AN ABSTRACT OF THE THESIS OF

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Abstract approved:

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Forest vegetation management (FVM) is an important component of reforestation in the Pacific Northwest (PNW). Several studies have demonstrated the benefits of vegetation management on planted conifer growth and survival. However, few reports have been published on the long-term effects of FVM treatments on total ecosystem biomass accumulation and aboveground net primary productivity (ANPP). In this study we assessed long-term effects of vegetation management on total tree and ecosystem biomass stock, and total tree and ecosystem ANPP for Douglas-fir, western hemlock, western redcedar, and grand fir growing in Oregon's central coast range (CR) and Douglas-fir and western redcedar growing in Oregon's cascade foothills (CF). This study represents the first known attempt to quantify how FVM treatments impact long-term ecosystem biomass accumulation and ANPP of four different conifer species planted in the PNW.

This study contained two vegetation management treatments: control (C) and vegetation management (VM). Both the C and VM plots received a fall site preparation treatment. The VM plots then had sustained vegetation control using herbicides during the first 5 years after planting. Measurements were carried out during growing seasons 16 and 17 at the CR site and 15 and 16 at the CF site. Crop tree aboveground biomass was assessed using inventory data and species-specific

allometric functions developed in this study. Ecosystem aboveground biomass was assessed by measuring, in addition to crop tree, midstory, understory and forest floor biomass. ANPP was calculated as the one-year increment in aboveground ecosystem biomass plus litterfall during the same period.

At age 16, at the CR site, average crop tree biomass stock of C plots was 95.3, 48.6, 19.0, and 38.2 Mg ha^{-1}, for Douglas-fir, western hemlock, western redcedar, and grand fir, respectively. VM plots increased crop tree biomass stock by 26.5, 91.2, 44.7, and 96.1 Mg ha^{-1} for the same species. At the same age, at the CF site, average crop tree biomass stock of C plots was 76.6 and 18.7 Mg ha^{-1}, for Douglas-fir and western redcedar, respectively. At this site, the gain of VM treatments over the control was 48.1 Mg ha^{-1} for Douglas-fir and 42.2 Mg ha^{-1} for western redcedar.

Ecosystem biomass stock was not affected by VM treatment on western hemlock, western redcedar and grand fir at the CR site, and only increased in treated plots of Douglas-fir at both sites and western redcedar at the CF site. Midstory of C plots at the CR site averaged 52.9, 64.7, and 36.0 Mg ha^{-1}, for western hemlock, western redcedar, and grand fir, respectively. At the CF site, midstory of C plots was 1.2 and 5.9 Mg ha^{-1}, for Douglas-fir and western redcedar, respectively.

The average crop tree ANPP of C plots growing at the CR site was 14.5, 12.6, 2.6, and 10.2 Mg ha^{-1} yr^{-1}, for Douglas-fir, western hemlock, western redcedar, and grand fir, respectively. At the CF site, crop tree ANPP of C plots was 11.0 and 3.2 Mg ha^{-1} yr^{-1}, for Douglas-fir and western redcedar, respectively. Eleven years after vegetation management treatment ended, the crop tree ANPP of VM plots was greater than the C plots by 11.2, 7.9, and 14.4 Mg ha^{-1} yr^{-1} for western hemlock, western redcedar, and grand fir, respectively, at the CR site and 4.6 Mg ha^{-1} yr^{-1} for Douglas-fir and 6.5 Mg ha^{-1} yr^{-1} for western redcedar at the CF site. There was no effect of treatments on ecosystem ANPP (including production of understory and midstory biomass) at the CR site.

The results of this analysis demonstrate that sustained FVM treatments during the first 5 years of stand establishment increases both the biomass stock and ANPP. This suggests that FVM treatments can accelerate the long-term carbon sequestration rate of planted forests in the PNW. However, in analyzing other ecosystem components, there was no increase in ecosystem biomass stock and ANPP for western hemlock, western redcedar, and grand fir stands growing in the CR site at age 16. These results provide managers with options for FVM, depending on management objectives and site conditions. Differences observed between sites also serve to inform forest managers to know their site, i.e. temperature, annual rainfall, and competing vegetation species composition to develop an appropriate vegetation management plan.

Long-term Effects of Vegetation Management on Biomass Stock and Aboveground Net Primary Productivity on Four Coniferous Species in the PNW

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

Herman Noe Flamenco, Jr., Author

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Chapter 1: Introduction and Literature Review

Introduction

Forest vegetation management (FVM) is an integral part of reforestation in the Pacific Northwest (PNW). Early control of competing vegetation is known to reduce competition for light, water, and nutrients between crop trees and undesired vegetation, and in turn achieve a desired yield in a shorter amount of time. In the PNW, and in other parts of the world, the most effective FVM method has been herbicide use since it reduces the amount of competing vegetation, improving seedling growth and survival (Ketchum et al. 1999, Maguire et al. 2009, Rose et al. 2006). Among other reasons, herbicides can be applied relatively quickly on large or difficult areas in comparison to mechanical methods and fewer treatments are needed to control regeneration, reducing costs. Herbicides are also versatile in that they are selective of target weeds and minimize damage to crop trees (Freedman 2008).

This chapter will provide a background on PNW plantation forestry, FVM and herbicide use, and the importance of quantifying forest biomass production.

Literature Review

Forests of the Pacific Northwest

The PNW refers to the region in western North America composed of the states of Washington and Oregon, in addition to Northern California and southwestern British Columbia. The region is most notable for its evergreen coniferous forests. Many of the tree species in these forests are known for their size and longevity of life (Waring and Franklin 1979). Apart from their aesthetics and ecological importance, these forests are also of great economic importance.

About half, 47%, of the total land area in Oregon is forestland with 36% in timber production, 33% is in multi-resource forest, and 31% in reserve (OFRI). Oregon accounted for 17% of the total US production of softwood lumber in 2015 with 5.2 billion board feet, making it the leader for several years running. Washington accounted for 12% and California for 6% of US softwood lumber production. Oregon also leads the nation in plywood production accounting for 29% of total US production and Washington accounts for an additional 9%. In 2013 and into 2014 Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) accounted for about 70% of timber volume harvested and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) accounted for about 11%. True firs (*Abies*) accounted for 8% and cedar (*Cedrus*, *Thuja*) for about 2% during this time (Simmons et al. 2016). All the forests within Oregon are subject to state forest practice regulations regardless of their use.

Forest Practices in Oregon

In 1971, Oregon became the first state to pass a law regulating forest practices (OFRI). Washington and California were not far behind in passing their own forest practice regulations. Each state has a slightly different set of rules, but share the same overall goals of regulating forest establishment, management, and harvesting to protect soil, water and fish, and wildlife habitat. Oregon's Forest Practice Rules require that any forested area must be "free to grow" within six years of timber harvest, specifically the area must be well stocked with vigorous trees that are dominant over undesired vegetation and will remain vigorous (Rose and Haase 2006). This is not an easy task to accomplish when mangers have ungulate browsing and competing vegetation to deal with. Considering this, vegetation management becomes of major importance when reforesting an area, not just for economic reasons, but for law compliancy as well.

Forest Vegetation Management

Ketchum et al. (1999) defines forest vegetation management (FVM) as the manipulation of colonizing vegetation to steer the ecosystem to a desired set of conditions. In the case of timber production-oriented forests, managers want to promote tree growth to maximize their revenue at rotation age. Promoting crop tree growth requires, in many cases, large early investments. Wagner et al. (2000), stated that a failure to understand how competing vegetation influences the survival and growth of tree seedlings leads to failed plantations, substantial reductions in early stand growth, and/or overspending on vegetation control that may or may not be successful.

After a harvest, site resources, such as light, water, and nutrients, are made readily available and early seral species will quickly use those resources and occupy the site. Research has shown that controlling vegetation for at least two years leads to an increase in the growth of crop species (Newton and Preest 1988, Rose et al. 2006). Contrary to public perception, studies have also shown that years after herbicide treatments, there are no adverse effects on understory species richness and diversity of competing vegetation (Boyd et al. 1995, Boateng et al. 2000).

Competing vegetation can be divided into different life forms and these life forms can differ in competitiveness (Balandier et al. 2005). Graminoids have been found to increase moisture stress and reduce tree seedling growth (Cole and Newton 1986, Davies 1987). Graminoid growth is variable. They can be short or tall and grow in low density or in high densities creating continuous canopies and thick root layers, increasing competition for light and soil water (Balandier et al. 2005). Herbaceous species can occupy large areas during the growing season in the PNW. When water becomes a limiting resource, they can pose a threat to seedling growth and survival (Rose et al. 1999, Newton and Preest 1988). Shrubs and hardwoods are considered to be highly competitive in young stands. They have a high dominance potential, meaning once established, they can become quite large and overtop crop tree seedlings and be tough competitors for available resources. Rose et al. (2006) found that the competitiveness of herbaceous species declined over time, whereas the competitiveness of shrubs and hardwoods increased over time. Thus, establishing a cohesive vegetation management plan is important, as graminoids and herbaceous species can cause high mortality during stand establishment and shrubs and hardwoods can continue to reduce stand growth of crop trees.

Herbicide use has become a common practice in forestry around the world, as it reduces vegetation competition with crop trees, preventing yield loss. The use of mechanical treatments and broadcast burns for site preparation have been on the decline, with chemical use rising. Site preparation and the use of herbicide in years 1 and 2 have also risen, decreasing shrub and hardwood release methods (cutting, trimming, or a combination of few lesions on the stem and an herbicide application) over several years (Briggs 2007). In the PNW, a standard herbicide application includes a pre-planting treatment in the fall and one or more post-planting applications in the spring (Maguire et al. 2009). Although other methods exist, herbicides have proven to be the most effective form of vegetation management (Ketchum et al. 1999).

Vegetation management effects are site specific. Rose et al. (1999, 2005, and 2006) evaluated eight herbicide treatments 3, 8, and 12 years after application at two different sites, one in the central Oregon coast range (Summit, near one of the sites used in this study) and the other in the western Cascade Range (Marcola). Controlling shrubs and hardwoods had little effect at the Marcola site since there were few competitive species, whereas at Summit volume production increased significantly. In a recent study, Vargas et al (2017) reported that the response of *Eucalyptus globulus* plantations to VM treatments depended on the amount of competing vegetation biomass produced during the first two years after planting. This difference in research results demonstrates the site-specific nature of FVM treatment responses.

FVM studies seek to understand both the effectiveness of vegetation management treatments and optimal timing for treatment application. It is essential for forest managers to know when to begin to control competing vegetation and when to stop to ensure adequate stand growth and survival while conserving economic resources. Maguire et al. (2009) analyzed eight herbicide regimes applied over 5 years at three coastal Douglas-fir plantations and found that the critical period, which corresponds to the period of stand establishment when competing vegetation must be controlled to prevent substantial yield losses (Swanton and Weise 1991, Knezevic et al. 2002), for maximizing yield in Douglas-fir was between the ages of 2 and 4 years. Another important finding was that critical period differed depending on the competing vegetation species composition. Gonzalez-Benecke and Wightman (2017) reported that for western hemlock, western redcedar, and grand fir, vegetation management in the first-year post planting is necessary to avoid significant yield reduction.

Although the consecutive use of release treatments appears to be promising, information on long term effects is needed. In the PNW, most studies have focused on the short-term effects of vegetation management (Clark et al. 2009). Only a few studies have monitored long-term effects of vegetation management (Albaugh et al. 2015 (Chile), Nillson and Allen 2003 (SE USA), Vargas et al. 2017 (Chile)). In this study we analyzed the effects of a treatment of continuous vegetation control carried out during the first 5 years after planting. The evaluations were developed 11 years after the vegetation control treatment ended (stand ages of 15 and 16).

Forest Biomass and Carbon Sequestration

Forests are not only important from an economic stand point of timber production; they also provide important ecological and social goods and services, such as carbon sequestration. Forests in the PNW are known for their large accumulation of biomass (Waring and Franklin 1979). Biomass is the organic matter accumulated in forests and the main storage of vegetation carbon (Le Toan et al. 2011). Birdsey (1992) reported that on average, across the United States, most of the carbon stored in forest ecosystems is found in the soil (about 59%) and in the overstory trees (about 30%). In the past, forests in the PNW have accounted for 39% of the 57.8 billion tons of carbon stored in U.S. forests (Birdsey 1992). While mature forests have high carbon storage, young forests accumulate carbon at a higher rate (Gray et al. 2016).

Forest biomass is also useful in measuring forest productivity. Net primary productivity (NPP), which is an important variable of terrestrial ecosystems and a key component of the global carbon cycle, is defined as the amount of carbon uptake after subtracting plant respiration from gross primary productivity (Lambers et al. 2008). NPP can be estimated as the net change in biomass over a period of time. Studying forests primary productivity helps researchers understand the impact that environmental factors and management practices can have on forest production and carbon sequestration (Waring and Running 1998).

Objectives and Hypothesis

The main objective of this study was to investigate the long-term effects of vegetation management on aboveground biomass stock and aboveground net primary productivity of the whole-ecosystem. The following hypotheses encapsulate the hypotheses examined in the following two chapters. At age 16, 11 years after the treatment of 5 years of sustained vegetation control ended:

1. There are still differences in component tree and ecosystem biomass stock between treatments.
2. There are still differences in component tree and ecosystem ANPP between treatments.
3. Treatment effects differ between sites due to differences in site characteristics.

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Chapter 2: Long-Term Effects of Vegetation Management on Stem Volume and Biomass Stock

Introduction

Forest biomass, net primary productivity (NPP), and leaf area, separate or in combination, are useful indices of productivity, light use efficiency, maturity and stability of forest ecosystems, and their economic importance (Gholz et al. 1982). These stand attributes are often overlooked as other stand attributes, such as stem volume, basal area (BA), and mean diameter at breast height (DBH), and dominant height are of most popular interest to forestry plantation managers. Stem volume has been the measurement most used by foresters for determining stand production, with biomass gaining interest since the early 1970s (Parde 1980). Parde (1980) attributes this interest to the need of the pulp and paper industries to deal in weight rather than volume, to a research interest in estimating biological productivity, and to the oil crisis leading to interest in biofuels. In addition, quantifying forest biomass is also of use for carbon accounting and for monitoring changes in terrestrial carbon storage (Le Toan et al. 2011).

Forest biomass is expressed in terms of dry organic matter per unit land area. Since a stand is composed by a population of individual trees, it is necessary to estimate biomass of individual trees. Allometric functions are the most common method of estimating individual tree biomass. To develop allometric functions, trees that are representative of the stand are chosen to be destructively sampled. Each sampled tree is then separated into several components such as: main stem, bark, crown (branches and foliage), and in some instances cones and roots. Linear and non-linear models are most commonly fit to the data using easy to measure predicting variables such as DBH, height, age, and live crown length (Parresol 1999). Some authors have included stands attributes as BA and trees per hectare as additional covariates in biomass functions (Antonio et al. 2007, Gonzalez-Benecke et al. 2014).

Forest stands are not only composed of planted overstory trees. To estimate forest biomass, other ecosystem components must also be accounted for. These include vegetation in the midstory and the understory, forest floor, and soil organic matter. While allometric functions exist for many midstory species, other ecosystem components must be determined by direct field samplings.

This chapter covers the background of biomass equations, their application in estimating total and component tree biomass, and forest biomass stock. As a side product of stem and bark biomass estimation, stem and bark volume functions were also determined. The development of biomass equations for this study and ecosystem biomass accounting are described. The long-term effects of vegetation management treatments on stem volume, total and component tree biomass and total and component ecosystem biomass stock for four coniferous species was tested and the results are presented in this chapter. Furthermore, we tested for differences between the four species and between two sites.

Literature Review

Stem Volume Equations

Estimating total and merchantable volume has been of the upmost importance for land managers. The most common method of estimating tree volume has been the use of volume equations, which are typically species-specific regression equations. Volume equations have been developed to be used both at the local and national level. Generalized functions are broadly applicable and can be developed for geographic regions by using data collected from a variety of areas within a region (Feller 1992). Temesgen et al. (2015) found that using generalized volume equations could introduce more error as form of trees can differ between areas. Management practices are also known to alter the growth form of trees and therefore affect volume estimates. Volume functions found in computer software and literature can be based off of older and larger trees in different geographic regions (Han 1994, PNW-FIA 2010). The trees in our study sites are reaching the upper limit of being considered small. Using localized and age appropriate volume functions would result in more precise estimates of stand volume and volume production.

Biomass Equations

There are different methods for estimating total and component tree biomass such as the mean tree method, the harvest method, dimensional analysis and allometry, and multi-stage sampling (Parde 1980). The most commonly used method is dimensional analysis and allometry by means of biomass equations. Biomass equations have been used for many years and have been developed for many economically and ecologically important species all over the world. Generalized biomass equations have also been developed to maintain consistency across agencies and for estimating carbon budgets, among other reasons (Chojnacky et al. 2013, Zianis et al. 2005 (Europe), Jenkins et al. 2003, Lambert et al. 1996 (Canada)). Generalized biomass equations pool available data pertaining to a particular species or genus, and develop a general biomass equation that is widely applicable. However, estimates can be more accurate if local biomass equations are used (Nam et al. 2016, Poudel and Temesgen 2016, de-Miguel et al. 2014). Local biomass equations use data pertaining to a specific region, more commonly the area of study. Furthermore, Tumwebaze et al. (2013) and Van Lear et al. (1986) found that biomass equations developed for natural forests might not be suitable for plantation forests.

Forest Biomass

Aboveground biomass of trees varies between species. Some species are slower growing than others and so biomass accumulates at a slower rate. Tree species also differ in the allocation of biomass, but most species allocate significant biomass to the stem, which makes up most of the aboveground biomass in forests (Nunes et al. 2013). Stem biomass accounted for about 80-90% of total biomass, live branches less than 10%, and foliage less than 5% in the120-200-year-old coniferous forests that Gholz et al. (1982) studied. Satoo (1970a) found similar results in a 39-year-old plantation of *Larix leptolepis*.

Aboveground tree biomass is only one component of the forest ecosystem biomass. The midstory and the understory are components that tend to be overlooked, primarily because they are not of economic interest, and also due to the fact that in many cases the understory can amount to less than 1% of mature forest biomass (Gilliam 2007). However, in other forests with more open canopies, understory biomass can represent as much as 7% of total ecosystem biomass (Gonzalez et al. 2013). Midstory species have the potential to play a greater role in biomass accumulation than understory vegetation. This is primarily due to plant life form. Midstory species for the most part are woody plants and stem biomass amounts for a large portion of aboveground biomass.

Studies and practice have shown that management practices have an impact on tree growth, but few studies have shown the impact that silviculture has on forest biomass (Temesgen et al. 2015). Du Toit 2007 found that removing all harvesting residues before planting, resulted in a reduced biomass production in eucalyptus plantations in South Africa, mainly due to the impact on nutrient cycling. Hynynen et al. (2015) reported intensively managed forests are more efficient in capturing carbon from the atmosphere than extensively managed forests. Intensively managed forests are high in capital and labor to maximize production, while extensively managed forests aim to bridge the gap between managed and natural forests. Jokela et al. (2010) and Vogel et al. (2011) reported similar results in southern pine plantations. In these studies, weed control increased growth rates and biomass accumulation. However, the latter author also reported that sustained competing vegetation control decreased carbon pools and nitrogen retention in the forest floor and the soil. Vogel et al. (2011) concluded that the understory may play an important role in carbon and nitrogen dynamics in southern pine planted forests.

Gaining more knowledge on how forest management impacts forest biomass is of high importance as forests are expected to have a significant role in carbon sequestration and carbon offset (Harmon 2001, Sedio et al. 1997). Increasing forest productivity can increase carbon sequestration, if the period between harvests is not reduced (McKinley et al. 2011). New growth and yield models are including ecosystem biomass as part of their modeling capabilities (Gonzalez-Benecke et al. 2010, 2011, and 2015).

Objectives and Hypotheses

The primary objective in this chapter was to quantify the long-term effects of vegetation management on biomass stock at age 16 on planted stands of four conifer species growing on two sites in the PNW. A secondary objective was to develop site and species-specific volume and biomass equations. We hypothesize that at age 16, 11 years after vegetation management ended:

1. Trees growing on plots that had sustained elimination of competing vegetation during the first 5 years after planting will have higher total and component biomass stock.
2. Tree response in above ground biomass stock to vegetation management differs between species and sites.
3. In plots without vegetation control, understory and midstory vegetation play a major role in terms of biomass stock, partially counteracting the positive effects of vegetation control on crop tree growth, when compared with treated plots.
4. Ecosystem biomass stock is larger in treated plots, and the response in above ground biomass stock to vegetation management differs between species and sites.

Methods

Description of Sites

The two study sites are located in the central Coast Range (CR) near Summit, OR, and the Cascade foothills (CF) near Sweet Home, OR. The CR site was established in January of 2000 on Starker Forests, Inc. land. It is located approximately 40 km from the coast (44.62°N, 123.57°W). The mean annual temperature is 11.1°C, and the mean annual rainfall is 1,707 mm. The site is characterized by fine loamy soil. The CF site was established in February of 2001 on Cascade Timber Consulting, Inc. land. It is located approximately 110 km from the coast (44.48°N, 122.73°W). The mean annual temperature is 12.4°C and the mean annual rainfall is 1,179 mm. The site is characterized by silty clay loam soil.

Study Design

A randomized complete-block experiment with eight treatments was implemented at both sites (Appendix Figures 1 and 2). Plots were planted with Styro-15 seedlings in six by six rows at 3 m (10-ft) spacing. A buffer row was included on all four sides for a plot size of about 0.06 ha. At the CR site, four coniferous species were planted Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata Donn ex D. Don*), and grand fir (*Abies grandis (Dougl. ex D. Don) Lindl.*). There are four blocks of Douglas-fir and western hemlock, and three blocks for western redcedar and grand fir. The CF site was planted with only Douglas-fir and western redcedar, each with four blocks.

Treatments

All plots on both sites received a fall site preparation herbicide application prior to planting in the winter. The eight different treatments were spring release applications that can be defined by the number and timing of herbicide treatments (T) applied during the first 5 years after planting. For this study, only the control (C) and the 5 consecutive years of spring release vegetation managment treatment (VM) were used. Further details on treatment of the whole study can be found in Maguire et al. (2009).

