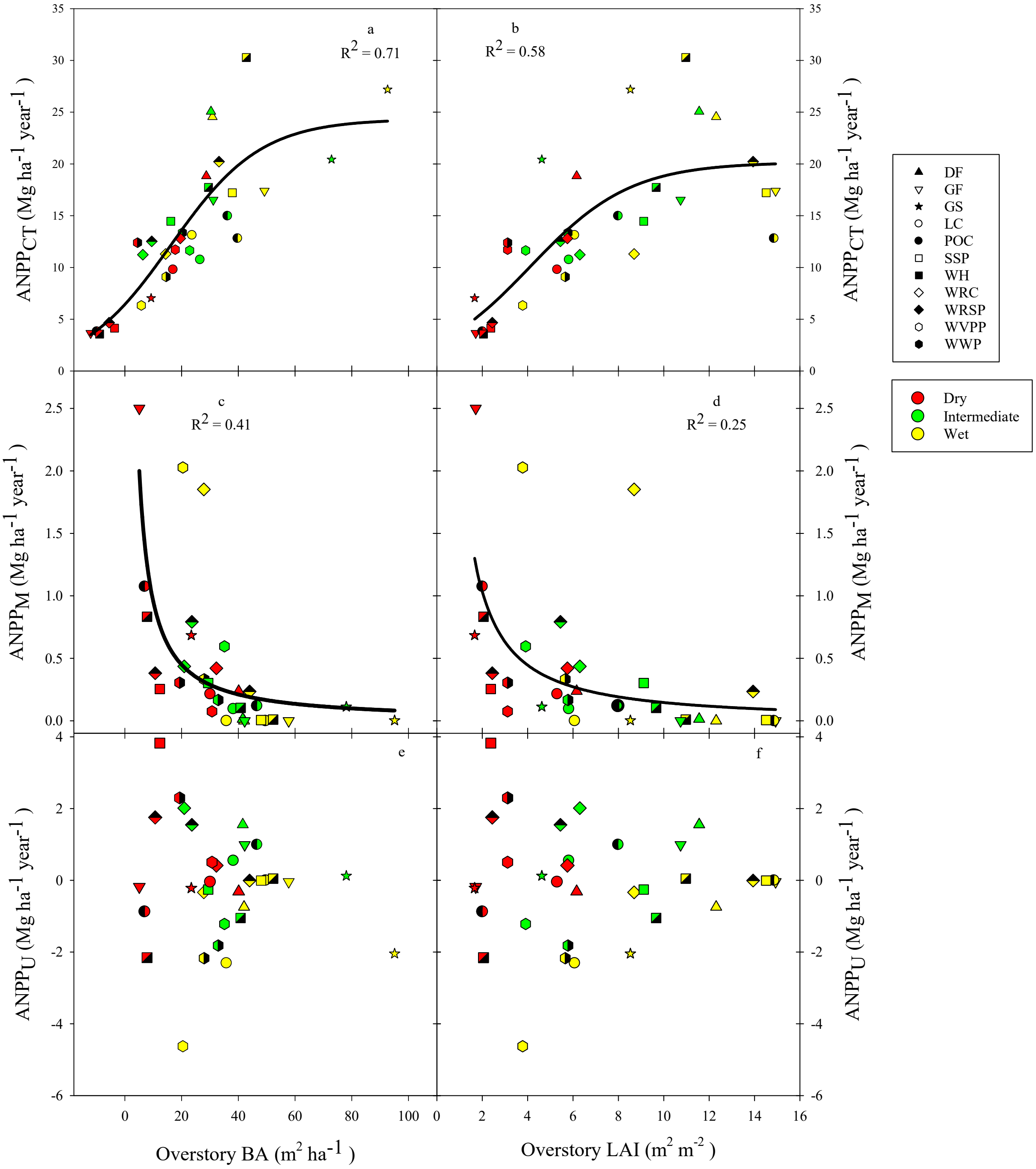

Figure 3.10. Relationship between overstory basal area (BA, m^2 ha^{-1}) (a, c, e) and projected leaf area index (LAI, m^2 m^{-2}) (b, d, f) of planted crop tress, and crop trees aboveground net primary productivity (ANPP$_{CT}$, Mg ha^{-1} year^{-1}) (a, c) and midstory aboveground net primary productivity (ANPP$_M$, Mg ha^{-1} year^{-1}) (c, d), understory aboveground net primary productivity (ANPP$_U$ Mg ha^{-1} year^{-1}) (e,f) for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 3.1.

Table 3.2 shows the parameter estimates and fit statistics for the relationships between BA and LAI, and $ANPP_{CT}$ and $ANPP_M$.

Table 3.2. Parameter estimates and fit statistics of the equations for predicting crop tree ($ANPP_{CT}$, Mg ha^{-1} year^{-1}) and midstory ($ANPP_M$, Mg ha^{-1} year^{-1}) ANPP from overstory basal area (BA, m^2 ha^{-1}) and projected leaf area index (LAI) for stands planted with conifer species across wet (Huffman) intermediate (Underhill), and dry (Campbell) sites in central Oregon.

