AN ABSTRACT OF THE THESIS OF

<u>Callan Cannon</u> for the degree of <u>Master of Science</u> in <u>Sustainable Forest Management</u> presented on <u>May 29, 2020</u>.

Title: <u>Long-term Effects of Vegetation Management on Plant and Soil Derived Nutrient Budgets</u> for Plantations of Four Western Conifer Species.

Carly Gonthen 3

Abstract approved:

Carlos Gonzalez-Benecke

Forest Vegetation Management (VM) is an important tool used in the Pacific Northwest (PNW) for reforestation. It has been well documented that VM increases seedling survival and crop tree volume growth. What is less understood, is how altering the plant community and successional trajectory affects the way the ecosystem uses and distributes nutrients in the long term. In this study, we investigate long-term effects of vegetation management on nutrient concentration and content of various tissues and ecosystem components of 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 mountain foothills (CF) under two contrasting VM treatments. This is the first study of its kind to investigate how VM affects distribution of several nutrients throughout both plant derived tissue and soil.

The two VM treatments represent operational extremes of VM regimes and consist of: Control, which received no herbicide application post planting, and VM, which received five years of spring release herbicide application. Both treatments include a fall site preparation herbicide application. The ecosystem was broken down into crop trees (separated into foliage, live branches, stembark, and stemwood), midstory species (separated into foliage and stem), understory, forest floor, fine roots, and mineral soil (with depth increments 0.0-0.2 m, 0.2-0.4 m, 0.4-0.6 m, and 0.6-1.0 m). Samples of crop tree, understory, forest floor, and soil from 0.0-0.2 m samples were taken during the 16th and 17th growing season (the CF site was planted one year later). Midstory and remaining mineral soil samples were collected during the 18th and 19th growing season.

All samples were analyzed for concentration of carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), boron (B), copper (Cu), iron (Fe), manganese (Mn), sodium (Na), and zinc (Zn). Concentrations of CNS for all samples was determined by dry combustion. The remaining nutrients were determined by inductively coupled plasma optical emission spectroscopy (ICP-OES) from dry ash extractions (for plant tissue) and nitric acid microwave digestion (for determination of total soil nutrients). These concentrations were scaled to tissue content using empirically derived biomass equations from Gonzalez-Benecke et al. (2018) and updated biomass measurements taken at year 16 by Flamenco et al. (2019).

VM effects on tissue concentration varied by nutrient, overstory species (species), tissue, and site. Forest floor and crop tree stembark, followed by fine roots, were the tissue types that showed the greatest number of treatment effects (greatest number of nutrients affected) across all species. Soil concentrations were generally unaffected by treatment, except for surface soil concentrations of Mg, and Ca (which were only significant for certain species) and deep soil carbon and N (which was only detected for Douglas-fir at the CR site). All detectable concentration differences between treatments showed higher concentrations in VM plots. The exception to this trend was soil N for WRC at the CR site which had significantly lower concentrations in VM plots for the 0.2-0.4 and 0.4-0.6 depth increments. Soil concentrations showed much greater variation between sites than between species or treatments.

VM effects on total plant derived nutrients masses were more prominent than differences in concentrations. Ca was the only nutrient for which all species showed higher plant derived masses in the VM condition. Plant derived tissue content of, C, Cu, P, and B, all tended to be higher in VM plots, with the exception of western redcedar plots at the CR site. This case was an

outlier due to the fact that Control plots developed significantly more biomass due to high midstory biomass, whereas the VM plots developed relatively little midstory and crop tree biomass. There were few differences in soil content between species and treatments, and those that were significant were unable to be explained by differences in uptake by plant species. Notably, total soil N of WRC at the CR site, however was significantly lower for VM plots. This may indicate the potential for VM applied to a slow growing species, such as WRC, to reduce ecosystem retention of N. With the exception of C and N, total soil nutrient reserves were orders of magnitude greater than total plant derived masses. This indicated that there is low probability of an adverse effect of VM on soil nutrient stores.

Treatment effects on foliar nutrition varied by site and species, though crop trees at the CF site tended to have diluted concentrations of P and K and increases in Ca, Mg, and Fe in the VM treatment. Nutrient use efficiency (NUE) for the different stands was computed from ratios between the mass of all plant derived carbon and all other plant derived nutrients. VM significantly increased the NUE of N, P, Mg, S, and Cu across all species. When the NUE was calculated with only the carbon stored in crop tree stemwood, VM increased the NUE of all nutrients.

The results of this analysis indicate that sustained VM during the first five years of stand establishment affected nutrient content of various pools more than concentration, though both tissue concentration and content vary more strongly by site and species. While total plant derived masses of Ca, C, Cu, P, and B all tended to be higher in VM plots, trends varied greatly by nutrient, site, and species. Overstory species exert control over the nutrient requirements of the ecosystem, but VM does tend to increase the NUE, especially with respect to N, P, Mg, S, and Cu. Stands growing under sustained competing vegetation control did tend to produce more harvestable and plant-derived carbon per unit nutrient fixed in plant tissues, improving the efficiency of nutrient use for stands that are being managed for carbon sequestration as well as for timber harvest. While total soil reserves were generally unaffected by VM treatment and are unlikely to be adversely affected by VM in the long term, it is possible that VM can reduce soil N retention for slow growing species like WRC. Managers can use this information to make better decisions about site preparation treatments. ©Copyright by Callan Cannon

May 29, 2020

All Rights Reserved

Long-term Effects of Vegetation Management on Plant and Soil Derived Nutrient Budgets for Plantations of Four Western Conifer Species

> by Callan Cannon

A THESIS

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Master of Science

Presented May 29, 2020 Commencement June 2020

ACKNOWLEDGEMENTS

I would like to express sincere appreciation for the many different types of support provided by many important parties. I would like to thank Carlos Gonzalez-Benecke, my advisor, for his support on all aspects of this project, his confidence in me, and the many doorways he has helped open. I would also like to thank my committee members, Drs. Matt Powers, David Myrold, and Jeff Hatten for their guidance and all the things I have learned from them. I would like to thank Maxwell Wightman for logistical help coordinating research as well as help editing.

I would like to thank the Vegetation Management Research Cooperative (VMRC) and all its members for financial support. I would like to thank Starker Forests Inc. and Cascade Timber Consulting for allowing me to use their property to conduct this study.

I would like to thank all who assisted in data collection and processing in any way. I specifically want to thank Gloria Ambrowiak, Adam Fund, and Marcus Kleber in the Central Analytical Laboratory at Oregon State for advice on analytical techniques, running ICP-OES samples, and for allowing me use of shared lab space. I would like to thank Jeff Hatten and Adrian Gallo with help designing soil sampling regimes and lending equipment.

I would also like to thank a number of people in my personal life for their help and support throughout this process. To my parents for helping from afar, especially my mother for her help with statistics and editing. To my sister and my friends at Oregon State who have helped keep me afloat. To my partners, for everything. I was able to do all of this thanks to you.

TABLE OF CONTENTS

1	Introduction	and Literature Review	1
	1.1 Ir	ntroduction	1
	1.2 L	iterature Review	2
	1.2.1	Forests of the Pacific Northwest	2
	1.2.2	Forest Nutrition	3
	1.2.3	Nutrient Cycling	5
	1.2.4	Plants and Nutrient Cycling 1	0
	1.2.5	Nutrient Budgets and Nutrient Use Efficiency 1	2
	1.2.6	Nutrients in Managed forests 1	2
	1.3 S	tudy Design 1	5
	1.4 O	bjectives and Hypotheses 1	6
	1.5 R	eferences 1	7
2.	Nutrient Con	centrations in Plant and Soil Pools of Four Western Conifer Stands	4
	2.1.	Introduction	4
	2.2.	Literature Review	5
	2.2.1	. Nutrient Concentrations in Plant Tissues	5
	2.2.2	. Nutrient Concentrations in Soils 2	8
	2.2.3	. Silvicultural Management Effects on Nutrient Concentrations 2	9
	2.3.	Questions and Hypotheses	1
	2.4.	Methods	1
	2.4.1	. Description of Sites	1
	2.4.2	. Study Design	2
	2.4.3	. Nutrient Analysis	4

TABLE OF CONTENTS (Continued)

	2.4.4.	Statistical Analysis	
	2.5.	Results	
	2.6.	Discussion	
	2.7.	Management Implications	49
	2.8.	References	49
3.	Nutrient Cont	ents in Plant and Soil Pools of Four Western Conifer Stands	56
	3.1.	Introduction	56
	3.2.	Literature Review	57
	3.2.1.	Nutrient Content in Plant Tissues	57
	3.2.2.	Nutrient Content in Soils	59
	3.2.3.	Management Effects on Nutrient Content	59
	3.3.	Questions and Hypotheses	61
	3.4.	Methods	
	3.4.1.	Description of Sites	
	3.4.2.	Study Design	
	3.4.3.	Soil Characterization	63
	3.4.4.	Biomass Calculations	63
	3.4.5.	Nutrient Budget Calculations	64
	3.4.6.	Statistical Analysis	65
	3.5.	Results	65
	3.5.1.	Stand Inventory and Soil Properties	65
	3.5.2.	Nutrient Budget Summary	67
	3.5.3.	Carbon Budget	68

TABLE OF CONTENTS (Continued)

3.5.4.	Nitrogen Budget	70
3.5.5.	Phosphorous Budget	71
3.5.6.	Potassium Budget	72
3.5.7.	Boron Budget	73
3.5.8.	Iron Budget	74
3.5.9.	Nutrients in Harvestable Pools	75
3.6.	Discussion	77
3.6.1.	Plant derived nutrient content	77
3.6.2.	Soil nutrient content	81
3.7.	Management Implications	82
3.8.	References	82
4 Nutrient Ratio	os, Foliar Vector Analysis, and Nutrient Use Efficiency of Four Western	
Conifers Stands G	rowing Under Contrasting Competing Vegetation Control Treatments	89
4.1 In	troduction	89
4.2 Li	terature Review	90
4.2.1	Nutrient Ratios in Plant Tissues	90
4.2.2	Management Effects on Nutrient Ratios	92
4.2.3	Nutrient Use Efficiency	92
4.2.4	Vector Analysis	94
4.3 Qu	uestions and Hypotheses	96
4.4 M	ethods	97
4.4.1	Description of Sites	97
4.4.2	Study Design	98
4.4.3	Nutrient Ratios	98

TABLE OF CONTENTS (Continued)

4.4.4	Vector Analysis	
4.4.5	5 Statistical Analysis	
4.5 R	Results	
4.5.1	Nutrient Ratios	
4.5.2	2 Foliar Vector Analysis	106
4.6 D	Discussion	111
4.6.1	Nutrient ratios	111
4.6.2	2 Nutrient Use Efficiency	112
4.6.3	Vector Analysis	113
4.7 M	Aanagement Implications	115
4.8 R	References	115
Conclusions		120
5.1.	Summary of Findings	120
5.2.	Management Implications	121
5.3.	Future Directions	122
5.4.	References	122
Appendix		120
5.1.	Chapter 2 Appendix	120
5.2.	Chapter 3 Appendix	137
5.3.	Chapter 4 Appendix	122

5.

6.

LIST OF FIGURES

Figure

Page

Figure 2.2. Crop tree tissue concentrations of nitrogen, phosphorous, potassium, and calcium for 16-year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) grown in the Oregon Coast Range. Concentrations are averaged between Control and VM treatments. Significant species differences within a tissue type are denoted by letters (P<0.05).

Figure 2.3. Crop tree tissue concentrations of boron, manganese, zinc, and sodium for 16-yearold stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) grown in the Oregon Coast Range. Concentrations are averaged between Control and VM treatments. Significant species differences within a tissue type are denoted by letters (P<0.05). 45

LIST OF FIGURES (Continued)

Figure

Figure 4.2. Relationship between crop tree biomass increment (Mg ha-1 yr-1) and total crop tree derived nutrient ratios of Cu:N for 18 and 19-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Regressions derived from the linear model are plotted for each treatment. 102

LIST OF FIGURES (Continued)

<u>Figure</u>

Figure 4.5. Examples of carbon:nutrient ratios for micronutrients. Ratios of plant derived carbon mass to plant derived boron (C:B, upper panel) and Fe (C:Fe, lower panel) for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species. 106

Figure 4.9. Vector diagrams for western redcedar foliar concentrations and content of for macronutrients (top) and micronutrients (bottom) of 18 and 19-year old stands at the CF site (circles) and CR site (diamonds). Treatments include control (black) and VM 4.1.1.1 (white) indicating five years herbicide application post-planting. CF VM and CR VM concentrations and content have been normalized to the Control treatment at their respective site (Control). 110

LIST OF TABLES

Table

Table 2.4. P values of site effect for concentration of C, N, P, K, Mg, Ca, S, B, Cu, Fe, Mn, Na, and Zn for each nutrient pool for 16-18 year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range and the Cascade foothills of western Oregon. Green cells indicate that the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the Site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site and white cells indicate the concentration was higher at the CR site.

Table 2.5. P values of species effect for concentration of C, N, P, K, Mg, Ca, S, B, Cu, Fe, Mn, Na, and Zn for each nutrient pool for 16-18 year-old Douglas-fir, western hemlock, western redcedar and grand fir, stands growing under contrasting treatments of vegetation management in the central Oregon Coast Range. Blank cells indicate no significant differences across species.

Table 3.1 Average trees per ha (TPHA, ha–1), mean height (height, m), quadratic mean diameter (QMD, cm), crop tree basal area (BA, m2 ha–1) and midstory basal area (BA, m2 ha–1), for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) planted stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon. Control: no post- planting vegetation control, VM: sustained vegetation control for first 5 years post planting.

LIST OF TABLES (Continued)

Table

Table 4.1. Critical and optimal macronutrient ratios for conifers (Ingestad, 1979; van denDreissche, 1974). Table adapted from Garrison and Moore (1998). All ratios are expressed as apercentage.92

Table 4.2. Average foliar nutrient ratios for 18 year old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing in the Oregon Coast Range (CR) and Cascade Foothills (CF). Values presented are not scaled to percentages and are averaged across treatments. Standard errors for each measurement are shown in parentheses. 100

LIST OF TABLES (Continued)

Table Table 4.5. Results of ANOVA test for differences between carbon:nutrient ratios of plant derived matter (crop trees, midstory, understory, and forest floor) for Douglas-fir, western hemlock,

western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). 104

LIST OF APPENDIX FIGURES

<u>Figure</u>

<u>Page</u>

LIST OF APPENDIX FIGURES (Continued)

Figure

Appendix Figure S.3.7. Average magnesium (Mg) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences

Appendix Figure S.3.8. Average manganese (Mn) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences

Appendix Figure S.3.9. Average nitrogen (N) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no postplanting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM

Appendix Figure S.3.10. Average sodium stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM

Appendix Figure S.3.11. Average phosphorous (P) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences

Appendix Figure S.3.12. Average Sulfur (S) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no postplanting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM

LIST OF APPENDIX FIGURES (Continued)

Figure

LIST OF APPENDIX TABLES

Table

Appendix Table S.2.4. Concentration (ppm) of Boron (B) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

Appendix Table S.2.5. Concentration (%) of carbon (C) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

Appendix Table S.2.6. Concentration (%) of calcium (Ca) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

Table

Appendix Table S.2.7. Concentration (ppm) of copper (Cu) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

Appendix Table S.2.8. Concentration (ppm) of iron (Fe) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

Appendix Table S.2.11. Concentration (ppm) of manganese (Mn) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

Appendix Table S.2.12. Concentration (%) of nitrogen (N) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

Table

Appendix Table S.2.13. Concentration (ppm) of sodium (Na) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at

Appendix Table S.2.14. Concentration (%) of phosphorus (P) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites locate d in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in **bold** if the difference in concentration was significant at

Appendix Table S.2.15. Concentration (%) of Sulfur (S) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in **bold** if the difference in concentration was significant at α =0.05.

Appendix Table S.2.16. Concentration (ppm) of zinc (Zn) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in **bold** if the difference in concentration was significant at α =0.05. 137

Appendix Table S.3.1. Results of ANOVA test for potassium (K) and sodium (Na) plant derived nutrient pools for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). High concentration assumes stem tissue concentrations of 1.5 ppm Na and 0.03% K in all species. Low concentration assumes stem tissue concentrations of 0.05 ppm and 0.01% K in all species.

Appendix Table S.3.2. Results of ANOVA test for nutrient pools of plant and soil derived boron (B) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are

Table

Appendix Table S.3.5. Results of ANOVA test for nutrient pools of plant and soil derived copper (Cu) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.6. Results of ANOVA test for nutrient pools of plant and soil derived iron (Fe) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Table

Appendix Table S.3.11. Results of ANOVA test for nutrient pools of plant and soil derived sodium masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.14. Results of ANOVA test for nutrient pools of plant and soil derived zinc (Zn) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

<u>Table</u>

<u>Page</u>

Appendix Table S.3.17. Mass (kg ha ⁻¹) of carbon (C) of tree and ecosystem components for 18- year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.18. Mass (kg ha ⁻¹) of carbon (C) of tree and ecosystem components for 18- year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.19. Mass (kg ha ⁻¹) of calcium (Ca) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.20. Mass (kg ha ⁻¹) of calcium (Ca) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.21. Mass (kg ha ⁻¹) of copper (Cu) of tree and ecosystem components for 18- year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.22. Mass (kg ha ⁻¹) of copper (Cu) of tree and ecosystem components for 18- year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.23. Mass (kg ha ⁻¹) of Fe of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05

<u>Table</u>

Appendix Table S.3.24. Mass (kg ha ⁻¹) of Fe of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.25. Mass (kg ha ⁻¹) of potassium (K) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.26. Mass (kg ha ⁻¹) of potassium (K) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.27. Mass (kg ha ⁻¹) of magnesium (Mg) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.28. Mass (kg ha ⁻¹) of magnesium (Mg) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.29. Mass (kg ha ⁻¹) of manganese (Mn) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.30. Mass (kg ha ⁻¹) of manganese (Mn) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05

xxvi

<u>Table</u>

Appendix Table S.3.31. Mass (kg ha ⁻¹) of nitrogen (N) of tree and ecosystem components for 18- year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.32. Mass (kg ha ⁻¹) of nitrogen (N) of tree and ecosystem components for 18- year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.33. Mass (kg ha ⁻¹) of sodium (Na) of tree and ecosystem components for 18- year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.34. Mass (kg ha ⁻¹) of sodium (Na) of tree and ecosystem components for 18- year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.35. Mass (kg ha ⁻¹) of phosphorous (P) of tree and ecosystem components for 18 year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.36. Mass (kg ha ⁻¹) of phosphorous (P) of tree and ecosystem components for 18 year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05
Appendix Table S.3.37. Mass (kg ha ⁻¹) of Sulfur (S) of tree and ecosystem components for 18- year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05

Table

1 Introduction and Literature Review

1.1 Introduction

Timber is an important sustainable material that has many uses. As a construction medium it is unique in that it is carbon neutral and renewable, and replacing other building materials with it may be an effective was to combat climate change (Sathre and O'Connor, 2010). Forest management increases forest ecosystem benefits, which helps satisfy production demand while maintaining other values that society puts on forests (O'Hara, 2016; Vierikko et al., 2008). One, increasingly common idea in forest management is the triad approach, which suggests that forested lands be divided into three overarching management regimes (Seymour and Hunter, 2016). It divides the landscape into high intensity production forestry on lands that are amenable, extensive management on forests that are not amenable to intensive management, and lands in reserve that are minimally managed to meet recreation and biodiversity conservation needs. This study is focused on high intensity plantations where silviculturalists are developing increasingly more intensive management regimes in order to maximize profit and meet production demand (Fox et al., 2007; Vance et al., 2010).

Trees, and plants in general, serve an important role in the ecosystem as primary producers. They are the main terrestrial organisms capable of converting solar energy into chemical energy which serves as the source of energy for all secondary producers in an ecosystem. This capacity to capture energy and turn it into biomass and stored energy is measured by net primary productivity (Perry et al., 2008). Certain conditions need to be met so that trees can continue to produce the biomass that humans harvest for our own needs, and on which ecosystem functions depend. While there are many factors that play into primary productivity, the most basic requirements are: light, water, and nutrient availability. Light serves as the energy source, water serves as the solvent in which the chemistry of life occurs, and nutrients are combined to make the very chemicals needed for biological functions (Perry et al. 2008).

In order for timber to be harvested continually, harvest practices must be sustainable. While there are many definitions and nuances to the concept of sustainability (e.g. ecological sustainability, economic sustainability and cultural sustainability), one of the fundamental aspects with regards to sustainable forestry is long term productivity (Vierikko et al., 2008). In order to achieve this goal, management activities must maintain certain aspects of the ecosystem to ensure continued productivity. To do this, we must understand how forest management practices alter ecosystem processes that are important for sustained primary production, such as nutrient cycling (Vierikko et al., 2008).

Nutrient cycling is an important ecosystem process as it controls the rate at which nutrients are supplied to trees (Cole, 1995; van Breemen, 1995). If this process is disrupted, it may lead to lower cycling rates which could result in less nutrient availability to trees, resulting in reduced productivity (Attiwill and Adams, 1993; Kershaw et al., 1996; Perry et al., 2008). In order to ensure sustained productivity, nutrient use must be sustainable. Research on the effects of silvicultural treatments has shown that long term effects vary based on intensity and frequency of removal as well as on site characteristics and planted species (Hoepting et al., 2011; Slesak et al., 2016; Vadeboncoeur et al., 2014). In order to ensure long term nutrient supply, it is important to study the effects that these treatments might have and how they may vary across sites and species.

1.2 Literature Review

1.2.1 Forests of the Pacific Northwest

The Pacific Northwest, a region that stretches from northern California to British Columbia, is known for its coniferous forests. They are considered valuable for recreation and as a source of timber. A state study in Oregon reported that outdoor recreation generates \$12.8 billion a year in consumer spending, in addition to creating over 100,000 State jobs and almost \$1 billion in state tax revenue (Oregon Parks and Recreation Department, 2017). In addition to recreation, the state of Oregon has led the nation in softwood lumber and plywood production for several years, followed by Washington. The forest products industry in Oregon employed over 60,00 people in 2019 and generated \$8.1 billion in GDP (Oregon Forest Resources Institute, 2019a). The state has almost 300 million acres of forest, most (60%) owned by the federal government. Large private landowners, which only make up 22% of acreage, account for more than 60% of timber harvest (Oregon Forest Resources Institute, 2019b).

The Douglas-fir is the most iconic species of the region, for its prominence both as a timber species and because of its dominance over large areas of landscape. It accounted for 70% of harvested volume in 2013. The next most significant species is western hemlock accounting

for 11%, followed by true firs which accounted for 8%, followed by pine, cedar and spruce (Simmons et al., 2014).

There are three main forest ecotypes important for timber production in the Pacific Northwest- the Pacific Coastal Ranges, the Cascade Mountains, and the dry interior forests (the latter of which will not be covered here). The Pacific Coastal Ranges, including the Oregon Coast Range and the Olympic mountains, are known for high rainfall (sometimes exceeding 2,000 mm annually) and productivity. The Cascade Mountains are a large mountain range influenced by volcanic activity which receive lots of winter precipitation but experience long summer drought. Forests in these ranges typically have thick organic layers and mineral soils high in organic matter (20-30%). These forests are traditionally thought to be nitrogen limited, and fertilization with urea is a common silvicultural treatment. However, many stands do not demonstrate a positive growth response to nitrogen fertilization (Mainwaring et al., 2014).

The Oregon Forest Practices act was passed in 1971, and similar regulations were soon established in Washington and California, though there are differences from state to state. One important aspect of these laws is that they regulate the amount of time between harvest and regeneration. In Oregon, trees must be "free to grow" six years after harvest. In order to meet this and other regeneration requirements, managers often turn to intensive forest management practices to ensure rapid plantation establishment. Though there is not as long of a history of intensive management as there is in the loblolly pine plantations in the Southeastern United States, commercial forest management regimes are becoming more intensive for private landowners. Seedling genetic improvement, harvest residues management, herbicidal vegetation management, thinnings and urea fertilization are common silvicultural treatments for intensively managed forests in this area (Vance et al., 2010).

1.2.2 Forest Nutrition

Plants need nutrients to function. Nutrients play key roles in biotic processes by forming cellular structures and assisting important cellular functions. They make up cell walls and membranes that are required to maintain for plant structure (Marschner and Marschner, 2012; Pallardy, 2008). As DNA, they store the information needed for plants to perform essential biotic processes from beginning to end of their life cycles. As enzymes and cofactors, they manipulate the chemical environment of the cell in a controlled manner in order to maintain suitable

conditions for life. As metabolites, they serve as a way to store energy as well as transport it throughout the organism. Essential plant nutrients are generally divided into two categories, macronutrients and micronutrients, depending on relative amount required (Marschner and Marschner, 2012; Pallardy, 2008).

Macronutrients are required in large amounts and generally play a structural role in the organism or play a role in cellular processes that are so ubiquitous they are required in large amounts. These seven nutrients are: carbon, nitrogen, phosphorous, potassium, calcium, magnesium, and sulfur (Brady and Weil, 2016). Carbon (along with as hydrogen and oxygen, which will not be focused on here) forms the backbone of most important structural moleculesparticularly cellulose in plants. These same three elements form sugars and other forms of reduced carbon that serve as energy stores for the plant. Nitrogen (N) is incorporated into the backbone of all proteins, which may serve a structural or biochemical role. The most abundant protein in plants is the enzyme rubisco, which is used in the Calvin cycle to catalyze the first step of carbon fixation (Pallardy, 2008). Nitrogen and phosphorous (P) are part of the structure of nucleic acids such as DNA and ribosomes (the machinery used to make proteins) (Marschner and Marschner, 2012). Potassium (K) is important in many processes, including protein synthesis, maintaining turgor pressure, and stomatal regulation. Calcium (Ca) is key in stabilizing membranes, as a component of secondary cell walls, and acts as a strong secondary messenger in certain plant signaling pathways (Hepler and Winship, 2010; Marschner and Marschner, 2012). Magnesium (Mg) plays its primary role in cellular chemistry. It coordinates the phosphate moieties of ATP (and other phosphate containing metabolites) better than any other element and is important for any cellular energy transfer that oxidizes or reduces phosphate (Pallardy, 2008). Additionally, there is one magnesium ion coordinated at the center of every chlorophyll molecule (Marschner and Marschner, 2012). Sulfur (S) is an essential constituent of several amino acids (methionine and cysteine) which serve special functions in proteins due to the unique redox chemistry of this nutrient.

Micronutrients are generally used by enzymes to catalyze some biochemical function. Since they are not widely used in structural elements and are only used for specific biochemical reactions, they are required in much smaller amounts than the macronutrients (Marschner and Marschner, 2012; Pallardy, 2008). The exact list of micronutrients depends on the kingdom of life being studied and the reference material. This study is concerned with the following six micronutrients: boron, copper, iron, manganese, sodium, and zinc. The function of boron (B) in plants was poorly understood for years, but it is now understood that it is important in cell division (Marschner and Marschner, 2012; Perry et al., 2008). Copper (Cu) is required for structure of important metabolic proteins in both the chloroplast and mitochondria as well as a cofactor in proteins that mediate oxidative stress. Iron (Fe) is notable in plants for its function in photosynthesis. Ferredoxin, an abundant iron containing protein, is an important part of the electron transport chain (Pallardy, 2008). Manganese (Mn) is also an important redox agent in photosynthesis. It is part of the enzyme complex that splits water molecules to produce gaseous oxygen, the reaction that serves as the source of electrons for the electron transport chain. Sodium (Na) is not considered an essential plant nutrient; however, it is a common cation in soil solution and is often used to maintain osmotic balance (Binkley and Fischer, 2013; Marschner and Marschner, 2012). Zinc (Zn) is an important structural and regulatory factor for a wide variety of enzymes (Marschner and Marschner, 2012; Pallardy, 2008).

A lack of any given nutrient can lead to nutrient deficiencies and limit production. Leibeg's Law of the Minimum states that a system is only as productive as its most limiting nutrient allows. This idea of single-nutrient limitation has guided thinking about forest nutrition in the Pacific Northwest for decades, but it is now becoming clear that co-limitation of ecosystems is common (Harpole et al., 2011). While some studies have shown response to phosphorous fertilizer application, another common limiting nutrient, there is sparse information about forest nutrition of other nutrients (Mainwaring et al., 2014). These nutrients are not unlimited, and their availability to plants are modulated by many important and often complicated processes.

1.2.3 Nutrient Cycling

Nutrients, with the exception of carbon (C), are largely taken up by plant roots and associated mycorrhizae (Marschner and Marschner, 2012). Plants and certain microorganisms are unique in their ability to uptake inorganic forms of nutrients and fix them into organic forms. Nutrients can be stored in the soil in many different forms, depending on the chemistry of the nutrient. Nutrients that are soluble can be found freely dissolved in the soil solution and are easy for plants to access, though this pool is often a small portion of the total pool. Some nutrients can

be found bound to soil particles by a large variety of interactions (Binkley and Fischer, 2013; McBride, 1994). Clay particles have negatively charged surfaces and organic matter often has negatively charged acidic functional groups. Nutrients with positive charges can adsorb to the surface of these particles or to negatively charged organic matter (the amount of positively charged ions a soil can hold is known as the cation exchange capacity). Depending on the exact chemistry of this interaction, these nutrients are generally readily exchangeable with the bulk soil solution. Plants and other organisms secrete protons and other cations to displace these nutrients from the exchange complex and make them available for uptake (Brady and Weil, 2016; McBride, 1994).

Some nutrients are derived from primary minerals, which are bound in the parent material of the soil and become available through weathering. This process can be relatively slow, though plants and other soil organisms are capable of accelerating it locally (Brady and Weil, 2016). They may also be stored in secondary minerals, which form as soils age and minerals precipitate from solution(McBride, 1994). Organic matter is a significant source of soil nutrients. It is derived from dead organic tissue and its nutrients are made available through decomposition and enzymatic activity that breaks these complex organic molecules into simple compounds ready for uptake (Binkley and Fischer, 2013). Some of these nutrients are easily accessible, but over time they can become tied up in recalcitrant complexes that have very slow turnover rates. In highly weathered soils like the tropics, organic matter is a significant source of nutrients (Perry et al., 2008).

Nutrients are cycled in interacting cycles on multiple scales. The influential model developed by Switzer and Nelson categorizes these processes into three different cycles on different spatial and temporal scales (Switzer and Nelson, 1972). The largest scale, the geochemical cycle, considers geochemical processes that serve as outputs and inputs into the system. Inputs to and exports from an ecosystem occur by exchanges with the atmosphere- by deposition, respiration and volatilization- with the lithosphere- by weathering and precipitation (formation of secondary minerals)- and from the hydrosphere- by leaching, sea spray, erosion and rainfall. On a smaller scale, the biogeochemical cycle, nutrients are cycled within an ecosystem by interactions between plants and the soil (Perry et al., 2008). Nutrient capital within the ecosystem is taken up by plants and then by secondary producers and cycled back when

organisms die or produce litter. This litter is then degraded and made available again for uptake by primary producers or detritivores. Nutrients are also cycled within a living organism, a process known as the biochemical cycle. In order to produce new foliage and new flushes of fine roots, plants mobilize nutrients from places they are not needed (Marschner and Marschner, 2012; Pallardy, 2008). Before trees shed their foliage, they remove as much of the nutrient content as they need. In conifers, needles decline in almost every nutrient as they age, with the exception of calcium which increases (Marschner and Marschner, 2012). Plants also mobilize nutrients from areas they are not needed to areas of active growth. Each nutrient has different cycles that are specific to its chemistry, use in plants, and origin (Perry et al., 2008).

Carbon is unique among other nutrients as its primary source is the atmosphere as CO₂ and its uptake is through leaves, instead of roots. While some C containing metabolites are taken up by roots or exchanged between roots and mycorrhizae, recycled carbon is a very minor source of plant biomass (Marschner and Marschner, 2012; Pallardy, 2008). C in litterfall is utilized by heterotrophs in the forest floor and soil for energy and for structure, however it is primarily cycled back to the atmosphere as organisms respire (Marschner and Marschner, 2012; Perry et al., 2008).

Nitrogen, while present in large quantities in the atmosphere, only added to an ecosystem through atmospheric deposition and the activity of certain specialized microorganisms. In managed landscapes, fertilization in the form of urea or other chemicals is another important source of nitrogen input (Binkley and Fischer, 2013; Brady and Weil, 2016). These processes produce ammonia that turns to ammonium when protonated, and can be converted further to nitrate via nitrification. In acidic forest soils, nitrification is inhibited and ammonium is the most common form of plant accessible nitrogen. Both nitrate and ammonium are soluble which makes them susceptible to loss via leaching- this is especially true of nitrate, as it is negatively charged and cannot interact with the wide variety of negative charges in soil (Binkley and Fischer, 2013; Perry et al., 2008). N may also be lost from the system by denitrification, a process where anaerobic bacteria use nitrate as an electron acceptor, ultimately releasing it as N₂ gas (Perry et al., 2008). N is largely cycled locally, with litterfall being the primary source of N for plant uptake- especially in places where deposition and fixation rates are low (Brady and Weil, 2016). The forest floor, however, can serve as a N sink. As heterotrophs degrade organic matter, they

preferentially consume carbon, enriching the content of nitrogen and other minerals in (Piatek and Allen, 2001). In Oregon, atmospheric deposition rates are generally low, but may be elevated in the Oregon Coast Range (National Atmospheric Deposition Program. 2020). However, a large N gradient across the Oregon Coast range is created by legacies of N fixing alder, though this species is often not present in intensively managed plantations (Hynicka et al., 2016; Perakis et al., 2006).

Mg K Ca Na are stored in parent material and become accessible through weathering, precipitation, and ocean spray (Binkley and Fischer, 2013). Mg K and Ca are known as the base cations, and are all macronutrients that are primarily found as cations in the soil (Na is also a cation but not a macronutrient) (Marschner and Marschner, 2012). Since they are found in nature as cations, they interact with negatively charged clays and organic matter which prevents leaching unless soils are saturated. Soils with higher cation exchange capacity are better at maintaining these nutrients (Binkley and Fischer, 2013; McBride, 1994). Both Mg and Ca have fairly large mineral reserves, depending on parent material (Binkley and Fischer, 2013). Weathering rates can be slow in forest soils, though mass balance studies show that they are an important source for long term biomass growth (Uroz et al., 2009). Aboveground litter serves an important source for Ca, K, and Na. However, since they are mobile and highly soluble, they are subject to leaching and often do leave the ecosystem in large quantities (Sollins et al., 1980). Of these nutrients, Ca cycling in particular has been tied with N cycling though similar trends have also been observed for Mg and K. When N supply is higher than demand, Ca and N leach in high quantities which may deplete soil Ca stores, (Homann et al., 1992; Hynicka et al., 2016; Perakis and Pett-Ridge, 2019).

K is added to an ecosystem mainly by weathering, but also may be added by rainfall, which is relatively dilute. K is a constituent of various types of clays and minerals and its availability in the soil depends on the composition and abundance of these substances (Marschner and Marschner, 2012). K is very mobile in soils and in plant matter. It leaches readily from litter, which may be the largest source in a forest (compared to contributions from parent material, rainfall, and deposition) (Brady and Weil, 2016; Sollins et al., 1980).

Phosphorous is unique amongst other nutrients in its low solubility and negative charge. The low solubility makes it much less susceptible to leaching. It also means that it is less
available through weathering and is often stored in forms that are harder for plants to access (Binkley and Fischer, 2013; McBride, 1994). Indeed, plants and soil organisms devote a large amount of energy to weathering P from primary minerals or from organic matter. P solubility changes with soil pH. At pH above 7, P forms insoluble complexes with divalent cations such as Ca. At more acidic pH, which is generally more relevant to forest soils, P forms insoluble complexes with aluminum and iron(Binkley and Fischer, 2013; McBride, 1994). Organic molecules in the soil can interact with aluminum and iron particles, shielding phosphorous from sorbing. Plants and mycorrhizae secrete small organic compounds to displace this adsorbed P and increase its availability. Plants and soil microorganisms also scavenge P from organic matter by secreting phosphatases into the soil, liberating accessible phosphate moieties (Binkley and Fischer, 2013; Brady and Weil, 2016). As soils age, P stores in primary minerals decline, and more phosphorous is stored in recalcitrant organic matter complexes (Compton and Cole, 1998). Since the forms in the soil are often hard to access, P is largely locally cycled, meaning that its main source in mature forests is litter (Perry et al., 2008; Sollins et al., 1980). This is especially true in the tropic where highly weathered soils are full of iron and aluminum that immobilizes most phosphorous in the soil (Perry et al., 2008).

Sulfur is added to ecosystems both via wet and dry deposition as well as mineral weathering (Brady and Weil, 2016). Deposition is especially important in areas where industrial pollution is high, though this type of pollution has been on the decline in many countries due to environmental regulations (Brady and Weil, 2016). Depending on location, input from deposition may be greater than the amount returned to the soil by litterfall (Marschner and Rengel, 2012). In areas with high organic matter, a large amount of S can be stored in organic complexes in the surface layers of soil. It can also be stored in anion exchange complexes, especially in weathered soils with high Al and Fe content (Johnson, 1984; Marschner and Rengel, 2012). Depending on minerology of a site, it can be stored in weatherable minerals such as gypsum, though certain parent material and soil series have low inorganic S reserves. When soils are saturated, leaching is common and losses are often equivalent to inputs from deposition (Brady and Weil, 2016).

Micronutrients are also sourced from parent material, though they are required in smaller amounts and harder for plants to access. Most information about micronutrient cycling comes from agricultural systems (Brady and Weil, 2016; Marschner and Rengel, 2012). Some forests are known to be limited by micronutrients, such as radiata pine plantations which are often fertilized with B (Lambert et al., 1997; Stone, 1990). B is taken up by plants as boric acid or borate, which may be bound up in insoluble complexes with iron oxides. Metallic micronutrients can exist in the soil in many oxidation states, though typically are more available in their reduced forms and are more soluble at lower pH (Brady and Weil, 2016; Marschner and Marschner, 2012). Fe and Mn are the most abundant micronutrients in soil and are generally found as oxides in soils but can also be major structural components of silicate minerals. While these nutrients are the most abundant, they are often in inaccessible forms. Zn can be found as substitute elements in silicates and clays. Micronutrients are also stored in organic matter complexes, especially Cu, Mn, and Zn, though these may be held in tight complexes (Brady and Weil, 2016; Marschner and Marschner, 2012). In order for plants and soil organisms to uptake heavy metals (Cu, Fe, Mn, Zn), they secrete chelating agents and may decrease local soil pH which help increase solubility and ease of transport.

1.2.4 Plants and Nutrient Cycling

Plants have an important role in the biogeochemical cycle as primary producers. As the main source of biomass in a forest, plants serve to immobilize nutrients which help maintain nutrient capital on a site. Plant litter is the main source of recycled nutrients within an ecosystem (Perry et al., 2008). For certain elements like P, these recycled nutrients are the main source of nutrients for new growth (Compton and Cole, 1998; Perry et al., 2008; Sollins et al., 1980). Plants are important in soil forming processes, which liberates nutrients and determines the ability of a site to retain nutrients (Binkley and Fischer, 2013). Plants and associated mycorrhizae serve crucial functions by scavenging nutrients that are currently in unavailable forms. This can either occur by etching, where roots and associated biota actively secrete compounds that accelerate weathering, or symbiotic N fixation (Homann et al., 1992; Perakis and Pett-Ridge, 2019).

Different plants use nutrients differently, and these differences play an important role in the way an ecosystem stores and cycles these nutrients. Plants require nutrients in different ratios and store them in different ways. Western redcedar trees, for example, store large amounts of calcium in their foliage, meaning that less is available deeper in the mineral soil, but more is available in the forest floor due to contributions from litter (Cross and Perakis, 2011). Broadleaf plants store large amounts of nutrients in their leaves which are more metabolically expensive than the needles of conifers and require greater amounts of nutrients (Huang et al., 2007). Inclusion of broadleaves in a conifer dominated forest has been shown to increase nutrient cycling rates, though effects on production are inconsistent (Binkley, 2003; Kelty, 2006).

Red alder (*Alnus rubra* Bong.) is an important feature of northwest forests and an excellent example of how a plant species can alter nutrient cycling. Alders are a nitrogen fixing species that have been shown to also increase weathering rates and availability of phosphorous and calcium in pure and mixed stands (Homann et al., 1992; Perakis and Pett-Ridge, 2019). Since N species are highly mobile, they are able to influence the soil N of downhill soils up to 10 m and stream N levels correlate with alder basal area on a landscape scale (Compton et al., 2003; Hynicka et al., 2016; Rhoades and Binkley, 1992). Alder stands have greater uptake of phosphorous compared to pure conifer stands, and they return more phosphorous in litterfall. Thus, they accelerate the rate at which inorganic phosphorus stores are converted into organic phosphorus stores (Compton and Cole, 1998). Conifer stands with alder have been shown to increase cycling rates of nitrogen sulfur and phosphorous (Binkley et al., 1992; Rhoades and Binkley, 1992).

Overstory tree species alter certain aspects of nutrient cycling. Species differ in the timing and amount of litter shed and the rate at which their litter decomposes. Thus, canopy composition influences nitrogen, and potentially other nutrient, availability, as it affects the amount of nutrients returned to the soil as litter (Prescott, 2002). Trees may also influence nitrogen cycling by altering mineralization rates and leaching. A study of cycling in Northeastern hardwood forests revealed that potentially mineralizable nitrogen varied two fold among species (Lovett et al., 2004). They also observed that there were different rates of nitrification and nitrate leaching for the five different species. Overstory species composition also influences the availability and leaching of base cations (Homann et al., 1992; Hynicka et al., 2016).

Changes in plant community alter ecosystem nutrient use. Conversion of a Norway spruce plantation to various different species showed that each species utilized nutrients differently such that there were different trends for each species and nutrient (Carnol and Bazgir, 2013). The study found that reforestation with rowan (*Sorbus aucuparia* L.) increased soil exchangeable calcium magnesium and potassium (Carnol and Bazgir, 2013). Vegetation

management (VM) inherently alters the structure and composition of these plant communities, and thus affects the nutrients storage capabilities and nutrient cycling within a stand. Slesak et al. (2009) found that VM increased dissolved organic N and nitrate concentration. Since these N species are mobile in soils, this has the potential to increase nutrient leaching, meaning that plant community structure affects the ability of the site to retain nutrients. Similarly, after disturbance, when there is a reduction in living plants at a site, nutrients are more susceptible to leaching as there are fewer primary producers to immobilize them.

1.2.5 Nutrient Budgets and Nutrient Use Efficiency

Nutrient budgets are a way to visualize how ecosystems use a specific nutrient or nutrients. Traditionally used in industrial farming, nutrient budgets originated as a way for farmers to look at the inputs and losses of nutrients from the soil to help shape and evaluate management practices (Zhang et al., 2020). This agronomic tool has since been adapted as silvicultural tool to help understand effects of management on forest ecosystems (Vadeboncoeur et al., 2014; Zhang et al., 2020). Generally, they measure nutrient stocks in different aboveground and belowground pools and estimates fluxes of nutrients into and out of the system. In this study, we do not measure nutrient fluxes, but instead create a snapshot of where nutrients are stored in the stand at a single point in time.

Nutrient use efficiency is a measure of how efficient a plant or plant community is at producing biomass on a per nutrient basis. There are different ways of defining nutrient use efficiency, but typically it is expressed as growth per unit nutrient used. That growth can be measured as net primary productivity (NPP), aboveground net primary productivity (ANPP), biomass increment, or some other measure of growth (Binkley et al., 1992; Bridgham et al., 2016). For this study we will focus on the ratio of nutrient mass to total plant derived biomass, similar to the nutrient efficiency ratio used in crop science (Agüero and Kirschbaum, 2013; Baligar et al., 2001).

1.2.6 Nutrients in Managed forests

Management decisions alter the way systems store and cycle nutrients. Management activities such as harvest of stemwood or litter remove nutrients from the forest, while fertilizer application acts as an input. Other silvicultural treatments such as thinning and vegetation management, exert control over plant community and community structure, which in turn will have an effect on nutrient storage and cycling (see above).

Forest vegetation management (VM) is the practice of reducing competition between planted tree species and other, less desirable species, by physical removal or treatment with herbicide (Wagner et al., 2006). Favored practices vary by country or geographic region. In certain areas of Europe, mechanical VM is common, whereas in other regions such as South America and the U.S., herbicide use is much more prevalent (Ammer et al., 2011). The goal of reforesting for production-oriented timber plantations is to establish the stand as quickly and effectively as possible (this efficiency is often mandated by laws such as the Oregon Forest Practices Act). While the efficacy in increasing crop tree (those planted with intent to harvest) survival and growth is being documented (Hoepting et al., 2011; Sadanandan Nambiar, 1990; Wagner et al., 2006, 1996), the long-term effects of VM on ecosystem services, such as nutrient cycling, are poorly understood. There may be losses or changes to total ecosystem nutrients caused by skipping early successional phases of forest establishment. This study aims to investigate how sustained vegetation control using annual herbicide application in the Coast Range and Cascade Foothills of Oregon affects the total amount and distribution of nutrients in the forest ecosystem.

In the Pacific Northwest, annual herbicide application is the most common form of VM for plantation forestry. These practices increase seedling survival primarily by reducing water stress but also by increasing nutrient availability (Slesak et al., 2010; Wagner et al., 2006, 1996). In young plantation stands in the U.S. Pacific Northwest, crop trees associated with VM had larger stem, branch, and foliage biomass compared to trees in control plots with similar diameter at breast height (Flamenco et al., 2019; Petersen et al., 2008). Furthermore, it has been repeatedly demonstrated that the practice increased the yield of crop trees by 30-450% at the end of the rotation (Wagner et al., 2004).

Some studies have investigated on the effects of VM on nutrient dynamics. Effects of intensive management activities (e.g. slash removal and VM) on soil nutrient flux are monitored at certain sites in the Long-Term Soil Productivity Study (Scott, 2016). Slesak et al. published several papers focusing on two LTSPS sites in the Pacific Northwest, one in the Olympic Peninsula in Washington and one in the Cascade Foothills in Northern Oregon. Their studies

focusing on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) found that changes in soil nutrients vary based on site quality, as do treatment effects. Generally, effects of intensive management are more pronounced at lower quality sites (Slesak et al., 2016, 2011). For the nutrients examined (C, N, P, Mg, K, Ca) and the depths surveyed (up to 60 cm), nutrients tended to increase over the 5- and 10-year periods studied, but these increases were greater without VM (Slesak et al., 2016, 2011). A study at the Fall River LTSP site showed that for a 12-year-old Douglas-fir stand there was an increase in soil N in the surface layers and an increase in deep soil C with VM (Knight et al., 2014).

It is likely that the magnitude of VM effects on site nutrients is related to the size of the nutrient reserve in the mineral soil (Knight et al., 2014). While the results of the LTSPS do not suggest a rapid and intense degradation of soil in the PNW, studies from Florida suggest otherwise. Miller et al. (2006) studied the flux of soil and foliar nutrients on a loblolly pine (*Pinus taeda*) plantation for 15 years and showed that in all cases soil nutrients declined, and that this decline was exacerbated by VM practices.

Studies on crop tree nutrient status are even more limited and typically only focus on young, typically 5-year-old, Douglas-fir and loblolly pine. Studies of young Douglas-fir and seedling have shown that VM increased the nitrogen allocated to foliage and to the whole tree (Slesak et al., 2010). A different study on 5-year-old Douglas-fir found that macronutrient concentrations of N, P, K, S, Ca, Mg were the same for trees in treated plots and untreated plots, with the exception of branch N which had higher concentrations in absence of vegetation control (Petersen et al., 2008). Another study done on 5-year-old Douglas-fir seedlings found that there was no difference in N concentration between treated and untreated trees with this exception of one site where seedling boles contained more N than treated (Devine et al., 2011). A study of 15 year old loblolly pine demonstrated higher foliar potassium and levels with herbaceous vegetation control but no difference in foliar phosphorous, calcium, and magnesium (Miller et al., 2006). Generally, all these studies found that seedlings grown in treated plots attained significantly larger biomass, leading them to find that total nutrient content of trees was greater when growing in absence of competing vegetation.

Many of these studies are limited in scope, and reveal little about longer term trends. Because the demand for timber yield is projected to increase, it is likely that silvicultural practices will become more intensive in order to produce timber yields that fulfill future demand for timber products (Fox, 2000). Thus, it is crucial to understand the lasting effects of these treatments. Some studies, such as the LTSPS, focus on nutrient flux in the soil and how different intensive management practices affect this. These studies only focus on soil, and typically only monitor the nutrient flux over the first 5-10 years of stand development. It is likely that nutrient fluxes in this period are initially dominated by the effects of clearcutting and loss of vegetation, and then by the regrowth of new vegetation. The effects of clearcutting and initial regrowth fade over time as the stand returns and soil nutrient dynamics occur on longer time scales. Therefore, these studies may not provide insight into the long-term changes in nutrient availability and longer-term monitoring is needed (Grigal and Berguson, 1998; Powers et al., 2013). It is not known how differences in N distribution in Douglas-fir changes into maturity and how less common timber species- such as grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)- are affected.

By constructing nutrient budgets for each of these stands with and without sustained herbicide application, this study will illuminate how VM alters nutrient quantities and distribution in these ecosystems. Nutrient budgets will be reported as tables detailing concentration and mass of 6 macronutrients and 7 micronutrients in different pools within an ecosystem. This will allow us to calculate the total ecosystem mass of each nutrient for each species, site, and treatment. Using this data, we will be able to explore nutrient status and nutrient use efficiency by examining nutrient rations in different ecosystem compartments.

1.3 <u>Study Design</u>

A randomized complete block design with eight VM treatments was implemented at each of the two sites, one in the Oregon Coast Range (CR) and one in the Oregon Cascade foothills (CF). The eight different VM treatments consisted of spring release applications that differed in the number and timing of herbicide treatments applied during the first 5 years after planting. The CR site was planted with Douglas-fir, western hemlock, western redcedar and grand fir and the CF site was planted with Douglas-fir and western redcedar. Similar to Flamenco et al. (2019), for this study we used only the control (Control; only pre-planting vegetation control) and the 5 consecutive years of spring release vegetation management treatment (VM). Plots were

approximately 0.06 ha and were planted in 8 rows of 8 trees at a 3 x 3 m spacing, resulting in a planting density of 1100 trees per ha. All plots were planted with a single tree species. All DF plots received pre-commercial thinning at year 12 and thinning residues were left on site.

The ecosystem was divided into soil pools and plant derived pools. The plant derived pools were broken down into overstory (planted crop trees), midstory (hardwoods and natural conifer regeneration), understory (shrubs, grasses, forbs, ferns and moss) and forest floor (including coarse woody debris). The overstory was divided into foliage, live branches, stemwood, stembark, and fine roots. The midstory was broken down into foliage and bole (stemwood and stembark). The soil was divided into four layers (0-0.2 m, 0.2-0.4 m, 0.4-0.6 m, and 0.6-1 m).

1.4 Objectives and Hypotheses

The goal of this project is to understand how intensive silvicultural practices affect longterm site quality. The first objective is to measure the nutrient contents of several different biomass pools in treated and untreated stands. We will measure the following nutrient pools: crop trees (which are divided into branches, stem wood, bark, and foliage) fine roots, understory, forest floor, midstory, and multiple strata of mineral soil. The second objective is to construct nutrient budgets for stands of different species and sites. The last objective is to compare nutrient concentrations, total ecosystem masses, and ratios between VM and control across species and sites.

We hypothesize that midstory trees increase the nutrient storage capacity of conifer dominated ecosystems because they store a large quantity of nutrients in their foliage. If this is true, total ecosystem nutrient content will be higher in plots that did not receive herbicide treatment and where a midstory has developed. We also hypothesize that stands treated with herbicide will produce more biomass per unit nutrient than untreated stands as treated stands store a large fraction of biomass in conifer boles, which serve as a large store of carbon but are not a significant pool of other nutrients. If this is true, the ratio of plant derived carbon mass to plant derived mass of macro and micronutrients will be higher in stands that are treated with herbicide.