On both sites, the herbicides applied for fall for site preparation consisted of sulfometuron (0.15 L/ha), metsulfuron (0.04 L/ha), and glyphosate (4.68 L/ha). Atrazine (4.5-4.9 kg/ha) and clopyralid (0.58-0.73 L/ha) were applied for the spring release treatments. If competing vegetation cover exceeded a 25% threshold during the growing season, glyphosate (1.5%-2.0%) was applied during the summer.

Stand Structure

Prior to the start of this study, the last stand inventories were conducted at age 12 years, corresponding to 2011 for the CR site and 2012 for the CF site. At both sites, Douglas-fir plots were thinned from below to reduce stocking by 20% at this age. In this study, inventories of tree height and DBH were conducted in March of 2016 and 2017. Table 2.1 summarizes stand characteristics in March of 2016. In treated plots, trees were larger and had higher survivability.

Table 2.1. Average trees per ha (TPHA, ha^{-1}), basal area (BA, $m^2\ ha^{-1}$), quadratic mean diameter (QMD, cm), and volume outside bark (VOB, $m^3\ ha^{-1}$) for 15-16 year old Douglas-fir, western hemlock, western redcedar, and grand fir trees growing under contrasting treatments of vegetation management on sites located in the central coast range (CR; 16 years) and the cascade foothills (CF; 15 years) of western Oregon.

Site	Species	Treatment	TPHA	BA	QMD	VOB
CR	Douglas-fir	C	688	18.4	18.5	127.4
		VM	696	23.6	20.8	169.7
	western hemlock	C	868	13.7	18.4	44.1
		VM	1025	33.1	27.8	124.8
	western redcedar	C	798	4.7	10.6	19.8
		VM	967	17.9	20.6	83.2
	grand fir	C	927	11.1	16.7	29.8
		VM	997	31.8	27.7	97.5
CF	Douglas-fir	C	696	12.8	15.9	73.9
		VM	710	21.6	20.2	139.6
	western redcedar	C	351	4.2	12.5	18.6
		VM	935	14.4	15.9	64.9

Overstory Biomass

In March of 2016 treatments plots at both study sites were inventoried. DBH and height of all living measurement trees were measured with metric diameter tapes (mm) and Haglof Vertex IV (cm), respectively.

Selection of Biomass Trees

Sample trees for developing biomass equations were selected using the 2016 inventory data. Trees were categorized by DBH into the following four classes: between the 1st and 24th percentile, the 25th and 49th percentile, the 50th and 74th percentile, and the 75th and 99th percentile. The mean DBH within each class was the target DBH for selected sample trees. These DBH targets were randomly assigned to a plot and the tree closest to the target DBH was selected from the buffer row (Appendix Figure 3). Proximity to desired DBH and ease of felling were factors for tree selection. Four trees per species, treatment, and site were selected for biomass determination.

Tree Biomass Measurements

In June and July of 2016, all selected trees were felled (32 trees at the CR site, 16 trees at the CF site). Once on the ground, the height (cm) and the length of the living crown (cm) or each tree were measured. The diameters of all branches were then measured at the stem insertion point using calipers (mm). The position of each branch in the main stem, as distance from the base (cm), was also recorded. Main stem diameter (mm) and bark thickness (mm) were measured at stump height (50 cm), breast height (DBH, at 137 cm) and every two meters from stump height using a metric diameter tape and a metric Haglof Barktax Bark Gauge, respectively.

Component Biomass Samples

Once the diameter at insertion point and position on the stem were recorded for all living and dead branches, the living crown of each tree was divided into thirds and two living branches were collected from each third (6 samples per tree, 48 samples per species). If there were dead branches below the start of the living crown, two dead branches were also collected on each tree. To facilitate manipulation of samples, a blue tarp was extended on the ground where branches were placed after being excised from the main stem. Later the sample branches were cut into smaller sections and placed into labeled Ziploc bags. All samples were then placed in a cooler with ice packs. From the main stem, five cross sections of 5-10 cm in width were taken at: i) stump height, ii) breast height, iii) between breast height and crown base, iv) crown base, and v) between crown base and top of the tree. All cross sections were labeled with a red wax pencil and placed in a cooler with the branch samples. Samples that were not being processed during the same day were stored in a cold room, at 8°C, located in the Oak Creek Complex at Oregon State University.

Processing and Weighing of Biomass Samples

In the laboratory, one branchlet encompassing the full range of foliage ages was placed in a small Ziploc bag, labeled, and stored in a refrigerator for specific leaf area determination. Each branch sample was separated into wood and foliage and placed in marked aluminum bins. They were then placed in a Moore-Kiln REI TT drying oven which was set to 74°C. Samples were left in the oven for at least 72 hours. After that time, the weight of wood and foliage of each branch sample was determined using an OHAUS NV4101 scale (g).

Each wood disc was first scanned with an HP Scanjet G4050. Then, the diameter and thickness of the cross section were measured with a meter stick (mm) in four directions by turning the sample 45° clockwise. From the four diameter and thickness measurements taken from the five cross section samples, an average diameter and thickness was calculated for each cross section and the fresh volume for each sample (inside and outside bark) was determined as a cylinder (cm^3). Volume of the bark was then determined as the difference. The bark was then removed and the cross sections and the bark were placed in the drying oven at 74°C for at least 72 hours. After that time, the dry weight of wood and bark of each disc sample was determined (g). Then the density of wood and bark was calculated as dry weight over fresh volume (g cm^{-3}).

Leaf Area

Projected specific leaf area (SLA, cm^2 g^{-1}) was estimated for each branch sample using the first order branches previously stored in the refrigerator. At least 60 needles were scanned for each Douglas-fir, western hemlock, and grand fir sample. For western redcedar at least one foliage spray was scanned. The projected area of the needles and the foliage sprays was estimated using ImageJ software (https://imagej.nih.gov) and the scanned images. Both the scanned subsamples and the first order branch sample were placed in the drying oven for at least 72 hours. They were weighed separately and then added to the weight of the overall branch sample. The SLA of each branch was determined as the ratio between the projected area and the dry mass of each sample (Appendix Table 2). Leaf area (LA, cm^2) of each branch was calculated as the product of SLA and dry weight of foliage.

Estimating Stemwood Biomass

Using Smalian's Formula and the diameter measured at 2 m intervals, the volume of the wood and bark at each 2 m section was determined (cm^3). The volume for the stump (50 cm in height) was calculated as a cylinder. The volume for the top of the tree was calculated as a cone. A wood density was assigned to each 2 m interval depending on its position on the tree and the position at which the cross-section sample was derived (average wood and bark density values can be found in Appendix Table 2). By multiplying the volume and the density, the dry weight of wood and bark of each 2 m section was determined (kg). The sum of these values represents the dry weight of the stem wood and bark for the whole tree.

Estimating Branch Biomass

Using Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC), several non-linear regression models were fitted to the branch samples to develop species-specific branch biomass equations. Models were selected based on BIC and

R^2 values. Models were fit for dead branchwood, live branchwood, foliage mass, and leaf area. For each species, in addition to diameter at branch insertion point and position on the main stem, site and treatment were tested as covariates. The selected equations were then applied to the full set of branch measurements of the 48 trees sampled. The sum of these values resulted in the dry weight of the dead branchwood, live branchwood, foliage, and leaf area for the whole tree.

Tree Level Biomass and Leaf Area Equations

Once the total volume of stemwood and bark, the total projected LA, and stemwood, bark, dead branchwood, live branchwood, and foliage biomass of all sampled trees was calculated, predictive equations were developed to estimate these variables using DBH and height as main predictors. Various non-linear models were tested. Different equations were developed for each site, species, and treatment. Models were selected based on BIC and R^2 values.

Stand Level Biomass Estimations

The selected tree level species-specific equations for total volume of stemwood and bark, the total projected LA, and stemwood, bark, dead branchwood, live branchwood, and foliage biomass were then applied to the age 16 years stand inventory. Each of these variables was then summed up by plot and expressed in m^3/ac for volume, m^2/ac for LA, and Mg/ac for biomass.

Thinning Residues

At both sites, all Douglas-fir plots were pre-commercially thinned (CR site in 2011, CF in 2012) and as all cut trees were left on site, this biomass had to be accounted for. As the DBH and height, and thus the biomass, of the trees removed on each plot was known from plot inventories at time of thinning, the current biomass of the thinned stems (currently on the ground) was determined by accounting for changes in stem wood density over the past 5 or 6 years. To accomplish this, in May of 2017, 10 stem samples were randomly collected from the thinned Douglas-fir stems at each site. The samples were 50 cm in length and cut from different sections at different positions along the stem. The density of stemwood residues 5 years after thinning was determined for each sample as described above for wood discs.

Midstory Biomass

In each plot, six 4 m^2 subplots were randomly placed using a cross made of pvc pipes (Appendix Figure 3). Subplots were sampled in May of 2016. All the hardwoods that were greater than 1.37 m in height that were within the subplot limits were measured and the species was recorded. Generalized biomass functions from Chojnacky et al. (2014), Ohmann et al. (1976), and Ter-Mikaelian and Korzukhin (1997) were applied to estimate the aboveground biomass for all hardwood species found at the sites with the exception of cascara buckthorn. (*Rhanmus purshiana* (D.C.) Cooper) (Table 2.2). Within the 0.06 ha measurement plot, all non-crop trees that were larger than 15 cm in DBH, were considered volunteer trees. The DBH of all these trees was measured and the species was recorded. For conifer volunteers, primarily Douglas-fir in C plots of the other three species, the biomass equations developed for crop trees were used.

Table 2.2. List of hardwood species and range of diameter at breast height (DBH, 1.37 m) measured in the year 2016.

Code	Species	DBH Range (cm)
ACCI	vine maple (*Acer circinatum* Pursh.)	1.0-4.0
ACMA	bigleaf maple (*Acer macrophyllum* Pursh)	1.5-20.0
ALRH	white alder (*Alnus rhombifolia* Nutt.)	0.1-2.8
ALRU	red alder (*Alnus rubra* Bong.)	0.5-19.0
CHCH	golden chinquapin (*Chrysolepis chrysophylla* (Douglas x Hook.) Hjelmqvist)	13.5
COCO	beaked hazelnut (*Corylus cornuta* Marsh.)	0.8-2.9
PREM	bitter cherry (*Prunus emarginata* (Dougl. ex Hook.) D. Dietr.)	0.5-12
RHPU	cascara buckthorn (*Rhanmus purshiana* (D.C.) Cooper)	0.7-7.8

Biomass Equation for Cascara Buckthorn

A species-specific biomass function was developed for cascara buckthorn as we did not find species-specific equations in the literature. In July of 2016, seven trees were selected at the CR site for destructive sampling. The DBH of sampled trees encompassed the range of DBH's measured in the subplots. The trees were cut at ground level, and total height and DBH were measured. Branches were cut from the stem and placed in Ziploc bags along with the foliage. The stem was cut into smaller sections to facilitate transportation. In the lab branches were separated from foliage, placed in aluminum trays, and put in the drying oven at 74°C for at least 72 hours and then weighed using an OHAUS NV4101 scale. An equation was created using DBH as the main predictor. Biomass equations of hardwood species were then applied to the age 16 years midstory and volunteer inventory. Biomass was summed up per plot and expressed in Mg/ac. For the midstory, biomass per ha was estimated using an expansion factor of 0.024. Biomass of volunteer trees per ha was estimated in the same manner as overstory tree biomass.

Understory Biomass and Forest Floor

The understory and forest floor biomass of each plot was determined in each of the six subplots where the midstory was measured. Samples were collected in August of 2016 using a 0.6 x 0.6 frame that was placed over the center of the 4 m^2 subplots. Previous to biomass collection, the percent cover of the understory was estimated visually by life form (moss, graminoids, forbs, and small shrubs/vine shrub) in each 0.36 m^2 subplot. All vegetation inside the subplot was then clipped at ground level and placed into bags. Vegetation that came over the top of the metal frame and belonged to a plant that was less than 1.37 m in height was also clipped. Once the vegetation was sampled, the forest floor was raked and collected down to bare mineral soil and placed in a labelled bag. In the case of the Douglas-fir plots that were thinned, thinning residues were left on site. Along with forest floor, fine woody debris (FWD), consisting mainly of branches, was also collected from each 0.36 m^2 subplot.

In the laboratory, understory and forest floor samples were placed in the drying oven in aluminum bins and dried at 74°C for at least 72 hours. After that time, understory samples were separated by life form and weighed. Forest floor and FWD were also weighed using the OHAUS NV4101 scale. Understory and forest floor was then summed up per plot and expressed in Mg/ac. The understory and forest floor biomass per ha was estimated using an expansion factor of 0.00036.

Fine Roots, Soil Bulk Density, and Soil Organic Matter

In May 2016, at the same time as the midstory DBH measurement, a soil core was extracted at the center of the six subplots. The soil cores were sampled using pvc tubes of 5.1 cm in diameter and 20 cm in length. All six cores from each treatment plot were placed into one bag, providing one composite sample per plot.

In the laboratory, the soil samples were sieved in a 2 mm sieve and fine roots were removed. Soil and fine root samples were placed in aluminum trays and put in the drying oven at 74°C for at least 72 hours. After that time, dry weight of fine roots and soil was determined using the OHAUS NV4101 scale.

Bulk density (g cm^{-3}) was estimated using the dry weight of the soil and the volume of the soil core. Two grams of each soil sample were stored in a glass vial for soil organic matter determination.

In the Forest Soils Lab at Oregon State University, a ceramic crucible was weighed for every two grams of soil that were stored in glass vials. The weight of the crucible with the soil sample was also recorded. Samples were then heated in muffle furnace set at 288°C for 24 hours. After that time, samples were reweighed. Soil organic matter percentage (SOM %) was calculated as the quotient of the difference between sample weight and the dry weight and the difference between sample weight and the weight of the crucible.

Data Analysis and Model Fitting

SAS verstion 9.4 was used for testing all volume and biomass equations. All equations were developed using PROC REG. When considering site-specific equations, the confidence interval of predictor variables were analyzed and since there was overlap, only species-specific equations were developed. To determine predictor variables, the stepwise method was used on log transformed data. For models, differences among species were assessed using analysis of variance (ANOVA).

SAS version 9.4 was used for all statistical analysis. All analyses were conducted using PROC MIXED. Treatment and site means were compared for tree and ecosystem components of all species with Tukey multiple comparisons tests (μ_i - μ_j). Mean tree and ecosystem differences between site, species, and treatments, as well as interactions between site, species, and treatments were tested for using ANOVA.

CurveExpert Professional version 2.6.3 (Hyams Development) was used for exploratory curve analysis. SigmaPlot version 13.0 (Systat Software, Inc. San Jose, CA) was used for linear model fitting and for creating all figures.

Results

Stem Volume

Parameter estimates and fit statistics of the models to estimate volume outside bark (VOB, m^3) and volume inside bark (VIB, m^3) for planted Douglas-fir, western hemlock, western redcedar, and grand fir are shown in Appendix: Table 3. As there were no differences in parameter estimates across sites ($P>0.25$), data were pooled to estimate volume functions that can be broadly applied. The coefficient of determination (R^2) was larger than 0.99 for all species. Height (HT) was not a significant parameter for estimating VOB or VIB for western redcedar.

The current annual increment in stem VOB (CAI, $m^3\ ha^{-1}\ yr^{-1}$), between the ages of 16 and 17 at the CR site, and 15 and 16 at the CF site, was calculated for each plot using the equations shown in Appendix: Table 3 and plot inventory data (Figure 2.1). There was a large gain in stem volume production for all species on both sites in response to sustained VM treatments ($P<0.05$), except for Douglas-fir growing at the CR site which showed no difference between treatments ($P=0.32$). Western hemlock and grand fir in VM treatment plots had the largest CAI, about 42 $m^3\ ha^{-1}\ year^{-1}$. On average, VM treated western hemlock and grand fir continue growing 20-25 $m^3\ ha^{-1}\ yr^{-1}$ more than the C plots. At the CF site, VM treated Douglas-fir continues to grow about 16 $m^3\ ha^{-1}\ yr^{-1}$ larger than the C treatment. When comparing sites, Douglas-fir in C plots had lower CAI at the CF site. Sustained VM treated Douglas-fir had similar CAI across both sites. Western redcedar was the opposite; CAI was similar in the C plots across both sites, and higher with sustained VM at the CR site.

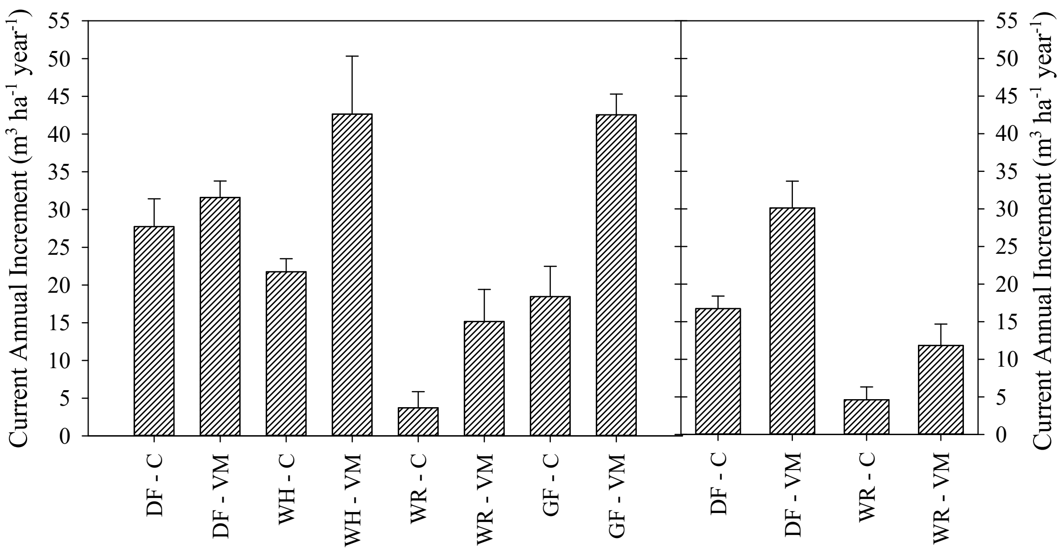

Figure 2.1. Average current annual increment in stem volume outside bark (CAI, m^3 ha^{-1} yr^{-1}) for Douglas-fir (DF), western hemlock (WH), western redcedar (WR), and grand fir (GF) stands growing under contrasting treatments of vegetation control on sites located in the coast range (CR, 16-17 year old, left panel) and in the cascade foothills (CF, 15-16 year old, right panel). C: control, VM: sustained vegetation management for first 5 years post planting. Error bars represents standard error.

Branch Level Biomass and Leaf Area Equations

Parameter estimates and fit statistics of the models to estimate branch wood biomass, foliage, and projected leaf area for all species is shown in Appendix: Table 4. As there were no differences in parameter estimates across sites (P>0.25), data was pooled to estimate functions that can be broadly applied. The coefficients of determination (R^2) ranged between 0.84 and 0.98. Dead branch biomass (BD) depended only on branch diameter at insertion point (D_b). In most cases, including branch relative depth into the living crown (Hr) improved the model fitting. These functions were used to estimate tree-level biomass and projected leaf area equations.

Tree Level Biomass and Leaf Area Equations

Parameter estimates and fit statistics for estimating stem wood (W), stem bark (B), live branch (LB), dead branch (DB), and foliage (F) biomass (kg $tree^{-1}$), as well as projected leaf area (LA, m^2 $tree^{-1}$), are shown in Appendix: Table 5. Similar to stem volume, as there were no differences in parameter estimates across sites

(P>0.32), data was pooled. Overall, R^2 ranged between 0.74 and 0.99. For Douglas-fir and western hemlock trees, W depended on DBH and HT. For grand fir trees, W biomass depended only on DBH and western redcedar depended only on HT. For all species, all other variables, including LA, depended only on DBH. The exception was B for grand fir which depended on both, DBH and HT.

Leaf Area Index

Projected leaf area index (LAI, $m^2 m^{-2}$) was calculated using the leaf area equations shown in Appendix: Table 4 and the inventory data collected at age 16 at both sites. There was a significant increase in LAI under sustained VM treatments at both sites (P<0.01) (Figure 2.2). LAI of western hemlock was greater than the other species. There was no difference in LAI between sites (P>0.46).

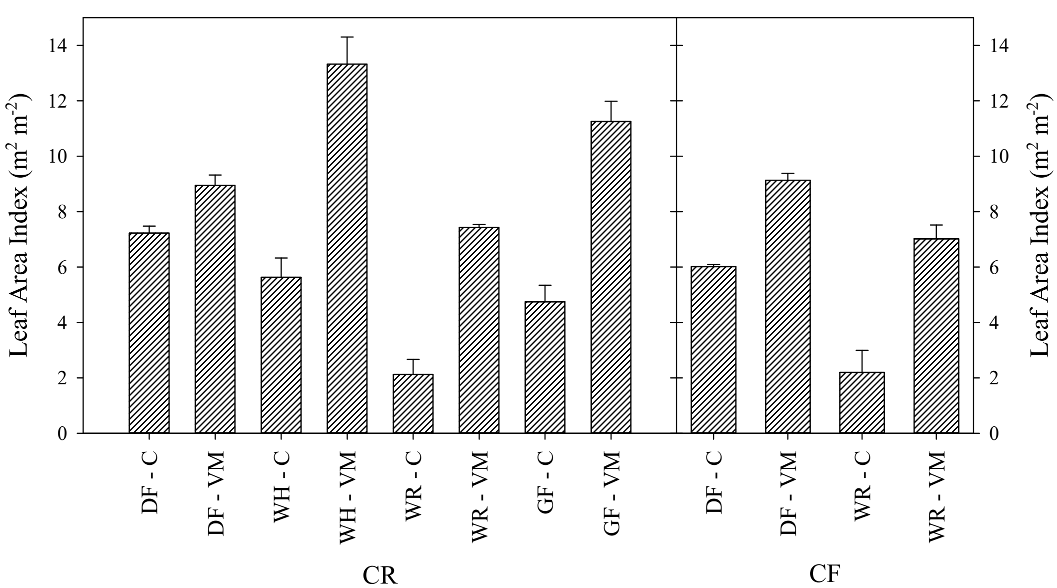

Figure 2.2. Projected leaf area index ($m^2 m^{-2}$) for 16-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WR), and grand fir (GF) stands growing under contrasting treatments of vegetation control on sites located in the coast range (CR, left panel) and in the cascade foothills (CF, right panel). C: control, VM: sustained vegetation management for first 5 years post planting. Error bars represents standard error.