Model	Parameter	Parameter Estimate	SE	R^2	RMSE
$ANPP_{CT} = \frac{a}{(1+\exp(-\frac{(BA-c)}{b}))}$	a	24.3288	2.786	0.71	3.626
	b	13.6325	3.3046		
	c	29.4235	4.1033		
$ANPP_{CT} = \frac{a}{(1+\exp(-\frac{(LAI-c)}{b}))}$	a	20.1553	1.9355	0.58	4.361
	b	2.2166	0.7688		
	c	4.1152	0.7217		
$ANPP_M = a*(BA^b)$	a	11.8056	0.483	0.41	0.468
	b	-1.0912	0.483		
$ANPP_M = a*(LAI^b)$	a	2.4119	0.546	0.25	0.529
	b	-1.2180	0.546		

3.4.8 Growth Efficiency

Across all species, the dry (Campbell) site showed the highest ANPP growth efficiency (GE, Mg m^{-2} year^{-1}), averaging, 2.6 Mg m^{-2} year^{-1}. The intermediate (Underhill) site showed the second-highest GE, averaging 2.2 Mg m^{-2} year^{-1} (15% lower than the dry site), followed by the wet (Underhill) site that averaged 1.7 Mg m^{-2} year^{-1} (30.7% less than the dry site) (Figure 3.11). When observing GE of each species, GS showed the highest GE, averaging 4 Mg m^{-2} year^{-1} across sites. WVPP and WWP at the dry and intermediate sites showed similar GE of 3.7 and 3.9 Mg m^{-2} year^{-1}, respectively. While most of species had decreasing trend from wet to dry conditions, LC and WH showed an opposite trend.

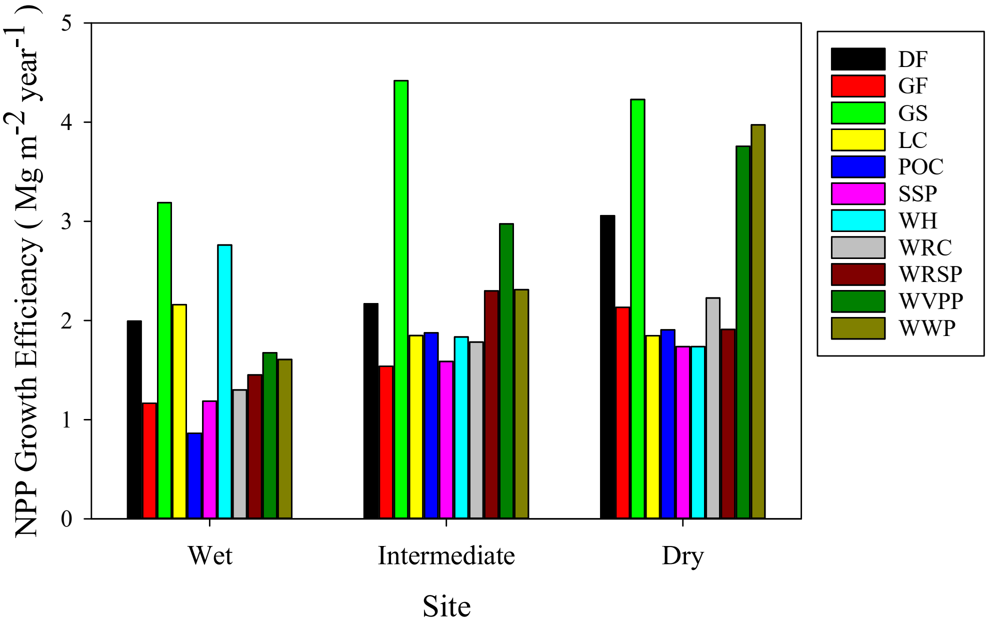

Figure 3.11. NPP Growth efficiency (Mg m^{-2} year^{-1}) for each species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites.

The relationship between overstory GE (measured between years 2021 and 2022) and LAI (measured in year 2022), are shown in Figure 3.12. The slope of the relationships between GE and LAI was not different across the sites ($P > 0.4$), but different models were fitted for two groups of species due to their differences in that relationship: Group 1, which includes species with high sensitivity of GE to changes in LAI, having large GE under low LAI (DF and GS), and Group 2, which includes species with low GE, sensitivity of GE to changes in LAI, having GE with little changes under different LAI (GF, LC, POC, SSP, WRC and WRSP). Pine species (WVPP and WWP) as well as WH were left out of this analysis, as for those species, changes in GE were not related to changes in LAI. For Group 1, an average reduction of GE of about 0.1 Mg m^{-2} year^{-1} was observed for 1 m^{2} m^{-2} LAI increment. For Group 2, an average reduction of GE of about 0.02 Mg m^{-2} year^{-1} was observed for 1 m^{2} m^{-2} LAI increment.

