AN ABSTRACT OF THE THESIS OF

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Signature redacted for privacy.

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Kermit Cromack, Jr.

Effects of partial understory removal on belowground and aboveground ecosystem properties were investigated in 5 and 15 yr old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) experimental plantations in western Oregon. Seedling survival was not affected by understory removal at age 5 yr. But through age 15 yr, understory removal increased seedling survival up to 30% on some of the plots. At plantation age 5 yr, tree biomass accumulation was increased nearly 12-fold with complete shrub and herb removal from the sites. However, total aboveground biomass was the same among treatments at age 5 yr. At plantation age 15 yr, tree biomass accumulation was 336% greater with complete understory removal from the Douglas-fir only plots (DFO). Even though Douglas-fir needle N concentrations were significantly higher on DFC plots at age 5 yr, this difference was not detected at plantation age 15 yr. However, Douglas-fir foliar nutrient concentrations decreased significantly between 5 and 15 yr for: Ca, Mn, Fe, Cu, B, and Zn. The total aboveground N

pool was greater for DFC plots due to the greater amount of aboveground biomass present in shrubs and herbs at age 5 yr. From plantation age 5 to 15 yr, the total aboveground N pool dramatically increased. However, the aboveground total N pool was not significantly different among plots. On the other hand, the aboveground P pool was 86% and Ca pool 87% higher on DFO than on DFC plots. At age 15 yr, the upper 15 cm of soil had more than 20% greater bulk density on DFO than on DFC plots. Soil C concentration in the < 2 mm soil fraction was reduced by 27% with complete understory removal at age 5 yr. DFO plot soil had 49% less exchangeable Ca than DFC plot soil by age 15 yr. At age 5 yr, net mineralizable NH_4^+ was the lowest on DFO plots. However, incorporation of organic matter into mineral soil during vegetation removal, and the decreased demand in plant uptake, increased total inorganic N on exchange resins in DFO soil. In the upper 15 cm of soil, $\delta^{15}N$ was enriched due to understory removal.

Ecosystem Effects of Vegetation Removal in Coastal Oregon Douglas-fir
Experimental Plantations: Impacts on Ecosystem Production, Tree Growth,
Nutrients, and Soils

by

Oktay Yildiz

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CONTRIBUTION OF AUTHORS

Dr. Cromack was involved in data collection, analysis and writing of each manuscript. Dr. Radosevich and Dr. Wagner were involved in the design and establishment of the experiments. Dr. Baham assisted in the interpretation of soil data.

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Ecosystem Effects of Vegetation Removal in Coastal Oregon Douglas-fir Experimental Plantations: Impacts on Ecosystem Production, Tree Growth, Nutrients, and Soils

CHAPTER 1

General Introduction

There are about 28 million hectares of timberland along the Pacific Coast, according to the 1993 timber assessment report by the USDA Forest Service. This coastal forestland accounts for about 14% of total timberland in the United States (Haynes et al. 1995). Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) comprises about 50% of the standing timber in western forests, and second growth Douglas-fir stands may produce more than 180 m^3 ha^{-1} of wood in less than 50 yr (Harlow et al. 1979). Coastal Oregon forests are characterized by soil and environmental conditions favoring high productivity (Waring and Franklin 1979; Cromack et al. 1999). Favorable climate and soil conditions allow vegetation to photosynthesize throughout the year. Mild winter temperatures permit substantial winter photosynthesis, and almost half of the annual net C assimilation by Douglas-fir occurs between mid-fall and late spring (Waring and Franklin 1979; Waring and Running 1998). Aboveground net primary productivity may average 10 metric tons ha^{-1} yr^{-1} for Pacific Northwest Douglas-fir forests (Waring 1986).

In the Pacific Northwest, management for timber production has converted large areas of coniferous forestlands to younger plantations in

various stages of development, and patches dominated by early successional shrubs and trees (Spies et al. 1994). After forest disturbance by harvesting practices, these early seral and disturbance-resistant species can contribute significantly to species richness, or even dominate a site for years before canopy closure of the stand (Bailey et al. 1998). Salmonberry (*Rubus spectabilis* Pursh) can fully occupy newly disturbed sites through vegetative regeneration and make it very difficult for other species to become established. Stemwood accumulation is usually the major interest in commodity-based forest management, and one of the management objectives in commercial plantation forestry is weed control around trees in order to maximize stemwood growth (Nambiar and Sands 1993). In order to secure seedling survival and maximize wood production from these plantations, understory removal and subsequent release of conifer seedlings from salmonberry competition until seedlings overtop shrubs during the stem exclusion stage is a necessary silvicultural management (Jensen et al. 1995). Thus, after seedlings are planted, plantations are often subjected to intensive weed control (Radosevich et al. 1997), and competing species removal from these sites has become routine in the Pacific Northwest (Knowe et al. 1992).

However, understory clearing after harvesting may disturb the ecological integrity of these highly productive forest ecosystems. Besides contributing to biological diversity, understory vegetation can affect forest ecosystem processes in a variety of ways, such as providing soil stability,

and food and cover for wildlife (Waring 1986; Jensen et al. 1995). Forest understory vegetation may play key role in soil fertility, even though it may be a relatively small component of the total forest ecosystem biomass (Busse et al. 1996). Ecosystem productivity and nutrient retention increase with interspecific differences in resource requirements (Tilman et al. 1997). Species mixtures might be more productive than monocultures, if different species adaptations within the mixture result in a more complete use of resources than possible by one species alone (Perry 1994). Thus, a species mixture, with shrubs and herbs as ecosystem components, may provide greater biomass yield as a result of improved site resource use. Higher plant productivity may also reduce ecosystem nutrient losses, leading to long-term increases in ecosystem C and nutrient stores which, in turn, increase productivity (Tilman et al. 1997).

The chemical quality of organic substrates affects mineralization and immobilization processes. Leaf litter residues with low N concentrations and high C:N ratios from Douglas-fir and other coniferous species, are expected to decompose more slowly, immobilize N during decomposition, and slow net nutrient mineralization rates relative to herb and shrub litter (Waring and Running 1998; Fisher and Binkley 2000). Pure Douglas-fir sites would have poorer litter quality than those with Douglas-fir, shrubs and herbs present. Thus, the accumulated forest floor under a Douglas-fir forest with total understory removal may become a significant repository of a site's nutrients. On the other hand, this slow nutrient release from

decomposing organic matter may cause a substantial decline in soil nutrient supply, especially during the stage of high nutrient demand by trees, resulting in a substantially lower canopy nutrient content. This nutrient supply decline may impact the growth of a young Douglas-fir forest that obtains half of its N from litter (Waring and Franklin 1979). If nutrients are sequestered in tree woody tissues, and understory removal occurs, then nutrients may be limited for future generations. Apparently, understory removal may have an effect on soil organic matter turnover and nutrient cycling.

Soil generally is the least renewable ecosystem resource. Thus, if the ecosystem soil component is altered in such a way that the ecosystem cannot recover, then resource sustainability will be reduced (Kimmins 1996). Organic matter is an important component of most forest soils because it maintains and improves soil nutrient storage, as well as soil physical properties (Russell 1973; Vitousek and Reiners 1975; Wild 1988; Tiessen et al. 1994; Hillel 1998). Thus, the amount of organic matter and its biochemical substrate quality are important in maintaining and improving soil fertility (Tiessen et al. 1994; Drinkwater et al. 1998). Storage of essential nutrients, such as N, is mainly in organic forms (Stevenson 1986; Waring and Running 1998). Substantial amounts of other soil nutrients, such as P and S, are also incorporated into soil organic matter (Stevenson 1986; Wild 1988). Soil organic matter also contributes to the soil exchange

capacity, and can be important in increasing the soil capacity for exchangeable cations such as Ca, K and Mg (Brady and Weil 1996).