There was a strong linear relationship between basal area (BA, m^2 ha^{-1}) and LAI. This stems from the pipe model theory, which proposes that a unit weight of foliage is supported by a specific cross-sectional area of sapwood (Waring et al. 1982). All species across both sites shared the same relationship ($P<0.001$, $R^2=0.98$) (Figure 2.3).

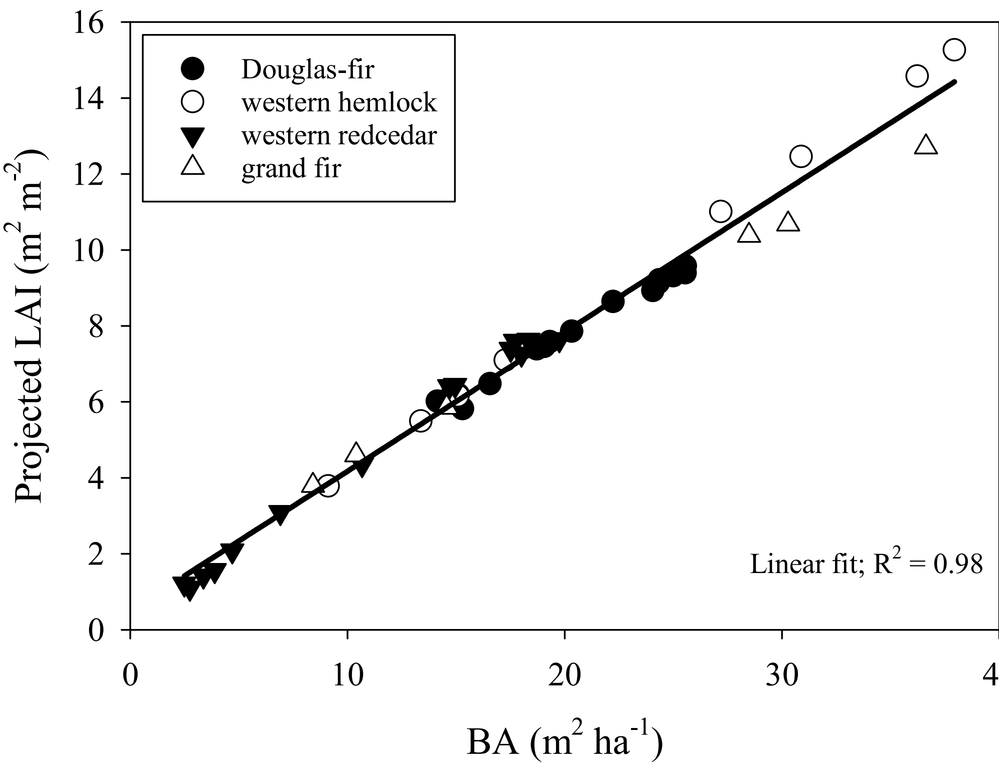

Figure 2.3. Relationship between basal area (BA, m^2 ha^{-1}) and projected leaf area index (LAI, m^2 m^{-2}) for 16-year-old Douglas-fir, western hemlock, western redcedar, and grand fir stands. A similar relationship was shared for all species growing under contrasting treatments of vegetation control on both sites.

Parameter estimates and fit statistics for the relationships between BA and projected LAI are shown in Table 2.3. On average, for every 1 m^2 ha^{-1} BA increment, LAI increased by 0.367 m^2 m^{-2}.

Table 2.3. Parameter estimates and fit statistic of the equation for predicting projected leaf area index (LAI, $m^2\ m^{-2}$) for Douglas-fir, western hemlock, western redcedar, and grand fir stands growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Model	Parameter	Parameter Estimate	SE	R^2	RMSE
$LAI = a + b \cdot BA$	a	0.5038	0.1463	0.98	0.428
	b	0.3670	0.0073		

BA: crop tree basal area ($m^2\ ha^{-1}$); LAI: projected leaf area index ($m^2\ m^{-2}$); R^2: coefficient of determination; RMSE: root mean square error. For all parameter estimates: $P < 0.05$.

Crop Tree Biomass

Similar to stem volume, using the equations shown in Appendix: Table 5 and plot inventory data measured at age 16 on both sites, aboveground stand biomass was calculated for each plot (Figure 2.4). At both sites, stand-level tree biomass was greatly increased under sustained VM treatments. At the CR site, average biomass gain was 26.5, 91.2, 44.7, and 96.1 Mg ha^{-1} for Douglas-fir, western hemlock, western redcedar, and grand fir, respectively. At the CF site, the average biomass gain was 48.1 Mg ha^{-1} for Douglas-fir and 42.2 Mg ha^{-1} for western redcedar. Differences in biomass allocation among the species were observed. Western redcedar allocated more biomass to foliage and live branches than the other species ($P<0.0001$). The other species allocated more biomass to stemwood and bark. Total tree biomass was significantly different ($P<0.009$) between treatments for all species at both sites. These differences were primarily observed in stem and bark. However, differences in biomass allocation were not observed between sites for Douglas-fir and western redcedar.

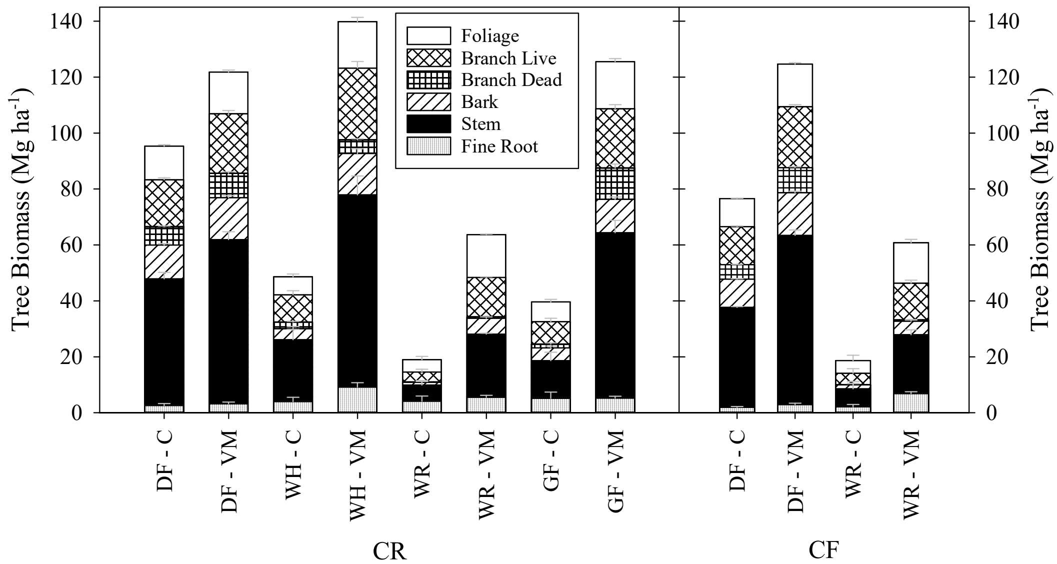

Figure 2.4. Biomass stock (Mg ha^{-1}) of tree components for 16-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WR), and grand fir (GF) stands growing under contrasting treatments of vegetation control on sites located in the Coast Range (CR, left panel) and in the Cascade foothills (CF, right panel).). C: control, VM: sustained vegetation management for first 5 years post planting. Error bars represents standard error.

Ecosystem Biomass

When other ecosystem components, such as midstory, understory, forest floor and thinning residues, are taken into account, total ecosystem biomass was greater with sustained VM with the exception of western hemlock, western redcedar, and grand fir at the CR site (Figure 2.5). At the CR site, the average total ecosystem biomass of the Douglas-fir, western hemlock, western redcedar and grand fir C plots was 124.9, 116.2, 38.2 and 89.2 Mg ha^{-1}, respectively. The increase in total ecosystem biomass due to VM was 32.5, 31.6, and 47.9 Mg ha^{-1} for Douglas-fir, western hemlock, and grand fir, respectively. The C plots for western redcedar at the CR site had 24.8 Mg ha^{-1} greater total ecosystem biomass than the VM treated plots due to a more established midstory. At the CF site, the average total ecosystem biomass for control Douglas-fir and western redcedar stands was 98.0 and 38.0 Mg ha^{-1}, respectively. At this site, the increase due to sustained VM was 56.9 and 34.3 Mg ha^{-1}, for Douglas-fir and western redcedar, respectively.

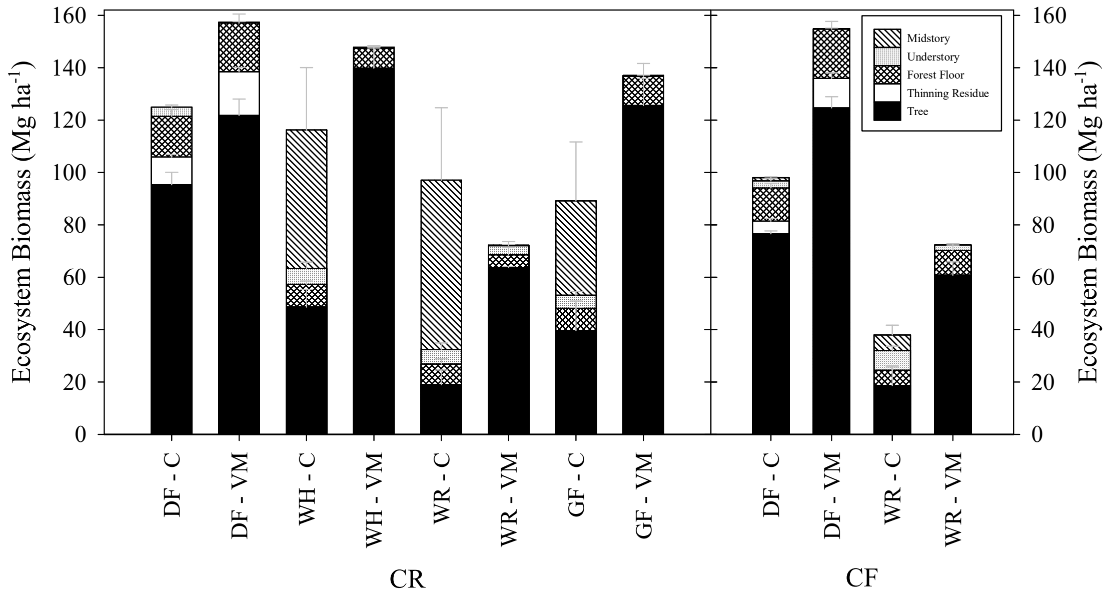

Figure 2.5. Average biomass stock (Mg ha^{-1}) of ecosystem components for 16-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation control on sites located in the Coast Range (CR, left panel) and in the Cascade foothills (CF, right panel). C: control, VM: sustained vegetation management for first 5 years post planting. Error bars represents standard error.

The models and parameter estimates used to estimate biomass for all midstory species are shown in Appendix: Table 6. In C plots of the CR site, the midstory represented a large component of the ecosystem biomass of western hemlock, western redcedar, and grand fir plots. The diversity of hardwood species growing in the midstory differs between crop species, however bitter cherry was the most prevalent species with an average biomass ranging between 26-41 Mg ha^{-1} (Figure 2.6). As all midstory was removed when the Douglas-fir plots were pre-commercially thinned, negligible midstory biomass was observed in those plots. At the CF site, midstory biomass was a minor component of ecosystem biomass.

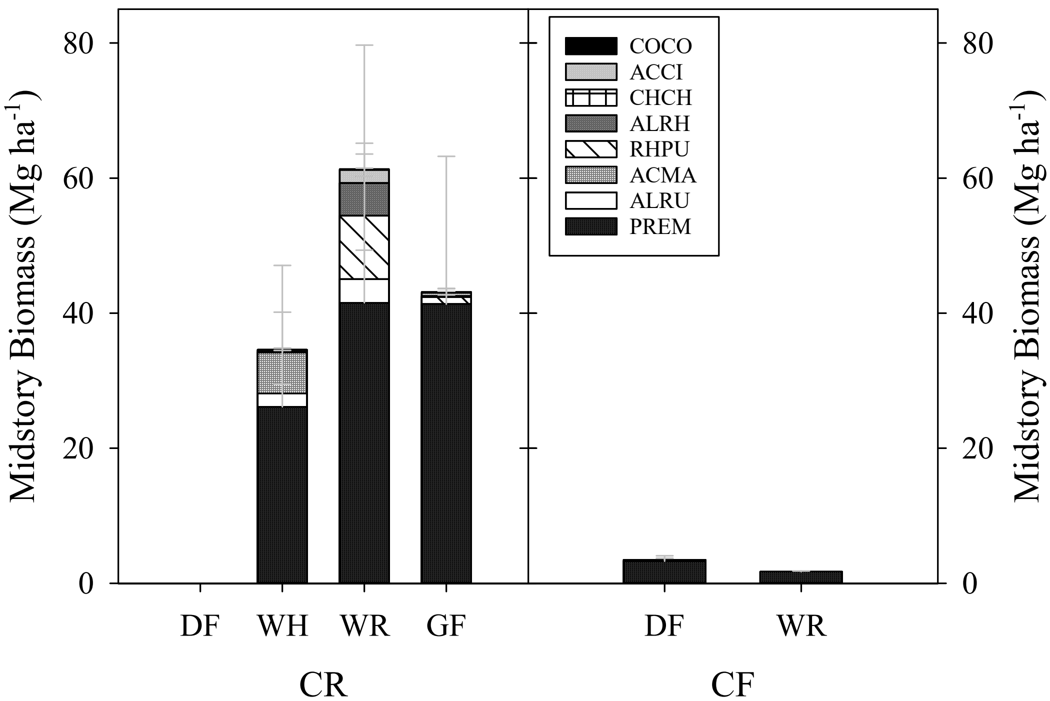

Figure 2.6. Average biomass stock (Mg ha^{-1}) of midstory for stands of 16-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under no vegetation control after planting (control treatment) on sites located in the Coast Range (CR, left panel) and in the Cascade foothills (CF, right panel). See Table 2.2 for species code description.

All life forms were grouped together in understory, as biomass of graminoids and forbs was minimal. However, moss was a large component of understory biomass in comparison to other life forms and we decided to analyze it separately. A relationship between understory percent cover and understory biomass and moss percent cover and moss biomass are shown in Figure 2.7. On average for an understory cover percent of 50, understory biomass was about 1.1 Mg ha^{-1}. For the same cover percent, moss biomass was 3.3 Mg ha^{-1}. Although cover percent could be the same between understory and moss, moss was denser than understory vegetation life forms.

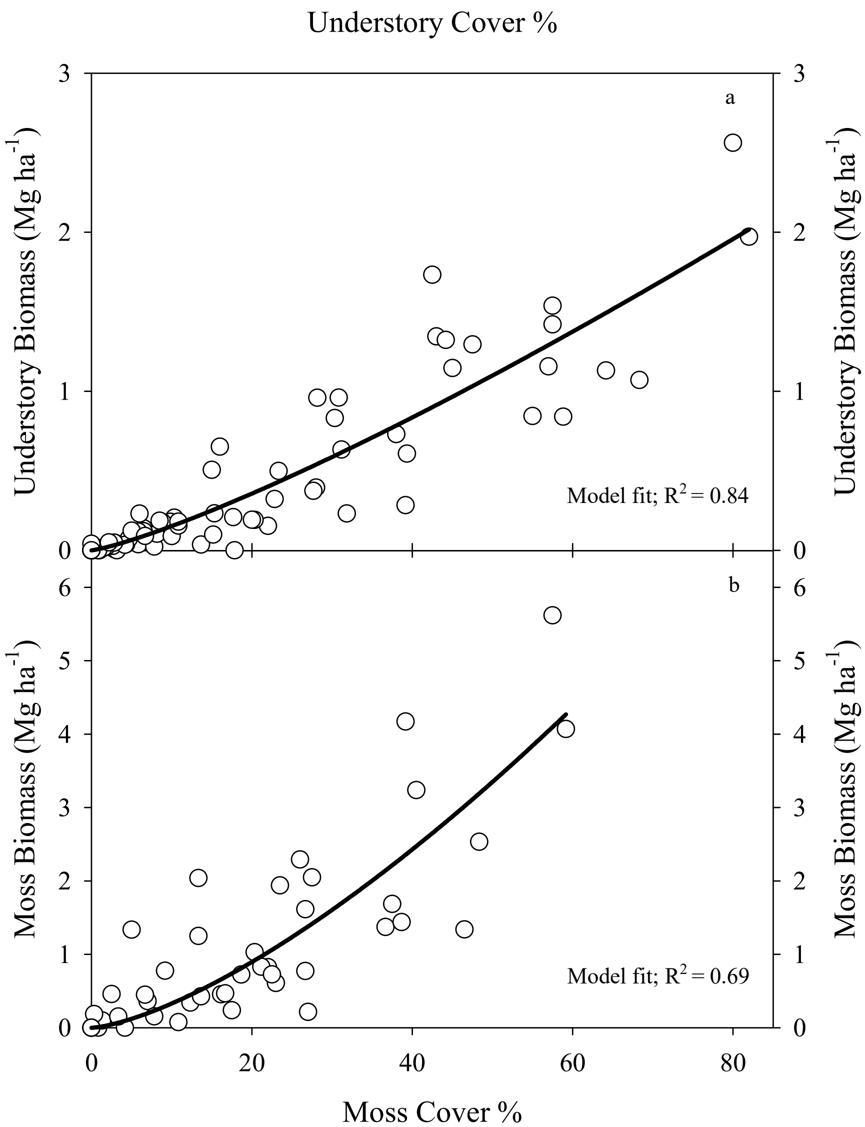

Figure 2.7. Relationship between a) understory percent cover and understory biomass (Mg ha^{-1}) and b) moss cover percent and moss biomass (Mg ha^{-1}) for 16-17-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing on sites located in the central coast range and the cascade foothills of western Oregon.

Parameter estimates and fit statistics for the relationships between understory percent cover and understory biomass and moss percent cover and moss biomass are shown in Table 2.4.

Table 2.4. Parameter estimates and fit statistic of the equations for predicting understory and moss biomass (Mg ha^{-1}) for Douglas-fir, western hemlock, western redcedar, and grand fir stands growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Model	Parameter	Parameter Estimate	SE	R^2	RMSE
$Understory\ biomass = a \cdot \%\ cover^{b}$	a	0.0090	0.0034	0.84	0.2119
	b	1.2278	0.0931		
$Moss\ biomass = a \cdot \%cover^{b}$	a	0.0120	0.0089	0.69	0.7028
	b	1.4396	0.1966		

%cover: visual estimation of cover percent; SE: standard error; R^2: coefficient of determination; RMSE: root mean square error. For all parameter estimates: $P < 0.05$.

Density of thinning residues was 23% lower than density of standing stemwood (P<0.05) (Figure 2.8). There was no difference in density of thinning residues between sites (P>0.35). The average decay rate for stemwood, determined as a negative exponential, was 6.0 and 6.6% at the CR site and the CF site, respectively. The bark of thinning residues was not accounted for.

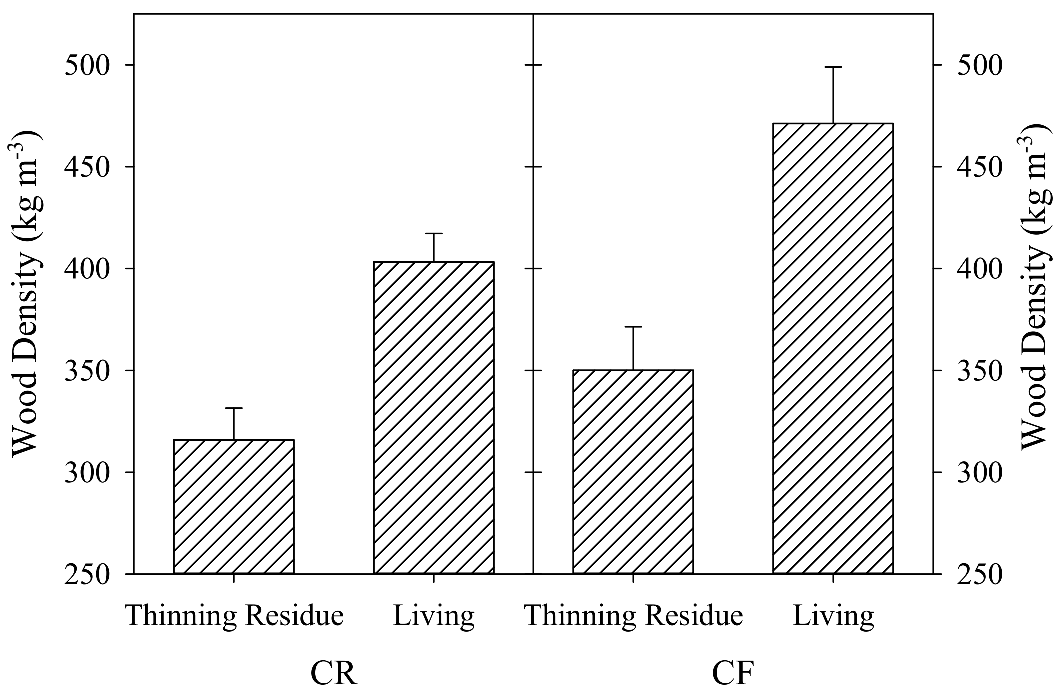

Figure 2.8. Average wood density (kg m^{-3}) of thinning residues 6-7 years after cut and 16-year-old standing stemwood of Douglas-fir located in the Coast Range (CR, left panel) and in the Cascade foothills (CF, right panel).

There was a trend of increased bulk density, decreased organic matter concentration, and decreased organic matter content of top soil on VM treated plots, however, these differences were not significant between treatments and sites (Table 2.5).

Table 2.5. Soil bulk density, organic matter concentration (OM%), and organic matter content (OMC) of 0-20 cm depth of soils for Douglas-fir, western hemlock, western redcedar, and grand fir stands growing under contrasting vegetation control treatments in the Coastal Range (CR) and Cascade foothills (CF). SE is the standard error.