- Agüero, J.J., Kirschbaum, D.S., 2013. Approaches to Nutrient Use Efficiency of Different Strawberry Genotypes. Int. J. Fruit Sci. 13, 139–148. https://doi.org/10.1080/15538362.2012.697047
- Ammer, C., Balandier, P., Bentsen, N.S., Coll, L., Löf, M., 2011. Forest vegetation management under debate: An introduction. Eur. J. For. Res. 130, 1–5. https://doi.org/10.1007/s10342-010-0452-6
- Attiwill, P.M., Adams, M.A., 1993. Nutrient cycling in forests. New Phytol. 124, 561–582. https://doi.org/10.1111/j.1469-8137.1993.tb03847.x
- Baligar, V.C., Fageria, N.K., He, Z.L., 2001. Nutrient use efficiency in plants. Commun. Soil Sci. Plant Anal. 32, 921–950. https://doi.org/10.1081/CSS-100104098
- Binkley, D., 2003. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Can. J. For. Res. 33, 2274–2279. https://doi.org/10.1139/x03-158
- Binkley, D., Fischer, R.F., 2013. Ecology and management of forest soils, 4th ed. ed. Wiley, Hoboken, NJ.
- Binkley, D., Sollins, P., Bell, R., Sachs, D., Myrold, D., 1992. Biogeochemistry of Adjacent Conifer and Alder-Conifer Stands. Ecology 73, 2022–2033.
- Brady, N.C., Weil, R.R., 2016. The Nature and Properties of Soils, Fifteenth. ed. Columbus, Ohio : Pearson, Columbus, Ohio.
- Bridgham, S.D., Pastor, J., Mcclaugherty, C.A., Curtis, J., Richardson, C.J., 2016. Nutrient-Use
 Efficiency : A Litterfall Index , a Model , and a Test Along a Nutrient- Availability
 Gradient in North Carolina Peatlands Published by : The University of Chicago Press for
 The American Society of Naturalists Stable URL : http://www.jstor.or 145, 1–21.
- Carnol, M., Bazgir, M., 2013. Nutrient return to the forest floor through litter and throughfall under 7 forest species after conversion from Norway spruce. For. Ecol. Manage. 309, 66– 75. https://doi.org/10.1016/j.foreco.2013.04.008

- Cole, D.W., 1995. Soil nutrient supply in natural and managed forests. Plant Soil 168–169, 43– 53. https://doi.org/10.1007/BF00029312
- Compton, J.E., Church, M.R., Larned, S.T., Hogsett, W.E., 2003. Nitrogen Export from Forested Watersheds in the Oregon Coast Range: The Role of N2-fixing Red Alder. Ecosystems 6, 773–785. https://doi.org/10.1007/s10021-002-0207-4
- Compton, J.E., Cole, D.W., 1998. Phosphorus cycling and soil P fractions in Douglas-fir and red alder stands. For. Ecol. Manage. 110, 101–112. https://doi.org/10.1016/S0378-1127(98)00278-3
- Cross, A., Perakis, S.S., 2011. Tree species and soil nutrient profiles in old-growth forests of the Oregon Coast Range. Can. J. For. Res. 41, 195–210. https://doi.org/10.1139/x10-199
- Devine, W.D., Harrington, T.B., Terry, T.A., Harrison, R.B., Slesak, R.A., Peter, D.H., Harrington, C.A., Shilling, C.J., Schoenholtz, S.H., 2011. Five-year vegetation control effects on aboveground biomass and nitrogen content and allocation in Douglas-fir plantations on three contrasting sites. For. Ecol. Manage. 262, 2187–2198. https://doi.org/10.1016/j.foreco.2011.08.010
- Flamenco, H.N., Gonzalez-Benecke, C.A., Wightman, M.G., 2019. Long-term effects of vegetation management on biomass stock of four coniferous species in the Pacific Northwest United States. For. Ecol. Manage. 432, 276–285. https://doi.org/10.1016/j.foreco.2018.09.033
- Fox, T.R., 2000. Sustained productivity in intensively managed forest plantations. For. Ecol. Manage. 138, 187–202. https://doi.org/10.1016/S0378-1127(00)00396-0
- Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The development of pine plantation silviculture in the Southern United States. J. For. 105, 337–347. https://doi.org/10.1093/jof/105.7.337
- Grigal, D.F., Berguson, W.E., 1998. Soil carbon changes associated with short-rotation systems. Biomass and Bioenergy 14, 371–377. https://doi.org/10.1016/S0961-9534(97)10073-3
- Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B., Smith, J.E., 2011. Nutrient co-limitation

of primary producer communities. Ecol. Lett. 14, 852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x

- Hepler, P.K., Winship, L.J., 2010. Calcium at the cell wall-cytoplast interface. J. Integr. Plant Biol. 52, 147–160. https://doi.org/10.1111/j.1744-7909.2010.00923.x
- Hoepting, M.K., Wagner, R.G., McLaughlin, J., Pitt, D.G., 2011. Timing and duration of herbaceous vegetation control in northern conifer plantations: 15th-year tree growth and soil nutrient effects. For. Chron. 87, 398–413. https://doi.org/10.5558/tfc2011-030
- Homann, P.S., Miegroet, H. Van, Cole, D.W., Wolfe, G. V, 1992. Cation Distribution, Cycling , and Removal from Mineral Soil in Douglas-Fir and Red Alder Forests 16, 121–150. https://doi.org/10.1007/BF00002828
- Huang, J., Wang, X., Yan, E., 2007. Leaf nutrient concentration, nutrient resorption and litter decomposition in an evergreen broad-leaved forest in eastern China. For. Ecol. Manage. 239, 150–158. https://doi.org/10.1016/j.foreco.2006.11.019
- Hynicka, J.D., Pett-Ridge, J.C., Perakis, S.S., 2016. Nitrogen enrichment regulates calcium sources in forests. Glob. Chang. Biol. 22, 4067–4079. https://doi.org/10.1111/gcb.13335
- Johnson, D.W., 1984. Sulfur cycling in forests. Biogeochemistry 1, 29–43.
- Kelty, M.J., 2006. The role of species mixtures in plantation forestry. For. Ecol. Manage. 233, 195–204. https://doi.org/10.1016/j.foreco.2006.05.011
- Kershaw, H.M., Jeglum, J.K., Morris, D.M., 1996. Long-term Productivity of Boreal Forest Ecosystems II . Expert Opinion on the Impact of Forestry Practices. Natural Resources Canada, Canadian Forest Service-Sault Ste. Marie, Sault Ste. Marie, ON.
- Knight, E., Footen, P., Harrison, R., Terry, T., Holub, S., 2014. Competing Vegetation Effects on Soil Carbon and Nitrogen in a Douglas-fir Plantation. Soil Sci. Soc. Am. J. 78, S146– S151. https://doi.org/10.2136/sssaj2013.07.0320nafsc
- Lambert, M.J., Turner, J., Knott, J., 1997. Boron nutrition of radiata pine plantations in Australia. Boron soils plants Proc. Int. Symp. Boron Soils Plants held Chiang Mai, Thailand, 7-11 Sept. 1997.

- Lovett, G.M., Weathers, K.C., Arthur, M.A., Schultz, J.C., 2004. Nitrogen cycling in a northern hardwood forest: Do species matter? Biogeochemistry 67, 289–308. https://doi.org/10.1023/B:BIOG.0000015786.65466.f5
- Mainwaring, D.B., Maguire, D.A., Perakis, S.S., 2014. Three-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington. For. Ecol. Manage. 327, 178–188. https://doi.org/10.1016/j.foreco.2014.05.005
- Marschner, H., Marschner, P., 2012. Marschner's mineral nutrition of higher plants.
- Marschner, P., Rengel, Z., 2012. Soil Biology, Nutrient Cycling in Terrestrial Ecosystems, Springer. https://doi.org/10.1017/CBO9781107415324.004
- McBride, M.B., 1994. Environmental chemistry of soils. Oxford University Press, New York (USA).
- Miller, J.H., Allen, H.L., Zutter, B.R., Zedaker, S.M., Newbold, R.A., 2006. Soil and pine foliage nutrient responses 15 years after competing-vegetation control and their correlation with growth for 13 loblolly pine plantations in the southern United States. Can. J. For. Res. 36, 2412–2425. https://doi.org/10.1139/x06-164
- National Atmospheric Deposition Program (NRSP-3). 2020. NADP Program Office, Wisconsin State Laboratory of Hygiene, 465 Henry Mall, Madison, WI 53706.
- O'Hara, K.L., 2016. What is close-to-nature silviculture in a changing world? Forestry 89, 1–6. https://doi.org/10.1093/forestry/cpv043
- Oregon Forest Resources Institute, 2019a. 2019 Forest Report: an Economic Snapshot of Oregon's Forest Sector.
- Oregon Forest Resources Institute, 2019b. Oregon Forest Facts.
- Pallardy, S.G., 2008. Physiology of woody plants.
- Perakis, S.S., Maguire, D.A., Bullen, T.D., Cromack, K., Waring, R.H., Boyle, J.R., 2006. Coupled nitrogen and calcium cycles in forests of the Oregon Coast Range. Ecosystems 9, 63–74. https://doi.org/10.1007/s10021-004-0039-5

- Perakis, S.S., Pett-Ridge, J.C., 2019. Nitrogen-fixing red alder trees tap rock-derived nutrients. Proc. Natl. Acad. Sci. 201814782. https://doi.org/10.1073/pnas.1814782116
- Perry, D.A., Oren, R., Hart, S.C., 2008. Forest ecosystems, Second edi. ed. The Johns Hopkins University Press, Baltimore, Maryland.
- Petersen, K.S., Ares, A., Terry, T.A., Harrison, R.B., 2008. Vegetation competition effects on aboveground biomass and macronutrients, leaf area, and crown structure in 5-year old Douglas-fir. New For. 35, 299–311. https://doi.org/10.1007/s11056-007-9078-z
- Piatek, K.B., Allen, H.L., 2001. Are forest floors in mid-rotation stands of loblolly pine (pinus taeda) a sink for nitrogen and phosphorus? Can. J. For. Res. 31, 1164–1174. https://doi.org/10.1139/x01-049
- Powers, R.F., Busse, M.D., McFarlane, K.J., Zhang, J., Young, D.H., 2013. Long-term effects of silviculture on soil carbon storage: Does vegetation control make a difference? Forestry 86, 47–58. https://doi.org/10.1093/forestry/cps067
- Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. 22, 1193–1200. https://doi.org/10.1093/treephys/22.15-16.1193
- Rhoades, C.C., Binkley, D., 1992. Spatial extent of impact of red alder on soil chemistry of adjacent conifer stands. Can. J. For. Res. 22, 1434–1437. https://doi.org/10.1139/x92-192
- Sadanandan Nambiar, E.K., 1990. Interplay between nutrients, water, root growth and productivity in young plantations. For. Ecol. Manage. 30, 213–232.
- Sathre, R., O'Connor, J., 2010. Meta-analysis of greenhouse gas displacement factors of wood product substitution. Environ. Sci. Policy 13, 104–114. https://doi.org/10.1016/j.envsci.2009.12.005
- Scott, D.A., 2016. A brief overview of the 25-year-old Long-Term Soil Productivity study in the South. Proc. 18th Bienn. South. Silvic. Res. Conf. 2-5 March 2015, Knoxville, TN. e–Gen. Tech. Rep. SRS–212. Asheville, NC U.S. Dep. Agric. For. Serv. South. Res. Stn. 18–26.

- Seymour, R.S., Hunter, M.L., 2016. New Forestry in Eastern Spruce-Fir Forests : Principles and Applications to Maine New Forestry in Eastern Spruce-Fir Forests : Principles and Applications to Maine.
- Simmons, E.A., Hayes, S.W., Morgan, T.A., Keegan, C.E., Witt, C., 2014. Oregon's Forest Products Industry and Timber Harvest 2013 With Trends Through 2013, USDA Forest Service - General Technical Report. https://doi.org/10.2737/RMRS-RB-19
- Slesak, R.A., Harrington, T.B., Peter, D.H., DeBruler, D.G., Schoenholtz, S.H., Strahm, B.D., 2016. Effects of intensive management practices on 10-year Douglas-fir growth, soil nutrient pools, and vegetation communities in the Pacific Northwest, USA. For. Ecol. Manage. 365, 22–33. https://doi.org/10.1016/j.foreco.2016.01.019
- Slesak, R.A., Harrington, T.B., Schoenholtz, S.H., 2010. Soil and Douglas-fir (Pseudotsuga menziesii) foliar nitrogen responses to variable logging-debris retention and competing vegetation control in the Pacific Northwest. Can. J. For. Res. 40, 254–264. https://doi.org/10.1139/X09-188
- Slesak, R.A., Schoenholtz, S.H., Harrington, T.B., 2011. Soil carbon and nutrient pools in Douglas-fir plantations 5years after manipulating biomass and competing vegetation in the Pacific Northwest. For. Ecol. Manage. 262, 1722–1728. https://doi.org/10.1016/j.foreco.2011.07.021
- Sollins, P., Grier, C.C., McCorison, F.M., Cromack, K., Fogel, R., Fredriksen, R.L., 1980. The Internal Element Cycles of an Old-Growth Douglas-Fir Ecosystem in Western Oregon. Ecol. Monogr. 50, 261–285. https://doi.org/10.2307/2937252
- Stone, E.L., 1990. Boron deficiency and excess in forest trees: a review. For. Ecol. Manage. 1, 49–75.
- Switzer, G.L., Nelson, L.E., 1972. Nutrient Accumulation and Cycling in Loblolly Pine (Pinus taeda L.) Plantation Ecosystems: The First Twenty Years. Soil Sci. Soc. Am. J. 36, 143– 147.

- Uroz, S., Calvaruso, C., Turpault, M.P., Frey-Klett, P., 2009. Mineral weathering by bacteria: ecology, actors and mechanisms. Trends Microbiol. 17, 378–387. https://doi.org/10.1016/j.tim.2009.05.004
- Vadeboncoeur, M.A., Hamburg, S.P., Yanai, R.D., Blum, J.D., 2014. Rates of sustainable forest harvest depend on rotation length and weathering of soil minerals. For. Ecol. Manage. 318, 194–205. https://doi.org/10.1016/j.foreco.2014.01.012
- van Breemen, N., 1995. Nutrient cycling strategies. Plant Soil 168–169, 321–326. https://doi.org/10.1007/BF00029344
- Vance, E.D., Maguire, D.A., Zalesny, R.S., 2010. Research strategies for increasing productivity of intensively managed forest plantations. J. For. 108, 183–192. https://doi.org/10.1093/jof/108.4.183
- Vierikko, K., Vehkamäki, S., Niemelä, J., Pellikka, J., Lindén, H., 2008. Meeting the ecological, social and economic needs of sustainable forest management at a regional scale. Scand. J. For. Res. 23, 431–444. https://doi.org/10.1080/02827580802284693
- Wagner, R.G., Little, K.M., Richardson, B., McNabb, K., 2006. The role of vegetation management for enhancing productivity of the world's forests. Forestry 79, 57–79. https://doi.org/10.1093/forestry/cpi057
- Wagner, R.G., Newton, M., Cole, E.C., Miller, J.H., Shiver, B.D., 2004. The role of herbicides for enhancing forest productivity and conserving land for biodiversity in North America. Wildl. Soc. Bull. 32, 1028–1041.
- Wagner, R.G., Noland, T.L., Mohammed, G.H., 1996. Timing and duration of herbaceous vegetation control around four northern coniferous species. New Zeal. J. For. Sci. 26, 39– 52.
- Zhang, X., Davidson, E.A., Zou, T., Lassaletta, L., Quan, Z., Li, T., Zhang, W., 2020. Quantifying Nutrient Budgets for Sustainable Nutrient Management. Global Biogeochem. Cycles 34, 1–25. https://doi.org/10.1029/2018GB006060

2. Nutrient Concentrations in Plant and Soil Pools of Four Western Conifer Stands

2.1. Introduction

Tissue and soil nutrient concentrations are useful measures in order to determine the nutrient status of a stand as well as potential for nutrient deficiencies or soil nutrient depletion (DeBruler et al., 2019; Slesak et al., 2016; Stone, 1990; Turner et al., 1977). They are the basis for various nutrient management guidelines such as Diagnosis and Integrated Recommendation system (DRIS) and the Kinsey regime which allow development of site-specific fertilization prescriptions (Beaufils, 1973; Mainwaring et al., 2014). Nutrient concentrations are useful in this respect because they indicate how much of a resource is available in the exploitable soil as well as understanding whether plant foliage is optimally equipped to meet a plant's physiological needs. If a plant is lacking a particular nutrient or set of nutrients such that its physiological processes are limited, it will have a suboptimal concentration of nutrients in its foliage. The lowest foliar concentration where nutrients do not significantly limit growth is known as the critical concentration (Binkley and Fischer, 2013; Ulrich, 1952).

Nutrient concentrations are also important for calculating nutrient content. In order to determine the mass of a nutrient in a given tissue, you must first determine the mass of the tissue and the proportion of that mass that is a given nutrient (its concentration). For this reason they are also important for building proper models of nutrient export (Augusto et al., 2008; Johnson and Turner, 2019). In order to estimate the amount of nutrients removed from a system by harvest, you need to have reliable information about how nutrients are stored in the different tissues that are being removed.

Silvicultural treatments, such as vegetation management, during the establishment phase set the trajectory for stand development. These treatments may affect plants by altering the concentration of nutrients in a tissue or in soil (Burger and Pritchett, 1988; Powers et al., 2005; Powers and Reynolds, 1999). Looking at the content of a tissue may not reveal physiologically important changes and may only show trends in biomass if concentrations remain the same. A decrease in tissue nutrient concentration may mean that an organism is having difficulty meeting its physiological needs for that nutrient, whereas a decrease in content can be the result of a number of factors such as reduced biomass or changes in allocation.

2.2. Literature Review

2.2.1. Nutrient Concentrations in Plant Tissues

Plants distribute nutrients throughout their tissues in order to satisfy their physiological needs. These nutrients are often divided into two categories, based on the relative requirements of plants. The following are considered macronutrients and are required in larger amounts: carbon (C), nitrogen (N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S). The following are considered micronutrients and are required in much smaller amounts: boron (B), copper (Cu), iron (Fe), manganese (Mn), sodium (Na), and zinc (Zn) (see Chapter 1 for more details).

Foliage is generally the tissue type that contains the greatest concentration of nutrients with the exception of Ca which may be higher in the branches and phloem (Augusto et al., 2008; Cole and Gessel, 1992; Marschner and Marschner, 2012). While foliage comprises approximately 4% of aboveground biomass in a 40 year old Douglas-fir stand, it contains roughly 70% of the total aboveground nitrogen (Cole and Gessel, 1992; Turner, 1981; Turner and Long, 1975). Trees allocate a significant portion of nutrients to their foliage as this is where the majority of physiological process occur, including stomatal regulation, photosynthesis and respiration (Marschner and Marschner, 2012). Foliar nutrient concentrations vary over the lifetime of the foliage. In conifers, which tend to have longer lived foliage, these concentrations decrease after the foliage reaches maturity- particularly before shedding the leaf (Perry et al., 2008). The one exception to this rule is Ca, which tends to increase in concentration over time. This is due to the tree mobilizing its nutrients to other tissue, such as newer foliage and areas of active growth. Calcium is the exception to this rule because it is less mobile in foliage, a large portion of it being bound to the cell wall and pectin (Hepler and Winship, 2010). After foliage, the next highest concentrations are typically found in the live branches, phloem, or fine rootsdepending on the tree species and nutrient. Stemwood generally contains low concentrations of nutrients, especially in the heartwood, where there is no living tissue (Augusto et al., 2008; Marschner and Marschner, 2012).

Plant nutrient uptake is generally classified into four regions- deficient, critical, luxury, and toxic (Binkley, 1986). At levels below luxury, plant productivity is correlated with nutrient uptake. Foliar concentrations are often studied as they provide the best insight into the nutrient status and

production potential of a plant. Critical concentrations in plant foliage refer to the concentration at which productivity is 90% of the maximum. These concentrations are different for different species and are defined by current year foliage, ideally sampled during the height of the growing season when plants are most stressed for nutrients (Powers, 1983; Ulrich, 1952). Some research suggests that nutrient ratios are a better indicator than concentrations, as this accounts for systematic error in analytical techniques (Colbert and Allen, 1996; Powers, 1983). In order to maintain optimum productivity, trees should be kept above critical nutrient concentrations. While these critical concentrations vary from species to species, a summary of macronutrient concentrations for species in this study can be found in Table 2.1.

Table 2.1. Foliar critical concentrations (%) for N, P, K, Ca, and Mg for the conifer species Douglas-fir, western hemlock, western redcedar, and grad fir. Unless otherwise noted, all values are from Binkley and Fischer (2013).

Nutrient	Douglas-fir	Western hemlock	Western redcedar	Grand fir
Ν	1.0-1.4	1.0-1.2	1.1-1.3	1.0-1.2
Р	0.08-0.12	0.11-0.15	0.10-0.13	0.12-0.15
Κ	0.35-0.60	0.40-0.45	0.35-0.40	0.50-0.60
Ca	0.15-0.20	0.06-0.08	0.10-0.20	0.12 1
Mg	0.06-0.09	0.06-0.08	0.05-0.09	0.9 ²

 1 - value taken from critical concentration of true firs as listed in Moore et al (2004)

 2 - value taken from "slight deficiency" concentration of white fir (*Abies alba*) as listed in Evers (1994)

Nutrient concentration in plant tissues is subject to change as stands develop- though the exact effects are not well understood. Most studies which track nutrients over time look for trends in nutrient mass as opposed to concentration (Binkley, 2003; Turner, 1981; Wang et al., 2019). A study on 13 different loblolly pine plantations tracking foliar nutrients at years 2, 6 and 15 found that fascicle mass changed over time, peaking at 6 years (around canopy closure). Foliar phosphorous concentration peaked around the same time, but the differences were not as great as fascicle mass. Potassium concentrations peaked at age 6, and declined to lowest levels at age 15. This, however, varied with vegetation management treatment, with some showing a steady decline over time. Nitrogen and calcium generally decreased at year 6 and maintained these concentrations through year 15, though the site with the highest soil calcium levels showed the opposite trend. Magnesium concentrations were highest at year 15 and trends between year 2 and 6 varied by site and vegetation management treatment (Miller et al., 2006). Due to the lack of similar published datasets, it is difficult to discern how general these trends are and whether they will persist as stands mature.

Similar species growing at different sites often have different tissue nutrient concentrations (Alexander, 2014; Moore et al., 2004; Radwan and DeBell, 1980; Radwan and Harrington, 1986). Some of this may be explained by water availability, soil nutrient availability and parent material type (Alexander, 2014; Hynicka et al., 2016). Miller et al. found that there was a significant trend between foliar phosphorous and available soil phosphorous, though correlations were weaker for other nutrients (Miller et al., 2006). Nitrogen concentrations in crop trees and vegetation have been shown to correlate with total soil N content in Douglas-fir stands (Devine et al., 2011). In forests, measures of soluble soil nitrogen may correlate poorly with growth and nutrient status. Instead measures of mineralizable nitrogen correlate better with growth than the current available concentration (Binkley and Fischer, 2013; Binkley and Hart, 1989; Ingestad, 1982; Powers, 1980).

Micronutrients refer to a group of nutrients that are required in smaller amounts than the macronutrients (N, P, K, Ca, Mg, and S). They are not as well studied as the macronutrients (with N, P, and K receiving the most attention). Most studies of micronutrient concentrations in conifers refer to foliar values. The range of concentrations in foliage is large, and coniferous trees have been shown to accumulate some micronutrients far in excess of physiological needs (Moore et al., 2004; Radwan et al., 1979). One study of Mn fertilization of Douglas-fir trees raised foliar concentrations from 200 ppm to over 1000 ppm with no noticeable differences in growth rate, and then to over 3,000 ppm with no noticeable toxicity (Radwan et al., 1979). In Douglas-fir trees, concentrations may vary from 11 to 892 ppm (Mn), 50 to 760 ppm (Fe), and 5 to 148 ppm (Zn) (Zinke and Stangenberger, 1979). These ranges span orders of magnitude and signify a wide range of luxury uptake that is not toxic. A study of 25 to 27 year-old western redcedar trees across the cascades and coast of the PNW reported foliar concentrations of 13-48 ppm (Zn), 4-19 ppm (Cu), 69-380 ppm (Mn), 37-83 ppm (Fe) (Radwan and Harrington, 1986). Western Hemlock in the Oregon Cascades have shown foliar concentrations from 13-24 ppm (Zn), 4.7-5.3 ppm (Cu), 736-1213 ppm (Mn), and 105-329 ppm (Fe), with concentrations in the Oregon Coast Range around 1/2 to 3/4 of these values (Zasoski et al., 1990).

Boron is one of the most common limiting micronutrients, though its deficiency in forests is still poorly understood, especially in western conifers (Green and Carter, 1993; Lambert et al.,

1997; Stone, 1990). Boron critical concentrations in foliage are generally cited as 10 ppm for Douglas-fir, true fir, and other conifer species (Moore et al., 2004). The first fertilizer study to confirm boron deficiency in coastal Douglas-fir reported that trees were deficient with foliar concentrations less than 12 ppm (Green and Carter, 1993). Reported intermediate foliar concentrations for grand fir are 22-28 ppm and around 29 ppm for western hemlock. Deficiency levels for western hemlock have been reported at 7 ppm (Stone, 1990). Analysis of a series of western hemlock forests in the PNW reported boron foliar concentrations between 13 and 29 ppm (Radwan and DeBell, 1980). Unlike some of the heavy metals, elevated boron levels can result in acute toxicity (Stone, 1990).

2.2.2. Nutrient Concentrations in Soils

Nutrient concentrations in forest soils can be measured in various ways. Due to each nutrient's distinct chemistry, there are different ways of quantifying different pools. These different pools are generally classified with respect to their availability to plants. Phosphorous, for example, can be labile, moderately-labile, moderately-recalcitrant or stored in Ca complexes-though these 4 categories do not account for all the phosphorous in the soil (DeBruler et al., 2019). Some studies only measure the labile, or available pools, though these are highly dynamic and can change over the course of a year. Additionally, some of these measures, such as nitrite or nitrate concentrations, may be poor indicators of long-term availability and potential for growth (Binkley and Hart, 1989; Powers, 1980). For the purpose of this study, the main concern is the total amount of nutrients in all pools and not the distribution of various soil fractions within the total pool.

Most studies of forest soil study, at the very least, the top 0.2 m of soil. However, forests are able to exploit a much greater soil volume and many studies look at trends in the top 0.5 to 1 m. Effective rooting depth is generally considered to be 1 m, and while there may be significant nutrient reserves up to 3 m in depth, it is not clear whether trees utilize nutrients from deep soil reserves if available (Callesen et al., 2016). Nutrient reserves are greatest near the surface for many nutrients, especially N, as this is where most of the biotic activity occurs in the soil and inputs from fine root turnover and aboveground litter tend to be highest. Trends with depth depend on the mineralogy at a site, and concentrations may increase with depth depending on soil properties and parent material chemistry (Callesen et al., 2016).

Soil nutrient properties depend on parent material and other soil forming factors. Different minerals will weather at different rates and release different nutrients depending on their chemical makeup. Sandstone and siltstone bedrock are nutrient poor relative to igneous rock, and thus may not be as rich of a source of weathered nutrients (Reichle, 1973). Soil age is also important, particularly for N and P. Young soils tend to be high in phosphorous and low in nitrogen, as bedrock is the main source of phosphorus in soils, and legacies of biotic activity are the source of nitrogen. As soils develop, nitrogen fixing activity combined with deposition and leaf litter contribute more N to soils as the P is slowly depleted. Indeed, the trend of young nitrogen limitation in young soils changing to phosphorous limitation in old soils has been observed on a global scale (Lambers et al., 2008). Additionally, history of land use can play a significant role. Agricultural processes have been shown to deplete soil nutrient reserves and alter physical and chemical properties. On the other hand, afforestation has significant effects on soil properties such as texture and nutrient concentration (Berthrong et al., 2009; Sauer et al., 2012).

2.2.3. Silvicultural Management Effects on Nutrient Concentrations

Fertilization and its effects on nutrient concentrations is very well studied. Nitrogen fertilization has been shown to increase foliar N concentration for the first year to two years after fertilizer application, the increase in concentration slowly returning to pre application values over a few years (the exact time varying by nutrient, site and species). As the concentration in the foliage lowers, it is mobilized to create new foliage and increase leaf area (Brix, 1993; Carlson et al., 2014). Fertilization is unique in that it provides a large pulse of plant available nutrients in a short amount of time. Other silvicultural prescriptions, like thinning or vegetation management, allow crop trees a larger share of site resources and may have some effects on nutrient supply. These changes however will likely not be as extreme as fertilizer application.

The effects of vegetation management (VM) on plant nutrient concentrations has been studied, though generally in younger tree seedlings. VM, while allowing trees greater access to site resources, has varying effect on tissue nutrient concentration. It more commonly increases affecting nutrient content as treatment as herbicide treatment produces higher biomass of a given tissue (Devine et al., 2011; Petersen et al., 2008). Nevertheless, some studies show significant effects on nutrient concentration. Five year old Douglas-fir seedling have shown increased foliar

N with vegetation control (Devine et al., 2011; Slesak et al., 2010). These trends varied between sites and concentration effects were only significant at the study level and not at the site level (Devine et al., 2011). A study in the Oregon Coast Range showed N was higher in VM treated Douglas-fir seedlings after the first year of growth but not the second. Boron, in contrast, showed a significant decrease in VM treated plots but only after the second year of growth (Rose and Ketchum, 2002). Differences in concentrations are not always observed, as Petersen et al. found that there were no differences in foliar N, P, K, S, Ca and Mg (Petersen et al., 2008).

The effects of VM on foliar nutrients changes over time. Across a gradient of site conditions, foliar N and P concentrations were greater for treated plots early in stand development. These differences disappeared at ages 7 and 9 for all sites, except for N concentrations at the site that had lowest N levels and untreated trees displayed signs of N deficiency (Powers and Reynolds, 1999). One study of loblolly pine conducted at mid-rotation found that eradication of herbaceous vegetation during stand establishment resulted in a decrease in foliar N and K (Miller et al., 2006). They found that all available soil nutrients declined over time but this decline was greater for C, N and Ca.

The effect of silvicultural management on soil concentration has also been studied, with most studies focusing on different forms of N or P. The Long Term Soil Productivity (LTSP) study has investigated the effects of different intensive management practices across the US, including sites in the PNW (Powers et al., 2005). Sites in Oregon show that after planting, soil nutrients (exchangeable Ca, Mg, K, and total N) tend to increase after 10 years in the top 0.3 m of soil, though the increase is greater when there is no vegetation control after planting (Slesak et al., 2016). Total soil P is more complicated, tending to decrease 10 years after planting in the top 0.3 m. At one site the decrease was less when harvest residues were left on site and there is no vegetation control after planting (Slesak et al., 2016). This study looked at total P and different pools of labile to less labile P which all showed roughly the same result: at one site, when there was a detectable difference in P concentrations of any pool, concentrations were higher with no annual vegetation control while the other site showed the opposite trend (DeBruler et al., 2019). A similar study from the Fall River LTSP site in Washington showed

that total soil N concentrations in the top 0.15 m of soil decreased 10 years after planting (Knight et al., 2014).

Most studies look at only a few nutrients, and few attempt to quantify total soil pools and total plant derived pools. They also tend to focus on younger trees and only one or two crop species (typically Douglas-fir and Ponderosa pine in Oregon). In this study we will investigate how vegetation management affects both of these on multiple conifer species (Douglas-fir, western hemlock, western redcedar, and grand fir) in two important timber producing ecoregions in Oregon (the Oregon Cascade foothills and the Oregon Coast Range).

2.3. Questions and Hypotheses

The objective of this study was to measure the nutrient contents of several different biomass pools in treated and untreated stands. We will measure the following nutrient pools: crop trees (which are divided into branches, stem wood, bark, and foliage), fine roots, understory, forest floor, midstory, and multiple strata of mineral soil up to 1 m depth.

We hypothesize that at age 19 there will be few differences in nutrient concentrations of crop tree tissues and total soil nutrients between treated and untreated plots within each species, but that there will be significant differences between species and sites driven by different nutrient availabilities between sites.

2.4. Methods

2.4.1. Description of Sites

The Coastal Range (CR) site is located at 44.62°N, 123.57°W near Summit, OR approximately 40 km from the coast. The site was planted in year 2000 and experiences a mean annual temperature of 11.1°C and average annual rainfall of 1,707 mm. The soil at this site is fine and loamy (Flamenco et al. 2019). The CR site was planted with Douglas-fir (DF) and western hemlock (WH) (four replicates each), and grand fir (GF) and western redcedar (WRC) (three replicates each). Soils at the CR site are part of the Preacher-Bohannon complex which is derived from siltstone and sandstone (USGS). This soil complex is classified as an Andic Dystrudept, meaning that while it is not an Andosol, it has high aluminum and iron activity (Soil Survey Staff 2015). This site sits near the western edge of the Tyee formation, a sedimentary rock formation that composed largely of marine micaceous sandstone and siltstone. The Cascade Foothills (CF) site is located at 44.48°N, 122.73°W near Sweet Home, OR and was planted in year 2001 with DF and WRC (four replicates each). The site has a mean annual temperature of 12.4°C and an average annual rainfall of 1,179 mm. The soil at this site is a silty clay loam (Flamenco et al. 2019). Soils at the CF site are from the Bellpine series which is derived from sedimentary rock (Soil Survey Staff 2015). Soils of this series are classified as Xeric Haplohumults, indicating an Ultisol with high organic matter content that experiences seasonal drought. These soils are well drained and characterized by a more xeric moisture regime from the CR site. The bedrock is a mixture of basalt, sedimentary rocks, and tuff. Similar to the CR site, these soils are derived from sedimentary bedrock, however tuff and mafic intrusions will lend different chemical characteristics to these soils. Mafic rocks tend to be higher in iron and magnesium than sandstone. This site was formerly agricultural land that was not sufficiently productive and was purchased by Cascade Timber Company.

Soil potassium levels in the PNW are low compared to the rest of the country due to a lack of K feldspar in the parent material. According to the USGS, concentrations near the study sites should range from 0.8 to 1.2% in the top 0.05 m and A horizon, though soil at 1 m depth by the CR site may have lower concentrations (USGS). Copper concentrations are high in the areas of both of these sites, ranging from 30 to 300 ppm or more in the top meter of soil (USGS). Mn high 880-1210 ppm through A horizon, samples at 1 m depth have higher concentrations near the CR site (USGS). Zn also high 80-100 ppm at both sites with possible higher concentration in the A horizon of the CF site. Fe also high in OR, with concentrations ranging from 3 ppm to 14 ppm (USGS). Mg concentrations are higher in the Oregon Cascades than the Coast Range due to differences in parent material. Concentrations near the CF site range from 1 to 13% in the top 0.05 m and A horizon, whereas the range from 0.7 to 1.2 % near the CR site (USGS)

2.4.2. Study Design

A randomized complete block design with eight VM treatments was implemented at each of the two sites. The eight different VM treatments consisted of spring release applications that differed in the number and timing of herbicide treatments applied during the first 5 years after planting. Similar to Flamenco et al. (2019), for this study we used only the control (Control; only pre-planting vegetation control) and the 5 consecutive years of spring release vegetation management treatment (VM). Plots were approximately 0.06 ha and were planted in 8 rows of 8

trees at a 3 x 3 m spacing, resulting in a planting density of 1100 trees per ha. All plots were planted with a single tree species. All DF plots received pre-commercial thinning at year 12 and thinning residues were left on site.

The ecosystem was divided into soil pools and plant derived pools. The plant derived pools were broken down into overstory (planted crop trees), midstory (hardwoods and natural conifer regeneration), understory (shrubs, grasses, forbs, ferns and moss) and forest floor (including coarse woody debris). The overstory was divided into foliage, live branches, stemwood, stembark, and fine roots. The midstory was broken down into foliage and bole (stemwood and stembark). The soil was divided into four layers (0-0.2 m, 0.2-0.4 m, 0.4-0.6 m, and 0.6-1 m).

Soil samples were taken during June 2019. Soil mass for each layer was computed from the bulk density (methods describe below) and calculated volume of the layer (assuming a rectangular prism with two faces 0.2 ha and a depth of either 0.2 or 0.4 m).

Overstory tissue for nutrient analysis were obtained from samples collected by Flamenco et al. (2019), who destructively sampled 4 trees for each species and treatment at each site. Stemwood samples were collected by removing a stem section (or cookie) at DBH. Stem bark samples were obtained by removing the bark from the cookie taken at DBH. Branches and foliage samples were collected from the middle of the living crown.

As dominant midstory species are the same across sites, samples for nutritional analysis were taken only at the CR site without respect to treatment. Midstory tissue samples for nutrient analysis (foliage and stemwood) were collected from midstory trees during the July 2019. Only the four most prevalent species were sampled: red alder (*Alnus rubra* Bong.), bigleaf maple (*Acer macrophyllum* Pursh), Oregon cherry (*Prunus emarginata* (Douglas ex Hook.) D. Dietr.), and cascara buckthorn (*Rhamnus purshiana* DC.). These four species account for 98% of the midstory biomass (Flamenco et al., 2019). Stemwood samples were collected at DBH using a 12-mm increment borer from four different individuals from each species.

Understory, forest floor and fine roots were collected from 6 subplots (0.6 m x 0.6 m) per plot. All vegetation in or hanging over these plots was collected. The forest floor was manually removed down to the organic horizon and included woody debris, duff, and litter. Researchers then collected a core of the top 0.2 m of mineral soil and used a 2 mm sieve to collect fine roots

(Flamenco et al., 2019). Within a plot, all six subsamples were combined for nutrient analysis. The lower layers were collected in spring 2019 on one sample per layer per plot using 50 mm x 50 mm soil cores (AMS, bulk density soil sampling kit). Fine roots were collected from each soil sample using a 2 mm sieve.

2.4.3. Nutrient Analysis

All plant samples were oven-dried at 65°C until reaching constant weight and ground to pass a 0.425 mm sieve. These tissues were then prepared for nutrient extraction by overnight combustion in quartz tubes at 580°C. Samples were extracted in 20% v/v HCl for 15 minutes and then diluted 1:1 with distilled water. These extracts were filtered and stored at 4°C until analysis. Total soil nutrients were extracted by microwave digestion. Samples were heated to 175°C in an Anton-Paar MicrowaveGO and held at that temperature for 4.5 minutes in a solution of 70% HNO₃. Digested samples were diluted 1:1 with distilled water, filtered, and stored at 4°C until analysis. Carbon (C), nitrogen (N) and sulfur (S) concentrations were determined by dry combustion using an Elementar vario MACRO cube. All other nutrients (phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), boron (B), copper (Cu), iron (Fe), manganese (Mn), sodium (Na), and zinc (Zn)), were determined by analyzing extracts with an Agilent ICP-OES 5110. All analyses were carried out at the Central Analytical Laboratory at Oregon State University.

2.4.4. Statistical Analysis

The Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC) was used for all statistical analysis. Analysis of variance, including Tukey multiple comparisons tests, was used to test the effects of site, species and treatments on all soil and plant derived pools (PROC MIXED, SAS Institute Inc. Cary, NC). SigmaPlot version 14 (Systat Software, Inc. San Jose, CA) was used to create all figures.

2.5. Results

Average nutrient concentrations for crop tree (overstory), forest floor and soil are reported in Table 2.2 (macronutrient) and Table 2.3 (micronutrient). Since nutrient concentrations were generally not affected by vegetation management, average values reported include both treatments (any significant treatment or species x treatment effect is denoted in the respective table). For the sake of simplicity, both tables show average nutrient concentration across sites, however there was a significant effect of site for 42% of all tissue types measured (Table 4). Soil nutrient concentrations were highly site dependent for all depths, with the exception of C, N and Zn. Concentration of midstory species and average understory can be found in Appendix Tables 2.1 and 2.2. Site and treatment specific nutrient concentrations are located in Appendix Tables 2.4 to 2.16.

For all species, the largest N, P and K concentrations were observed in foliage, ranging between 0.978 to 1.252% (N), 0.116 to 0.255% (P) and 0.381 to 0.607% (K). On the other hand, larger Mg, Ca and S was observed in forest floor, ranging between 0.116 to 0.146% (Mg), 0.754 to 1.600% (Ca) and 0.090 to 0.111% (S). Within crop tree tissues, fine roots showed the lowest C concentration, ranging between 27.4 to 33.9%, while all other crop tree tissues ranged from 46% to 50%. Nutrient concentration in mineral soil decreased with depth for C, N, P and Ca, but no clear trend was observed for K and Mg. K and Na were below detectable levels for all stemwood samples (both understory and midstory trees). The limit of detection of the ICP for these elements was 2 ppm (Na) and 0.04% (K).

Cu and Fe both had the highest concentrations in fine roots ranging between 4.8 and 6.4 ppm (Cu) and 1209 and 1554 ppm (Fe). The forest floor also contained a notably high concentration of Fe ranging from 914 to 1281 ppm. The concentrations of Mn were highest in the forest floor for all species except WRC, with concentrations ranging from 449 to 833 ppm. The concentration of B was highest in foliage for all species except for WRC, with concentrations averaging between 22.3 and 12.4 ppm. For Zn, the concentrations were highest in different tissues for each species. The concentration of Na was highest in fine roots and forest floor, averaging between 118 and 162 ppm. In WRC, concentrations of Zn, B, and Mn were highest in fine roots. While these root samples are a composite of fine roots from all species, this suggests that WRC invests more micronutrients to fine roots than the other species. Nutrient concentrations of soils decreased with increasing depth for Mn and Zn. Other micronutrients showed no pattern, but in the case of Na, the top layer of soil contained the lowest concentration across all species.

Table 2.2. Average concentrations (%) and standard errors (SE) of the macronutrients carbon, nitrogen, phosphorous, potassium, magnesium,
calcium, and sulfur for each nutrient pool of 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF)
stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range and Cascade foothills of western
Oregon. Averages were taken across sites and treatments.

	5	ow cognitudes we	Carb	00 1	o und u cu Nitre	Dgen	Phosph	orous	Potas	sium	Маеп	esium	Calc	ium	Sul	fur
Foliage 9.440 0.171 1.32 0.064 0.015 0.005 0.037 0.005 0.037 0.005 0.037 0.005 0.037 0.005 0.037 0.005 0.037 0.003 0.017 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 <t< th=""><th></th><th></th><th>%</th><th>SE</th><th>%</th><th>SE</th><th>%</th><th>SE</th><th>%</th><th>SE</th><th>° %</th><th>SE</th><th>%</th><th>SE</th><th>%</th><th>SE</th></t<>			%	SE	%	SE	%	SE	%	SE	° %	SE	%	SE	%	SE
Wood 4723 0.010 0.274 0.019 0.006 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.003 0.007 0.001 0.007 0.007 0.003 0.003 0.001 0.007 0.003 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0		Foliage	49.460	0.171	1.252	0.064	0.184	0.009	0.607	0.037	0.097	0.005	0.600	0.038	0.125	0.010
		Branch	47.234	0.100	0.274	0.019	0.060	0.005	0.236	0.020	0.040	0.004	0.319	0.030	0.057	0.002
		Wood	47.781	0.086	0.077	0.013	0.005	0.001	BLD	ı	0.009	0.001	0.051	0.012	0.032	0.001
Rote 37.32 1.34 0.59 0.03 0.17 0.04 0.14 0.00 0.13 0.03 0.17 0.04 0.07 0.00 0.014 0.016 0.015 0.013 0.014 0.016 0.015 0.013 0.014 0.014 0.015 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013		Bark	49.225	0.361	0.294	0.018	0.056	0.002	0.222	0.015	0.036	0.002	0.300	0.027	0.053	0.003
$ Forst Phot = 7543 \ 1756 \ 0.015 \ 0.176 \ 0.016 \ 0.176 \ 0.016 \ 0.016 \ 0.028 \ 0.042 \ 0.012 \ 0.011 \ 0.015 \ 0.028 \ 0.041 \ 0.011 \ 0.013 \ 0.028 \ 0.041 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.013 \ 0.0$		Root	28.253	1.244	0.591	0.024	0.077	0.004	0.143	0.020	0.068	0.003	0.477	0.040	0.076	0.002
		Forest Floor	37.392	1.738	0.986	0.053	0.091	0.003	0.176	0.016	0.116	0.006	0.860	0.042	0.111	0.004
		Soil 0-0.2 m	4.198	0.275	0.250	0.014	0.763	0.063	0.129	0.011	0.219	0.018	0.258	0.341	ı	I
Said0.4.0 m 0.17 0.110 0.010 0.014 0.112 0.014 0.125 0.014 0.015 0.014 0.016 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013		Soil 0.2-0.4 m	2.811	0.242	0.165	0.013	0.674	0.067	0.114	0.012	0.229	0.018	0.234	0.370	ı	I
Soliol-10m 0.703 0.073 0.073 0.073 0.073 0.073 0.014 0.003 0.073 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.013 0.003 0.013 0.003 0.013 0.003 0.013 0.003 0.013 0.003 0.013		Soil 0.4-0.6 m	1.410	0.175	0.101	0.010	0.550	0.043	0.112	0.014	0.226	0.021	0.154	0.246	ı	I
		Soil 0.6-1.0 m	0.705	0.072	0.055^{-2}	0.004	0.498	0.068	0.114	0.015	0.227	0.023	0.103	0.228	ı	I
	H	Foliage	49.315	0.264	1.033	0.032	0.255	0.027	0.549	0.043	0.114	0.009	0.669	0.078	0.101	0.013
		Branch	46.505	0.117	0.261	0.017	0.044	0.003	0.163	0.020	0.033	0.003	0.259	0.022	0.051	0.002
		Wood	47.740	0.205	0.072	0.004	0.010	0.002	BLD	,	0.015	0.001	0.076	0.008	0.032	0.001
		Bark	46.131	0.644	0.301	0.025	0.086	0.006	0.282	0.032	0.043	0.004	0.393	0.024	0.056	0.003
$ \begin{array}{{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$		Root	33.904	1.737	0.522	0.026	0.084	0.006	0.159	0.019	0.094	0.005	0.409	0.029	0.071	0.002
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		Forest Floor	40.966	1.314	0.903	0.086	0.107	0.003	0.179	0.028	0.146	0.015	0.754	0.039	0.105	0.004
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		Soil 0-0.2 m	4.960	0.306	0.206	0.012	0.691	0.079	0.144	0.008	0.257	0.004	0.111	0.132	ı	I
		Soil 0.2-0.4 m	2.693	3.755	0.351	0.204	0.627	0.094	0.142	0.007	0.271	0.006	0.078	0.166	,	I
		Soil 0.4-0.6 m	1.513^{2}	0.308	0.106^{2}	0.017	0.523	0.048	0.139	0.007	0.275	0.009	0.070	0.157	ı	I
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		Soil 0.6-1.0 m	0.658	0.100	0.056^{2}	0.004	0.347	0.038	0.135	0.009	0.261	0.018	0.037	0.020	ı	I
$ \begin{array}{llllllllllllllllllllllllllllllllllll$	S	Foliage	48.675	0.209	0.978	0.080	0.116	0.005	0.381	0.027	0.105	0.008	1.300	0.069	0.074	0.004
		Branch	45.646	0.965	0.216	0.021	0.039	0.003	0.146	0.015	0.035	0.003	0.624	0.048	0.045	0.002
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		Wood	47.748	0.352	0.238	0.042	0.006	0.000	BLD	·	0.017	0.001	0.142	0.021	0.036	0.001
Root 27.354 1.664 0.552 0.021 0.076 0.004 0.119 0.011 0.079 0.006 0.577 0.047 0.077 0.002 Forest Flor 39.943 1.826 0.774 0.085 0.077 0.009 0.222 0.021 0.127 0.019 1.123 0.100 0.090 0.006 Soil $0-0.2.0.4 m$ 3.079 0.218 0.014 0.745 0.029 0.012 0.223 0.021 0.218 0.365 $ -$ Soil $0.4-0.6 m$ 1.464 0.201 0.1014 0.745 0.005 0.120 0.021 0.218 0.365 $ -$ Soil $0.4-0.6 m$ 1.464 0.201 0.014 0.745 0.004 0.115 0.011 0.226 0.021 0.218 0.097 0.096 Soil $0.6-1.0 m$ 0.608 0.094 0.1146 0.0012 0.122 0.021 0.218 0.021 0.007 Soil $0.6-1.0 m$ 0.096 0.991 0.014 0.146 0.012 0.122 0.021 0.226 0.021 Soil $0.6-1.0 m$ 0.006 0.77 0.007 0.014 0.174 0.075 0.021 0.021 0.071 Soil $0.6-1.0 m$ 0.096 0.971 0.090 0.001 0.012 0.123 0.011 0.012 0.071 0.007 Soil $0.6-1.0 m$ 0.096 0.090 0.090 0.001 0.012 0.025 0.021 0.071 0.07		Bark	47.871	0.300	0.262	0.015	0.049	0.003	0.154	0.013	0.052	0.003	1.009	0.051	0.053	0.003
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		Root	27.354	1.664	0.552	0.021	0.076	0.004	0.119	0.011	0.079	0.006	0.577	0.047	0.077	0.002
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		Forest Floor	39.943	1.826	0.774	0.085	0.077	0.009	0.222	0.050	0.127	0.019	1.123	0.100	0.090	0.006
$ \begin{array}{llllllllllllllllllllllllllllllllllll$		Soil 0-0.2 m	4.867	0.266	0.250	0.012	0.978	0.079	0.140	0.012	0.215	0.021	0.278	0.365	ı	I
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		Soil 0.2-0.4 m	3.079	0.318	0.178	0.014	0.745	0.059	0.120	0.012	0.223	0.021	0.219	0.326	ı	I
$ \begin{array}{l c c c c c c c c c c c c c c c c c c c$		Soil 0.4-0.6 m	1.464	0.201	0.108	0.011	0.583	0.044	0.115	0.014	0.226	0.021	0.178	0.263		ı
7Foliage 48.667 0.122 1.111 0.047 0.146 0.009 0.509 0.047 0.130 0.012 1.205 0.097 0.096 0.006 Branch 46.347 0.240 0.379 0.090 0.088 0.015 0.373 0.052 0.054 0.010 0.453 0.042 0.061 0.005 Wood 47.360 0.096 0.091 0.010 0.007 0.007 0.037 0.067 0.007 0.037 0.007 0.037 0.007 0.037 0.007 0.007 0.003 0.001 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.007 0.002 0.002 0.002 0.002 0.002 0.002 0.002 0.002 0.002 0.002 0		Soil 0.6-1.0 m	0.608	0.049	0.062	0.005	0.474	0.050	0.122	0.020	0.220	0.023	0.144	0.377		
$ \begin{array}{llllllllllllllllllllllllllllllllllll$	[T _1	Foliage	48.667	0.122	1.111	0.047	0.146	0.009	0.509	0.047	0.130	0.012	1.205	0.097	0.096	0.009
Wood 47.360 0.096 0.091 0.010 0.007 0.001 BLD - 0.016 0.001 0.087 0.007 0.034 0.001 Bark 46.708 0.376 0.348 0.038 0.065 0.007 0.305 0.005 0.715 0.083 0.058 0.001 Root 27.373 1.733 0.597 0.059 0.104 0.010 0.136 0.011 0.105 0.005 0.488 0.033 0.038 0.003 Forest Floor 35.490 1.831 1.005 0.114 0.105 0.008 0.1122 0.004 1.600 0.176 0.109 0.006 Soil 0-0.2 m 6.119 0.705 0.292 0.032 0.827 0.116 0.176 0.284 0.013 0.106 0.006 Soil 0-2.0.4 m 2.541 0.2262 0.015 0.284 0.013 0.126 0.005 0.176 0.106 0.006 Soil 0.4-0.6 m 1.625 0.243		Branch	46.347	0.240	0.379	0.090	0.088	0.015	0.373	0.052	0.054	0.010	0.453	0.042	0.061	0.005
Bark 46.708 0.376 0.348 0.038 0.065 0.007 0.305 0.044 0.055 0.005 0.715 0.083 0.058 0.002 Root 27.373 1.733 0.597 0.059 0.104 0.010 0.136 0.011 0.105 0.005 0.468 0.045 0.079 0.003 Forest Floor 35.490 1.831 1.005 0.114 0.105 0.008 0.132 0.015 0.122 0.004 1.600 0.176 0.006 Soil 0-0.2 m 6.119 0.705 0.292 0.032 0.827 0.116 0.176 0.012 0.284 0.013 0.106 0.006 Soil 0.2-0.4 m 2.541 0.226 0.162 0.015 0.557 0.085 0.150 0.007 0.300 0.018 0.183 - - - - - - - - - - - - - - - - - -		Wood	47.360	0.096	0.091	0.010	0.007	0.001	BLD	ı	0.016	0.001	0.087	0.007	0.034	0.001
Root 27.373 1.733 0.597 0.059 0.104 0.010 0.136 0.011 0.105 0.068 0.045 0.079 0.003 Forest Floor 35.490 1.831 1.005 0.114 0.105 0.008 0.1122 0.004 1.600 0.176 0.100 0.006 Soil 0-0.2 m 6.119 0.705 0.292 0.032 0.827 0.116 0.176 0.013 0.187 0.126 - - Soil 0-2.0 4 m 2.541 0.226 0.162 0.015 0.557 0.085 0.156 0.007 0.300 0.187 0.126 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -		Bark	46.708	0.376	0.348	0.038	0.065	0.007	0.305	0.044	0.055	0.005	0.715	0.083	0.058	0.002
Forest Floor 35.490 1.831 1.005 0.114 0.105 0.008 0.132 0.015 0.122 0.004 1.600 0.176 0.100 0.006 Soil 0-0.2 m 6.119 0.705 0.292 0.032 0.827 0.116 0.176 0.012 0.284 0.013 0.126 - - Soil 0-2.0.4 m 2.541 0.226 0.162 0.015 0.557 0.085 0.150 0.007 0.300 0.005 0.183 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -		Root	27.373	1.733	0.597	0.059	0.104	0.010	0.136	0.011	0.105	0.005	0.468	0.045	0.079	0.003
Soil 0-0.2 m 6.119 0.705 0.292 0.032 0.827 0.116 0.176 0.012 0.284 0.013 0.187 0.126 Soil 0.2-0.4 m 2.541 0.226 0.162 0.015 0.557 0.085 0.150 0.007 0.300 0.005 0.109 0.183 Soil 0.4-0.6 m 1.625 0.243 0.106 0.013 0.490 0.078 0.154 0.012 0.303 0.011 0.085 0.172 Soil 0.6-1.0 m 0.648 0.144 0.059 0.008 0.374 0.072 0.177 0.020 0.308 0.013 0.071 0.161		Forest Floor	35.490	1.831	1.005	0.114	0.105	0.008	0.132	0.015	0.122	0.004	1.600	0.176	0.100	0.006
Soil 0.2-0.4 m 2.541 0.226 0.162 0.015 0.557 0.085 0.150 0.007 0.300 0.005 0.109 0.183 Soil 0.4-0.6 m 1.625 0.243 0.106 0.013 0.490 0.078 0.154 0.012 0.303 0.011 0.085 0.172 Soil 0.6-1.0 m 0.648 0.144 0.059 0.008 0.374 0.072 0.177 0.020 0.308 0.013 0.071 0.161		Soil 0-0.2 m	6.119	0.705	0.292	0.032	0.827	0.116	0.176	0.012	0.284	0.013	0.187	0.126	ı	I
Soil 0.4-0.6 m 1.625 0.243 0.106 0.013 0.490 0.078 0.154 0.012 0.303 0.011 0.085 0.172 Soil 0.6-1.0 m 0.648 0.144 0.059 0.008 0.374 0.072 0.177 0.020 0.308 0.013 0.071 0.161		Soil 0.2-0.4 m	2.541	0.226	0.162	0.015	0.557	0.085	0.150	0.007	0.300	0.005	0.109	0.183	·	I
Soil 0.6-1.0 m 0.648 0.144 0.059 0.008 0.374 0.072 0.177 0.020 0.308 0.013 0.071 0.161		Soil 0.4-0.6 m	1.625	0.243	0.106	0.013	0.490	0.078	0.154	0.012	0.303	0.011	0.085	0.172		I
		Soil 0.6-1.0 m	0.648	0.144	0.059	0.008	0.374	0.072	0.177	0.020	0.308	0.013	0.071	0.161		ı

Table 2.3. Average concentrations (ppm) and standard errors (SE) of the micronutrients boron, copper, iron, manganese, sodium, and zinc for each nutrient pool of 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range and Cascade foothills of western Oregon. Averages were taken across sites and treatments

regon.	. Averages were	e taken acı	ross sites	and treatn	nents.							i	
		Bor	on	Cop	per	Iro	u I	Manga	nese	Sodi	um	Zi	ן נ
		mdd	SE	mdd	SE	mdd	SE	ndd	SE	mdd	SE	mdd	SE
DF	Foliage	17.034	1.796	2.961	0.131	52.860	3.946	369.047	28.631	135.670	19.454	11.439	0.838
	Branch	10.284	0.675	3.619	0.146	31.329	5.673	119.420	17.436	22.405	6.901	16.423	1.146
	Wood	1.967	0.187	1.311	0.192	19.596	1.961	20.550	2.777	BLD	ı	4.054	0.358
	Bark	7.629	0.214	3.608	0.129	45.304	4.561	129.875	16.471	106.382	35.786	17.479 1	0.843
	Root	14.143	0.769	5.379 1	0.220	1549.2	82.1	382.418	57.283	117.595	11.097	11.782	0.550
	Forest Floor	14.970	0.796	3.699^{-1}	0.353	1281.2	69.4	638.222	57.97	150.120	6.938	12.511	0.957
	Soil 0-0.2 m	48.715	4.561	28.918	1.934	21917	996	2155.74	307.36	151.554	8.253	65.090	3.439
	Soil 0.2-0.4 m	58.596	5.623	32.707	2.872	22882	871	1788.44	315.91	176.304	6.656	62.755	3.275
	Soil 0.4-0.6 m	59.284	5.565	34.817	3.015	23310	957	1019.24	162.92	186.797	14.348	57.233	3.122
	Soil 0.6-1.0 m	62.565	8.668	34.291	3.015	23640	1052	663.11	150.95	143.978	6.998	51.710	3.710
ΗM	Foliage	22.255	2.334	3.351	0.505	55.198	14.770	936.251	146.375	130.058	18.224	11.013	0.666
	Branch	10.132	0.598	4.776	0.214	29.735	2.933	218.387	20.791	4.171	2.377	8.448	1.336
	Wood	2.381	0.173	1.523	0.129	19.847	4.596	72.358	15.333	BLD		3.406	0.499
	Bark	10.147	1.086	3.694	0.339	46.132	8.651	268.174	18.738	83.081	11.005	6.146^{1}	0.888
	Root	10.437	0.898	4.428	0.220	1297.6	125.9	222.632	11.498	125.196	5.496	10.402	0.686
	Forest Floor	13.295	0.808	3.969^{-1}	0.414	913.6	157.1	833.346	149.956	161.855	5.740	13.428	0.920
	Soil 0-0.2 m	33.726	0.974	23.111	1.043	19676	374	1050.64	81.79	155.685	3.915	67.011	2.214
	Soil 0.2-0.4 m	43.475	2.205	25.391	1.128	21215	382	931.66	102.62	196.372	8.923	68.181	2.906
	Soil 0.4-0.6 m	45.126	0.944	26.761	0.930	21518	229	783.24	104.26	189.093	8.202	66.351	2.748
	Soil 0.6-1.0 m	42.264	1.840	26.067	1.198	22069	239	413.27	77.67	149.796	4.386	53.755	2.573
WRC	Foliage	12.390	0.673	3.781 2	0.299	77.395	12.774	177.280	14.185	89.757	12.735	14.357	0.772
	Branch	8.257	0.667	2.535	0.193	41.744	9.418	42.749	4.114	5.058	4.249	8.742	0.853
	Wood	2.969	0.171	1.270	0.102	26.215	7.233	8.266	0.976	BLD		2.608	0.224
	Bark	14.506	0.944	3.266	0.172	56.389	6.326	61.002	6.423	40.538	5.594	13.131	1.668
	Root	16.481	1.221	6.390^{-1}	0.560	1554.2	131.3	529.184	73.419	127.050	16.858	20.736	5.319
	Forest Floor	15.031	1.397	3.839^{-1}	0.399	1133.9	140.6	448.912	96.881	134.839	13.224	13.360	1.722
	Soil 0-0.2 m	63.536	7.910	32.258	1.766	23069	1022	3174.29	459.79	144.226	5.955	77.349	3.726
	Soil 0.2-0.4 m	63.985	6.813	36.622	2.306	23724	872	2749.14	366.04	216.366	8.387	74.005	3.067
	Soil 0.4-0.6 m	63.709	5.365	39.261	2.653	24409	837	1756.18	244.79	154.218	7.571	67.836	3.170
	Soil 0.6-1.0 m	62.968	5.989	37.497	3.106	24605	938	831.00	114.31	146.445	9.767	54.405	4.006
GF	Foliage	15.653	1.927	3.583	0.213	72.338	7.932	549.387	63.859	69.935	8.716	24.834	2.809
	Branch	14.590	2.257	6.399	1.880	38.428	5.555	136.476	27.601	33.656	9.246	15.458	1.965
	Wood	2.838	0.409	1.604	0.120	19.368	3.615	35.335	5.523	BLD	ı	4.016	0.451
	Bark	11.878	1.483	4.144	0.483	98.706	31.807	243.977	42.910	56.709	5.072	13.299 ¹	2.178
	Root	11.895^{-1}	1.315	4.832	0.442	1384.5	80.0	263.310	16.927	140.396	15.263	15.657	2.425
	Forest Floor	13.399	0.775	3.377	0.202	1208.9	121.2	686.560 1	63.508	138.020	4.359	19.118	1.810
	Soil 0-0.2 m	26.596	2.722	21.228	1.216	17734	1272	1443.65	179.80	181.352	8.418	74.804	5.096
	Soil 0.2-0.4 m	33.997	3.177	23.900	1.041	18687	1184	1161.23	152.37	209.191	10.326	75.210	4.750
	Soil 0.4-0.6 m	41.097	4.706	26.378	1.298	19664	1347	937.51	176.77	186.769	3.882	70.850	4.441
	Soil 0.6-1.0 m	37.015	4.893	27.147	1.691	20202	1569	443.71	110.72	169.210	12.984	56.942	3.321
1- I	Denotes a sign	ificant T ₁	reatment	effect (P	< 0.05)	2-De	notes a s	ignificant	Species	x Treatm	ent effec	t (P < 0.)) 5)

Table 2.4. P values of site effect for concentration of C, N, P, K, Mg, Ca, S, B, Cu, Fe, Mn, Na, and Zn for each nutrient pool for 16-18 year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range and the Cascade foothills of western Oregon. Green cells indicate that the concentration was higher at the CR site and white cells indicate the concentration was higher at the CF site. Blank cells indicate no significant differences across sites.