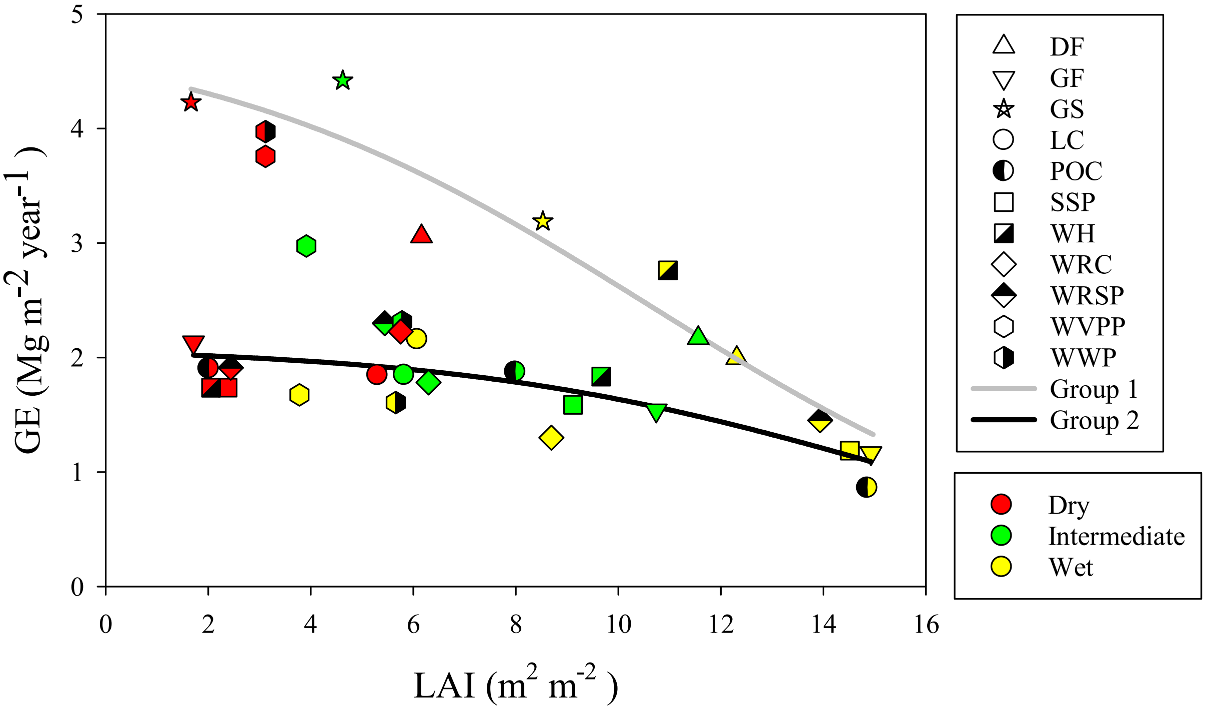

Figure 3.12. Relationship between Leaf area index (LAI, m^2 m^{-2}) of planted crop trees, and crop tree growth efficiency (GE, Mg m^{-2} year^{-1}) for stands planted with different conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. Group 1 includes DF and GS; Group 2 includes GF, LC, POC, SSP, WRC, and WRSP. Species description can be found in Table 3.1.

Parameter estimates and fit statistics for the equations to estimate GE from LAI are shown in Table 3.3.

Table 3.3. Parameter estimates and fit statistics of the equations for predicting growth efficiency (GE, Mg m^{-2} year^{-1}) from overstory leaf area index (LAI, m^2 m^{-2}) for stands planted with conifer species across the wet (Huffman) intermediate (Underhill), and dry (Campbell) sites. G1: Group 1 (GS, DF), G2: Group 2 (GF, LC, POC, SSP, WRC, WRSP).

Model		Parameter	Parameter Estimate	SE	R^2	RMSE
Group 1	$GE = \frac{a}{(1+\exp(-\frac{(LAI-c)}{b}))}$	a	4.919	1.51	0.88	1.43
		b	-4.3986	3.07		
		c	10.6045	3.03		
Group 2	$GE = \frac{a}{(1+\exp(-\frac{(LAI-c)}{b}))}$	a	2.0991	0.23	0.71	3.42
		b	-4.1761	2.08		
		c	15.2550	1.10		

3.5 Discussion

The annual amount of litterfall was highest at the wet (Huffman) site followed by intermediate (Underhill), and dry (Campbell) sites. This result agrees with Souza et al. (2019) who concluded that foliage production was regulated by water availability, in addition to temperature and forest structure. While around 41% of NPP in old-growth tropical forests is derived from litterfall (Kennan at al., 1995; Chen, 2017), this percentage varied between 16 and 54% by site and species in our study. Furthermore, most species' annual litterfall decreased from the wet to the dry site, while the opposite was true of WVPP and WWP annual litterfall due to their reduced productivity in the wet (Huffman) site. A similar trend for forest floor accumulation was reported in chapter 2.

Genetic and environmental factors control litterfall phenology. In our study, for most species across the three sites, litterfall peaked in October. Other studies showed a similar pattern of maximum litter fall in October for DF (Dimmock II, 1958), GS (Stohlgren, 1988) and ponderosa pine (Klemmedson, 1990). Nevertheless, DF, WVPP, and LC growing at the dry (Campbell) site exhibited peak litterfall in August. In addition, for WH, litterfall peaked in August at all sites. A similar result was reported by Kennen (1995). Seasonal dynamics in litterfall are frequently influenced by crown disturbance factors, such as cold, windstorms, and hail, as well as weather variations, such as water stress resulting from drought conditions (Gonzalez-Benecke et al., 2012; and Dimmock II. 1958).

Gholz (1982) reported that maximum LAI was associated with a simple index of growing season water balance. Grier et al. (1977) reported that stand LAI was reduced in regions where water was limited. In our observation, LAI ranged between 1.6 and 14.9 m^2 m^{-2}, where in most cases LAI decreased from wet to dry sites due to increasing water deficit during growing season.

Furthermore, at the wet (Huffman) site, most species had an LAI larger than 10 m^2 m^{-2}, which is a very large value for most temperature forests (Waring et al., 1979). As Gholz (1982) pointed out, in the PNW maximum LAI is correlated with mean minimum air temperature in January, as well as growing season water balance (both higher at the wet site). In water-limited environments, NPP is at least as closely related to LAI as it is to moisture availability (Grier et al., 1979). In this study, the wet (Huffman) site had more water availability, and less summer drought, and therefore had more NPP and LAI compared to the other sites. Further, NPP and LAI both significantly decreased at the dry (Campbell) site, which had larger water deficit. Forest production is linked to intercepted radiation, and therefore has a strong relationship with LAI (Flamenco, 2018). High LAI of overstory result in lower light available for understory and midstory species. In our study, most plots in the wet site showed very low abundance of understory and midstory vegetation.