		CR					CF					
Species	Characteristics	C	SE	VM	SE	P-Value	C	SE	VM	SE	P-Value	P-Value*
Douglas-fir	Bulk Density	0.74	0.04	0.76	0.03	0.632	0.66	0.06	0.71	0.05	0.477	0.086
	OM%	19.2	0.02	18.3	0.01	0.684	18.9	0.01	19.2	0.01	0.855	0.795
	OMC	282.3	27.2	276.8	11.0	0.836	246.4	7.18	269.2	9.35	0.067	0.137
western hemlock	Bulk Density	0.67	0.04	0.68	0.02	0.823						
	OM%	19.7	0.01	19.5	0.01	0.862						
	OMC	263.6	6.42	265.9	8.45	0.810						
western redcedar	Bulk Density	0.64	0.05	0.73	0.05	0.168	0.71	0.05	0.75	0.04	0.542	0.255
	OM%	22.2	0.04	17.9	0.01	0.248	17.1	0.01	16.7	0.02	0.793	0.096
	OMC	277.5	28.9	259.5	11.4	0.518	246.3	31.8	248.3	23.3	0.955	0.355
grand fir	Bulk Density	0.69	0.07	0.71	0.05	0.849						
	OM%	19.9	0.04	19.3	0.03	0.858						
	OMC	272.6	27.2	271.4	32.7	0.974						

Bulk density: g cm^{-3}; OM%: soil organic matter concentration (%); OMC: soil organic matter content (Mg ha^{-1}). C: control, VM: sustained vegetation management for first 5 years post planting. P-Value for treatment differences within sites. P-Value* for site differences.

A summary of all biomass pools is presented in Table 2.6, except for soil organic matter content (Table 2.5). Significant ($P<0.05$) differences are highlighted in bold. Biomass of fine roots only differed between treatments for western hemlock at the CR site ($P=0.04$). Understory biomass was significantly different for all species at both sites, with the exception of western redcedar at the CR site ($P=0.54$). Midstory biomass was only significantly different between treatments for Douglas-fir at the CF site ($P<0.01$). Forest floor biomass did not differ between treatments for any species for both sites. Total ecosystem biomass did differ between treatments for western hemlock, western redcedar, and grand fir at the CR site ($P>0.13$).

Table 2.6. Biomass stock (Mg ha^{-1}) of tree and ecosystem components for 16-year-old Douglas-fir, western hemlock, western redcedar, and grand fir stands growing under contrasting treatments of vegetation control on sites located in the Coast Range (CR) and in the Cascade foothills (CF). SE is the standard error. The P-value shown, for each site, is in bold if the difference in biomass stock was significant at α=0.05.

		CR					CF					
Species	Component	C	SE	VM	SE	P-Value	C	SE	VM	SE	P-Value	P-Value*
Douglas-fir	Tree	95.3	4.8	121.8	5.6	**0.006**	76.6	1.1	124.7	4.2	**<0.0001**	0.478
	Fine Roots	2.6	0.7	3.2	0.6	0.483	1.9	0.3	2.9	0.5	0.074	0.343
	Foliage	12.0	0.5	14.9	0.7	**0.009**	10.0	0.1	15.2	0.5	**<0.0001**	0.486
	Branch	23.3	0.9	30.0	1.7	**0.007**	18.8	0.4	30.7	1.1	**<0.0001**	0.497
	Stem	45.2	2.3	58.7	2.8	**0.005**	35.7	0.3	60.5	1.9	**<0.0001**	0.499
	Bark	12.1	0.5	15.0	0.7	**0.009**	10.1	0.1	15.3	0.5	**<0.0001**	0.485
	Thinning Res	10.6	1.0	16.6	1.7	**0.011**	4.9	1.0	11.2	2.1	**0.021**	**0.018**
	Midstory	0.0	0.0	0.0	0.0	-	1.2	0.3	0.0	0.0	-	-
	Understory	3.5	0.9	0.4	0.2	**0.007**	2.7	0.8	0.2	0.1	**0.011**	0.587
	Forest Floor	15.5	2.6	18.6	3.5	0.450	12.6	1.8	18.8	2.9	0.083	0.621
	Total	124.9	2.3	157.4	7.5	**0.003**	98.0	1.8	154.9	5.0	**<0.0001**	0.275
western hemlock	Tree	48.6	8.6	139.8	11.8	**0.0004**						
	Fine Roots	4.0	1.5	9.2	1.6	**0.035**						
	Foliage	6.5	1.0	16.6	1.5	**0.001**						
	Branch	12.1	1.8	30.5	2.7	**0.001**						
	Stem	22.2	3.7	68.7	6.7	**0.0004**						
	Bark	3.9	0.8	14.8	1.7	**0.001**						
	Midstory	52.9	23.8	0.0	0.0	-						
	Understory	6.0	2.5	0.5	0.2	**0.042**						
	Forest Floor	8.7	1.2	7.5	1.1	0.420						
	Total	116.2	22.0	147.8	12.3	0.198						
western redcedar	Tree	19.0	6.8	63.7	7.7	**0.001**	18.7	7.7	60.8	5.1	**0.002**	0.907
	Fine Roots	4.1	2.3	5.5	0.8	0.759	2.1	0.8	6.8	0.7	**0.002**	0.809
	Foliage	4.4	1.4	15.3	1.9	**0.001**	4.5	1.9	14.5	1.2	**0.002**	0.914
	Branch	3.7	1.3	14.6	1.7	**0.001**	4.2	1.7	13.6	1.1	**0.002**	0.929
	Stem	5.8	2.0	22.6	2.7	**0.001**	6.5	2.7	21.0	1.7	**0.002**	0.929
	Bark	1.0	0.4	5.7	0.5	**0.001**	1.4	0.5	4.9	0.4	**0.001**	0.878
	Midstory	64.7	33.8	0.2	0.3	0.102	5.9	3.7	0.0	0.0	-	0.086
	Understory	5.5	3.1	3.5	1.9	0.535	7.5	1.7	2.1	0.4	**0.011**	0.867
	Forest Floor	7.9	2.4	4.9	3.4	0.433	5.9	1.3	9.5	2.1	0.135	0.527
	Total	97.1	24.4	72.3	1.7	0.282	38.0	11.0	72.3	4.6	**0.016**	**0.043**
grand fir	Tree	38.2	10.3	134.3	10.5	**0.002**						
	Fine Roots	5.1	2.8	5.2	0.8	0.976						
	Foliage	7.0	1.1	16.9	1.4	**0.002**						
	Branch	8.0	3.5	41.2	8.4	**0.011**						
	Stem	13.5	3.7	59.1	5.4	**0.001**						
	Bark	4.6	0.8	12.0	1.1	**0.002**						
	Midstory	36.0	27.5	0.0	0.0	-						
	Understory	5.0	1.7	0.3	0.1	**0.027**						
	Forest Floor	8.5	3.4	11.2	6.0	0.662						
	Total	89.2	26.0	137.0	16.4	0.129						

P-Value for treatment differences within sites. P-Value* for site differences.

Table 2.7 summarizes analysis of variance (ANOVA) results. Significant (P<0.05) differences are highlighted in bold. A significant interaction between site, species, and treatment was only observed for midstory biomass. There was a significant interaction between species and treatment for total and component tree biomass. This interaction was also observed for whole-ecosystem biomass, as well as an interaction between site and treatment. There was a significant interaction between site and species for midstory biomass. Total and component tree biomass was significantly different between species and treatments. Midstory and understory biomass was significantly different between treatments. Understory biomass was significantly different between sites. Whole-ecosystem biomass was significantly different between sites, species, and treatments.

Table 2.7. Analysis of covariance (ANOVA) testing differences and interactions in total and component tree biomass stock and total and component ecosystem biomass stock. P-value is in bold if significant at $\alpha=0.05$.

Component	Site	Species	Treatment	Site x Species	Site x Treatment	Species x Treatment	Site x Species x Treatment
Tree	0.275	**<0.0001**	**<0.0001**	0.467	0.276	**<0.0001**	0.171
Fine Roots	0.570	**0.002**	**0.0004**	0.931	0.203	**0.026**	0.319
Foliage	0.367	**0.0003**	**<0.0001**	0.709	0.601	**<0.0001**	0.226
Branch	0.465	**<0.0001**	**<0.0001**	0.586	0.522	**<0.0001**	0.263
Stem	0.295	**<0.0001**	**<0.0001**	0.402	0.270	**<0.0001**	0.105
Bark	0.281	**<0.0001**	**<0.0001**	0.496	0.573	**<0.0001**	0.071
Midstory	0.066	0.089	**0.0004**	**0.047**	0.068	0.090	**0.048**
Understory	0.914	**0.012**	**<0.0001**	0.621	0.391	0.422	0.232
Forest Floor	0.995	**<0.0001**	0.092	0.428	0.143	0.495	0.599
Ecosystem	**0.007**	**<0.0001**	**<0.0001**	0.343	**0.011**	**0.021**	0.267
Bulk Density	0.715	0.655	0.171	**0.042**	0.783	0.824	0.451
OM%	0.183	0.971	0.459	0.105	0.235	0.579	0.516
OMC	0.088	0.743	0.737	0.983	0.330	0.878	0.867

Discussion

The research presented in this chapter represents one of the few attempts to quantify how FVM treatments impact the long-term ecosystem biomass accumulation of conifer plantations in the PNW. Species-specific biomass functions were developed for all four of the conifer species tested in this study. These functions are useful for estimating the biomass and leaf area of conifer stands in the PNW using simple inventory data.

Stem Volume Production

Eleven years after treatments ended, plots that had sustained VM treatment for 5 years post planting showed larger volume production from the C plots. This result indicates that the benefits of FVM treatments persist long after the treatments are applied. The largest CAI was observed on western hemlock and grand fir VM plots, averaging 43 Mg ha^{-1} yr^{-1}. That is comparable to (or even larger than) other fast-growing conifers, such as *Pinus taeda*, in the Southeast United states (Jokela et al., 2010) or *Pinus radiata*, in Chile and New Zealand (Lamprecht, 1990).

The reduced CAI of Douglas-fir (compared with western hemlock and grand fir) is assumed to be an effect of the reduced stocking due to a pre-commercial thinning at age 12. DBH and height of individual trees was fairly similar at age 15-16 between Douglas-fir, western hemlock, and grand fir. A pre-commercial thinning was carried out to deter intraspecific competition in Douglas-fir. Unthinned stands of western hemlock and grand fir may soon experience intraspecific competition as stand density index is approaching 39 and 54% of maximum, respectively.

Leaf Area Index

LAI of Douglas-fir was within the range of what has been reported for young Douglas-fir growing in the Oregon coast range (Weiskittel and Maguire 2007, Velazquez-Martinez et al. 1992). In most cases, LAI of crop trees was observed to be higher in treated plots, even though it has been 11 years since vegetation management ended. This larger LAI in stands without competing vegetation reflects lower mortality and larger resource availability for surviving trees as LAI has been shown to be correlated with nutrient (Velazquez-Martinez et al. 1992) and water availability (Grier and Running 1977). LAI of treated Douglas-fir and western redcedar did not differ per site.

Several studies have shown a strong relationship between sapwood area and leaf area (Bancalari and Perry 1986, Waring et al. 1982). In this chapter we presented a strong relationship between BA and LAI for the four species studied, indicating that all species have a similar sapwood to leaf area ratio, as the trees have little to no heartwood development at the age of sampling. Even though a similar trend has been reported in other studies (Eckrich et al. 2013, O'Grady et al. 2000), this is the first study reporting the same relationship for Douglas-fir, western hemlock, western redcedar, and grand fir trees of the same age. This relationship is helpful as BA can be easily determined and be used as a method of estimating LAI for stands of similar age.

Tree Biomass

We had to partly reject our first hypothesis, that trees growing in plots that had sustained vegetation management for first 5 years post planting have higher total tree and component biomass stock. Biomass stock in trees was greater in plots with sustained vegetation control, as were tree components with the exception of fine roots. It is important to note that coarse roots were not included in this study. To properly compare with values reported in literature, it is better to express biomass stock at a given age as mean annual increment (MAI, current biomass divided by age, Mg ha^{-1} yr^{-1}). The MAI of biomass of VM treated Douglas-fir (7.6 Mg ha^{-1} yr^{-1}) was larger than the values reported by Turner and Long (1975) for 22-year-old Douglas-fir growing in western Washington, (5.9 Mg ha^{-1} yr^{-1}). The MAI of VM treated western hemlock (8.7 Mg ha^{-1} yr^{-1}) was also larger than the values reported by Fujimori (1971) for a 26-year-old stand growing in the central Oregon coast (7.4 Mg ha^{-1} yr^{-1}). These other studies were conducted on naturally regenerated stands.

However, results from this study serve to show the remarkable productivity of stands without interspecific competition and reduced mortality.

Our second hypothesis, that tree response to sustained vegetation management differs between species and site, was also partly rejected. Mean total and component tree biomass was found to be significantly different between species, but no differences were observed between sites. Western redcedar allocated more biomass into branches and foliage, whereas the other species allocated more biomass into stemwood. In our study, the stemwood to crown biomass ratio for western redcedar was about 2.1 to 2.7 times lower that the other three species. The larger stemwood to crown biomass ratio observed in VM plots indicates that trees growing under condition of no interspecific competition are more effective at partitioning biomass towards stem production, which increases volume yield with less investment in crown tissue. A significant interaction in total tree biomass between species and treatment was also observed, suggesting that some species were more susceptible to competition than others. Douglas-fir appears to be the most tolerant species to competition at both sites.

Ecosystem Biomass

The third hypothesis, that the understory and midstory in plots without vegetation management served to partially counteract the positive effects of vegetation control on crop tree growth, was supported by our results. The midstory accounted for a large fraction of above ground ecosystem biomass for western hemlock, western redcedar, and grand fir plots that did not receive post planting competing vegetation control. We expect that the midstory of control Douglas-fir would have been a factor, had it not been cut in the pre-commercial thinning. Furthermore, for western redcedar growing at the CR site, the midstory accounted for 68% of total biomass. Without vegetation management, competing species, particularly bitter cherry, were allowed to outgrow western redcedar. The understory was not as big of a factor as the midstory. Turner and Long (1975) reported that understory biomass ranged between 1.1 and 7.6 Mg ha^{-1}, for stands with BA ranging between 32 and 57 m^{2} ha^{-1}. In our study, understory biomass ranged between 0.2 and 7.9 Mg ha^{-1}. For VM plots, it is expected that LAI will continue increasing and in turn further decrease understory biomass.

The fourth hypothesis, that ecosystem biomass stock is larger in sustained vegetation management plots and that it differs between species and sites, was partially rejected. When understory, midstory, and forest floor were accounted for, no differences in total ecosystem aboveground biomass were found between VM and C plots of western hemlock, western redcedar, and grand fir at the CR site. In C plots, total tree biomass accounted for about 75, 47, 19, and 43% of total aboveground biomass, for Douglas-fir, western hemlock, western redcedar, and grand fir stands, respectively. Turner and Long (1975) reported a value of 82% for 22-year-old Douglas-fir stands. Ecosystem biomass did differ between species. This resulted from differences between crop tress, as no differences were observed between midstory and understory biomass. Differences in ecosystem biomass between sites were minimal for western redcedar ($P=0.051$). This more than likely stemmed from the large store of biomass from the midstory at the CR site.

Forest floor biomass accumulation was found to be different across species, accounting for between 5 and 16% of total ecosystem biomass. The large forest floor accumulation observed in Douglas-fir stands (between 13 and 19 Mg ha^{-1}) is in part an effect of the accumulation of residues from the pre-commercial thinning and pruning carried out in the years of 2011 and 2012. Our observations are in agreement with Turner and Long (1975), who reported a forest floor biomass of 20.5 Mg ha^{-1} for a 22-year-old Douglas-fir stand.

Soil Organic Matter Content

The soil held the highest amount of biomass. This study only sampled the upper 20 cm of soil, but found that vegetation management had no effect on SOM. Johnson (1992) reported that a major disturbance such as clearcut harvests had minimal impact on SOM. In our study, SOM % ranged between 18 and 22% at the CR site and between 17 and 19% at the CF site. These values were lower than what was reported by Griffiths and Swanson (2001), about 24%, for a 15-year-old Douglas-fir stand in the central Oregon Cascade mountains. Due to trends observed across treatments, where OM% tend to be higher in C plots, we consider that future research should be conducted to assess the effects of treatments on SOM for deeper soil profiles.

Summary

The results of this study demonstrate that sustained FVM treatments during the first 5 years of stand establishment increased the biomass stock of Douglas-fir, western hemlock, western redcedar, and grand fir stands at age 16. This suggests that FVM treatments can accelerate the long-term carbon sequestration rate of planted forests in the PNW. However, in analyzing other ecosystem components, there was no increase in ecosystem biomass stock for western hemlock, western redcedar, and grand fir stands growing in the CR site at age 16. These results provide managers with options for FVM, depending on management objectives and site conditions. Differences observed between sites also serve to inform forest managers to know site characteristics, i.e. temperature, annual rainfall, and competing vegetation composition to develop an appropriate vegetation management plan.

The relationship observed between BA and projected LAI is a useful tool. LAI is a difficult variable to estimate, but is a key component in some process based models, as LAI is closely related to forest productivity and is the driving force of water and carbon gas exchange (Breda 2003), while BA is a common variable estimated in most forest inventories and growth and yield models. Additionally, the high productivity in the western hemlock and grand fir treated plots (CAI of 42 m^3 ha^{-1} $year^{-1}$) was found to be comparable to other fast-growing conifer species intensively managed in other parts of the world. The CAI of the Douglas-fir plots was less than that of western hemlock and grand fir, maybe due to a pre-commercial thinning treatment applied to the Douglas-fir plots, but we expect that the CAI of un-thinned Douglas-fir stands would be equal to or greater than these other species.

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Chapter 3: Long-term Effects of Vegetation Management on Aboveground Net Primary Productivity

Introduction

Sustainable intensive forest management should balance maximizing tree growth and protecting ecological services of forest. Intensive forest management includes different silvicultural practices such as genetic improvement, soil preparation, tree spacing at time of planting, vegetation management, fertilization, and thinning (Fox et al. 2007). These practices can result in an increased wood yield, but the long-term effects on ecological services, such as carbon sequestration are still poorly understood. It is important for forest managers to understand the long-term effects of intensive forest management, including forest vegetation management (FVM), on timber production and carbon sequestration, including not only crop trees, but all vegetation growing in the forest.

Net primary productivity (NPP, Mg ha^{-1} $year^{-1}$) is a widely used measure of forest productivity. It represents the net flux of C from the atmosphere into organic matter (i.e. foliage, branches, stems, reproductive organs, and roots). It can be measured as the sum of new organic matter retained by vegetation at the end of an established interval, and the organic matter that was produced and lost by vegetation in that same interval (Newbould 1967). When only the aboveground NPP (ANPP) is to be determined, and herbivory is assumed negligible, what is typically measured is litterfall and aboveground biomass increment.

While there has been research conducted on the ANPP of forests in the PNW, there has been little research on the effects that vegetation management has on ANPP (Bormann et al. 2015). Litterfall, a necessary component in estimating ANPP, has also been of research interest. While studies have been conducted on quantifying the effects of thinning (Dimmock II 1958, Reukema 1964), analyzing the effects that vegetation management is also lacking.

The Vegetation Management Research Cooperative (VMRC) at OSU installed two study sites in 2000 and 2001. These field installations are important resources for studying the long-term effects of FVM treatments on planted conifer growth and survival in the PNW. Both sites contain a wide range of vegetation management treatments tested on multiple crop tree species and have over 16 years of measurement data. This, in addition to the large differences between the treatments, made these sites ideal candidates to assess the impact of FVM on ecosystem processes.

This chapter covers the long-term effects of vegetation management at establishment on ANPP, including relationships between stand attributes and ANPP. This chapter also includes a review of reports on studies that have estimated ANPP of forests in the PNW. The method for estimating ANPP is described. Total tree ANPP ($ANPP_T$) and component tree ANPP (i.e. fine roots, stemwood, bark, live branches, and foliage) are reported. In addition to $ANPP_T$, in this study we quantified the biomass production of understory and midstory vegetation. We refer to the sum of crop tree + understory + midstory biomass production as ecosystem ANPP ($ANPP_E$). We also tested the effects of vegetation management treatment on both $ANPP_T$ and $ANPP_E$, including the differences between species and sites; results are presented in this chapter.

Literature Review

Litterfall

Litterfall is said to play an integral role in carbon cycling and soil fertility, thus is important in maintaining forest productivity (Dimmock II 1958). It can be used as an indicator for ANPP and be used to determine nutrient-use efficiency (Keenan et al. 1995). Abee and Lavender (1975) reported that for a 450-year-old Douglas-fir stand, 72% of the aboveground nutrient return was from litterfall. Amount of litterfall can vary due to factors such as soil fertility, forest cover type, stand density, stand age, and climate (Dimmock II 1958).

Quality of litterfall has been observed to differ between species (Ogden and Schmidt 1997). Litterfall of hardwood species have been shown to have higher concentrations of nutrients and to decompose faster than conifer species (Ogden and Schimdt 1997, Fried et al. 1990, Harmon et al. 1990). Silvicultural practices have been shown to have an impact on the amount of litterfall. Increasing thinning intensity reduced the amount of litterfall (Dimmock II 1958, Reukema 1964). In time, fertilization has been shown to increase amount of litterfall and has been shown to increase availability of limiting nutrients (Tanner et al. 1992, Theodorou and Bowen 1990).

Litterfall has been shown to differ seasonally (Gresham 1982, Lawrence 2005) and by forest type (Zhang et al. 2014). Zhang et al. (2014) reported that litterfall peaked in the spring or winter during the drought season, in temperate broadleaved and evergreen forests, peaks occurred at various seasons, and in temperate deciduous broadleaved forests and boreal evergreen forests, peaks occurred in autumn. For old-growth forest stands of Douglas-fir growing in the western Cascade Mountains, Abee and Lavender (1975) reported that the peak in litterfall was during the winter. Some litterfall models have been developed (Dixon 1976, Zeilhofer et al. 2012) to quantify spatial and temporal patterns, while other models use algorithms that assume litterfall occurs in one period (Sitch et al. 2003) or evenly throughout the year (Ryan and Law 2005) (Zhang et al. 2014). Seasonal patterns of litterfall can also be used to track seasonal patterns of leaf area index (Liu et al. 2015).