Species	s Tissue	С	Ν	Р	K	Mg	Ca	S	В	Cu	Fe	Mn	Na	Zn
DF	Foliage				0.005				0.009		0.039		0.002	
	Branch		0.032					0.028					0.020	
	Bark					0.004					0.003		0.042	
	Wood									0.040	0.001	0.002		0.040
	Root	0.014			< 0.001	0.001	< 0.001		0.001		0.002	0.001	0.022	
	Understory	0.011	0.013	0.033			0.034		0.015					-
	Forest floor	0.033			0.029		0.006		0.004	0.006		< 0.001	0.022	0.018
	Soil 0.0-0.2 m			< 0.001	0.001	< 0.001	< 0.001		< 0.001	0.001	< 0.001	< 0.001	< 0.001	
	Soil 0.2-0.4 m			< 0.001	0.002	< 0.001	0.002		< 0.001	0.004	< 0.001	0.004		-
	Soil 0.4-0.6 m			0.001	0.001	< 0.001	0.016		< 0.001	0.008	< 0.001	0.038	< 0.001	
	Soil 0.6-1.0 m			0.001	< 0.001	< 0.001	0.047		< 0.001	0.003	< 0.001	0.013	0.001	
WRC	Foliage					0.024								
	Branch									< 0.001				
	Bark		0.010		0.002		0.001				-		< 0.001	
	Wood		< 0.001			-		-						-
	Root	0.033			0.009	0.029	0.017			0.012	0.019	< 0.001		
	Understory						0.009		0.022			0.036		
	Forest floor					0.036		0.049					< 0.001	
	Soil 0.0-0.2 m				0.002	< 0.001	0.008		0.002	0.002	< 0.001	0.006		-
	Soil 0.2-0.4 m				0.001	< 0.001	0.014		0.001	< 0.001	< 0.001	0.019		
	Soil 0.4-0.6 m					< 0.001	< 0.001		0.007	< 0.001	< 0.001	0.038	< 0.001	
	Soil 0.6-1.0 m				0.001	< 0.001	0.021		0.016	0.018	0.001	0.020	< 0.001	

Concentrations of N were lower at the CR site for the understory of DF and the bark and wood of WRC, but the concentration was higher for the branches of DF (Table 2.4). B concentrations were lower at the CR site in the forest floor, foliage, roots, and understory of DF. Concentrations of C at the CR site were lower in the forest floor and understory of DF, but higher for roots of both DF and WRC. Ca concentrations were lower at the CR site for roots and understory of both DF and WRC, but higher in the bark of WRC. Fe concentrations were lower at the CR site for the bark, foliage, and wood of DF and lower in the fine roots of both DF and WRC. K concentrations were lower at the CR site for the forest floor and foliage of DF, but higher for the bark of WRC and the fine roots of both DF and WRC. Concentrations of Mg were higher at the CR site for the bark and roots of DF and the forest floor, foliage and roots of WRC. Concentrations of Mg were higher at the CR site for the bark and roots of DF and the forest floor, roots, and wood of DF and for

the roots and understory of WRC. Concentrations of Na were higher at the CR site for the bark, branches, forest floor, foliage, and fine roots of DF and for the bark and forest floor of WRC.

Table 2.5. P values of species effect for concentration of C, N, P, K, Mg, Ca, S, B, Cu, Fe, Mn, Na, and Zn for each nutrient pool for 16-18 year-old Douglas-fir, western hemlock, western redcedar and grand fir, stands growing under contrasting treatments of vegetation management in the central Oregon Coast Range. Blank cells indicate no significant differences across species.

Sample	C	Ν	Р	K	Mg	Ca	S	В	Cu	Fe	Mn	Na	Zn
Foliage			0.004	0.027		0.004		0.018			0.003	0.002	0.003
Branch	< 0.001		0.001	< 0.001		< 0.001	0.006	0.016			0.011	0.045	< 0.001
Bark	0.027	0.023	< 0.001	0.027	0.005	< 0.001		0.030			0.002	0.039	0.001
Wood	0.005	0.006	0.001		0.002			0.012	0.014		0.005		0.033
Root					0.011								
Understory	0.032												
Forest floor	0.031			0.033	0.022	< 0.001					0.004	0.037	
Soil 0.0-0.2 m	0.050		0.042		0.016							0.021	
Soil 0.2-0.4 m					0.001						0.004	0.007	
Soil 0.4-0.6 m					0.035							0.008	
Soil 0.6-1.0 m													

Generally, soil concentrations were similar between species (only 17% of all nutrients and depths effected), but species had a significant effect on 46% of all nutrients and tissue types, Table 2.5. Carbon and Mn were the two elements whose plant derived concentrations were most effected by species, each with 5 tissue types effected. Western Hemlock had the highest Mn concentrations across all tissue types, except for bark (WH and GF were not distinguishable but both were significantly higher than other species) forest floor where the top 3 species had indistinguishable concentrations (though WH tended to have higher concentrations in the forest floor). Western redcedar had the lowest concentrations in foliage branches, forest floor, and bark (though bark concentrations were indistinguishable from DF). Na an Mg were the two elements whose soil concentrations were affected greatest by species, with 0-20 cm, 20-40 cm and 40-60 cm all significantly affected. For Mg, WH had the lowest concentrations in the top three layers of soil, though in the 0-20 and 20-60 cm layers, the concentrations were only significantly lower than DF at α =0.05. For sodium, DF soil concentrations were the lowest in the 20-40 and 40-60 cm layers, though at 20-40 the concentration was not significantly different from WH. In the 0-20 layer, sodium tended to be lower in WH plots, though the concentrations were not significantly different from any other species at α =0.05. It should be noted that there were no detectable species differences in the deepest layer (60-100 cm) for any nutrient.

There were relatively few treatment effect on soil concentrations. Notably, there were two depths (0.2-0.4 m and 0.4-0.6 m) for which there was a significantly lower soil N concentration under WRC at the CF site (P<0.05) and one layer (0.6-1.0m) for which this trend was marginally significant (P=0.07). Soil N concentrations were higher under DF at the CF site for the 0.6-1.0 m depth (P<0.05). Soil carbon concentrations were higher in the 0.4-0.6 m depth for WRC (P<0.05).



Figure 2.1. Concentrations of phosphorous, magnesium, copper, and manganese at different soil depths for 18-yearold stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) grown in the Oregon Coast Range. Concentrations are averaged between Control and VM treatments. Significant species differences within a layer are denoted by lowercase letters and differences between depths for a given species are marked with capital letters (P<0.05).

Bark and branches were the two tissue types whose nutrient concentrations differed most between species, followed by wood and then foliage. The top layer of soil displayed the most differences between species. In the 0-0.2 m layer, C and P concentrations were lowest for DF though only significantly different from GF. Magnesium and sodium tended to be lower for WH in this layer, though only significantly different from DF magnesium.

2.6. Discussion

The foliar nutrient concentrations measured here generally agree with published values. Moore et al. (2004) measured foliar concentrations of unfertilized grand fir and DF in the inner mountain west, calculating percentiles for each nutrient. DF foliar nutrient concentrations in this study generally fell within the ranges published for N, P, Mn, Fe, and Cu. Measured concentrations for K, Mg, and B ranged from 40th percentile to below levels measured in the study, whereas S concentrations ranged from 80th percentile to greater than observed concentrations. Measured concentrations for two of the elements were entirely outside of these published ranges- Ca concentrations being higher than highest reported value, and Zn concentrations being lower. These differences may be due to different nutrient availabilities in different soil types- as the measured Ca concentrations in DF foliage agree better with data from sites in Oregon (Mainwaring et al., 2014). A study of old growth DF showed similar trends for N, P, Mg, and K. However, our reported Ca values were lower, though by less than a factor of 2 (Cross and Perakis, 2011).

Nutrient concentrations of GF were less in line with concentrations in the inner mountain west as reported by Moore et al. (2004), even though grand fir was the most variable of the species measured. Only N, P, S, Mg, and Zn fall entirely in the reported ranges. All other nutrients fell outside the published range, with Ca, Mn, Fe, and Cu being greater and K and B being lower (Moore et al., 2004). Foliar concentrations of N, P, K, and Ca are at or below critical concentrations for true firs grown in California (Powers 1983). This may be due to the different sampling regimes. Our study uses a composite sample of foliage of all age classes as opposed to new growth, which was used in the cited studies. Older foliage tends to be lower in most concentrations with the exception of Ca, which tends to increase with foliage age (Binkley and Fischer, 2013; Littke and Zabowski, 2007; Perry et al., 2008).

Foliar nutrients of WRC also generally agree with published literature values. Radawan and Harrington (2011) measured foliar concentrations of WRC trees sampled from a range of different sites in Washington and British Columbia, with a couple of sites in Oregon. The concentrations measured here are generally within the published range for N, P, K, Mg, and, S-though the lowest concentrations measured by this study were lower than those of Radawan and Harrington (2011). However, the Ca concentrations measured in this study were almost two-fold higher than their published data. When compared to foliar concentrations from a different study in British Columbia- measured N, P, K, S, and Mg concentrations were lower than published values, whereas Ca concentrations are higher (Kranabetter et al., 2003). Similar differences in sampling regimes may explain these discrepancies. Comparison with foliar concentrations of old growth WRC in the Oregon Coast range show similar trends for N, P, Mg, and K- however our Ca concentrations were all lower than the ones reported (Cross and Perakis, 2011).

As with the other species, most published foliar values of WH report concentrations in current year foliage. Foliar N was lower than values from old growth specimens in the coast range and stands in western Washington (Cross and Perakis, 2011; Radwan and DeBell, 1980). Concentrations of P, however, were higher than those reported for old growth specimens, slightly higher than coastal stands reported by Radwan and DeBell (1980), but fitting with stands in the Cascades. Ca values, as with other species, were higher than other published values (Cross and Perakis, 2011; Kranabetter et al., 2003; Radwan and DeBell, 1980). K concentrations were similar but slightly higher than old growth species in the Oregon Coast range, but lower than stands in western Washington and British Columbia. Mg concentrations measured in this study were similar to but slightly lower than old growth specimens in the Coast Range but higher than stands in the Washington Cascades (Radwan and DeBell, 1980). Micronutrient concentrations (Zn, Cu, and Mn) measured were also generally lower than reported values, though Fe concentrations were 2-fold higher than stands in western Washington).



Figure 2.2. Crop tree tissue concentrations of nitrogen, phosphorous, potassium, and calcium for 16-year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) grown in the Oregon Coast Range. Concentrations are averaged between Control and VM treatments. Significant species differences within a tissue type are denoted by letters (P<0.05).

It should be noted that critical concentrations are generally developed from fertilization studies using current year foliage. The foliar samples in this study were taken as a composite sample, as this gives a better representation of the average concentration of all foliage. This method is better for the purposes of this study, which is to calculate total foliar nutrients in a stand as opposed to determining stand nutrient status. If this study were to have relied only on measurements current year foliage, it would likely overestimate foliar content of all nutrients except Ca, as these nutrient concentrations are lower in older needle cohorts.

Soil concentrations of C, N, and P are in line with other studies in the Oregon Coast Range (Cromack et al., 1999; Cross and Perakis, 2011). Concentrations of C and N from both sites are similar to the STR and CTC sites in Mainwaring et al. (2014), which are geographically very close to the CR and CF sites respectively. Soil concentrations of Cu Mn and Zn are in or near the ranges predicted by the USGS, with Cu and Zn concentrations slightly lower than the predicted ranges. Concentrations of Ca, K and Mg are lower than USGS predictions by approximately an order of magnitude. Measurements of Ca in soil residue (<2 mm) in the Oregon Coast Range averaged 0.25% on sedimentary bedrock to 0.77% on basaltic bedrock (Hynicka et al., 2016). These values are only two-fold higher than the 0.13% average at the CR site (located on sedimentary bedrock) and 0.35% at the CF site (located on basaltic bedrock). It should be noted that the Basaltic bedrock sites in Hynicka et al. (2016) were from basaltic sites in the Oregon Coast range and not in the Cascade foothills.

Treatment effects on nutrient concentration varied by site, tissue, and nutrient. Bark and forest floor were the two nutrient pools most affected by vegetation control treatment, followed by fine roots. Crop tree foliage, branches, and stemwood all showed no treatment differences for all species at both sites. The forest floor was the tissue type most affected by treatment. This makes sense as the litter from the VM plots was almost entirely composed of conifer litter, with some inclusion of understory litter, whereas the forest floor of the C plots contained litter from midstory species, whose foliar nutrition differs significantly from the conifers. Concentrations of Cu and Mg were higher in the forest floor for control plots, though this trend was less pronounced for DF and WRC at the CF site, since untreated plots had less robust midstory development (Flamenco et al. 2018). Concentrations of K in forest floor were also higher in forest floor of VM plots, which makes sense because conifers are accumulators of this nutrient. As observed elsewhere, RHPU also accumulated high concentrations of Mn in its foliage, but other midstory species did not (Zasoski et al., 1990).


Figure 2.3. Crop tree tissue concentrations of boron, manganese, zinc, and sodium for 16-year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) grown in the Oregon Coast Range. Concentrations are averaged between Control and VM treatments. Significant species differences within a tissue type are denoted by letters (P<0.05).

Bark was the tissue type second most often affected by treatment, with effects seen for P, K, Mg, and Ca. Generally, with the exception of DF K concentrations, bark nutrient concentrations were higher in Control plots at the CF site. Based on comparisons with a dataset that separated bark, phloem, and wood, it is likely that the bark samples in this study contained the phloem, which contains a significant portion of stem nutrients (Augusto et al., 2008). While the current foliage of trees tends to represent the current nutritional status, the bark is

accumulated over the lifespan of the tree. P and K are highly mobile in tree tissues and are easily translocated, and Mg concentrations show similar patterns in bark tissue implying that it is also somewhat mobile (Helmisaari and Siltala, 1989). The fact that these concentrations are higher in Control plots may indicate that they had higher nutrient concentrations in the inner bark at the time of sampling or may suggest a larger portion of live inner bark. Generally, if this were the case it would be expected that foliage concentrations would show a similar pattern which they do not. While difficult to study in depth due to the small annual increment in bark tissues, it has been shown that certain nutrients (N, P, K, Ca, Mg and possibly Zn) are retranslocated from the bark, though this is likely a small overall source of nutrients (Helmisaari and Siltala, 1989; Hendrickson, 1987; Laclau et al., 2003). Thus, higher bark concentrations may indicate that these nutrients were poorly retranslocated from the outer bark before the tissue became dormant. This would suggest that the trees in the Control plots were less stressed for these nutrients over their lifetime resulting in a lower retranslocation efficiency.

There were a few treatment differences on soil nutrient concentrations, though not many. Soil N concentration was affected by treatment differently for different species and soil depths. For DF, soil N concentrations were higher in deep soil. However, for WRC at the CR site, soil N concentrations were significantly lower from 0.2-0.6 m with the deepest soil increment showing marginally lower concentrations. N is a common limiting element in these forests and this indicates that for this slow growing species, sustained vegetation control may reduce the ability of the ecosystem to retain N, as was shown by Miller et al. (2006). Concentrations of C were higher in the Control under one species and only for one layer. Across all species, soil concentrations of Ca and Mg were higher in one layer of the VM treated plots. Slesak et al. (2016) noted less C under VM and greater N at one site, which agrees partially with our results. However, they noted greater increases in soil cations in plots without control of competing vegetation (though it should be noted they were measuring exchangeable cation pools and not total soil cations). Our study did not note any treatment differences in P and K concentrations, both of which were noted in Slesak et al. (2016). Another study of similar design conducted in Western Washington noted no treatment differences in total soil N for all depths, but did note more C in the 0.6-1.0 m layer in herbicide treated plots (Knight et al., 2014). Additionally, this study did not note any difference in total soil P concentrations between vegetation management treatments.

Differences in concentration between site varied by nutrient and tissue type. Similar trends were noticed for both species, though DF displayed more site dependent nutrient differences. Most of the differences in tissue nutrient concentration were associated with differences in total soil nutrient concentration (Appendix Table 2.3). Generally, soils at the CR site had higher concentrations of K, Mg, and Na while soils at the CF site had higher concentrations of Ca, B, Cu, Fe, and Mn. When there were differences in tissue concentrations, they generally followed similar trends, with the exception of branch Cu and bark Ca in WRC as well as forest floor and foliage K in DF. This suggests that, while the soil nutrients measured were total pools as opposed to accessible pools, they may be indicative of trends in available pools between sites. A previous study of WRC nutrition noted that foliar concentrations of N, P, K, Ca, Mg, and S were all significantly higher at inland sites than coastal sites- which contrasts with what was noted in this study (Radwan and Harrington, 1986). All of the coastal sites in Radwan and Harrington (1986) were situated on the Olympic Peninsula which has different mineralogy (soils in the Washington Cascades are also distinct from soils in the Oregon Cascades).

Differences in parent material are able to explain some of the soil concentration differences between the two sites. Basaltic rocks tend to have higher concentrations of Fe, Mg, and Ca than sedimentary rock, though this can change depending upon the nature of the sedimentary material. This study found that there were higher soil concentrations of Fe at the CF site which is more volcanic, but less Mg. It is possible that this is due to the nature of sedimentary rock at the CR site or land use history at the CF site. The CF site was previously agricultural land that was relatively low yielding. It may be that farming procedures decreased soil Mg. It has been shown that application of lime in the form of Ca carbonate depletes the exchangeable Mg, though this may only be a small portion of the total Mg at a site. Additionally, studies at soils formed on the Tyee formation (which the CR site is located on) show that these sites contain a large amount of montmorillonite, a clay which commonly has Mg isomorphous substitutions in the Al layer.

P is almost entirely sourced from bedrock, with soil reserves declining with age. The bedrock from the Tyee formation formed in the middle Eocene, somewhere between 54 and 36 Ma. The bedrock that the CF site is located on is estimated to be between 32 and 11 Ma in

various parts of the range. Additionally, the Oregon Coast Range (CR site) generally experiences greater rainfall and higher NPP than the West Cascades (CF site) (Hudiburg et al., 2009). Both plant activity and moisture are important soil forming factors. Given this information it is reasonable to suspect that soils at the CR site are more developed which may have resulted in less soil P than the CF site.

Species differences in concentrations were more common than treatment differences and showed notably different, but expected, patterns when compared to site differences. Species differences in soil concentration were most common in the top 0.2 m, which is to be expected as this is where the greatest quantity of fine roots are found. The species effect was significant across all species for 5 nutrients (Table 2.5). However, when comparing one species to another, these trends were often not significant (Figure 2.1). Lower soil C for DF may reflect a lower rate of fine root turnover or a higher rate of microbial respiration. Mg generally had the lowest concentrations under WH. This may indicate that there is greater uptake or leaching of this nutrient under this species. It may also indicate that there is a blocking effect on soil Mg concentrations or that the sampling regime was too simple to characterize soil heterogeneity (though it should be noted that block was included as a random factor in the mixed model).

It is difficult to draw general trends for species differences in aboveground tissue concentrations. Elements such as B and Zn did not have strong trends that indicate the tendency of one species to accumulate more of a nutrient across all tissue types. Similarly, no tissue type tended to have higher concentrations of all or most nutrients in any given species. Mn had significantly higher tissue concentrations in the wood, bark, branches, and foliage of WH, which indicates that this species may accumulate more Mn than other species. WH, as a species, is capable of growing at lower soil pH than other conifers and soil Mn becomes more available at lower pH. The trend observed here may indicate that WH has adapted to survive with higher tissue concentrations of Mn due to its preference for acidic soils. Concentrations of P were highest for wood, bark and foliage of WH. This differs from old growth species in the Oregon Coast Range which showed DF species as having not significantly higher foliar concentrations than WH (Cross and Perakis, 2011). A study of WRC and WH in coastal British Columbia showed no differences across species on a number of different site types (Kranabetter et al., 2003).

2.7. Management Implications

Since the treatment had little effect on foliar nutrient concentrations, we expect the physiology, including photosynthetic efficiency of the foliage, to also be similar between competing vegetation control treatments. This means that crop tree growth differences between Control and VM treatments cannot be explained by the foliar nutrient status at year 16-18.

Most differences in soil nutrient content (with the exception of C) indicated higher concentrations under the VM treatment. This study does not indicate the potential for total soil nutrient reserves to be depleted by even sustained vegetation management treatment. WRC at the CR site was a notable exception, where VM plots showed significantly lower N concentrations. This may indicate the potential for reduced N retention when stands of WRC, a slow growing species, receive five years of post-planting herbicide application. This study did not attempt to quantify fluxes between various available and unavailable soil nutrient pools, and as such there may be treatment differences in nutrient availability that cannot be observed from this data.

2.8. <u>References</u>

- Alexander, E.B., 2014. Foliar Analyses of Conifers On Serpentine and Gabbro Soils In the Klamath Mountains. Madroño 61, 77–81. https://doi.org/10.3120/0024-9637-61.1.77
- Augusto, L., Meredieu, C., Bert, D., Trichet, P., Porté, A., Bosc, A., Lagane, F., Loustau, D., Pellerin, S., Danjon, F., Ranger, J., Gelpe, J., 2008. Improving models of forest nutrient export with equations that predict the nutrient concentration of tree compartments. Ann. For. Sci. 65. https://doi.org/10.1051/forest:2008059
- Beaufils, E.R., 1973. Diagnosis and recommendation integrated system (DRIS). Soil Sci. Bull. 1, 1–132.
- Berthrong, S.T., Jobbágy, E.G., Jackson, R.B., 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. Ecol. Appl. 19, 2228– 2241. https://doi.org/10.1890/08-1730.1
- Binkley, D., 2003. Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Can. J. For. Res. 33, 2274–2279. https://doi.org/10.1139/x03-158

- Binkley, D., Fischer, R.F., 2013. Ecology and management of forest soils, 4th ed. ed. Wiley, Hoboken, NJ.
- Binkley, D., Hart, S.C., 1989. The Components of Nitrogen Availability Assessments in Forest Soils, in: Stewart, B.A. (Ed.), Advances in Soil Science: Volume 10. Springer New York, New York, NY, pp. 57–112. https://doi.org/10.1007/978-1-4613-8847-0_2
- Brix, H., 1993. Fertilization and Thinning Effect on a Douglas-fir Ecosystem at Shawnigan Lake: A Synthesis of Project Results.
- Burger, J.A., Pritchett, W.L.L., 1988. Site preparation effects on soil moisture and available nutrients in a pine plantation in the Florida flatwoods. For. Sci. 34, 77–87.
- Callesen, I., Harrison, R., Stupak, I., Hatten, J., Raulund-Rasmussen, K., Boyle, J., Clarke, N., Zabowski, D., 2016. Carbon storage and nutrient mobilization from soil minerals by deep roots and rhizospheres. For. Ecol. Manage. 359, 322–331. https://doi.org/10.1016/j.foreco.2015.08.019
- Carlson, C.A., Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R.A., Stape, J.L., 2014. Growth responses of loblolly pine in the southeast united states to midrotation applications of nitrogen, phosphorus, potassium, and micronutrients. For. Sci. 60, 157–169. https://doi.org/10.5849/forsci.12-158
- Colbert, S.R., Allen, H.L., 1996. Factors contributing to variability in loblolly pine foliar nutrient concentrations. South. J. Appl. For. 20, 45–52. https://doi.org/10.1093/sjaf/20.1.45
- Cole, D.W., Gessel, S.P., 1992. Fundamentals of Tree Nutrition, in: Chappell, H.N., Weetman,
 G.F., Miller, R.E. (Eds.), Forest Fertilization: Sustaining and Improving Nutrition and
 Growth of Western Forests. College of Forest Resorces, University of Washington,
 Seattle, pp. 7–16.
- Cromack, K., Miller, R.E., Anderson, H.W., Helgerson, O.T., Smith, R.B., 1999. Soil Carbon and Nutrients in a Coastal Oregon Douglas-Fir Plantation with Red Alder. Soil Sci. Soc. Am. J. 63, 232–239. https://doi.org/10.2136/sssaj1999.03615995006300010034x
- Cross, A., Perakis, S.S., 2011. Tree species and soil nutrient profiles in old-growth forests of the Oregon Coast Range. Can. J. For. Res. 41, 195–210. https://doi.org/10.1139/x10-199

- DeBruler, D.G., Schoenholtz, S.H., Slesak, R.A., Strahm, B.D., Harrington, T.B., 2019. Soil phosphorus fractions vary with harvest intensity and vegetation control at two contrasting Douglas-fir sites in the Pacific northwest. Geoderma 350, 73–83. https://doi.org/10.1016/j.geoderma.2019.04.038
- Devine, W.D., Harrington, T.B., Terry, T.A., Harrison, R.B., Slesak, R.A., Peter, D.H., Harrington, C.A., Shilling, C.J., Schoenholtz, S.H., 2011. Five-year vegetation control effects on aboveground biomass and nitrogen content and allocation in Douglas-fir plantations on three contrasting sites. For. Ecol. Manage. 262, 2187–2198. https://doi.org/10.1016/j.foreco.2011.08.010
- Evers, F.H., 1994. Magnesiummangel, eine verbreitete Erscheinung in Waldbeständen—
 Symptome und analytische Schwellenwerte. Mitteilungen des Vereins für Forstl.
 Standortskartierung und Forstpflanzenzüchtung 37, 7–15.
- Green, R.N., Carter, R.E., 1993. Boron and Magnesium Fertilization of a Coastal Douglas-Fir Plantation. West. J. Appl. For. 8, 48–53. https://doi.org/10.1093/wjaf/8.2.48
- Helmisaari, H.S., Siltala, T., 1989. Variation in nutrient concentrations of pinus sylvestris stems. Scand. J. For. Res. 4, 443–451. https://doi.org/10.1080/02827588909382580
- Hendrickson, O., 1987. Winter Branch Nutrients in Northern Conifers and Hardwoods. For. Sci. 33, 1068–1074.
- Hepler, P.K., Winship, L.J., 2010. Calcium at the cell wall-cytoplast interface. J. Integr. Plant Biol. 52, 147–160. https://doi.org/10.1111/j.1744-7909.2010.00923.x
- Hudiburg, T., Law, B., Turner, D.P., Campbell, J., Donato, D., Duane, M., 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecol. Appl. 19, 163–180. https://doi.org/10.1890/07-2006.1
- Hynicka, J.D., Pett-Ridge, J.C., Perakis, S.S., 2016. Nitrogen enrichment regulates calcium sources in forests. Glob. Chang. Biol. 22, 4067–4079. https://doi.org/10.1111/gcb.13335
- Ingestad, T., 1982. Relative addition rate and external concentration; Driving variables used in plant nutrition research. Plant. Cell Environ. 5, 443–453. https://doi.org/10.1111/1365-3040.ep11611714

- Johnson, D.W., Turner, J., 2019. Nutrient cycling in forests: A historical look and newer developments. For. Ecol. Manage. 444, 344–373. https://doi.org/10.1016/j.foreco.2019.04.052
- Knight, E., Footen, P., Harrison, R., Terry, T., Holub, S., 2014. Competing Vegetation Effects on Soil Carbon and Nitrogen in a Douglas-fir Plantation. Soil Sci. Soc. Am. J. 78, S146– S151. https://doi.org/10.2136/sssaj2013.07.0320nafsc
- Kranabetter, J.M., Banner, A., Shaw, J., 2003. Growth and nutrition of three conifer species across site gradients of north coastal British Columbia. Can. J. For. Res. 33, 313–324. https://doi.org/10.1139/x02-188
- Laclau, J.P., Deleporte, P., Ranger, J., Bouillet, J.P., Kazotti, G., 2003. Nutrient dynamics throughout the rotation of Eucalyptus clonal stands in Congo. Ann. Bot. 91, 879–892. https://doi.org/10.1093/aob/mcg093
- Lambers, H., Chapin, F.S., Pons, T.L., 2008. Plant Physiological Ecology. Springer New York, New York, New York.
- Lambert, M.J., Turner, J., Knott, J., 1997. Boron nutrition of radiata pine plantations in Australia. Boron soils plants Proc. Int. Symp. Boron Soils Plants held Chiang Mai, Thailand, 7-11 Sept. 1997.
- Littke, K.M., Zabowski, D., 2007. Influence of calcium fertilization on Douglas-fir foliar nutrition, soil nutrient availability, and sinuosity in coastal Washington. For. Ecol. Manage. 247, 140–148. https://doi.org/10.1016/j.foreco.2007.04.027
- Mainwaring, D.B., Maguire, D.A., Perakis, S.S., 2014. Three-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington. For. Ecol. Manage. 327, 178–188. https://doi.org/10.1016/j.foreco.2014.05.005
- Marschner, H., Marschner, P., 2012. Marschner's mineral nutrition of higher plants.
- Miller, J.H., Allen, H.L., Zutter, B.R., Zedaker, S.M., Newbold, R.A., 2006. Soil and pine foliage nutrient responses 15 years after competing-vegetation control and their

correlation with growth for 13 loblolly pine plantations in the southern United States 1. Can. J. For. Res. 36, 2412–2425. https://doi.org/10.1139/x06-164

- Moore, J.A., Mika, P.G., Shaw, T.M., Garrison-Johnston, M.I., 2004. Foliar nutrient characteristics of four conifer species in the interior Northwest United States. West. J. Appl. For. 19, 13–24. https://doi.org/10.1093/wjaf/19.1.13
- Perry, D.A., Oren, R., Hart, S.C., 2008. Forest ecosystems, Second edi. ed. The Johns Hopkins University Press, Baltimore, Maryland.
- Petersen, K.S., Ares, A., Terry, T.A., Harrison, R.B., 2008. Vegetation competition effects on aboveground biomass and macronutrients, leaf area, and crown structure in 5-year old Douglas-fir. New For. 35, 299–311. https://doi.org/10.1007/s11056-007-9078-z
- Powers, R.F., 1983. Forest Fertilization Research in California, in: Ballard, R., Gessel, S.P. (Eds.), IUFRO Symposium on Forest Site and Continuous Productivity. Gen. Tech. Rep. PNW-163. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, pp. 388–397.
- Powers, R.F., 1980. Mineralizable Soil Nitrogen as an Index of Nitrogen Availability to Forest Trees. Soil Sci. Soc. Am. J. 44, 1314–1320. https://doi.org/10.2136/sssaj1980.03615995004400060037x
- Powers, R.F., Reynolds, P.E., 1999. Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. Can. J. For. Res. 29, 1027–1038. https://doi.org/10.1139/x99-104
- Powers, R.F., Scott, D.A., Sanchez, F.G., Voldseth, R.A., Page-dumroese, D., Elioff, J.D., Stone, D.M., 2005. The North American long-term soil productivity experiment : Findings from the first decade of research 220, 31–50. https://doi.org/10.1016/j.foreco.2005.08.003
- Radwan, M.A., DeBell, D.S., 1980. Site index, growth, and foliar chemical composition relationships in western hemlock. For. Sci. 26, 283–290.
- Radwan, M.A., Harrington, C.A., 1986. Foliar chemical concentrations, growth, and site productivity relations in western red cedar. Can. J. For. Res. 16, 1069–1075. https://doi.org/10.1139/x86-185

- Radwan, M.A., Shumway, J.S., DeBell, D.S., 1979. Effects of manganese and manganesenitrogen applications on growth and nutrition of Douglas-fir seedlings /, Effects of manganese and manganese-nitrogen applications on growth and nutrition of Douglas-fir seedlings /. https://doi.org/10.5962/bhl.title.94198
- Reichle, D.E., 1973. Analysis of Temperate Forest Ecosystems, First. ed. Springer-Verlag, New York, New York.
- Rose, R., Ketchum, J.S., 2002. Interaction of vegetation control and fertilization on conifer species across the Pacific Northwest. Can. J. For. Res. 32, 136–152. https://doi.org/10.1139/x01-180
- Sauer, T.J., James, D.E., Cambardella, C.A., Hernandez-Ramirez, G., 2012. Soil properties following reforestation or afforestation of marginal cropland. Plant Soil 360, 375–390. https://doi.org/10.1007/s11104-012-1258-8
- Slesak, R.A., Harrington, T.B., Peter, D.H., DeBruler, D.G., Schoenholtz, S.H., Strahm, B.D., 2016. Effects of intensive management practices on 10-year Douglas-fir growth, soil nutrient pools, and vegetation communities in the Pacific Northwest, USA. For. Ecol. Manage. 365, 22–33. https://doi.org/10.1016/j.foreco.2016.01.019
- Slesak, R.A., Harrington, T.B., Schoenholtz, S.H., 2010. Soil and Douglas-fir (Pseudotsuga menziesii) foliar nitrogen responses to variable logging-debris retention and competing vegetation control in the Pacific Northwest. Can. J. For. Res. 40, 254–264. https://doi.org/10.1139/X09-188
- Soil Survey Staff. 2015. Illustrated guide to soil taxonomy. U.S. Department of Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, Nebraska.
- Stone, E.L., 1990. Boron deficiency and excess in forest trees: a review. For. Ecol. Manage. 1, 49–75.
- Turner, J., 1981. Nutrient cycling in an age sequence of western Washington douglas-fir stands. Ann. Bot. 48, 159–170. https://doi.org/10.1093/oxfordjournals.aob.a086109

- Turner, J., Lambert, M.J., Gessel, S.P., 1977. Use of foliage sulphat concentration to predics response to urea application by Douglas-fir. Can. J. For. Res. 7, 476–480. https://doi.org/https://doi.org/10.1139/x77-061
- Turner, J., Long, J.N., 1975. Accumulation of Organic Matter in a Series of Douglas-fir Stands. Can. J. For. Res. 5, 681–690.
- Ulrich, A., 1952. Physiological Bases for Assessing the Nutritional Requirements of Plants. Annu. Rev. Plant Physiol. 3, 207–228. https://doi.org/10.1146/annurev.pp.03.060152.001231
- Wang, H., Chen, D., Sun, X., 2019. Nutrient allocation to different compartments of agesequence larch plantations in China. Forests 10, 1–15. https://doi.org/10.3390/f10090759
- Zasoski, R.J., Porada, H.J., Ryan, P.J., Greenleaf-Jenkins, J., Gessel, S.P., 1990. Observations of copper, zinc, iron and manganese status in western Washington forests. For. Ecol. Manage. 37, 7–25. https://doi.org/10.1016/0378-1127(90)90043-B
- Zinke, P.J., Stangenberger, A.G., 1979. Ponderosa pine and Douglas–fir foliage analyses arrayed in probability distributions. Pp., in: S. P. Gessel, P. M. Kenady, and W. A. Atkinson (Eds.), Proceedings of the Forest Fertilization Conference. pp. 221–225.

3. Nutrient Contents in Plant and Soil Pools of Four Western Conifer Stands

3.1. Introduction

Measures of tissue nutrient content are important for understanding the ways an ecosystem uses nutrients. They have been used to calculate nutrient budgets which have in turn been used to measure various processes including internal nutrient cycling in forests (Sollins et al., 1980). They have been used to estimate harvest removals from a system under different harvest scenarios. They can also be used to quantify total soil nutrient reserves, which can help managers make decisions (Augusto et al., 2003; Callesen et al., 2016; Vadeboncoeur et al., 2014).

Nutrient budgets are estimates of total nutrient mass stored in various ecosystem pools. They originated as an agricultural tool to help farmers determine needs for fertilizer application. Since then, they have been used to study how forest ecosystems store nutrients. When measurements of internal nutrient transfers are also included, nutrient budgets can illuminate how a forest ecosystem cycles nutrients internally (Sollins et al., 1980). They can also be used comparatively, to see how ecosystem components and internal transfers are different between two stands (Compton and Cole, 1998) or look at how stand nutrient storage chances with age (Turner, 1981). The ability to compare nutrient budgets of different stands is useful when trying to understand the way different species use nutrients, how similar species use nutrients differently at different sites, and how stands use nutrients differently under different treatments.

Silviculture has the potential to change the way a forest uses nutrients. It can change the amount of nutrients stored in a tissue type or it can change the way nutrients are distributed between different pools. Vegetation management, for example, reduces the amount of nutrients stored in competing vegetation and allows the system to reallocate these nutrients to crop trees (Devine et al., 2011). It also changes the allometry of crop trees, which will affect the way they distribute nutrients to different tissues (Gonzalez-Benecke et al., 2018).

3.2. Literature Review

3.2.1. Nutrient Content in Plant Tissues

Plants distribute nutrients throughout their tissues in order to satisfy their physiological needs. These nutrients are often divided into two categories, based on the relative requirements of plants. The following are considered macronutrients and are required in larger amounts: carbon (C), nitrogen (N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S). The following are considered micronutrients and are required in much smaller amounts: boron (B), copper (Cu), iron (Fe), manganese (Mn), sodium (Na), and zinc (Zn) (see Chapter 1 for more details).

Foliage contains a disproportionately large amount of nutrients compared to its biomass. While comprising only 4% of aboveground biomass in a 40 year old Douglas-fir stand, it contains 70% of the total aboveground N (Cole and Gessel, 1992; Turner, 1981; Turner and Long, 1975). Trees allocate a significant portion of nutrients to their foliage as this is where the majority of physiological process occur (Marschner and Marschner, 2012). As with concentration, nutrient content of leaves changes over time, declining after the needle reaches maturity. Stemwood, on the other hand, contains a large amount of biomass in established forests, but relatively little nutrient mass, with the exception of Ca. Heartwood, the portion of stemwood that is dead, contains relatively little nutrients, except carbon and calcium, which are associated with cellular structural elements and difficult to mobilize before tissue senescence.

Forest floor contents are highly dependent on litter chemistry and vary as tree species change (Cross and Perakis, 2011; Homann et al., 1992). A study in the Oregon coast range looked at forest floor nutrient content under several different species. Nutrient content was highest under Douglas-fir, second highest under western hemlock, and lowest under western redcedar (except for forest floor calcium, where western redcedar was second highest). Nutrient content ranged from 6.8–12.4 Mg/ha (C), 149.9–345.8 kg/ha (N), 12.7–28.2 kg/ha (P), 179.8–385.0 kg/ha (Ca), 13.9–26.3 kg/ha (Mg), and 9.7–18.2 kg/ha (K) under all species including big leaf maple. The nutrient content of the forest floor changes over the life of a stand, especially in managed stands where harvesting may disturb or significantly reduce forest floor mass. It also changes composition over time, young stands tend to have forest floors composed mostly of leaf litter, with increasing proportion of woody material over time (Turner and Long, 1975). Forest

floor mass increases continually (for at least the first 100 years) and decomposition rates decline with age (Turner, 1981). They also change in chemical composition, as forest floor in old-growth forests tends to have more lignin and lower concentrations of more easily degradable components such as simple sugar and hemicellulose (Entry and Emmingham, 1998). This lends more weight to the idea that the forest floor serves as a nutrient sink (Piatek and Allen, 2001; Turner, 1981).

Understory plants can contain a large portion of nutrients and may account for a large portion of transpiration as well as production. In fertilization trials, the understory has been shown to take up a significant amount of added nutrients, occasionally more than crop trees (Chang et al., 1996). After heavy thinning of Norway spruce plantations, understory vegetation transpiration was 35% that of crop tree respiration (Gebhardt et al., 2014). In a series of Douglas-fir stands, understory composed only 5% of standing biomass, but up to 17% of aboveground production and up to 43% of liter returned to the forest floor (Turner and Long, 1975). Thus understory species also have an important influence on forest floor chemistry. Under well stocked forests with high canopy cover, understory biomass tends to decline with age. This is largely due to the reduction in light availability for understory plants.

Midstory nutrient reserves are less studied than other ecosystem components, largely due to their intentional eradication in managed stands or the inclusion of these species in overstory calculations. However, when they are allowed to develop they are capable of accumulating significant biomass (Flamenco et al., 2019). In the Pacific Northwest, midstory species are often hardwoods, which invest more nutrients in their foliage. This combined with the fact that canopies exert important control over nutrient cycling, implies that they can be a significant component that is worth studying (Prescott, 2002).

Nutrient content changes over the life of the stand, as trees add biomass to different biomass pools. The rate at which this occurs depends on the productivity of the stand, with less productive stands having reduced biomass and nutrient contents compared to stands of similar ages (Turner, 1981; Turner and Long, 1975). An age sequence of Douglas-fir stands in Washington reveals some interesting trends, though it should be noted that these stands were N limited and relatively low productivity. Crown and foliar biomass and nutrient content tended to increase until age 40-50 after which it remained somewhat constant (the exception being foliar Ca content, which continued to increase over the life of the stand). Stem and forest floor biomass and nutrient content, however, continued to increase with increasing stand age (Turner, 1981). As stems continue to grow while foliage content stabilizes, the proportion of aboveground biomass stored as C increases.

3.2.2. Nutrient Content in Soils

The LTSP sites at Mollala, OR (about 50 miles north of our study site located in Cascades foothills) has total soil content of 170 Mg ha⁻¹, 7220 kg ha⁻¹ and 5050 kg ha⁻¹ of C, N, and P respectively in the top 0.6 m of soil. The Matlock site in the Olympic Peninsula has total soil content of 92.4 Mg ha⁻¹, 3300 kg ha⁻¹, and 3290 kg ha⁻¹ of C, N, and P respectively in the top 0.6 cm of soil (DeBruler et al., 2019). A stand of Douglas-fir with volunteer red alder trees in the Oregon Coast range had 175.62 Mg ha⁻¹, 8327 kg ha⁻¹, and 3337 kg ha⁻¹ of C, N, and P respectively in the top meter of soil (Cromack et al., 1999). Under a Douglas-fir forest in the cascade foothills in Washington, total cation masses were 33000 kg ha⁻¹ 21000 kg ha⁻¹ and 17000 kg ha⁻¹ for Ca, Mg, and K in the top 0.45 m of soil. These cation concentrations tended to increase slightly as depth increased, though the authors do not comment on whether these trends are significant (Homann et al., 1992). As researchers tend to measure exchangeable cations as opposed to total cations, it is difficult to find comparable datasets.

3.2.3. Management Effects on Nutrient Content

Management can affect nutrient content in two main ways. It can alter the concentration in a given tissue or it can alter the mass of a given tissue, or in many cases it may do both. Site preparation, planting techniques, competition control, and fertilization all lead to increased biomass, and as such they all will lead to an increase in tissue nutrient content (Fox et al., 2007). Since total root system masses are not often quantified, shifts in allocation from belowground to aboveground can produce this effect as well.

In studies of VM effects during the first few years after planting, nutrient content differences generally occur due to significant treatment effects on biomass. Since tissue concentrations are generally (though not always) unaffected, treatments that produce bigger crop trees and/or higher seedling survival result in larger aboveground nutrient content. Vegetation management (VM) is an important silvicultural tool particularly because it increases seedling growth rates and survival (its effects on seedling tissue concentration are equivocal- see Chapter 2 Literature Review for more). In young plantation stands in the U.S. Pacific Northwest, crop trees associated with VM had larger stem, branch, and foliage biomass compared to trees in control plots with similar diameter at breast height (Petersen et al., 2008).

Studies of VM and crop tree nutrient content typically only focus on young, generally 5year-old, Douglas-fir and Loblolly pine. A study of 13 year old loblolly pine demonstrated higher foliar potassium and nitrogen mass with herbaceous vegetation control but no difference in foliar phosphorous, calcium, and magnesium mass (Miller et al., 2006). A study of young Douglas-fir and seedlings at the Long Term Soil Productivity sites at Mollala, OR Matlock, WA and Fall River, WA, showed that VM increased crop tree biomass as well as the nitrogen content of foliage and whole tree (Devine et al., 2011; Slesak et al., 2010). A different study on 5-yearold Douglas-fir found that foliage concentrations of N, P, K, S, Ca, Mg remained largely the same, but changes in aboveground biomass led to a greater than two fold increase in macronutrient content (Petersen et al., 2008). Generally, all these studies found that seedlings grown in treated plots attained significantly larger biomass, leading them to find that total nutrient content of trees was greater when growing in absence of competing vegetation.

Management effects on total soil nutrient content are similar to soil nutrient concentrations effects since silvicultural prescriptions generally do not increase soil mass or bulk density (soil compaction upon harvesting being an exception). Generally, when there are differences in nutrient content, they tend to be in the top 0.2 m of soil and more pronounced at poor quality sites (Slesak et al., 2011). Studies of soil nutrients often focus on N or P but will occasionally investigate exchangeable cations.

Long Term Soil Productivity (LTSP) sites in Oregon show that soil nutrients (exchangeable Ca, Mg, K, and total N) tend to increase 10 years after planting in the top 0.3 m of soil. However, the increase is greater when there is no vegetation control after planting (Slesak et al., 2016). Total soil tends to decrease after planting. At one site the decrease was less with no vegetation control after planting, while at the other site the decrease was less with annual vegetation control after planting (Slesak et al., 2016). A follow up study looking at different P pools showed the same result: at one site, when there was a detectable difference in P concentrations of any pool, concentrations were higher with no annual vegetation control while the other site showed the opposite trend (DeBruler et al., 2019). Studies from different sites and with different species yield different results. A similar study from the Fall River LTSP site in WA showed that total soil N concentrations in the top 0.15 m of soil decreased 10 years after planting (Knight et al., 2014). One study of loblolly pine conducted at mid-rotation found that all available soil nutrients declined over time but this decline was greater for C, N and Ca (Miller et al., 2006). A study of jack pine, red pine, western white pine and black spruce showed that changes to soil nutrients caused by VM vary by nutrient and species. Jack pine and red pine showed no statistically significant decrease in soil nutrients, white pine plots showed a decline in C and N, and black spruce plots showed declines in C, N, Ca and K (Hoepting et al., 2011). In a study of loblolly and slash pine at rotation age, Vogel et al (2011) found that weed control reduced fine root biomass in deep soil layers and a decrease in soil carbon from 0.66 – 1.0 m and increase N in the surface (0.0-0.33 m) mineral soil.

Most of these studies investigate young stands of only one or two crop species. They also typically only focus on only a few plant/soil pools (such as crop tree foliage or soil to a certain depth) and a few nutrients (typically N, P, K and occasionally Ca and Mg). In this study we will investigate how vegetation management affects the nutrient mass of wide variety of plant and soil pools of multiple conifer species (Douglas-fir, western hemlock, western redcedar, and grand fir) in two important timber producing ecoregions in Oregon (the Oregon Cascades Mountains foothills and the Oregon Coast Range). We will combine this mass information to also investigate how treatment affects the nutrient masses of all plant derived and soil derived pools as a whole.

3.3. Questions and Hypotheses

The overarching goal of this project is to understand how intensive silvicultural practices affect long-term site quality. The specific objective of this study is to construct nutrient budgets for stands of different species and sites and to compare total ecosystem, plant derived, and soil nutrient masses between VM and control.

We hypothesize that midstory trees increase the nutrient storage capacity of conifer dominated ecosystems because they store a large quantity of nutrients in their foliage. If this is true, total ecosystem nutrient content will be higher in plots that did not receive herbicide treatment and where understory and midstory has developed.

3.4. Methods

3.4.1. Description of Sites

The Coastal Range (CR) site is located at 44.62°N, 123.57°W near Summit, OR approximately 40 km from the coast. The site was planted in year 2000 and experiences a mean annual temperature of 11.1°C and average annual rainfall of 1,707 mm. The soil at this site is fine and loamy (Flamenco et al. 2019). The CR site was planted with Douglas-fir (DF) and western hemlock (WH) (four replicates each), and grand fir (GF) and western redcedar (WRC) (three replicates each). Soils at the CR site are part of the Preacher-Bohannon complex which is derived from siltstone and sandstone (USGS). This soil complex is classified as an Andic Dystrudept, meaning that while it is not an Andisol, it has high aluminum and iron activity (Soil Survey Staff 2015). This site sits near the western edge of the Tyee formation, a sedimentary rock formation that composed largely of marine micaceous sandstone and siltstone.

The Cascade Foothills (CF) site is located at 44.48°N, 122.73°W near Sweet Home, OR and was planted in year 2001 with DF and WRC (four replicates each). The site has a mean annual temperature of 12.4°C and an average annual rainfall of 1,179 mm. The soil at this site is a silty clay loam (Flamenco et al. 2019). Soils at the CF site are from the Bellpine series which is derived from sedimentary rock (Soil Survey Staff 2015). Soils of this series are classified as Xeric Haplohumults, indicating an Ultisol with high organic matter content that experiences seasonal drought. These soils are well drained and characterized by a more xeric moisture regime from the CR site. The bedrock is a mixture of basalt, sedimentary rocks, and tuff. Similar to the CR site, these soils are derived from sedimentary bedrock, however tuff and mafic intrusions will lend different chemical characteristics to these soils. Mafic rocks tend to be higher in iron and magnesium than sandstone. This site was formerly agricultural land that was not sufficiently productive and was purchased by Cascade Timber Company.

3.4.2. Study Design

A randomized complete block design with eight VM treatments was implemented at each of the two sites. The eight different VM treatments consisted of spring release applications that differed in the number and timing of herbicide treatments applied during the first 5 years after planting. Similar to Flamenco et al. (2019), for this study we used only the control (Control; only pre-planting vegetation control) and the 5 consecutive years of spring release vegetation

management treatment (VM). Plots were approximately 0.06 ha and were planted in 8 rows of 8 trees at a 3 x 3 m spacing, resulting in a planting density of 1100 trees per ha. All plots were planted with a single tree species. All DF plots received pre-commercial thinning at year 12 and thinning residues were left on site.

The ecosystem was divided into soil pools and plant derived pools. The plant derived pools were broken down into overstory (planted crop trees), midstory (hardwoods and natural conifer regeneration), understory (shrubs, grasses, forbs, ferns and moss) and forest floor (including coarse woody debris). The overstory was divided into foliage, live branches, stemwood, stembark, and fine roots. The midstory was broken down into foliage and bole (stemwood and stembark). The soil was divided into four layers (0-0.2 m, 0.2-0.4 m, 0.4-0.6 m, and 0.6-1 m).

3.4.3. Soil Characterization

Soil pH was measured in 1:1 soil to water ratio using a Hanna Instruments HI5522. Four plots from each site were chosen for texture analysis. In order to measure soil texture, 50 g of soil was resuspended in a 1% sodium metaphosphate solution by shaking for 4 hours and resuspending the soil mixture in a 1 L graduated cylinder. Solution density was measured using a hydrometer at 45 seconds and again at 7.5 hours. These densities were used to calculate percentages of sand, silt, and clay according to Miller et al., 2013.

3.4.4. Biomass Calculations

Overstory (crop tree) biomass was computed using tree inventory (DBH and height) data at age 18 years (CR site in January 2018; CF site in January 2019) and the species and sitespecific biomass functions reported in Gonzalez-Benecke et al. (2018). Midstory biomass was computed using tree inventory (DBH) data from July 2019 and the species-specific biomass functions reported in Flamenco et al. (2019). Species specific biomass functions were also used to calculate midstory foliar biomass for the main four midstory species: red alder (*Alnus rubra* Bong.), bigleaf maple (*Acer macrophyllum* Pursh), cascara buckthorn (*Rhamnus purshiana* Don.), and Oregon bittercherry (*Prunus emarginata* (Dougl. ex Hook.) Eaton) (Busing et al., 1993; Flamenco et al., 2019; J.A. Kendall Snell, 1983). Since species specific foliage biomass equations were not available for Oregon bittercherry, an equation for pin cherry (*P. pensylvanica* L.f.) was used. Forerest floor biomass were taken from Flamenco et al. (2019). Understory mass was adjusted from Flamenco et al (2019) based on empirically derived equations relating understory mass and crop tree basal area. Soil samples were taken during June 2019. Soil mass for each layer was computed from the bulk density (methods describe below) and calculated volume of the layer (assuming a rectangular prism with two faces 0.2 ha and a depth of either 0.2 or 0.4 m).