Vegetation removal can result in greatly increased soil organic matter and nutrient losses (Bormann and Likens 1979; Wild 1988; Mao et al. 1992). Losses of nutrients or organic matter during harvesting and post-harvesting practices may reduce future productivity. Thus, revegetation of the site by disturbance-resistant and pioneering species, which occupy newly disturbed sites, may play an important role in ameliorating the effects of severe ecological disturbance, such as clear-cutting, by retaining nutrients and key soil organisms during the period of tree reestablishment (Marks and Bormann 1972; Bormann and Likens 1979; Kimmins 1996; Waring and Running 1998). Management practices that reduce cover of these pioneering plants can lead to nutrient losses, may reduce ecological diversity, and may possibly affect sustainability (Perry 1988).

Maintaining forest productivity will be a major challenge as population and its demand for forest products rise. The success of future generations will depend on balancing the demand for resources with the capacity of the landscape to maintain its functional integrity (Waring and Running 1998). Restoration of degraded forestlands will be an important future goal for many countries, and will be aided by basic ecosystems research on forest productivity and soil fertility (Mao et al. 1992). Increased retention of limiting nutrients, such as N, is desirable as management component (Johnson 1992). In addition, a better understanding of N

recycling, together with managing for increased organic inputs as component parts of current studies in sustainable forestry and agriculture, may help us to understand better the maintenance of long-term site productivity. Moreover, the effects of excess inorganic N inputs, which in some cases may not enhance soil C accretion (Nadelhoffer et al. 1999), even with some increases in ecosystem productivity. Nutrient imbalance increase ecosystem stress and increase incidence of forest insects and diseases (Waring and Running 1998).

Drastic changes in species composition of the stand are likely to lead not only to increased productivity of target species for wood production, but also may lead to changes in the site's nutritional status. Thus, the retention or removal of understory or overstory vegetation components is of general interest with regard to both competition and to total ecosystem productivity (Wagner and Radosevich 1998; Waring and Running 1998), together with understory contribution to maintenance of long-term soil fertility (Busse et al. 1996).

The effects of understory vegetation on young conifer seedling survival and growth through competition for light, water and nutrients are well documented (Newton and Preest 1988; Tesch and Hobbs 1989; Hughes et al. 1990; Tesch et al. 1993; Roth and Newton 1996; Harrrington and Tappeiner 1997; Rose et al. 1999). However, literature is lacking in: (1) changes in total ecosystem properties due to species composition manipulation or (2) residual effects of understory removal during the early

years of stand establishment on the performance of trees and other plant species 10 yr later. In this study, an effort was made to analyze the ecosystem structural and functional characteristics induced by changes in species composition. Alteration of net ecosystem productivity which may have occurred by selected understory shrub and/or herb removal was investigated on the same Douglas-fir experimental plots at age 5 yr and 15 yr. Ecosystem characteristics at 15 yr were evaluated, based on a comparison with the same properties at age 5 yr. The objectives of this study were: (1) to evaluate forest ecosystem productivity based on the difference between the biomass that a target tree species attains in the absence of some or all understory shrubs and herbs, compared to tree biomass with understory retention in its presence, (2) to examine changes in ecosystem nutrient pool sizes in response to experimental vegetation removal, and (3) to investigate the soil chemical and physical properties affecting nutrient cycling at the ecosystem level.

Literature Cited

Bailey, J.D., Mayrsohn, C., Doescher, P.S., Pierre, E.S., and Tappeiner, J.C., II. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. For. Ecol. and Manage. **112**: 289-302.

Bormann, F.H., and Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Brady, N.C., and Weil, R.R. 1996. The nature and property of soils. 11th ed. Prentice-Hall, Upper Saddle River, New Jersey.

Busse, M.D., Cochran, P.H., and Barrett, J.W. 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. Soil Sci. Soc. Amer. J. **60**: 614-1621.

Cromack, K., Jr., Miller, R. E., Helgerson, O. T., Smith, R.B., and Anderson, H.W. 1999. Soil carbon and nutrients in a coastal Oregon Douglas-fir plantation with red alder. Soil Sci. Soc. Amer. J. **63**: 232-239.

Drinkwater, L. E., Wagoner, P., and Sarrantonio, M. 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. Nature, **396**: 262-265.

Fisher, R.F., and Binkley, D. 2000. Ecology and management of forest soils. 3rd ed. John Wiley and Sons, New York.

Harlow, W. M., Harror, E. S., and White, F. M. 1979. Textbook of dendrology: Covering the important forests of the United States and Canada. 6th ed. McGraw-Hill Book Co., New York.

Harrington, T.B., and Tappeiner, J.C.,II. 1997. Growth responses of young Douglas-fir and tanoak 11 years after various levels of hardwood removal and understory suppression in southwestern Oregon, USA. For. Ecol. Manage. **96**: 1-11.

Haynes, R. W., Adams, D. M., and Mills, J. R. 1995. The 1993 RPA timber assessment update. USDA For. Serv. Gen. Tech. Rep. RM-GTR-259.

Hillel, D. 1998. Environmental soil physics. Academic Press, New York.

Hughes, T.F., Tappeiner, J.C., II.,and Newton, M. 1990. Relationship of Pacific madrone sprouts to productivity of Douglas-fir seedlings and understory vegetation. West. J. Appl. For. **5**: 20-24.

Jensen, E.C., and Anderson, D.J., Zasada, J.C., and Tappeiner, J.C.,II 1995. The reproductive ecology of broadleaved trees and shrubs: Salmonberry (*Rubus spectabilis* Pursh). Forest Research Laboratory, Oregon State University, Corvallis. Res. Publ. 9e. 7p.

Johnson, D.W. 1992. Nitrogen retention in forest soils. J. Environ. Qual. **21**: 1-12.

Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. Soil Sci. Soc. Amer. J. **60**: 1643-1654.

Knowe, S.A., Harrington, T.B., and Shula, R.G. 1992. Incorporating the effects of interspecific competition and vegetation management treatments in diameter distribution for Douglas-fir saplings. Can. J. For. Res. **22**: 1255-1262.

Mao, D.M., Min, Y.W., Yu, L. L., Martens, R., and Insam, H. 1992. Effects of afforestation on microbial biomass and activity in soils of tropical China. Soil Biol. Biochem. **24**: 865-877.

Marks, P.L., and Bormann, F.H. 1972. Revegetation following forest cutting: mechanisms for the return to steady state nutrient cycling. Science, **176**: 914-915.

Nadelhoffer, K.J., Emmett, B.A., Gundersen, P., Kjonaas, O.J., Koopmans, C.J., Schleppi, P., Tietema, A., and Wright, R.F. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature, **398**: 145-148.

Nambiar, E. K. S., and Sands, R. 1993. Competition for water and nutrients in forests. Can. J. For. Res. **23**: 1955-1968.

Newton, M., and Preest, D. S. 1988. Growth and water relations of Douglas-fir seedlings under different weed control regimes. Weed Sci. **36**: 653-662.

Perry, D. A. 1988. An overview of sustainable forestry. J. Pesticide Reform, **8**: 8-12.

Perry, D. A. 1994. Forest ecosystems. Johns Hopkins University Press. Baltimore, Maryland.

Radosevich, S., Halt, J., and Ghersa, C. 1997. Weed ecology. Implications for management. John Wiley & Sons, Inc. 2nd ed., New York.

Rose, R., Ketchum, J.S., and Hanson, D.E. 1999. Three-year survival and growth of Douglas-fir seedlings under various vegetation-free regimes. For. Sci. **45**: 117-126.

Roth, B.E., and Newton, M. 1996. Survival and growth of Douglas-fir relating to weeding, fertilization, and seed source. West. J. Appl. For. **11**: 62-69.

Russell, E.W. 1973. Soil conditions and plant growth. 10th ed., Longman, London.

Spies, T.A., Ripple, W.J., and Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. **4**: 555 -568.