Leaf Area Index

Projected leaf area index (LAI, $m^2 m^{-2}$), is defined as the projected area of green foliage per unit ground surface area (Chen and Black 1992). LAI is closely related to forest productivity as it has a strong influence on photosynthetic capacity and potential transpiration (Gholz et al. 1982). Because of this, LAI is useful for studying atmosphere and vegetation interactions and thus is an important parameter in many process-based models (Liu et al. 2015). Aside from varying seasonally, LAI can also depend on factors such as species composition, site, and management practices. LAI has been shown to range between 0.4 to 16.9 $m^2 m^{-2}$ (Jonckheere et al. 2004). LAI can be difficult and time consuming to measure and so it has been of interest to find indirect forms of measurement (Gonzalez-Benecke et al. 2012, Jonckheere et al. 2004, Liu et al. 2015).

Aboveground Net Primary Productivity

Forests of the Pacific Northwest (PNW) are regarded as some of the most productive forests in North America (Grier 1979). In a comparison of forest regions, Grier (1979) reported that forests in the PNW have a slow initial growth, but soon after canopy closure, they become highly productive forests. These forests are also long lived and can accumulate large amounts of biomass. Within this region, forests growing along the coast are the most productive. NPP in the PNW can range from <1 to 37 Mg ha^{-1} yr^{-1}, with an average of 12 Mg ha^{-1} yr^{-1} (Gholz 1982, Grier 1979).

NPP has been shown to be dependent on the amount of foliage, as light interception and photosynthetic material is the basis of dry matter production (Waring and Running 2007). Conifers are known to have greater foliage biomass in comparison to hardwood species (Waring 1979), and as is observed, are more productive (Grier 1979). For different types of forests, a strong relationship has been reported between NPP and foliage biomass (Satoo 1968, 1971, 1974) or leaf area (Gholz 1982, Stape 2002, Martin and Jokela 2004).

There are several factors that have been shown to have an effect on NPP such as light (Helms et al. 1976), moisture stress (Brix 1972, 1979), and nutrients (Brix 1972, 1979). Through different silvicultural practices, managers can alter these factors, thus impacting forest productivity. Brix (1971) reported that nitrogen fertilization increased photosynthetic capacity of Douglas-fir in favorable conditions. Furthermore, a combination of nitrogen fertilization and a thinning from below, removal of suppressed trees, can have large positive effects on foliage mass and crown structure (Brix 1981). Wagner et al. (2004) reported that the use of herbicides for vegetation management increased forest productivity, measured as wood volume yield. Similar trends were observed by Dinger and Rose (2009). Vegetation management increased available soil water, reducing water stress and possibly extending the growing season.

In analyzing ANPP of forests, other ecosystem components must be taken into account, as a forest is made up of more than just overstory trees. There is vegetation in the midstory and the understory. Bormann et al. (2015) reported that mixed stands of conifers and hardwoods had double the ANPP than stands of pure low-planting density Douglas-fir with vegetation management. Furthermore, the midstory added biodiversity and stabilized soil organic matter in the B-horizon, both important factors of forest sustainability. Vogel et al. (2011) concluded that the understory played an important role in soil and forest floor carbon accumulation.

The high productivity of young forests has led to the idea of promoting carbon sequestration of plantation forests (Sedjo 1999). It has been demonstrated that through management, forest productivity can be increased and in turn increase carbon storage (Johnsen et al. 2014). However, the increase in carbon storage is only observed if harvest intervals do not change (McKinley et al. 2011). Harmon (2001) further elaborates on other processes that should be considered when accounting for carbon sequestration aside from tree growth, such as photosynthesis and plant respiration, tree mortality and litterfall, decomposition and formation of soil organic matter, disturbances, and manufacturing, use, and disposal of wood products.

While the focus has been on the effects of intensive vegetation management on crop trees, few studies have focused on effects on soil, particularly the loss of an understory component (Powers et al. 2013). Vogel et al. (2011) warns about the risks of focusing on crop tree development and the importance of studying the long-term effects of vegetation management. They report that 18 years after weed control treatments had ended, forest floor carbon was reduced and continued to decrease. The understory was an important component of forest sustainability in southern pines in Florida. Powers et al. (2013) reported contrasting results. Vegetation management had no impact on forest floor carbon accumulation. With intensive management, there has been a loss of biodiversity and early-seral stages across the landscape (Bormann et al. 2015). The results from these studies highlight the importance of understanding the long-term effects of vegetation management on all ecosystem components.

Objectives and Hypotheses

The primary objective was to quantify the long-term effects of vegetation management on total and tree component ANPP, as well as total and ecosystem component ANPP, in planted stands of four conifer species growing in two sites in the PNW. We hypothesize that 10-11 years after vegetation management ended:

1. Trees growing on plots that had sustained elimination of competing vegetation during the first five years after planting have higher total and component $ANPP_T$.
2. The response in $ANPP_T$ to vegetation management differs between species and sites.
3. In plots without vegetation control, understory and midstory vegetation play a major role in the $ANPP_E$.
4. $ANPP_E$ is larger in vegetation management treated plots, and the response differs between species and sites.
5. There is a positive correlation between ANPP and LAI and basal.

Methods

Description of Sites

The two study sites are located in the Central Coast Range (CR) near Summit, OR, and the Cascade foothills (CF) near Sweet Home, OR. The CR site was established in January of 2000 on Starker Forests, Inc. land. It is located approximately 40 km from the coast (44.62°N, 123.57°W). The mean annual temperature is 11.1°C, and the mean annual rainfall is 1,707 mm. The site is characterized by fine loamy soil. The CF site was established in February of 2001 on Cascade Timber Consulting, Inc. land. It is located approximately 110 km from the coast (44.48°N, 122.73°W). The mean annual temperature is 12.4°C and the mean annual rainfall is 1,179 mm. The site is characterized silty clay loam soil.

Study Design

A randomized complete-block experiment with eight treatments was implemented (Appendix Figures 1 and2). Plots were planted with Styro-15 seedlings in six by six rows at 3 m (10-ft) spacing. A buffer row was included on all four sides for a plot size of about 0.06 ha. At the CR site, four coniferous species were planted: Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata Donn ex D. Don*), and grand fir (*Abies grandis (Dougl. ex D. Don) Lindl.*). There are four blocks of Douglas-fir and western hemlock, and three blocks for western redcedar and grand fir. The CF site was planted with only Douglas-fir and western redcedar, each with four blocks.

Treatments

All plots on both sites received a fall site preparation herbicide application during the fall season prior to planting. The eight different treatments were spring release (SR) applications that can be defined by the number and timing of herbicide treatments (T) applied during the first 5 years after planting. For this study, only the control (C) and the 5 consecutive years of SR treatment (VM) were used. Further details of treatment of the whole study can be found in Maguire et al. (2009).

On both sites, the herbicedes applied for fall for site preparation consisted of sulfometuron (0.15 L/ha), metsulfuron (0.04 L/ha), and glyphosate (4.68 L/ha). Atrazine (4.5-4.9 kg/ha) and clopyralid (0.58-0.73 L/ha) were applied for the spring release treatments. If competing vegetation cover exceeded a 25% threshold during the growing season, glyphosate (1.5%-2.0%) was applied in the summer.

Stand Structure

Prior to the start of this study, the last stand inventories were conducted at age 12 years, corresponding to 2011 for the CR site and 2012 for the CF site. At both sites, Douglas-fir stands were thinned from below, reducing the stocking by 20%. Treatment plots were inventoried in March of 2016 and 2017. Table 3.1 summarizes stand characteristics in March 2017. In VM plots, trees were larger and had higher survival.

Table 3.1. Average trees per ha (TPHA, ha^{-1}), basal area (BA, $m^2\ ha^{-1}$), quadratic mean diameter (QMD, cm), and volume outside bark (VOB, $m^3\ ha^{-1}$) for Douglas-fir, western hemlock, western redcedar, and grand fir trees growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR; 17 years) and the Cascade foothills (CF; 16 years) of western Oregon.

Site	Species	Treatment	TPHA	BA	QMD	VOB
CR	Douglas-fir	C	688	20.8	19.6	154
		VM	696	26.4	21.6	202.9
	western hemlock	C	868	15.9	19.7	59.2
		VM	1025	35.8	28.7	152.9
	western redcedar	C	798	5.5	10.9	23.5
		VM	967	20.8	22.2	98.4
	grand fir	C	927	13.2	17.8	42.7
		VM	997	35.9	29.4	120.8
CF	Douglas-fir	C	696	14.8	16.5	96.5
		VM	710	24.2	20.8	177.7
	western redcedar	C	351	5.2	13.7	23.2
		VM	935	16.8	15.1	76.7

Litterfall

In February of 2016, 0.5 m^2 circular litterfall traps made of plastic tubing and mesh net were placed in each study plot, 28 at the Coastal Range (CR) site and 16 at the Cascade foothills (CF) site. A total of five traps were randomly placed in each plot (Appendix Figure 3). Between February 2016 and February 2017, litterfall was collected approximately every four weeks and dried in a Moore-Kiln REI TT drying oven at 74°C for a minimum of 72 hours. After that time, dry litter was separated into foliage of the crop species, foliage of all other species (including midstory and understory), and woody material of all species. Dry mass of all litterfall components was determined using an OHAUS NV4101 scale (g).

Crop Tree ANPP

In March of 2016 and 2017, treatment plots at both study sites were inventoried. Diameter at breast height (DBH, 1.37m) and height of all living trees were measured with metric diameter tapes (mm) and Haglof Vertex IV (cm), respectively. Aboveground biomass, total and tree components, was estimated using species specific biomass equations developed from trees sampled at both sites (see Chapter 2). Equations used can be found in Appendix: Table 5. For each tree component, biomass production was calculated as the change in biomass between March 2016 and March 2017 (no tree mortality was detected during the evaluation period). Foliage biomass production was computed as the change in biomass + the sum of foliage in litterfall traps. $ANPP_T$ (Mg ha^{-1} $year^{-1}$) was determined as the sum of foliage + branch + bark + stemwood biomass production.

Ecosystem ANPP

In addition to $ANPP_T$, $ANPP_E$ (Mg ha^{-1} $year^{-1}$) includes biomass production of understory and midstory. In May of 2016 and 2017, hardwoods were subsampled in each plot using six 4 m^2 subpots (7% of total area sampled). All the hardwoods that were greater than 1.37 m in height that were within the subplot limits were measured and species was recorded. Generalized biomass functions from Chojnacky et al. 2014, Ter-Mikaelian and Korzukhin 1997, and Ohmann et al. 1976 were applied to estimate the aboveground biomass for all hardwood species (Table 3.2) found at the sites with the exception of cascara buckthorn (*Rhanmus purshiana* (D.C.) Cooper). For cascara buckthorn, aboveground biomass was estimated using a species-specific function developed in this study (see Chapter 2). Within the 0.06 ha measurement experimental unit, all non-crop trees that were larger than 15 cm in DBH were considered volunteer trees. The DBH of all these trees was measured and the species was recorded. For conifer volunteers, the biomass equations developed for the corresponding species of crop trees were used. Midstory biomass production was calculated as the change in biomass between years 2016 and 2017. The sum of non-crop conifer foliage in litterfall traps was added to midstory biomass production. For Douglas-fir C plots, as midstory was not present, the sum of non-crop conifer foliage in litterfall traps was added to the understory biomass production.

Table 3.2. List of hardwood species and range of diameter at breast height (DBH, 1.37 m) measured on both sites in the year 2017.

Species	DBH Range (cm)
vine maple (*Acer circinatum* Pursh.)	1.0-4.0
bigleaf maple (*Acer macrophyllum* Pursh)	1.5-20.0
white alder (*Alnus rhombifolia* Nutt.)	0.1-2.8
red alder (*Alnus rubra* Bong.)	0.5-19.0
golden chinquapin (*Chrysolepis chrysophylla* (Douglas x Hook.) Hjelmqvist)	13.5
beaked hazelnut (*Corylus cornuta* Marsh.)	0.8-2.9
bitter cherry (*Prunus emarginata* (Dougl. ex Hook.) D. Dietr.)	0.5-12
cascara buckthorn (*Rhanmus purshiana* (D.C.) Cooper)	0.7-7.8

The understory was sampled in August of 2016 and June of 2017 in the same six subplots as the midstory. In 2016, clip plots were taken using a 0.6 m x 0.6 m frame that was placed at the center of the 4 m^2 subplots. In 2017, clip plots were taken on either side of the remnants of the 2016 sample. Previous to biomass collection, the percentage of cover by life form was recorded on each 0.36 m^2 clipped subplot. All the vegetation inside was clipped and placed into labeled Ziploc bags. Samples were kept in coolers while in the field and for transportation. In the laboratory, samples were place in labeled aluminum trays and then placed in a Moore-Kiln REI TT drying oven at 74°C for at least 72 hours. After that time, understory samples were separated by life form and weighed using an OHAUS NV4101 scale (g). Understory biomass production was calculated as the change in biomass between years 2016 and 2017.

Data Analysis and Model Fitting

Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC) was used for statistical analysis, including non-linear model fitting. All analyses were conducted using PROC MIXED. Treatment and site means were compared for tree and ecosystem components of all species with Tukey multiple comparisons tests (μ_i - μ_j). Mean tree and ecosystem differences between site, species, and treatments, as well as interactions between site, species, and treatments were tested for using ANOVA. For models, differences among species were assessed using ANOVA.

CurveExpert Professional version 2.6.3 (Hyams Development) was used for exploratory analysis of model fitting. SigmaPlot version 13.0 (Systat Software, Inc. San Jose, CA) was used for linear model fitting and for creating all figures.

Results

Litterfall

For all species at the CR site, monthly litterfall (kg ha^{-1} $month^{-1}$) peaked in the period of October-November (Figure 3.1). During the year of observation, Douglas-fir monthly litterfall showed a biomodal shape, having a second peak in the period of June-July. Large differences in seasonal litterfall of crop trees and midstory was observed. For example, for western hemlock C treatment plots at the CR site, foliage fall of crop trees was 21 kg ha^{-1} between March and October 2016 and 95 kg ha^{-1} between November 2016 and February 2017. At the same time, for western hemlock VM treatment plots, foliage fall of crop trees was 379 kg ha^{-1} between March and October 2016 and 398 kg ha^{-1} between November 2016 and February 2017. On plots of the same crop species, midstory vegetation litterfall averaged about 977 kg ha^{-1} between March and October 2016, and 626 kg ha^{-1} between November 2016 and February 2017.

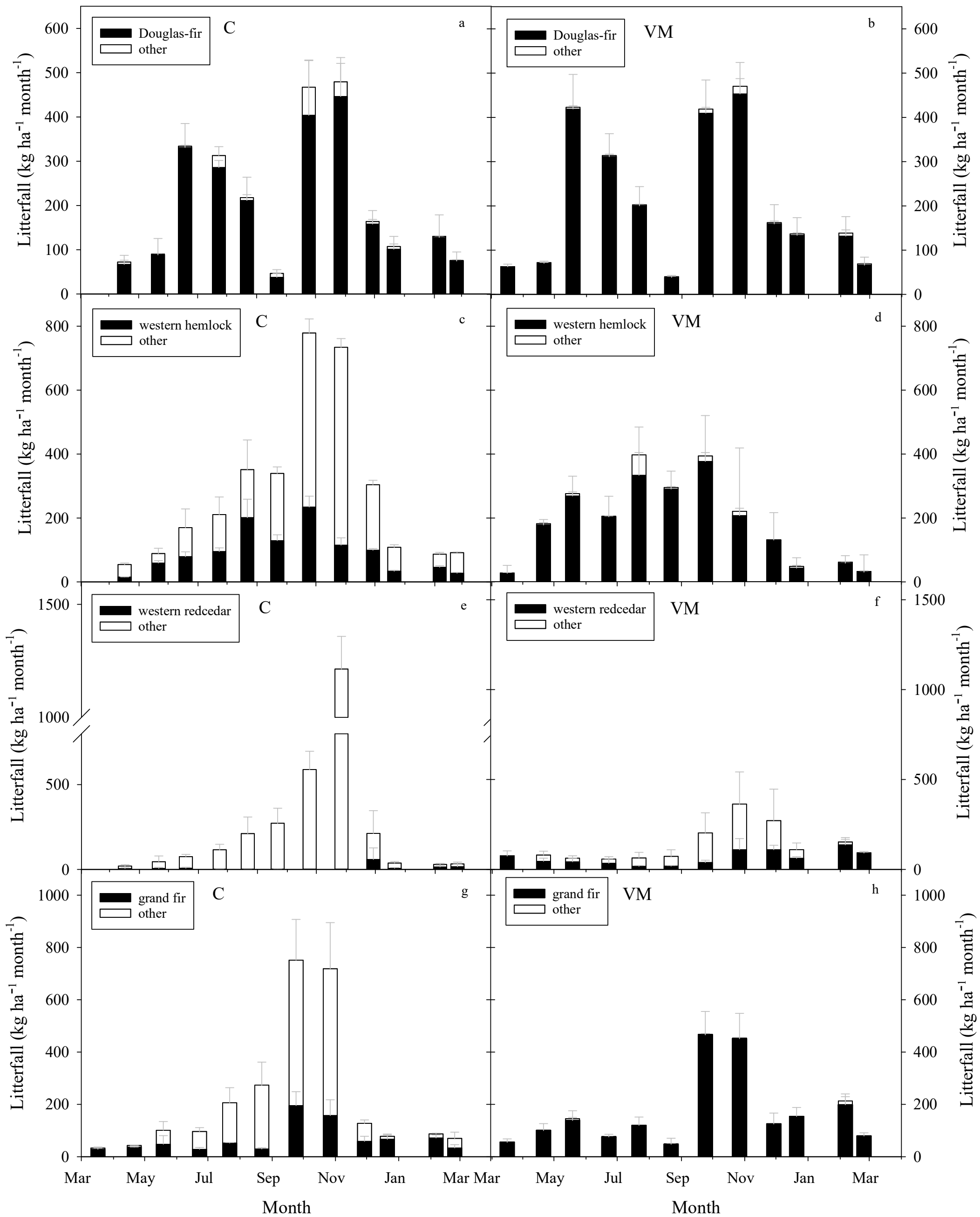

Figure 3.1. Monthly litterfall from March 2016 to February 2017 of of Douglas-fir (a,b), western hemlock (c,d), western redcedar (e,f), and grand fir (g,h) stands growing under contrasting treatments of vegetation management (control, C, left panel; sustained vegetation management for first 5 years post planting, VM, right panel) on a site located in the central Coast Range.

At the CF site, monthly litterfall followed similar patterns as the CR site. Douglas-fir monthly litterfall showed a bimodal shape, but had the second peak in the period of May-June (Figure 3.2). On C plots of western redcedar most of the litterfall was from other vegetation, while in treated redcedar, almost all litterfall was from western redcedar trees. Interestingly, western redcedar on treated plots showed a large peak of litterfall of about 1000 kg ha^{-1} $month^{-1}$ during October.

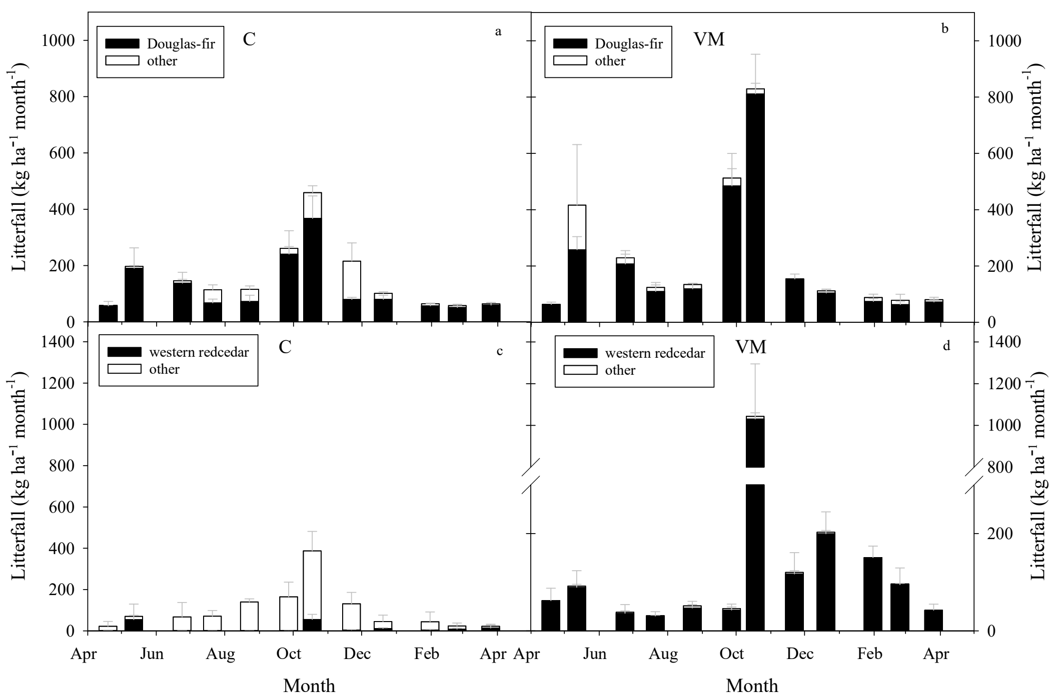

Figure 3.2. Monthly litterfall from April 2016 to March 2017 of Douglas-fir (a,b) and western redcedar (c,d) stands growing under contrasting treatments of vegetation management (control, C, left panel; sustained vegetation management for first 5 years post planting, VM, right panel) on a site located in the Cascade foothills.

Table 3.3 summarizes annual litterfall (Mg ha^{-1} $year^{-1}$) collected between March 2016 and February 2017 at the CR site and between April 2016 and March 2017 at the CF site. Eleven years after vegetation management treatments ended, all species at both sites ($P<0.029$), except for Douglas-fir at the CR site ($P=0.766$) showed larger annual crop tree foliage fall on VM plots. Foliage fall of midstory and understory vegetation was large on C plots for all species at both sites ($P<0.039$), with the exception of Douglas-fir at the CR site ($P=0.894$). Total litterfall was not different between sites for both Douglas-fir and western redcedar (P>0.069). On average, yearly litterfall of woody material accounted for 1 to 10% of total litterfall, averaging 6 and 3%, for C and VM plots, respectively.