Mineral soil samples were collected at 4 depth increments: 0-0.2 m, 0.2-0.4 m, 0.4-0.6 m, and 0.6-1.0 m. The top 0.2 m was sampled in spring 2017 using a 5-cm diameter PVC core (6 samples per plot; Flamenco et al. 2019). The lower layers were collected in spring 2019 on one sample per layer per plot using 5 cm x 5 cm soil cores (AMS, bulk density soil sampling kit). Soil samples were dried at 70°C and ground to pass a 2mm sieve. Dry soil mass was measured and used to calculate the bulk density of the layer.

Fine roots were collected from each soil sample using a 2 mm sieve. Fine root biomass for each layer was calculated by scaling the mass of fine roots collected from the soil cores proportionally to the volume of the layer determined using a rectangular prism. This biomass was summed for all layers in a plot to calculate total fine root biomass. This biomass was partitioned into crop tree fine roots and vegetation fine roots allometrically. This was done by calculating a ratio between crop tree basal area and fine root biomass for the VM plots (where vegetation fine roots were assumed to be negligible) and applying this ratio to the Control plotswhere any remaining fine root biomass was attributed to competing vegetation (understory and midstory.

3.4.5. Nutrient Budget Calculations

Nutrient concentrations for each pool in each plot, calculated in Chapter 2, were multiplied by the calculated biomass of each pool in each plot (see above) to determine the total mass of each nutrient in a given pool in each plot. Average values for each site, species, and treatment were computed by averaging across replicates. For each site, species, treatment, and nutrient, calculated nutrient masses of plant derived nutrient pools were summed as were total soil nutrient pools. ICP analysis failed to detect K and Na in the stemwood samples of all species of overstory and midstory trees. The limit of detection is 2ppm for Na and 0.04% K (400 ppm) in undiluted tissue. Since it is known that actual concentrations of these nutrient are non-zero, they were assumed to be a fixed value for all species. Nutrient budgets were constructed assuming stemwood concentrations of 0.5 ppm, 1 ppm and 1.5 ppm Na and 0.01%, 0.02% and 0.03% for K. Treatment differences for total plant derived Na and K mass were analyzed (see next section for details) for each assumption in order to determine how sensitive the analysis was to this parameter. Since there was no statistical difference (Appendix Table S.3.1), the largest concentrations (1.5 ppm Na and 0.03% K) were used for further analysis.

3.4.6. Statistical Analysis

The Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC) was used for all statistical analysis. Analysis of variance, including Tukey multiple comparisons tests, was used to test the effects of site, species and treatments on all soil and plant derived pools (PROC MIXED, SAS Institute Inc. Cary, NC). SigmaPlot version 14 (Systat Software, Inc. San Jose, CA) was used to create all figures.

All P values for DF and WRC as well as all Site parameters and interactions (Site*Trt, Site*Spp, and Site*Spp*Trt) were calculated from a mixed linear model using a reduced dataset excluding western hemlock and grand fir plots. All P values for WH and GF, as well as Spp, Trt, and Spp*Trt parameters were calculated from a mixed linear model using a reduced dataset excluding all plots from the CF site.

3.5. <u>Results</u>

3.5.1. Stand Inventory and Soil Properties

A summary of stand attributes at age 18-years is provided in Table 3.1. In general, the VM treatment increased the mean height, quadratic mean diameter (QMD, cm) and basal area (BA, $m^2 ha^{-1}$) of crop trees at both sites. For example, DF in the VM treatment were on average 1 and 2.3 m taller than the Control treatment for the CR and CF sites, respectively. Although the BA of crop trees was larger in the VM treatment (reaching 42.5 m² ha⁻¹ for WH and GF), the Control treatment tended to have much higher midstory BA ranging between 16.1 and 29.3 m² ha⁻¹ at the CR site and 2.7 to 4.5 m² ha⁻¹ at the CF site. There was no midstory for any of the VM treatment plots with the exception of WRC at CR which had 0.7 m² ha⁻¹ of midstory BA.

Table 3.1 Average trees per ha (TPHA, ha-1), mean height (height, m), quadratic mean diameter (QMD, cm), crop tree basal area (BA, m2 ha-1) and midstory basal area (BA, m2 ha-1), for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) planted stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon. Control: no post- planting vegetation control, VM: sustained vegetation control for first 5 years post planting.

Site	Species	Treatment	TPHA (ha ⁻¹)	Height (m)	QMD (cm)	Crop tree BA (m ² ha ⁻¹)	Midstory BA (m ² ha ⁻¹)
CR	DF	Control	681	17.1	8.5	25.1	0.0
		VM	725	18.1	9.2	31.0	0.0
	WH	Control	868	13.5	6.7	19.4	16.1
		VM	1032	17.2	9.0	42.6	0.0
	WRC	Control	748	6.2	4.1	7.0	29.3
		VM	967	10.7	7.0	24.0	0.7
	GF	Control	907	11.8	5.9	16.5	17.7
		VM	987	15.6	9.2	42.5	0.0
CF	DF	Control	696	14.8	7.2	18.4	4.5
		VM	718	17.1	8.9	28.5	0.0
	WRC	Control	352	8.7	6.4	7.0	2.7
		VM	935	9.6	6.3	19.1	0.0

There was a trend for the stocking of plots with VM to be higher than Control plots and this effect was particularly strong for WRC at the CF site which averaged 935 and 352 trees ha⁻¹ for the Control and VM plots, respectively. VM treatment effects were significant for all stand metrics (TPA, Height, QMD, crop tree BA, and midstory BA), Table 3.1. Plant derived biomass for each treatment is plotted in Figure 3.1.



Figure 3.1. Average biomass (Mg ha⁻¹) of plant derived pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

Midstory components differed between species and sites. DF plots did not tend to develop midstories without VM, though there was some development on plots at the CF site. Western hemlock plots accumulated dense conifer regeneration in Control plots, especially ones that were close to the adjacent mature Douglas-fir stands, though they also contained various hardwood species. Grand fir Control plots developed a similar basal are of midstory species compared to western hemlock, but this was mostly composed of native broadleaf species, with less conifer regeneration. Midstory development in western redcedar plots had remarkably different trajectories at the two different sites. At the CF site there was very little midstory development even though there was significant crop tree mortality. At the CR site, there was less crop tree mortality, however there was significant, dense midstory composed largely of broadleaf species.

Soil physical and chemical properties are listed in Table 3.2. Soils at both sites were acidic with pH averaging 4.85 at the CR site and 5.05 at the CF site for all depths, and no significant differences across species or treatments. Soil bulk density did not vary by treatment but did vary significantly in the 0.4-0.6 m layer for grand fir, Table 3.3.

<u> </u>			Bulk Density	Sand	Clay	Silt
Site	Depth	рН	(g cm- ³)	(%)	(%)	(%)
CR	0-0.2 m	4.71 (0.04)	0.704 (0.013)	30.4 (4.4)	38.0 (4.7)	31.6 (3.6)
	0.2-0.4 m	4.88 (0.04)	0.790 (0.015)	21.3 (5.4)	48.9 (7.3)	29.8 (2.6)
	0.4-0.6 m	4.92 (0.03)	0.822 (0.018)	14.6 (2.8)	60.4 (4.6)	25.0 (3.1)
	0.6-1.0 m	-	-	15.9 (4.4)	58.1 (3.9)	26.0 (2.2)
CF	0-0.2 m	5.19 (0.07)	0.706 (0.021)	21.8 (1.8)	34.3 (1.7)	43.9 (0.4)
	0.2-4 m	5.05 (0.07)	0.738 (0.022)	13.9 (1.5)	42.6 (1.9)	43.5 (0.8)
	0.4-6 m	4.81 (0.05)	0.814 (0.019)	14.0 (2.3)	40.9 (2.6)	45.1 (2.3)
	0.6-1.0 m	-	-	17.0 (3.0)	43.5 (2.7)	39.5 (0.6)

Table 3.2. Average pH, bulk density, and texture of four layers of soil (0-0.2 m, 0.2-0.4 m, 0.40-0.6 m, and 0.6-1.0 m) for study sites in the Oregon Coast Range (CR) and Cascade Foothills (CF). Standard errors are included in parentheses.

3.5.2. Nutrient Budget Summary

Summary of ANOVA tables including P-values for all effects for macro and micro nutrient mass in all ecosystem pools can be found in Appendix Tables S.3.2-S.3.14. Similarly, while several nutrient budgets will be highlighted in this section, all budgets can be found in Appendix Figures S.3.1-13. Masses of each nutrient stored in each tissue for all sites, species, and treatments can be found presented in table format in Appendix Tables S.3.15-S.3.40. In general, macro nutrient masses stored in aboveground crop tree tissues (specifically foliage,

branches, bark, and stemwood) displayed a significant species x treatment effect, largely because the biomass of crop trees responded to treatment differently for each species (data not shown).

A summary of the ANOVA tables for the effects of site, species, treatment, and their interactions on total plant derived and total soil nutrient mass is shown in Table 3.3. For simplicity, this table only looks at total plant derived nutrients (calculated as the sum of crop tree, midstory, understory, and forest floor masses) and total soil derived nutrients (calculated as the sum of all soil depths masses). Total plant derived mass of carbon, Mg and S had a site x species x treatment interaction suggesting that the effect of VM on storage of these elements varies widely with site and crop species. Total plant derived masses of P displayed a significant treatment effect only for WH and GF, VM effect on K was only significant for GF. B, Mn, Cu, and Zn were the only micronutrients that displayed a significant treatment effect, though for all this effect varied by species. Ca was the only nutrients that showed consistent differences across species (no spp x trt interaction, Table 3.3). Ca was the only nutrients to be affected by VM independent of site and species. With the exception of C, N and Zn there was a significant effect of site on total soil nutrient mass (soil S masses were not quantified in this study). The only nutrient where total soil nutrient mass varied by treatment was Mg (Table 3.3).

3.5.3. Carbon Budget

Figure 3.2 displays the carbon mass at age 18 years. Vegetation management plots had a significantly higher mass of carbon stored in plant derived tissues across species (P=0.003). The only exception to this was WRC at the CR site, where crop tree growth was reduced but the midstory contained significant biomass (difference not significant, P=0.102). In WRC Control plots, the midstory and understory contributed 75% of the total carbon mass at the CR site and 32% at the CF site. Due to this, the carbon mass of the Control treatment was greater than the VM at CR, but the opposite was true at CF, although these differences were not significant. In Control plots of GF and WH, the midstory and understory contributed around 47% of total carbon mass. Soil carbon stocks were, in general, not significantly affected by treatment or site across all species (P=0.332). The exception was WRC were VM plots showed reduced total soil carbon mass (P=0.018).

Table 3.3. Results of ANOVA test for stand characteristics, nutrient pools of plant derived matter and soil characteristics for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Stand characteristics include: stand trees per hectare (TPHA), mean height, basal area (BA) and quadratic mean diameter (QMD). Nutrient pools include plant derived matter (sum of crop trees, midstory, understory, and forest floor) and total soil pool (0-1 m). Soil characteristics include: bulk density for the top three layers (0-0.2 m, 0.2-0.4 m and 0.4-0.6 m). Significant differences are highlighted in bold.

Stand Characteristi	с	Site	Spp	Trt	Site x Spp	Site x Trt	Spp x Trt	Site x Spp x Trt
TPHA		0.031	0.012	<0.001	0.026	0.071	0.002	0.012
Height		0.999	<0.001	<0.001	0.008	0.142	0.118	<0.001
BA		0.018	<0.001	<0.001	0.456	0.983	<0.001	0.104
QMD		0.252	<0.001	<0.001	0.008	0.213	0.350	<0.001
Nutrient	Pool*	Site	Spp	Trt	Site x Spp	Site x Trt	Spp x Trt	Site x Spp x Trt
С	Plant	<0.001	0.048	0.003	0.013	0.003	0.001	0.018
	Soil	0.469	0.403	0.332	0.975	0.198	0.501	0.305
Ν	Plant	0.012	0.732	0.341	0.282	0.075	0.013	0.067
	Soil	0.445	0.087	0.161	0.802	0.316	0.341	0.287
Р	Plant	0.009	0.002	0.045	0.027	0.036	0.002	0.105
	Soil	0.002	0.256	0.835	0.340	0.735	0.964	0.975
Κ	Plant	0.343	0.015	0.654	0.491	0.123	0.019	0.120
	Soil	<0.001	0.052	0.323	0.726	0.261	0.937	0.272
Mg	Plant	0.001	0.196	0.001	0.080	0.004	0.021	0.020
	Soil	<0.001	0.018	0.051	0.254	0.369	0.537	0.461
Ca	Plant	0.215	0.011	0.016	0.132	0.222	0.245	0.930
	Soil	<0.001	0.071	0.205	0.688	0.817	0.749	0.833
S	Plant	0.001	0.703	0.013	0.024	0.005	0.069	0.003
В	Plant	0.211	0.004	0.002	0.060	0.155	0.005	0.123
	Soil	<0.001	0.701	0.436	0.814	0.779	0.728	0.803
Mn	Plant	<0.001	<0.001	<0.001	0.709	0.288	0.001	0.912
	Soil	<0.001	0.080	0.494	0.543	0.766	0.739	0.517
Fe	Plant	0.207	0.299	0.246	0.207	0.206	0.299	0.207
	Soil	<0.001	0.674	0.296	0.759	0.666	0.785	0.920
Cu	Plant	0.271	0.009	0.019	0.002	<0.001	<0.001	0.095
	Soil	<0.001	0.739	0.059	0.975	0.465	0.828	0.022
Na	Plant	<0.001	<0.001	0.907	<0.001	0.124	0.260	0.266
	Soil	<0.001	0.007	0.227	0.214	0.449	0.125	0.312
Zn	Plant	0.338	0.008	0.015	0.907	0.255	0.005	0.695
	Soil	0.708	0.229	0.314	0.563	0.970	0.720	0.897
Soil Characteristic	Depth	Site	Spp	Trt	Site x Spp	Site x Trt	Spp x Trt	Site x Spp x Trt
Bulk Density	0-0.2 m	0.713	0.651	0.033	0.041	0.872	0.853	0.451
	0.2-0.4 m	0.201	0.572	0.802	0.869	0.999	0.046	0.523
	0.4-0.6 m	0.369	0.017	0.483	0.287	0.222	0.485	0.677

*: Plant is plant derived matter (sum of crop trees, midstory, understory, and forest floor) and Soil is total soil pool (0-1 m)



Figure 3.2. Average carbon stocks (Mg ha-1) of soil and plant derived nutrient pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

3.5.4. Nitrogen Budget

There was a significant species x treatment effect for N plant derived mass (P=0.013, figure 3.3). At the CR site the N mass was larger in the VM treatment for WH (P=0.032), but no difference was detected for other species (P>0.1). This was, in part, due to the robust understory and midstory in the WH and WRC Control plots which contained 48% and 66% of total plant derived N mass, respectively. At the CF site the plant derived N mass was larger in DF than in WRC. In Control plots, total crop tree biomass was significantly reduced, resulting in lower nitrogen mass stored in the crop tree tissue types. Total soil N mass did vary by site, but was affected by VM treatment for WH and WRC. For WH, soil N was larger in VM plots and for WRC soil N was larger in Control plots (P=0.021 and P=0.039 respectively).



Figure 3.3. Average nitrogen (N) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

3.5.5. Phosphorous Budget

There was a significant species x treatment effect (P=0.002) for total plant derived P stocks such that only WH and GF displayed treatment effects (Figure 3.4). WH and GF had more total plant derived P mass in VM plots. On the other hand, WRC had more plant derived P mass in Control plots at the CR site (P=0.046). For these plots, there was less P in crop tree derived tissues and much in the midstory and understory, which accounted for 44% of total plant phosphorous. This effect was opposite at the CF site due to a less abundant midstory. Total soil pools were not affected by VM treatments but were significantly lower at the CR site (P=0.853 and P=0.002 respectively).



Figure 3.4. Average phosphorous (P) stocks (kg ha-1) of soil and plant derived nutrient pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

3.5.6. Potassium Budget

There was a significant species x treatment effect (P=0.019) for plant derived K mass such that VM only increased K mass in GF (Figure 3.5). Plant derived K mass was similar between treatments for all other species at both sites (P=0.654). Total soil K mass was larger at the CR site (P<0.001) and was not affected by VM treatments.



Figure 3.5. Average potassium (K) stocks (kg ha-1) of soil and plant derived nutrient pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

3.5.7. Boron Budget

There was a significant effect of VM treatments on plant derived mass of B across all species (P=0.002, Figure 3.6). WRC was the only exception, showing no differences between treated and untreated plots (P>0.2). In WRC Control plots, the midstory and understory contributed 41% of total B mass at the CR site and 49% at the CF site. In GF and WH plots, the midstory and understory contributed 49% and 52% of total B mass respectively. Soil pools varied significantly by site (P<0.01), with the CR site having significantly reduced mass. Interestingly, DF foliar concentrations of B were significantly lower at the CR site and indicate marginal B bioavailability (Stone 1990).



Figure 3.6. Average boron (B) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

3.5.8. Iron Budget

Unlike previous nutrients, Fe was disproportionately stored in fine roots and forest floor, and very little was stored in aboveground, living plant tissue (Figure 3.7). There were significant differences in Fe mass stored in many different crop tree derived tissues across sites and across treatments (P<0.05, Appendix Tables S.3.23 and S.3.24), though there was no significant effect on total plant derived Fe mass. Since the concentrations in these crop tree pools do not vary by site or treatment, this difference was largely driven by differences in biomass. The total soil mass of Fe was greater at the CF site, but was unaffected by treatment.



Figure 3.7. Average iron stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old stands of Douglasfir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

3.5.9. Nutrients in Harvestable Pools

Distribution between tissues is important with regards to harvest removals. As typical harvest practices remove only the boles of trees, nutrients with high stemwood and stembark content are going to be removed in greater quantities. Table 3.4 reports the percentage of each nutrient stored in crop tree stem bark as a proportion of the mass stored in aboveground tissue. As VM increases the biomass allocation to crop trees, it is no surprise that for almost all of these nutrients, a greater percentage of the total plant derived nutrients are stored in crop tree stems in VM plots. Removals are generally lowest for WRC C plots since the crop trees represent a

proportionately small amount of overall nutrient storage. Removals are generally highest for WH VM followed by GF VM, which also makes sense since these were the conditions where crop tree biomass was greatest.

Table 3.5 shows the mass of each nutrient in stembark and stemwood, standardized by the mass of wood produced in Mg. At the CR site, WRC contained the most N, Ca, Mg, S, B, Fe and Zn in harvestable tissue when normalized to wood production and WH contained the most P, Cu, and Mn. DF had the lowest quantities of several nutrients, including N, Ca, Mg, B, Cu, and Fe contained in stemwood and stembark per unit wood produced. Differences between sites are less apparent than differences between species. At the CF site, both species contain notably more N in their stemwood and stembark, and DF contained more Mn. At the CR site, WRC contained more Ca and Fe in its stembark and stemwood. This shows that the different allocations to different tissues has a potentially meaningful effect on how nutrients would be removed in a harvest. At both sites, DF was the species that tended to contain less nutrient mass in harvestable tissues per unit of stemwood. However, it should be noted that this is only a snapshot of where nutrients are stored at 18 to 19 years and further study is needed to confirm whether or not these trends continue to a rotation age.

Table 3.4. Percentage of total plant derived nutrient mass stored in crop tree stembark and stemwood for pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM).

Site	Species	Treatment	С	Ν	Р	K	Ca	Mg	S	В	Cu	Fe	Mn	Na	Zn
CR	DF	С	59.1	13.4	15.8	21.2	23.3	17.7	32.8	23.0	31.3	3.4	10.8	32.0	34.8
		VM	61.2	13.6	17.4	31.8	15.8	21.4	34.3	24.8	34.0	3.8	11.4	18.6	37.7
	WH	С	29.3	7.2	9.9	11.1	12.8	9.6	12.3	14.7	17.1	3.6	13.3	8.6	16.0
		VM	65.3	25.6	25.2	30.3	31.8	28.7	47.1	28.7	45.2	8.4	28.1	22.1	39.9
	WRC	С	7.9	2.2	2.0	2.4	6.6	2.7	2.9	5.3	4.1	0.6	2.2	2.1	5.8
		VM	41.7	10.3	9.3	13.4	24.4	16.4	27.0	24.3	21.7	6.3	6.2	9.5	21.5
	GF	С	29.9	10.0	9.3	13.2	14.7	10.2	11.3	16.1	20.2	3.1	13.7	8.4	21.4
		VM	67.0	20.8	15.8	20.2	22.3	27.0	45.5	31.7	38.9	13.7	20.7	14.2	28.2
CF	DF	С	50.6	18.2	14.0	14.8	14.7	12.4	24.6	18.1	31.8	4.6	13.4	8.8	35.3
		VM	59.8	19.3	15.8	22.0	15.4	18.4	36.0	21.1	46.5	6.7	11.3	15.3	41.9
	WRC	С	23.3	12.5	4.5	3.6	8.4	5.3	11.6	7.2	9.9	1.0	1.4	1.8	6.6
		VM	38.3	24.6	8.9	9.6	11.7	12.5	23.0	16.3	17.7	2.2	2.5	4.4	15.3

here a	ere are for the VM treated plots only.														
		Macronutirents (g nutrient/Mg wood)							Micronutirents (mg nutrient/Mg wood)						
Site	Species	Ν	Р	K	Ca	Mg	S	В	Cu	Fe	Mn	Na	Zn		
CR	DF	23.6	3.5	19.8	18.4	3.9	9.5	0.71	0.31	4.13	7.32	5.21	20.05		
	WH	27.2	5.2	15.6	31.4	4.1	9.0	0.77	0.47	5.01	31.04	3.40	16.96		
	WRC	33.8	3.6	15.0	110.8	7.5	10.9	1.49	0.42	13.33	4.62	3.82	49.97		
	GF	26.3	3.0	13.2	33.3	4.7	8.7	0.92	0.46	8.37	13.51	1.77	20.56		
CF	DF	32.2	3.5	14.8	21.8	3.1	9.3	0.77	0.61	8.35	11.60	2.37	18.35		
	WRC	90.1	3.9	15.4	64.7	5.6	10.0	1.45	0.43	7.74	4.66	1.38	47.85		

Table 3.5. Mass of nutrients stored in crop tree stembark and stemwood standardized by mass of stemwood produced for pools for 18 year-old stands of Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF). Stands were grown under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM), but the values presented here are for the VM treated plots only.

3.6. Discussion

3.6.1. Plant derived nutrient content

Nutrient content depends partially on the biomass of each component. VM treatments resulted in different stand characteristics. The stocking, height, basal area, and quadratic mean diameter were all greater under the VM treatment. This means that there were more crop trees in the VM plots and that they were larger in both height and diameter. The inverse is true with regards to midstory and understory development. VM plots had less midstory BA and tended to have lower understory mass (it should be noted that previous understory biomass calculations were adjusted based on an empirically derived inverse relationship between understory biomass and crop tree basal area). DF was a notable exception to this trend, as these stands tended not to develop a large midstory or understory biomass even in the Control plots. At this point in stand development, the midstory and understory biomasses were generally seen to decline (except for stands with low crop tree survival). This is because they are being overtopped by the crop trees and dying due to lack of light.

The age series presented by Turner and Long (1975) and Turner (1981) provides an excellent opportunity to compare datasets of macronutrient masses in Douglas-fir stands. In their analysis, the stands were grown under poor, severely N limited conditions in WA state. The stocking (822-2756 trees ha⁻¹) and basal area (32-57 m² ha⁻¹) of all stands in their age series were greater than the stands presented here, which averaged 703 trees ha⁻¹ and 28 m² ha⁻¹ at the CR site and 707 trees ha⁻¹ and 23 m² ha⁻¹ at the CF site. Lower stocking in our study may be due to thinning that occurred in DF stands at age 12. The foliar biomass in Douglas-fir stands in this

analysis were greater than the maximum noted in Turner and Long (1975), which peaked around 40-50 years. The biomass of stemwood, however, was less than that of the 22-year-old Turner stand. The weight of the bark and forest floor in this analysis was around that of the 30 year old stand in Turner, though the forest floor mass was higher, but not as high as the 42 year old stand (Turner and Long, 1975). With the exception of N, the macronutrient masses followed a similar trend. In general, foliage masses of P, K, and Ca were similar to that of the 42-year-old stand (note that with the exception of Ca, this is when foliage masses reached their maximum in the age series). The foliar nitrogen masses observed in our analysis were unsurprisingly higher than any of the stands in Turner (1981). Bark and stemwood masses of P, K, Ca were similar to or less than the 22-year-old stand whereas N bark and stemwood mass was comparable to the 30 year old. The forest floor mass of all nutrients was similar to the 42-year-old stand in Turner (1981). The most notable differences between these analyses were the significantly greater foliar biomass and relative mass of N caused by the N limitations of the WA stands. All other nutrient masses were comparable based on stands with similar biomass (Turner, 1981). Plant derived masses of Ca, Mg, and K are comparable to those of 50 year old Douglas-fir stands in the WA Cascade foothills, though Mg and K masses were 47% and 36% greater respectively at the CR site (Homann et al., 1992).

3.6.1.1. Treatment effects

Calcium is the only element that displayed treatment differences without respect to site and species. All other nutrients with notable treatment effects varied either by site or by species or both. Mn, N, and K all displayed significant species x treatment effects. All other nutrients that were affected by treatment showed different responses to treatment based either on site (Cu, P), species (B, Cu, P, Zn), or site and species (C, Mg, S). Cu and N all displayed a marginally significant Site x spp x trt interaction (P<0.1). This means that general trends about treatment effects can only be made for Ca. With very few exceptions, all crop tree tissues (foliage, branches, bark, and wood) had significantly greater masses with VM treatment for all species and nutrients. This is due to significant treatment differences in biomass for these tissues. Midstory tissues (midstory foliage and midstory wood) only showed significant treatment differences for WRC, with Control plots having higher nutrient mass. Understory nutrient masses generally only had significant treatment differences for DF, with Control plots having greater nutrient mass. Forest floor nutrient masses displayed very few treatment effects. The balance of these treatment effects on different tissues governed the responses of the total plant derived nutrient masses to treatment.

WRC plots responded very differently to the control treatment based on site. Differences in stand development were the driving factors behind the numerous site x species x treatment effects were for plant derived nutrient masses. At both sites, there was significant crop tree mortality in the absence of vegetation control, though it was more pronounced at the CF site. At the CR site, which experiences higher rainfall and shorter summer drought, there was significant recruitment of midstory species with an average basal area of 29.3 m² ha⁻¹ in the Control plots (not including crop trees). At the CF site, there was little midstory development, only 2.7 m² ha⁻¹ in the Control plots (Table 3.1). This may be due to differences in rainfall and summer drought, but may also be attributable to previous land use practices. The CF site in on reforested agricultural land and may not have as robust of a seed source or resprouting source for native hardwoods. At the CR site, Control plots developed more biomass due to the rapid accumulation of early seral hardwoods such as cherry and red alder, which were more productive than the shade tolerant western redcedar trees. At the CF site, the lack of midstory growth in Control plots led to a lower biomass accumulation than VM plots. Generally, aboveground nutrients followed the same trend, with Control plots having more plant derived nutrients at the CR site and VM plot having more at the CF site.

If the CR WRC data is excluded from the analysis, several nutrients display a constant treatment trend. C, Cu, P, and B all tend to have greater plant derived masses in VM plots (with the exception of WRC plots at the CR site). This suggests that for these four elements, the direction of treatment effects depends largely on the development of midstory in the absence of VM.

Treatment effects of Ca were not altered by this difference in midstory development, and the WRC VM plots at the CR site had greater mass than did the Control plots. This is partially due to the fact that WRC tends to sequester more Ca and generally has higher tissue concentrations than did the midstory species (Chapter 2, Table 2.2 and Appendix Table S.2.1). The VM plots had higher crop tree survival and growth, and averaged 3.5 times more aboveground crop tree biomass. This combined with the elevated tissue concentrations, overwhelmed the effect of the midstory.

3.6.1.2. Site effects

Site effects on plant derived nutrients were driven by differences in plant derived biomass between sites in some circumstances, but were also driven by differences in tissue concentrations between sites, such as with Mn. DF and WRC stands growing at the CR site tended to have greater plant derived biomass, which generally led to increased nutrient mass if there were no notable site-based concentration differences (with the exception of K, Ca, and Cu). B, Fe, and Mn had higher plant nutrient concentrations for various tissues of DF and WRC at the CF site. Due to this, B and Fe did not have significant Site effects. Mn, however, had a significant Site effect. The concentration differences between sites were so large, that the CF site had higher plant derived Mn mass.

3.6.1.3. Species effects

Ca was the only nutrient that displayed species effects on plant derived nutrient content without any interactions. WRC and GF had greater plant derived Ca when compared to other species with at the same site under the same treatment (see Appendix Figure S.3.3). This is in agreements with studies in the inner mountain west that show GF to have more aboveground Ca content than DF (Parent and Coleman, 2016). The finding that WRC has high nutrient content compared to other species is unsurprising given that high Ca tissue concentrations are well documented and the species has been referred to as a 'calciphile' (Gessel et al., 1951; Krajina, 1969; Radwan and Harrington, 1986)

3.6.1.4. Nutrient distribution between tissues

Fe has a notably different nutrient budget than some of the others presented. The nutrient content is concentrated primarily in the fine roots and forest floor, whereas many other nutrients are preferentially allocated in leaves and other aboveground tissues. Iron is a unique nutrient in many ways. It is required in high amounts in meristems of actively growing tissue (Marschner and Marschner, 2012; Mengel, 1994). It tends to accumulate in root apoplasts and bind to hemicellulose, often in concentrations orders of magnitude higher than in the leaves (Marschner and Marschner, 2012; Mengel, 1994; Strasser et al., 1999). These stores may function to help prevent against Fe deficiency if plants are able to effectively mobilize this nutrient (Zhu et al., 2016). Notably, when Fe arrives at its destination in aboveground tissue, it is often permanently immobilized, and is unable to be retranslocated from older to newer tissue. This means that the
concentration of iron in litter is likely to be higher than in living tissue. For a similar reason, it is less likely than more mobile nutrients to leach from litter. This may explain why the forest floor is enriched with iron compared to other tissues, though one study suggests that these inputs are too small and high forest floor concentrations are due to bioturbation of Fe from mineral soil into the litter layer (Li et al., 2017).

3.6.2. Soil nutrient content

Soil nutrient content for N and K in the top 0.6 m are similar to the Matlock, WA site in the LTSP. Soil P content however, was around half of that site, much closer to the "lower quality" site near Mollala, OR (DeBruler et al., 2019). The soil contents of N, P, and K in the top 1 m of soil at the CR site, agree well with data from another site in the Oregon Coast Range (Cromack et al., 1999). Soil cation masses were between 87% and 54% lower than those reported under a DF stand in the Washington Cascade Foothills. (Homann et al., 1992). The largest difference was between Ca soil mass reported by Homann et al. (1992) and the Ca soil mass at the CR site. This is to be expected somewhat, as high N content in the Oregon Coast range has been linked with Ca leaching (Compton et al., 2003; Homann et al., 1992; Hynicka et al., 2016).

There were relatively few effects on soil nutrient content. Site effects on soil nutrient content show similar patterns to soil nutrient concentration, as soil bulk densities (and thus mass of soil layers) were similar between sites. Mg was the only element that displayed marginally significant treatment effect across all species. Cu displayed a significant Site x Species x Trt interaction due to the large difference between soil content in treatments for DF at the CF site. Mg and Na displayed significant differences between species. Mg generally had the lowest concentrations under WH. This may indicate that there is greater uptake or leaching of this nutrient under this species. It may also indicate that there is a blocking effect on soil Mg concentrations or that the sampling regime was too simple to characterize soil heterogeneity (though it should be noted that block was included as a random factor in the mixed model). There was a significant Site x Spp x Trt effect for soil C in the 0.4 m – 0.6 m depth increment (Appendix Table S.3.3) with C masses tending to be larger in Control plots. This is contrary to the findings at the Fall River LTSP site which found higher deep soil carbon with VM (Knight et al. 2014). Notably, the reduced soil N concentration in VM plot of WRC at the CR site resulted in an overall decrease in total soil N mass. This may indicate the potential for VM applied to a

slow growing species, such as WRC, to reduce ecosystem retention of N. As N is a common limiting nutrient in these forests, this has the potential to reduce growth of current and future stands (Mainwaring et al., 2014).

Generally, the lack of treatment differences in soil nutrient masses can be attributed to the fact that total soil nutrient reserves were one to three orders of magnitude greater than plant derived pools (with the exception of C and N). Any treatment differences in these nutrients (such as Cu or Mg) thus can likely not be explained entirely by differences in plant uptake, but may instead reflect soil heterogeneity, differences in leaching, or sampling/analysis error. The average standard error for Mg soil measurements for a given site, species, treatment, and depth was 570 kg ha⁻¹ and the maximum plant derived mass was ~120 kg ha⁻¹.

3.7. Management Implications

Sustained vegetation management regimes tend to increase nutrient mass stored in crop tree tissues while having little effect on concentration. When other ecosystem components are included, the differences in plant derived nutrient mass between VM and Control plots become much less pronounced, and in some cases, Control plots even have higher nutrient masses such as for WRC at the CR site.

Total soil nutrient reserves are 10 to 1000 times greater than the amount stored in plant tissue (excluding C, which is not taken up via plant roots). Given that standard harvesting practices only remove stemwood and bark, the proportion of nutrient capital removed by harvesting is relatively low compared to total ecosystem nutrient storage. WRC at the CR site, however, showed reduced total soil N mass under VM, indicating the potential for sustained vegetation control to reduce ecosystem N retention when this treatment is applied to a slow growing species, such as WRC. Nevertheless, it should be noted that this study quantified total soil nutrient pools and not exchangeable/plant accessible nutrient pools.

3.8. References

Augusto, L., Ranger, J., Ponette, Q., Rapp, M., 2003. Relationships between forest tree species, stand production and stand nutrient amount. Ann. For. Sci. 57, 313–324. https://doi.org/10.1051/forest:2000122

- Brunner, I., Brodbeck, S., Walthert, L., 2002. Fine root chemistry, starch concentration, and "vitality" of subalpine conifer forests in relation to soil pH. For. Ecol. Manage. 165, 75– 84. https://doi.org/10.1016/S0378-1127(01)00633-8
- Busing, R., Clebsch, E.E., White, P., 1993. Biomass and Production of Southern Appalachian Cove Forests Reexamined. Can. J. For. Res. 23, 760–765.
- Callesen, I., Harrison, R., Stupak, I., Hatten, J., Raulund-Rasmussen, K., Boyle, J., Clarke, N.,
 Zabowski, D., 2016. Carbon storage and nutrient mobilization from soil minerals by deep roots and rhizospheres. For. Ecol. Manage. 359, 322–331. https://doi.org/10.1016/j.foreco.2015.08.019
- Chang, S.X., Preston, C.M., McCullogh, K., Weetman, G.F., Barker, J., 1996. Effect of understory competition on distribution and recovery of 15N applied to a western red cedar–western hemlock clear-cut site. Can. J. For. Res. 26, 313–321.
- Cole, D.W., Gessel, S.P., 1992. Fundamentals of Tree Nutrition, in: Chappell, H.N., Weetman, G.F., Miller, R.E. (Eds.), Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests. College of Forest Resorces, University of Washington, Seattle, pp. 7–16.
- Compton, J.E., Church, M.R., Larned, S.T., Hogsett, W.E., 2003. Nitrogen Export from Forested Watersheds in the Oregon Coast Range: The Role of N2-fixing Red Alder. Ecosystems 6, 773–785. https://doi.org/10.1007/s10021-002-0207-4
- Compton, J.E., Cole, D.W., 1998. Phosphorus cycling and soil P fractions in Douglas-fir and red alder stands. For. Ecol. Manage. 110, 101–112. https://doi.org/10.1016/S0378-1127(98)00278-3
- Cromack, K., Miller, R.E., Anderson, H.W., Helgerson, O.T., Smith, R.B., 1999. Soil Carbon and Nutrients in a Coastal Oregon Douglas-Fir Plantation with Red Alder. Soil Sci. Soc. Am. J. 63, 232–239. https://doi.org/10.2136/sssaj1999.03615995006300010034x

- Cross, A., Perakis, S.S., 2011. Tree species and soil nutrient profiles in old-growth forests of the Oregon Coast Range. Can. J. For. Res. 41, 195–210. https://doi.org/10.1139/x10-199
- DeBruler, D.G., Schoenholtz, S.H., Slesak, R.A., Strahm, B.D., Harrington, T.B., 2019. Soil phosphorus fractions vary with harvest intensity and vegetation control at two contrasting Douglas-fir sites in the Pacific northwest. Geoderma 350, 73–83. https://doi.org/10.1016/j.geoderma.2019.04.038
- Devine, W.D., Harrington, T.B., Terry, T.A., Harrison, R.B., Slesak, R.A., Peter, D.H., Harrington, C.A., Shilling, C.J., Schoenholtz, S.H., 2011. Five-year vegetation control effects on aboveground biomass and nitrogen content and allocation in Douglas-fir plantations on three contrasting sites. For. Ecol. Manage. 262, 2187–2198. https://doi.org/10.1016/j.foreco.2011.08.010
- Entry, J.A., Emmingham, W.H., 1998. Influence of forest age on forms of carbon in Douglas-fir soils in the Oregon Coast Range. Can. J. For. Res. 28, 390–395. https://doi.org/10.1139/x98-002
- Flamenco, H.N., Gonzalez-Benecke, C.A., Wightman, M.G., 2019. Long-term effects of vegetation management on biomass stock of four coniferous species in the Pacific Northwest United States. For. Ecol. Manage. 432, 276–285. https://doi.org/10.1016/j.foreco.2018.09.033
- Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The development of pine plantation silviculture in the Southern United States. J. For. 105, 337–347. https://doi.org/10.1093/jof/105.7.337
- Gebhardt, T., Häberle, K.H., Matyssek, R., Schulz, C., Ammer, C., 2014. The more, the better? Water relations of Norway spruce stands after progressive thinning. Agric. For. Meteorol. 197, 235–243. https://doi.org/10.1016/j.agrformet.2014.05.013
- Gessel, S.P., Walker, R.B., Haddock, P.G., 1951. Preliminary Report on Mineral Deficiencies in Douglas-fir and Western Red Cedar. Soil Sci. Soc. Am. J. 15, 364–369.

- Gonzalez-Benecke, C.A., Flamenco, H.N., Wightman, M.G., 2018. Effect of vegetation management and site conditions on volume, biomass and leaf area allometry of four coniferous species in the Pacific Northwest United States. Forests 9. https://doi.org/10.3390/f9090581
- Hoepting, M.K., Wagner, R.G., McLaughlin, J., Pitt, D.G., 2011. Timing and duration of herbaceous vegetation control in northern conifer plantations: 15th-year tree growth and soil nutrient effects. For. Chron. 87, 398–413. https://doi.org/10.5558/tfc2011-030
- Homann, P.S., Miegroet, H. Van, Cole, D.W., Wolfe, G. V, 1992. Cation Distribution, Cycling , and Removal from Mineral Soil in Douglas-Fir and Red Alder Forests 16, 121–150. https://doi.org/10.1007/BF00002828
- Hynicka, J.D., Pett-Ridge, J.C., Perakis, S.S., 2016. Nitrogen enrichment regulates calcium sources in forests. Glob. Chang. Biol. 22, 4067–4079. https://doi.org/10.1111/gcb.13335
- J.A. Kendall Snell, S.N.L., 1983. Predicting Crown Weight and Bole Volume of Five Western Hardwoods.
- Knight, E., Footen, P., Harrison, R., Terry, T., Holub, S., 2014. Competing Vegetation Effects on Soil Carbon and Nitrogen in a Douglas-fir Plantation. Soil Sci. Soc. Am. J. 78, S146–S151. https://doi.org/10.2136/sssaj2013.07.0320nafsc
- Krajina, V.J., 1969. Ecology of forest trees in British Columbia. Vancouver : Dept. of Botany, University of British Columbia, Vancouver.
- Li, J., Richter, D., Mendoza, A., Heine, P., 2017. Four-Decade Responses of Soil Trace Elements to an Aggrading Old-Field Forest: B, Mn, Zn, Cu, and Fe Author (s): Jianwei Li, Daniel deB. Richter, Arlene Mendoza and Paul Heine Published by: Wiley on behalf of the Ecological Society of America S 89, 2911–2923.
- Marschner, H., Marschner, P., 2012. Marschner's mineral nutrition of higher plants.

- Mengel, K., 1994. Iron availability in plant tissues-iron chlorosis on calcareous soils. Plant Soil 165, 275–283. https://doi.org/10.1007/BF00008070
- Miller, J.H., Allen, H.L., Zutter, B.R., Zedaker, S.M., Newbold, R.A., 2006. Soil and pine foliage nutrient responses 15 years after competing-vegetation control and their correlation with growth for 13 loblolly pine plantations in the southern United States 1. Can. J. For. Res. 36, 2412–2425. https://doi.org/10.1139/x06-164
- Miller, R.O., Gavlak, R., Horneck, D., 2013. Soil, Plant and Water Reference Methods for the Western Region, 4th ed. Western Rural Development Center, Corvallis, OR.
- Parent, D.R., Coleman, M.D., 2016. Grand fir nutrient management in the Inland Northwestern USA. Forests 7, 1–15. https://doi.org/10.3390/f7110261
- Petersen, K.S., Ares, A., Terry, T.A., Harrison, R.B., 2008. Vegetation competition effects on aboveground biomass and macronutrients, leaf area, and crown structure in 5-year old Douglas-fir. New For. 35, 299–311. https://doi.org/10.1007/s11056-007-9078-z
- Piatek, K.B., Lee Allen, H., 2001. Are forest floors in mid-rotation stands of loblolly pine (pinus taeda) a sink for nitrogen and phosphorus? Can. J. For. Res. 31, 1164–1174. https://doi.org/10.1139/x01-049
- Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. 22, 1193–1200. https://doi.org/10.1093/treephys/22.15-16.1193
- Radwan, M.A., Harrington, C.A., 1986. Foliar chemical concentrations, growth, and site productivity relations in western red cedar. Can. J. For. Res. 16, 1069–1075. https://doi.org/10.1139/x86-185
- Slesak, R.A., Harrington, T.B., Peter, D.H., DeBruler, D.G., Schoenholtz, S.H., Strahm, B.D., 2016. Effects of intensive management practices on 10-year Douglas-fir growth, soil nutrient pools, and vegetation communities in the Pacific Northwest, USA. For. Ecol. Manage. 365, 22–33. https://doi.org/10.1016/j.foreco.2016.01.019

- Slesak, R.A., Harrington, T.B., Schoenholtz, S.H., 2010. Soil and Douglas-fir (Pseudotsuga menziesii) foliar nitrogen responses to variable logging-debris retention and competing vegetation control in the Pacific Northwest. Can. J. For. Res. 40, 254–264. https://doi.org/10.1139/X09-188
- Slesak, R.A., Schoenholtz, S.H., Harrington, T.B., 2011. Soil carbon and nutrient pools in Douglas-fir plantations 5years after manipulating biomass and competing vegetation in the Pacific Northwest. For. Ecol. Manage. 262, 1722–1728. https://doi.org/10.1016/j.foreco.2011.07.021
- Sollins, P., Grier, C.C., McCorison, F.M., Cromack, K., Fogel, R., Fredriksen, R.L., 1980. The Internal Element Cycles of an Old-Growth Douglas-Fir Ecosystem in Western Oregon. Ecol. Monogr. 50, 261–285. https://doi.org/10.2307/2937252
- Strasser, O., Köhl, K., Römheld, V., 1999. Overestimation of apoplastic Fe in roots of soil grown plants. Plant Soil 210, 179–189. https://doi.org/10.1023/A:1004650506592
- Turner, J., 1981. Nutrient cycling in an age sequence of western Washington douglas-fir stands. Ann. Bot. 48, 159–170. https://doi.org/10.1093/oxfordjournals.aob.a086109
- Turner, J., Long, J.N., 1975. Accumulation of Organic Matter in a Series of Douglas-fir Stands. Can. J. For. Res. 5, 681–690.
- Vadeboncoeur, M.A., Hamburg, S.P., Yanai, R.D., Blum, J.D., 2014. Rates of sustainable forest harvest depend on rotation length and weathering of soil minerals. For. Ecol. Manage. 318, 194–205. https://doi.org/10.1016/j.foreco.2014.01.012
- Vogel, J.G., Suau, L.J., Martin, T.A., Jokela, E.J., 2011. Long-term effects of weed control and fertilization on the carbon and nitrogen pools of a slash and loblolly pine forest in northcentral Florida. Can. J. For. Res. 41, 552–567. https://doi.org/10.1139/X10-234
- Vogt, K.A., Dahlgren, R., Ugolini, F., Zabowski, D., Moore, E.E., Zasoski, R., 1987. Aluminum, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above- and belowground biomass. II. Pools and

circulation in a subalpine Abies amabilis stand. Biogeochemistry 4, 295–311. https://doi.org/10.1007/BF02187372

Zhu, X.F., Wang, B., Song, W.F., Zheng, S.J., Shen, R.F., 2016. Putrescine alleviates iron deficiency via NO-dependent reutilization of root cell-wall Fe in Arabidopsis Plant Physiol. 170, 558–567. https://doi.org/10.1104/pp.15.01617

4 Nutrient Ratios, Foliar Vector Analysis, and Nutrient Use Efficiency of Four Western Conifers Stands Growing Under Contrasting Competing Vegetation Control Treatments

4.1 Introduction

Plants require nutrients in certain amounts in order to satisfy their physiological needs. The proportion of the concentration between different nutrients (nutrient ratios) in different components of the tree, specifically foliar ratios, are useful to investigate the nutrient status of a stand. These ratios are considered a better way to diagnose nutrient deficiencies, as they may be more reliable than nutrient concentration and less susceptible to systematic error. Additionally, they are used as guidelines for predicting responses to fertilizer application. For example, foliage with a high N:S ratio indicates that those trees are not equipped with enough sulfur to synthesize more proteins, as two key amino acids contain S. This means that addition of N fertilizer, which helps plant synthesize more foliar proteins and expand photosynthetic capacity, may not be very effective, since protein synthesis may be limited by S.

Nutrient use efficiency (NUE) is a concept borrowed by forestry from agriculture. NUE generally refers to a ratio of some measure of primary productivity on a basis of nutrients taken up by the stand (Chapin, 1980). Since nutrient use and recycling in forests is complicated and measuring total plant nutrient uptake is more difficult in forests than in annual crops, different researchers have defined different ways to calculate this efficiency. Vitousek (1982), for example, suggests calculating NUE in terms of litterfall production per mass nutrient shed in litterfall- as nutrients lost in litterfall must be replaced via nutrient uptake. Other publications measure NUE as some measurement of growth (net primary productivity (NPP), aboveground net primary productivity (ANPP), biomass increment etc., respiration) (Binkley et al., 1992; Bridgham et al., 2016; Chapin, 1980). In the absence of annual uptake data and annual productivity data, we will be exploring a proxy for NUE that more closely resembles the nutrient efficiency ratio in crop science (Agüero and Kirschbaum, 2013). This will be calculated by dividing the plant derived carbon or the carbon in crop tree boles by the total plant derived masses of various nutrients. While this way of investigating NUE may not be as interesting to ecosystem ecologists, we think it will be useful for managers hoping to maximize carbon storage or timber yield while using a minimal amount of site nutrients.

Vector analysis provides an alternative way of judging the effects of silvicultural treatments on nutrient status of plants as well as an alternative way to understand nutrient deficiencies outside of critical concentrations or ratios (Haase and Rose, 1995). This technique involves comparison of nutrient concentration, nutrient content, as well as some growth measurement between two or more stands. It can be used to detect nutrient imbalances and help diagnose nutrient limitations (Timmer and Armstrong, 1987). As a technique it is useful in that it does not require previous determination of critical nutrient values, as the effects of silvicultural treatment are seen comparatively. Additionally, tree species are able to reduce growth rates in order to maintain sufficient foliar nutrient levels, which may make deficiencies hard to detect in some cases (Haase and Rose, 1995).

4.2 <u>Literature Review</u>

4.2.1 Nutrient Ratios in Plant Tissues

Plants distribute nutrients throughout their tissues in order to satisfy their physiological needs. These nutrients are often divided into two categories, based on the relative requirements of plants. The following are considered macronutrients and are required in larger amounts: carbon (C), nitrogen (N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S). The following are considered micronutrients and are required in much smaller amounts: boron (B), copper (Cu), iron (Fe), manganese (Mn), sodium (Na), and zinc (Zn) (see Chapter 1 for more details).

The Redfield ratio is an important ecological concept concerning the behavior of plankton growth and nutrient use. On a global scale, all plankton communities conform quite strictly to a specific C:N:P ratio of 106:16:1 in their biomass (Redfield, 1934). This concept was foundational for developing an understanding of algal physiology and nutrient limitation in these communities of primary producers. Terrestrial plants, however, behave somewhat differently, specifically due to their higher affinity for carbon than their single celled marine counterparts. This extra carbon is structural elements needed to support standing plant tissue, which algae have no need for. From a whole organism standpoint, there is no Redfield-like ratio for woody terrestrial plants. There is, however, some consistency in foliar, litter, and fine root nutrient ratios across terrestrial forested biomes (Jackson et al., 1997; McGroddy et al., 2004). These ratios-foliage (1212:28:1), litter (3007:45:1), and fine roots (450:11:1) indicate a higher affinity for C

than in algal systems as well as a slightly higher affinity for N over P in foliage and litter. When C is not included in the calculations, and ratios are taken with respect to N, all terrestrial plant foliage has similar optimal foliar ratios due to similar physiological needs (Binkley, 1986; Knecht and Göransson, 2004).

As with nutrient concentrations and content, foliage is the tissue type most studied for trends in nutrient ratios (though fine roots and litter have also received some study). This is because, like nutrient concentrations, foliar nutrient ratios have been shown to correlate to measures of primary productivity as well as nutrient status of a stand. Certain critical concentrations, particularly sulfur, are derived from optimal foliar nutrient ratios as opposed to from empirical fertilization studies (Garrison et al., 2000; Moore et al., 2004; Turner et al., 1979, 1977).

The N:S ratio is relatively constant across many herbaceous crop species (Dijkshoorn and van Wijk, 1967). This is because most of the S in plant foliage is used in proteins as the amino acids cysteine and methionine. When foliage has sufficient S to form the protein needed, excess is stored in inorganic form as sulfate. If foliar levels are inadequate, little will be stored as sulfate, and the N:S ratio will higher. Sufficient N:S for conifer species varies somewhat, but reported values for Douglas-fir, radiata pine, and lodgepole pine are around 14.7, and any individuals with foliar ratios below this number are considered S sufficient (Blake et al., 1990; Brockley, 2001a; Turner et al., 1979, 1977). This ratio is in agreement with many studies of legumes and gramineous plants (Dijkshoorn and van Wijk, 1967). This value is generally used to calculate sufficiency levels for most conifers, though it should be noted that some conifer species, such as radiata pine and Norway spruce, are sufficient at higher ratios (Kelly and Lambert, 1972; Linder, 1995).

Optimum nutrient requirements have been studied for a number of species using controlled seedling experiments by Swedish scientists in the 1950s through the 1980s. In these experiments, seedings were grown in a controlled environment and supplied with nutrients in certain ratios. The growth and foliar nutrition were measured so that optimal foliar concentrations could be derived (Ingestad, 1979, 1962; van den Dreissche, 1974). While these ratios vary between plant families and species, generalized optimal and critical ratios for conifer macronutrients (expressed as a fraction on N) have been calculated and are presented in Table 4.1. Similar to critical concentrations, plants whose foliar nutrition drops below these ratios will have their growth limited by the non-nitrogen nutrient (assuming that N foliar levels are sufficient). Generalized optimal micronutrient ratios are: Fe/N = 0.7% Mn/N = 0.4% B/N 0.2% Cu/N 0.03% Zn/N 0.03% Na/N 0.003%, though it should be noted that these are expressed as a percentage and have been scaled by 100 (Ingestad, 1979).

Critical	Optimal
50%	65%
8%	15%
5%	10%
5%	10%
	Critical 50% 8% 5% 5%

Table 4.1. Critical and optimal macronutrient ratios for conifers (Ingestad, 1979; van den Dreissche, 1974). Table adapted from Garrison and Moor<u>e (1998). All ratios are expressed as a percentage.</u>

4.2.2 Management Effects on Nutrient Ratios

Management effect on foliar nutrient ratios are generally studied with respect to fertilizer application. Fertilizer application of N tends to enrich foliar N concentrations, increasing N:nutrient ratios. In certain circumstances, this can cause other nutrients to become limiting, notably S. Guidelines for N fertilizer application indicate that stands with foliar N:S ratios of 12-13 or greater will not respond well to application, as N enrichment in the leaves will elevate the ratio above the 14.7 threshold causing a weak fertilizer response (Brockley, 2001b, 2001a).

4.2.3 Nutrient Use Efficiency

There are many ways to define NUE. Generally it refers to the ratio of annual NPP to annual nutrient uptake (Binkley et al., 2004; Chapin, 1980). A very influential paper in the field of production ecology has defined it as the mass of litterfall divided by the mass of nutrients lost in litterfall (Vitousek, 1982). In theory, this makes sense because nutrients lost in litter must be replaced via uptake and assuming that litterfall is well correlated with ANPP. The definition used by Vitousek (1982) has received much attention, though it is flawed. One problem is that there is autocorrelation between the two parts of the ratio, (Bridgham et al., 2016; Knops et al., 1997). Additionally, it assumes that litterfall mass is a good proxy for ANPP, when in reality, as production increases, litterfall represents a smaller and smaller fraction of ANPP (Binkley et al., 2004).

In this study, since no data for NPP or annual uptake are available, we will investigate a proxy for NUE that, while potentially less interesting to production ecologists, will be of interest to managers interested in optimizing timber yield or carbon storage in plant matter while minimizing site nutrient use. We will calculate this efficiency by taking the ratio between either all plant derived C (or the amount of carbon stored in crop tree stems) and the total plant derived mass of other nutrients. Total plant derived carbon is not an exact measurement of stand productivity. Total plant derived nutrients are also not an exact measurement of annual plant uptake or even total plant uptake, as plants lose nutrients to above and belowground litter, canopy throughfall, and stemflow. However, if we assume that nutrients lost to litterfall are either made available again to plants or remain in the litter layer, then this measure does approximate the amount of nutrients removed from soil pools over the life of the stand. While it may not be a traditional measurement of NUE, we think these ratios are useful to judge the amount of nutrients required by a system to produce a given amount of biomass.

When the idea of NUE originated, it was theorized that plants growing on nutrient poor sites would be more efficient with their nutrients or that plants adapted to low nutrient environments would have higher NUE. Research since then has not proven neither of these to be true. Plants adapted to infertile environments, when grown alongside plants adapted to more fertile environments tend to grow slower and have higher tissue nutrient concentrations, indicating lower NUE (Chapin, 1980). A meta-analysis of studies of the same species growing across a gradient of site fertility show that moderate fertility sites and high fertility sites have higher NUE (if there is any trend at all) (Knops et al., 1997).