Stevenson, F.J. 1986. Cycles of soil, carbon, nitrogen, phosphorus, sulfur, and micronutrients. John Wiley and Sons, Inc. New York.

Tesch, S.D., and Hobbs, S.D. 1989. Impact of shrub sprout competition on Douglas-fir seedling development. West. J. Appl. For. **4**: 89-92.

Tesch, S.D., Korpela, E.J., and Hobbs, S.D. 1993. Effects of sclerophyllous shrub competition and root and shoot development and biomass partitioning of Douglas-fir seedlings. Can. J. For. Res. **23**: 1415-1426.

Tiessen, H., Cueva, E., and Chacon, P. 1994. The role of soil organic matter in soil fertility. Nature, **371**: 783-785.

Tilman, D., Lehman, C. L., and Thomson, K. T. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Nat. Acad. Sci. USA, **94**: 1857-1861.

Vitousek, P.M., and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience, **25**: 376-381

Wagner, R.G., and Radosevich, S. R. 1998. Neighborhood approach for quantifying interspecific competition in a coastal Oregon forest. Ecol. Appl. **8**: 779-794.

Waring, R. H. 1986. The ecological foundation for forestry in the Northwest- limits and opportunities. *In* Forests of the Northwest: A time for reflection. 1986 Starker Lectures. Oregon State University, Corvallis. pp. 1-8.

Waring, R. H., and Franklin, J. F. 1979. Evergreen coniferous forests of the Pacific Northwest. Science, **204**: 1380-1386.

Waring, R. H., and Running, S. W. 1998. Forest ecosystems: Analysis at multiple scales. 2nd ed. Academic Press. San Diego .

Wild, A. 1988. Russell's soil conditions and plant growth. 11th ed. Longman Scientific and Technical, Essex, England.

CHAPTER 2

FOREST ECOSYSTEM RESPONSES TO INTENSIVE MANAGEMENT: EFFECTS OF UNDERSTORY VEGETATION REMOVAL ON DOUGLAS-FIR GROWTH, NUTRIENTS AND SOILS

Oktay Yildiz, Kermit Cromack, Jr., Steven R. Radosevich, John E. Baham, and Robert G. Wagner

Prepared for

Abstract

Effects of partial understory removal on belowground and aboveground ecosystem properties were investigated in 15 yr old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) experimental plantations in western Oregon. Understory removal increased seedling survival up to 30% on some of the plots. Tree biomass accumulation was significantly increased (336%) with complete shrub and herb removal from the plots (DFO). Total aboveground biomass was 46% lower when there was no understory vegetation removal (DFC). Carbon concentrations in Douglas-fir needles were significantly lower in the DFC treatment. Even though Douglas-fir needle N concentration was significantly higher on DFC plots, this difference was not detected at plantation age 15 yr. The total aboveground N pool dramatically increased from plantation age 5 yr to 15 yr. However, the aboveground total N pool was not affected by understory vegetation removal. On the other hand, the aboveground P pool was 86% higher on DFO plots than DFC plots. Understory modification also affected $\delta^{13}C$ values in shrub branches and herbs. The DFO plots accumulated 2.5 times more forest floor material than DFC plots. The upper 15 cm of soil had significantly greater bulk density (22%) after complete understory vegetation removal (DFO). Soil C concentration in the < 2 mm soil fraction was reduced by 27% with complete understory removal (DFO) at age 5 yr. Soil in the < 2 mm fraction on DFC sites had 15%, 25% and 32% lower Fe, Al and Ca concentrations, respectively, than the same soil fraction on DFO

plots at age 5 yr. DFO plot soil had 49% less exchangeable Ca than DFC

soil on plots at age 15 yr.

Introduction

In the Pacific Northwest, management for timber production has converted large areas of coniferous forestlands to younger plantations with presumably higher demands for nutrients and, with patches dominated by early successional shrubs and trees (Spies et al. 1994). After forest disturbance by harvesting practices, these early seral and disturbance-resistant species can significantly contribute to species richness, or even dominate a site for years before canopy closure of the stand (Bailey et al. 1998). This rapid site colonization by pioneer species may delay the establishment of economically desirable target species because of competition for sunlight, moisture, and nutrients (Newton and Preest 1988; Tesch et al. 1993; Harrington and Tappeiner 1997; Jobidon 2000).

Salmonberry (*Rubus spectabilis* Pursh) can fully occupy newly disturbed sites through vegetative regeneration and make it very difficult for other species to become established. Vegetation management practices have been focused on channeling resources to desired species by eliminating unwanted plants (Walstad and Kuch 1987). Thus, during stand initiation stage, conifer seedlings should be released from competition with salmonberry until seedlings overtop shrubs during the stem exclusion stage (Jensen et al. 1995). Accumulation of stemwood is usually the major interest in forestry, and one of the management objectives in commercial plantation forestry is to control weeds surrounding trees in order to maximize stemwood growth (Nambiar and Sands 1993). Vegetation

management practices that release commercial species from competitive shrubs, herbs, and grasses is a key requirement on productive sites in the Pacific Northwest (Walstad et al. 1987). Thus, after seedlings are planted, plantations are often subjected to intensive weed control (Radosevich et al. 1997).

Removal of competing species from plantation sites has become a routine silvicultural practice in the Pacific Northwest (Knowe et al. 1992). However, intensive management practices such as brush clearing after harvesting or herbicide treatments may disturb the ecological integrity of these highly productive forest ecosystems. Drastic changes in species composition of the stand are likely to lead not only to productivity of target species for wood production, but also may lead to changes in the site's nutritional status. These management practices may affect soil microorganisms that have ecologically significant functions such as N fixation (Bormann et al. 1994). Besides contributing to biological diversity of forest ecosystems, understory vegetation can affect ecosystem processes in a variety of ways. For example, a dense network of salmonberry rhizomes contributes to soil stability. Brush removal from a site may weaken root networks which hold the soil mantle together and make it two to three times stronger (Waring 1986). Salmonberry may slow the development of large woody debris needed for fish habitat by forming dense thickets that inhibit conifer establishment. These management practices may also limit browse available to ungulates. For example,

having highly palatable leaves and fruits, salmonberry also provides an important source of food and cover for mountain beavers, deer, elk, rabbits, beavers, bears, chipmunks, deer mice, raccoons, and various birds (Jensen et al. 1995).

Ecosystem productivity and nutrient retention generally increase with interspecific differences in resource requirements (Tilman 1987). Mixtures of species might be more productive than monocultures if different adaptations among species within the mixture result in a more complete use of resources than possible by one species alone. Examples of this would be extending light absorption by a variety of shade-tolerant understory species, or rooting of species in different parts of the soil profile, thereby accessing water and nutrients that are out of the other species' root depletion zones (Perry 1994). For example, in Cole and Newton's (1986) examination of the effects of grass and red alder competition with Douglas-fir seedlings in three Coast Range plantations, the presence of herbs was associated with a significant increase in P concentration in 5 yr old Douglas-fir tree foliage (0.133% vs. 0.143%). Thus, a mixture of species (when shrubs and herbs were part of the ecosystem) may provide greater biomass yield as a result of improved use of site resources.

Higher plant diversity may also reduce ecosystem nutrient losses, leading to increases in ecosystem C and nutrient stores which, in turn, increase long-term productivity (Tilman et al. 1997). Apparently, changes in species composition, such as understory removal, alter nutrient cycling.

Ecosystems are open systems (Vitousek and Reiners 1975). Through biogeochemical pathways, nutrients have several sources and sinks. Nutrient losses from an ecosystem may occur through a variety of different pathways (leaching, root exudation, etc.). Most nutrients that return to the soil through one of the recycling pathways enter the general soil nutrient pool, and cannot simply be taken up again by some plants (Berendse and Elberse 1990). Some trees and shrubs can take up nutrients, such as N, directly from organic sources (Waring and Running 1998; Nasholm et al. 1998). Aboveground plant parts recycled to soil usually account for a major source of available soil nutrients.