Table 3.3. Cumulated planted crop tree foliage fall (CT Foliage, Mg ha^{-1} year^{-1}) foliage fall of midstory and understory (V Foliage, Mg ha^{-1} year^{-1}), woody and miscellaneous litterfall (Other, Mg ha^{-1} year^{-1}), and total litterfall (Total, Mg ha^{-1} year^{-1}) for Douglas-fir, western hemlock, western redcedar, and grand fir stands growing under contrasting treatments of vegetation control on sites located in the Coast Range (CR) and in the Cascade foothills (CF). SE is the standard error.

		CR					CF					
Species	Litterfall Type	C	SE	VM	SE	P-Value	C	SE	VM	SE	P-Value	P-Value*
Douglas-fir	CT Foliage	2.3	0.4	2.4	0.2	0.766	1.5	0.2	2.5	0.2	**0.002**	0.119
	V Foliage	-	-	-	-	0.894	0.4	0.1	-	-	**0.004**	**0.035**
	Other	0.2	0.1	-	-	0.167	-	-	0.3	0.2	0.070	0.537
	Total	2.5	0.4	2.4	0.2	0.996	1.9	0.1	2.8	0.3	**0.012**	0.418
western hemlock	CT Foliage	1.0	0.1	2.1	0.2	**0.001**						
	V Foliage	2.0	0.5	0.1	0.1	**0.002**						
	Other	0.2	0.1	-	-	0.078						
	Total	3.2	0.4	2.2	0.1	**0.034**						
western redcedar	CT Foliage	0.1	0.1	0.8	0.2	**0.008**	0.2	0.1	1.9	0.3	**0.001**	0.270
	V Foliage	2.5	0.4	0.7	0.6	**0.039**	1.0	0.3	-	-	**0.019**	**0.031**
	Other	0.2	0.1	0.1	0.1	0.059	0.1	0.04	-	-	0.089	**0.028**
	Total	2.8	0.4	1.6	0.7	0.114	1.3	0.4	1.9	0.3	0.178	0.069
grand fir	CT Foliage	0.8	0.1	2.0	0.4	**0.026**						
	V Foliage	1.6	0.4	-	-	**0.009**						
	Other	0.2	0.02	-	-	**0.009**						
	Total	2.6	0.4	2	0.5	0.329						

C: control treatment; VM: sustained vegetation management treatment for first 5 years post planting. P-Value for treatment differences within sites. P-Value* for differences across sites. P-value in bold indicates that the difference in litterfall was significant at α=0.05. At the CR site, sampling period was March 2016 to February 2017. At the CF site, sampling period was April 2016 to March 2017.

The relationships between BA at the beginning of the evaluation period (March 2016) and crop tree (CT) and vegetation (V, understory + midstory) yearly foliage loss (Mg ha^{-1} year^{-1}) between 2016 and 2017 are shown in Figure 3.3. For CT foliage loss, the relationship was different between Douglas-fir (DF) and the other three species (WH, WR, and GF), so separate sigmoidal functions were fitted for each group (Figure 3.3a). On average, for a BA of 20 m^2 ha^{-1}, the annual foliage loss of DF was about 2.1 Mg ha^{-1} year^{-1}. For the same BA, WH, WR, and GF had an annual foliage loss of about 1.2 Mg ha^{-1} year^{-1}. For V foliage loss, a non-linear relationship across species was fitted, decreasing exponentially as BA increased (Figure 3.3b). For a BA larger than about 20 m^2 ha^{-1}, V foliage loss was negligible.

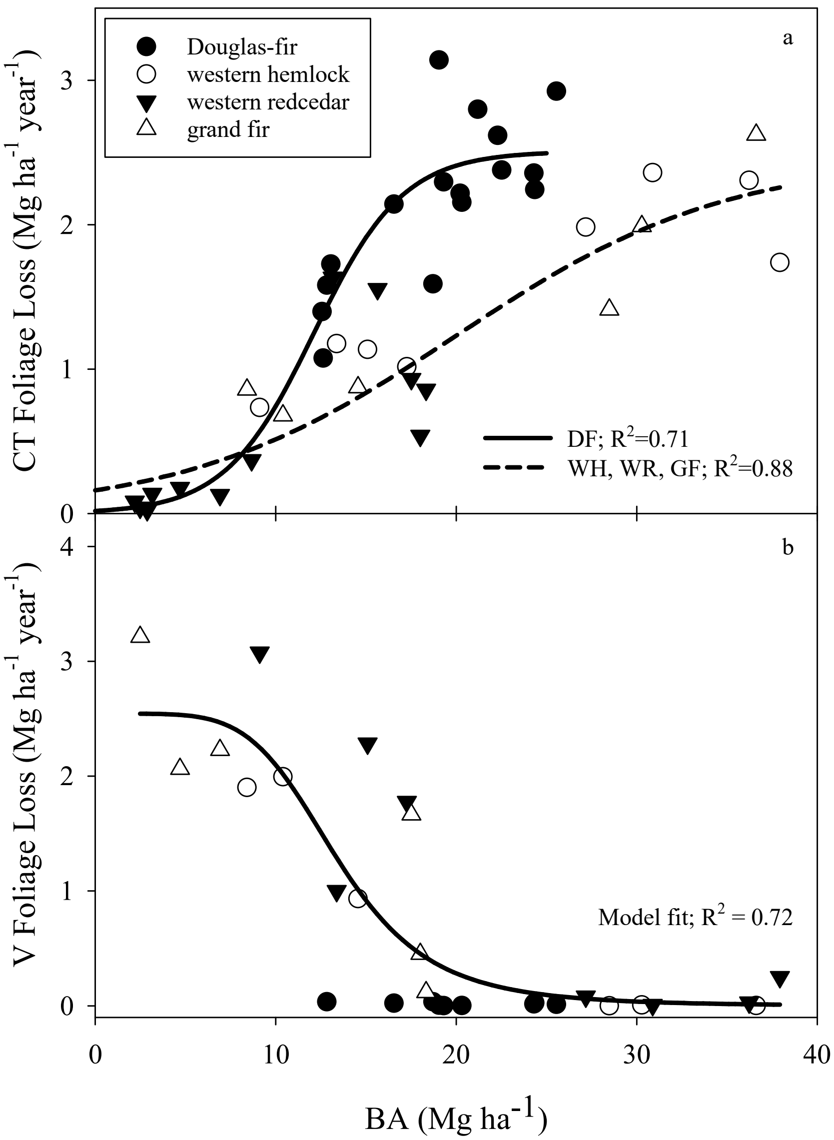

Figure 3.3. Relationship between basal area (BA, m^2 ha^{-1}) at the beginning of the evaluation period and a) crop tree (CT) and b) vegetation (V) foliage loss for 16-17 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Parameter estimates and fit statistics for the relationships between BA and CT and V yearly foliage loss are shown in Table 3.4.

Table 3.4. Parameter estimates and fit statistics of the equations for predicting crop tree (CT) and vegetation (V) foliage loss (Mg ha^{-1} yr^{-1}) for Douglas-fir, western hemlock, western redcedar, and grand fir stands growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Model	Species	Parameter	Parameter Estimate	SE	R^2	RMSE
$CT\ Foliage\ Loss = \frac{a}{1 + b * exp(-c \cdot BA)}$	DF	a	2.5086	0.2261	0.71	0.578
		b	137.0973	567.9611		
		c	0.4057	0.3057		
	WH	a	2.4676	0.3533	0.88	0.544
	WRC	b	14.3036	12.2289		
	GF	c	0.1329	0.0466		
$V\ Foliage\ Loss = \frac{1}{a + b * BA^c}$	All	a	0.3931	0.0538	0.72	0.770
		b	0.000000495	0.00000029		
		c	5.2279	2.1439		

BA: crop tree basal area (m^2 ha^{-1}) at the beginning of the evaluation period; R^2: coefficient of determination; RMSE: root mean square error. For all parameter estimates: $P < 0.05$.

Tree Aboveground Net Primary Productivity

Plots with sustained VM for 5 years after planting showed larger $ANPP_T$ eleven years after treatment ended. At the CR site on C plots, $ANPP_T$ averaged 14.5, 12.6, 2.6, 10.2 Mg ha^{-1} yr^{-1}, for Douglas-fir, western hemlock, western redcedar, and grand fir respectively. On VM plots, there was an average gain of 1.7, 11.2, 7.9, and 14.4 Mg ha^{-1} yr^{-1} for same species (Figure 3.4). At the CF site, C plots of Douglas-fir and western redcedar had an average $ANPP_T$ of 11.0 and 3.2 Mg ha^{-1} yr^{-1}, respectively. VM plots showed an average gain of 4.6 and 6.5 Mg ha^{-1} yr^{-1}, respectively.

On C plots, foliage production averaged 26, 19, 30, and 26 % of $ANPP_T$ for Douglas-fir, western hemlock, western redcedar, and grand fir at the CR site, and 21 and 27% for Douglas-fir and western redcedar at the CF site. On VM plots at the CR site, $ANPP_T$ allocation to foliage was reduced to 23, 28, and19% for Douglas-fir, western redcedar, and grand fir, but increased to 22% on western hemlock. At the CF site $ANPP_T$ allocation to foliage for VM Douglas-fir and western hemlock was 21 and 40%, respectively.

Large differences in $ANPP_T$ allocation to crown (foliage + branch) were observed across species. At the CR site, $ANPP_T$ allocation to crown averaged 39, 28, and 28% for Douglas-fir, western hemlock, and grand fir, but 52% for western redcedar. At the CF site, average $ANPP_T$ allocation to crown was 40 and 56% for Douglas-fir and western redcedar, respectively.

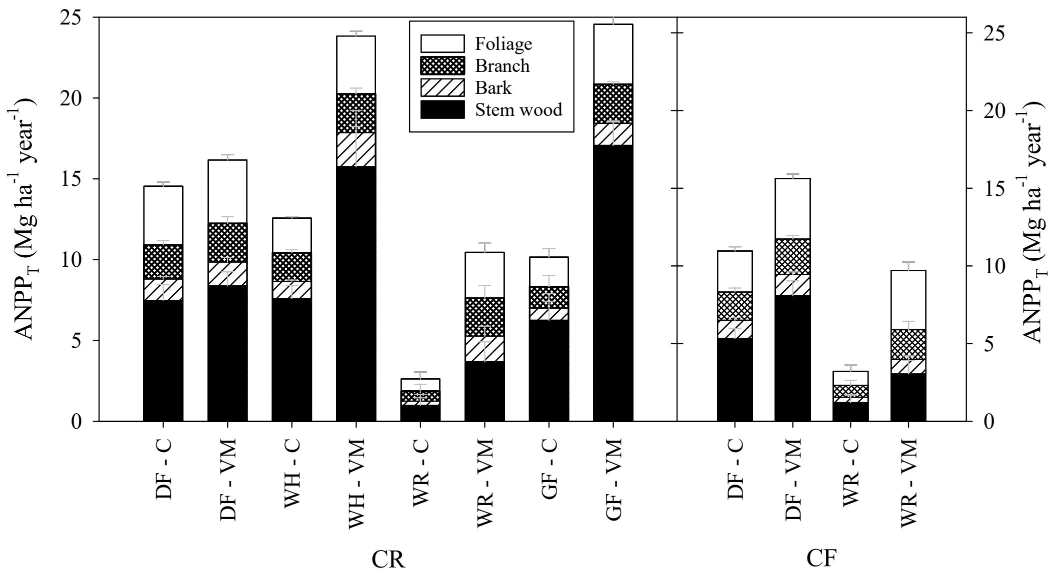

Figure 3.4. Average ANPP (Mg ha^{-1} yr^{-1}) of tree components for Douglas-fir (DF), western hemlock (WH), western redcedar (WR), and grand fir (GF) stands growing under contrasting treatments of vegetation control (C: control treatment, VM: sustained vegetation management treatment for first 5 years post planting) on sites located in the central Coast Range (CR, 16-17-year-old, left panel) and in the Cascade foothills (CF, 15-16 year old, right panel). Error bars represent the standard error.

Ecosystem Aboveground Net Primary Productivity

To facilitate the analysis on $ANPP_E$, $ANPP_T$ was divided into foliage and woody (branch + bark + stemwood) components, and understory and midstory were pooled into a single vegetation component ($ANPP_V$). On C plots at the CR site, $ANPP_V$ accounted for a large fraction of $ANPP_E$, counteracting the differences in $ANPP_T$ across treatments. At the CF site, $ANPP_V$ accounted for a small fraction of $ANPP_E$. Negative values of $ANPP_E$ indicate a reduction in understory vegetation production (Figure 3.5).

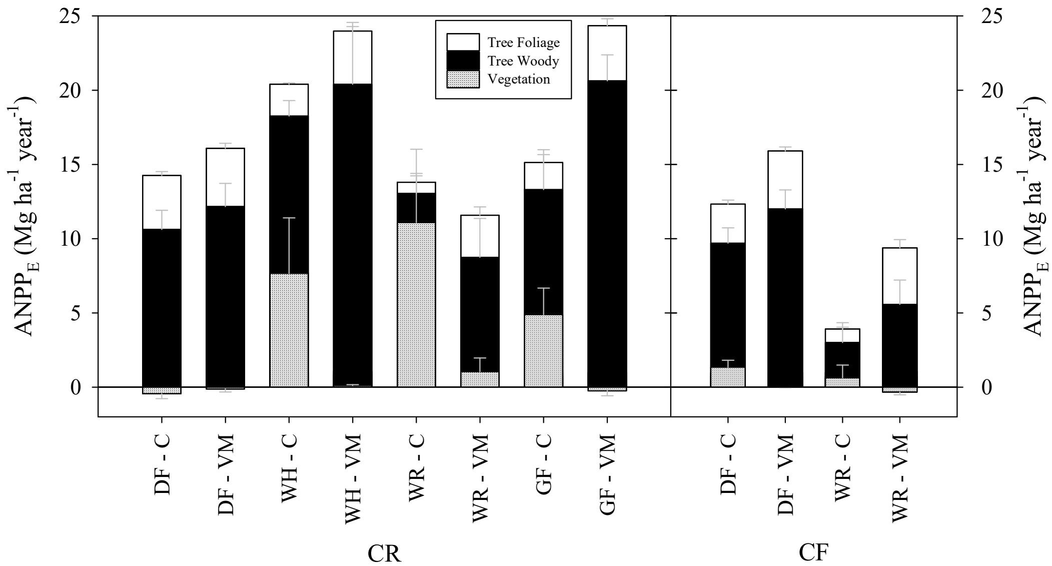

Figure 3.5. Average ANPP (Mg ha^{-1} yr^{-1}) of ecosystem components for Douglas-fir (DF), western hemlock (WH), western redcedar (WR), and grand fir (GF) stands growing under contrasting treatments of vegetation control (C: control treatment, VM: sustained vegetation management treatment for first 5 years post planting) on sites located in the central Coast range (CR, 16-17-year-old, left panel) and in the Cascade foothills (CF, 15-16 year old, right panel). Error bars represent the standard error.

A summary of all ANPP$_E$ components is shown in Table 3.5. At the CR site, C plots showed an average ANPP$_E$ of 14.1, 20.2, 13.7, and 15.0 Mg ha^{-1} yr^{-1}, for Douglas-fir, western hemlock, western redcedar, and grand fir, respectively, and were no different than VM plots ($P>0.086$). For the same species, plots with VM had an average ANPP$_E$ of 16.0, 24.0, 11.5, and 24.3 Mg ha^{-1} yr^{-1}. At the CF site, C plots of Douglas-fir and western redcedar showed an average ANPP$_E$ of 12.3 and 3.9 Mg ha^{-1} yr^{-1}, respectively. At this site, VM plots of Douglas-fir and western redcedar had a gain in ANPP$_E$ of 3.3 and 5.5 Mg ha^{-1} yr^{-1}, respectively ($P<0.051$). For most of the plots on both sites, understory ANPP was neutral or negative, ranging between -0.9 and 0.2 Mg ha^{-1} yr^{-1}.

Table 3.5. ANPP (Mg ha^{-1} yr^{-1}) of tree and ecosystem components for 16-17-year-old Douglas-fir, western hemlock, western redcedar, and grand fir stands in the central Coast Range (CR) and 15-16-year-old Douglas fir and western redcedar in the Cascade foothills (CF), growing under contrasting vegetation management treatments. SE is the standard error. P-value in bold indicates that the difference in biomass production was significant at α=0.05.

		CR					CF					
Species	Component	C	SE	VM	SE	P-Value	C	SE	VM	SE	P-Value	P-Value*
Douglas-fir	$ANPP_T$	14.5	1.3	16.2	1.8	0.469	11.0	1.3	15.6	1.5	**0.028**	0.217
	Foliage	3.6	0.3	3.9	0.3	0.468	2.6	0.3	3.9	0.3	**0.009**	0.154
	Live Branches	2.1	0.3	2.4	0.4	0.549	1.8	0.3	2.3	0.2	0.169	0.458
	Bark	1.3	0.2	1.5	0.3	0.583	1.2	0.2	1.4	0.2	0.377	0.452
	Stemwood	7.5	1.0	8.4	0.9	0.460	5.3	0.6	8.1	1.0	**0.033**	0.189
	$ANPP_V$	-0.4	-0.3	-0.1	-0.1	0.391	1.3	0.8	0.0	0.0	**-**	**0.019**
	Midstory	0.0	0.0	0.0	0.0	-	1.5	0.5	0.0	0.0	**-**	**0.047**
	Understory	-0.4	0.3	-0.1	0.2	0.391	-0.2	0.3	0.0	0.0	-	0.384
	$ANPP_E$	14.1	1.4	16.0	1.8	0.392	12.3	1.5	15.6	1.5	0.105	0.486
western hemlock	$ANPP_T$	12.6	1.1	23.8	4.4	**0.029**						
	Foliage	2.1	0.1	3.6	0.3	**0.002**						
	Live Branches	1.8	0.2	2.4	0.4	0.126						
	Bark	1.1	0.1	2.1	0.4	**0.019**						
	Stemwood	7.6	0.8	15.8	3.5	**0.039**						
	$ANPP_V$	7.7	4.4	0.1	0.1	0.058						
	Midstory	7.7	3.9	0.0	0.0	0.061						
	Understory	0.0	0.2	0.1	0.1	-						
	$ANPP_E$	20.2	3.5	24.0	4.4	0.488						
western redcedar	$ANPP_T$	2.6	1.8	10.5	3.2	**0.058**	3.2	1.4	9.7	2.1	**0.028**	0.961
	Foliage	0.8	0.4	2.8	0.6	**0.023**	0.9	0.4	3.8	0.6	**0.003**	0.527
	Live Branches	0.6	0.4	2.3	0.8	0.078	0.8	0.3	1.9	0.5	0.078	0.813
	Bark	0.3	0.2	1.6	0.6	0.069	0.4	0.1	0.9	0.2	0.051	0.453
	Stemwood	1.0	0.7	3.7	1.2	0.079	1.2	0.5	3.1	0.9	0.079	0.824
	$ANPP_V$	11.1	7.8	1.0	0.7	0.070	0.6	0.4	-0.3	-0.2	0.248	**0.037**
	Midstory	11.1	4.9	0.8	1.0	0.066	0.8	0.5	0.0	0.0	-	**0.047**
	Understory	0.0	0.0	0.2	0.2	-	-0.1	0.5	-0.3	0.2	0.697	0.247
	$ANPP_E$	13.7	3.2	11.5	2.3	0.526	3.9	2.3	9.4	2.2	0.094	**0.022**
grand fir	$ANPP_T$	10.2	3.2	24.6	2.1	**0.011**						
	Foliage	1.8	0.5	3.7	0.5	**0.031**						
	Live Branches	1.3	0.7	2.4	0.2	0.135						
	Bark	0.8	0.4	1.4	0.1	0.135						
	Stemwood	6.3	1.6	17.1	1.5	**0.004**						
	$ANPP_V$	4.9	3.5	-0.2	-0.2	**0.026**						
	Midstory	5.8	2.2	0.0	0.0	-						
	Understory	-0.9	0.6	-0.2	0.3	0.275						
	$ANPP_E$	15.0	4.2	24.3	2.5	0.081						

C: control treatment, VM: sustained vegetation management for first 5 years post planting. P-Value for treatment differences within sites. P-Value* for site differences.

Table 3.6 summarizes analysis of variance (ANOVA) results. Significant (P<0.05) differences are highlighted in bold. Only the midstory was significantly different between sites and species. Total tree and tree components with the exception of live branches was significantly different between species. All ecosystem components were significantly different between treatments. There was a significant interaction between site and species for the midstory and understory ANPP, between species and treatment for $ANPP_T$, including crop tree foliage and bark ANPP. Only midstory ANPP was found to have a significant interaction between site, species, and treatment.

Table 3.6. Analysis of covariance testing differences and interactions in total and component tree $ANPP_E$ for 16-17-year-old Douglas-fir, western hemlock, western redcedar, and grand fir stands growing under contrasting vegetation management treatments on sites located in the central Coast Range and the Cascade foothills.

Component	Site	Species	Treatment	Site x Species	Site x Treatment	Species x Treatment	Site x Species x Treatment
$ANPP_T$	0.438	**<0.0001**	**<0.0001**	0.497	0.714	**0.021**	0.382
Foliage	0.922	**0.001**	**<0.0001**	**0.027**	0.061	**0.004**	0.852
Branches	0.481	**0.034**	**0.0002**	0.899	0.704	0.166	0.444
Bark	0.193	**0.002**	**<0.0001**	0.609	0.258	0.078	0.222
Stemwood	0.416	**<0.0001**	**<0.0001**	0.564	0.775	**0.002**	0.442
$ANPP_V$	**0.022**	**0.039**	**0.0001**	**0.002**	0.080	0.078	**0.014**
Midstory	**0.027**	0.065	**<0.0001**	**0.005**	0.065	0.109	**0.013**
Understory	0.716	0.082	0.197	0.147	0.409	0.650	0.701
$ANPP_e$	**0.036**	**0.0002**	**0.003**	0.133	0.155	0.202	0.366

The relationships between initial BA and LAI at the beginning of the evaluation period (March 2016) and $ANPP_T$ and $ANPP_V$ (between 2016 and 2017) are shown in Figure 3.6. As the slope of the relationship between BA and LAI with $ANPP_T$ was not different across species (P=0.32 for BA; P=0.18 for LAI) and sites (P=0.43 for BA; P=0.32 for LAI), data from both sites was pooled and a non-linear relationship across species was fitted in each case (P<0.001). For $ANPP_T$, the relationship was sigmoidal as BA and LAI increased. For $ANPP_V$, the relationship was an exponential decay as BA and LAI increased. For a BA larger than about 20 m^2 ha^{-1}, $ANPP_V$ was negligible.