A similar response to water availability was observed for $ANPP_{CT}$, where the wet (Huffman) site had the highest $ANPP_{CT}$ among all sites. During the relatively mild and wet autumn and winter months, photosynthesis and nutrient uptake are possible. However, during the warm, dry summer, reduced soil moisture and high evaporative demand may reduce stomatal conductance (and hence, photosynthesis). Waring and Franklin (1979) concluded that temperature and water availability are the most significant climatic factors limiting global net primary productivity. In our study, at the wet (Huffman) site, $ANPP_{CT}$ of WH was the highest (30.2 Mg ha^{-1} $year^{-1}$), followed by the GS (27.1 Mg ha^{-1} $year^{-1}$). These results were similar, but slightly lower than the $ANPP_{CT}$ of 36 Mg ha^{-1} $year^{-1}$ reported by Fujimori (1971) for a 26-year-old WH stand in western Oregon coast, where WH can thrive due to high water availability (Burns and Honkala, 1990). $ANPP_{CT}$ of GS, WH, and WRSP had a similar trend which is a sharp decline from wet to dry conditions. Westman (1966) reported that the ANPP of an old GS stand ranged between 5 and 19

Mg ha^{-1} year^{-1}, while young GS stands can have more than 20 Mg ha^{-1} year^{-1} (Busing and Fujimori, 2005). Our results are agreement with those reports, as GS ANPP$_{CT}$ ranged between 7 Mg ha^{-1} year^{-1} at the dry (Campbell) site, and 27 Mg ha^{-1} year^{-1} wet (Huffman). As Rundel (1972) highlighted, productivity of GS can be highly affected by water availability.

For DF, GF, LC, POC, SSP, and WRC, ANPP$_{CT}$ was very stable between wet and intermediate sites, but had a reduction from the intermediate to dry site (more pronounced for GF, POC and SSP; less pronounced for LC and DF). According to these results, dry site factors such as higher water deficit, temperature and VPD, limit productivity of GF, SSP and POC. A similar effect was reported by Gholz (1982), where NPP was positively correlated with higher (more positive) water balance. Flamenco (2018) reported ANPP$_{CT}$ of GF growing in coastal Oregon (near the intermediate (Underhill) site) between 10.2 and 24.6 Mg ha^{-1} year^{-1}, for stands subjected contrasting competing vegetation control. Similar values were obtained in this study. Productivity of POC was very high in the wet (Huffman) and intermediate (Underhill) sites, which makes sense given that POC dominates on moist and cooler sites, reaching its greatest size and commercial value on productive coastal soils near its northern range limit (Zobel et al., 1985). Even though DF and LC are more resilient to drought and high VPD than most of the species included in this study (Niemiera 2018), future increasing VPD and temperatures may negatively affect even these species (Restaino, et al., 2016). Our result agrees with this idea, as increased water deficit from wet to dry sites reduced ANPP$_{CT}$ of DF and LC, although less so than most other species.

Antos et al. (2016) indicated that WRC is tolerant to a wide range of environmental conditions, from highly-productive to nutrient-poor or wet soils. We observed that the productivity of WRC was very stable across sites (11.2 and 12.8 Mg ha $^{-1}$ year^{-1}, at the wet and dry sites, respectively). Flamenco (2018) reported similar ANPP$_{CT}$ for WRC at age 16 in western Oregon growing under sustained control of competing vegetation (10.5 Mg ha^{-1}year^{-1}). On the other hand, WVPP, and WWP showed an opposite trend, with increasing productivity from the wet to dry conditions. Scianna (2011) concluded that while WVPP is drought tolerant, it is very sensitive to humid coastal environments. Our observed trend implies that these pine species are well-adapted to drought and/or mal-adapted to wet conditions.

Even thought $ANPP_E$ was largely controlled by the productivity of planted trees (in most plots, $ANPP_M$ represented less than 10% of $ANPP_E$), $ANPP_M$ accounted for a large proportion of $ANPP_E$ in some plots. On the WVPP plot at the wet (Huffman) site, midstory accounted for 54% of $ANPP_E$. At the dry (Campbell) site, midstory accounted for 41 and 37% of $ANPP_E$ on GF and WH plots, respectively. In DF, GS, POC, and LC plots at the wet (Huffman) site, $ANPP_M$ was zero. Even though several plots showed negative $ANPP_U$ (mostly at the wet site), and other plots showed small $ANNP_U$ (between 0 and 4 Mg ha^{-1} year^{-1}), there was no clear relationship between overstory BA or LAI and $ANPP_U$. Negative $ANPP_U$ indicates that the understory abundance is decreasing due to mortality caused by reduced light availability for understory vegetation (Flamenco, 2018). While overstory BA or LAI had a positive sigmoidal relationship with $ANPP_{CT,}$ our observations showed a negative power relationship with $ANPP_M$. Similar relationships were reported by Flamenco (2018). As overstory crop trees will continue to grow, less light will be available for other vegetation to grow.