The amounts of some important nutrients, such as N, circulated annually in an ecosystem is often 10 to 20 times greater than the amount received from outside the system (Schlesinger 1997). Internal nutrient cycling and retention in the ecosystem may profoundly influence plant growth. Understory vegetation cycles nutrients within the system in different forms, at different times, and in different amounts than do conifers (Jensen and Anderson 1995). A plant that annually loses a large percentage of nutrients from its biomass must absorb more nutrients for biomass maintenance than a plant that is more economical with its acquired nutrients (Berendse and Elberse 1990).

Conifers generally require lower quantities of nutrients and use them more efficiently. Less than 20% of coniferous foliage is replaced annually, and nutrient redistribution from senescent needles may result in nutrient

storage in tree biomass, slowing nutrient cycling, which may lead to the depletion of available nutrients in the soil (Waring and Franklin 1979). In a review paper, Binkley and Giardina (1998) calculated a 20% to 50% difference in the rates of litterfall mass and litterfall N contents among species where climate, parent material and previous land use were held constant. Litter chemistry on these sites may differ due to different vegetation cover. Pure Douglas-fir sites would have poorer litter quality than those with Douglas-fir, shrubs and herbs present. Furthermore, the chemical quality of the organic substrate affects mineralization and immobilization processes.

The C:N ratio of organic matter can be used as an index of resource quality, as can other indices, such as the lignin:N ratio (Killham 1994). Leaf litter residues with low a N concentration and a high C:N ratio such as Douglas-fir and other coniferous species, are expected to decompose more slowly, immobilize N during decomposition, and slow net nutrient mineralization rates. Assuming that other factors are similar, bacteria tend to be more important in deciduous angiosperm leaf decomposition, which is more rapid. On the other hand, fungi dominate decomposition of evergreen gymnosperms, but this decomposition is slow due to plant material physical and chemical characteristics (Paul and Clark 1996; Kimmins 1997).

Poorer quality litter from Douglas-fir may decompose more slowly relative to herb and shrub litter. Thus, the accumulated forest floor under a Douglas-fir forest with total understory removal may become a significant

repository of a site's nutrients. On the other hand, this slow nutrient release from decomposing organic matter may cause a substantial decline in the soil nutrient supply, especially during the stage of high nutrient demand by trees, resulting in a substantially lower canopy nutrient content. This decline in nutrient supply may have an impact on the growth of a young Douglas-fir forest that obtains half of its N from litter (Waring and Franklin 1979). If nutrients are sequestered in woody tissues of trees, and understory shrubs and herbs are removed, this may cause nutrient limitation for future generations. Apparently, the different types of understory vegetation may have an effect on soil organic matter turnover and nutrient cycling by determining the quality of decomposing materials.

Soil generally is the least renewable ecosystem resource. Thus, if the soil component of the ecosystem is altered in such a way that the ecosystem cannot recover, then soil resources will be reduced substantially (Kimmins 1996). For most soils, nutrient retention is related to soil organic matter retention (Vitousek and Reiners 1975). Having the function of maintaining and improving soil nutrient storage, as well as soil physical properties, organic matter is an important component of forest soils (Russell 1973; Wild 1988; Tiessen et al. 1994; Hillel 1998). Thus, the amounts of organic matter and its biochemical substrate quality are important in improving soil fertility (Tiessen et al. 1994; Drinkwater et al. 1998). Storage of essential nutrients, such as N, is mainly in organic forms (Stevenson 1986; Waring and Running 1998). Substantial amounts of other soil

nutrients, such as P and S, are also incorporated into soil organic matter (Stevenson 1986; Wild 1988). Soil organic matter also contributes to the soil exchange capacity, and can be important in increasing the soil capacity for exchangeable cations such as Ca, K and Mg (Brady and Weil 1996).

Vegetation removal can result in greatly increased losses of soil organic matter and nutrients (Bormann and Likens 1979; Wild 1988; Mao et al. 1992). In a site very similar to the present study, Cromack et al. (1999) reported a six-fold forest floor litter biomass decrease, and a seven-fold C, ten-fold N, and five-fold P concentration decrease in nutrient capital of the forest floor in a 9 yr old Douglas-fir plantation compared to an adjacent 150 yr old Douglas-fir forest.

Losses of nutrients or organic matter during harvesting and post-harvesting practices may reduce future productivity. Disturbances such as clearcutting may cause rapid nutrient losses from soil before the rates of biomass uptake increase to where nutrients are utilized. Nutrients in the soil profile that exceed plant uptake and microbial demand can be transported below the rooting zone via water movement through the soil profile. Increased nutrient uptake by vegetation maintains low concentrations in soil solution, and thus lessens the potential for nutrient leaching in forest ecosystems (Barnes et al. 1998).

Prompt recolonization of disturbed sites facilitates rapid nutrient uptake, thus minimizing nutrient and soil organic matter losses (Marks and Bormann 1972; Bormann and Likens 1979; Kimmins 1996; Waring and

Running 1998). Thus, revegetation of the site by disturbance-resistant and pioneering species, which occupy newly disturbed sites, may play an important role in ameliorating the effects of severe ecological disturbance, such as clearcutting, by retaining nutrients and key soil organisms during the period of tree reestablishment. The importance that understory vegetation plays in a forest, thus may far exceed the biomass it represents (Busse et al. 1996). Management practices that reduce cover of these pioneering plants can lead to nutrient losses, may reduce ecological diversity, and may possibly affect sustainability of the forest ecosystem (Perry 1988). The implications for tree growth of retaining or removing the understory is a balance between the understory's detrimental effect on competition and its beneficial effects on soil fertility.

Effects of understory vegetation on survival and growth of young conifer seedlings through competition for light, water and nutrients are well documented (Newton and Preest 1988; Tesch and Hobbs 1989; Hughes et al. 1990; Tesch et al. 1993; Roth and Newton 1996; Harrington and Tappeiner 1997; Rose et al. 1999). However, literature is lacking in: (1) changes in total ecosystem properties due to manipulation of species composition, and (2) residual effects of understory removal during the early years of stand establishment on the performance of trees and other plant species after ten years of stand age. The question arises as to whether partial or complete removal of some or all understory components enhances or limits nutrient availability for tree growth in new plantations.

Although competing species can be detrimental to seedling growth in the early stages of stand establishment, excessive understory vegetation control may, in some cases, be ecologically undesirable.

In this study, an effort was made to analyze the ecosystem structural and functional characteristics induced by changes in species composition. Alteration of net ecosystem productivity which may have occurred by selected shrub and/or herb removal as understory vegetation components were investigated in 15 yr old Douglas-fir plantations. Ecosystem characteristics of the 15 yr old stands were compared and evaluated based on the properties when they were 5 yr old.

The objectives of this study were: (1) to evaluate forest ecosystem productivity based on the difference between the biomass that a target species attains in the absence of some or all shrubs and herbs, compared to its biomass in the presence of all shrubs and herbs, (2) to examine changes in the ecosystem's nutrient pool sizes in response to experimental vegetation removal, and (3) to investigate the soil chemical and physical properties affecting nutrient cycling at the ecosystem level.

Materials and Methods

Site Location

Sites were selected based on vegetation zones and topographic

aspect. Two vegetation zones were located: a Sitka spruce (*Picea*

sitchensis) zone that stretches along a narrow band parallel to the Pacific

Ocean and a western hemlock (*Tsuga heterophylla*) zone situated several

kilometers further inland. The north and south facing sites are located at

380 and 230 meters elevation, respectively. The spruce zone sites are

situated about 11 km east of the Pacific Ocean near Lincoln City, Oregon.

The hemlock zone sites are located at 400 m elevation, about 19 km east of

the Pacific Ocean near Waldport, Oregon. Specific locations of the sites

are presented in Table 2.1 (Wagner and Radosevich 1989).