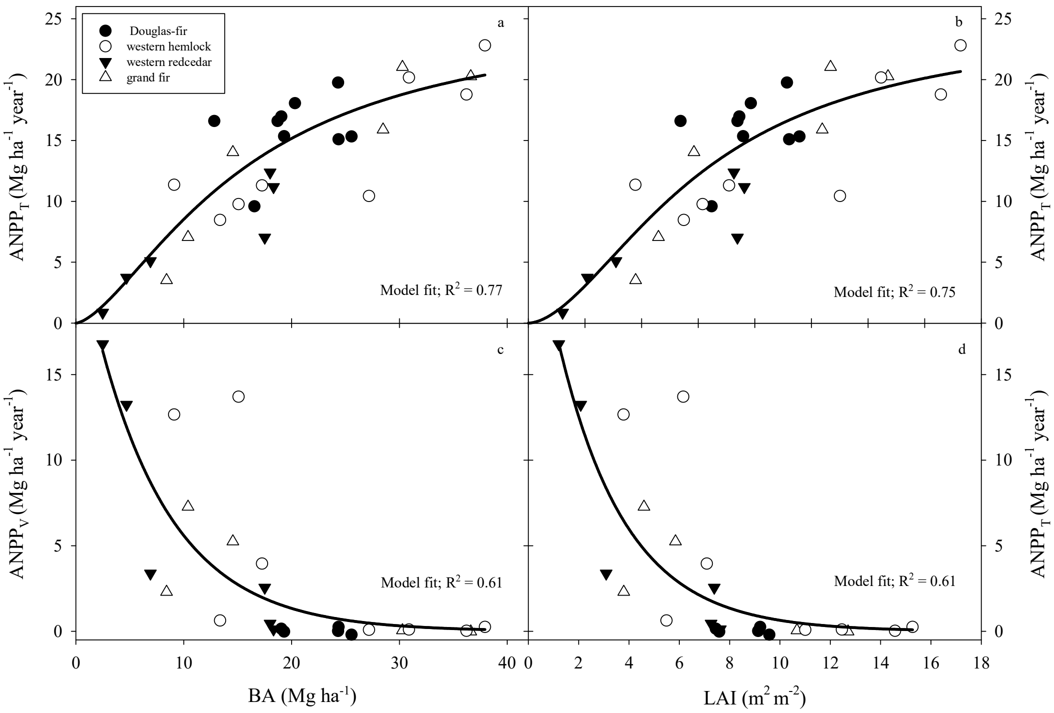

Figure 3.6. Relationship between initial basal area (BA, m^2 ha^{-1}) (a, c) and initial projected leaf area index (LAI, m^2 m^2) (c, d) of planted crop tress and tree aboveground net primary productivity ($ANPP_T$, Mg ha^{-1} yr^{-1}) (a, b) and vegetation (midstory + understory) aboveground net primary productivity ($ANPP_V$, Mg ha^{-1} yr^{-1}) (c, d) for Douglas-fir, western hemlock, western redcedar, and grand fir stands growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Parameter estimates and fit statistics for the regression of $ANPP_T$ and $ANPP_V$ on BA and LAI are shown in Table 3.7. On average, for every 1 m^2 ha^{-1} BA increment, $ANPP_T$ increased 0.573 Mg ha^{-1} yr^{-1}, and $ANPP_V$ decreased by 14.3%. For every 1 m^2 m^{-2} LAI increment, $ANPP_T$ increased 1.52 Mg ha^{-1} yr^{-1}, and $ANPP_V$ decreased by 14.29%.

Table 3.7. Parameter estimates and fit statistics of the equations for predicting crop tree ANPP ($ANPP_T$, Mg ha^{-1} yr^{-1}) and vegetation ANPP ($ANPP_V$, Mg ha^{-1} yr^{-1}) for Douglas-fir, western hemlock, western redcedar, and grand fir stands growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Model	Parameter	Parameter Estimate	SE	R^2	RMSE
$ANPP_T = \frac{a}{1 + b * exp(-c \cdot BA)}$	a	25.603	6.310	0.89	3.027
	b	-1.542	0.479		
	c	15.688	5.575		
$ANPP_V = a \cdot exp\,(-b \cdot BA)$	a	23.5255	4.8486	0.79	3.085
	b	0.1435	0.0288		
$ANPP_T = \frac{a}{1 + b * exp(-c \cdot LAI)}$	a	24.850	5.708	0.75	3.127
	b	-1.754	0.554		
	c	6.136	1.792		
$ANPP_V = a \cdot exp\,(-b \cdot LAI)$	a	23.3683	5.0051	0.61	3.198
	b	0.1429	0.0298		

BA: crop tree basal area (m^2 ha^{-1}) at the beginning of the evaluation period; LAI: projected leaf area index (m^2 m^{-2}) at the beginning of the evaluation period; R^2: coefficient of determination; RMSE: root mean square error. For all parameter estimates: $P < 0.05$.

Discussion

Litterfall

Dimmock II (1958) reported that litterfall of 45-year-old Douglas-fir stands growing in western Washington was not evenly distributed throughout the year. Litterfall increased as the growing season progressed reaching a maximum in October, followed by a gradual decline without a clear low point. A similar trend was observed in this study. However, Dimmock II (1958) reports variations found between years due to cold weather. In our study, total yearly litterfall of VM plots was similar for all species.

The relationship between BA and yearly foliage loss allows for fluxes of dead foliage into the forest floor to be estimated. In a similar approach, Gonzalez-Benecke et al. (2012) developed a set of equations to estimate LAI and litterfall from basal area, and the number of trees per hectare. As stands reached a BA of about 10 m^2 ha^{-1}, there was a sharp decline in vegetation foliage loss. That value of BA corresponds with the time of canopy closure for the stands assessed in the study (VMRC; data not shown). If, in addition to BA, foliage decomposition rate is known, needle accumulation in the forest floorcan be estimated. For example, Fogel and Cromack (1977) reported needle decomposition rates that ranged between 0.27 and 0.44 $year^{-1}$, for Douglas-fir growing in western Oregon. Using this information, together with a growth and yield simulator that can estimate dynamics in BA, it is possible to estimate leaf litter accumulation in the forest floor (Gonzalez-Benecke et al. 2015).

Litterfall of understory vegetation that was shorter than the height of the litterfall traps (<50cm), was not accounted for.

Tree Aboveground Net Primary Productivity

Our first hypothesis, that trees growing on plots that had sustained vegetation management for the first five years post planting have higher total and component tree ANPP was partially accepted, as $ANPP_T$ was observed to be higher in VM plots for all species, with the exception of Douglas-fir at the CR site. $ANPP_T$ of Douglas-fir was about double what was reported by Turner and Long (1975), 8.7 Mg ha^{-1} yr^{-1}, for 22-year-old Douglas-fir growing on a poor site in western Washington. Fujimori (1971) reported a higher $ANPP_T$, 36 Mg ha^{-1} yr^{-1}, for a 26-year-old stand of western hemlock growing in the central Oregon coast. It is important to remark that the annual production estimates of Fujimori (1971), were assessed in a stand with 6,627 trees per ha, that estimate included roots (5.5 Mg ha^{-1} yr^{-1}), and that biomass increment for all components was calculated with an alternative method of analyzing ring growth for stems and branches with a magnifying lens. Perhaps the differences in stand structure and analytical methods invalidate any comparison. Using a similar method to ours, Gholz et al. (1982) reported that ANPP of crop trees in PNW forests can range between 4.2 and 15 Mg $ha^{-1}yr^{-1}$. Foliage ANPP was found to differ between treatments for all species at both sites, with the exception of Douglas-fir at the CR site. Stem and branch ANPP were higher, while foliage was only half the rate that Gholz et al. (1982) reported. When our values are expressed as ANPP per unit LAI, our results are comparable with those of Gholz (1982).

When competing vegetation was eliminated, Douglas-fir, western hemlock, and grand fir showed similar $ANPP_T$. This result suggests that when these conifer species have full access to site resources, especially soil water, they have similar growth potential (at least over the age range assessed here). Even though western redcedar showed lower productivity, the common relationship between LAI and $ANPP_T$ indicates a similar trend in light use efficiency across the four conifer species tested.

The second hypothesis, that response in $ANPP_T$ to vegetation management differs between species and site, was partially accepted. Total and component tree ANPP were found to differ between species, with the exception of branch ANPP. Stemwood and total tree ANPP were found to be different between species. Grier (1976) and Fujimori (1971) reported western hemlock stands had high stem production. In our study, grand fir and western hemlock had the largest stemwood production and no change in ANPP allocation to stem was observed across treatments. On the other hand, in C plots, foliage production differed across species. This response was mainly due to the low productivity of C western redcedar. Even with sustained vegetation control, $ANPP_T$ of western redcedar was the lowest of all four species. Western redcedar is a shade tolerant species and may not be able to take full advantage of available resources. No differences in $ANPP_T$ were observed between sites.

The interaction between species and VM treatment observed for $ANPP_T$ suggests some species responded better to vegetation management. Brix (1979) reported that western hemlock was more susceptible to water stress than Douglas-fir and western redcedar is most likely more susceptible than western hemlock. McCulloh et al. (2014) showed that western hemlock, western redcedar, and grand fir have higher xylem vulnerability to cavitation than Douglas-fir. This may explain, at least partially, why Douglas-fir was the least responsive species to VM treatments, assuming that similar levels of water stress, Douglas-fir experiences much lower reduction in water transport, therefore lower reduction in growth.

Ecosystem Aboveground Net Primary Productivity

Our third hypothesis that in the C plots the midstory and understory play a major role in $ANPP_{E,}$ and fourth hypothesis, that $ANPP_E$ is larger in treated plots and the response differs between species and sites, were partially rejected. Sustained vegetation management for 5 years post planting increased $ANPP_T$, but not $ANPP_E$, with the exception of western redcedar growing at the CF site, where that response was attributed to a lack of a midstory at the site. With VM treatments, the productivity of the ecosystem was not reduced, but rather distributed to the crop trees. In our study $ANPP_E$ of Douglas-fir was 60% larger than what Turner and Long (1975) reported (5.7 to 11.5 Mg ha^{-1} yr^{-1}, for 22-year-old Douglas-fir stands) and most of the productivity stemmed from the overstory. Bormann et al. (2015) reported aboveground biomass increment of about 18 Mg ha^{-1} yr^{-1} for an early-seral plantation that included Douglas-fir among plentiful shrub and hardwood regeneration in southern Oregon. Similar values were found in this study.

Midstory vegetation accounted for a large proportion of $ANPP_E$ in C plots. This response was not observed for Douglas-fir where the midstory was eliminated when the pre-commercial thinning was carried out. Understory vegetation production was lower than what Turner and Long (1975) reported, 1.9 Mg ha^{-1} yr^{-1}. Furthermore, it was negative in most of the cases, indicating that the presence of understory species is being reduced and will continue to decrease as the overstory continues growing, reducing the light availability for the vegetation living in the understory. Similar decrease in understory vegetation with the increase of overstory canopy has been reported in other studies (Satoo 1970; Usoltev et al. 2002; Lindh 2005; Gonzalez-Benecke et al. 2010 and 2015).

There is some discussion regarding the lack of early-successional stages on the landscape in areas dominated by planted forests, like the Coastal Range and Cascade foothills in western Oregon. Early-successional stages add resiliency and sustainability to the landscape (Bormann et al. 2015). These authors found that biodiversity and aboveground biomass increment were much larger in plots where vegetation control was absent and early seral species were promoted. It is important to remark that in that study, Douglas-fir was scatter planted. In our study, for all four species tested, the monoculture stands that grew under sustained VM, showed similar ecosystem productivity to the stands where understory and midstory species were allowed to grow and occupy the site. If carbon sequestration is the main objective, both management schemes seem to be viable options for forest managers. If timber production is the main objective, large stem volume and biomass growth is possible to attain without reducing total ecosystem productivity.

Basal area and LAI Relationships with ANPP

Our final hypothesis, that BA and LAI have a positive correlation with ANPP was accepted. Forest production is tightly linked to intercepted radiation, thus it is strongly related to LAI (Luo et al. 2014, Webb et al. 1983). In this chapter we presented functions to estimate $ANPP_T$ from LAI. These functions have a strong potential use, but LAI is not readily available. In Chapter 1 we presented an equation that describes the relationship between BA and LAI for the four species studied. Based on that result we decided to present an alternative function to estimate $ANPP_T$ using BA. The relationship observed between BA and ANPP reflects that BA is a viable proxy for estimating $ANPP_T$ in western Oregon.

A negative exponential relationship between BA and $ANPP_V$ was observed. As stands reach a BA larger than 20 $m^2\ ha^{-1}$ (or LAI larger than 8 $m^2\ m^{-2}$) vegetation production was almost eliminated due to minimal light reaching the ground. Conifers have been shown to reach high LAI and unlike deciduous species, they maintain a canopy cover year-round allowing to less cumulative light to penetrate their canopy.

The functions reported in this study provide a practical way to estimate litterfall and ANPP of planted forests in the PNW. Continued measurements are needed to cover similar range in BA or LAI across the species in order to better compare our current results and to further expand their predictive ability.

Summary

The results of this study demonstrate that sustained FVM treatments during the first five years of stand establishment increased tree ANPP of western hemlock, western redcedar, and grand fir stands at age 16-17 at the CR site, and Douglas-fir and western redcedar stands at age 15-16 at the CF site. This suggests that FVM treatments can increase stand productivity of planted forests in the PNW, but this response can be site dependent, as was observed in Douglas-fir. However, in analyzing other ecosystem components, there was no increase in ecosystem ANPP for all species and sites. These results serve to inform forest managers and other parties of interest, that FVM does not have an effect on ecosystem productivity. With FVM, site resources are allocated to the crop trees, whereas without FVM, site resources are dispersed among crop trees and vegetation in the midstory and the understory.

The relationship observed between BA and $ANPP_T$ and between LAI and $ANPP_T$ is a useful tool. $ANPP_T$ and LAI are difficult variables to estimate, but BA is a common variable estimated in most forest inventories and growth and yield models.

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Chapter 4: Conclusions

Summary of Findings

In this study we determined that hypotheses 1-3 for Chapter 2 were likely true. At age 16, 11 years after vegetation management ended, trees growing with VM treatment had higher total and component biomass stock. Overall tree response to vegetation management treatments, in terms of biomass stock, did differ between species. Tree component biomass, with the exception of fine roots also differed. However, there were no differences in tree biomass stock, between sites. Hypothesis 4 was determined to be partly true. For western hemlock, western redcedar, and grand fir without vegetation management treatments growing at the CR site, the understory and midstory vegetation counteracted the positive effects of vegetation control on crop tree growth when compared with treated plots. Hypothesis 5 was determined to be partially true. Ecosystem biomass stock was not higher in treated plots in all cases. Ecosystem biomass stock was not larger in treated plots of western hemlock, western redcedar, and grand fir at the CR site.

For Chapter 3 we determined that hypothesis 1-4 were partially true. Trees in treated plots had a higher total and component ANPP 11 years after vegetation management ended, with the exception of Douglas-fir growing at the CR site. Overall tree response to aggressive vegetation management, in terms of ANPP, differed between species. Foliage and live branch ANPP did not differ between species. In the case of Douglas-fir, overall tree and stemwood ANPP response to vegetation management did differ between sites. $ANPP_E$ was observed to be higher in treated plots at the CF site. A positive correlation between basal area and $ANPP_T$ was observed to be true across all species and sites.

Overview of Results

Planted conifers growing in stands with sustained vegetation management during the first 5 years after planting showed larger aboveground tree biomass and aboveground net primary productivity (ANPP) 11 years after treatment had ended.

This gain was for all species at both sites, yet the magnitude differed between species. Western hemlock and grand fir were the most productive species when growing under sustained control of competing vegetation. Under conditions of no vegetation control after planting, Douglas-fir was the most productive species. Even though western redcedar was the most responsive species (73% increase in crop tree biomass stock and 72% increase in crop tree ANPP), the magnitude of the biomass yield and productivity was less than 60% of that of the other conifer species. The large relative response of western redcedar is mainly due to large mortality and low productivity under water-limited conditions. The low absolute biomass production is thought to be related to a reduced intrinsic productivity at the sites tested of this shade-tolerant species.

Management Implications

The relationships between BA and LAI and ANPP observed in this study can be useful for researchers and managers to estimate stand productivity and other ecosystem services and processes related to canopy growth such as carbon sequestration (Chen et al. 1999, Felzer et al. 2004), vegetation abundance and species richness (McBride et al. 2014, Kirkman et al. 2001), wildfire risks (Eastaugh and Hasenauer 2013, Waring and Coops 2016), and evapotranspiration (McLaughlin et al. 2013, Sun et al. 2015) among others.

Vegetation control did not affect ecosystem productivity. In our study, the four conifer species showed similar ecosystem productivity, independent of them growing as monocultures, with sustained vegetation management, or as multi-species, where the understory and midstory were allowed to grow. For this study, we also observed no difference in soil organic matter content in the upper 20 cm with and without vegetation management. From a carbon sequestration stand point, both management schemes seem to be viable options. If timber production is the main objective, large volume yield is attainable without reducing total ecosystem productivity under the intensive vegetation management treatment.

Future Directions

In continuation with this study, samples will be used for nutrient analysis as sub-samples from al oven-dried material were kept for future analysis. Although our findings gave a good overview of the responses in terms of biomass production, it is of high interest to test if there are differences in nutrient content between VM and C plots. Although we found no differences in soil organic matter content in the top 0-20 cm soil profile, it is important to confirm the trend at lower layers of the soil. Samples will therefore be taken up to 1.5 m in depth.

In this study we reported one year of litterfall and ANPP, however, we collected two years of litterfall. Another inventory is planned for this winter which will increase ANPP assessment to two years. Depending on funding availability, it is expected that litterfall collection and inventory measurements will continue for two more years. Furthermore, the assessments carried out in this study are planned to be repeated every 15-20 years. It will be beneficial to see if the effects of vegetation management are still present along the whole rotation.

Another valuable study is planned, i.e. performing an uncertainty analysis of biomass and ANPP estimates. Uncertainty analysis will help validate our findings by presenting the “true” error in our estimates.

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Appendix

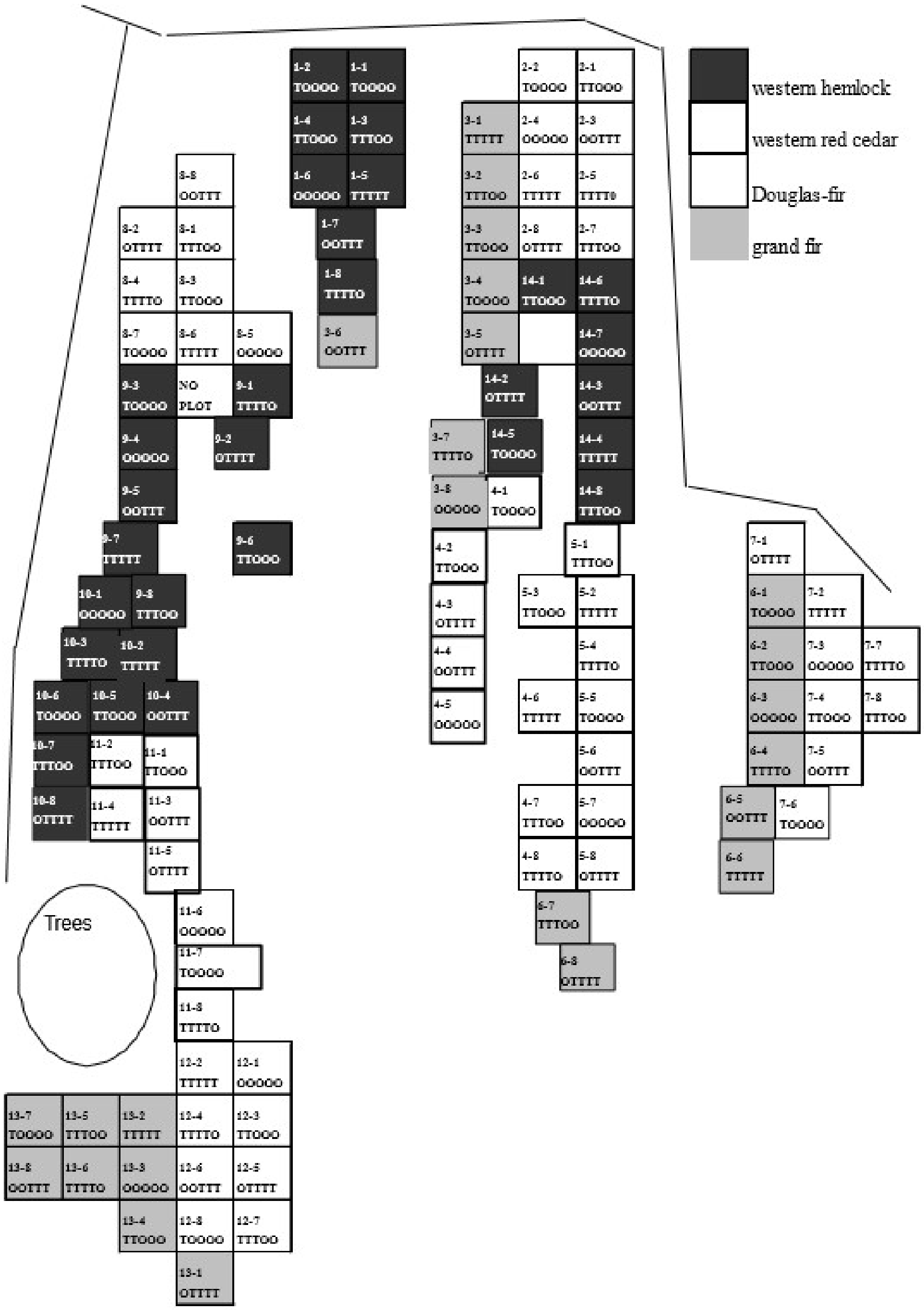

Figure 1. Map of central Coast Range site. See Appendix Table 1 for treatment description.