The amount of NPP per unit LAI (GE) decreased as moisture availability increased. In our study, the wet (Huffman) site had higher LAI and moisture availability, but lower GE. A similar response was reported by Jose and Gillespie (1997), who pointed out that as LAI increased along a gradient of increasing moisture availability, growth efficiency declined. The exception was WH which had a higher GE at the wet (Huffman), mainly due to high mortality at the dry (Campbell) site. When comparing species across sites, GS had the largest GE, POC and SSP had the lowest GE, and DF had an intermediate position. This result implies that GS can grow more with a similar and even lower amount of foliage that all other conifer species tested in this study. When observing the relationship between LAI and GE, two groups emerged: GS and DF showed larger GE for lower LAI, while other species, such as GF, LC, POC, SSP, WRC and WRSP, showed lower GE for similar low LAI. Nevertheless, both groups trended to converge to similar GE when LAI was larger than 12 m^2 m^{-2}.

3.6 Conclusions

We determined NPP, LAI, and GE of eleven conifer species on three sites covering a range of water availability. In general, in terms of NPP and LAI, the wet (Huffman) site had higher productivity than the intermediate (Underhill) site, followed by the dry (Campbell) site. However, GE had an opposite trend increasing from wet (Huffman) to dry (Campbell) sites. While the amount of carbon sequestration was higher in WH, GS, and DF species (around 25 Mg ha^{-1} $year^{-1}$) at the wet (Huffman) site and decreased from wet to dry sites in WH and GS plots, NPP of DF, LC and WRC was relatively stable across the sites. GS was the species with the greatest GE, implying that GS can grow more with a similar and even lower amount of foliage, making this species a good option for biomass production in the PNW.

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Chapter 4 Conclusions

4.1 Summary

In chapter 2, this study focused on determining the variation in productivity in terms of ecosystem biomass stocks including overstory, midstory, understory, forest floor and belowground biomass (soil and roots) for 26-year-old stands planted with 11 different species under contrasting levels of water deficit in western Oregon in order to determine differences in species. Whole ecosystem tree biomass stock of 11 species vary by species and site. While the amount of biomass of WH, GF, GS, WRSP, and SSP declined with decreasing water availability from wet to dry site, WVPP and WWP had the opposite trend. The amount of biomass of DF, LC, WRC was the most stable across sites. In terms of ecosystem biomass stock, the wet site had highest biomass accumulation, followed the intermediate and dry sites. The distribution of plant-derived biomass indicated that biomass stock was largely controlled by planted trees. When SOMC was included into the ecosystem biomass stock, belowground biomass was larger than aboveground biomass stock.

In chapter 3, we determined NPP, LAI, and GE of eleven conifer species on three sites covering a range of water availability. In general, in terms of NPP and LAI, the wet (Huffman) site had higher productivity than the intermediate (Underhill) site, followed by the dry (Campbell) site. However, GE had the opposite trend increasing from wet (Huffman) to dry (Campbell) sites. While the amount of carbon sequestration was higher in WH, GS, and DF species (around 25 Mg ha^{-1} year^{-1}) at the wet (Huffman) site and decreased from wet to dry site in WH and GS plots, NPP of DF, LC and WRC was relatively stable across the sites. GS was the species with the highest GE, implying that GS can grow more with a similar and even lower amount of foliage, making this species a great option for biomass production in the PNW.

4.2 Management Implications

This study demonstrates that species vary in their susceptibility to water deficits and climate variability in terms of biomass accumulation, leaf area index (LAI), and productivity. While water deficit was the most important factor affecting growth on all productivity metrics, species varied in their sensitivity to climate variables such as water supply and evaporative demand.

Those three study sites were established with alternative production species or to increase the pest- and disease-resilience or climate sensitivity of single-species stands across a water deficit gradient. DF is regarded as one of the most valuable and major timber species in the Pacific Northwest and has demonstrated exceptional drought resistance, which would be advantageous for maintaining productivity in the face of anticipated climate change. In terms of alternative species, this study will be helpful for species selections, reforestation efforts and increasing biodiversity across a water deficit gradient. Observations made clear that WH, GF, and GS were more productive than DF at the Huffman (wet) site. Although DF was more productive at the intermediate (Underhill) site, GS and GF did not differ significantly. Therefore, these species (WH, GF, GS) may be alternatives available for reforestation and timber production of the Oregon Coast Range.

For the Willamette valley, at the dry (Campbell) site most of species had a limited amount of productivity except DF, some of species such as WWP, WVPP, WRC, and LC had a comparable productivity. In our observation, those four species (WWP, WVPP, WRC, and LC) are more drought tolerant species, and had higher survival rate among the others in the dry (Campbell) site. Therefore, these species may be alternatives available for reforestation and timber production of the Oregon cascade foothill range.

The relationship between BA, biomass stock and NPP are useful tool to calculate aboveground biomass and NPP. While estimating aboveground biomass and NPP are more complex and time consuming, overstory basal area is a variable that is commonly estimated in most forest inventories and growth and yield models.

4.3 Future directions

In this study, we reported one year of litterfall and ANPP, but we just finished the second year of litterfall collection and the third year of tree inventory (February 2023), and it is anticipated that understory and midstory measurements will be carried out during this year. These measurements will extend the assessment period for ANPP to two years. Extended measurement will help to better understand how carbon sequestration changes under varying weather conditions. In addition, having more observations may allow us to improve the statistical power, allowing for better testing of climate variability effects on species' productivity and growth efficiency.

In addition, this is a non-replicate because each study sites had a single plot. Further research may be needed to understand alternative species in western Oregon. These include site replicate with each plot and seed sources. Also, specific site species biomass equation is needed for each species at each plot to estimate total biomass more accurately in future studies.