Table 2.1. Geographic locations of the study sites (blocks) in the Oregon
Coast Range.

Site	Survey location	Aspect	Vegetation zone
Erickson-Round	S10, T7S R10W, WM	south	*Picea sitchensis*
Minski-Bald	S14, T7S R10W, WM	north	*Picea sitchensis*
Tidewater	S30, T13S R9W, WM	south	*Tsuga heterophylla*
Cannibal	S10, T14S R10W, WM	north	*Tsuga heterophylla*

Climate

Both vegetation zones have a mild, wet, maritime climate with more

than 180 cm average annual precipitation, more than 90% of which occurs

during the winter. The climate in the spruce zone is characterized by more summer fog and less variation in precipitation and temperature than in the hemlock zone. Both zones have mild, wet winters and relatively warm, dry summers; the growing season is characterized by 15-20°C daytime average temperatures. The coast is influenced by a maritime climate, and narrow seasonal temperature fluctuations. Winters are extremely wet, and freezing temperatures are rare as a result of cyclonic storms generated from the Aleutian Low. Summers are under the influence of the east Pacific Subtropical High, and thus are cool and relatively dry (Waring and Franklin 1979; Sea and Whitlock 1995).

Soils

Soils in these two zones are deep, relatively fertile, and well drained. They are derived from Flournoy sandstone, and are high in soil C and N, but may be low in S (Cromack et al. 1999). They have a low bulk density (0.5-0.6 g cm^{-3}) and are highly porous (> 20 cm hr^{-1} permeability), resulting in a highly permeable profile that maintains generally aerobic conditions that favor rapid turnover of organic matter and nutrient release (Wagner 1989). Soils in the spruce zone are classified as Typic Haplumbrept. Hemlock zone soils are classified as Pachic Haplumbrept.

History

The spruce zone sites were clear-cut in 1983 (two years before planting), but not burned. The north-facing site in the hemlock zone was clear-cut and then subjected to a low intensity prescribed burn in 1978. The south-facing site was clear-cut in 1971 and unsuccessfully regenerated until the experiment commenced.

Experimental Design

This study utilized a previously established, large-scale project where the understory vegetation was differentially controlled in Douglas-fir plantations (Wagner 1989). The experiment used a randomized block design with four blocks. Each block (site) site was divided into seven 20 x 20 m plots. Treatments included seven randomly assigned levels of salmonberry (*Rubus spectabilis* Pursh) and herbaceous vegetation control. In addition to salmonberry, some other shrub species were present in small amounts. These included thimbleberry (*Rubus parviflorus* Nutt.), red elderberry (*Sambucus racemosa* L.var. *arborescens* [T. & Gray]), vine maple (*Acer circinatum* Pursh), cascara (*Rhamnus purshiana* DC.), red huckleberry (*Vaccinium parvifolium* Smith) and bitter cherry (*Prunus emarginata* Dougl.). The most abundant herbaceous species was velvet-grass (*Holcus lanatus* L.), with lesser amounts of swordfern (*Polystichum munitum* [Kaulf] Presl.), pearly everlasting (*Anaphalis margaritacea* [L.] B.

& H.), foxglove (*Digitalis purpurea* L.) and woodland groundsel (*Senecio sylvaticus* L.).

In March 1985, all shrubs were cleared by hand and chainsaw, and in April, Douglas-fir seedlings (2-0 bare-root stock) were planted at a 3 x 3 m spacing. A control plot received no vegetation removal after initial establishment with Douglas-fir seedlings (DFC). On three of the plots, 25, 50 and 75% of the shrubs were removed in 2 m wide corridors that were located randomly. Herbaceous vegetation was allowed to invade and occupy these corridors after shrub removal. On one of the plots, shrubs were completely removed, leaving only herbs and Douglas-fir (DFH). On another plot, all shrubs and 50% of the herbs were removed. Finally, complete removal of shrubs and herbs was included in the array of treatments, leaving only Douglas-fir (DFO). Each treatment was maintained manually through the growing seasons from 1985 to 1989 (Wagner 1989). To minimize deer, elk and rodent damage, each experimental site was surrounded by a 2.5 m tall, woven wire fence and, after planting, every seedling in all of the experimental plots was enclosed in a cylindrical, open-top chicken-wire cage (Wagner 1989).

Data Collection and Analysis

Biomass

Tree height, length of widest branches perpendicular to the trunk, and height to live crown were measured in early spring of both 1989 and 1999, before bud break, using a PVC pole graduated in centimeters. Diameter at breast height (137 cm) (DBH) and diameter at 10 cm above the soil surface (only for 1989) were measured at the same time tree heights were measured, using tapes recording diameters to the nearest mm. Biomass of Douglas-fir and its components (leaf, branch and bole) was estimated for the average number of trees on each plot, and total tree biomass per hectare was calculated using the diameter at 10 cm above the soil surface (DST) for 1989 data, and the diameter at breast height (DBH) for 1999 data as independent variables in the equations developed by Helgerson et al. (1988). For 5 year old trees (1989):

Ln Y = a + b ln (DST)

Where Y is total weight, leaf weight, branch weight, or bole weight (g). Intercept (a) = 4.593, 2.922, 2.340 and 4.279 for total, leaf, branch and bole weight, respectively. Slope (b) = 2.036, 1.936, 2.393, and 1.965 for total, leaf, branch, and bole weight, respectively. The independent variable (DST) is the geometric mean stump diameter (cm), including the bark, at 15 cm height. For 15 year old trees (1999):

$$\ln Y = a + b \ln (DBH)$$

Where Y is total weight, leaf weight, branch weight or bole weight (g). For 5 year old trees (1989): Intercept (a) = 4.984, 3.329, 2.856 and 4.639 for total, leaf, branch and bole weight, respectively. Slope (b) = 2.186, 2.031, 2.503, and 2.120 for total, leaf, branch and bole weight, respectively. The independent variable (DBH) is the geometric mean diameter (cm), including the bark, at breast height.

Increment core samples from Douglas-fir trees were taken during summer of 1999. Nine randomly chosen trees per plot were cored. Using DBH, bark thickness and heartwood lengths, sapwood areas were calculated for each sample. Douglas-fir leaf areas were estimated from sapwood areas, using the coefficient of leaf area:sapwood ratio developed for the same species by Waring et al. (1982). During the summers of both 1989 and 1999, needles from 15 randomly chosen trees per plot were collected to estimate specific Douglas-fir leaf areas (Waring and Running 1998). The projected surface area of a needle was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Washington). In 1999, light interception by the canopy was estimated using a sunfleck ceptometer with 80 sensors (Decagon Devices, Inc. Pullman, WA). To determine the incoming solar radiation above the canopy, 10 readings every half hour were recorded in the open, then 100 readings were recorded in random location under the canopy between 11 am and 1 pm on a clear day in August, 1999.

For both 1989 and 1999, shrub samples were collected from two randomly located 9 m^2 quadrats on each experimental unit (plot). Branches and leaves were separated, and fresh weights were recorded in the field. Each sample from every component on each plot was sub-sampled to determine its moisture and nutrient content. Total shrub dry biomass (kg ha^{-1}) was estimated after adjusting for moisture content calculated from sub-samples that were weighed fresh and oven dried at 70°C for two days.

Herbs were sampled on five randomly located 1 m^2 quadrats on each experimental unit. Sample moisture content was calculated after samples were weighed fresh and oven dried at 70°C for two days. After correcting for moisture content, the total herb biomass was calculated (kg ha^{-1}). After calculating the biomass of individual components for each vegetation treatment, values were summed to estimate total aboveground biomass.

Nutrients

For both age 5 and 15 yr, Douglas-fir needles were collected from trees only on three treatments (DFC, DFH, and DFO). Five trees from each plot were randomly chosen, and three samples were collected from three crown positions (low, medium and high). Samples were air-dried, then ground using a coffee-grinder. Needle total N and C concentrations were determined using a dry combustion method in a LECO CNS 2000 Carbon Analyzer (LECO Corp., St. Joseph, MI) (Nelson and Sommers 1996).