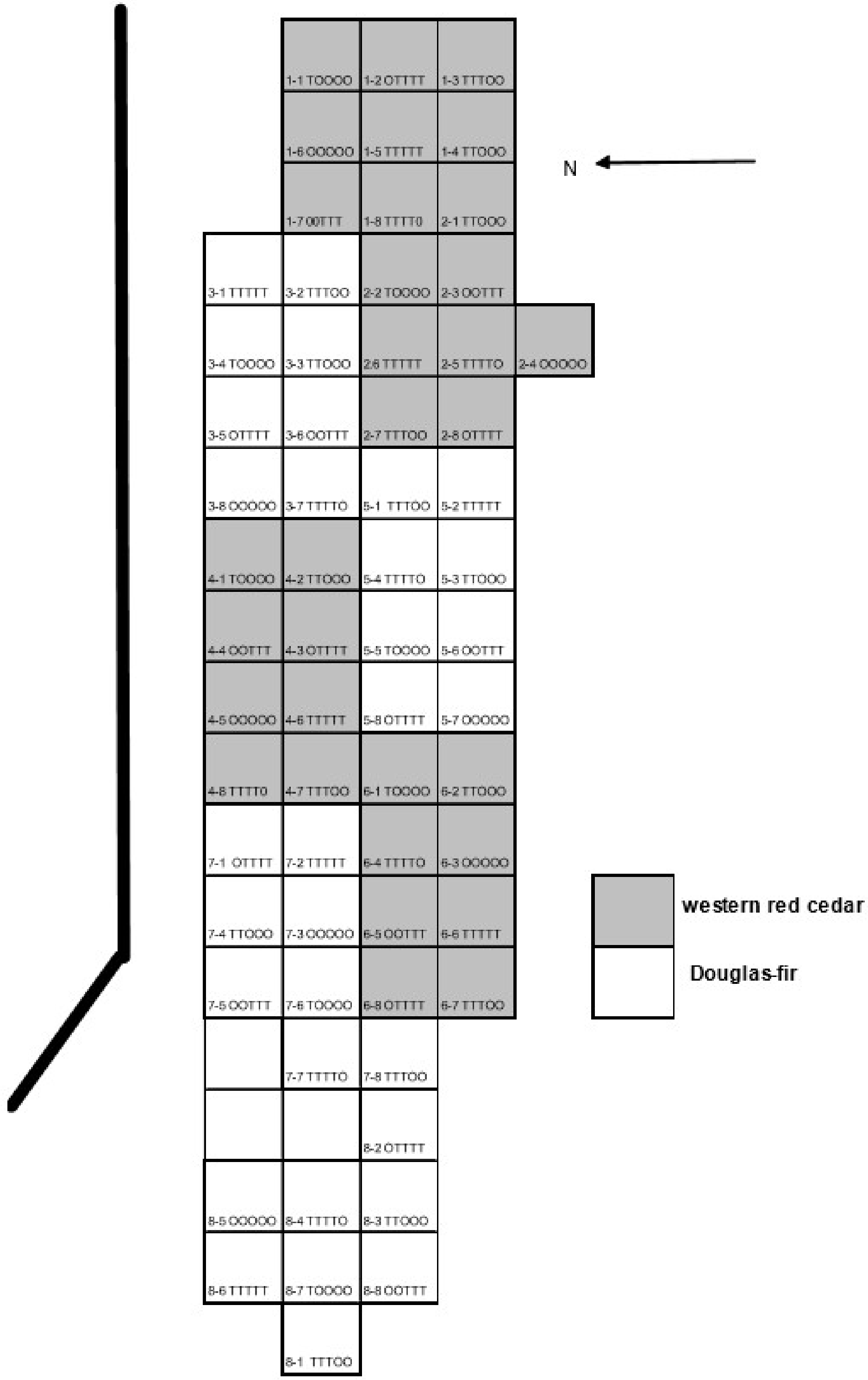

Figure 2. Map of Cascade foothills site. See Appendix Table 1 for treatment description.

Table 1. List of eight treatments applied at the central Coast Range and Cascade foothills sites. Control treatment (OOOOO) and VM treatment (TTTTT).

Treatment	Fall SP	SR1	SR2	SR3	SR4	SR5
OOOOO	**SP**	**O**	**O**	**O**	**O**	**O**
TOOOO	SP	T	O	O	O	O
TTOOO	SP	T	T	O	O	O
TTTOO	SP	T	T	T	O	O
TTTTO	SP	T	T	T	T	O
TTTTT	**SP**	**T**	**T**	**T**	**T**	**T**
OTTTT	SP	O	T	T	T	T
OOTTT	SP	O	O	T	T	T

SP: site preparation treatment; SR: spring release treatment; O: no treatment applied; T: treatment applied

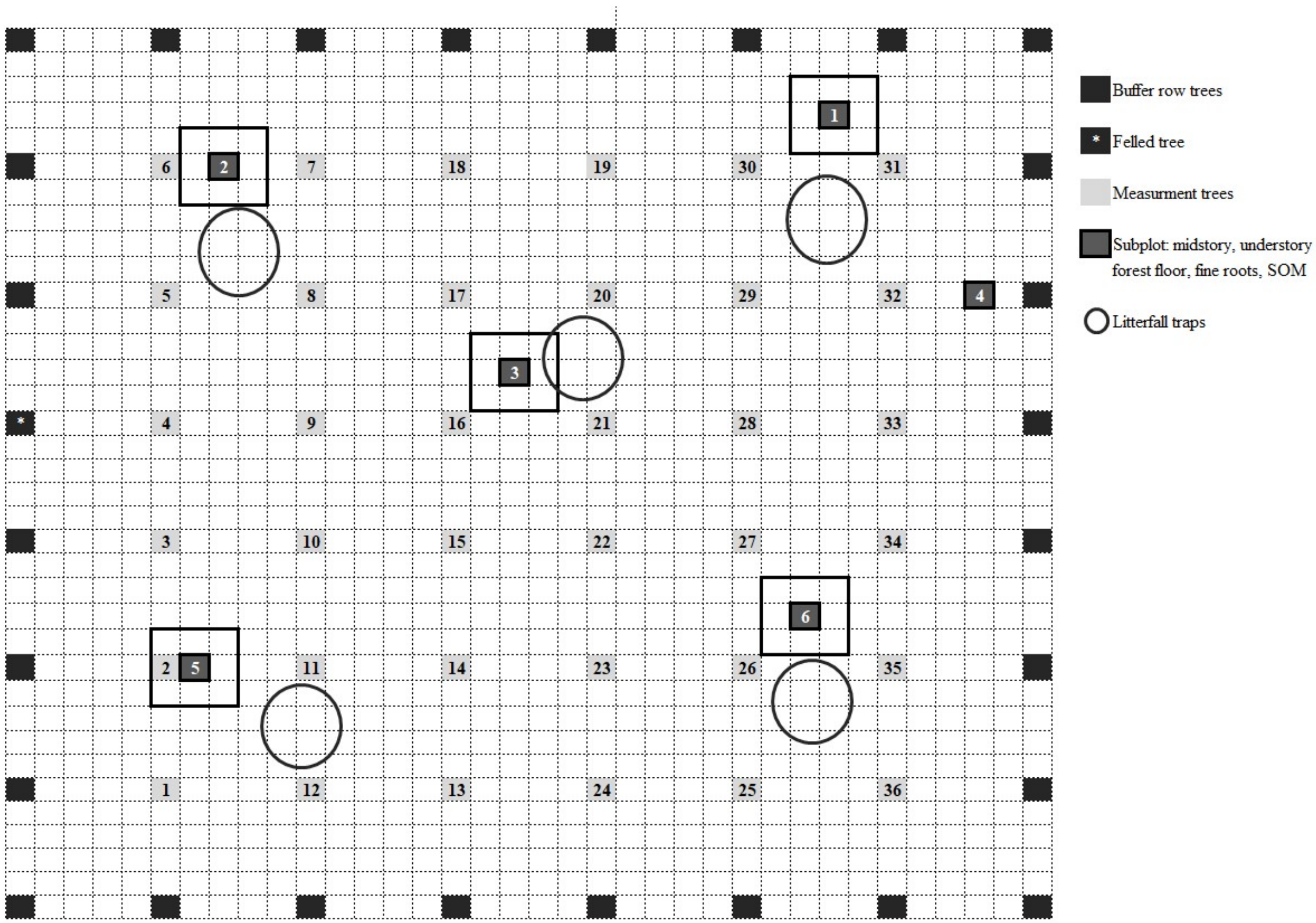

Figure 3. Measurement plot layout.

Table 2. Average specific leaf area ($m^2\ kg^{-1}$) and stemwood and stembark density ($kg\ m^{-3}$) for destructively sampled 15-16-year-old Douglas-fir, western hemlock, western redcedar and grand fir trees growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

		CR				CF			
Species	Variable	C	SE	VM	SE	C	SE	VM	SE
Douglas-fir	SLA	5.60	0.07	5.63	0.06	5.51	0.04	5.55	0.07
	W Density	394.6	21.6	379.0	25.1	477.7	37.8	569.1	28.1
	B Density	414.6	12.6	392.6	26.5	527.0	43.1	608.1	46.2
western hemlock	SLA	5.54	0.03	5.49	0.09				
	W Density	413.1	32.5	410.7	15.7				
	B Density	372.4	22.5	443.8	31.3				
western redcedar	SLA	3.08	0.12	3.05	0.09	2.98	0.03	3.00	0.10
	W Density	347.6	25.8	287.2	42.1	300.3	10.2	389.7	14.9
	B Density	321.7	30.1	285.0	14.3	346.3	54.8	463.9	48.6
grand fir	SLA	4.25	0.08	4.31	0.06				
	W Density	338.0	15.1	416.0	10.9				
	B Density	337.0	36.6	420.0	18.1				

C: control treatment; VM: sustained vegetation management treatment for first 5 years post planting; SLA: Specific leaf area ($m^2\ kg^{-1}$); W Density: stemwood density ($kg\ m^{-3}$); B Density: stembark density ($kg\ m^{-3}$); SE: standard error.

Table 3. Parameter estimates and fit statistics of equations for predicting stem volume outside bark (VOB) and stem volume inside bark (VIB) for 15 to 16-year-old Douglas-fir, western hemlock, western redcedar and grand fir trees growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Species	Model	Parameter	Parameter Estimate	SE	R^2	RMSE	CV
Douglas-fir	$VOB = a*(DBH^b)*(HT^c)$	a	0.000055	0.000027	0.996	0.014	6.9
		b	1.703752	0.203596			
		c	1.190193	0.306222			
	$VIB = a*(DBH^b)*(HT^c)$	a	0.000034	0.000018	0.995	0.012	7.5
		b	1.671631	0.219626			
		c	1.327253	0.333032			
western hemlock	$VOB = a*(DBH^b)*(HT^c)$	a	0.000027	0.000019	0.997	0.009	6.3
		b	2.027001	0.099639			
		c	1.083405	0.242174			
	$VIB = a*(DBH^b)*(HT^c)$	a	0.000018	0.000016	0.995	0.011	8.2
		b	1.890755	0.129699			
		c	1.335256	0.308443			
western redcedar	$VOB = a*(DBH^b)$	a	0.000177	0.000052	0.993	0.006	10.3
		b	2.253929	0.102283			
	$VIB = a*(DBH^b)$	a	0.000148	0.000051	0.991	0.006	12.2
		b	2.255902	0.121304			
grand fir	$VOB = a*(DBH^b)*(HT^c)$	a	0.000039	0.000010	0.999	0.004	4.0
		b	2.047817	0.075631			
		c	0.923092	0.105001			
	$VIB = a*(DBH^b)*(HT^c)$	a	0.000017	0.000007	0.998	0.006	6.0
		b	2.257204	0.119024			
		c	0.934745	0.159914			

VOB: stem volume over-bark (m^3); VIB:stem volume inside bark (m^3) DBH: diameter at breast height (cm at 1.37 m), HT: tree height (m), SE: standard error, R^2: coefficient of determination, RMSE: root mean square error. CV: coefficient of variation (100·RMSE/mean). For all parameter estimates: $P < 0.05$.

Table 4. Parameter estimates and fit statistics of branch-level biomass functions of foliage, live branches, and dead branches and leaf area for 15-16-year-old Douglas-fir, western hemlock, western redcedar and grand fir trees growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Species	Component	Model	Parameter	Parameter Estimate	SE	R^2	RMSE	CV
Douglas-fir	BF	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.242740	0.111243	0.900	43.874	41.9
			b	2.234609	0.153935			
			c	0.325534	0.070549			
	BWB	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.104009	0.030414	0.969	40.342	24.3
			b	2.520137	0.093530			
			c	-0.083128	0.023099			
	BD	$= a \cdot D_b^b$	*a*	0.322141	0.157709	0.968	34.485	22.1
			b	2.175812	0.158788			
	BLA	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.001583	0.000812	0.883	0.400	45.6
			b	2.297381	0.170593			
			c	0.266067	0.072168			
			b	1.242950	0.827991			
western hemlock	BF	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.409374	0.183901	0.899	26.031	40.9
			b	2.079810	0.153200			
			c	0.386665	0.080550			
	BWB	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.258027	0.100716	0.953	28.206	28.8
			b	2.172031	0.128320			
			c	-0.100870	0.030428			
	BD	$= a \cdot D_b^b$	*a*	0.296655	0.161302	0.976	28.392	19.7
			b	2.169103	0.172334			
	BLA	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.006060	0.002824	0.905	0.218	40.6
			b	1.845332	0.160453			
			c	0.302019	0.074047			
western redcedar	BF	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.887282	0.264078	0.937	42.222	33.5
			b	1.811325	0.094996			
			c	0.101805	0.038719			
	BWB	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.043754	0.029673	0.837	54.141	65.3
			b	2.581373	0.206244			
			c	-0.135667	0.048691			
	BD	$= a \cdot D_b^b$	*a*	0.025267	0.044227	0.944	3.137	29.9
			b	2.848520	0.752131			
	BLA	$= a \cdot D_b^b$	*a*	0.003206	0.000994	0.935	0.198	33.8
			b	1.853035	0.097849			
grand fir	BF	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.263667	0.184964	0.841	37.831	55.7
			b	2.201609	0.239199			
			c	0.185972	0.074089			
	BWB	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.113294	0.048466	0.956	21.431	30.0
			b	2.338510	0.142954			
			c	-0.154903	0.024570			
	BD	$= a \cdot D_b^b$	*a*	0.390743	0.296059	0.943	37.788	35.3
			b	2.091764	0.242813			
	BLA	$= a \cdot D_b^b \cdot Hr^c$	*a*	0.002418	0.001487	0.875	0.226	46.0
			b	2.141783	0.211811			
			c	0.311511	0.104361			

D_b: diameter outside-bark at base (mm), Hr: relative depth into the living crown, BF: Total foliage biomass (kg), BWB: Total live branch biomass (kg), BLA: Leaf area (m^2), BD: Total dead branch biomass (kg), SE: standard error, R^2: coefficient of determination, RMSE: root mean square error, CV: coefficient of variation (100·RMSE/mean). For all parameter estimates: $P < 0.05$.

Table 5. Parameter estimates and fit statistics of equations predicting dry weight (kg) of wood, bark, live branch, dead branch and foliage for 15-16-year-old Douglas-fir, western hemlock, western redcedar and grand fir trees growing on sites located in the central Coast Range and the Cascade foothills of western Oregon.

Species	Component	Model	Parameter	Parameter Estimate	SE	R^2	RMSE	CV
Douglas-fir	W	$= a \cdot \text{dbh}^b \cdot \text{ht}^c$	*a*	0.085982	0.079190	0.983	9.548	13.8
			b	1.743391	0.410895			
			c	0.588628	0.592671			
	B	$= a \cdot \text{dbh}^b$	*a*	0.143963	0.124467	0.970	3.237	18.3
			b	1.650530	0.289199			
	F	$= a \cdot \text{dbh}^b$	*a*	0.127946	0.126649	0.962	3.663	20.8
			b	1.687964	0.330921			
	LB	$= a \cdot \text{dbh}^b$	*a*	0.091734	0.124809	0.934	6.883	27.8
			b	1.914700	0.453363			
	DB	$= a \cdot \text{dbh}^b$	*a*	0.013202	0.040815	0.744	6.009	61.2
			b	2.257778	1.025492			
	LA	$= a \cdot \text{dbh}^b$	*a*	0.809925	0.790337	0.962	21.795	20.6
			b	1.671241	0.326305			
western hemlock	W	$= a \cdot \text{dbh}^b \cdot \text{ht}^c$	*a*	0.007047	0.004370	0.99	2.928	6.00
			b	1.571966	0.097645			
			c	1.662778	0.219399			
	B	$= a \cdot \text{dbh}^b$	*a*	0.000498	0.000253	0.995	0.888	9.95
			b	3.381269	0.161567			
	F	$= a \cdot \text{dbh}^b$	*a*	0.022128	0.011911	0.990	1.335	11.9
			b	2.189509	0.175570			
	LB	$= a \cdot \text{dbh}^b$	*a*	0.026507	0.010002	0.995	1.419	8.32
			b	2.271618	0.122826			
	DB	$= a \cdot \text{dbh}^b$	*a*	0.048264	0.087975	0.888	1.482	37.2
			b	1.531550	0.605645			
	LA	$= a \cdot \text{dbh}^b$	*a*	0.378075	0.186953	0.991	10.329	11.2
			b	1.942013	0.162359			
western redcedar	W	$= a \cdot \text{dbh}^b$	*a*	0.084895	0.057711	0.961	4.275	24.9
			b	2.053715	0.237990			
	B	$= a \cdot \text{dbh}^b$	*a*	0.000772	0.001259	0.892	1.870	46.1
			b	3.204432	0.556574			
	F	$= a \cdot \text{dbh}^b$	*a*	0.140835	0.039597	0.992	1.329	10.9
			b	1.736489	0.099446			
	LB	$= a \cdot \text{dbh}^b$	*a*	0.048643	0.028102	0.972	2.245	21.1
			b	2.083644	0.202075			
	DB	$= a \cdot \text{dbh}^b$	*a*	0.003620	0.009308	0.938	0.044	29.2
			b	1.825111	1.152156			
	LA	$= a \cdot \text{dbh}^b$	*a*	0.632243	0.197693	0.989	7.109	12.1
			b	1.764259	0.110488			
grand fir	W	$= a \cdot \text{dbh}^b \cdot \text{ht}^c$	*a*	0.001790	0.001526	0.969	4.664	31.8
			b	2.367067	0.238453			
			c	1.292649	0.331163			
	B	$= a \cdot \text{dbh}^b$	*a*	0.054515	0.050308	0.967	1.638	22.2
			b	1.799409	0.308392			
	F	$= a \cdot \text{dbh}^b$	*a*	0.141392	0.084277	0.983	1.675	15.5
			b	1.599511	0.200387			
	LB	$= a \cdot \text{dbh}^b$	*a*	0.096273	0.069479	0.979	2.265	17.4
			b	1.799857	0.241167			
	DB	$= a \cdot \text{dbh}^b$	*a*	0.000009	0.000035	0.899	2.497	42.9
			b	4.570093	1.150185			
	LA	$= a \cdot \text{dbh}^b$	*a*	1.015881	0.615344	0.982	11.524	15.9
			b	1.575135	0.203806			

dbh: diameter outside-bark at 1.37 m height (cm), ht: total tree height (m), W: Total stem wood biomass (kg), B: Total bark biomass (kg), F: Total foliage biomass (kg), LB: Total live branch biomass (kg), LA: Leaf area (m^2 $tree^{-1}$), DB: Total dead branch biomass (kg), SE: standard error, R^2: coefficient of determination, RMSE: root mean square error, CV: coefficient of variation (100·RMSE/mean). For all parameter estimates: $P < 0.05$.

Table 6. Parameter estimates for aboveground biomass of hardwood species.

Species	Component	a	b	Model	R^2	Source
ACCI	Total AG	-2.047	2.3852	$= a + b \cdot \ln(DBH)$	0.84	Chojnacky et al. 2014
ACMA	Total AG	-2.047	2.3852	$= a + b \cdot \ln(DBH)$	0.84	Chojnacky et al. 2014
ALRH	Total AG	-2.5932	2.5349	$= a + b \cdot \ln(DBH)$	0.81	Chojnacky et al. 2014
ALRU	Total AG	-2.5932	2.5349	$= a + b \cdot \ln(DBH)$	0.81	Chojnacky et al. 2014
CHCH	SW	0.024	2.658	$= a \cdot DBH^b$	0.98	Ter-Mikaelian and
	SB	0.0026	2.989	$= a \cdot DBH^b$	0.97	Korzukhin 1997
	FL	0.0401	1.6930	$= a \cdot DBH^b$	0.81	
	BR	0.0092	2.5760	$= a \cdot DBH^b$	0.89	
COCO	Total AG	54.1	1.229	$= a \cdot DBH^b$	-	Ohmann et al. 1976
PREM	Total AG	-2.2118	2.4133	$= a + b \cdot \ln(DBH)$	0.79	Chojnacky et al. 2014
RHPU	FL	0.000003	6.788099	$= a \cdot DBH^b$	0.96	This study
	SW+BR	0.174466	2.161457	$= a \cdot DBH^b$	0.99	

ACCI: *Acer circinatum* Pursh., ACMA: *Acer macrophyllum* Pursh, ALRH: *Alnus rhombifolia* Nutt., ALRU: *Alnus rubra* Bong., CHCH: Chrysolepis chrysophylla (Douglas x Hook.) Hjelmqvist, COCO: *Corylus cornuta* Marsh., PREM: *Prunus emarginata* (Dougl. ex Hook.) D. Dietr., RHPU: *Rhanmus purshiana* (D.C.) Cooper. DBH: diameter at breast height (1.37 m), cm. Total AG: Total aboveground biomass (kg), SW: Stemwood (kg), SB: Stem bark (kg), FL: Foliage (kg), BR: Branch (kg).