Appendix

Appendix 1: The volume equations and species-specific coefficients used in chapter 2, as well as their associated reference, are listed below:

Where: *DBHin* is DBH in inches; *HTft* is height in feet; *DBH* is DBH in centimeters; *HT* is height in meters; and *Age* is age in years.

Gonzalez-Benecke (et al. 2018):

$$DF = 0.00899 * (DBHin^{1.9448}) * (HTft^{0.7154}) * (Age^{-0.0473})$$

$$WH = 0.00681 * (DBHin^{1.9757}) * (HTft^{0.8061}) * (Age^{-0.1123})$$

$$WRC = 0.01960 * (DBHin^{1.9403}) * (HTft^{0.6847}) * (Age^{-0.2911})$$

Wensel & Krumland (1983):

$$GS = 0.0007903 * (DBHin^{1.792}) * (HTft^{1.282})$$

$$WH = 0.0005621 * (DBHin^{1.648}) * (HTft^{1.473})$$

$$GF = 0.0005621 * (DBHin^{1.648}) * (HTft^{1.473})$$

Zhou & Hemstrom (2010):

$$SSP = 10^{-2.700574 + 1.754171 * \log(DBHin) + 1.164531 * \log(HTft)}$$

$$WRSP = 10^{-2.700574 + 1.754171 * \log(DBHin) + 1.164531 * \log(HTft)}$$

Zianis et al. (2005):

$$POC = \frac{DBH^{1.85298} * HT^{0.86717} * e^{-2.33706}}{28.317}$$

Pillsbury et al. (1998):

$$LC = 0.005764 * (DBHin^{2.260353}) * (HTft^{0.630129})$$

Poudel et al. (2019):

$$WVPP = e^{(-10.5808 + 2.1110 * \log(DBH) + 0.9126 * \log HT)} * 35.315$$

$$WWP = e^{(-9.5997 + 1.4028 * \log(DBH) + 1.4115 * \log HT)} * 35.315$$

Appendix 2. List of references of biomass equations available for each species. One equation was selected for each species.

Species	Reference
DF	Chojnacky et al. (2014); Gonzalez-Benecke et al. (2018), Poudel et al. (2019), Zhou et al. (2009 and 2010)
GF	Chojnacky et al. (2014); Gonzalez-Benecke et al. (2018), Poudel et al. (2019), Zhou et al. (2009)
GS	Chojnacky et al. (2014), Poudel et al. (2019), Sillet et al. (2019), Zhou et al. (2010)
LC	Chojnacky et al. (2014)
POC	Chojnacky et al. (2014), Zhou et al. (2009)
SSP	Chojnacky et al. (2014). Poudel et al. (2019), Zhou et al. (2009 and 2010)
WH	Chojnacky et al. (2014), Gonzalez-Benecke et al. (2018), Poudel et al. (2016 and 2019), Zhou et al. (2009 and 2010),
WRC	Chojnacky et al. (2014), Gonzalez-Benecke et al. (2018), Poudel et al. (2019), Zhou et al. (2009 and 2010)
WRSP	Poudel et al. (2019)
WVPP	Chojnacky et al. (2014), Poudel et al. (2016 and 2019), Zhou et al. (2009 and 2010)
WWP	Chojnacky et al. (2014), Zhou et al. (2009 and 2010)

Appendix 3. Soil bulk density and organic matter (%) at 0-15, 15-30, 30-50 and 50-100 cm depth, on plots planted with 11 conifer species, including a naturally regenerated unplanted (UP) plot, at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 2.1.

		Soil Bulk Density (g cm^{-3})				Soil Organic Matter (%)			
Site	Species	0 – 15	15 - 30	30 - 50	50 - 100	0 - 15	15 - 30	30 - 50	50 - 100
Wet	DF	0.72	0.91	0.93	0.95	20.81	8.50	5.91	4.31
	GF	0.56	0.80	0.88	0.88	13.72	6.65	13.31	6.57
	GS	0.69	0.68	0.84	0.88	8.62	6.53	4.68	3.48
	LC	0.66	0.74	0.74	0.89	14.70	12.76	7.25	5.42
	POC	0.79	0.95	0.84	0.97	15.77	6.15	4.86	3.71
	SSP	0.68	0.76	0.87	0.89	16.95	12.54	8.83	6.01
	WH	0.62	0.90	0.75	0.87	18.50	15.38	15.09	7.84
	WRC	0.73	0.79	0.83	0.92	14.97	8.01	5.77	4.43
	WRSP	0.58	1.00	0.96	0.92	14.72	7.53	4.67	5.59
	WVPP	0.80	0.81	0.92	0.93	14.05	12.61	6.97	6.01
	WWP	0.92	1.06	0.96	0.86	14.44	8.92	6.49	6.59
	UP	0.69	0.69	0.70	0.69	13.64	13.26	12.80	13.31
Intermediate	DF	0.84	0.83	1.06	0.85	13.09	5.89	4.39	3.79
	GF	0.96	1.06	1.05	1.11	8.46	5.04	3.99	3.08
	GS	0.90	1.00	0.99	0.98	13.30	6.85	4.13	3.00
	LC	0.88	0.80	0.88	0.88	12.52	6.21	4.63	2.88
	POC	0.74	1.02	1.08	0.85	13.97	6.06	3.30	3.26
	SSP	0.75	0.77	0.94	0.93	8.47	5.74	3.65	2.97
	WH	0.78	0.86	1.02	0.95	7.33	7.09	4.21	3.51
	WRC	0.89	0.88	1.03	1.12	8.73	5.96	4.68	3.52
	WRSP	0.76	1.10	0.95	1.02	8.58	4.21	3.46	2.98
	WVPP	0.86	1.11	0.94	0.81	5.11	4.14	3.77	3.12
	WWP	0.95	1.05	1.02	1.04	6.01	6.08	3.61	3.31
	UP	0.77	0.95	0.89	1.02	12.60	6.32	3.99	3.00
Dry	DF	0.80	0.80	0.97	1.05	12.36	6.15	5.45	3.67
	GF	0.90	1.10	0.95	0.99	8.52	4.32	3.39	3.26
	GS	0.83	0.90	0.93	0.99	12.61	6.40	5.55	4.64
	LC	1.01	0.95	0.90	1.10	12.90	12.36	6.76	5.95
	POC	0.76	0.96	0.76	0.91	8.74	7.80	6.76	5.17
	SSP	0.82	0.75	0.82	0.90	7.96	6.71	5.05	5.36
	WH	0.79	0.79	0.87	0.90	8.46	7.60	3.83	4.05
	WRC	0.97	0.94	0.99	1.05	7.43	6.38	5.00	4.42
	WRSP	0.78	1.08	1.14	1.03	7.90	6.03	4.40	3.93
	WVPP	0.94	0.92	1.03	0.96	7.04	5.96	5.35	5.10
	WWP	0.87	0.97	0.89	1.14	8.21	5.93	5.35	4.75
	UP	0.94	1.01	0.92	1.15	5.98	4.72	4.76	3.44