Needle concentrations for P, K, Ca, S, Mg, Mn, Fe, Cu, B, Zn, and Al were analyzed using an inductively coupled plasma spectrometer (ICP) following nitric acid digestion in a microwave oven (Jones and Case 1990). The nutrient content of Douglas-fir boles and branches was estimated using nutrient concentration data acquired from a 22-yr old plantation growing on a similar site in western Washington State (Cole and Rapp 1981).

Shrub and herb nutrient concentrations were determined from sub-samples collected during destructive biomass sampling. Shrub and herb samples were prepared and analyzed for total C, N and P following the same procedures employed for needles, except that total N and P were determined from micro-Kjeldahl digests (Nelson and Sommers 1996; Cromack et al. 1999). Using concentration and biomass data for each vegetation component, total nutrient content in all aboveground portions of the vegetation was determined.

Needle and shrub samples were also analyzed for their ^{13}C and ^{15}N stable isotope values using a continuous flow method and a Finnigan Delta Isotope Ratio Mass Spectrometer with ± 0.2‰ sensitivity for both C and N.

Soil

Soil samples were collected from 0-7.5 cm and 7.5-15 cm soil depths at 5 randomly selected locations on each plot, using a double-cylinder sliding-hammer core sampler (Blake and Hartge 1986). Soil samples were sub-sampled and dried at 105°C for 24 hr to determine soil moisture

content and calculate bulk density. The remaining portions of the soil core samples were separated into coarse and fine fractions, using USA Standard Testing Sieves with 2 mm, 4 mm and 6.3 mm openings. Soil for 1989 was air dried and then sieved. Soil for 1999 was moist sieved.

For 1999, field moist soils from DFC, DFH and DFO were sub-sampled for separation of light (LF)- and heavy-fraction (HF) organic material. Twenty grams of soil from < 2 mm fractions was dispersed in sodium polytungstate (NPT) solution (1.7 g cm^{-3}) over 24 hr. After stirring, the HF was allowed to settle for 48 hr at room temperature, then the solution was aspirated to separate LF using the methods developed by Strickland and Sollins (1987). For 1989 and 1999, both coarse- and fine-fractions of remaining soil portions were ground into powder with a heavy duty rock grinder.

Total C concentrations were analyzed using a dry combustion method in a LECO CNS 2000 Carbon Analyzer (Nelson and Sommers 1980, Nelson and Sommers 1996). Total soil N was analyzed after samples were digested using the micro-Kjeldahl method, and analyzed with an Autoanalyzer (Technicon autoanalyzer, Technicon Industrial Systems, Tarrytown, NY) (Nelson and Sommers 1980). Total soil P was analyzed from the same micro-Kjeldahl digests (Cromack et al. 1999). Total soil nutrient content (kg ha^{-1}) was estimated, taking into account the amount of fine (< 2 mm) and coarse ($\geq$ 2 mm) soil fractions with their respective nutrient concentrations, and the soil bulk density. Total soil C and N in the

coarse soil fraction (≥ 2 mm) were determined by dry combustion in a LECO CNS 2000 Carbon Analyzer (LECO Corp., St. Joseph, MI) (Nelson and Sommers 1996). After nitric and perchloric acid digestion, total P was analyzed using the molybdate blue method (Kuo 1996). Total soil C and nutrients in the 0-15 cm depth of mineral soil were estimated taking into account bulk densities determined on the least disturbed plots (DFC).

Net N mineralization was determined using an anaerobic incubation method (Keeney and Bremner 1966) as modified by McNabb et al. (1986). The amount of N leached from the soil was estimated using in-situ ion-exchange resin bags for a period of 8 months. Fine mesh nylon resin bags, each containing 10 g of a mixed-bed resin with both cation and anion resin beads (J.T. Baker M-614), were placed in duplicate sets at 5 cm soil depth below the mineral soil surface in three randomly selected locations on each plot, following the methods of Waring et al. (1987) and Binkley and Matson (1983). On DFO sites, three additional resin bags also were placed close to trees to determine if there was any difference in the amount of mineral N leached due to tree proximity. The bags were marked with string tags and retrieved after 8 months.

Stable isotopes ^{13}C and ^{15}N of the LF and HF were determined following the same analytical procedures used on needles.

Soil total elemental analysis for P, K, Ca, Mg, S, Mn, Fe, Cu, Zn, and Al was done by digesting mineral soil from the <2mm size fraction in a

microwave digest with nitric acid and HF (Hosner 1996), followed by ICP analysis (Soltanpour et al. 1996).

Statistical Analysis

The effects of treatments on concentration and content of nutrients and biomass for each major vegetation component, species, and for the whole ecosystem were tested with an analysis of variance procedure for a randomized block design. Tukey's HSD test with $\alpha = 0.05$ was performed to permit separation of means. In order to determine treatment effects on soil density fractionation, ^{13}C values were analyzed for both LF and HF. Then, differences between LF and HF were analyzed with an analysis of variance procedure for a randomized block design. Repeated measurement analysis with a mixed model was run using data from 1989 and 1999 to determine the changes in treatment effects over this time period. SAS was used for all statistical analyses (SAS 1996). Results were considered significant at $P < 0.05$. For isotopes, results were considered significant at $P < 0.1$.

Results

Aboveground

Survival and growth

At the end of the fifth growing season (1989) about 93% of the seedlings had survived in all treatments. Thus, the presence of shrubs and herbs did not appear to affect seedling survival. However, when the plantations were 15 yr old, the vegetation zone, which may be associated with aspect, had some influence on Douglas-fir survival. For example, seedling survival in the southern spruce zone site was 30% higher than that of the southern hemlock zone (Table 2. 2).

Table 2.2. Numbers of standing Douglas-fir trees per plot and average survival (%) at age 15 yr (original tree number for each plot was 25).

Treatments (removal)	Spruce zone (south)	Spruce zone (north)	Hemlock zone (south)	Hemlock zone (north)	Survival (%)
No removal	25	17	12	6	60
25% shrub	24	16	11	14	65
50% shrub	24	17	17	16	74
75% shrub	22	23	20	22	87
100% shrub	23	24	22	21	90
100% shrub + 50% herb	24	25	22	24	95
100% shrub + 100% herb	23	25	21	20	89

When the plantations were 5 yr old, Douglas-fir seedlings were almost twice as tall and had diameters 3.5 times larger on DFO plots than on DFC plots (Figures 2.1 and 2.2). Thus, understory vegetation removal significantly increased Douglas-fir tree growth in the first five years following plantation establishment.