Some studies have been conducted on the NUE of mixed species stands. A comparison of adjacent Douglas-fir and Douglas-fir/red alder stands showed that the mixed species stands had lower NUE for all nutrients measured, largely since the red alder trees were less efficient (Binkley et al., 1992). A meta-analysis comparing planted monocultures and planted mixed species plantations found that NUE increased in 65% of the cases, but that NUE decreased more than 10% in more than 40% of the studies (Richards et al., 2010). Since these mixed species stands were planned and mixtures were intentionally chosen, we can assume that spurious mixtures such as those caused by lack of vegetation management practices will be more likely to decrease NUE.

4.2.4 Vector Analysis

Vector analysis was pioneered in the 1960s but later gained traction in the 1990s largely due to work done by V. R. Timmer who applied the technique to many different situations (Haase and Rose, 1995). The analysis involves comparison of two or more stands (typically before and after some treatment or suite of treatments) and is accomplished by the construction and interpretation of a vector diagram (Haase and Rose, 1995). It has been used to diagnose nutrient deficiencies in fertilizer studies (Timmer and Stone, 1978), test effects of drought stress on seedlings (Timmer and Miller, 1991), determine shifts in C and N partitioning to shoots and roots (Timmer and Miller 1991), and investigate silvicultural effects on non-nutrient compounds like foliar terpene levels (Clancy et al. 1993).

This vector diagram plots the nutrient concentration vs. nutrient content of dried plant tissue of the various treatments. It may be the concentration and content of all foliage, a set number of needles, the entire stem, roots, or some combination (Haase and Rose, 1995). The choice depends on what the researcher expects to be a predictor of future growth. For conifer species with determinant growth, weight of a set number of needles is appropriate (Haase and Rose, 1995; Timmer and Stone, 1978). For the purpose of this paper, we will use total foliage mass as the amount of foliage has been proven to relate to stand productivity (Gholz, 1982; Waring, 1983). This data is typically normalized to some control or reference condition, by dividing the concentration and content of all the nutrients of each treatment by that of the reference stand and multiplying by 100. This allows the researcher to easily plot multiple nutrients on the same scale even if their contents and concentrations are very different. Also typically plotted, are several lines through the origin representing relative dry weight. Relative dry weight of 100% will be a line passing from the origin with a slope of 1, that will intersect the reference point plotted at (100,100) and relative dry weight of 80% and 120% will be a similar line though the origin but with a slopes of 0.8 and 1.2, respectively. It should be noted that when multiple nutrients are plotted for each treatment, they will all fall along a single line through the origin, as content and concentration are always related by the same ratio, which is the dry mass of the tissue.

An example diagram shows the six possible scenarios of a vector diagram, Figure 4.1. Scenario A involves an increase in nutrient content and dry weight, but a decrease in nutrient content. This scenario is referred to as a dilution, where the extra growth in this scenario was not compensated by a similar increase in nutrient content, and indicates that the nutrient was not likely limiting growth. Scenario B is similar to Scenario A but the relative nutrient concentration remained the same, indicating the supply is likely sufficient and the nutrient was not likely limiting. Scenario C indicates that the nutrient content and concentration both increased as well as the dry mass. This indicates that growth was improved when the concentration of the given nutrient was increased, suggesting that it may have been limiting growth in the reference condition. Scenario D involves an increase in content and concentration that did not result in an increase in tissue mass. This indicates luxury consumption that was above sufficiency levels but does not indicate any sort of toxicity. Scenario E indicates that the nutrient may be taken up at toxic levels (in the absence of some other growth constraint). Scenario F indicates some antagonistic effect that reduced the ability of the plant to uptake that particular nutrient (Timmer and Stone, 1978). Generally, the longest vector (largest shift from the control) represents the most responsive nutrient (Haase and Rose, 1995).



Figure 4.1. Example vector analysis diagram plotting the standardized reference point and 6 possible outcomes of various silvicultural treatments labeled A-F. Adapted from Haas and Rose (1995) and Timmer and Stone (1978).

4.3 **Questions and Hypotheses**

The objective of this study was to determine long term effects of VM treatment on foliar and total plant derived nutrient ratios, NUE, as well as foliar nutrient content and concentration on four conifer species growing in two sites in Central Oregon. We will do this by constructing nutrient ratios and determining NUE from plant derived nutrient masses as well as by constructing vector diagrams showing how foliar nutrients responded to VM treatment on each species and site.

We hypothesize that at age 18 there will be few differences in nutrient ratios of total crop tree tissues and total plant tissues between treated and untreated plots within each species, but that there will be significant differences between species and sites driven by different nutrient availabilities between sites and nutrient requirements of each plant. We also hypothesize that VM treatment (sustained vegetation control during first five years after planting) will increase the NUE of the ecosystem, both in terms of producing plant derived carbon and in terms of producing crop tree stemwood. Lastly, we hypothesize that shifts on a vector diagram will share some similarities within a site or certain species, but that each species and each site will respond uniquely to the treatment.

4.4 <u>Methods</u>

4.4.1 Description of Sites

The Coastal Range (CR) site is located at 44.62°N, 123.57°W near Summit, OR approximately 40 km from the coast. The site was planted in year 2000 and experiences a mean annual temperature of 11.1°C and average annual rainfall of 1,707 mm. The soil at this site is fine and loamy (Flamenco et al. 2019). The CR site was planted with Douglas-fir (DF) and western hemlock (WH) (four replicates each), and grand fir (GF) and western redcedar (WRC) (three replicates each). Soils at the CR site are part of the Preacher-Bohannon complex which is derived from siltstone and sandstone (USGS). This soil complex is classified as an Andic Dystrudept, meaning that while it is not an Andosol, it has high aluminum and iron activity (Soil Survey Staff 2015). This site sits near the western edge of the Tyee formation, a sedimentary rock formation that composed largely of marine micaceous sandstone and siltstone.

The Cascade Foothills (CF) site is located at 44.48°N, 122.73°W near Sweet Home, OR and was planted in year 2001 with DF and WRC (four replicates each). The site has a mean annual temperature of 12.4°C and an average annual rainfall of 1,179 mm. The soil at this site is a silty clay loam (Flamenco et al. 2019). Soils at the CF site are from the Bellpine series which is derived from sedimentary rock (Soil Survey Staff 2015). Soils of this series are classified as Xeric Haplohumults, indicating an Ultisol with high organic matter content that experiences seasonal drought. These soils are well drained and characterized by a more xeric moisture regime from the CR site. The bedrock is a mixture of basalt, sedimentary rocks, and tuff. Similar to the CR site, these soils are derived from sedimentary bedrock, however tuff and mafic intrusions will lend different chemical characteristics to these soils. Mafic rocks tend to be higher in iron and magnesium than sandstone. This site was formerly agricultural land that was not sufficiently productive and was purchased by Cascade Timber Company.

4.4.2 Study Design

A randomized complete block design with eight VM treatments was implemented at each of the two sites. The eight different VM treatments consisted of spring release applications that differed in the number and timing of herbicide treatments applied during the first 5 years after planting. Similar to Flamenco et al. (2019), for this study we used only the control (Control; only pre-planting vegetation control) and the 5 consecutive years of spring release vegetation management treatment (VM). Plots were approximately 0.06 ha and were planted in 8 rows of 8 trees at a 3 x 3 m spacing, resulting in a planting density of 1100 trees per ha. All plots were planted with a single tree species. All DF plots received pre-commercial thinning at year 12 and thinning residues were left on site.

The ecosystem was divided into soil pools and plant derived pools. The plant derived pools were broken down into overstory (planted crop trees), midstory (hardwoods and natural conifer regeneration), understory (shrubs, grasses, forbs, ferns and moss) and forest floor (including coarse woody debris). The overstory was divided into foliage, live branches, stemwood, stembark, and fine roots. The midstory was broken down into foliage and bole (stemwood and stembark). The soil was divided into four layers (0-0.2 m, 0.2-0.4 m, 0.4-0.6 m, and 0.6-1 m).

4.4.3 Nutrient Ratios

Four foliage samples were collected per treatment (note that this does not mean one per plot, see Chapter 3 or Flamenco et al. 2019). Nutrient ratios for foliar nutrients were determined by dividing the concentration of one foliar nutrient by that of another taken from the same foliage sample. Four ratios were calculated for each treatment (one per sample) and then averaged across treatments and sites when applicable.

Nutrient ratios for total crop tree nutrients and total plant derived nutrients were calculated from the total nutrient masses of the appropriate pools in each plot. For crop tree nutrient ratios, the masses of crop tree foliage, branches, stembark, and stemwood were used. For total plant derived nutrient ratios, nutrient masses of all plant derived nutrient pools were used (all crop tree tissues, midstory foliage and stemwood, understory, forest floor, and fine roots). Ratios between total plant derived carbon and total plant derived nutrients for NUE

determination were calculated in a similar manner. Methods for determination of nutrient concentration and content can be found in Chapters 2 and 3 respectively.

4.4.4 Vector Analysis

Foliar nutrient content (calculated per plot in Chapter 3) was averaged by treatment. Foliar nutrient concentrations were taken from Chapter 2 (all concentrations were originally averaged per treatment from four foliage samples). Vector diagrams were constructed for each species by plotting the normalized foliar nutrient content as a function of the normalized foliar concentration for each nutrient. Within each site, concentrations and content for each nutrient of the VM plot was normalized to the Control plot so that content and concentration of Control were both equal to 100. For DF and WRC, each of the four conditions were normalized to the Control for that given site, so that the content and concentration for the Control at the CR and CF sites were equal to 100. Regressions for each condition were then plotted so that the relationship between concentration and content passed through the origin for each site and treatment.

4.4.5 Statistical Analysis

The Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC) was used for all statistical analysis. Analysis of variance, including Tukey multiple comparisons tests, was used to test the effects of site, species and treatments on all soil and plant derived pools (PROC MIXED, SAS Institute Inc. Cary, NC). A generalized linear model was used to determine the relationships between nutrient ratios and biomass increment (PROC GLM, SAS Institute Inc. Cary, NC). Models began with the full model using ratio, species, site and treatment, and all interactions to predict biomass increment. The least significant parameters were removed stepwise until all remaining parameters were significant at α =0.05 or until all parameters including ratio were removed. SigmaPlot version 14 (Systat Software, Inc. San Jose, CA) was used to create all figures.

4.5 <u>Results</u>

4.5.1 Nutrient Ratios

Foliar nutrient ratios for each species at each site are presented in Table 4.2. Ratios for each treatment are not shown as treatment only had an effect on two of the ratios, Ca:Mg and K:Ca (Table 4.3). Nutrient ratios were suboptimal for several species and ratios, and a few were below critical ratios derived for all conifers (Garrison and Moore, 1998; Ingestad, 1979). Only WH and DF at the CF site had P:N ratios at or above the optimal ratio of 0.16. K:N ratios were

below the optimal ratio of 0.65 for all species and sites, and DF, WH, and GF at the CR site were all below the critical ratio of 0.5. WRC at the CR site was the only species that had a S:N ratio above the optimal 14.7. All species at both sites were above the optimal N:Ca ratio of 0.1. DF at both sites were below the optimal N:Mg ratio of 0.1.

Table 4.2. Average foliar nutrient ratios for 18 year old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing in the Oregon Coast Range (CR) and Cascade Foothills (CF). Values presented are not scaled to percentages and are averaged across treatments. Standard errors for each measurement are shown in parentheses.

		C	CF			
Ratio	DF	WH	WRC	GF	DF	WRC
P:N	0.140 (0.016)	0.247 (0.024)	0.120 (0.011)	0.133 (0.009)	0.164 (0.010)	0.130 (0.009)
K:N	0.434 (0.044)	0.530 (0.034)	0.350 (0.053)	0.460 (0.041)	0.569 (0.043)	0.519 (0.066)
N:S	9.386 (0.363)	11.89 (1.95)	16.69 (2.39)	12.58 (1.68)	11.03 (0.24)	11.02 (1.28)
Ca:N	0.481 (0.072)	0.657 (0.089)	1.183 (0.109)	1.111 (0.119)	0.511 (0.031)	1.736 (0.247)
Mg:N	0.086 (0.009)	0.111 (0.009)	0.123 (0.012)	0.117 (0.009)	0.074 (0.005)	0.101 (0.008)
Mn:N	263.1 (49.0)	933.6 (177.6)	163.5 (18.2)	503.1 (62.6)	345.8 (15.3)	244.9 (47.3)
Cu:N	2.326 (0.201)	3.203 (0.420)	3.398 (0.286)	3.281 (0.267)	2.519 (0.151)	5.116 (0.857)
Zn:N	8.97 (1.04)	10.75 (0.78)	14.19 (1.44)	22.54 (2.57)	9.83 (1.13)	16.80 (1.41)
B:N	9.33 (1.11)	21.62 (2.21)	11.52 (1.35)	14.39 (2.09)	18.30 (1.26)	15.75 (1.51)
Na:N	161.9 (27.9)	125.3 (15.5)	112.1 (18.6)	64.2 (8.1)	67.1 (8.0)	89.0 (21.1)
Fe:N	36.42 (2.12)	52.35 (12.73)	52.02 (3.94)	66.97 (8.79)	49.28 (5.32)	131.31 (32.41)
Ca:Mg	5.511 (0.558)	6.241 (0.909)	10.32 (1.13)	10.04 (1.44)	7.055 (0.442)	17.41 (2.44)
Na:K	384.3 (65.3)	242.8 (32.3)	422.7 (146.2)	144.8 (22.9)	120.2 (12.7)	154.6 (37.7)
K:Ca	0.968 (0.097)	0.908 (0.125)	0.312 (0.055)	0.444 (0.051)	1.123 (0.079)	0.318 (0.046)

Both site and species had significant effects on several foliar nutrient ratios (Table 4.3). WH had the highest P:N (P<0.005) and K:N ratio (not significant) at the CR site (0.247 and 0.530 respectively) and DF had the highest P:N (P=0.05) and K:N ratio (not significant) at the CF site (0.164 and 0.569 respectively). DF had the lowest N:S ratio at the CR site (9.386) and the two species at the CF site had comparable ratios, around 11.0. WRC had the higher Ca:N ratio at both sites, 1.183 at the CR site and 1.736 at the CF site. WRC also had the highest N:Mg at both sites, 0.123 at the CR site and 0.101 at the CR site. Across sites, the CF site generally had higher ratios, including K:N, N:Mn, N:B, and Ca:Mg. Several other ratios tended to be higher but the differences were not statistically significant.

Table 4.3. Results of ANOVA test for foliar nutrient ratios of Douglas-fir, western hemlock, western redcedar and grand fir (Spp) stands growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range and the Cascade foothills of western Oregon (Site). Significant differences are highlighted in bold.

Ratio	Site	Spp	Trt	Site*Spp	Site*Trt	Spp*Trt	Site*Spp*Trt
P:N	0.191	0.001	0.707	0.600	0.510	0.678	0.208
K:N	0.024	0.129	0.953	0.715	0.200	0.064	0.420
Mg:N	0.107	0.126	0.082	0.771	0.046	0.730	0.672
Ca:N	0.082	<0.001	0.511	0.193	0.687	0.723	0.718
N:S	0.194	0.177	0.427	0.016	0.226	0.626	0.079
B:N	<0.001	0.002	0.946	0.108	0.467	0.987	0.323
Mn:N	0.050	<0.001	0.348	0.896	0.915	0.633	0.539
Fe:N	0.070	0.080	0.684	0.259	0.551	0.494	0.737
Cu:N	0.175	0.094	0.603	0.313	0.608	0.625	0.662
Na:N	0.022	0.014	0.437	0.050	0.385	0.396	0.234
Zn:N	0.203	0.002	0.641	0.601	0.247	0.297	0.249
Ca:Mg	0.010	0.037	0.042	0.077	0.439	0.420	0.996
Na:K	0.012	0.197	0.842	0.984	0.868	0.042	0.056
K:Ca	0.288	<0.001	0.022	0.355	0.350	0.021	0.852

Nutrient ratios for all plant derived biomass were more variable than foliar nutrient ratios (Table 4.4). Fe:N was the only ratio that was not significantly affected by site, species, treatment or any interactions. P:N, Mg:N, and Fe:N were the only ratios that did not vary significantly by site. K:N, B:N, and Fe:N were the only ratios that did not vary significantly by species or any interaction with species. K:N and Fe:N were the only ratios that did not vary significantly by site or any interaction with site.

Table 4.4. Results of ANOVA test for total plant derived nutrient ratios of Douglas-fir, western hemlock, western redcedar and grand fir (Spp) stands growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range and the Cascade foothills of western Oregon (Site). Significant differences are highlighted in bold.

moninging	d m oola.						
Ratio	Site	Spp	Trt	Site*Spp	Site*Trt	Spp*Trt	Site*Spp*Trt
P:N	0.231	<0.001	0.006	0.368	0.718	0.016	0.935
K:N	0.011	0.327	0.860	0.245	0.665	0.090	0.878
Mg:N	0.065	0.001	< 0.001	0.704	0.803	0.925	0.611
Ca:N	0.021	< 0.001	<0.001	0.449	0.357	<0.001	0.045
N:S	0.002	0.003	0.131	0.007	0.010	0.384	0.009
B:N	<0.001	0.629	0.024	0.400	0.364	0.086	0.556
Mn:N	<0.001	0.002	0.001	0.192	0.681	0.001	0.295
Fe:N	0.217	0.570	0.484	0.217	0.216	0.572	0.216
Cu:N	0.001	<0.001	0.001	0.018	0.100	0.001	0.480
Na:N	<0.001	0.074	0.968	0.002	0.854	0.429	0.029
Zn:N	0.022	0.001	0.016	0.192	0.789	0.141	0.095

Includes all crop tree tissues, midstory foliage and stemwood, understory, forest floor, and fine roots.

Several nutrient ratios significantly predicted total plant increment and one significantly predicted crop tree increment (Figures 4.2 and 4.3). Total plant derived nutrient ratios of P:N, Cu:N, and Zn:N had significant positive correlations with total plant derived biomass increment (P<0.05). All three of these models were significantly improved by the inclusion of a Ratio x Spp interaction, meaning that the slope of this relationship was significantly different between species (P<0.05). For two of the ratios, Cu:N and P:N, the slope of the relationship was the same for WH and DF (Figures 4.3a and 4.3b). For the Zn:N ratio, the slope for WH was not significantly different from the slope of the relationship for GF. Generally, GF had a higher slope for the relationship between total plant derived biomass increment and nutrient ratios compared to other species for the 18 and 19-year-old stands studied here.



Figure 4.2. Relationship between crop tree biomass increment (Mg ha-1 yr-1) and total crop tree derived nutrient ratios of Cu:N for 18 and 19-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Regressions derived from the linear model are plotted for each treatment.



Figure 4.3. Relationship between total plant derived biomass increment (Mg ha-1 yr-1) and total plant derived nutrient ratios of Zn:N (a), Cu:N (b), and P:N (c) for 18-year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Regressions derived from the linear model are plotted for each species, if significantly different.

Only the Cu:N ratio for crop tree derived nutrients was significantly correlated with crop tree growth (Figure 4.2). The parameter for the interaction between the Cu:N ratio and treatment was significant, meaning that the relationship between the nutrient ratio and crop tree growth was different under different treatments. Specifically, the slope of the relationship was higher for VM plots, meaning that they tended to produce more crop tree biomass at the same crop tree derived ratio when compared to the Control plots.Nutrient Use Efficiency

Using the carbon:nutrient ratio from nutrient mass data obtained for the plant derived tissues we can explore a proxy of NUE. Overall, VM plots had a lower carbon:nutrient ratio for N, K, Mg, S, and Cu (Table 4.5), implying that pure conifer stands, where understory and hardwoods were excluded, are able to amass comparably larger amount of carbon per unit nutrient stored in biomass. That response varied across species (Spp x Trt interaction) for N, Mg and S.

Table 4.5. Results of ANOVA test for differences between carbon:nutrient ratios of plant derived matter (crop trees, midstory, understory, and forest floor) for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site).

Nutrient	Site	Spp	Trt	Site*Spp	Site*Trt	Spp*Trt	Site*Spp*Trt
C:N	0.123	<0.001	<0.001	0.074	0.057	0.010	0.388
C:P	0.002	0.002	0.074	0.135	0.072	0.540	0.160
C:K	<0.001	0.038	0.001	0.009	0.121	0.140	0.348
C:Mg	0.745	<0.001	<0.001	0.209	0.075	0.033	0.324
C:Ca	0.001	<0.001	0.493	0.136	0.057	0.104	0.015
C:S	0.098	0.007	<0.001	0.879	0.477	<0.001	0.053
C:B	<0.001	0.033	0.165	0.146	0.009	0.518	0.056
C:Mn	0.001	0.632	0.141	0.026	0.074	0.601	0.074
C:Fe	0.024	0.013	0.360	0.035	0.124	0.240	0.060
C:Cu	<0.001	0.017	0.004	0.575	0.880	0.068	0.002
C:Na	0.020	0.212	0.138	0.001	0.035	0.932	0.033
C:Zn	<0.001	0.001	0.218	0.001	0.016	0.194	0.005

Ratios for C mass to N (C:N), P (C:P) and K (C:K) mass are displayed in Figure 4.4. There was a significant reduction in the amount of K per mass of C stored (higher K use efficiency) in WH and DF (P=0.008 and P<0.001 respectively). There was a significant reduction in C:P ratio for DF at the CF site (P=0.016). Lastly, there a significant reduction in C:N ratio for WH and WRC at the CF site (P=0.008 and P=0.027 respectively).



Figure 4.4. Plots of carbon:nutrient ratios for macronutrients. Ratios of plant derived carbon mass to plant derived nitrogen (C:N, upper panel), phosphorus (C:P, center panel) and potassium mass (C:K, lower panel) for 18 year-old Douglas-fir (DF), western hemlock(WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

Ratios for C mass to B (C:B) and Fe (C:Fe) mass are displayed in Figure 4.5. There was a significant reduction in the amount of B per mass of B stored (higher B use efficiency) for DF and WRC at the CF site (P=0.033 and P=0.045 respectively). There was no significant reduction in the amount of Fe used for any species (P>0.1).



Figure 4.5. Examples of carbon:nutrient ratios for micronutrients. Ratios of plant derived carbon mass to plant derived boron (C:B, upper panel) and Fe (C:Fe, lower panel) for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

4.5.2 Foliar Vector Analysis

The effects of vegetation management on foliage mass, foliar nutrient content, and foliar nutrient concentration of 18-year old DF, WH, GF and WRC stands are presented on vector diagrams in Figures 4.6, 4.7, 4.9 and 4.9, respectively. For all species and sites, the foliar concentrations and content of VM treatments were normalized to the Control treatment to 100.



Figure 4.6. Vector diagrams for Douglas-fir foliar concentrations and content of for macronutrients (top) and micronutrients (bottom) of 18-year-old stands at the CF site (circles) and CR site (diamonds). Treatments include control (filled) and VM (open) indicating five years herbicide application post-planting.

At the CR site, Douglas-fir K, Mg, and Zn were diluted in foliage of VM plots, meaning that while foliage mass increased, concentration decreased (so much so in K that overall content

also decreased). C, Ca, P, B, and Cu all increased in mass with little change in concentration. N, S, Fe, Mn, and Na increased in both concentration and content. At the CF site, Douglas-fir P, K, and Zn were diluted in the foliage of VM plots. C, S, B, Mn, and Cu all maintained similar concentrations while increasing in content. N, Ca, Mg, Na, and Fe all increased in both concentration and content.

For WH growing at the CR site, P, K, Mg, S, and Zn were diluted in foliage of VM plots, meaning that while foliage mass increased, concentration decreased. C, N, and B all increased in mass with little change in concentration. Ca, Mn, Fe, Cu, and Na increased in both concentration and content (Figure 4.7).



Figure 4.7. Vector diagram for western hemlock foliar nutrient concentrations and content of 19-year old stands at. Treatments include control (black) and VM (white) indicating five years herbicide application post-planting. All concentrations and content have been normalized to the Control treatment (Control).

For GF growing at the CR site, N, Mg, Ca, S, and Fe were diluted in foliage of VM plots, meaning that while foliage mass increased, concentration decreased. C, Mn, Cu, and Zn all increased in mass with little change in concentration. P, K, B, and Na increased in both concentration and content (Figure 4.8).



Figure 4.8. Vector diagram for grand fir foliar nutrient concentrations and content of 19-year old stands at. Treatments include control (black) and VM (white) indicating five years herbicide application post-planting. All concentrations and content have been normalized to the Control treatment (Control).

For WRC growing at the CR site, P, Mg, S, Fe, Cu, Na, and Zn were diluted in foliage of VM plots, meaning that while foliage mass increased, concentration decreased. C, K, B, and Mn all increased in mass with little change in concentration. N and Ca increased in both concentration and content (Figure 4.9a). At the CF site, N, P, K, S, Mn, and Na of WRC were diluted in the foliage of VM plots (so much so in S and Mn that content of these nutrients also decreased). C was the only nutrient that similar concentration while increasing in content. Mg, Ca, B, Fe, Cu, and Zn all increased in both concentration and content (Figure 4.9b).



Figure 4.9. Vector diagrams for western redcedar foliar concentrations and content of for macronutrients (top) and micronutrients (bottom) of 18 and 19-year old stands at the CF site (circles) and CR site (diamonds). Treatments include control (black) and VM 4.1.1.1 (white) indicating five years herbicide application post-planting. CF VM and CR VM concentrations and content have been normalized to the Control treatment at their respective site (Control).

4.6 Discussion

4.6.1 Nutrient ratios

Conclusions based on comparisons to critical and optimal ratios should be done cautiously. The foliage sampling regime used here is not the same as that used to derive these critical and optimal ratios. The samples analyzed were a composite sample of multiple needle cohorts as opposed to current year foliage which is typically used to study stand nutritional status. On the other hand, our results reflect the overall nutritional status of the whole foliage canopy of the planted crop conifer trees. For example, Ca:N ratios were the only ones that were consistently 5-10 times the optimal ratio. This is likely because Ca is not retranslocated from older foliage as efficiently as other more mobile nutrients like K or N. Conversely, K, which is generally stored as an ion in solution and is highly mobile showed the most suboptimal and subcritical ratios. This could indicate that the plants are limited by K, or it may indicate that K is recycled more efficiently from older needle cohorts than N. S:N ratios are likely to be more reliable, as N and S are both mainly stored in proteins and because they were determined using the same analytical technique at the laboratory. Even as foliar nutrients are recycled, the N:S stoichiometry should remain close. Thus it is safer to claim that the WRC plots at the CR site which have a ratio above the critical ratio of 14.7 are potentially limited by sulfur. This is further supported by the fact that S was diluted in foliage of WRC in the VM plots (see the Vector Analysis section below for more).

There was a marginally significant Spp x Trt effect for foliar K:N (P=0.064). For DF, Control plots had a foliar K:N ratio similar to the critical, but the VM plots were below the critical ratio. This is in agreement with Miller et. al (2006), while the authors themselves do not comment on nutrient ratios, they report a significant decline in K concentration that is greater than the significant decline in N concentration in the herbaceous VM treatment (since the authors do not calculate this ratio themselves, it cannot be determined if this difference is significant). For WH, Control plots had a foliar K:N similar to the optimal ratio, but the VM plots were similar to the critical ratio (difference not significant, P=0.2). On the other hand, VM plots for GF had a foliar K:N ratio above the critical ratio but Control plots were below the critical ratio (difference significant, P=0.022). While using this critical ratio may not be the perfect test for foliar nutrient status (see above), these trends suggest that the foliar nutrition of different species responded very differently to the vegetation control treatment.

There were several strong trends between total ecosystem increment and total ecosystem nutrient ratios. While it is more common to see trends in growth analyzed via foliar concentrations and ratios, these trends provide insight into the nutrient requirements for growth of the entire ecosystem (it should be noted that the design of this experiment precluded robust analysis of growth vs foliar nutrients). Total plant derived P:N, Cu:N and Zn:N ratios were strongly correlated with ecosystem biomass increment. While treatment and site did not affect this trend, crop tree species did. This shows that overstory species composition exhibits strong control over the nutrient requirements of the entire ecosystem. This especially surprising, given the fact that treatment (which governed crop tree survival and biomass) was not a significant factor. This may be useful information for managers dealing with sites that are known to be deficient in these nutrients (especially P, which is a commonly limiting nutrient). Based on this data, GF is able to achieve higher increment while requiring less P relative to N. There was also a trend for increased crop tree growth with larger Cu:N ratios. The slope of this relationship was greater for VM treated plots, implying that VM treatment increases the efficiency with which copper is used to produce crop tree biomass, something that we explored more deeply with NUE.

4.6.2 Nutrient Use Efficiency

NUE, as used in this analysis, is a measurement of how much carbon was stored in plant derived tissues per unit mass of another nutrient stored in plant derived tissues. While this is not an exact measurement of nutrient uptake, it accounts for all nutrients taken up over the life of the stand, with the exception of nutrients lost via throughfall and leached from litter (above and belowground) as it decomposes- both of which should be partially retained on site by soil processes. This is why we chose to compare it to ecosystem carbon (not including mineral soil) as opposed to increment, as ecosystem carbon is also an aggregate of productivity over the life of the stand.

Different treatments and species produced different masses of carbon, for a given mass of nutrients stored in plant derived tissues, meaning that crop tree species composition, as well as vegetation management treatment had significant effects on the NUE of the entire ecosystem (not including mineral soil). Species effects were significant for all nutrients except for Mn and Na, showing again that overstory species composition exhibits strong control over the nutrient requirements of the ecosystem. Site effects and Site x Spp effects were also common. Generally, stands at the CF site had lower NUE than stands at the CR site, especially for WRC. VM treated plots were statistically more efficient with the use of N, K, Mg, S, and Cu. This is especially important for N which is a common limiting nutrient in the region. This treatment effect is especially pronounced if the NUE is calculated using the mass of C stored only in crop tree stems, which is an important metric for managers concerned with maximizing timber production in a sustainable manner (Appendix Table S.4.1). This is because the differences in crop tree stemwood production between treatments are much greater than the difference between total ecosystem carbon.

The largest single pool of carbon for all species and treatments is the stemwood of crop tree species. VM plots tend to have more stemwood biomass than C plots. Since stemwood has a relatively low concentration of nutrients compared to all other tissue types, it follows that plots with more stem biomass have a lower ratio of C to other nutrients. The measurements in this study were taken at year 18, roughly one third to one half the length of the standard DF rotation. We suspect that over time, VM plots will continue to develop stemwood biomass at a faster rate than C plots, which will accentuate these differences in nutrient use efficiency.

4.6.3 Vector Analysis

Since the VM treatment always increased foliage biomass and crop tree productivity, all of the shifts on the vector diagram can be categorized as either dilution, sufficiency, or potential deficiency (Haase and Rose, 1995). Generally, nutrients that decreased in concentration are said to be diluted, those that stayed approximately the same are sufficient, and those that increased were potentially deficient in the reference condition (in this case the Control treatment). Crop trees in the VM treatment are subject to less interspecific competition, and are allowed to utilize a greater proportion of site nutrients. Any nutrient that increases in foliar concentration as growth is improved may have been limiting growth in the Control (though other factors e.g. summer moisture or light competition may also have influenced growth differences). Conversely, any nutrient that decreases in concentration (dilution) may means that the trees were not able to uptake enough nutrients to maintain the same foliar concentration. This can mean that either

consumption in the Control trees was greater than required, or that crop trees in the VM plots are becoming unable to meet their physiological requirements.

For all species and sites, C concentration was unchanged by treatment. At the CF site, P and K were diluted for both DF and WRC. Both of these nutrients are commonly limiting, and it may suggest that at these sites, increased crop tree growth is not able to maintain appropriate uptake of these nutrients. At the CR site, Mg was diluted for all species, and S and Zn were diluted for 3 out of 4 species. For DF and WH, K was one of the most diluted nutrients, so much so that in the DF stands, K content was decreased even as total foliage biomass increased. Conversely, at the same site, GF saw the opposite trend, where K was the most enriched foliar nutrient in VM stands, implying that K may have been growth limiting in the Control (see Nutrient Ratios section for more).

At the CF site, both species showed increases in concentration and content in the VM treatment for Ca, Mg, and Fe. This indicates that at this site, competition between crop trees and understory species may be highest for these nutrients. Among these three nutrients, Mg was the only nutrient with lower total soil concentrations at this site compared to the CR site. While higher total soil magnesium generally indicated higher exchangeable magnesium, total concentrations are not always good indicators of nutrient availability to plants (Haby et al., 1990; Metson, 1974). At the CR site, VM plots had higher foliar concentrations of Na for three species (DF, WH, and GF) and higher concentrations of N for two species (DF and WRC). Since Na is generally used as a counter ion and is not generally considered an essential plant nutrient, it is not likely that this was a limiting nutrient in Control plots. It is difficult to draw general trends for species at the CR site, indicating that the foliar nutrition of each species responded in a unique manner at this site. DF had a more consistent foliar nutrient response between sites when compared to WRC. At both sites, foliar concentrations of K and Zn were lower in VM plots, while foliar concentrations of N, Fe, and Na were all higher in VM plots, and concentrations of C, B, and Cu all remained relatively unchanged. Thus, DF foliar nutrients responded fairly similarly across sites, while the only similarities for WRC were an increase in Ca and a decrease in Fe in VM plots. This is likely due to the fact the WRC Control plots experienced very different conditions at the two sites, with the CR site developing a much more robust midstory,

whereas DF had a much smaller volume response to VM and did not tend to develop a midstory in Control plots (Flamenco et al., 2019).

4.7 <u>Management Implications</u>

Vegetation management treatments generally increased the amount of carbon stored in plant derived tissues as well as the carbon stored in crop tree stems per unit of nutrient in plant derived tissues. Controlling competing vegetation with herbicide may improve the nutrient use efficiency of forests that are managed for aboveground carbon sequestration as well as timber yield.

The species of the dominant overstory tree had a significant effect on the nutrient requirements of the stand as seen through foliar nutrient ratios, ratios of total plant derived nutrients, and relationships between these ratios and biomass production. While more research is needed, this may indicate that GF is able to obtain larger increments for a given ratio of P:N in plant derived tissue, indicating that it may be a more efficient species at sites in the Oregon coast Range that are known or suspected to be limited by P.

Crop tree foliar responses to VM treatment varied by site and by species, suggesting that each species responds in a unique way at each site to competing vegetation control even 18 to 19 years after planting.

4.8 <u>References</u>

Agüero, J.J., Kirschbaum, D.S., 2013. Approaches to nutrient use efficiency of different strawberry genotypes. Int. J. Fruit Sci. 13, 139–148. https://doi.org/10.1080/15538362.2012.697047

Binkley, D., 1986. Forest Nutrition Management. New York : Wiley, New York.

- Binkley, D., Sollins, P., Bell, R., Sachs, D., Myrold, D., 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73, 2022–2033.
- Binkley, D., Stape, J.L., Ryan, M.G., 2004. Thinking about efficiency of resource use in forests. For. Ecol. Manage. 193, 5–16. https://doi.org/10.1016/j.foreco.2004.01.019

- Blake, J.I., Chappell, H.N., Bennett, W.S., Gessel, S.P., Webster, S.R., 1990. Douglas-fir growth and foliar nutrient responses to nitrogen and sulfur fertilization. Soil Sci. Soc. Am. J. 54, 257–262. https://doi.org/10.2136/sssaj1990.03615995005400010041x
- Bridgham, S.D., Pastor, J., Mcclaugherty, C.A., Curtis, J., Richardson, C.J., 2016. Nutrient-use efficiency : a litterfall index , a model , and a test along a nutrient- availability gradient in North Carolina peatlands 145, 1–21.
- Brockley, R.P., 2001a. Foliar sampling guidelines and nutrient interpretative criteria for Lodgepole Pine. Minist. For. Res. Progr. Ext. Note No. 52 8 p.
- Brockley, R.P., 2001b. Foliar analysis as a planning tool for operational fertilization. Enhanc. For. Manag. Fertil. Econ. Conf. 6.
- Chapin, F.S., 1980. The Mineral Nutrition of Wild Plants. Annu. Rev. Plant Physiol. 11, 233–260. https://doi.org/10.1146/annurev.pp.31.060180.001323
- Dijkshoorn, W., van Wijk, A.L., 1967. The sulphur requirements of plants as evidenced by the sulphur-nitrogen ratio in the organic matter a review of published data. Plant Soil 26, 129–157. https://doi.org/10.1007/BF01978680
- Flamenco, H.N., Gonzalez-Benecke, C.A., Wightman, M.G., 2019. Long-term effects of vegetation management on biomass stock of four coniferous species in the Pacific Northwest United States. For. Ecol. Manage. 432, 276–285. https://doi.org/10.1016/j.foreco.2018.09.033
- Garrison, M.T., Moore, J.A., 1998. Nutrient management : A summary and review, Intermountain Forest Tree Nutrition Cooperative Supplemental Report 98-5.
- Garrison, M.T., Moore, J.A., Shaw, T.M., Mika, P.G., 2000. Foliar nutrient and tree growth response of mixed-conifer stands to three fertilization treatments in northeast Oregon and north central Washington. For. Ecol. Manage. 132, 183–198. https://doi.org/10.1016/S0378-1127(99)00228-5
- Gholz, H.L., 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology 63, 469–481. https://doi.org/10.2307/1938964
- Gonzalez-Benecke, C.A., Flamenco, H. N., & Wightman, M. G. 2018. Effect of vegetation management and site conditions on volume, biomass and leaf area allometry of four coniferous species in the Pacific Northwest United States. Forests, 9, 581; doi:10.3390/f9090581
- Haase, D.L., Rose, R., 1995. Vector analysis and its use for interpreting plant nutrient shifts in response to silvicultural treatments. For. Sci. 41, 54–66. https://doi.org/10.1093/forestscience/41.1.54
- Haby, V.A., Russelle, M.P., Skogley, E.O., 1990. Testing Soils for Potassium, Calcium, and Magnesium, in: Westerman, R.L. (Ed.), Soil Testing and Plant Analysis. Soil Science Society of America, Madison, WI, pp. 181–227. https://doi.org/10.2136/sssabookser3.3ed.c8
- Ingestad, T., 1979. Mineral nutrient requirements of Pinus silvestris and Picea abies seedlings. Physiol. Plant. 45, 373–380. https://doi.org/10.1111/j.1399-3054.1979.tb02599.x
- Ingestad, T., 1962. Macro element nutrition of pine, spruce, and birch seedlings in nutrient solutions. Medd. Statens Skogsforskningsinst 51, 1–150.
- Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sci. U. S. A. 94, 7362–7366. https://doi.org/10.1073/pnas.94.14.7362
- Kelly, J., Lambert, M.J., 1972. The relationship between sulphur and nitrogen in the foliage of Pinus radiata. Plants Soil 37, 395–407.
- Knecht, M.F., Göransson, A., 2004. Terrestrial plants require nutrients in similar proportions. Tree Physiol. 24, 447–460. https://doi.org/10.1093/treephys/24.4.447
- Knops, J.M.H., Koenig, W.D., Nash, T.H., 1997. On the relationship between nutrient use efficiency and fertility in forest ecosystems. Oecologia 110, 550–559. https://doi.org/10.1007/s004420050194
- Linder, S., 1995. Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. Ecol. Bull. 178–190.

- McGroddy, M.E., Daufresne, T., Hedin, L.O., 2004. Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios. Ecology 85, 2390–2401. https://doi.org/10.1890/03-0351
- Metson, A.J., 1974. Some factors governing the availability of soil magnesium: A review. New Zeal. J. Exp. Agric. 2, 277–319. https://doi.org/10.1080/03015521.1974.10427689
- Moore, J.A., Mika, P.G., Shaw, T.M., Garrison-Johnston, M.I., 2004. Foliar nutrient characteristics of four conifer species in the interior Northwest United States. West. J. Appl. For. 19, 13–24. https://doi.org/10.1093/wjaf/19.1.13
- Redfield, A.C., 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. James Johnstone Meml. 176, 176–192.
- Richards, A.E., Forrester, D.I., Bauhus, J., Scherer-Lorenzen, M., 2010. The influence of mixed tree plantations on the nutrition of individual species: A review. Tree Physiol. 30, 1192– 1208. https://doi.org/10.1093/treephys/tpq035
- Timmer, V.R., Armstrong, G., 1987. Diagnosing nutritional status of containerized tree seedlings: comparative plant analyses. Soil Sci. Soc. Am. J. 51, 1082–1086. https://doi.org/10.2136/sssaj1987.03615995005100040048x
- Timmer, V.R., Miller, B.D., 1991. Effects of contrasting fertilization and moisture regimes on biomass, nutrients, and water relations of container grown red pine seedlings. New For. 5, 335–348. https://doi.org/10.1007/BF00118861
- Timmer, V.R., Stone, E.L., 1978. Comparative foliar analysis of young Balsam fir fertilized with nitrogen, phosphorus, potassium, and lime. Soil Sci. Soc. Am. J. 42, 125–130. https://doi.org/10.2136/sssaj1978.03615995004200010027x
- Turner, J., Lambert, M., Gessel, S., 1979. Sulfur requirements of nitrogen fertilized Douglas-fir. For. Sci. 25, 461–467.
- Turner, J., Lambert, M.J., Gessel, S.P., 1977. Use of foliage sulphat concentration to predics response to urea application by Douglas-fir. Can. J. For. Res. 7, 476–480. https://doi.org/https://doi.org/10.1139/x77-061

- van den Dreissche, R., 1974. Prediction of mineral nutrient status of trees by foliar analysis. Bot. Rev. 40, 347–394.
- Vitousek, P., 1982. Nutrient Cycling and Nutrient Use Efficiency. Am. Nat. 119, 553–572. https://doi.org/10.1086/283931
- Waring, R.H., 1983. Estimating Forest Growth and Efficiency in Relation to Canopy Leaf Area. Adv. Ecol. Res. 13, 327–354. https://doi.org/10.1016/S0065-2504(08)60111-7

5. Conclusions

5.1. Summary of Findings

In Chapter 2, we found that effects of vegetation management (VM) on tissue nutrient concentrations at age 18 varied by site, species, nutrient, and tissue. Bark and forest floor were the two tissue types that were most sensitive to VM treatment. Differences in forest floor nutrient concentrations are likely driven by the changes in plant species composition between VM and Control plots, with midstory and understory species contributing chemically distinct litter in many Control plots. Differences in bark concentrations may indicate differences in nutrient retranslocation over the lives of the different stands. Few treatment effects on soil were discovered and varied by species, site, and depth. When differences were detectable, soil concentrations of nitrogen (N), calcium (Ca), and magnesium (Mg) were higher in VM plots. The one exception was that soil N concentrations for WRC at the CR site were significantly lower for 0.2-0.4 m and 0.4-0.6 m depth increments in VM plots. Generally, tissue concentrations were most affected by species and soil concentrations were most affected by site.

In Chapter 3, we proved our hypothesis that Control plots would hold more plant derived nutrient content to be false. Ca was the only nutrient for which plant derived nutrient content varied only by treatment and not by site or species. For all other nutrients, treatment effects on plant derived nutrient content varied by site and species. Western redcedar (WRC) plots at the Coast Range (CR) site was the only site and species for which this trend was true for almost all nutrients, due to the large amount of midstory biomass in Control plots and comparatively small crop tree biomass in VM plots. If WRC CR plot were to be excluded from analysis, carbon (C), copper (Cu), phosphorous (P), and boron (B), all tended to show higher plant derived nutrient content in VM plots. Of all tissue types, nutrient content of crop tree branches, bark, foliage, and stemwood had generally greater nutrient content in VM plots as the biomass of all these tissues was significantly greater for all species. As soil nutrient content tended to be orders of magnitude higher than plant derived content (with the exception of C and N), there were few treatment and species differences in soil content. Total soil N of WRC at the CR site, however was significantly lower for VM plots. This may indicate the potential for VM applied to a slow growing species, such as WRC, to reduce ecosystem retention of N. As N is a common limiting

120

nutrient in these forests, this has the potential to reduce growth of current and future stands (Mainwaring et al., 2014).

Mg soil content displayed a marginally significant treatment effect, while Mg and sodium (Na) displayed differences between species.

In Chapter 4, we saw that foliar nutrient ratios did not have a strong response to treatment. Instead, each species foliar nutrition responded differently to VM, though there were similarities among sites. Species at the Cascade mountain foothills (CF) site tended to have diluted concentrations of P and potassium (K) and increases in Ca, Mg, and iron (Fe) in the VM treatment. Species at the CR site, all showed dilutions of Mg and increases in Na. Total plant biomass increment was well correlated with total plant Cu:N, Zn:N, and P:N, such that the slope of that relationship varied by species. Total crop tree biomass increment trended with crop tree Cu:N such that the slope varied by treatment. VM increased nutrient use efficiency (NUE), increasing the amount of total plant derived carbon produced per unit of nutrient fixed in plant tissue for N, P, Mg, sulfur (S), and Cu. When NUE was calculated in terms of crop bole carbon produced per unit nutrient fixed in plant tissue, VM increased NUE of all nutrients.

5.2. Management Implications

Sustained VM resulted in few differences in tissue nutrient concentrations, with bark and forest floor being the most notable exceptions. While VM tended to increase the biomass and nutrient content of crop tree tissues, when all plant derived tissues are considered as a whole, the differences in plant derived nutrient mass between VM and Control plots become much less pronounced, and in some cases, Control plots even have higher nutrient masses such as for WRC at the CR site. Nevertheless, nutrient mass in WRC Control plots was similar or lower than in VM plots of the other species tested at each site.

Most differences in soil nutrient content (with the exception of C) indicated higher concentrations under the VM treatment. Total soil nutrient reserves are 10 to 1000 times greater than the amount stored in plant tissue (excluding C, which is not taken up via plant roots). This study does not indicate the potential for total soil nutrient reserves to be depleted by even sustained vegetation management treatment. WRC at the CR site, showed reduced total soil N mass under VM, indicating the potential for sustained vegetation control to reduce ecosystem N retention when this treatment is applied to a slow growing species, such as WRC. However, this study did not attempt to quantify fluxes between various available and unavailable soil nutrient pools, and as such there may be treatment differences in nutrient availability that cannot be observed from this data.

VM plots, however, did tend to produce more harvestable and plant-derived carbon per unit nutrient fixed in plant tissues. This means that VM treatments may improve the efficiency of nutrient use for stands that are being managed for carbon sequestration as well as for timber harvest.

The dominant overstory species has a significant effect on the nutrient requirements of the whole stand. While more research is needed, grand fir may be able to obtain higher increment for a given P:N ratio which could be important for sites in the Oregon Coast Range limited by P.

5.3. Future Directions

The Vegetation Management Cooperative (VMRC) which oversaw this and related projects, has collected litterfall data for several years. This could be used to calculate net primary productivity which may have interesting relationships with nutrient content, concentrations, or ratios. Additionally, the litterfall collection would allow for chemical characterization of litter which would facilitate a different manner of NUE calculations (Vitousek, 1982). It would also allow investigation into how crop trees and midstory species are recycling their nutrients.

A reassessment of this study is planned for 15-20 years in the future which will allow a better understanding of how these trends of nutrient use continue through rotation age. It will also allow more accurate estimates of how harvest removals will differ between species and treatments.

5.4. <u>References</u>

- Vitousek, P., 1982. Nutrient Cycling and Nutrient Use Efficiency. Am. Nat. 119, 553–572. https://doi.org/10.1086/283931
- Mainwaring, D.B., Maguire, D.A., Perakis, S.S., 2014. Three-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington. For. Ecol. Manage. 327, 178–188. https://doi.org/10.1016/j.foreco.2014.05.005

Appendix Table S.S.2.1. Average concentrations in percent and standard errors (SE) of the macronutrients carbon,
nitrogen, phosphorous, potassium, magnesium, calcium, and sulfur for the understory and the foliage and wood of the
midstory species: bigleaf maple (ACMA), red alder (ALRU), Oregon bitter cherry (PREM), and cascara buckthorn
RHPU). Understory average was taken across sites, species, and treatments.

		Carb	00	Nitro	ngen	Phospl	lorous	Potas	sium	Magn	esium	Calc	ium	Sul	fur
		%	SE	%	SE	%	SE	%	SE	%	SE	%	SE	%	SE
ACMA	Foliage	44.917	0.380	3.010	0.116	0.371	0.043	1.496	0.034	0.344	0.014	1.163	0.134	0.204	0.010
	Stem	45.472	0.127	0.117	0.002	0.017	0.005	BLD	ı	0.036	0.001	0.082	0.003	0.043	0.000
ALRU	Foliage	47.240	0.330	2.938	0.154	0.147	0.007	1.083	0.142	0.253	0.003	0.590	0.052	0.087	0.010
	Stem	53.112	0.448	0.552	0.004	0.009	0.001	BLD	ı	0.026	0.002	0.087	0.015	0.048	0.003
PREM	Foliage	44.108	0.576	3.248	0.100	0.412	0.032	1.506	0.049	0.397	0.018	1.147	0.126	0.160	0.002
	Stem	44.916	0.088	0.110	0.003	0.021	0.010	BLD		0.027	0.005	0.124	0.017	0.049	0.003
RHPU	Foliage	42.813	0.101	2.678	0.049	0.331	0.009	1.709	0.056	0.351	0.012	1.213	0.082	0.117	0.002
	Stem	45.212	0.095	0.143	0.005	0.007	0.002	BLD	ı	0.042	0.001	0.125	0.008	0.045	0.001
Understory	Total	40.834	0.845	1.375	0.059	0.180	0.011	1.177	0.104	0.272	0.015	0.907	0.049	0.000	0.000

boron, copper, iron, sodium, and zinc for the understory and the foliage and wood of the midstory species: bigleaf Appendix Table S.S.2.2. Average concentrations in mg kg⁻¹ (ppm) and standard errors (SE) of the micronutrients maple (ACMA), red alder (ALRU), Oregon bitter cherry (PREM), and cascara buckthorn (RHPU). Understory average was taken across sites, species, and treatments.