Appendix 4. Aboveground ecosystem biomass (Mg ha^{-1}), on plots planted with 11 conifer species, including a naturally regenerated unplanted (UP) plot, at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 2.1. B_R

	Wet					Intermediate					Dry				
Species	B_{FF}	B_U	B_M	B_R	B_O	B_{FF}	B_U	B_M	B_R	B_O	B_{FF}	B_U	B_M	B_R	B_O
DF	13.1	0.2	0	59.5	267.1	9.4	4.5	0.1	57.2	257.3	9.4	0.1	2.3	48.1	213.2
GF	7.2	0	0	67.7	307.9	6.3	1.3	0	49.2	222.9	3.8	2.8	21.7	9.5	19.7
GS	7.5	0.8	0.2	58.5	272.2	6.2	0.4	0	39.6	181.5	3.3	2.1	0.4	9.6	42.6
LC	16.1	1.5	0	35.3	158.7	8	2.8	0.5	35.4	156.7	7.2	0	0.7	27.9	122.6
POC	6.5	0	0	43.9	197.6	6.4	1.8	0.4	42.2	189.4	4.3	2.2	5.9	7.5	26.7
SSP	18.7	0	0	37.4	168.3	6.2	0.1	1	21.1	92.9	3.2	5.7	1.4	7.7	32
WH	9.6	0.1	0.5	63.5	286.7	11.3	1.2	0.1	45.3	204.3	4.7	7.4	3.1	6.4	24.5
WRC	6.8	0.7	10	18.6	72.5	7.9	2.3	3.1	13.8	57.4	4.4	0.8	4.5	21.4	90.2
WRSP	16.2	0	0	38.5	172.9	4.9	2.1	1.5	18.0	78.1	2.8	2.4	1.5	7.4	29.9
WVPP	12.2	4.3	6.7	21.8	90.3	11.7	3.6	3	35.1	153.1	13	2.7	0.5	30.0	132.5
WWP	6.3	3.1	3.6	27.7	120.3	9.4	3.6	0.5	32.0	143.3	9.8	3.6	4.1	19.1	80.9
UP	N.D.	5.5	16.3	3.9	0	N.D.	4.8	14.3	3.4	0	N.D.	4.4	10.1	2.4	0

B_{FF}: Forest floor biomass (Mg ha^{-1}); B_U: Understory biomass (Mg ha^{-1}); B_M: Midstory biomass (Mg ha^{-1}); B_R: sum of midstory and overstory root biomass B_O: Overstory crop tree biomass (Mg ha^{-1}); N.D.: Not determined.

Appendix 5. Ecosystem Aboveground Net Primary Productivity (NPP_E, Mg ha^{-1} year^{-1}), including litterfall (LF, Mg ha^{-1} year^{-1}),understory biomass increment (U, Mg ha^{-1} year^{-1}), midstory biomass increment (M, Mg ha^{-1} year^{-1}) and overstory crop tree biomass increment (CT, Mg ha^{-1} year^{-1}) for…… at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 2.1.

	Wet				Intermediate				Dry			
Species	LF	U	M	CT	LF	U	M	CT	LF	U	M	CT
DF	4.0	-0.7	0.0	20.6	4.8	1.6	0.0	20.3	3.1	-0.3	0.2	15.8
GF	4.8	0.0	0.0	12.6	5.4	1.0	0.0	11.1	1.4	-0.2	2.5	2.2
GS	6.1	-2.0	0.0	21.1	4.2	0.1	0.0	16.3	2.2	-0.2	0.1	4.9
LC	7.2	-2.3	0.0	5.9	5.1	0.6	0.0	5.7	3.7	0.0	0.1	6.1
POC	6.5	0.0	0.0	6.3	4.4	1.0	0.0	10.6	2.0	-0.9	0.7	1.8
SSP	6.2	0.0	0.0	11.0	5.8	-0.3	0.3	8.7	1.1	3.8	0.2	3.0
WH	5.6	0.0	0.0	24.7	3.0	-1.0	0.0	14.7	1.7	-2.2	0.7	1.9
WRC	3.3	-0.3	1.2	8.0	4.0	2.0	0.4	7.2	4.1	0.4	-0.4	8.7
WRSP	5.7	0.0	0.0	14.5	3.9	1.5	0.6	8.6	0.9	1.8	0.3	3.7
WVPP	2.0	-4.6	0.7	4.3	4.0	-1.2	0.5	7.6	3.5	0.5	0.1	8.2
WWP	3.5	-2.2	0.3	5.6	4.0	-1.8	0.0	9.3	4.4	2.3	0.3	8.0