Figure 2.1 Mean and SE of Douglas-fir seedling heights (cm) at age 5 yr with partial understory vegetation removal. (Treatment 1: no removal, treatment 2: 25% shrub removal, treatment 3: 50% shrub removal, treatment 4: 75% shrub removal, treatment 5: 100% shrub removal, treatment 6: 100% shrub + 50% herb removal, treatment 7: total understory removal).
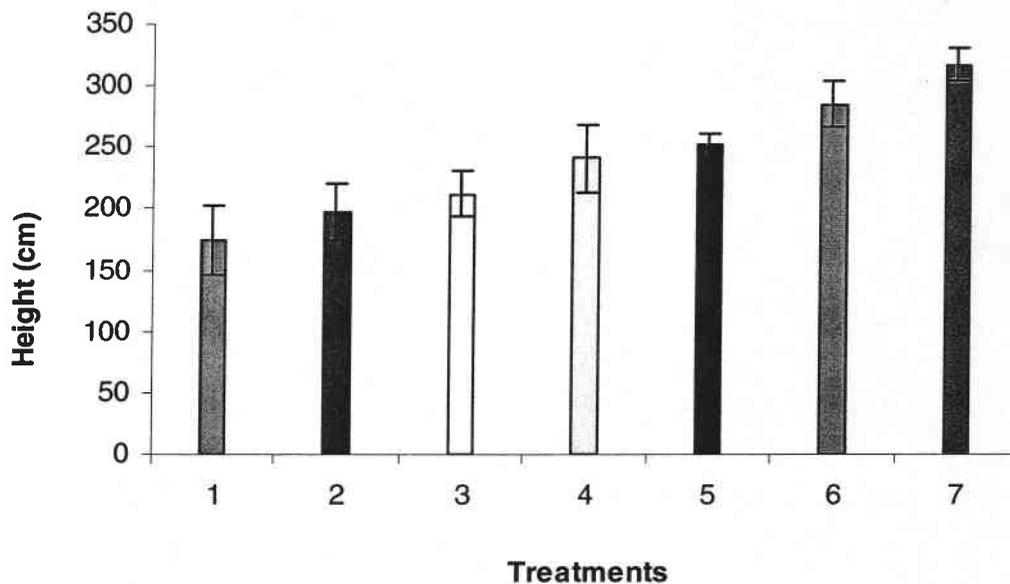
Figure 2.2. Mean and SE of Douglas-fir diameter (mm), 10 cm above the soil surface, at age 5 yr with partial understory vegetation removal. (Treatment 1: no removal, treatment 2: 25% shrub removal, treatment 3: 50% shrub removal, treatment 4: 75% shrub removal, treatment 5: 100% shrub removal, treatment 6: 100% shrub + 50% herb removal, treatment 7: total understory removal).
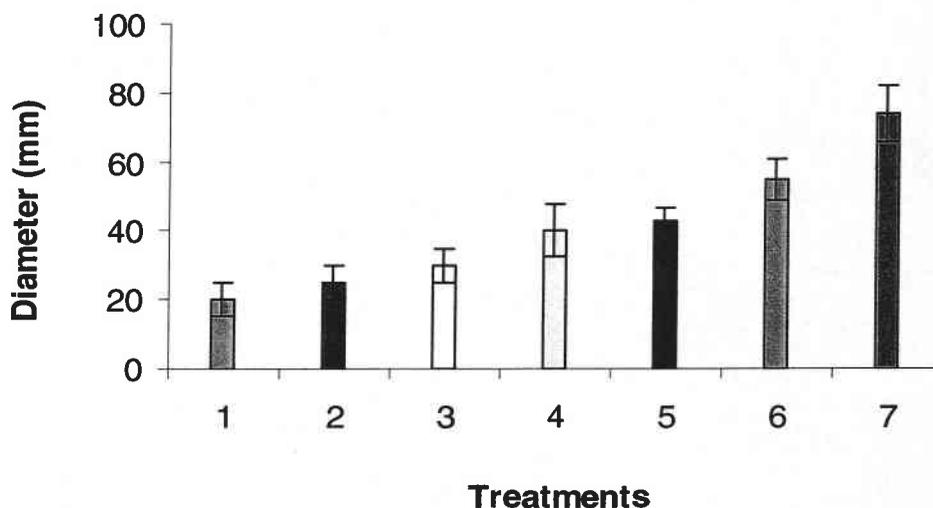
At age 5 yr, tree biomass was significantly reduced in the presence of understory vegetation (P < 0.0001). With total understory removal, tree biomass was 12 times that of the control (Figure 2.3).

Figure 2.3. Mean and SE of Douglas-fir seedling biomass (kg ha $^{-1}$) at age 5 yr with partial understory vegetation removal. (Treatment 1: no removal, treatment 2: 25% shrub removal, treatment 3: 50% shrub removal, treatment 4: 75% shrub removal, treatment 5: 100% shrub removal, treatment 6: 100% shrub + 50% herb removal, treatment 7: total understory removal).
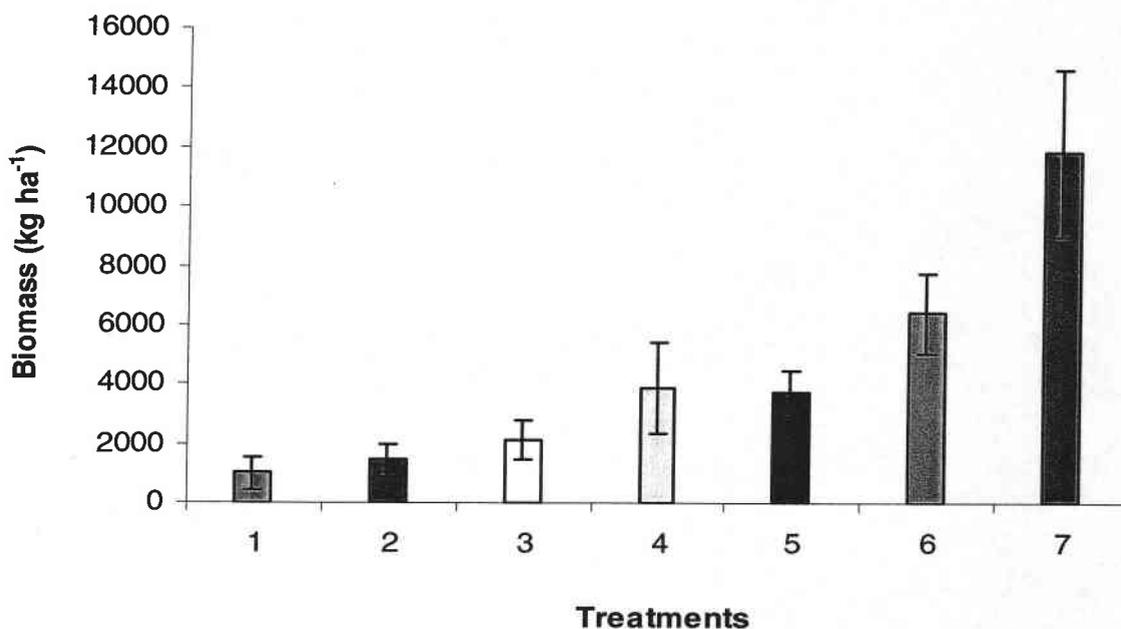
Douglas-fir specific leaf areas differed significantly (P < 0.04) among treatments. Trees on DFH plots had the lowest, while those on DFC plots (controls) had the highest specific leaf areas. Douglas-fir needles on DFC plots had 20% higher specific leaf areas than needles on DFH plots. $\delta^{13}C$ values of Douglas-fir needles were not significantly different between treatments. But, $\delta^{15}N$ values were significantly different at $\alpha = 0.1$ (P < 0.074); DFH plots had the most negative $\delta^{15}N$ values (Table 2.3).

Table 2.3. Mean and SE for aboveground biomass and related properties of trees, shrubs and herbs in 5 yr old Douglas-fir plantations.

		No removal	100% shrub removal	Pure Douglas-fir
Douglas-fir	Height (cm)	174.3 (28.5) a	253.4 (9.3) b	317 (13.3) c
	10 cm surface diam. (mm)	20 (5.3) a	42.7 (4.1) b	73.6 (7.9) c
	Leaf dry weight (g)	165 (83) a	582 (104) a	1731 (345) b
	Branch dry weight (g)	185 (108) a	769 (163) a	2919 (696) b
	Bole dry weight (g)	681 (353) a	2483 (458) a	7732 (1600) b
	Total tree weight (kg)	1.03 (0.55) a	3.83 (0.74) a	12.38 (2.70) b
	Tree biomass (kg ha^{-1})	1008 (543) a	3702 (749) a	11800 (2807) b
	Projected SLA (cm^2 g^{-1})	81.7 (6.6) a	65.8 (1) b	69.5 (1.1) ab
	Needle length (cm)	2.8 (0.1) a	2.96 (0.015) a	3.03 (0.02) a
	δ^{13}C-needle	-29.1 (0.3) A	-28.6 (0.26) A	-28.7 (0.07) A
	δ^{15}N-needle	-1.54 (0.27) A	-2.32 (0.22) B	-1.14 (0.33) A
Understory	Biomass (kg ha^{-1})	10111 (1642) a	5400 (1009) b	0
	Shrub biomass (kg ha^{-1})	9142 (1633)	0	0
	Herb biomass (kg ha^{-1})	969.5 (244) a	5400 (1009) b	0
Total	Biomass (kg ha^{-1})	11119 (1869) a	9102 (1700) a	11800 (2807) a

Note: Within a row, means with a common lowercase letter are not significantly different at P = 0.05, while means with a common uppercase letter are not significantly different at P = 0.10.