		Bor	uo.	Cop	per	In	n	Mang	anese	Sodi	m	Zin	c
		bpm	SE	bpm	SE	bpm	SE	mqq	SE	bpm	SE	bpm	SE
ACMA	Foliage	14.66	2.91	6.589	0.381	100.00	17.40	180.98	15.05	192.61	31.74	52.05	4.65
	Stem	2.70	0.10	3.332	0.598	100.46	10.53	24.51	4.02	BLD	ı	5.66	0.81
ALRU	Foliage	15.50	0.42	8.179	0.458	62.62	4.17	229.03	16.38	166.26	23.17	26.30	2.61
	Stem	2.36	0.08	2.239	0.097	135.46	29.79	17.74	0.69	BLD	ı	5.09	0.32
PREM	Foliage	18.53	1.29	5.681	0.478	156.25	1.79	58.01	3.16	93.55	19.47	11.73	1.66
	Stem	3.62	0.44	2.121	0.246	89.29	5.48	4.74	0.11	BLD	ı	2.49	0.19
RHPU	Foliage	32.07	0.34	6.845	0.684	138.71	9.10	833.53	12.75	157.24	11.48	23.73	1.44
	Stem	2.72	0.09	2.377	0.412	109.86	38.47	31.32	1.13	BLD	ı	2.37	0.39
Understory	Total	27.67	2.59	5.839	0.330	918.54	115.52	562.36	55.27	195.19	11.32	22.24	1.84

6. Appendix

Appendix Table S.5.3. P-values of Pearson correlation coefficients for correlation between nutrient concentrations (P, K, Mg, Ca, B, Cu, Fe, Mn, and Na) for each plant derived nutrient pool and average soil concentrations (averaged across all depths). Data for 18 year- old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range and the Cascade foothills of western Oregon. P values only shown for tissues and nutrients for which there was a significant difference in concentration between sites (see Appendix Table S.2.4)

Species	Tissue	Р	K	Mg	Ca	В	Cu	Fe	Mn	Na
DF	Foliage		0.053 1			< 0.001		0.439		0.001
	Branch									0.005
	Bark			0.003				0.117		0.027
	Wood						0.114	0.008	0.084	
	Root		< 0.001	0.001	< 0.001	0.001		0.002	0.001	0.010
	Understory	0.086			0.001	0.013				
	Forest floor		0.038 1		0.001	0.014	0.059			0.003
WRC	Foliage			0.035						
	Branch						<0.001 1			
	Bark		0.913		0.003 1					< 0.001
	Wood									
	Root		0.016	0.090	0.142		0.043	0.002	0.001	
	Understory				0.002	0.001			< 0.001	
	Forest floor			0.109						< 0.001

¹- indicates negative Pearson correlation coefficient

Appendix Table S.5.4. Concentration (ppm) of Boron (B) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR Y	VM	CF C	ontrol	CF	VM		P-val	ue
Species	Tissue	ppm	SE	ppm	SE	ppm	SE	ppm	SE	Trt	Site	Site x Trt
DF	Foliage	10.914	1.928	11.617	1.182	23.098	2.606	22.505	2.851	0.973	0.001	0.797
	Branches	9.899	1.824	9.690	0.544	10.693	1.194	10.852	1.933	0.905	0.548	0.818
	Bark	7.504	0.051	7.478	0.452	8.185	0.686	7.349	0.306	0.313	0.484	0.266
	Wood	1.720	0.138	1.663	0.123	2.522	0.691	1.963	0.186	0.421	0.162	0.511
	Understory	19.118	3.226	15.199	2.463	41.661	7.804	38.091	5.529	0.225	0.006	0.952
	Forest Floor	11.987	0.442	13.105	0.414	18.414	1.437	16.372	1.223	0.622	0.001	0.118
	Fine Roots	11.357	0.764	12.492	1.348	17.234	0.570	15.491	1.350	0.764	0.002	0.180
	Soil 0.0-0.2 m	n 30.999	1.536	33.548	2.026	68.333	5.279	61.978	3.670	0.575	<0.001	0.225
	Soil 0.2-0.4 m	n 36.972	1.128	39.072	2.617	77.365	7.351	80.975	1.696	0.486	< 0.001	0.852
	Soil 0.4-0.6 m	n 39.868	1.565	38.512	4.634	80.367	6.925	78.389	2.853	0.716	< 0.001	0.946
	Soil 0.6-1.0 m	n 34.418	3.029	34.865	2.701	89.667	19.769	91.309	7.435	0.924	< 0.001	0.957
WH	Foliage	22.988	4.664	21.522	1.819	-	-	-	-	0.772	-	-
	Branches	10.329	0.586	9.935	1.140	-	-	-	-	0.692	-	-
	Bark	11.573	2.012	8.721	0.309	-	-	-	-	0.211	-	-
	Wood	2.751	0.220	2.011	0.018	-	-	-	-	0.015	-	-
	Understory	22.641	4.799	16.540	1.894	-	-	-	-	0.282	-	-
	Forest Floor	11.909	0.272	14.681	1.300	-	-	-	-	0.082	-	-
	Fine Roots	12.136	1.263	8.738	0.491	-	-	-	-	0.046	-	-
	Soil 0.0-0.2 m	n 33.444	1.547	34.008	1.409	-	-	-	-	0.477	-	-
	Soil 0.2-0.4 m	n 45.462	4.239	41.488	1.445	-	-	-	-	0.268	-	-
	Soil 0.4-0.6 m	n 45.086	0.921	45.166	1.820	-	-	-	-	0.970	-	-
	Soil 0.6-1.0 m	n 44.221	2.651	40.307	2.494	-	-	-	-	0.356	-	-
WRC	Foliage	11.887	2.347	11.503	1.030	12.808	0.266	13.362	1.302	0.954	0.355	0.751
	Branches	8.400	1.472	8.632	0.631	7.585	1.726	8.411	1.771	0.726	0.731	0.844
	Bark	15.462	2.152	14.338	2.858	12.977	1.406	15.248	1.329	0.783	0.705	0.420
	Wood	2.711	0.144	2.865	0.414	3.267	0.155	3.033	0.558	0.448	0.184	0.315
	Understory	15.225	3.043	20.714	4.394	40.545	9.775	50.863	15.728	0.496	0.033	0.833
	Forest Floor	17.847	0.592	13.231	3.281	14.523	2.772	14.777	3.667	0.492	0.777	0.444
	Fine Roots	14.134	1.842	12.470	0.928	20.454	2.547	17.277	1.767	0.152	0.071	0.622
	Soil 0.0-0.2 m	n 31.926	1.856	33.282	0.995	85.150	5.952	88.319	8.501	0.276	< 0.001	0.645
	Soil 0.2-0.4 m	n 36.815	1.111	39.018	5.055	88.387	6.714	78.683	5.886	0.413	<0.001	0.215
	Soil 0.4-0.6 m	n 44.924	0.001	43.435	1.703	76.366	7.199	80.346	6.826	0.672	< 0.001	0.369
	Soil 0.6-1.0 m	n 47.372	4.158	40.433	3.883	77.805	2.860	76.729	13.980	0.643	0.014	0.733
GF	Foliage	15.357	1.701	15.948	3.792	-	-	-	-	0.925	-	-
	Branches	11.809	0.953	17.371	4.208	-	-	-	-	0.245	-	-
	Bark	13.149	2.700	10.606	1.376	-	-	-	-	0.282	-	-
	Wood	2.734	0.734	2.941	0.486	-	-	-	-	0.822	-	-
	Understory	26.539	6.626	17.110	3.275	-	-	-	-	0.271	-	-
	Forest Floor	14.308	1.217	12.489	0.834	-	-	-	-	0.285	-	-
	Fine Roots	13.500	2.284	10.290	0.924	-	-	-	-	0.263	-	-
	Soil 0.0-0.2 m	n 23.793	5.267	29.399	1.208	-	-	-	-	0.358	-	-
	Soil 0.2-0.4 m	n 28.730	3.508	39.265	3.226	-	-	-	-	0.092	-	-
	Soil 0.4-0.6 m	n 40.802	10.373	41.393	1.737	-	-	-	-	0.953	-	-
	Soil 0.6-1.0 m	1 33.694	9.363	40.336	4.585	-	-	-	-	0.442	-	-

Appendix Table S.5.5. Concentration (%) of carbon (C) of tree and ecosystem components for 18 year-old Douglasfir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR Co	ontrol	CR	VM	CF Co	ntrol	CF	VM		P-va	lue
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Foliage	49.198	0.233	49.260	0.574	50.004	0.042	49.379	0.248	0.439	0.267	0.310
	Branches	47.316	0.241	47.450	0.110	47.071	0.189	47.099	0.250	0.700	0.172	0.800
	Bark	48.317	0.743	49.210	1.113	49.738	0.491	49.634	0.401	0.702	0.182	0.595
	Wood	47.766	0.079	47.566	0.179	47.762	0.258	48.030	0.083	0.827	0.234	0.190
	Understory	37.224	5.545	31.499	1.869	42.310	1.722	44.338	0.760	0.559	0.013	0.231
	Forest Floor	31.218	4.077	35.340	2.264	41.640	1.973	41.370	3.060	0.527	0.017	0.472
	Fine Roots	31.738	2.063	30.568	2.010	23.863	2.821	26.845	1.323	0.676	0.027	0.350
	Soil 0.0-0.2 m	3.805	0.124	4.197	1.035	4.256	0.457	4.535	0.356	0.584	0.521	0.925
	Soil 0.2-0.4 m	2.875	0.581	2.432	0.487	2.798	0.529	3.140	0.487	0.849	0.038	0.168
	Soil 0.4-0.6 m	2.366	0.240	1.094	0.262	0.818	0.143	1.363	0.106	0.102	0.012	0.002
	Soil 0.6-1.0 m	0.654	0.227	0.818	0.025	0.539	0.123	0.808	0.135	0.166	0.945	0.711
WH	Foliage	49.220	0.534	49.410	0.187	-	-	-	-	0.719	-	-
	Branches	46.683	0.099	46.328	0.183	-	-	-	-	0.060	-	-
	Bark	47.080	1.065	45.183	0.449	-	-	-	-	0.152	-	-
	Wood	47.625	0.414	47.854	0.128	-	-	-	-	0.544	-	-
	Understory	42.050	1.252	42.189	0.761	-	-	-	-	0.928	-	-
	Forest Floor	40.928	1.699	41.005	2.273	-	-	-	-	0.976	-	-
	Fine Roots	32.731	3.508	35.076	0.927	-	-	-	-	0.542	-	-
	Soil 0.0-0.2 m	4.635	0.418	5.285	0.437	-	-	-	-	0.324	-	-
	Soil 0.2-0.4 m	2.747	0.892	2.640	0.223	-	-	-	-	0.906	-	-
	Soil 0.4-0.6 m	1.109	0.217	1.919	0.536	-	-	-	-	0.234	-	-
	Soil 0.6-1.0 m	0.708	0.162	0.609	0.137	-	-	-	-	0.659	-	-
WRC	Foliage	48.924	0.466	48.069	0.561	48.894	0.356	48.812	0.230	0.288	0.415	0.378
	Branches	46.974	0.114	46.686	0.118	46.060	0.239	42.865	3.868	0.353	0.288	0.429
	Bark	48.347	0.189	48.949	0.628	47.042	0.602	47.145	0.375	0.302	0.015	0.338
	Wood	48.623	0.036	48.517	0.096	46.974	0.955	46.878	0.805	0.793	0.001	0.592
	Understory	43.587	0.200	36.950	5.724	41.622	1.832	44.055	0.545	0.437	0.439	0.124
	Forest Floor	39.320	0.945	38.153	4.024	42.548	4.349	39.148	4.443	0.368	0.434	0.650
	Fine Roots	34.517	4.095	29.843	1.724	24.278	2.879	23.193	0.729	0.290	0.026	0.490
	Soil 0.0-0.2 m	5.287	0.884	4.624	0.173	4.750	0.354	4.850	0.690	0.646	0.799	0.535
	Soil 0.2-0.4 m	3.907	1.130	2.709	0.428	3.155	0.467	2.661	0.568	0.087	0.250	0.419
	Soil 0.4-0.6 m	2.230	0.438	1.330	0.251	1.676	0.388	0.779	0.116	0.018	0.114	0.998
	Soil 0.6-1.0 m	0.615	0.168	0.498	0.077	0.739	0.057	0.556	0.083	0.156	0.374	0.745
GF	Foliage	48.729	0.128	48.605	0.226	-	-	-	-	0.650	-	-
	Branches	46.700	0.306	45.994	0.304	-	-	-	-	0.153	-	-
	Bark	46.812	0.550	46.605	0.593	-	-	-	-	0.044	-	-
	Wood	47.285	0.123	47.436	0.156	-	-	-	-	0.374	-	-
	Understory	44.327	0.127	40.323	1.382	-	-	-	-	0.099	-	-
	Forest Floor	34.173	3.389	36.807	1.881	-	-	-	-	0.534	-	-
	Fine Roots	27.791	2.740	26.954	2.708	-	-	-	-	0.839	-	-
	Soil 0.0-0.2 m	6.713	1.420	5.525	0.342	-	-	-	-	0.462	-	-
	Soil 0.2-0.4 m	2.469	0.074	2.613	0.494	-	-	-	-	0.787	-	-
	Soil 0.4-0.6 m	1.548	0.213	1.702	0.494	-	-	-	-	0.790	-	-
	Soil 0.6-1.0 m	0.782	0.265	0.515	0.128	-	-	-	-	0.415	-	-

Appendix Table S.5.6. Concentration (%) of calcium (Ca) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF C	ontrol	CF	VM		P-val	ue
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Foliage	0.561	0.108	0.573	0.090	0.627	0.046	0.641	0.069	0.878	0.426	0.994
	Branches	0.352	0.076	0.344	0.073	0.293	0.031	0.285	0.067	0.638	0.532	0.752
	Bark	0.324	0.040	0.228	0.055	0.355	0.071	0.294	0.042	0.121	0.228	0.717
	Wood	0.086	0.047	0.036	0.001	0.045	0.006	0.036	0.000	0.232	0.402	0.409
	Understory	0.649	0.114	0.606	0.055	1.216	0.312	1.037	0.121	0.545	0.016	0.712
	Forest Floor	0.707	0.065	0.749	0.038	0.987	0.054	0.996	0.061	0.660	0.003	0.774
	Fine Roots	0.387	0.045	0.320	0.037	0.679	0.059	0.521	0.028	0.024	< 0.001	0.322
	Soil 0.0-0.2 m	0.151	0.034	0.133	0.022	0.371	0.049	0.378	0.034	0.878	< 0.001	0.748
	Soil 0.2-0.4 m	0.108	0.030	0.113	0.048	0.339	0.057	0.376	0.019	0.512	< 0.001	0.606
	Soil 0.4-0.6 m	0.103	0.037	0.062	0.016	0.231	0.047	0.221	0.034	0.369	0.038	0.587
	Soil 0.6-1.0 m	0.048	0.013	0.041	0.008	0.183	0.054	0.141	0.049	0.336	0.118	0.479
WH	Foliage	0.577	0.120	0.761	0.092	-	-	-	-	0.295	-	-
	Branches	0.252	0.042	0.265	0.022	-	-	-	-	0.790	-	-
	Bark	0.347	0.027	0.439	0.022	-	-	-	-	0.040	-	-
	Wood	0.085	0.014	0.066	0.004	-	-	-	-	0.232	-	-
	Understory	0.803	0.068	0.747	0.056	-	-	-	-	0.565	-	-
	Forest Floor	0.759	0.059	0.749	0.061	-	-	-	-	0.905	-	-
	Fine Roots	0.451	0.023	0.367	0.048	-	-	-	-	0.166	-	-
	Soil 0.0-0.2 m	0.106	0.018	0.116	0.022	-	-	-	-	0.736	-	-
	Soil 0.2-0.4 m	0.080	0.034	0.076	0.011	-	-	-	-	0.927	-	-
	Soil 0.4-0.6 m	0.083	0.032	0.057	0.006	-	-	-	-	0.466	-	-
	Soil 0.6-1.0 m	0.034	0.002	0.040	0.003	-	-	-	-	0.184	-	-
WRC	Foliage	1.138	0.158	1.265	0.103	1.446	0.152	1.350	0.142	0.950	0.339	0.609
	Branches	0.563	0.095	0.666	0.074	0.774	0.121	0.493	0.031	0.337	0.846	0.052
	Bark	1.230	0.077	1.078	0.047	0.936	0.079	0.790	0.053	0.042	0.001	0.959
	Wood	0.125	0.003	0.210	0.082	0.124	0.003	0.107	0.006	0.369	0.194	0.251
	Understory	0.896	0.086	0.785	0.018	1.313	0.139	1.106	0.128	0.206	0.011	0.690
	Forest Floor	1.084	0.107	1.080	0.130	0.897	0.165	1.411	0.257	0.117	0.796	0.114
	Fine Roots	0.495	0.093	0.412	0.013	0.683	0.089	0.655	0.086	0.519	0.027	0.753
	Soil 0.0-0.2 m	0.169	0.063	0.147	0.037	0.418	0.052	0.317	0.023	0.212	0.004	0.398
	Soil 0.2-0.4 m	0.137	0.009	0.082	0.022	0.342	0.044	0.260	0.044	0.007	0.002	0.414
	Soil 0.4-0.6 m	0.110	0.022	0.045	0.002	0.270	0.010	0.238	0.023	0.019	< 0.001	0.371
	Soil 0.6-1.0 m	0.055	0.005	0.042	0.006	0.181	0.040	0.250	0.105	0.683	0.031	0.550
GF	Foliage	1.254	0.192	1.156	0.075	-	-	-	-	0.836	-	-
	Branches	0.438	0.074	0.468	0.050	-	-	-	-	0.751	-	-
	Bark	0.869	0.128	0.562	0.021	-	-	-	-	0.055	-	-
	Wood	0.092	0.011	0.082	0.008	-	-	-	-	0.466	-	-
	Understory	0.743	0.175	0.915	0.015	-	-	-	-	0.399	-	-
	Forest Floor	1.408	0.322	1.792	0.120	-	-	-	-	0.350	-	-
	Fine Roots	0.531	0.039	0.404	0.068	-	-	-	-	0.190	-	-
	Soil 0.0-0.2 m	0.187	0.023	0.186	0.017	-	-	-	-	0.961	-	-
	Soil 0.2-0.4 m	0.108	0.017	0.110	0.037	-	-	-	-	0.950	-	-
	Soil 0.4-0.6 m	0.107	0.028	0.063	0.015	-	-	-	-	0.160	-	-
	Soil 0.6-1.0 m	0.082	0.031	0.060	0.015	-	-	-	-	0.302	-	-

Appendix Table S.5.7. Concentration (ppm) of copper (Cu) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR Co	ontrol	CR Y	VM	CF Co	ontrol	CF V	VM		P-val	ue
Species	Tissue	ppm	SE	ppm	SE	ppm	SE	ppm	SE	Trt	Site	Site x Trt
DF	Foliage	2.821	0.296	2.760	0.171	3.125	0.199	3.135	0.382	0.977	0.214	0.990
	Branches	4.097	0.348	3.679	0.157	3.321	0.242	3.380	0.312	0.497	0.119	0.383
	Bark	3.163	0.219	3.558	0.226	3.728	0.339	3.982	0.049	0.188	0.055	0.767
	Wood	0.980	0.193	0.668	0.124	1.623	0.451	1.974	0.359	0.965	0.016	0.289
	Understory	7.299	2.644	5.558	1.081	5.588	0.282	5.629	0.629	0.574	0.587	0.556
	Forest Floor	2.591	0.368	2.717	0.307	5.497	0.597	3.991	0.268	0.050	0.001	0.027
	Fine Roots	5.472	0.462	4.780	0.504	6.205	0.272	5.060	0.211	0.015	0.204	0.462
	Soil 0.0-0.2 m	21.488	1.366	23.100	2.299	34.138	2.300	36.947	1.454	0.239	<0.001	0.739
	Soil 0.2-0.4 m	23.435	1.899	22.904	1.560	39.889	3.648	44.601	4.543	0.110	<0.001	0.055
	Soil 0.4-0.6 m	25.346	2.176	25.383	1.879	40.184	4.020	48.353	5.205	0.034	<0.001	0.036
	Soil 0.6-1.0 m	26.786	1.575	25.605	1.904	32.147	3.515	52.624	2.422	0.001	<0.001	0.001
WH	Foliage	3.219	0.415	3.482	1.004	-	-	-	-	0.817	-	-
	Branches	5.036	0.225	4.516	0.343	-	-	-	-	0.098	-	-
	Bark	4.270	0.464	3.117	0.318	-	-	-	-	0.032	-	-
	Wood	1.374	0.228	1.672	0.102	-	-	-	-	0.181	-	-
	Understory	6.412	0.734	3.327	0.262	-	-	-	-	0.022	-	-
	Forest Floor	4.497	0.644	3.441	0.448	-	-	-	-	0.227	-	-
	Fine Roots	4.689	0.332	4.168	0.265	-	-	-	-	0.164	-	-
	Soil 0.0-0.2 m	23.383	0.642	22.839	2.147	-	-	-	-	0.764	-	-
	Soil 0.2-0.4 m	25.657	1.331	25.124	2.029	-	-	-	-	0.793	-	-
	Soil 0.4-0.6 m	25.295	0.936	28.228	1.313	-	-	-	-	0.143	-	-
	Soil 0.6-1.0 m	25.344	1.860	26.789	1.701	-	-	-	-	0.052	-	-
WRC	Foliage	3.766	0.401	3.107	0.207	4.580	0.893	3.672	0.650	0.013	0.036	0.679
	Branches	3.131	0.400	3.173	0.133	1.984	0.198	1.851	0.119	0.854	< 0.001	0.723
	Bark	3.104	0.111	3.008	0.235	3.487	0.349	3.465	0.585	0.941	0.363	0.873
	Wood	1.309	0.224	1.121	0.117	1.515	0.303	1.137	0.131	0.207	0.531	0.447
	Understory	6.137	1.438	4.660	1.062	6.453	0.761	7.421	0.804	0.673	0.179	0.077
	Forest Floor	5.269	1.067	2.943	0.333	3.767	0.256	3.512	0.991	0.107	0.597	0.181
	Fine Roots	5.202	0.571	4.553	0.795	8.444	1.194	6.605	0.483	0.181	0.012	0.507
	Soil 0.0-0.2 m	25.250	0.545	25.630	0.749	37.249	1.868	37.493	1.642	0.754	< 0.001	0.946
	Soil 0.2-0.4 m	28.743	1.705	27.367	0.770	43.444	2.803	42.652	2.547	0.658	< 0.001	0.905
	Soil 0.4-0.6 m	29.174	1.398	29.736	1.692	47.158	3.378	46.073	2.921	0.927	< 0.001	0.774
	Soil 0.6-1.0 m	28.440	0.316	30.504	2.314	47.089	4.222	39.943	7.768	0.643	0.025	0.407
GF	Foliage	3.604	0.251	3.561	0.386	-	-	-	-	0.929	-	-
	Branches	4.350	0.246	8.449	3.691	-	-	-	-	0.224	-	-
	Bark	4.917	0.619	3.371	0.556	-	-	-	-	0.113	-	-
	Wood	1.492	0.196	1.717	0.143	-	-	-	-	0.384	-	-
	Understory	5.797	1.227	5.459	0.006	-	-	-	-	0.797	-	-
	Forest Floor	3.588	0.204	3.166	0.345	-	-	-	-	0.101	-	-
	Fine Roots	5.211	0.727	4.452	0.550	-	-	-	-	0.445	-	-
	Soil 0.0-0.2 m	19.904	2.373	22.552	0.117	-	-	-	-	0.362	-	-
	Soil 0.2-0.4 m	22.744	1.796	25.057	0.925	-	-	-	-	0.361	-	-
	Soil 0.4-0.6 m	25.506	2.670	27.250	0.732	-	-	-	-	0.489	-	-
	Soil 0.6-1.0 m	25.516	3.262	28.778	0.993	-	-	-	-	0.316	-	-

Appendix Table S.5.8. Concentration (ppm) of iron (Fe) of tree and ecosystem components for 18 year-old Douglasfir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR Co	ontrol	CR Y	VM	CF Co	ontrol	CF	VM		P-val	ue
Species	Tissue	ppm	SE	ppm	SE	ppm	SE	ppm	SE	Trt	Site	Site x Trt
DF	Foliage	40.374	3.729	49.468	4.865	52.809	2.079	68.790	11.367	0.079	0.032	0.608
	Branches	32.965	6.804	31.799	7.397	19.074	3.130	41.479	21.153	0.386	0.862	0.338
	Bark	32.919	2.797	33.206	4.116	54.570	10.560	60.521	8.608	0.675	0.006	0.703
	Wood	15.673	2.541	12.119	0.381	24.705	4.188	25.887	2.668	0.679	0.002	0.414
	Understory	746.5	321.0	1199.1	241.2	1016.8	787.2	439.7	99.0	0.874	0.865	0.212
	Forest Floor	1355.6	157.3	1244.1	131.4	1204.0	83.9	1321.1	206.2	0.986	0.809	0.465
	Fine Roots	1332.1	86.6	1313.1	67.9	1854.4	213.8	1697.1	66.2	0.493	0.003	0.589
	Soil 0.0-0.2 m	18052.1	932.6	18670.7	534.4	25710.8	545.6	25234.2	492.5	0.915	<0.001	0.417
	Soil 0.2-0.4 m	19436.1	243.4	19776.3	770.1	26251.6	432.1	26065.6	85.5	0.870	<0.001	0.578
	Soil 0.4-0.6 m	20095.5	450.7	19477.7	1124.6	26734.7	478.1	26930.5	122.9	0.745	<0.001	0.536
	Soil 0.6-1.0 m	19961.9	956.5	19936.3	769.4	26681.4	1329.1	27978.8	663.9	0.522	<0.001	0.505
WH	Foliage	42.439	6.768	67.957	29.388	-	-	-	-	0.430	-	-
	Branches	25.985	3.878	33.484	3.966	-	-	-	-	0.225	-	-
	Bark	38.260	12.915	54.005	11.879	-	-	-	-	0.378	-	-
	Wood	26.125	8.471	13.569	0.725	-	-	-	-	0.217	-	-
	Understory	691.6	195.1	1070.4	146.1	-	-	-	-	0.171	-	-
	Forest Floor	836.7	177.8	990.5	282.2	-	-	-	-	0.587	-	-
	Fine Roots	1365.3	250.6	1229.8	90.1	-	-	-	-	0.629	-	-
	Soil 0.0-0.2 m	19842.0	228.0	19509.3	763.8	-	-	-	-	0.636	-	-
	Soil 0.2-0.4 m	21842.0	466.4	20587.4	447.2	-	-	-	-	0.046	-	-
	Soil 0.4-0.6 m	21574.0	433.2	21461.8	233.2	-	-	-	-	0.829	-	-
	Soil 0.6-1.0 m	22407.9	343.9	21729.7	267.0	-	-	-	-	0.170	-	-
WRC	Foliage	55.945	2.035	49.319	3.265	108.640	35.892	95.675	33.281	0.483	0.515	0.929
	Branches	35.320	6.059	49.661	16.892	64.994	32.138	17.001	0.599	0.408	0.893	0.127
	Bark	41.827	3.792	59.508	21.698	67.886	12.104	56.334	7.116	0.796	0.515	0.300
	Wood	17.690	4.188	46.565	28.724	18.277	3.498	22.328	1.780	0.283	0.435	0.413
	Understory	710.9	161.8	1269.6	262.2	1488.4	799.3	436.7	99.0	0.628	0.956	0.134
	Forest Floor	1009.5	155.7	1275.7	151.4	1076.1	448.1	1178.7	254.7	0.534	0.958	0.779
	Fine Roots	1045.1	273.2	1207.4	233.3	1827.3	162.1	1923.2	73.5	0.459	0.009	0.843
	Soil 0.0-0.2 m	18753.6	527.5	19124.6	216.0	25953.2	586.6	26380.8	596.3	0.073	< 0.001	0.878
	Soil 0.2-0.4 m	20710.5	453.7	19802.2	1024.9	26331.3	414.7	26317.4	335.8	0.344	< 0.001	0.358
	Soil 0.4-0.6 m	20918.1	241.2	21072.0	307.6	27076.7	488.9	26862.0	307.4	0.895	< 0.001	0.435
	Soil 0.6-1.0 m	22655.4	1529.0	20397.1	1157.8	27408.0	407.3	26420.7	1493.5	0.212	0.001	0.613
GF	Foliage	75.395	13.104	69.281	10.755	-	-	-	-	0.796	-	-
	Branches	42.971	9.619	33.885	6.139	-	-	-	-	0.456	-	-
	Bark	100.507	48.424	96.906	48.725	-	-	-	-	0.224	-	-
	Wood	12.196	1.599	26.540	4.913	-	-	-	-	0.032	-	-
	Understory	524.4	347.0	1514.9	66.2	-	-	-	-	0.075	-	-
	Forest Floor	1356.7	199.2	1061.1	109.4	-	-	-	-	0.263	-	-
	Fine Roots	1364.9	157.2	1404.0	83.2	-	-	-	-	0.670	-	-
	Soil 0.0-0.2 m	16258.4	2412.4	19208.8	300.2	-	-	-	-	0.292	-	-
	Soil 0.2-0.4 m	16941.2	1953.2	20431.8	386.1	-	-	-	-	0.154	-	-
	Soil 0.4-0.6 m	18975.3	2909.6	20353.0	363.7	-	-	-	-	0.643	-	-
	Soil 0.6-1.0 m	18841.3	3189.8	21688.8	326.8	-	-	-	-	0.451	-	_

Appendix Table S.5.9. Concentration (%) of potassium (K) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF C	ontrol	CF	VM		P-val	ue
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Foliage	0.580	0.042	0.446	0.026	0.750	0.056	0.654	0.069	0.043	0.003	0.720
	Branches	0.235	0.061	0.229	0.016	0.266	0.033	0.215	0.052	0.523	0.850	0.611
	Bark	0.230	0.013	0.283	0.034	0.200	0.012	0.175	0.027	0.576	0.052	0.065
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	1.465	0.652	0.770	0.368	1.702	0.233	1.528	0.412	0.345	0.310	0.565
	Forest Floor	0.155	0.025	0.117	0.014	0.251	0.024	0.179	0.016	0.014	0.004	0.326
	Fine Roots	0.208	0.026	0.199	0.044	0.091	0.010	0.075	0.012	0.645	0.001	0.906
	Soil 0.0-0.2 m	0.166	0.000	0.169	0.021	0.095	0.004	0.087	0.006	0.841	< 0.001	0.647
	Soil 0.2-0.4 m	0.160	0.020	0.145	0.019	0.081	0.009	0.069	0.005	0.345	< 0.001	0.900
	Soil 0.4-0.6 m	0.164	0.019	0.159	0.017	0.059	0.003	0.068	0.006	0.896	<0.001	0.581
	Soil 0.6-1.0 m	0.173	0.009	0.162	0.019	0.057	0.002	0.064	0.007	0.838	< 0.001	0.383
WH	Foliage	0.620	0.062	0.478	0.036	-	-	-	-	0.094	-	-
	Branches	0.157	0.007	0.169	0.043	-	-	-	-	0.791	-	-
	Bark	0.333	0.045	0.232	0.032	-	-	-	-	0.113	-	-
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	1.175	0.401	0.840	0.182	-	-	-	-	0.476	-	-
	Forest Floor	0.210	0.048	0.148	0.024	-	-	-	-	0.295	-	-
	Fine Roots	0.174	0.027	0.144	0.030	-	-	-	-	0.037	-	-
	Soil 0.0-0.2 m	0.153	0.015	0.135	0.006	-	-	-	-	0.289	-	-
	Soil 0.2-0.4 m	0.146	0.012	0.138	0.007	-	-	-	-	0.585	-	-
	Soil 0.4-0.6 m	0.135	0.012	0.144	0.009	-	-	-	-	0.579	-	-
	Soil 0.6-1.0 m	0.124	0.012	0.146	0.014	-	-	-	-	0.286	-	-
WRC	Foliage	0.339	0.071	0.346	0.031	0.358	0.042	0.482	0.045	0.068	0.243	0.423
	Branches	0.133	0.027	0.116	0.036	0.191	0.026	0.145	0.023	0.212	0.608	0.488
	Bark	0.162	0.041	0.140	0.017	0.146	0.020	0.170	0.030	0.995	0.468	0.933
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	1.024	0.488	0.790	0.370	1.147	0.206	1.540	0.171	0.641	0.762	0.112
	Forest Floor	0.431	0.148	0.160	0.025	0.185	0.070	0.149	0.087	0.122	0.186	0.226
	Fine Roots	0.177	0.016	0.129	0.010	0.108	0.011	0.078	0.010	0.009	0.001	0.469
	Soil 0.0-0.2 m	0.176	0.011	0.180	0.022	0.127	0.019	0.094	0.006	0.364	0.002	0.265
	Soil 0.2-0.4 m	0.171	0.005	0.166	0.013	0.082	0.011	0.086	0.011	0.967	< 0.001	0.380
	Soil 0.4-0.6 m	0.164	0.005	0.172	0.020	0.074	0.013	0.078	0.008	0.602	< 0.001	0.872
	Soil 0.6-1.0 m	0.182	0.036	0.201	0.036	0.079	0.018	0.061	0.010	0.990	0.001	0.371
GF	Foliage	0.433	0.034	0.586	0.072	-	-	-	-	0.064	-	-
	Branches	0.277	0.048	0.469	0.063	-	-	-	-	0.074	-	-
	Bark	0.371	0.071	0.240	0.032	-	-	-	-	0.140	-	-
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	1.263	0.254	0.627	0.063	-	-	-	-	0.082	-	-
	Forest Floor	0.153	0.021	0.111	0.017	-	-	-	-	0.068	-	-
	Fine Roots	0.130	0.015	0.142	0.018	-	-	-	-	0.438	-	-
	Soil 0.0-0.2 m	0.178	0.023	0.174	0.014	-	-	-	-	0.892	-	-
	Soil 0.2-0.4 m	0.141	0.009	0.159	0.010	-	-	-	-	0.241	-	-
	Soil 0.4-0.6 m	0.141	0.004	0.166	0.022	-	-	-	-	0.337	-	-
	Soil 0.6-1.0 m	0.157	0.017	0.196	0.037	-	-	-	-	0.396	-	_

Appendix Table S.5.10. Concentration (%) of magnesium (Mg) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF C	ontrol	CF	VM		P-val	ue
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Foliage	0.108	0.016	0.100	0.008	0.079	0.003	0.103	0.007	0.311	0.184	0.161
	Branches	0.052	0.015	0.039	0.004	0.032	0.003	0.035	0.003	0.305	0.393	0.168
	Bark	0.046	0.004	0.038	0.004	0.029	0.003	0.032	0.002	0.502	0.004	0.143
	Wood	0.011	0.002	0.010	0.001	0.009	0.001	0.007	0.000	0.196	0.144	0.594
	Understory	0.244	0.046	0.188	0.037	0.289	0.026	0.321	0.031	0.697	0.166	0.180
	Forest Floor	0.121	0.004	0.102	0.002	0.146	0.005	0.096	0.010	< 0.001	0.051	0.016
	Fine Roots	0.083	0.002	0.070	0.004	0.064	0.003	0.053	0.001	0.001	< 0.001	0.819
	Soil 0.0-0.2 m	0.287	0.009	0.287	0.013	0.146	0.009	0.157	0.015	0.650	< 0.001	0.641
	Soil 0.2-0.4 m	0.296	0.009	0.297	0.007	0.153	0.010	0.172	0.010	0.290	<0.001	0.351
	Soil 0.4-0.6 m	0.304	0.012	0.303	0.008	0.143	0.011	0.155	0.019	0.505	< 0.001	0.454
	Soil 0.6-1.0 m	0.315	0.013	0.306	0.015	0.142	0.011	0.145	0.026	0.866	<0.001	0.748
WH	Foliage	0.130	0.013	0.097	0.005	-	-	-	-	0.042	-	-
	Branches	0.035	0.003	0.031	0.005	-	-	-	-	0.258	-	-
	Bark	0.050	0.006	0.035	0.000	-	-	-	-	0.048	-	-
	Wood	0.017	0.002	0.013	0.000	-	-	-	-	0.125	-	-
	Understory	0.343	0.076	0.228	0.037	-	-	-	-	0.226	-	-
	Forest Floor	0.168	0.019	0.123	0.018	-	-	-	-	0.129	-	-
	Fine Roots	0.100	0.006	0.088	0.008	-	-	-	-	0.297	-	-
	Soil 0.0-0.2 m	0.257	0.006	0.258	0.006	-	-	-	-	0.816	-	-
	Soil 0.2-0.4 m	0.267	0.007	0.274	0.010	-	-	-	-	0.567	-	-
	Soil 0.4-0.6 m	0.272	0.011	0.278	0.015	-	-	-	-	0.743	-	-
	Soil 0.6-1.0 m	0.235	0.030	0.286	0.012	-	-	-	-	0.161	-	-
WRC	Foliage	0.138	0.016	0.108	0.015	0.092	0.009	0.083	0.015	0.149	0.063	0.417
	Branches	0.037	0.005	0.040	0.004	0.039	0.005	0.026	0.004	0.316	0.230	0.101
	Bark	0.064	0.006	0.049	0.005	0.049	0.004	0.046	0.004	0.079	0.065	0.223
	Wood	0.017	0.001	0.021	0.004	0.016	0.001	0.015	0.001	0.532	0.182	0.261
	Understory	0.242	0.065	0.264	0.092	0.274	0.074	0.329	0.021	0.486	0.614	0.764
	Forest Floor	0.232	0.033	0.111	0.014	0.098	0.018	0.089	0.030	0.030	0.019	0.054
	Fine Roots	0.091	0.017	0.095	0.010	0.071	0.007	0.067	0.008	0.997	0.045	0.741
	Soil 0.0-0.2 m	0.289	0.012	0.306	0.020	0.156	0.011	0.149	0.006	0.666	< 0.001	0.344
	Soil 0.2-0.4 m	0.298	0.003	0.314	0.015	0.160	0.010	0.161	0.012	0.364	< 0.001	0.456
	Soil 0.4-0.6 m	0.295	0.009	0.324	0.016	0.160	0.019	0.168	0.012	0.271	< 0.001	0.526
AF	Soil 0.6-1.0 m	0.276	0.014	0.329	0.030	0.147	0.027	0.171	0.024	0.162	0.000	0.585
GF	Foliage	0.137	0.019	0.124	0.015	-	-	-	-	0.306	-	-
	Branches	0.042	0.003	0.065	0.019	-	-	-	-	0.273	-	-
	Bark	0.062	0.007	0.048	0.004	-	-	-	-	0.151	-	-
	Wood	0.016	0.002	0.016	0.001	-	-	-	-	0.850	-	-
	Understory	0.326	0.062	0.203	0.027	-	-	-	-	0.143	-	-
	Forest Floor	0.129	0.005	0.116	0.004	-	-	-	-	0.112	-	-
	Fine Roots	0.109	0.005	0.101	0.010	-	-	-	-	0.476	-	-
	Soil 0.0-0.2 m	0.262	0.016	0.306	0.010	-	-	-	-	0.134	-	-
	Soil 0.2-0.4 m	0.290	0.004	0.309	0.003	-	-	-	-	0.057	-	-
	Soil 0.4-0.6 m	0.289	0.018	0.318	0.009	-	-	-	-	0.211	-	-
	5011 U.6- L.U m	0.295	0.025	0.321	0.009	-	-	-	-	LU. 578	-	-

Appendix Table S.5.11. Concentration (ppm) of manganese (Mn) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF Co	ontrol	CF	VM		P-val	ue
Species	Tissue	ppm	SE	ppm	SE	ppm	SE	ppm	SE	Trt	Site	Site x Trt
DF	Foliage	271.573	61.568	344.996	67.393	432.704	38.328	426.917	27.675	0.539	0.039	0.460
	Branches	129.633	71.133	106.285	28.216	121.678	7.842	120.083	8.276	0.394	0.483	0.422
	Bark	98.112	18.562	90.838	22.471	191.671	47.236	138.879	14.168	0.259	0.022	0.337
	Wood	11.539	1.825	14.203	2.188	33.353	5.435	23.106	4.387	0.335	0.002	0.113
	Understory	758.15	473.96	472.71	140.72	654.28	75.68	767.36	153.95	0.702	0.979	0.386
	Forest Floor	392.41	38.08	496.48	47.81	771.35	56.15	892.64	77.42	0.070	< 0.001	0.882
	Fine Roots	178.05	29.82	203.47	19.50	632.16	106.62	516.00	40.72	0.463	< 0.001	0.259
	Soil 0.0-0.2 m	1080.93	150.39	1060.01	196.26	3232.82	184.29	3249.19	473.06	0.994	<0.001	0.948
	Soil 0.2-0.4 m	a 870.24	175.56	804.17	165.54	2366.88	384.96	3112.45	699.82	0.426	0.002	0.346
	Soil 0.4-0.6 m	n 723.95	155.04	654.69	114.49	811.16	192.02	1887.14	343.45	0.033	0.046	0.020
	Soil 0.6-1.0 m	n 225.84	28.98	395.10	97.23	966.85	461.01	1064.67	246.35	0.625	0.021	0.896
WH	Foliage	799.005	168.960	01073.50	242.655	-	-	-	-	0.389	-	-
	Branches	189.007	25.444	247.766	28.186	-	-	-	-	0.152	-	-
	Bark	249.825	28.857	286.523	24.111	-	-	-	-	0.191	-	-
	Wood	51.259	27.149	93.457	7.957	-	-	-	-	0.176	-	-
	Understory	501.8	80.4	463.8	65.7	-	-	-	-	0.727	-	-
	Forest Floor	551.5	69.7	1115.2	217.1	-	-	-	-	0.045	-	-
	Fine Roots	235.7	20.2	209.6	9.7	-	-	-	-	0.230	-	-
	Soil 0.0-0.2 m	n 1062.1	167.1	1039.2	56.5	-	-	-	-	0.888	-	-
	Soil 0.2-0.4 m	923.2	201.5	940.1	92.1	-	-	-	-	0.942	-	-
	Soil 0.4-0.6 m	n 828.8	166.2	737.7	147.3	-	-	-	-	0.696	-	-
	Soil 0.6-1.0 m	n 524.8	135.6	301.8	38.4	-	-	-	-	0.165	-	-
WRC	Foliage	160.700	16.861	164.770	22.525	202.880	45.269	180.770	28.585	0.771	0.355	0.673
	Branches	37.941	5.153	45.612	12.221	54.784	8.177	32.658	1.734	0.425	0.623	0.113
	Bark	64.099	10.459	56.797	13.899	64.913	21.088	58.199	7.810	0.520	0.772	0.966
	Wood	11.506	2.547	5.116	1.292	9.005	1.786	7.436	0.699	0.128	0.810	0.297
	Understory	232.2	27.6	292.0	42.0	685.6	121.6	761.4	168.2	0.369	0.013	0.912
	Forest Floor	260.4	64.7	258.0	87.9	638.7	300.8	543.7	113.7	0.781	0.201	0.792
	Fine Roots	196.3	36.9	287.9	54.1	706.6	71.8	782.4	18.1	0.137	<0.001	0.881
	Soil 0.0-0.2 m	n 1393.0	206.3	1625.1	256.6	4086.6	682.5	4759.8	421.7	0.175	0.000	0.479
	Soil 0.2-0.4 m	n 1616.0	3.2	1409.3	245.8	3546.6	626.0	3806.4	505.7	0.924	0.003	0.416
	Soil 0.4-0.6 m	n 1298.1	204.8	1076.1	289.7	2603.5	397.5	1762.5	529.6	0.264	0.085	0.493
	Soil 0.6-1.0 m	n 525.4	147.3	554.8	230.6	1166.4	211.4	931.9	181.0	0.620	0.029	0.525
GF	Foliage	554.176	72.747	544.599	117.144	-	-	-	-	0.947	-	-
	Branches	121.206	15.724	151.747	56.146	-	-	-	-	0.619	-	-
	Bark	250.708	81.151	237.247	44.464	-	-	-	-	0.526	-	-
	Wood	38.854	8.016	31.816	8.358	-	-	-	-	0.478	-	-
	Understory	589.4	295.8	380.9	2.3	-	-	-	-	0.520	-	-
	Forest Floor	579.4	28.5	793.8	88.7	-	-	-	-	0.088	-	-
	Fine Roots	258.0	30.5	268.6	21.8	-	-	-	-	0.792	-	-
	Soil 0.0-0.2 m	n 1085.2	125.9	1802.1	131.4	-	-	-	-	0.017	-	-
	Soil 0.2-0.4 m	n 1047.6	145.0	1274.9	286.6	-	-	-	-	0.518	-	-
	Soil 0.4-0.6 m	1 757.2	230.0	1117.8	266.1	-	-	-	-	0.363	-	-
	Soil 0.6-1.0 m	437.8	201.8	449.6	143.2	-	-	-	-	0.964	-	-

Appendix Table S.5.12. Concentration (%) of nitrogen (N) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF C	ontrol	CF	VM		P-val	ue
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Foliage	1.174	0.044	1.348	0.267	1.232	0.061	1.255	0.028	0.495	0.901	0.598
	Branches	0.336	0.041	0.313	0.018	0.222	0.019	0.223	0.032	0.708	0.004	0.696
	Bark	0.338	0.044	0.313	0.042	0.256	0.017	0.270	0.036	0.874	0.109	0.594
	Wood	0.043	0.005	0.042	0.007	0.134	0.024	0.091	0.025	0.273	0.007	0.273
	Understory	1.344	0.378	1.034	0.034	1.378	0.134	1.638	0.091	0.902	0.181	0.181
	Forest Floor	0.938	0.201	1.080	0.074	0.968	0.025	0.958	0.078	0.571	0.719	0.511
	Fine Roots	0.647	0.027	0.611	0.066	0.580	0.054	0.525	0.017	0.291	0.114	0.824
	Soil 0.0-0.2 m	0.239	0.007	0.249	0.050	0.263	0.026	0.249	0.022	0.943	0.703	0.709
	Soil 0.2-0.4 m	0.162	0.023	0.113	0.004	0.179	0.027	0.206	0.026	0.547	0.016	0.061
	Soil 0.4-0.6 m	0.137	0.022	0.069	0.016	0.084	0.010	0.115	0.008	0.161	0.602	0.004
	Soil 0.6-1.0 m	0.046	0.003	0.061	0.004	0.048	0.008	0.066	0.009	0.011	0.144	0.791
WH	Foliage	1.065	0.024	1.002	0.059	-	-	-	-	0.237	-	-
	Branches	0.270	0.026	0.252	0.025	-	-	-	-	0.622	-	-
	Bark	0.283	0.049	0.320	0.020	-	-	-	-	0.506	-	-
	Wood	0.076	0.007	0.069	0.005	-	-	-	-	0.412	-	-
	Understory	1.625	0.219	1.319	0.074	-	-	-	-	0.275	-	-
	Forest Floor	1.125	0.027	0.680	0.028	-	-	-	-	< 0.001	-	-
	Fine Roots	0.538	0.053	0.506	0.014	-	-	-	-	0.592	-	-
	Soil 0.0-0.2 m	0.197	0.015	0.215	0.019	-	-	-	-	0.378	-	-
	Soil 0.2-0.4 m	0.148	0.036	0.156	0.013	-	-	-	-	0.817	-	-
	Soil 0.4-0.6 m	0.084	0.010	0.127	0.030	-	-	-	-	0.224	-	-
	Soil 0.6-1.0 m	0.059	0.006	0.053	0.006	-	-	-	-	0.502	-	-
WRC	Foliage	0.982	0.059	1.137	0.218	1.037	0.213	0.757	0.070	0.700	0.327	0.196
	Branches	0.262	0.046	0.264	0.033	0.223	0.023	0.117	0.015	0.120	0.012	0.111
	Bark	0.234	0.019	0.221	0.004	0.304	0.021	0.291	0.041	0.618	0.017	0.995
	Wood	0.114	0.013	0.097	0.020	0.390	0.050	0.350	0.096	0.345	0.006	0.570
	Understory	1.600	0.367	1.243	0.199	1.181	0.261	1.502	0.081	0.926	0.712	0.115
	Forest Floor	1.227	0.217	0.690	0.065	0.638	0.077	0.635	0.109	0.054	0.026	0.056
	Fine Roots	0.589	0.078	0.555	0.065	0.545	0.026	0.530	0.011	0.597	0.466	0.833
	Soil 0.0-0.2 m	0.299	0.029	0.223	0.019	0.240	0.022	0.244	0.010	0.107	0.359	0.077
	Soil 0.2-0.4 m	0.196	0.038	0.155	0.014	0.198	0.033	0.162	0.027	0.041	0.362	0.851
	Soil 0.4-0.6 m	0.140	0.024	0.089	0.016	0.128	0.027	0.078	0.006	0.034	0.580	0.998
	Soil 0.6-1.0 m	0.063	0.012	0.051	0.001	0.078	0.010	0.053	0.009	0.070	0.284	0.436
GF	Foliage	1.150	0.085	1.072	0.047	-	-	-	-	0.525	-	-
	Branches	0.281	0.045	0.476	0.170	-	-	-	-	0.312	-	-
	Bark	0.408	0.045	0.288	0.047	-	-	-	-	0.116	-	-
	Wood	0.096	0.010	0.086	0.020	-	-	-	-	0.708	-	-
	Understory	1.307	0.285	1.323	0.107	-	-	-	-	0.959	-	-
	Forest Floor	1.033	0.154	0.977	0.201	-	-	-	-	0.834	-	-
	Fine Roots	0.637	0.119	0.557	0.040	-	-	-	-	0.560	-	-
	Soil 0.0-0.2 m	0.322	0.064	0.262	0.011	-	-	-	-	0.411	-	-
	Soil 0.2-0.4 m	0.156	0.004	0.167	0.032	-	-	-	-	0.753	-	-
	Soil 0.4-0.6 m	0.105	0.010	0.107	0.026	-	-	-	-	0.965	-	-
	Soil 0 6-1 0 m	0.067	0.014	0.050	0.006	_	-	_	-	0 315	_	-

Appendix Table S.5.13. Concentration (ppm) of sodium (Na) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR V	VM	CF C	ontrol	CF V	M		P-val	ue
Species	Tissue	ppm	SE	ppm	SE	ppm	SE	ppm	SE	Trt	Site	Site x Trt
DF	Foliage	148.580	25.340	229.924	41.497	94.074	12.767	70.104	3.895	0.277	0.001	0.059
	Branches	47.097	20.326	33.214	4.105	2.848	3.269	6.462	7.574	0.619	0.018	0.417
	Bark	252.500	122.419	102.548	3.745	28.500	4.201	41.981	8.322	0.288	0.073	0.212
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	205.89	48.98	171.86	25.79	177.92	30.71	148.38	34.07	0.309	0.460	0.941
	Forest Floor	177.49	13.68	160.98	8.77	133.90	1.00	128.11	12.63	0.193	0.005	0.511
	Fine Roots	157.85	28.11	139.01	8.50	92.85	13.78	80.67	7.66	0.232	0.005	0.786
	Soil 0.0-0.2 m	173.16	14.92	186.22	5.97	122.03	2.45	124.80	3.52	0.360	< 0.001	0.548
	Soil 0.2-0.4 m	171.23	8.21	173.98	4.29	174.77	17.92	185.24	21.00	0.544	0.200	0.720
	Soil 0.4-0.6 m	217.99	12.33	255.96	15.92	137.91	3.83	135.33	9.93	0.055	< 0.001	0.034
	Soil 0.6-1.0 m	161.13	6.46	174.59	5.52	123.29	7.92	116.91	6.87	0.469	< 0.001	0.066
WH	Foliage	117.286	10.844	142.831	36.381	-	-	-	-	0.526	-	-
	Branches	1.778	4.232	6.563	2.151	-	-	-	-	0.165	-	-
	Bark	89.351	21.525	76.812	8.700	-	-	-	-	0.610	-	-
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	246.05	42.27	191.50	31.67	-	-	-	-	0.341	-	-
	Forest Floor	163.11	11.97	160.60	3.07	-	-	-	-	0.845	-	-
	Fine Roots	119.53	8.76	130.86	6.55	-	-	-	-	0.211	-	-
	Soil 0.0-0.2 m	153.37	3.94	158.00	7.24	-	-	-	-	0.595	-	-
	Soil 0.2-0.4 m	187.92	9.38	204.82	15.36	-	-	-	-	0.384	-	-
	Soil 0.4-0.6 m	188.64	9.19	189.55	15.14	-	-	-	-	0.954	-	-
	Soil 0.6-1.0 m	149.90	1.42	149.69	9.37	-	-	-	-	0.983	-	-
WRC	Foliage	130.180	36.392	96.327	5.043	66.372	29.553	66.150	9.657	0.409	0.122	0.416
	Branches	14.398	14.133	11.174	2.879	2.072	6.913	-7.412	2.992	0.450	0.082	0.707
	Bark	63.242	6.253	55.987	5.957	22.849	4.542	20.074	5.938	0.397	< 0.001	0.702
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	164.66	35.07	237.94	68.48	171.04	46.74	179.00	55.39	0.247	0.111	0.338
	Forest Floor	203.49	19.58	164.50	3.94	94.85	8.27	101.09	8.60	0.164	<0.001	0.074
	Fine Roots	180.45	58.79	132.43	4.16	131.37	31.66	78.64	7.98	0.126	0.193	0.937
	Soil 0.0-0.2 m	156.19	19.24	158.06	7.61	132.26	9.62	136.84	9.04	0.786	0.116	0.909
	Soil 0.2-0.4 m	229.57	16.06	212.81	22.44	189.91	12.14	235.59	11.64	0.365	0.592	0.068
	Soil 0.4-0.6 m	190.92	12.75	169.88	6.10	133.48	5.52	135.68	9.11	0.301	< 0.001	0.209
	Soil 0.6-1.0 m	180.45	9.67	188.02	7.09	116.35	8.89	119.86	6.11	0.510	< 0.001	0.808
GF	Foliage	67.127	15.166	72.742	10.920	-	-	-	-	0.774	-	-
	Branches	30.592	17.391	36.721	9.497	-	-	-	-	0.665	-	-
	Bark	62.789	6.010	50.629	7.701	-	-	-	-	0.083	-	-
	Wood	-	-	-	-	-	-	-	-	-	-	-
	Understory	248.70	21.53	222.58	1.61	-	-	-	-	0.337	-	-
	Forest Floor	135.31	4.48	140.73	8.22	-	-	-	-	0.302	-	-
	Fine Roots	122.17	9.84	158.62	27.13	-	-	-	-	0.268	-	-
	Soil 0.0-0.2 m	166.06	10.84	196.64	1.72	-	-	-	-	0.050	-	-
	Soil 0.2-0.4 m	206.18	4.78	212.21	22.39	-	-	-	-	0.812	-	-
	Soil 0.4-0.6 m	185.03	1.59	188.50	8.36	-	-	-	-	0.675	-	-
	Soil 0.6-1.0 m	178.57	16.87	159.85	21.69	-	-	_	-	0.353	-	-

Appendix Table S.5.14. Concentration (%) of phosphorus (P) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites locate d in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF C	ontrol	CF	VM		P-val	ue
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Foliage	0.163	0.018	0.169	0.019	0.213	0.005	0.193	0.023	0.664	0.084	0.462
	Branches	0.060	0.014	0.056	0.007	0.065	0.009	0.061	0.010	0.610	0.484	0.942
	Bark	0.059	0.005	0.059	0.006	0.055	0.002	0.053	0.003	0.780	0.417	0.927
	Wood	0.004	0.000	0.003	0.000	0.007	0.002	0.004	0.001	0.155	0.092	0.189
	Understory	0.146	0.046	0.105	0.012	0.207	0.027	0.254	0.034	0.895	0.008	0.088
	Forest Floor	0.087	0.009	0.089	0.006	0.093	0.008	0.096	0.006	0.730	0.371	0.991
	Fine Roots	0.078	0.004	0.080	0.012	0.068	0.002	0.081	0.009	0.242	0.334	0.378
	Soil 0.0-0.2 m	0.526	0.028	0.555	0.041	1.018	0.078	0.954	0.054	0.752	< 0.001	0.404
	Soil 0.2-0.4 m	0.561	0.120	0.380	0.024	0.879	0.086	0.877	0.080	0.276	0.001	0.285
	Soil 0.4-0.6 m	0.504	0.077	0.349	0.026	0.662	0.058	0.687	0.054	0.273	0.001	0.138
	Soil 0.6-1.0 m	0.273	0.028	0.334	0.028	0.736	0.193	0.647	0.048	0.892	0.002	0.475
WH	Foliage	0.280	0.044	0.230	0.031	-	-	-	-	0.397	-	-
	Branches	0.043	0.004	0.044	0.005	-	-	-	-	0.875	-	-
	Bark	0.095	0.009	0.077	0.005	-	-	-	-	0.127	-	-
	Wood	0.010	0.003	0.010	0.002	-	-	-	-	0.973	-	-
	Understory	0.197	0.044	0.157	0.005	-	-	-	-	0.405	-	-
	Forest Floor	0.105	0.004	0.109	0.005	-	-	-	-	0.413	-	-
	Fine Roots	0.086	0.006	0.083	0.012	-	-	-	-	0.695	-	-
	Soil 0.0-0.2 m	0.708	0.154	0.674	0.074	-	-	-	-	0.814	-	-
	Soil 0.2-0.4 m	0.637	0.174	0.617	0.103	-	-	-	-	0.921	-	-
	Soil 0.4-0.6 m	0.541	0.083	0.505	0.061	-	-	-	-	0.710	-	-
	Soil 0.6-1.0 m	0.362	0.071	0.332	0.039	-	-	-	-	0.408	-	-
WRC	Foliage	0.127	0.009	0.113	0.007	0.113	0.012	0.109	0.015	0.440	0.441	0.650
	Branches	0.031	0.006	0.039	0.004	0.044	0.005	0.042	0.007	0.700	0.361	0.404
	Bark	0.053	0.007	0.039	0.002	0.052	0.002	0.050	0.006	0.140	0.319	0.228
	Wood	0.005	0.000	0.006	0.001	0.007	0.001	0.006	0.001	0.694	0.133	0.250
	Understory	0.164	0.041	0.168	0.045	0.176	0.040	0.246	0.030	0.357	0.344	0.403
	Forest Floor	0.100	0.018	0.090	0.021	0.064	0.012	0.064	0.021	0.713	0.060	0.726
	Fine Roots	0.082	0.003	0.078	0.013	0.064	0.003	0.081	0.005	0.371	0.310	0.162
	Soil 0.0-0.2 m	0.763	0.084	0.826	0.076	1.083	0.161	1.150	0.180	0.438	0.005	0.981
	Soil 0.2-0.4 m	0.642	0.079	0.602	0.056	0.805	0.102	0.869	0.151	0.838	0.009	0.404
	Soil 0.4-0.6 m	0.560	0.008	0.484	0.030	0.683	0.111	0.575	0.103	0.112	0.018	0.749
	Soil 0.6-1.0 m	0.400	0.018	0.364	0.032	0.548	0.071	0.536	0.156	0.819	0.202	0.909
GF	Foliage	0.136	0.008	0.155	0.016	-	-	-	-	0.348	-	-
	Branches	0.064	0.009	0.112	0.025	-	-	-	-	0.122	-	-
	Bark	0.078	0.010	0.052	0.006	-	-	-	-	0.073	-	-
	Wood	0.006	0.000	0.007	0.002	-	-	-	-	0.547	-	-
	Understory	0.175	0.053	0.144	0.005	-	-	-	-	0.594	-	-
	Forest Floor	0.098	0.012	0.111	0.011	-	-	-	-	0.468	-	-
	Fine Roots	0.098	0.008	0.111	0.020	-	-	-	-	0.586	-	-
	Soil 0.0-0.2 m	0.732	0.174	0.923	0.166	-	-	-	-	0.471	-	-
	Soil 0.2-0.4 m	0.464	0.057	0.649	0.157	-	-	-	-	0.331	-	-
	Soil 0.4-0.6 m	0.481	0.148	0.498	0.091	-	-	-	-	0.925	-	-
	Soil 0 6-1 0 m	0.382	0 161	0 365	0.006	-	-	-	-	0.923	-	-