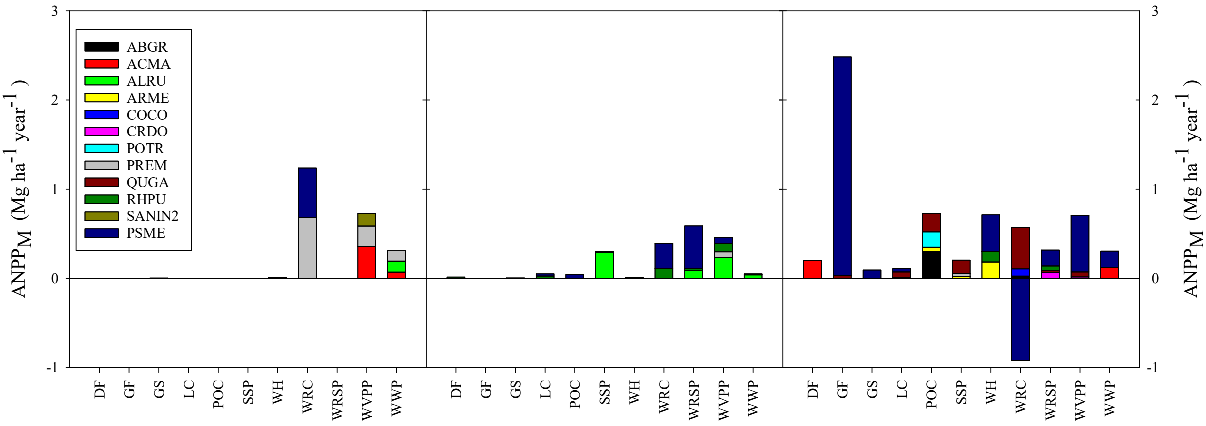
LF: Litterfall (Mg ha^{-1} year^{-1}); U: Understory Biomass Increment (Mg ha^{-1} year^{-1}); M: Midstory Biomass Increment (Mg ha^{-1} year^{-1}); CT: Overstory Crop Tree Biomass Increment (Mg ha^{-1} year^{-1})

Appendix 6. Aboveground Net Primary Productivity (Mg ha^{-1} y^{-1}) of understory (U), midstory trees (M), overstory crop trees (CT) and the sum of all parts (Ecosystem ANPP, E), on plots planted with 10 conifer species, at the wet (Huffman), intermediate (Underhill), and dry (Campbell) sites. Species description can be found in Table 2.1.

	Wet								Dry			
Species	U	M	CT	E	U	M	CT	E	U	M	CT	E
DF	-0.74	0	24.55	23.81	1.55	0.01	25.06	26.62	-0.31	0.24	18.84	18.77
GF	-0.04	0	17.39	17.35	0.99	0	16.52	17.51	-0.18	2.5	3.65	5.97
GS	-2.04	0	27.19	25.15	0.12	0.11	20.43	20.66	-0.22	0.68	7.04	7.50
LC	-2.31	0	13.12	10.81	0.55	0.1	10.75	11.40	-0.04	0.21	9.79	9.96
POC	0	0	12.81	12.81	1	0.12	14.98	16.10	-0.87	1.07	3.82	4.02
SSP	-0.01	0.01	17.22	17.22	-0.26	0.3	14.46	14.50	3.82	0.25	4.13	8.20
WH	0.05	0.01	30.28	30.34	-1.05	0.1	17.73	16.78	-2.16	0.83	3.57	2.24
WRC	-0.34	1.85	11.30	12.81	2.01	0.44	11.23	13.68	0.42	-0.43	12.81	12.80
WRSP	-0.01	0.23	20.22	20.44	1.55	0.79	12.51	14.85	1.75	0.38	4.66	6.79
WVPP	-4.63	2.03	6.33	3.73	-1.22	0.6	11.64	11.02	0.51	0.08	11.72	12.31
WWP	-2.17	0.33	9.09	7.25	-1.82	0.17	13.36	11.71	2.3	0.3	12.39	14.99

U: Understory ANPP (Mg ha^{-1} y^{-1}); M: Midstory ANPP (Mg ha^{-1} y^{-1}); CT: Crop Trees ANPP (Mg ha^{-1} y^{-1}); E: Ecosystem ANPP (U + M + CT; Mg ha^{-1} y^{-1});

Appendix 7. Midstory net primary productivity (ANNP$_{M}$; Mg ha^{-1} year^{-1}) in terms of plant species between 2021 and 2022 for stands planted with different conifer species across the wet (Huffman, left) intermediate (Underhill, center), and dry (Campbell, right) sites. Midstory vegetation includes all conifer and broadleaf species with DBH>2.5 cm identified by USDA species code (Table 2.3). Species description can be found in Table 3.1.



Appendix 8. Understory net primary productivity (ANNP$_U$; Mg ha^{-1} year^{-1}) in terms of each growth habit between 2021 and 2022 for stands planted with different conifer species across the wet (Huffman, left) intermediate (Underhill, center), and dry (Campbell, dry) sites. Species description can be found in Table 3.1.