Appendix Table S.5.15. Concentration (%) of Sulfur (S) of tree and ecosystem components for 18 year-old Douglasfir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF C	ontrol	CF	VM		P-val	ue
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Foliage	0.121	0.006	0.154	0.039	0.115	0.004	0.111	0.002	0.463	0.229	0.367
	Branches	0.065	0.005	0.061	0.004	0.049	0.002	0.052	0.003	0.244	0.006	0.024
	Bark	0.065	0.011	0.051	0.002	0.049	0.003	0.049	0.002	0.291	0.188	0.308
	Wood	0.032	0.001	0.034	0.003	0.030	0.000	0.033	0.001	0.244	0.509	0.790
	Understory	0.157	0.029	0.113	0.004	0.147	0.012	0.168	0.017	0.554	0.279	0.099
	Forest Floor	0.106	0.012	0.112	0.007	0.114	0.006	0.113	0.002	0.592	0.994	0.494
	Fine Roots	0.079	0.005	0.080	0.001	0.071	0.005	0.075	0.002	0.524	0.103	0.661
WH	Foliage	0.110	0.018	0.092	0.019	-	-	-	-	0.481	-	-
	Branches	0.052	0.003	0.050	0.003	-	-	-	-	0.370	-	-
	Bark	0.055	0.004	0.057	0.006	-	-	-	-	0.529	-	-
	Wood	0.032	0.000	0.032	0.001	-	-	-	-	0.878	-	-
	Understory	0.160	0.015	0.172	0.006	-	-	-	-	0.452	-	-
	Forest Floor	0.104	0.006	0.107	0.006	-	-	-	-	0.784	-	-
	Fine Roots	0.075	0.004	0.068	0.002	-	-	-	-	0.234	-	-
WRC	Foliage	0.077	0.011	0.058	0.001	0.084	0.003	0.078	0.003	0.071	0.071	0.399
	Branches	0.048	0.004	0.050	0.001	0.045	0.002	0.036	0.003	0.301	0.011	0.081
	Bark	0.063	0.010	0.055	0.004	0.048	0.000	0.047	0.001	0.429	0.012	0.449
	Wood	0.035	0.001	0.036	0.002	0.036	0.001	0.035	0.002	0.663	0.680	0.119
	Understory	0.148	0.014	0.150	0.016	0.121	0.012	0.122	0.003	0.886	0.026	0.957
	Forest Floor	0.116	0.017	0.100	0.015	0.080	0.005	0.074	0.005	0.302	0.027	0.648
	Fine Roots	0.079	0.005	0.080	0.005	0.074	0.003	0.076	0.002	0.524	0.103	0.661
GF	Foliage	0.102	0.015	0.090	0.011	-	-	-	-	0.900	-	-
	Branches	0.053	0.003	0.070	0.008	-	-	-	-	0.113	-	-
	Bark	0.062	0.002	0.053	0.002	-	-	-	-	0.019	-	-
	Wood	0.033	0.002	0.034	0.003	-	-	-	-	0.873	-	-
	Understory	0.187	0.019	0.150	0.005	-	-	-	-	0.134	-	-
	Forest Floor	0.101	0.007	0.099	0.011	-	-	-	-	0.885	-	-
	Fine Roots	0.084	0.004	0.074	0.004	-	-	-	-	11.520) _	-

Appendix Table S.5.16. Concentration (ppm) of zinc (Zn) of tree and ecosystem components for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR C	ontrol	CR	VM	CF C	ontrol	CF	VM		P-va	lue
Species	Tissue	ppm	SE	ppm	SE	ppm	SE	ppm	SE	Trt	Site	Site x Trt
DF	Foliage	11.031	2.015	10.416	0.856	12.386	1.079	11.922	2.705	0.897	0.841	0.881
	Branches	19.187	2.456	18.013	1.075	14.970	2.112	13.522	2.780	0.422	0.092	0.965
	Bark	16.825	0.555	18.194	1.248	17.993	3.263	16.904	1.087	0.927	0.997	0.515
	Wood	3.674	0.681	3.001	0.380	4.635	0.741	4.906	0.793	0.769	0.053	0.494
	Understory	26.617	11.655	16.493	6.024	21.821	2.580	33.762	5.748	0.903	0.408	0.155
	Forest Floor	9.793	1.488	10.135	1.217	15.676	1.857	14.442	1.495	0.777	0.020	0.620
	Fine Roots	10.979	0.876	12.399	1.642	12.767	1.252	10.983	0.367	0.836	0.799	0.102
	Soil 0.0-0.2 m	58.228	3.024	65.472	7.464	67.605	3.764	69.057	11.592	0.527	0.534	0.671
	Soil 0.2-0.4 m	61.790	2.428	56.924	6.136	62.827	3.904	69.478	11.360	0.892	0.471	0.396
	Soil 0.4-0.6 m	62.669	2.541	57.902	7.540	50.524	3.791	57.838	9.597	0.846	0.405	0.375
	Soil 0.6-1.0 m	50.815	4.120	54.975	5.893	49.460	12.250	51.591	8.244	0.679	0.658	0.893
WH	Foliage	11.686	0.896	10.341	0.983	-	-	-	-	0.351	-	-
	Branches	9.741	2.491	7.155	1.007	-	-	-	-	0.373	-	-
	Bark	7.075	1.283	5.218	1.207	-	-	-	-	0.333	-	-
	Wood	3.645	0.942	3.168	0.487	-	-	-	-	0.683	-	-
	Understory	27.572	7.117	13.608	0.456	-	-	-	-	0.131	-	-
	Forest Floor	14.366	0.997	12.490	1.538	-	-	-	-	0.346	-	-
	Fine Roots	10.428	0.565	10.376	1.370	-	-	-	-	0.973	-	-
	Soil 0.0-0.2 m	67.528	3.716	66.495	2.980	-	-	-	-	0.836	-	-
	Soil 0.2-0.4 m	70.611	4.061	65.751	4.357	-	-	-	-	0.446	-	-
	Soil 0.4-0.6 m	67.979	5.162	64.724	2.614	-	-	-	-	0.594	-	-
	Soil 0.6-1.0 m	53.941	5.279	53.569	1.731	-	-	-	-	0.935	-	-
WRC	Foliage	16.022	1.474	12.557	0.827	15.489	1.906	13.358	1.630	0.089	0.931	0.667
	Branches	10.508	1.384	9.513	0.823	9.059	2.663	5.889	0.947	0.225	0.145	0.516
	Bark	18.825	5.188	12.305	2.538	11.587	2.558	9.807	0.453	0.215	0.150	0.469
	Wood	2.012	0.044	2.494	0.350	2.889	0.592	3.038	0.564	0.492	0.136	0.716
	Understory	19.021	6.003	14.034	3.098	20.366	5.086	31.775	5.296	0.549	0.095	0.145
	Forest Floor	13.283	1.445	14.650	7.188	15.039	2.856	10.771	2.520	0.691	0.708	0.448
	Fine Roots	13.898	1.484	10.095	0.611	35.193	17.267	19.389	4.405	0.287	0.365	0.499
	Soil 0.0-0.2 m	67.375	7.071	71.251	4.990	80.082	9.555	86.671	4.025	0.292	0.036	0.772
	Soil 0.2-0.4 m	77.650	6.002	68.045	5.955	71.207	6.946	78.539	6.081	0.749	0.535	0.051
	Soil 0.4-0.6 m	75.434	9.748	66.819	4.836	62.587	6.037	68.148	5.730	0.823	0.604	0.334
	Soil 0.6-1.0 m	46.951	8.450	57.207	4.117	50.765	4.232	61.533	12.002	0.238	0.570	0.975
GF	Foliage	24.702	3.402	24.965	5.025	-	-	-	-	0.300	-	-
	Branches	14.174	3.192	16.743	2.596	-	-	-	-	0.562	-	-
	Bark	17.857	2.810	8.741	0.635	-	-	-	-	0.019	-	-
	Wood	4.353	0.877	3.680	0.325	-	-	-	-	0.499	-	-
	Understory	19.750	7.024	17.388	5.177	-	-	-	-	0.800	-	-
	Forest Floor	17.965	3.157	20.271	2.256	-	-	-	-	0.584	-	-
	Fine Roots	14.379	0.757	16.935	5.214	-	-	-	-	0.624	-	-
	Soil 0.0-0.2 m	65.707	1.521	83.900	6.691	-	-	-	-	0.078	-	-
	Soil 0.2-0.4 m	75.079	3.157	75.342	10.140	-	-	-	-	0.976	-	-
	Soil 0.4-0.6 m	66.434	2.161	75.266	8.629	-	-	-	-	0.377	-	-
	Soil 0.6-1.0 m	56.841	5.840	57.043	4.607	-	-	-	-	0.980	-	-

Appendix Table S.3.1. Results of ANOVA test for potassium (K) and sodium (Na) plant derived nutrient pools for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). High concentration assumes stem tissue concentrations of 1.5 ppm Na and 0.03% K in all species. Low concentration assumes stem tissue concentrations of 0.05 ppm and 0.01% K in all species. Significant differences are highlighted in bold.

Assumption	Nutrient	Spp	Site	Trt	Site x Spp	Spp x Trt	Site x Trt	Site x Spp x Trt
High	К	0.015	0.343	0.088	0.491	0.019	0.123	0.120
C	Na	< 0.001	<0.001	0.425	<0.001	0.260	0.124	0.266
Low	K	0.015	0.539	0.100	0.657	0.032	0.200	0.199
	Na	<0.001	<0.001	0.431	<0.001	0.266	0.134	0.248

Appendix Table S.3.2. Results of ANOVA test for nutrient pools of plant and soil derived boron (B) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

B - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.211	0.004	0.002	0.060	0.155	0.005	0.123
Foliage	<0.001	<0.001	<0.001	<0.001	0.344	<0.001	0.132
Bark	0.014	0.002	<0.001	0.662	0.190	0.007	0.085
Branch	0.030	<0.001	<0.001	0.822	0.611	<0.001	0.014
Wood	0.834	<0.001	<0.001	0.235	0.393	<0.001	0.196
Plant Roots	0.209	0.223	0.577	0.294	0.745	0.407	0.856
Mid Foliage	0.038	0.064	0.002	0.006	0.028	0.064	0.004
Mid Wood	0.015	0.091	0.001	0.003	0.016	0.097	0.003
Forest Floor	0.276	0.001	0.759	0.840	0.275	0.371	0.260
Understory	0.063	0.679	0.005	0.189	0.143	0.378	0.392
Veg Roots	<0.001	0.003	<0.001	<0.001	<0.001	0.004	<0.001
Soil	<0.001	0.701	0.436	0.814	0.779	0.728	0.803
0.0-0.2 m	<0.001	0.121	0.043	0.010	0.694	0.697	0.603
0.2-0.4 m	<0.001	0.129	0.227	0.801	0.932	0.386	0.148
0.4-0.6 m	<0.001	0.661	0.819	0.840	0.788	0.979	0.570
1.0-0.6 m	<0.001	0.594	0.855	0.256	0.823	0.574	0.715

western Oregon (S	western Oregon (Site). Significant differences are highlighted in bold.										
<u>C - Pool</u>	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt				
Plant	<0.001	0.048	0.003	0.013	0.003	0.001	0.018				
Foliage	0.073	0.006	<0.001	0.851	0.713	<0.001	0.156				
Bark	0.003	<0.001	<0.001	0.649	0.406	0.001	0.017				
Branch	0.001	<0.001	<0.001	0.437	0.633	0.003	0.026				
Wood	<0.001	<0.001	<0.001	0.023	0.568	<0.001	0.025				
Plant Roots	0.105	0.007	0.160	0.849	0.878	0.186	0.376				
Mid Foliage	0.104	0.071	0.004	0.026	0.076	0.071	0.019				
Mid Wood	0.009	0.067	0.001	0.002	0.008	0.072	0.001				
Forest Floor	0.585	0.010	0.516	0.881	0.338	0.609	0.630				
Understory	0.835	0.339	<0.001	0.593	0.515	0.636	0.405				
Veg Roots	<0.001	0.013	<0.001	<0.001	<0.001	0.014	<0.001				
Soil	0.469	0.403	0.332	0.975	0.198	0.501	0.305				
0.0-0.2 m	0.792	0.145	0.965	0.837	0.906	0.681	0.860				
0.2-0.4 m	0.781	0.866	0.443	0.455	0.176	0.905	0.716				
0.4-0.6 m	0.011	0.726	0.243	0.556	0.046	0.028	0.016				
1.0-0.6 m	0.797	0.549	0.570	0.355	0.881	0.486	0.578				

Appendix Table S.3.3. Results of ANOVA test for nutrient pools of plant and soil derived carbon (C) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.4. Results of ANOVA test for nutrient pools of plant and soil derived calcium (Ca) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Ca - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.215	0.011	0.016	0.132	0.222	0.245	0.930
Foliage	0.679	<0.001	<0.001	0.776	0.418	<0.001	0.158
Bark	0.008	0.040	<0.001	0.007	0.076	<0.001	0.002
Branch	<0.001	0.004	<0.001	0.586	0.012	<0.001	0.002
Wood	<0.001	0.001	<0.001	0.862	0.469	<0.001	<0.001
Plant Roots	0.051	0.047	0.645	0.510	0.896	0.536	0.613
Mid Foliage	0.035	0.072	0.001	0.004	0.017	0.074	0.002
Mid Wood	0.009	0.075	0.001	0.001	0.009	0.081	0.001
Forest Floor	0.226	0.010	0.650	0.971	0.019	0.592	0.171
Understory	0.181	0.299	0.005	0.438	0.121	0.703	0.363
Veg Roots	<0.001	0.011	<0.001	<0.001	<0.001	0.011	<0.001
Soil	<0.001	0.071	0.205	0.688	0.817	0.749	0.833
0.0-0.2 m	<0.001	0.148	0.984	0.825	0.647	0.981	0.271
0.2-0.4 m	<0.001	0.722	0.722	0.373	0.591	0.814	0.381
0.4-0.6 m	<0.001	0.518	0.021	0.431	0.649	0.786	0.851
1.0-0.6 m	<0.001	0.141	0.158	0.488	0.799	0.226	0.403

Appendix Table S.3.5. Results of ANOVA test for nutrient pools of plant and soil derived copper (Cu) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of

Cu - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.271	0.009	0.019	0.002	<0.001	<0.001	0.095
Foliage	0.948	<0.001	<0.001	0.809	0.884	<0.001	0.319
Bark	0.383	<0.001	<0.001	0.618	0.764	0.039	0.039
Branch	<0.001	<0.001	<0.001	0.260	0.612	<0.001	<0.001
Wood	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Plant Roots	0.263	0.224	0.214	0.082	0.609	0.120	0.308
Mid Foliage	0.028	0.058	0.001	0.006	0.022	0.058	0.004
Mid Wood	0.005	0.067	0.001	0.001	0.005	0.073	0.001
Forest Floor	0.123	0.033	0.613	0.214	0.349	0.344	0.190
Understory	0.653	0.706	0.002	0.177	0.381	0.465	0.131
Veg Roots	0.004	0.025	<0.001	0.003	0.003	0.024	0.003
Soil	<0.001	0.739	0.059	0.975	0.465	0.828	0.022
0.0-0.2 m	<0.001	0.560	0.037	0.495	0.869	0.450	0.664
0.2-0.4 m	<0.001	0.521	0.705	0.313	0.262	0.581	0.270
0.4-0.6 m	<0.001	0.555	0.095	0.924	0.981	0.808	0.483
1.0-0.6 m	<0.001	0.416	0.116	0.940	0.593	0.841	0.016

vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.6. Results of ANOVA test for nutrient pools of plant and soil derived iron (Fe) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Fe - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.207	0.299	0.246	0.207	0.206	0.299	0.207
Foliage	0.004	<0.001	<0.001	0.052	0.085	<0.001	0.756
Bark	0.001	<0.001	<0.001	<0.001	0.974	<0.001	<0.001
Branch	<0.001	0.007	<0.001	0.108	0.132	<0.001	<0.001
Wood	0.262	<0.001	<0.001	<0.001	0.561	<0.001	<0.001
Plant Roots	0.086	0.082	0.106	0.083	0.935	0.187	0.831
Mid Foliage	0.023	0.082	0.001	0.002	0.018	0.085	0.002
Mid Wood	0.006	0.056	0.001	0.001	0.004	0.061	0.001
Forest Floor	0.669	<0.001	0.808	0.261	0.067	0.847	0.902
Understory	0.568	0.225	0.155	0.791	0.110	0.571	0.231
Veg Roots	0.026	0.130	0.002	0.021	0.023	0.126	0.018
Soil	<0.001	0.674	0.296	0.759	0.666	0.785	0.920
0.0-0.2 m	<0.001	0.524	0.037	0.093	0.748	0.409	0.767
0.2-0.4 m	<0.001	0.181	0.358	0.616	0.687	0.373	0.785
0.4-0.6 m	<0.001	0.545	0.436	0.731	0.416	0.946	0.892
1.0-0.6 m	<0.001	0.434	0.563	0.959	0.661	0.776	0.738

Appendix Table S.3.7. Results of ANOVA test for nutrient pools of plant and soil derived potassium (K) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of

K - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.343	0.015	0.654	0.491	0.123	0.019	0.120
Foliage	0.020	<0.001	<0.001	0.306	0.018	<0.001	0.303
Bark	<0.001	<0.001	<0.001	<0.001	0.006	0.025	0.109
Branch	0.068	<0.001	<0.001	0.011	0.580	<0.001	0.642
Wood	<0.001	<0.001	<0.001	0.013	0.581	<0.001	0.037
Plant Roots	0.009	0.205	0.501	0.353	0.919	0.558	0.382
Mid Foliage	0.022	0.067	0.001	0.004	0.020	0.069	0.003
Mid Wood	0.010	0.069	0.001	0.002	0.009	0.074	0.001
Forest Floor	0.369	0.006	0.032	0.212	0.129	0.092	0.209
Understory	0.196	0.951	0.008	0.274	0.232	0.580	0.347
Veg Roots	<0.001	0.030	<0.001	<0.001	<0.001	0.030	<0.001
Soil	<0.001	0.052	0.323	0.726	0.261	0.937	0.272
0.0-0.2 m	<0.001	0.179	0.766	0.198	0.141	0.779	0.280
0.2-0.4 m	<0.001	0.722	0.999	0.777	0.761	0.886	0.903
0.4-0.6 m	<0.001	0.099	0.244	0.426	0.669	0.980	0.692
1.0-0.6 m	<0.001	0.043	0.248	0.968	0.380	0.898	0.273

vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.8. Results of ANOVA test for nutrient pools of plant and soil derived magnesium (Mg) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Mg - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.001	0.196	0.001	0.080	0.004	0.021	0.020
Foliage	<0.001	0.001	<0.001	0.094	0.955	0.001	0.009
Bark	<0.001	<0.001	<0.001	0.004	0.792	0.002	0.002
Branch	<0.001	<0.001	<0.001	0.003	0.778	<0.001	<0.001
Wood	<0.001	<0.001	<0.001	0.057	0.011	<0.001	0.007
Plant Roots	0.047	0.033	0.298	0.795	0.803	0.333	0.354
Mid Foliage	0.023	0.081	0.001	0.004	0.021	0.085	0.003
Mid Wood	0.002	0.049	0.001	<0.001	0.002	0.053	<0.001
Forest Floor	0.427	0.003	0.248	0.871	0.178	0.304	0.129
Understory	0.469	0.522	0.005	0.394	0.290	0.271	0.287
Veg Roots	<0.001	0.014	<0.001	<0.001	<0.001	0.014	<0.001
Soil	<0.001	0.018	0.051	0.254	0.369	0.537	0.461
0.0-0.2 m	<0.001	0.033	0.049	0.167	0.309	0.468	0.118
0.2-0.4 m	<0.001	0.371	0.288	0.659	0.500	0.240	0.275
0.4-0.6 m	<0.001	0.041	0.151	0.296	0.325	0.777	0.648
1.0-0.6 m	<0.001	0.008	0.071	0.210	0.472	0.507	0.725

Appendix Table S.3.9. Results of ANOVA test for nutrient pools of plant and soil derived manganese (Mn) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of

Mn - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	<0.001	<0.001	<0.001	0.709	0.288	0.001	0.912
Foliage	0.047	<0.001	<0.001	0.025	0.491	<0.001	0.348
Bark	<0.001	<0.001	<0.001	<0.001	0.144	<0.001	0.446
Branch	0.002	<0.001	<0.001	0.128	0.093	<0.001	<0.001
Wood	<0.001	<0.001	<0.001	<0.001	0.049	<0.001	0.008
Plant Roots	<0.001	0.045	0.031	0.016	0.816	0.116	0.292
Mid Foliage	0.385	0.091	0.018	0.213	0.190	0.089	0.095
Mid Wood	0.015	0.074	0.004	0.004	0.010	0.075	0.002
Forest Floor	0.009	0.008	0.080	0.252	0.245	0.548	0.938
Understory	0.395	0.964	0.029	0.109	0.379	0.598	0.111
Veg Roots	0.020	0.089	0.001	0.012	0.015	0.086	0.009
Soil	<0.001	0.080	0.494	0.543	0.766	0.739	0.517
0.0-0.2 m	<0.001	0.212	0.006	0.128	0.652	0.034	0.920
0.2-0.4 m	<0.001	0.024	0.847	0.927	0.282	0.992	0.573
0.4-0.6 m	<0.001	0.103	0.731	0.349	0.774	0.604	0.109
1.0-0.6 m	0.003	0.498	0.937	0.680	0.471	0.469	0.934

vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.10. Results of ANOVA test for nutrient pools of plant and soil derived nitrogen (N) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

N - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.012	0.732	0.341	0.282	0.075	0.013	0.067
Foliage	<0.001	0.234	<0.001	0.080	0.005	0.001	0.003
Bark	<0.001	<0.001	<0.001	<0.001	0.463	<0.001	0.018
Branch	<0.001	<0.001	<0.001	0.003	0.034	<0.001	0.001
Wood	<0.001	<0.001	<0.001	0.491	0.050	<0.001	0.037
Plant Roots	0.369	0.156	0.165	0.323	0.760	0.111	0.205
Mid Foliage	0.029	0.072	0.001	0.006	0.027	0.075	0.005
Mid Wood	0.037	0.070	0.001	0.015	0.015	0.045	0.004
Forest Floor	0.341	0.001	0.918	0.507	0.394	0.414	0.400
Understory	0.785	0.310	0.001	0.678	0.522	0.422	0.482
Veg Roots	0.001	0.008	<0.001	0.001	0.001	0.008	0.001
Soil	0.445	0.087	0.161	0.802	0.316	0.341	0.287
0.0-0.2 m	0.794	0.094	0.586	0.787	0.698	0.640	0.421
0.2-0.4 m	0.325	0.551	0.400	0.225	0.124	0.860	0.100
0.4-0.6 m	0.900	0.748	0.205	0.988	0.136	0.061	0.060
1.0-0.6 m	0.350	0.422	0.437	0.462	0.284	0.063	0.397

Appendix Table S.3.11. Results of ANOVA test for nutrient pools of plant and soil derived sodium masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of

Na - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	<0.001	<0.001	0.907	<0.001	0.124	0.260	0.266
Foliage	<0.001	<0.001	<0.001	<0.001	<0.001	0.004	0.011
Bark	<0.001	<0.001	0.680	<0.001	<0.001	<0.001	<0.001
Branch	<0.001	<0.001	<0.001	<0.001	0.988	<0.001	<0.001
Wood	<0.001	<0.001	<0.001	0.013	0.581	<0.001	0.037
Plant Roots	0.075	0.371	0.152	0.577	0.767	0.099	0.125
Mid Foliage	0.098	0.071	0.005	0.033	0.103	0.069	0.034
Mid Wood	0.268	0.085	0.009	0.122	0.271	0.084	0.123
Forest Floor	0.008	<0.001	0.962	0.136	0.108	0.490	0.487
Understory	0.960	0.524	0.003	0.627	0.214	0.198	0.134
Veg Roots	0.033	0.080	0.005	0.031	0.031	0.078	0.029
Soil	<0.001	0.007	0.227	0.214	0.449	0.125	0.312
0.0-0.2 m	<0.001	0.014	0.022	<0.001	0.479	0.650	0.956
0.2-0.4 m	0.449	0.054	0.774	0.437	0.221	0.433	0.551
0.4-0.6 m	<0.001	<0.001	0.305	0.002	0.215	0.080	0.073
1.0-0.6 m	<0.001	0.033	0.702	0.817	0.164	0.104	0.511

vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.12. Results of ANOVA test for nutrient pools of plant and soil derived phosphorous (P) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

P - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.009	0.002	0.045	0.027	0.036	0.002	0.105
Foliage	<0.001	<0.001	<0.001	0.061	0.654	0.001	0.217
Bark	<0.001	<0.001	<0.001	0.003	0.951	<0.001	0.171
Branch	<0.001	<0.001	<0.001	0.241	0.754	<0.001	0.022
Wood	<0.001	<0.001	<0.001	0.005	0.067	<0.001	0.573
Plant Roots	0.463	0.113	0.105	0.417	0.550	0.221	0.741
Mid Foliage	0.029	0.082	0.001	0.003	0.025	0.084	0.003
Mid Wood	0.034	0.125	0.002	0.007	0.037	0.131	0.007
Forest Floor	0.292	0.001	0.512	0.982	0.254	0.719	0.872
Understory	0.335	0.413	0.007	0.582	0.250	0.399	0.441
Veg Roots	<0.001	0.021	<0.001	<0.001	<0.001	0.021	<0.001
Soil	0.002	0.256	0.835	0.340	0.735	0.964	0.975
0.0-0.2 m	0.005	0.215	0.258	0.856	0.630	0.712	0.905
0.2-0.4 m	0.006	0.452	0.991	0.200	0.210	0.802	0.450
0.4-0.6 m	0.010	0.354	0.400	0.472	0.948	0.811	0.351
1.0-0.6 m	0.002	0.437	0.902	0.217	0.441	0.729	0.521

Appendix Table S.3.13. Results of ANOVA test for nutrient pools of plant and soil derived Sulfur (S) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of

S - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.001	0.703	0.013	0.024	0.005	0.069	0.003
Foliage	0.009	<0.001	<0.001	0.002	0.500	0.328	0.189
Bark	<0.001	<0.001	<0.001	0.030	0.494	<0.001	<0.001
Branch	<0.001	<0.001	<0.001	0.006	0.624	<0.001	0.002
Wood	<0.001	<0.001	<0.001	0.008	0.740	<0.001	0.027
Plant Roots	0.457	0.084	0.072	0.386	0.770	0.069	0.276
Mid Foliage	0.102	0.082	0.007	0.027	0.079	0.082	0.020
Mid Wood	0.024	0.131	0.002	0.004	0.026	0.138	0.005
Forest Floor	0.460	0.004	0.622	0.676	0.392	0.605	0.723
Understory	0.635	0.542	0.004	0.886	0.505	0.441	0.233
Veg Roots	0.001	0.027	<0.001	0.001	0.001	0.027	0.001

vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Appendix Table S.3.14. Results of ANOVA test for nutrient pools of plant and soil derived zinc (Zn) masses for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site). Significant differences are highlighted in bold.

Zn - Pool	Site	Spp	Trt	Site x Spp	Sit x Trt	Spp x Trt	Site x Spp x Trt
Plant	0.338	0.008	0.015	0.907	0.255	0.005	0.695
Foliage	0.409	<0.001	<0.001	0.468	0.921	<0.001	0.287
Bark	<0.001	<0.001	<0.001	0.460	0.181	0.217	0.206
Branch	<0.001	<0.001	<0.001	<0.001	0.249	<0.001	0.030
Wood	0.001	<0.001	<0.001	0.003	<0.001	<0.001	<0.001
Plant Roots	0.247	0.166	0.109	0.154	0.385	0.358	0.393
Mid Foliage	0.038	0.065	0.002	0.007	0.022	0.062	0.004
Mid Wood	0.014	0.075	0.001	0.003	0.010	0.076	0.002
Forest Floor	0.244	0.039	0.645	0.581	0.370	0.635	0.886
Understory	0.453	0.699	0.011	0.210	0.639	0.467	0.366
Veg Roots	0.005	0.009	<0.001	0.005	0.006	0.010	0.005
Soil	0.708	0.229	0.314	0.563	0.970	0.720	0.897
0.0-0.2 m	0.184	0.653	0.014	0.181	0.700	0.307	0.996
0.2-0.4 m	0.787	0.198	0.408	0.604	0.251	0.762	0.836
0.4-0.6 m	0.578	0.131	0.923	0.630	0.554	0.922	0.838
1.0-0.6 m	0.744	0.217	0.213	0.541	0.606	0.420	0.794



Appendix Figure S.3.1. Average boron (B) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no represent standard error. An * indicates significant differences between the Control and VM treatments for a given site and species.



Appendix Figure S.3.2. Average carbon stocks (Mg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.3. Average calcium (Ca) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 yearold Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of postplanting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.4. Average copper stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.5. Average iron (Fe) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.6. Average potassium (K) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 yearold Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of postplanting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.7. Average magnesium (Mg) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.8. Average manganese (Mn) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.


Appendix Figure S.3.9. Average nitrogen (N) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.10. Average sodium stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.11. Average phosphorous (P) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 yearold Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of postplanting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.12. Average Sulfur (S) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.



Appendix Figure S.3.13. Average zinc (Zn) stocks (kg ha⁻¹) of soil and plant derived nutrient pools for 18 year-old Douglas-fir (DF), western hemlock (WH), western redcedar (WRC), and grand fir (GF) stands growing under contrasting vegetation management treatments: no post-planting vegetation management (C), and 5-years of post-planting vegetation management (VM). Error bars represent standard error. An * indicates significant differences between the C and VM treatments for a given site and species.

Appendix Table S.3.15. Mass (kg ha⁻¹) of boron (B) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR			CF				P-value			
		Con	trol	VI	M	Con	trol	VN	Л			
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt	Site	Site x Trt
DF	Total Plant	1.009	0.022	1.121	0.079	1.206	0.077	1.306	0.055	0.043	0.051	0.885
	Foliage	0.120	0.005	0.150	0.006	0.199	0.003	0.278	0.006	<0.001	<0.001	0.001
	Branches	0.223	0.009	0.268	0.017	0.179	0.004	0.277	0.007	<0.001	0.130	0.030
	Bark	0.117	0.005	0.141	0.008	0.099	0.002	0.129	0.003	<0.001	0.012	0.561
	Wood	0.114	0.006	0.138	0.007	0.119	0.002	0.146	0.003	<0.001	0.231	0.690
	Tree Roots	0.098	0.026	0.062	0.003	0.106	0.020	0.064	0.006	0.037	0.815	0.863
	Mid Foliage	0.000	0.000	0.000	0.000	0.015	0.008	0.000	0.000	0.107	0.107	0.107
	Mid Wood	0.000	0.000	0.000	0.000	0.043	0.027	0.000	0.000	0.170	0.170	0.170
	Understory	0.067	0.020	0.007	0.004	0.122	0.046	0.005	0.003	0.012	0.335	0.292
	Forest Floor	0.269	0.039	0.355	0.070	0.323	0.056	0.406	0.035	0.146	0.354	0.977
	Veg Roots	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.002	0.002	0.002
	Total Soil	272.49	16.36	300.12	39.41	636.64	106.49	624.93	20.72	0.894	<0.001	0.742
	0.0-0.2 m	45.82	2.79	51.27	4.67	89.30	6.43	86.67	1.14	0.745	<0.001	0.361
	0.2-0.4 m	55.19	3.61	64.90	6.78	107.10	9.32	131.17	4.33	0.022	<0.001	0.285
	0.4-0.6 m	62.88	3.59	65.70	11.87	134.56	16.87	123.65	10.70	0.737	<0.001	<0.001
	0.6-1.0 m	108.60	10.75	118.25	16.59	305.68	83.88	283.43	11.49	0.887	0.001	0.720
WRC	Total Plant	0.997	0.054	0.908	0.056	0.812	0.112	1.007	0.055	0.524	0.607	0.109
	Foliage	0.074	0.025	0.226	0.009	0.076	0.025	0.216	0.014	0.001	0.862	0.770
	Branches	0.045	0.017	0.165	0.012	0.042	0.014	0.126	0.008	<0.001	0.132	0.199
	Bark	0.029	0.013	0.133	0.025	0.030	0.009	0.091	0.006	<0.001	0.147	0.143
	Wood	0.024	0.009	0.087	0.006	0.029	0.009	0.073	0.005	<0.001	0.568	0.227
	Tree Roots	0.087	0.069	0.157	0.031	0.144	0.018	0.195	0.021	0.136	0.249	0.800
	Mid Foliage	0.125	0.030	0.003	0.003	0.034	0.021	0.005	0.005	0.002	0.031	0.025
	Mid Wood	0.303	0.100	0.006	0.006	0.021	0.010	0.002	0.002	0.013	0.021	0.021
	Understory	0.082	0.047	0.067	0.033	0.335	0.145	0.108	0.038	0.216	0.140	0.275
	Forest Floor	0.151	0.041	0.063	0.028	0.096	0.025	0.191	0.095	0.958	0.568	0.172
	Veg Roots	0.077	0.012	0.001	0.001	0.006	0.002	0.000	0.000	0.001	0.001	0.001
	Total Soil	297.35	12.21	307.66	29.36	622.89	48.17	630.90	65.07	0.693	0.005	0.960
	0.0-0.2 m	40.40	1.71	48.69	4.05	122.41	15.08	131.82	12.09	0.301	0.002	0.945
	0.2-0.4 m	52.83	0.91	62.78	7.27	122.55	10.10	116.40	7.41	0.796	0.001	0.300
	0.4-0.6 m	65.71	0.86	68.38	3.42	124.67	13.75	132.30	11.65	0.433	0.007	0.699
	0.6-1.0 m	138.41	11.45	127.81	15.52	253.26	12.60	250.38	42.32	0.770	0.014	0.866

Appendix Table S.3.16. Mass (kg ha⁻¹) of boron (B) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	trol	VN	Л	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	1.369	0.089	1.510	0.101	0.036
	Foliage	0.218	0.023	0.473	0.029	<0.001
	Branches	0.149	0.016	0.340	0.021	<0.001
	Bark	0.082	0.010	0.197	0.015	<0.001
	Wood	0.119	0.016	0.236	0.023	0.006
	Tree Roots	0.137	0.035	0.130	0.023	0.879
	Mid Foliage	0.166	0.065	0.000	0.000	0.085
	Mid Wood	0.224	0.092	0.000	0.000	0.092
	Understory	0.137	0.065	0.008	0.003	0.093
	Forest Floor	0.105	0.015	0.126	0.026	0.458
	Veg Roots	0.032	0.013	0.000	0.000	0.098
	Total Soil	330.72	19.86	315.08	21.62	0.535
	0.0-0.2 m	45.23	4.36	46.37	2.37	0.766
	0.2-0.4 m	73.15	7.95	65.91	5.02	0.471
	0.4-0.6 m	71.30	5.43	72.71	5.69	0.841
	0.6-1.0 m	141.04	15.91	130.10	12.92	0.510
GF	Total Plant	1.094	0.089	1.581	0.145	0.052
	Foliage	0.147	0.025	0.339	0.016	0.019
	Branches	0.135	0.026	0.477	0.026	0.008
	Bark	0.085	0.017	0.165	0.009	0.041
	Wood	0.090	0.023	0.336	0.018	0.005
	Tree Roots	0.070	0.021	0.093	0.020	0.462
	Mid Foliage	0.060	0.029	0.000	0.000	0.174
	Mid Wood	0.197	0.096	0.000	0.000	0.176
	Understory	0.127	0.048	0.006	0.002	0.127
	Forest Floor	0.142	0.054	0.165	0.081	0.823
	Veg Roots	0.040	0.011	0.000	0.000	0.071
	Total Soil	284.95	56.53	318.92	8.03	0.584
	0.0-0.2 m	32.59	7.32	41.37	1.13	0.302
	0.2-0.4 m	49.85	3.40	59.05	7.22	0.313
	0.4-0.6 m	76.81	18.21	74.35	3.64	0.890
	0.6-1.0 m	125.70	29.78	144.16	12.87	0.541

Appendix Table S.3.17. Mass (kg ha⁻¹) of carbon (C) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR			CF				P-value			
		Con	trol	VN	M	Con	trol	VN	ſ			
Species	Tissue	%	SE	%	SE	%	SE	%	SE	Trt	Site	Site x Trt
DF	Total Plant	66621	2613	79526	3816	56444	3092	74402	2188	0.001	0.060	0.374
	Foliage	5428	237	6374	252	4304	67	6101	142	<0.001	0.003	0.045
	Branches	10653	440	13109	850	7890	167	12005	322	<0.001	0.003	0.131
	Bark	7553	321	9259	537	6030	98	8693	206	<0.001	0.009	0.176
	Wood	31792	1699	39429	2114	22507	310	35810	763	<0.001	0.001	0.069
	Tree Roots	2691	625	1567	199	1465	343	1162	223	0.057	0.123	0.225
	Mid Foliage	0	0	0	0	320	191	0	0	0.145	0.145	0.145
	Mid Wood	0	0	0	0	5560	3344	0	0	0.147	0.147	0.147
	Understory	1305	365	128	67	1136	264	81	52	0.002	0.674	0.784
	Forest Floor	7199	1548	9660	2065	7213	904	10549	1578	0.079	0.807	0.760
	Veg Roots	0	0	0	0	18	5	0	0	0.010	0.010	0.010
	Total Soil	155932	7429	149564	10599	126354	17133	162872	17212	0.223	0.629	0.102
	0.0-0.2 m	56116	1728	63608	15627	56888	8887	63608	4661	0.461	0.968	0.968
	0.2-0.4 m	41638	6549	41027	10047	38917	7525	51858	9534	0.247	0.727	0.209
	0.4-0.6 m	37140	3396	17436	2534	13235	1848	21433	2222	0.045	0.002	0.000
	0.6-1.0 m	21038	7883	27493	2420	17314	3356	25973	5548	0.086	0.698	0.774
WRC	Total Plant	65447	8301	46384	2401	22479	5585	36791	2771	0.627	0.006	0.015
	Foliage	3046	1033	9457	396	2904	965	7904	523	0.001	0.353	0.399
	Branches	2543	949	8929	650	2553	827	6434	430	<0.001	0.120	0.118
	Bark	916	415	4547	856	1070	309	2812	184	<0.001	0.110	0.063
	Wood	4238	1570	14806	1036	4171	1355	11277	754	<0.001	0.168	0.183
	Tree Roots	2039	1597	3645	423	1677	74	2700	419	0.104	0.396	0.701
	Mid Foliage	2946	786	92	92	964	601	168	168	0.004	0.084	0.065
	Mid Wood	42093	12511	1449	1449	3110	1576	214	214	0.008	0.016	0.014
	Understory	2401	1111	1161	518	3138	666	914	174	0.025	0.716	0.470
	Forest Floor	3311	865	2285	1366	2806	692	4369	1240	0.791	0.534	0.236
	Veg Roots	1914	346	14	14	84	32	0	0	0.001	0.002	0.002
	Total Soil	174523	7798	147100	10103	164489	15059	142188	13666	0.088	0.583	0.850
	0.0-0.2 m	67383	11774	67189	2110	68561	8887	72319	9796	0.852	0.741	0.836
	0.2-0.4 m	56523	16962	43663	6683	43741	6930	38878	7246	0.185	0.510	0.519
	0.4-0.6 m	32754	6841	20673	3332	27832	7693	12742	1806	0.037	0.282	0.796
	06-10m	17864	4676	15574	2181	24354	3124	18248	2760	0 2 2 9	0.192	0 573

Appendix Table S.3.18. Mass (kg ha⁻¹) of carbon (C) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Con	trol	VN	Λ	P-value
Species	Tissue	%	SE	%	SE	Trt
WH	Total Plant	81671	11754	101810	7935	0.029
	Foliage	4672	500	10862	658	<0.001
	Branches	6752	734	15832	971	<0.001
	Bark	3331	424	10210	757	<0.001
	Wood	20597	2721	56245	5509	0.001
	Tree Roots	3584	823	5119	648	0.193
	Mid Foliage	4595	1856	0	0	0.090
	Mid Wood	31074	12143	0	0	0.083
	Understory	2568	921	190	73	0.078
	Forest Floor	3566	412	3351	234	0.563
	Veg Roots	931	454	0	0	0.133
	Total Soil	147305	21462	162449	11440	0.394
	0.0-0.2 m	63081	8528	71586	4213	0.385
	0.2-0.4 m	44453	14789	41871	4567	0.873
	0.4-0.6 m	18063	4525	29767	7326	0.224
	0.6-1.0 m	21707	4153	19225	4094	0.685
GF	Total Plant	62473	13548	91719	6620	0.056
	Foliage	4669	806	10329	493	0.022
	Branches	5351	1040	12630	678	0.021
	Bark	3033	589	7236	388	0.021
	Wood	15617	4018	54183	2905	0.007
	Tree Roots	1379	229	2323	219	0.041
	Mid Foliage	1408	672	0	0	0.171
	Mid Wood	24566	12004	0	0	0.177
	Understory	2224	606	135	38	0.067
	Forest Floor	3388	1169	4883	2459	0.612
	Veg Roots	839	240	0	0	0.073
	Total Soil	193737	29985	166781	20902	0.502
	0.0-0.2 m	92061	19970	77568	1826	0.510
	0.2-0.4 m	43282	1088	39658	8843	0.714
	0.4-0.6 m	29312	2928	30902	9338	0.879
	0.6-1.0 m	29081	9074	18653	4940	0.402

Appendix Table S.3.19. Mass (kg ha⁻¹) of calcium (Ca) of tree and ecosystem components for 18-year-old Douglasfir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR			CF				P-value			
		Cont	rol	VN	1	Cont	rol	VN	1			
Species	Tissue	kg ha ⁻¹	SE	Trt	Site	Site x Trt						
DF	Total Plant	463.9	30.0	459.1	33.9	437.2	14.6	505.1	34.0	0.079	0.810	0.051
	Foliage	61.9	2.7	74.1	2.9	54.0	0.8	79.2	1.8	<0.001	0.541	0.014
	Branches	79.3	3.3	95.1	6.2	49.1	1.0	72.7	1.9	<0.001	<0.001	0.311
	Bark	50.7	2.2	42.8	2.5	43.0	0.7	51.4	1.2	0.884	0.797	0.001
	Wood	57.4	3.1	29.8	1.6	21.3	0.3	26.5	0.6	<0.001	<0.001	<0.001
	Tree Roots	30.1	2.3	15.9	1.1	41.2	7.4	22.2	3.3	0.001	0.158	0.414
	Mid Foliage	0.0	0.0	0.0	0.0	8.3	5.0	0.0	0.0	0.145	0.145	0.145
	Mid Wood	0.0	0.0	0.0	0.0	15.2	9.3	0.0	0.0	0.153	0.153	0.153
	Understory	23.2	7.5	2.7	1.5	36.0	15.6	1.7	1.0	0.019	0.523	0.459
	Forest Floor	161.3	28.7	198.7	30.0	168.6	14.1	251.3	31.5	0.059	0.328	0.413
	Veg Roots	0.0	0.0	0.0	0.0	0.5	0.1	0.0	0.0	<0.001	<0.001	<0.001
	Total Soil	6905	1522	6443	1203	19835	3863	19461	3007	0.826	0.007	0.981
	0.0-0.2 m	2229	504	2011	315	4939	774	5287	405	0.897	0.002	0.580
	0.2-0.4 m	1579	404	1957	900	4800	906	6126	538	0.166	0.005	0.415
	0.4-0.6 m	1600	557	1070	297	3860	834	3519	681	0.369	0.021	0.840
	0.6-1.0 m	1497	380	1405	330	6235	1994	4530	1742	0.391	0.053	0.439
WRC	Total Plant	519.3	69.3	673.7	36.2	385.4	51.5	623.4	60.6	0.007	0.139	0.482
	Foliage	70.9	24.0	248.9	10.4	85.9	28.5	218.7	14.5	0.001	0.754	0.324
	Branches	30.5	11.4	127.4	9.3	42.9	13.9	74.1	5.0	<0.001	0.084	0.012
	Bark	23.3	10.6	100.1	18.8	21.3	6.1	47.1	3.1	<0.001	0.020	0.028
	Wood	10.9	4.0	64.0	4.5	11.0	3.6	25.8	1.7	<0.001	<0.001	<0.001
	Tree Roots	34.1	27.0	51.5	9.8	47.1	4.0	72.6	4.9	0.119	0.206	0.756
	Mid Foliage	63.2	18.2	1.1	1.1	12.4	7.3	4.1	4.1	0.003	0.026	0.015
	Mid Wood	108.6	32.9	2.4	2.4	6.8	3.2	0.8	0.8	0.009	0.015	0.014
	Understory	53.6	27.0	26.9	12.1	100.8	24.2	23.3	5.4	0.022	0.284	0.215
	Forest Floor	97.3	37.6	51.0	26.3	54.9	12.5	157.0	43.5	0.280	0.468	0.024
	Veg Roots	26.9	5.5	0.2	0.2	2.3	0.9	0.0	0.0	0.001	0.004	0.003
	Total Soil	7309	1027	5479	866	21106	3004	21162	4753	0.798	0.001	0.785
	0.0-0.2 m	2152	787	2169	587	6035	1029	4711	267	0.387	0.011	0.376
	0.2-0.4 m	1964	162	1308	341	4724	598	3836	599	0.046	0.012	0.708
	0.4-0.6 m	1597	296	705	19	4414	333	3975	538	0.123	<0.001	0.579
	0.6-1.0 m	1597	111	1296	130	5932	1385	8640	3953	0.638	0.040	0.557

Appendix Table S.3.20. Mass (kg ha⁻¹) of calcium (Ca) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Control		VM		P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	480.5	41.6	554.4	38.7	0.015
	Foliage	54.7	5.9	167.2	10.1	<0.001
	Branches	36.4	4.0	90.6	5.6	<0.001
	Bark	24.5	3.1	99.2	7.4	<0.001
	Wood	36.9	4.9	77.3	7.6	0.004
	Tree Roots	50.5	11.9	54.5	10.5	0.812
	Mid Foliage	71.2	26.9	0.0	0.0	0.078
	Mid Wood	75.1	30.8	0.0	0.0	0.093
	Understory	51.3	20.2	3.5	1.5	0.099
	Forest Floor	67.3	12.0	62.1	8.3	0.724
	Veg Roots	12.4	5.2	0.0	0.0	0.099
	Total Soil	5056	916	5051	602	0.996
	0.0-0.2 m	1464	337	1583	302	0.801
	0.2-0.4 m	1293	560	1251	242	0.947
	0.4-0.6 m	1224	381	930	128	0.493
	0.6-1.0 m	1076	84	1287	145	0.221
GF	Total Plant	590.2	45.4	810.0	131.7	0.190
	Foliage	120.2	20.7	245.7	11.7	0.028
	Branches	50.2	9.8	128.5	6.9	0.017
	Bark	56.3	10.9	87.2	4.7	0.102
	Wood	30.4	7.8	93.3	5.0	0.009
	Tree Roots	26.7	5.4	34.1	3.2	0.306
	Mid Foliage	36.6	17.5	0.0	0.0	0.171
	Mid Wood	67.7	33.0	0.0	0.0	0.177
	Understory	36.3	14.3	3.1	1.0	0.133
	Forest Floor	149.4	61.8	218.2	101.7	0.594
	Veg Roots	16.4	5.2	0.0	0.0	0.088
	Total Soil	9896	1921	7642	951	0.155
	0.0-0.2 m	2604	432	2658	400	0.931
	0.2-0.4 m	1924	403	1692	605	0.753
	0.4-0.6 m	2112	607	1137	280	0.152
	0.6-1.0 m	3256	1336	2156	565	0.300

Appendix Table S.3.21. Mass (kg ha⁻¹) of copper (Cu) of tree and ecosystem components for 18-year-old Douglasfir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR			CF				P-value			
		Con	trol	VI	M	Con	trol	VI	М			
Species	Tissue	kg ha ⁻¹	SE	Trt	Site	Site x Trt						
DF	Total Plant	0.366	0.017	0.360	0.026	0.383	0.018	0.466	0.022	0.022	0.064	0.012
	Foliage	0.031	0.001	0.036	0.001	0.027	0.000	0.039	0.001	<0.001	0.597	0.006
	Branches	0.092	0.004	0.102	0.007	0.056	0.001	0.086	0.002	<0.001	<0.001	0.022
	Bark	0.049	0.002	0.067	0.004	0.045	0.001	0.070	0.002	<0.001	0.769	0.165
	Wood	0.065	0.003	0.055	0.003	0.076	0.001	0.147	0.003	<0.001	<0.001	<0.001
	Tree Roots	0.046	0.009	0.025	0.004	0.038	0.006	0.022	0.004	0.004	0.510	0.538
	Mid Foliage	0.000	0.000	0.000	0.000	0.004	0.002	0.000	0.000	0.127	0.127	0.127
	Mid Wood	0.000	0.000	0.000	0.000	0.027	0.016	0.000	0.000	0.142	0.142	0.142
	Understory	0.025	0.011	0.003	0.002	0.016	0.004	0.001	0.001	0.011	0.389	0.534
	Forest Floor	0.058	0.012	0.073	0.015	0.094	0.012	0.101	0.014	0.352	0.076	0.726
	Veg Roots	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	<0.001	<0.001	<0.001
	Total Soil	191.6	15.7	204.1	25.9	274.6	25.8	366.5	31.0	0.014	0.009	0.040
	0.0-0.2 m	31.7	2.1	35.5	4.8	45.4	5.9	52.5	4.6	0.172	0.030	0.659
	0.2-0.4 m	35.1	4.1	38.0	3.9	55.8	6.7	72.0	6.3	0.013	0.008	0.051
	0.4-0.6 m	40.1	4.3	43.3	6.0	67.6	10.2	76.6	10.1	0.309	0.023	0.612
	0.6-1.0 m	84.6	6.8	87.3	11.9	105.9	9.9	165.5	13.5	0.002	0.012	0.003
WRC	Total Plant	0.423	0.053	0.287	0.014	0.217	0.027	0.271	0.019	0.181	0.022	0.015
	Foliage	0.023	0.008	0.061	0.003	0.027	0.009	0.059	0.004	0.003	0.890	0.691
	Branches	0.017	0.006	0.061	0.004	0.011	0.004	0.028	0.002	<0.001	0.001	0.007
	Bark	0.006	0.003	0.028	0.005	0.008	0.002	0.021	0.001	<0.001	0.393	0.142
	Wood	0.011	0.004	0.034	0.002	0.013	0.004	0.027	0.002	<0.001	0.503	0.228
	Tree Roots	0.027	0.018	0.059	0.018	0.058	0.004	0.075	0.007	0.050	0.145	0.449
	Mid Foliage	0.035	0.010	0.002	0.002	0.006	0.004	0.001	0.001	0.010	0.037	0.029
	Mid Wood	0.200	0.054	0.006	0.006	0.013	0.007	0.001	0.001	0.005	0.011	0.009
	Understory	0.026	0.009	0.018	0.009	0.051	0.015	0.015	0.002	0.055	0.325	0.198
	Forest Floor	0.045	0.015	0.017	0.010	0.025	0.007	0.044	0.023	0.791	0.819	0.176
	Veg Roots	0.031	0.010	0.000	0.000	0.003	0.001	0.000	0.000	0.008	0.019	0.017
	Total Soil	199.1	3.9	224.6	12.2	342.8	19.5	324.0	17.1	0.841	<0.001	0.203
	0.0-0.2 m	32.1	2.2	37.3	1.0	52.7	2.8	56.4	4.9	0.238	<0.001	0.838
	0.2-0.4 m	41.2	1.9	44.2	1.9	60.2	4.4	63.4	4.5	0.445	0.001	0.989
	0.4-0.6 m	42.6	1.5	46.9	3.4	76.8	6.5	75.6	3.2	0.746	<0.001	0.562
	0.6-1.0 m	83.2	0.4	96.2	8.7	153.0	12.8	128.6	20.7	0.711	0.006	0.236

Appendix Table S.3.22. Mass (kg ha⁻¹) of copper (Cu) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Con	trol	VI	М	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	0.524	0.057	0.591	0.041	0.035
	Foliage	0.031	0.003	0.077	0.005	<0.001
	Branches	0.073	0.008	0.154	0.009	0.001
	Bark	0.030	0.004	0.070	0.005	0.001
	Wood	0.059	0.008	0.197	0.019	0.001
	Tree Roots	0.049	0.007	0.062	0.010	0.360
	Mid Foliage	0.037	0.013	0.000	0.000	0.069
	Mid Wood	0.150	0.061	0.000	0.000	0.092
	Understory	0.039	0.016	0.001	0.001	0.055
	Forest Floor	0.041	0.010	0.029	0.007	0.391
	Veg Roots	0.015	0.007	0.000	0.000	0.112
	Total Soil	192.6	15.2	202.5	16.9	0.504
	0.0-0.2 m	31.6	2.5	31.1	2.8	0.837
	0.2-0.4 m	41.1	2.6	40.1	4.8	0.809
	0.4-0.6 m	40.0	3.5	45.4	3.4	0.268
	0.6-1.0 m	79.9	8.0	86.0	7.1	0.268
GF	Total Plant	0.401	0.072	0.638	0.038	0.031
	Foliage	0.035	0.006	0.076	0.004	0.022
	Branches	0.050	0.010	0.232	0.012	0.006
	Bark	0.032	0.006	0.052	0.003	0.078
	Wood	0.049	0.013	0.196	0.011	0.005
	Tree Roots	0.026	0.006	0.041	0.011	0.310
	Mid Foliage	0.018	0.009	0.000	0.000	0.172
	Mid Wood	0.116	0.057	0.000	0.000	0.178
	Understory	0.026	0.004	0.002	0.001	0.017
	Forest Floor	0.034	0.010	0.040	0.017	0.787
	Veg Roots	0.015	0.003	0.000	0.000	0.044
	Total Soil	212.2	6.5	221.3	3.4	0.124
	0.0-0.2 m	27.2	2.3	31.9	2.1	0.217
	0.2-0.4 m	39.7	1.0	37.3	0.6	0.107
	0.4-0.6 m	48.4	3.1	48.9	0.3	0.883
	0.6-1.0 m	97.0	9.9	103.2	1.2	0.568

Appendix Table S.3.23. Mass (kg ha⁻¹) of Fe of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR		CF				P-value				
		Cont	trol	VN	M	Cont	trol	VN	ſ			
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt	Site	Site x Trt
DF	Total Plant	45.346	2.027	42.428	2.978	39.351	4.777	44.703	5.97	0.778	0.668	0.347
	Foliage	0.445	0.019	0.640	0.025	0.455	0.007	0.850	0.02	<0.001	<0.001	<0.001
	Branches	0.742	0.031	0.878	0.057	0.320	0.007	1.057	0.03	<0.001	0.005	<0.001
	Bark	0.515	0.022	0.625	0.036	0.662	0.011	1.060	0.03	<0.001	<0.001	<0.001
	Wood	1.043	0.056	1.005	0.054	1.164	0.016	1.930	0.04	<0.001	<0.001	<0.001
	Tree Roots	11.111	2.208	7.013	1.372	10.804	1.359	7.252	1.09	<0.001	0.988	0.581
	Mid Foliage	0.000	0.000	0.000	0.000	0.111	0.068	0.000	0.00	0.157	0.157	0.157
	Mid Wood	0.000	0.000	0.000	0.000	1.147	0.657	0.000	0.00	0.131	0.131	0.131
	Understory	2.254	1.167	0.367	0.187	3.811	3.311	0.107	0.09	0.150	0.734	0.611
	Forest Floor	29.236	3.170	31.899	2.439	20.740	2.440	32.446	5.07	0.060	0.272	0.215
	Veg Roots	0.000	0.000	0.000	0.000	0.138	0.027	0.000	0.00	0.002	0.002	0.002
	Total Soil	150073	5082	161559	15321	203747	13008	207794	9115	0.466	0.007	0.722
	0.0-0.2 m	26633	1373	28482	1794	33793	2205	35568	1719	0.248	0.015	0.980
	0.2-0.4 m	28926	1155	32790	2697	36514	1520	42316	1955	0.044	0.005	0.629
	0.4-0.6 m	31674	1306	32913	3891	44483	2895	42324	2614	0.874	0.002	0.560
	0.6-1.0 m	62840	3151	67375	7249	88957	8039	87587	3714	0.775	0.012	0.596
WRC	Total Plant	35.074	8.506	31.568	6.457	33.102	5.334	39.411	3.0	0.260	0.260	0.259
	Foliage	0.348	0.118	0.970	0.041	0.645	0.214	1.549	0.1	0.003	0.043	0.349
	Branches	0.191	0.071	0.950	0.069	0.360	0.117	0.255	0.0	0.002	0.009	<0.001
	Bark	0.079	0.036	0.553	0.104	0.154	0.045	0.336	0.0	<0.001	0.224	0.023
	Wood	0.154	0.057	1.421	0.099	0.162	0.053	0.537	0.0	<0.001	<0.001	<0.001
	Tree Roots	5.148	3.098	16.042	5.923	13.179	2.055	22.850	4.5	0.030	0.098	0.883
	Mid Foliage	0.782	0.255	0.012	0.012	0.113	0.063	0.025	0.0	0.004	0.017	0.014
	Mid Wood	8.723	2.537	0.370	0.370	0.300	0.125	0.014	0.0	0.007	0.013	0.009
	Understory	4.077	1.794	5.130	2.765	11.874	6.385	0.862	0.2	0.244	0.670	0.165
	Forest Floor	9.084	3.671	6.034	3.075	5.738	1.763	12.982	4.8	0.532	0.674	0.160
	Veg Roots	6.487	2.866	0.088	0.088	0.576	0.182	0.000	0.0	0.031	0.060	0.055
	Total Soil	150330	5140	157441	9280	207275	10015	209744	4039	0.552	<0.001	0.772
	0.0-0.2 m	23790	950	27919	1813	37093	3065	39445	1696	0.179	<0.001	0.700
	0.2-0.4 m	29725	264	31938	1164	36656	2248	39241	2568	0.276	0.007	0.930
	0.4-0.6 m	30587	46	33216	1613	44136	2194	44336	1904	0.461	<0.001	0.526
	0.6-1.0 m	66229	4245	64369	5246	89390	4586	86722	3300	0.616	<0.001	0.928

Appendix Table S.3.24. Mass (kg ha⁻¹) of Fe of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	trol	VN	ſ	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	38.933	2.642	33.675	3.276	0.163
	Foliage	0.403	0.043	1.494	0.090	<0.001
	Branches	0.376	0.041	1.144	0.070	<0.001
	Bark	0.271	0.034	1.220	0.090	<0.001
	Wood	1.130	0.149	1.595	0.156	0.075
	Tree Roots	15.211	4.318	18.539	3.822	0.585
	Mid Foliage	0.757	0.282	0.000	0.000	0.075
	Mid Wood	5.382	2.207	0.000	0.000	0.093
	Understory	3.531	1.648	0.545	0.232	0.123
	Forest Floor	7.791	1.997	9.137	3.677	0.714
	Veg Roots	4.082	1.661	0.000	0.000	0.091
	Total Soil	166737	8466	163495	6981	0.710
	0.0-0.2 m	26717	1759	26586	1213	0.944
	0.2-0.4 m	34988	1307	32744	2432	0.448
	0.4-0.6 m	34150	2727	34456	1817	0.897
	0.6-1.0 m	70881	5242	69708	3292	0.794
GF	Total Plant	33.872	2.134	33.147	5.395	0.894
	Foliage	0.722	0.125	1.472	0.070	0.028
	Branches	0.492	0.096	0.930	0.050	0.044
	Bark	0.651	0.127	1.505	0.081	0.023
	Wood	0.403	0.104	3.031	0.163	0.002
	Tree Roots	6.542	0.062	12.625	2.457	0.069
	Mid Foliage	0.497	0.237	0.000	0.000	0.170
	Mid Wood	4.912	2.412	0.000	0.000	0.179
	Understory	3.220	2.623	0.520	0.171	0.389
	Forest Floor	11.724	2.187	13.064	5.456	0.831
	Veg Roots	4.709	2.246	0.000	0.000	0.171
	Total Soil	158991	19919	172074	1283	0.548
	0.0-0.2 m	22282	3158	27109	1280	0.292
	0.2-0.4 m	29419	1802	30560	1676	0.667
	0.4-0.6 m	35988	4784	36546	872	0.908
	0.6-1.0 m	71303	10270	77858	631	0.559

Appendix Table S.3.25. Mass (kg ha⁻¹) of potassium (K) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR			CF				P-value			
		Con	trol	VN	N	Con	trol	VN	1			
Species	Tissue	kg ha ⁻¹	SE	Trt	Site	Site x Trt						
DF	Total Plant	264.17	25.69	245.63	7.80	260.17	20.55	241.28	10.13	0.298	0.831	0.992
	Foliage	63.98	2.79	57.69	2.28	64.59	1.01	80.77	1.88	0.036	<0.001	<0.001
	Branches	52.91	2.18	63.29	4.10	44.66	0.95	54.72	1.47	0.001	0.005	0.949
	Bark	35.95	1.53	53.16	3.08	24.26	0.39	30.63	0.73	<0.001	<0.001	<0.001
	Wood	19.97	1.07	24.87	1.33	14.14	0.19	22.37	0.48	<0.001	0.001	0.087
	Tree Roots	16.51	2.23	11.25	4.12	5.56	1.16	3.39	0.99	0.046	0.024	0.338
	Mid Foliage	0.00	0.00	0.00	0.00	11.10	6.50	0.00	0.00	0.138	0.138	0.138
	Mid Wood	0.00	0.00	0.00	0.00	3.70	2.24	0.00	0.00	0.150	0.150	0.150
	Understory	42.49	21.36	4.82	3.74	48.38	16.12	4.16	3.44	0.022	0.857	0.815
	Forest Floor	32.36	1.81	30.56	3.93	43.71	7.03	45.24	6.09	0.972	0.084	0.660
	Veg Roots	0.00	0.00	0.00	0.00	0.07	0.01	0.00	0.00	<0.001	<0.001	<0.001
	Total Soil	12862	840	13086	1673	5264	387	5455	559	0.795	0.001	0.983
	0.0-0.2 m	2456	107	2578	366	1253	120	1241	127	0.705	0.003	0.648
	0.2-0.4 m	2373	273	2419	418	1145	152	1130	104	0.954	0.001	0.910
	0.4-0.6 m	2575	263	2668	353	982	79	1068	130	0.589	0.002	0.982
	0.6-1.0 m	5458	280	5421	721	1884	132	2016	273	0.896	<0.001	0.817
WRC	Total Plant	232.77	10.06	165.55	24.37	166.48	28.03	180.57	12.04	0.195	0.336	0.071
	Foliage	21.08	7.15	67.99	2.84	21.24	7.06	78.07	5.17	<0.001	0.465	0.423
	Branches	7.20	2.69	22.14	1.61	10.60	3.43	21.82	1.46	0.004	0.581	0.495
	Bark	3.06	1.39	13.01	2.45	3.33	0.96	10.12	0.66	<0.001	0.358	0.275
	Wood	2.61	0.97	9.16	0.64	2.66	0.87	7.22	0.48	<0.001	0.243	0.221
	Tree Roots	10.66	7.92	15.78	1.98	7.60	0.87	8.84	1.18	0.387	0.186	0.594
	Mid Foliage	82.88	24.45	2.10	2.10	12.92	7.45	1.75	1.75	0.009	0.027	0.025
	Mid Wood	28.01	8.13	0.82	0.82	2.64	1.41	0.20	0.20	0.007	0.016	0.015
	Understory	35.44	12.93	26.67	19.44	92.47	31.96	29.94	1.99	0.125	0.188	0.236
	Forest Floor	31.78	7.05	7.82	3.72	12.65	5.36	22.60	17.50	0.551	0.852	0.165
	Veg Roots	10.04	2.31	0.06	0.06	0.39	0.14	0.00	0.00	0.003	0.005	0.004
	Total Soil	12457	1000	14245	1616	6779	1104	5967	643	0.569	0.003	0.166
	0.0-0.2 m	2245	210	2603	292	1850	326	1401	43	0.858	0.009	0.132
	0.2-0.4 m	2453	106	2688	243	1171	205	1263	104	0.216	0.002	0.562
	0.4-0.6 m	2398	42	2688	228	1198	206	1293	158	0.308	0.001	0.591
	0.6-1.0 m	5361	1129	6266	1041	2561	607	2010	358	0.795	0.010	0.310

Appendix Table S.3.26. Mass (kg ha⁻¹) of potassium (K) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	rol	VN	1	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	329.09	29.38	289.38	19.65	0.275
	Foliage	58.89	6.31	105.17	6.37	0.002
	Branches	22.70	2.47	57.75	3.54	<0.001
	Bark	23.55	3.00	52.34	3.88	0.001
	Wood	12.97	1.71	35.26	3.45	0.001
	Tree Roots	19.44	5.32	22.51	6.85	0.717
	Mid Foliage	81.91	30.19	0.00	0.00	0.073
	Mid Wood	22.49	8.72	0.00	0.00	0.082
	Understory	62.89	35.42	4.57	2.21	0.152
	Forest Floor	19.31	6.56	11.80	1.12	0.302
	Veg Roots	4.95	2.45	0.00	0.00	0.137
	Total Soil	10406	799	11016	706	0.588
	0.0-0.2 m	2080	279	1853	125	0.463
	0.2-0.4 m	2340	227	2183	176	0.605
	0.4-0.6 m	2097	120	2308	202	0.403
	0.6-1.0 m	3889	348	4672	481	0.235
GF	Total Plant	256.56	48.49	354.42	24.67	0.058
	Foliage	41.50	7.16	124.45	5.95	0.010
	Branches	31.71	6.16	128.66	6.90	0.007
	Bark	24.06	4.67	37.19	2.00	0.103
	Wood	9.91	2.55	34.27	1.84	0.007
	Tree Roots	6.44	1.23	12.09	0.45	0.013
	Mid Foliage	48.15	23.01	0.00	0.00	0.172
	Mid Wood	16.40	8.01	0.00	0.00	0.177
	Understory	59.97	17.62	2.08	0.56	0.078
	Forest Floor	14.00	3.71	15.68	8.12	0.860
	Veg Roots	4.43	2.04	0.00	0.00	0.162
	Total Soil	13803	1408	14804	1828	0.687
	0.0-0.2 m	2491	469	2484	347	0.992
	0.2-0.4 m	2488	292	2365	62	0.700
	0.4-0.6 m	2719	206	2967	334	0.561
	0.6-1.0 m	6105	939	6987	1152	0.585

Appendix Table S.3.27. Mass (kg ha⁻¹) of magnesium (Mg) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

			C	R		CF			P-value		ue	
		Cont	rol	VN	M	Con	trol	VN	Л			
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt	Site	Site x Trt
DF	Total Plant	80.036	3.906	71.016	4.951	63.762	5.269	60.128	4.554	0.026	0.074	0.256
	Foliage	11.876	0.518	12.893	0.510	6.835	0.107	12.754	0.297	<0.001	<0.001	<0.001
	Branches	11.791	0.487	10.910	0.708	5.345	0.113	8.828	0.237	0.013	<0.001	<0.001
	Bark	7.160	0.304	7.188	0.417	3.463	0.056	5.519	0.131	0.002	<0.001	0.003
	Wood	7.020	0.375	8.028	0.430	4.468	0.062	5.571	0.119	0.004	<0.001	0.874
	Tree Roots	6.876	1.252	3.644	0.583	3.876	0.584	2.281	0.399	0.001	0.076	0.088
	Mid Foliage	0.000	0.000	0.000	0.000	2.818	1.731	0.000	0.000	0.155	0.155	0.155
	Mid Wood	0.000	0.000	0.000	0.000	3.588	1.986	0.000	0.000	0.121	0.121	0.121
	Understory	8.279	2.391	0.913	0.567	7.827	2.045	0.501	0.290	0.002	0.812	0.990
	Forest Floor	27.033	3.575	27.441	4.968	25.494	3.699	24.674	3.980	0.957	0.648	0.872
	Veg Roots	0.000	0.000	0.000	0.000	0.048	0.008	0.000	0.000	0.001	0.001	0.001
	Total Soil	23378	1103	24620	1522	11145	706	12066	1769	0.381	<0.001	0.893
	0.0-0.2 m	4230	83	4358	246	1914	137	2205	187	0.245	<0.001	0.635
	0.2-0.4 m	4410	274	4918	365	2130	174	2795	243	0.052	<0.001	0.779
	0.4-0.6 m	4799	282	5095	418	2361	183	2444	385	0.439	0.001	0.660
	0.6-1.0 m	9940	621	10249	782	4740	510	4621	999	0.894	0.001	0.765
WRC	Total Plant	100.596	8.204	67.493	7.248	48.072	8.762	50.405	5.531	0.037	0.014	0.022
	Foliage	8.620	2.923	21.312	0.892	5.469	1.817	13.451	0.890	<0.001	0.010	0.209
	Branches	1.987	0.741	7.668	0.558	2.166	0.701	3.899	0.261	<0.001	0.012	0.007
	Bark	1.216	0.551	4.594	0.865	1.114	0.322	2.745	0.180	<0.001	0.070	0.100
	Wood	1.471	0.545	6.497	0.455	1.440	0.467	3.557	0.238	<0.001	0.006	0.007
	Tree Roots	6.335	5.129	11.737	2.344	4.948	0.441	7.515	0.639	0.128	0.270	0.569
	Mid Foliage	19.919	6.589	0.492	0.492	2.217	1.191	0.449	0.449	0.013	0.029	0.026
	Mid Wood	26.693	6.410	0.705	0.705	1.295	0.601	0.098	0.098	0.003	0.006	0.005
	Understory	10.304	3.857	8.713	5.323	22.584	10.428	6.863	1.396	0.232	0.461	0.324
	Forest Floor	19.176	4.850	5.724	2.897	6.589	1.911	11.828	6.942	0.419	0.521	0.084
	Veg Roots	4.873	0.649	0.052	0.052	0.250	0.095	0.000	0.000	<0.001	0.001	<0.001
	Total Soil	20360	59	24900	1303	11806	1450	13150	1517	0.055	<0.001	0.266
	0.0-0.2 m	3693	367	4432	206	2225	223	2224	24	0.125	<0.001	0.125
	0.2-0.4 m	4276	9	5076	328	2239	253	2386	162	0.061	<0.001	0.177
	0.4-0.6 m	4318	71	5088	230	2597	293	2799	317	0.108	<0.001	0.326
	0.6-1.0 m	8073	461	10305	802	4744	761	5740	1055	0.091	0.001	0.490

Appendix Table S.3.28. Mass (kg ha⁻¹) of magnesium (Mg) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	trol	VI	M	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	112.967	11.345	80.196	6.120	0.045
	Foliage	12.315	1.319	21.382	1.295	0.003
	Branches	5.101	0.555	10.609	0.651	0.001
	Bark	3.569	0.454	7.882	0.584	0.001
	Wood	7.272	0.961	15.174	1.486	0.004
	Tree Roots	11.342	2.824	13.228	2.670	0.645
	Mid Foliage	17.132	6.419	0.000	0.000	0.076
	Mid Wood	17.307	7.168	0.000	0.000	0.095
	Understory	21.426	10.233	1.146	0.528	0.095
	Forest Floor	14.828	2.827	10.775	3.064	0.369
	Veg Roots	2.676	1.088	0.000	0.000	0.091
	Total Soil	19369	1410	21577	1257	0.284
	0.0-0.2 m	3460	267	3517	108	0.840
	0.2-0.4 m	4283	191	4383	435	0.839
	0.4-0.6 m	4284	294	4473	360	0.698
	0.6-1.0 m	7342	952	9204	682	0.207
GF	Total Plant	90.516	10.399	93.593	11.013	0.443
	Foliage	13.131	2.266	26.245	1.254	0.030
	Branches	4.798	0.932	17.950	0.963	0.008
	Bark	4.007	0.778	7.493	0.402	0.046
	Wood	5.266	1.355	17.812	0.955	0.007
	Tree Roots	5.402	0.743	8.650	0.662	0.031
	Mid Foliage	12.626	6.010	0.000	0.000	0.171
	Mid Wood	14.978	7.390	0.000	0.000	0.180
	Understory	14.914	3.001	0.668	0.181	0.039
	Forest Floor	11.959	3.298	14.775	7.294	0.743
	Veg Roots	3.435	1.187	0.000	0.000	0.102
	Total Soil	25729	2444	26207	345	0.856
	0.0-0.2 m	3648	465	4346	400	0.319
	0.2-0.4 m	5098	209	4621	157	0.128
	0.4-0.6 m	5563	594	5706	66	0.823
	0.6-1.0 m	11420	1542	11534	201	0.945

Appendix Table S.3.29. Mass (kg ha⁻¹) of manganese (Mn) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

			С	R		CF				P-value		
		Con	trol	VN	N	Con	trol	VN	ſ			
Species	Tissue	kg ha ⁻¹	SE	Trt	Site	Site x Trt						
DF	Total Plant	21.384	1.902	25.342	3.454	28.980	2.242	36.895	2.661	0.060	0.012	0.471
	Foliage	2.996	0.131	4.464	0.177	3.725	0.058	5.275	0.123	<0.001	<0.001	0.755
	Branches	2.919	0.120	2.936	0.190	2.040	0.043	3.061	0.082	0.001	0.009	0.001
	Bark	1.534	0.065	1.709	0.099	2.324	0.038	2.433	0.058	0.061	<0.001	0.636
	Wood	0.768	0.041	1.177	0.063	1.572	0.022	1.723	0.037	<0.001	<0.001	0.011
	Tree Roots	1.434	0.280	1.053	0.175	3.525	0.308	2.164	0.268	0.001	0.003	0.015
	Mid Foliage	0.000	0.000	0.000	0.000	0.124	0.043	0.000	0.000	0.030	0.030	0.030
	Mid Wood	0.000	0.000	0.000	0.000	0.107	0.035	0.000	0.000	0.022	0.022	0.022
	Understory	3.217	2.360	0.244	0.174	1.936	0.643	0.100	0.055	0.080	0.605	0.636
	Forest Floor	8.516	0.889	13.758	3.410	13.582	2.401	22.140	2.160	0.023	0.036	0.494
	Veg Roots	0.000	0.000	0.000	0.000	0.047	0.010	0.000	0.000	0.004	0.004	0.004
	Total Soil	4742	773	5512	1113	12371	2948	16058	2520	0.299	0.001	0.491
	0.0-0.2 m	1617	288	1639	349	4295	529	4615	771	0.743	0.002	0.774
	0.2-0.4 m	1282	236	1370	325	3330	631	5187	1339	0.249	0.009	0.290
	0.4-0.6 m	1131	226	1139	265	1365	337	2998	651	0.054	0.063	0.056
	0.6-1.0 m	712	95	1365	379	3381	1789	3258	636	0.790	0.037	0.696
WRC	Total Plant	9.945	2.483	10.991	1.459	16.592	2.020	20.864	1.223	0.185	0.008	0.394
	Foliage	1.000	0.339	3.242	0.136	1.205	0.400	2.927	0.194	0.001	0.870	0.408
	Branches	0.205	0.077	0.872	0.064	0.304	0.098	0.490	0.033	<0.001	0.085	0.009
	Bark	0.121	0.055	0.528	0.099	0.148	0.043	0.347	0.023	<0.001	0.194	0.092
	Wood	0.100	0.037	0.156	0.011	0.080	0.026	0.179	0.012	0.008	0.959	0.379
	Tree Roots	1.152	0.806	3.812	1.392	5.015	0.672	9.205	1.599	0.019	0.004	0.547
	Mid Foliage	1.525	0.408	0.044	0.044	0.704	0.455	0.189	0.189	0.015	0.341	0.184
	Mid Wood	1.135	0.274	0.048	0.048	0.226	0.143	0.030	0.030	0.005	0.030	0.022
	Understory	1.156	0.506	1.140	0.569	5.182	1.224	1.478	0.349	0.042	0.066	0.043
	Forest Floor	2.400	1.116	1.127	0.737	3.516	1.223	6.018	2.221	0.709	0.090	0.266
	Veg Roots	1.149	0.404	0.021	0.021	0.213	0.065	0.000	0.000	0.010	0.046	0.039
	Total Soil	7481	609	8020	1814	19133	3118	18580	2057	0.997	0.012	0.758
	0.0-0.2 m	1742	176	2376	412	5965	1194	7069	474	0.261	0.004	0.746
	0.2-0.4 m	2321	26	2267	377	5074	1068	5590	589	0.745	0.013	0.690
	0.4-0.6 m	1891	275	1669	392	4297	789	2919	872	0.295	0.030	0.443
	0.6-1.0 m	1528	420	1708	653	3797	727	3002	489	0.622	0.038	0.443

Appendix Table S.3.30. Mass (kg ha⁻¹) of manganese (Mn) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	trol	VN	Л	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	29.954	1.734	62.025	5.210	0.006
	Foliage	7.584	0.812	23.598	1.429	<0.001
	Branches	2.734	0.297	8.467	0.519	<0.001
	Bark	1.768	0.225	6.475	0.480	<0.001
	Wood	2.217	0.293	10.984	1.076	<0.001
	Tree Roots	2.559	0.548	3.129	0.562	0.496
	Mid Foliage	2.745	1.301	0.000	0.000	0.126
	Mid Wood	1.108	0.519	0.000	0.000	0.123
	Understory	3.496	1.506	0.212	0.077	0.117
	Forest Floor	5.022	1.052	9.160	1.663	0.051
	Veg Roots	0.721	0.294	0.000	0.000	0.092
	Total Soil	5843	1051	5063	451	0.521
	0.0-0.2 m	1426	219	1418	92	0.965
	0.2-0.4 m	1489	344	1498	203	0.982
	0.4-0.6 m	1262	196	1175	236	0.787
	0.6-1.0 m	1666	483	972	143	0.218
GF	Total Plant	21.222	2.812	35.358	6.109	0.103
	Foliage	5.310	0.916	11.573	0.553	0.023
	Branches	1.389	0.270	4.167	0.224	0.012
	Bark	1.624	0.316	3.684	0.198	0.024
	Wood	1.283	0.330	3.634	0.195	0.012
	Tree Roots	1.235	0.022	2.320	0.187	0.024
	Mid Foliage	0.226	0.127	0.000	0.000	0.217
	Mid Wood	0.292	0.158	0.000	0.000	0.205
	Understory	3.359	2.363	0.129	0.038	0.301
	Forest Floor	5.627	1.948	9.852	5.046	0.479
	Veg Roots	0.877	0.402	0.000	0.000	0.161
	Total Soil	6400	1517	8119	1613	0.481
	0.0-0.2 m	1500	213	2527	73	0.010
	0.2-0.4 m	1814	154	1939	510	0.827
	0.4-0.6 m	1417	403	2021	507	0.404
	0.6-1.0 m	1669	807	1632	538	0.972

Appendix Table S.3.31. Mass (kg ha⁻¹) of nitrogen (N) of tree and ecosystem components for 18-year-old Douglasfir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

			C	R		CF			P-value		ue	
		Con	trol	VN	M	Con	trol	VN	A			
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt	Site	Site x Trt
DF	Total Plant	604.66	62.08	687.20	76.06	517.66	34.07	596.37	43.17	0.076	0.252	0.961
	Foliage	129.56	5.65	174.39	6.90	106.05	1.66	155.01	3.61	<0.001	0.001	0.681
	Branches	75.65	3.12	86.54	5.61	37.25	0.79	56.78	1.52	0.001	<0.001	0.218
	Bark	52.88	2.25	58.80	3.41	30.98	0.50	47.20	1.12	<0.001	<0.001	0.033
	Wood	28.29	1.51	34.40	1.84	63.03	0.87	68.03	1.45	0.003	<0.001	0.711
	Tree Roots	52.91	8.32	30.59	2.61	34.32	5.21	22.55	3.68	0.012	0.066	0.315
	Mid Foliage	0.00	0.00	0.00	0.00	23.00	14.17	0.00	0.00	0.156	0.156	0.156
	Mid Wood	0.00	0.00	0.00	0.00	15.29	7.79	0.00	0.00	0.097	0.097	0.097
	Understory	41.86	12.23	4.10	2.14	39.01	12.41	3.04	1.92	0.005	0.837	0.921
	Forest Floor	223.52	64.40	298.38	72.28	168.29	22.35	243.75	36.61	0.181	0.365	0.995
	Veg Roots	0.00	0.00	0.00	0.00	0.43	0.08	0.00	0.00	0.002	0.002	0.002
	Total Soil	9507	640	8859	935	8924	1004	10752	700	0.473	0.491	0.159
	0.0-0.2 m	3545	220	3798	820	3508	515	3482	236	0.827	0.736	0.789
	0.2-0.4 m	2377	253	1882	168	2494	403	3379	511	0.513	0.105	0.050
	0.4-0.6 m	2131	308	1100	150	1375	115	1796	134	0.109	0.896	0.004
	0.6-1.0 m	1454	133	2079	263	1547	197	2095	392	0.008	0.879	0.807
WRC	Total Plant	651.29	104.06	487.51	18.78	332.49	51.96	412.87	26.18	0.436	0.025	0.056
	Foliage	61.12	20.72	223.65	9.36	61.61	20.47	122.53	8.11	0.001	0.028	0.024
	Branches	14.18	5.29	50.40	3.67	12.38	4.01	17.59	1.18	<0.001	0.001	0.002
	Bark	4.43	2.01	20.52	3.86	6.91	2.00	17.36	1.14	<0.001	0.883	0.243
	Wood	9.94	3.68	29.45	2.06	34.63	11.25	84.22	5.63	0.004	0.005	0.080
	Tree Roots	29.07	20.66	69.09	13.09	38.20	1.17	61.30	8.23	0.021	0.961	0.415
	Mid Foliage	173.77	56.23	5.70	5.70	26.59	15.24	3.82	3.82	0.012	0.035	0.033
	Mid Wood	149.94	61.54	15.06	15.06	9.46	5.02	0.58	0.58	0.017	0.059	0.027
	Understory	70.53	26.58	39.48	17.86	98.42	40.39	30.43	4.43	0.102	0.739	0.517
	Forest Floor	103.93	32.20	33.90	17.50	42.49	10.88	75.05	30.92	0.464	0.710	0.082
	Veg Roots	34.39	9.10	0.27	0.27	1.80	0.62	0.00	0.00	0.005	0.008	0.008
	Total Soil	10548	188	8731	559	10921	1276	9026	501	0.079	0.711	0.965
	0.0-0.2 m	3830	513	3239	276	3434	454	3640	204	0.625	0.994	0.322
	0.2-0.4 m	2829	576	2495	219	2766	511	2380	349	0.252	0.882	0.929
	0.4-0.6 m	2055	381	1389	216	2127	550	1270	69	0.070	0.952	0.804
	0.6-1.0 m	1835	314	1607	70	2593	435	1736	295	0.121	0.296	0.329

Appendix Table S.3.32. Mass (kg ha⁻¹) of nitrogen (N) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	rol	VN	1	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	735.25	70.72	596.41	38.64	0.032
	Foliage	101.07	10.83	220.21	13.34	<0.001
	Branches	39.09	4.25	86.21	5.29	<0.001
	Bark	20.01	2.54	72.31	5.36	<0.001
	Wood	32.98	4.36	80.51	7.89	0.002
	Tree Roots	61.27	16.98	75.00	12.21	0.536
	Mid Foliage	173.75	63.08	0.00	0.00	0.071
	Mid Wood	97.78	30.56	0.00	0.00	0.049
	Understory	96.32	39.09	6.11	2.48	0.061
	Forest Floor	98.06	10.49	56.06	5.55	0.024
	Veg Roots	14.93	5.73	0.00	0.00	0.080
	Total Soil	8250	711	9071	754	0.021
	0.0-0.2 m	2673	334	2930	276	0.444
	0.2-0.4 m	2378	599	2476	264	0.886
	0.4-0.6 m	1353	233	1982	414	0.213
	0.6-1.0 m	1846	188	1683	193	0.570
GF	Total Plant	579.12	53.80	684.17	82.08	0.107
	Foliage	110.16	19.01	227.86	10.89	0.027
	Branches	32.22	6.26	130.64	7.01	0.007
	Bark	26.40	5.13	44.76	2.40	0.068
	Wood	31.54	8.11	97.66	5.24	0.009
	Tree Roots	31.59	6.70	49.03	7.14	0.149
	Mid Foliage	103.38	49.20	0.00	0.00	0.170
	Mid Wood	61.43	30.48	0.00	0.00	0.181
	Understory	57.88	7.99	4.57	1.61	0.019
	Forest Floor	106.38	41.89	129.65	57.90	0.761
	Veg Roots	18.13	3.75	0.00	0.00	0.040
	Total Soil	11663	1039	9974	1157	0.338
	0.0-0.2 m	4355	671	3687	99	0.380
	0.2-0.4 m	2752	222	2536	585	0.709
	0.4-0.6 m	2000	96	1935	505	0.906
	0.6-1.0 m	2556	524	1816	255	0.225

Appendix Table S.3.33. Mass (kg ha⁻¹) of sodium (Na) of tree and ecosystem components for 18-year-old Douglasfir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05

			С	R		CF			P-value		ue	
		Con	trol	VN	M	Cont	trol	VN	A			
Species	Tissue	kg ha ⁻¹	SE	Trt	Site	Site x Trt						
DF	Total Plant	12.659	0.370	11.015	0.567	4.752	0.319	5.539	0.626	0.369	<0.001	0.033
	Foliage	1.639	0.071	2.975	0.118	0.810	0.013	0.866	0.020	<0.001	<0.001	<0.001
	Branches	1.060	0.044	0.918	0.060	0.048	0.001	0.165	0.004	0.733	<0.001	0.004
	Bark	3.947	0.168	1.930	0.112	0.346	0.006	0.735	0.017	<0.001	<0.001	<0.001
	Wood	0.100	0.005	0.124	0.007	0.071	0.001	0.112	0.002	<0.001	0.001	0.087
	Tree Roots	1.436	0.561	0.735	0.141	0.562	0.115	0.356	0.082	0.087	0.130	0.307
	Mid Foliage	0.000	0.000	0.000	0.000	0.076	0.039	0.000	0.000	0.101	0.101	0.101
	Mid Wood	0.000	0.000	0.000	0.000	0.018	0.011	0.000	0.000	0.150	0.150	0.150
	Understory	0.633	0.109	0.081	0.048	0.505	0.190	0.039	0.030	0.002	0.531	0.672
	Forest Floor	3.843	0.290	4.252	0.572	2.310	0.245	3.266	0.520	0.139	0.013	0.538
	Veg Roots	0.000	0.000	0.000	0.000	0.007	0.001	0.000	0.000	0.003	0.003	0.003
	Total Soil	1359.7	50.3	1588.1	107.5	1044.0	84.6	1061.3	84.5	0.171	<0.001	0.234
	0.0-0.2 m	254.0	15.2	282.6	8.2	160.5	11.5	175.5	5.9	0.066	<0.001	0.539
	0.2-0.4 m	255.0	16.8	288.6	22.4	242.9	27.2	301.5	41.2	0.111	0.990	0.630
	0.4-0.6 m	342.3	15.3	428.1	36.4	229.2	14.1	213.3	23.3	0.171	<0.001	0.056
	0.6-1.0 m	508.4	29.9	588.9	56.2	411.4	42.4	371.0	41.6	0.604	0.019	0.150
WRC	Total Plant	6.433	1.445	5.938	0.580	3.667	0.614	3.577	0.34	0.713	0.008	0.799
	Foliage	0.810	0.275	1.895	0.079	0.394	0.131	1.071	0.07	<0.001	0.002	0.200
	Branches	0.078	0.029	0.214	0.016	0.011	0.004	-0.111	0.01	0.666	<0.001	<0.001
	Bark	0.120	0.054	0.520	0.098	0.052	0.015	0.120	0.01	0.001	0.001	0.006
	Wood	0.013	0.005	0.046	0.003	0.013	0.004	0.036	0.00	<0.001	0.243	0.221
	Tree Roots	0.924	0.557	1.634	0.242	0.938	0.248	0.933	0.19	0.288	0.344	0.282
	Mid Foliage	0.767	0.184	0.032	0.032	0.265	0.168	0.024	0.02	0.012	0.104	0.108
	Mid Wood	0.209	0.042	0.004	0.004	0.102	0.064	0.004	0.00	0.005	0.230	0.233
	Understory	0.732	0.270	0.693	0.376	1.242	0.409	0.321	0.05	0.154	0.830	0.187
	Forest Floor	1.657	0.327	0.893	0.510	0.599	0.101	1.179	0.38	0.778	0.351	0.082
	Veg Roots	1.123	0.564	0.007	0.007	0.050	0.024	0.000	0.00	0.055	0.073	0.071
	Total Soil	1336.3	63.4	1434.7	87.3	1048.9	75.9	1178.2	78.5	0.179	0.006	0.849
	0.0-0.2 m	197.7	23.0	231.6	23.3	186.9	12.6	205.0	16.2	0.187	0.331	0.673
	0.2-0.4 m	330.3	27.4	343.1	32.7	264.6	24.7	348.9	15.2	0.078	0.254	0.179
	0.4-0.6 m	279.7	22.3	268.3	19.6	217.6	13.7	225.7	23.7	0.938	0.028	0.642
	0.6-1.0 m	528.6	35.2	591.6	23.5	379.9	35.0	398.6	37.9	0.274	0.001	0.545

Appendix Table S.3.34. Mass (kg ha⁻¹) of sodium (Na) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	trol	VN	Л	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	8.096	0.952	8.652	0.488	0.619
	Foliage	1.113	0.119	3.140	0.190	<0.001
	Branches	0.026	0.003	0.224	0.014	<0.001
	Bark	0.632	0.080	1.736	0.129	<0.001
	Wood	0.065	0.009	0.176	0.017	<0.001
	Tree Roots	1.314	0.297	1.941	0.324	0.241
	Mid Foliage	1.220	0.509	0.000	0.000	0.096
	Mid Wood	0.393	0.174	0.000	0.000	0.110
	Understory	1.513	0.670	0.100	0.044	0.080
	Forest Floor	1.468	0.262	1.335	0.161	0.647
	Veg Roots	0.351	0.154	0.000	0.000	0.107
	Total Soil	1277.4	47.2	1320.0	39.1	0.513
	0.0-0.2 m	207.0	16.7	216.3	16.3	0.703
	0.2-0.4 m	301.8	20.9	325.6	33.2	0.566
	0.4-0.6 m	295.6	12.7	301.4	14.6	0.773
	0.6-1.0 m	473.1	29.6	476.7	14.8	0.916
GF	Total Plant	5.420	0.149	6.743	1.090	0.318
	Foliage	0.643	0.111	1.546	0.074	0.017
	Branches	0.350	0.068	1.008	0.054	0.013
	Bark	0.407	0.079	0.786	0.042	0.041
	Wood	0.050	0.013	0.171	0.009	0.007
	Tree Roots	0.601	0.083	1.332	0.064	0.016
	Mid Foliage	0.302	0.146	0.000	0.000	0.174
	Mid Wood	0.082	0.040	0.000	0.000	0.177
	Understory	1.293	0.399	0.075	0.022	0.084
	Forest Floor	1.275	0.368	1.823	0.855	0.587
	Veg Roots	0.42	0.19	0.00	0.00	0.161
	Total Soil	1624.4	9.1	1501.8	91.9	0.255
	0.0-0.2 m	228.0	10.5	277.7	14.9	0.052
	0.2-0.4 m	363.6	28.4	314.8	22.3	0.220
	0.4-0.6 m	354.6	17.0	338.5	16.2	0.524
	0.6-1.0 m	678.2	32.1	570.8	63.9	0.242

Appendix Table S.3.35. Mass (kg ha⁻¹) of phosphorous (P) of tree and ecosystem components for 18 year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

			С	R		CF			P-value		ue	
		Con	trol	VN	Л	Cont	trol	VN	Л			
Species	Tissue	kg ha ⁻¹	SE	Trt	Site	Site x Trt						
DF	Total Plant	74.300	3.907	79.466	3.339	70.302	4.202	79.299	2.572	0.049	0.632	0.531
	Foliage	18.010	0.785	21.878	0.866	18.315	0.287	23.786	0.554	<0.001	0.121	0.249
	Branches	13.397	0.553	15.471	1.003	10.894	0.231	15.449	0.414	<0.001	0.065	0.069
	Bark	9.210	0.392	11.034	0.640	6.653	0.108	9.323	0.221	<0.001	<0.001	0.305
	Wood	2.556	0.137	2.793	0.150	3.181	0.044	3.169	0.068	0.324	0.001	0.277
	Tree Roots	6.643	1.589	4.245	1.051	4.098	0.654	3.374	0.442	0.022	0.258	0.153
	Mid Foliage	0.000	0.000	0.000	0.000	2.879	1.812	0.000	0.000	0.163	0.163	0.163
	Mid Wood	0.000	0.000	0.000	0.000	2.322	1.622	0.000	0.000	0.202	0.202	0.202
	Understory	4.569	1.637	0.397	0.206	6.199	2.145	0.461	0.341	0.010	0.563	0.581
	Forest Floor	19.915	3.824	23.649	3.344	15.711	0.306	23.737	1.266	0.045	0.448	0.429
	Veg Roots	0.000	0.000	0.000	0.000	0.051	0.008	0.000	0.000	0.001	0.001	0.001
	Total Soil	32481	3186	32064	3546	61714	8810	58691	4162	0.757	<0.001	0.814
	0.0-0.2 m	7804	631	8502	924	13261	866	13358	241	0.590	<0.001	0.683
	0.2-0.4 m	8215	1579	6350	717	12287	1476	14327	1719	0.952	<0.001	0.196
	0.4-0.6 m	7870	1082	5898	753	11021	1171	10759	1002	0.292	0.002	0.415
	0.6-1.0 m	8591	820	11315	1480	25146	7866	20247	1641	0.796	0.009	0.372
WRC	Total Plant	72.723	4.725	56.488	4.241	39.545	8.251	49.077	3.424	0.590	0.020	0.078
	Foliage	7.894	2.677	22.231	0.930	6.713	2.231	17.710	1.172	0.001	0.205	0.408
	Branches	1.691	0.631	7.411	0.540	2.461	0.797	6.266	0.419	0.001	0.781	0.190
	Bark	1.005	0.455	3.601	0.678	1.181	0.341	3.002	0.196	0.000	0.620	0.371
	Wood	0.436	0.161	1.678	0.117	0.599	0.195	1.383	0.092	0.001	0.686	0.190
	Tree Roots	4.717	3.484	9.119	0.115	4.561	0.370	9.451	1.550	0.023	0.961	0.891
	Mid Foliage	21.061	6.690	0.285	0.285	3.842	2.238	0.502	0.502	0.003	0.021	0.019
	Mid Wood	15.969	6.212	0.258	0.258	1.345	0.671	0.070	0.070	0.023	0.038	0.040
	Understory	7.314	3.082	5.857	3.073	14.269	5.942	5.022	0.977	0.211	0.462	0.353
	Forest Floor	7.971	1.565	6.020	3.735	4.366	1.698	5.673	0.712	0.806	0.475	0.248
	Veg Roots	4.666	0.990	0.028	0.028	0.208	0.070	0.000	0.000	0.002	0.003	0.003
	Total Soil	38755	1617	40669	2259	56620	8674	56363	9748	0.606	0.186	0.503
	0.0-0.2 m	9593	713	12000	1084	15813	3144	17225	2717	0.262	0.136	0.756
	0.2-0.4 m	9249	1248	9704	761	11344	1779	12811	2017	0.416	0.281	0.660
	0.4-0.6 m	8193	8	7583	185	11393	2434	9293	1356	0.260	0.290	0.516
	0.6-1.0 m	11720	612	11382	594	18070	2780	17034	4449	0.800	0.156	0.897

Appendix Table S.3.36. Mass (kg ha⁻¹) of phosphorous (P) of tree and ecosystem components for 18 year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	trol	VM	I	P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	113.155	8.902	116.901	6.498	0.224
	Foliage	26.607	2.850	50.638	3.067	0.001
	Branches	6.255	0.680	15.122	0.928	<0.001
	Bark	6.718	0.854	17.353	1.287	0.001
	Wood	4.513	0.596	12.106	1.186	0.001
	Tree Roots	9.676	2.410	11.904	1.506	0.432
	Mid Foliage	23.183	8.758	0.000	0.000	0.077
	Mid Wood	13.508	5.514	0.000	0.000	0.092
	Understory	11.101	5.278	0.701	0.270	0.097
	Forest Floor	9.316	1.427	9.076	1.235	0.858
	Veg Roots	2.278	0.942	0.000	0.000	0.094
	Total Soil	39350	6339	37657	3740	0.756
	0.0-0.2 m	9713	2367	9221	1155	0.828
	0.2-0.4 m	10233	2860	9892	2072	0.926
	0.4-0.6 m	8314	760	8027	860	0.811
	0.6-1.0 m	11090	1627	10517	914	0.502
GF	Total Plant	76.268	15.253	103.996	8.215	0.121
	Foliage	13.061	2.254	32.967	1.575	0.015
	Branches	7.351	1.428	30.762	1.651	0.006
	Bark	5.055	0.982	8.138	0.437	0.085
	Wood	2.064	0.531	8.281	0.444	0.005
	Tree Roots	4.915	0.989	10.133	3.120	0.186
	Mid Foliage	13.094	6.221	0.000	0.000	0.170
	Mid Wood	11.301	5.440	0.000	0.000	0.173
	Understory	7.466	1.835	0.494	0.159	0.019
	Forest Floor	8.756	1.982	13.221	6.050	0.522
	Veg Roots	3.204	1.281	0.000	0.000	0.130
	Total Soil	41366	11310	44789	6587	0.807
	0.0-0.2 m	10106	2656	12787	1684	0.442
	0.2-0.4 m	8053	552	9868	2772	0.556
	0.4-0.6 m	8955	2451	9006	1781	0.988
	0.6-1.0 m	14252	6030	13128	498	0.862

Appendix Table S.3.37. Mass (kg ha⁻¹) of Sulfur (S) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

			Cl	R		CF			P-value		ue	
		Cont	trol	VM	1	Cont	rol	VM	ſ			
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt	Site	Site x Trt
DF	Total Plant	95.88	4.66	109.84	8.63	82.23	10.65	91.97	3.27	0.085	0.123	0.726
	Foliage	13.35	0.58	19.96	0.79	9.86	0.15	13.72	0.32	<0.001	<0.001	0.022
	Branches	14.69	0.61	16.71	1.08	8.17	0.17	13.19	0.35	<0.001	<0.001	0.040
	Bark	10.12	0.43	9.64	0.56	5.94	0.10	8.54	0.20	0.014	<0.001	0.001
	Wood	21.30	1.14	27.98	1.50	14.26	0.20	24.60	0.52	<0.001	<0.001	0.086
	Tree Roots	6.65	1.42	4.17	0.65	4.41	0.99	3.21	0.52	0.026	0.232	0.348
	Mid Foliage	0.00	0.00	0.00	0.00	0.59	0.26	0.00	0.00	0.067	0.067	0.067
	Mid Wood	0.00	0.00	0.00	0.00	15.54	10.53	0.00	0.00	0.191	0.191	0.191
	Understory	5.39	1.61	0.46	0.24	3.97	1.01	0.37	0.24	0.003	0.497	0.480
	Forest Floor	24.38	4.81	30.92	7.47	19.44	1.44	28.34	2.28	0.084	0.513	0.762
	Veg Roots	0.00	0.00	0.00	0.00	0.05	0.01	0.00	0.00	0.003	0.003	0.003
WRC	Total Plant	145.05	31.30	59.85	2.99	37.13	6.03	48.86	3.03	0.032	0.011	0.012
	Foliage	4.76	1.61	11.46	0.48	4.97	1.65	12.59	0.83	0.002	0.646	0.723
	Branches	2.57	0.96	9.52	0.69	2.47	0.80	5.45	0.36	<0.001	0.016	0.020
	Bark	1.19	0.54	5.12	0.96	1.10	0.32	2.80	0.18	<0.001	0.040	0.055
	Wood	3.08	1.14	11.06	0.77	3.20	1.04	8.42	0.56	<0.001	0.194	0.159
	Tree Roots	4.03	2.72	9.78	1.18	5.25	0.45	8.82	1.32	0.025	0.938	0.490
	Mid Foliage	6.00	1.05	0.15	0.15	2.22	1.42	0.28	0.28	0.002	0.088	0.071
	Mid Wood	101.88	39.12	1.30	1.30	2.84	1.22	0.04	0.04	0.025	0.029	0.030
	Understory	7.57	3.40	5.21	2.35	9.46	2.69	2.50	0.43	0.077	0.867	0.354
	Forest Floor	9.24	1.61	6.22	3.79	5.38	1.47	7.97	1.96	0.920	0.681	0.231
	Veg Roots	4.71	1.29	0.04	0.04	0.24	0.08	0.00	0.00	0.006	0.010	0.009

Appendix Table S.3.38. Mass (kg ha⁻¹) of Sulfur (S) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Cont	rol	VM		P-value
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	143.19	32.94	107.36	7.48	0.258
	Foliage	10.42	1.12	20.17	1.22	0.001
	Branches	7.52	0.82	17.00	1.04	<0.001
	Bark	3.89	0.49	12.94	0.96	<0.001
	Wood	13.73	1.81	37.61	3.68	0.001
	Tree Roots	7.94	1.27	10.01	1.47	0.328
	Mid Foliage	9.82	4.37	0.00	0.00	0.110
	Mid Wood	68.29	31.85	0.00	0.00	0.121
	Understory	10.30	4.21	0.79	0.30	0.107
	Forest Floor	9.01	0.92	8.84	1.08	0.533
	Veg Roots	2.27	1.00	0.00	0.00	0.109
GF	Total Plant	133.11	35.22	103.53	7.89	0.392
	Foliage	9.75	1.68	19.13	0.91	0.032
	Branches	6.10	1.19	19.08	1.02	0.011
	Bark	4.03	0.78	8.23	0.44	0.034
	Wood	10.98	2.83	38.84	2.08	0.006
	Tree Roots	4.20	0.75	6.53	0.94	0.124
	Mid Foliage	2.12	1.04	0.00	0.00	0.178
	Mid Wood	74.09	35.78	0.00	0.00	0.174
	Understory	9.83	3.40	0.51	0.14	0.104
	Forest Floor	9.34	2.50	11.21	4.36	0.728
	Veg Roots	2.67	0.96	0.00	0.00	0.109

Control: no post-planting vegetation control, VM: sustained vegetation control for first 5 years post planting. Trt:

Effect of vegetation management treatment

Appendix Table S.3.39. Mass (kg ha⁻¹) of zinc (Zn) of tree and ecosystem components for 18-year-old Douglas-fir (DF) and western redcedar (WRC) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		CR			CF				P-value			
		Control VM			Control VM							
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt	Site	Site x Trt
DF	Total Plant	1.460	0.094	1.569	0.114	1.238	0.020	1.579	0.081	0.008	0.355	0.090
	Foliage	0.122	0.005	0.135	0.005	0.107	0.002	0.147	0.003	<0.001	0.768	0.007
	Branches	0.432	0.018	0.498	0.032	0.251	0.005	0.345	0.009	0.001	<0.001	0.478
	Bark	0.263	0.011	0.342	0.020	0.218	0.004	0.296	0.007	<0.001	0.003	0.956
	Wood	0.245	0.013	0.249	0.013	0.218	0.003	0.366	0.008	<0.001	0.001	<0.001
	Tree Roots	0.089	0.012	0.062	0.008	0.074	0.006	0.046	0.006	0.009	0.167	0.957
	Mid Foliage	0.000	0.000	0.000	0.000	0.010	0.005	0.000	0.000	0.084	0.084	0.084
	Mid Wood	0.000	0.000	0.000	0.000	0.031	0.018	0.000	0.000	0.141	0.141	0.141
	Understory	0.081	0.043	0.010	0.007	0.059	0.018	0.008	0.005	0.023	0.616	0.670
	Forest Floor	0.228	0.055	0.274	0.062	0.269	0.039	0.371	0.064	0.196	0.298	0.600
	Veg Roots	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.006	0.006	0.006
	Total Soil	437.1	20.2	482.7	73.7	430.4	75.6	468.6	88.9	0.559	0.889	0.959
	0.0-0.2 m	86.0	4.8	100.8	15.0	89.2	8.8	97.4	17.5	0.350	0.993	0.778
	0.2-0.4 m	92.1	5.4	94.9	13.5	87.9	8.3	114.3	22.3	0.305	0.627	0.401
	0.4-0.6 m	98.6	3.9	99.2	18.8	84.6	10.2	91.8	18.5	0.780	0.507	0.815
	0.6-1.0 m	160.5	15.5	187.7	29.8	168.7	50.6	165.2	33.2	0.736	0.847	0.664
WRC	Total Plant	0.924	0.104	0.884	0.067	0.783	0.234	0.858	0.066	0.908	0.631	0.702
	Foliage	0.100	0.034	0.247	0.010	0.092	0.031	0.216	0.014	0.002	0.488	0.651
	Branches	0.057	0.021	0.182	0.013	0.050	0.016	0.088	0.006	<0.001	0.007	0.014
	Bark	0.036	0.016	0.114	0.022	0.026	0.008	0.058	0.004	0.001	0.025	0.089
	Wood	0.018	0.006	0.076	0.005	0.026	0.008	0.073	0.005	0.001	0.726	0.434
	Tree Roots	0.070	0.050	0.128	0.029	0.252	0.129	0.215	0.046	0.862	0.259	0.442
	Mid Foliage	0.096	0.023	0.005	0.005	0.024	0.015	0.009	0.009	0.004	0.036	0.024
	Mid Wood	0.273	0.077	0.014	0.014	0.038	0.023	0.002	0.002	0.006	0.025	0.017
	Understory	0.079	0.031	0.046	0.023	0.158	0.064	0.061	0.008	0.153	0.282	0.457
	Forest Floor	0.115	0.039	0.070	0.035	0.102	0.031	0.134	0.061	0.889	0.595	0.420
	Veg Roots	0.081	0.020	0.001	0.001	0.015	0.010	0.000	0.000	0.006	0.023	0.024
	Total Soil	443.3	46.9	499.8	42.7	484.8	55.2	554.5	43.3	0.059	0.490	0.808
	0.0-0.2 m	85.2	7.9	104.5	11.9	116.3	19.3	129.1	4.3	0.248	0.101	0.800
	0.2-0.4 m	111.3	7.2	109.6	8.0	100.6	14.3	115.5	3.8	0.509	0.826	0.414
	0.4-0.6 m	110.0	12.8	105.4	9.9	102.5	12.4	111.3	5.2	0.801	0.952	0.448
	0.6-1.0 m	136.9	23.2	180.2	14.7	165.4	14.7	198.6	33.3	0.034	0.496	0.718

Appendix Table S.3.40. Mass (kg ha⁻¹) of zinc (Zn) of tree and ecosystem components for 18-year-old western hemlock (WH) and grand fir (GF) stands growing under contrasting treatments of vegetation management on sites located in the central Coast Range (CR) and Cascade Foothills (CF) of western Oregon. SE is the standard error. The P-value shown is in bold if the difference in concentration was significant at α =0.05.

		Con	trol	\mathbf{V}	P-value	
Species	Tissue	kg ha ⁻¹	SE	kg ha ⁻¹	SE	Trt
WH	Total Plant	1.297	0.103	1.228	0.104	0.575
	Foliage	0.111	0.012	0.227	0.014	0.001
	Branches	0.141	0.015	0.245	0.015	0.003
	Bark	0.050	0.006	0.118	0.009	0.001
	Wood	0.158	0.021	0.372	0.036	0.002
	Tree Roots	0.117	0.028	0.158	0.041	0.446
	Mid Foliage	0.122	0.049	0.000	0.000	0.091
	Mid Wood	0.270	0.108	0.000	0.000	0.089
	Understory	0.174	0.089	0.006	0.002	0.108
	Forest Floor	0.127	0.021	0.102	0.014	0.354
	Veg Roots	0.028	0.012	0.000	0.000	0.095
	Total Soil	479.1	20.7	471.8	31.5	0.816
	0.0-0.2 m	91.3	8.9	90.5	3.5	0.919
	0.2-0.4 m	113.2	7.8	105.4	13.1	0.626
	0.4-0.6 m	105.9	3.7	103.9	7.0	0.809
	0.6-1.0 m	168.7	15.7	172.1	10.9	0.749
GF	Total Plant	1.215	0.181	1.972	0.232	0.051
	Foliage	0.237	0.041	0.531	0.025	0.021
	Branches	0.162	0.032	0.460	0.025	0.013
	Bark	0.116	0.022	0.136	0.007	0.454
	Wood	0.144	0.037	0.420	0.023	0.011
	Tree Roots	0.072	0.013	0.136	0.020	0.027
	Mid Foliage	0.038	0.019	0.000	0.000	0.176
	Mid Wood	0.137	0.067	0.000	0.000	0.178
	Understory	0.087	0.037	0.006	0.003	0.098
	Forest Floor	0.177	0.059	0.283	0.152	0.549
	Veg Roots	0.046	0.017	0.000	0.000	0.115
	Total Soil	567.6	18.4	571.6	57.1	0.952
	0.0-0.2 m	91.1	8.1	117.6	3.9	0.071
	0.2-0.4 m	132.7	12.8	113.6	19.7	0.255
	0.4-0.6 m	127.0	3.1	135.5	17.2	0.638
	0.6-1.0 m	216.9	21.1	204.9	17.3	0.682

located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site).								
Nutrient	Site	Spp	Trt	Site*Spp	Site*Trt	Spp*Trt	Site*Spp*Trt	
C:N	0.001	<0.001	<0.001	0.011	0.153	0.002	0.409	
C:P	0.652	<0.001	<0.001	0.324	0.825	<0.001	0.008	
C:K	0.592	<0.001	<0.001	0.678	0.544	<0.001	0.096	
C:Mg	<0.001	<0.001	<0.001	0.356	0.130	<0.001	0.052	
C:Ca	0.003	<0.001	<0.001	0.004	0.011	0.078	0.132	
C:S	0.049	<0.001	<0.001	0.370	0.058	<0.001	0.003	
C:B	0.014	<0.001	<0.001	0.020	0.757	0.004	0.375	
C:Mn	0.651	<0.001	<0.001	0.429	0.724	<0.001	0.100	
C:Fe	0.022	<0.001	<0.001	0.294	0.289	0.001	0.001	
C:Cu	0.089	<0.001	<0.001	0.878	0.220	0.001	0.212	
C:Na	0.037	<0.001	<0.001	0.012	0.723	0.006	0.031	
C:Zn	0.652	<0.001	<0.001	0.324	0.825	<0.001	0.008	

Appendix Table S.4.1. Results of ANOVA test for differences between carbon:nutrient ratios of crop tree stemwood carbon to plant derived nutrient (crop trees, midstory, understory, and forest floor) for Douglas-fir, western hemlock, western redcedar and grand fir (Spp) growing under contrasting treatments of vegetation management (Trt) on sites located in the central Coast Range (CR) and the Cascade foothills (CF) of western Oregon (Site).