When the stands were 15 yr old, trees in the pure Douglas-fir stand (DFO) had accumulated 336% more standing biomass ha^{-1} than those in control plots (DFC) due to understory vegetation removal in the DFO stands (Figure 2.4). These differences in tree biomass per hectare can be accounted for by: (1) survival differences on each plot. On average, 60% of the trees survived on the DFC plots, with a mean survival of 89% on the DFO plots (Table 2.4), and (2) performance of trees by treatments showed that tree diameter (dbh) on DFC plots averaged 10.3 cm, which was 41% lower than that of trees on DFO plots. Total tree biomass ha^{-1} on DFO sites was more than 4 times higher than those on DFC plots.

Figure 2.4. Mean and SE of Douglas-fir biomass at age fifteen. (Treatment 1: no removal, treatment 2: 25% shrub removal, treatment 3: 50% shrub removal, treatment 4: 75% shrub removal, treatment 5: 100% shrub removal, treatment 6: 100% shrub + 50% herb removal, treatment 7: total understory removal.)
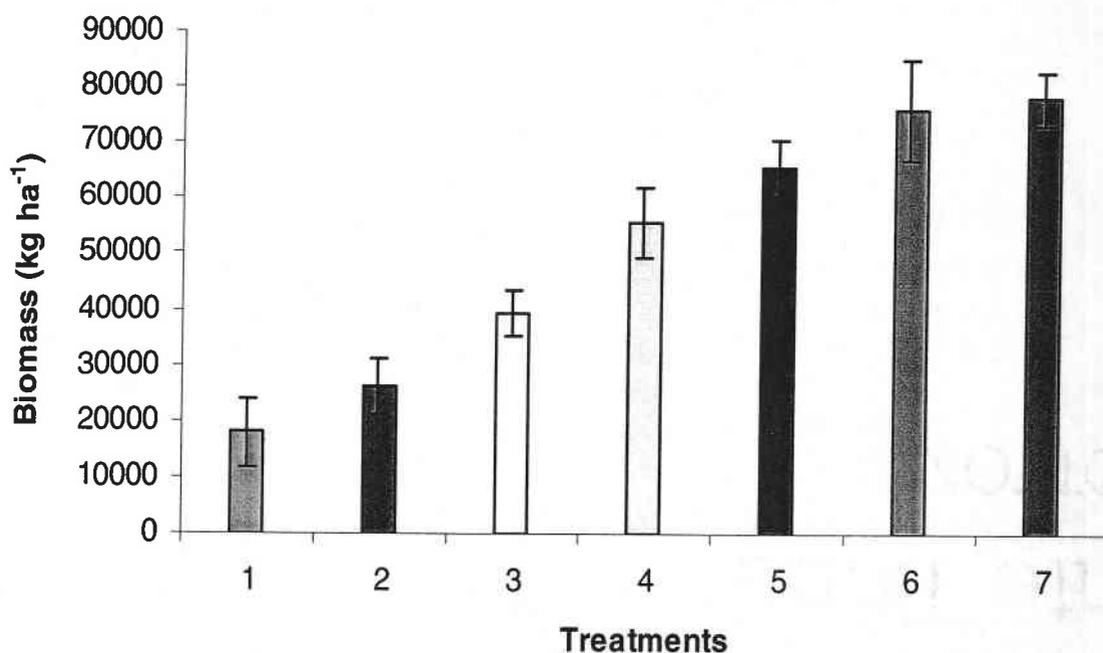
Differences in tree growth among plots may be attributed to significant variation in tree leaf area (LA). The availability of environmental resources expressed not only in growth, but also in 80% more leaf area on DFO plots than on DFC plots (Table 2.4). Thus, the presence of understory vegetation significantly reduced the standing biomass of Douglas-fir on a per tree basis ($P < 0.0001$). An average tree on DFO plots had 3 times greater biomass than a tree on DFC plots. Greater than 50% shrub removal resulted in no additional growth response by trees (Figure 2.4). Douglas-fir needle specific leaf area (SLA) was 20% higher on DFC sites than on DFO plots at age 5 yr, reflecting differences in shading (82 cm^2 g^{-1} vs. 69 cm^2 g^{-1}). By age 15 yr, there was no real difference among treatments (Table 2.4).

Table 2.4. Mean and SE for aboveground biomass of trees, shrubs and herbs on 15 yr old Douglas-fir plantations.

		No removal	100% shrub removal	Pure Douglas-fir
Douglas-fir	Height (m)	8.2 (0.3) a	10.2 (0.3) a	10.6 (0.1) a
	Dbh (cm)	10.3 (0.8) a	16.6 (0.5) b	17.5 (0.5) b
	Crown width (cm)	277 (43) a	353 (49) ab	411 (58) b
	Live crown ratio (%)	60 (3) a	65 (3) a	65 (4) a
	Leaf dry weight (kg)	3.6 (0.5) a	9 (0.7) b	10.4 (0.3) b
	Branch dry weight (kg)	7.4 (1.2) a	22 (2.1) b	26.1 (0.9) b
	Bole dry weight (kg)	16.8 (2.4) a	43 (3.5) b	49.9 (1.6) b
	Weight per tree (kg)	28 (4) a	73.6 (6) b	85.7 (2.8) b
	Tree biomass (kg ha^{-1})	17891(5977) a	65594 (5062) b	78099 (4733) b
	Projected SLA (cm^2 g^{-1})	59.5 (0.9) a	55.7 (3.6) a	59.3 (1) a
	LA per tree (m^2)	50.2 (3.1) a	81.1 (1.9) b	89.5 (5.2) b
	LAI (ha ha^{-1})	2.96 (0.85) a	7.2 (0.24) b	8.2 (0.7) b
Understory	Biomass (kg ha^{-1})	15177 (3527) a	3777 (988) a	0
	Shrub biomass (kg ha^{-1})	15020 (3556) a	3516 (1085) b	0
	Herb biomass (kg ha^{-1})	156 (70) a	261 (132) a	0
Total	Biomass (kg ha^{-1})	33068 (4259) a	69372 (5871) b	78099 (4733) b

Note: Within a row, means with a common lowercase letter are not significantly different at $P = 0.05$.

Removing up to 50% of understory biomass from some of the plots during the five years following tree planting in 1985, secured successful tree establishment in those treatments with higher overall survival rate and biomass accumulation for Douglas-firs on the sites. After understory removal was completed in 1989, some of the shrubs and herbs reestablished on the sites (Figure 2.5). However, at plantation age 15 yr, there was a significant difference in the amount of understory biomass between plots (P < 0.0005). Plots that received total shrub removal each year from 1985 through 1989 (DFH) had accumulated about 25% of the understory biomass present on DFC plots. Plots which received 50% and 25% shrub removal 10 yr before, had about the same amount of understory biomass (~ 16000 kg ha^{-1}) present on DFC plots at the end of plantation year 15. More than 95% of the understory biomass on each plot was made up of shrubs (salmonberry) (Figure 2.5).

Figure 2.5. Mean and SE of understory biomass (kg ha^{-1}) in 15 yr old Douglas-fir plantations. (Treatment 1: no removal, treatment 2: 25% shrub removal, treatment 3: 50% shrub removal, treatment 4: 75% shrub removal, treatment 5: 100% shrub removal.)
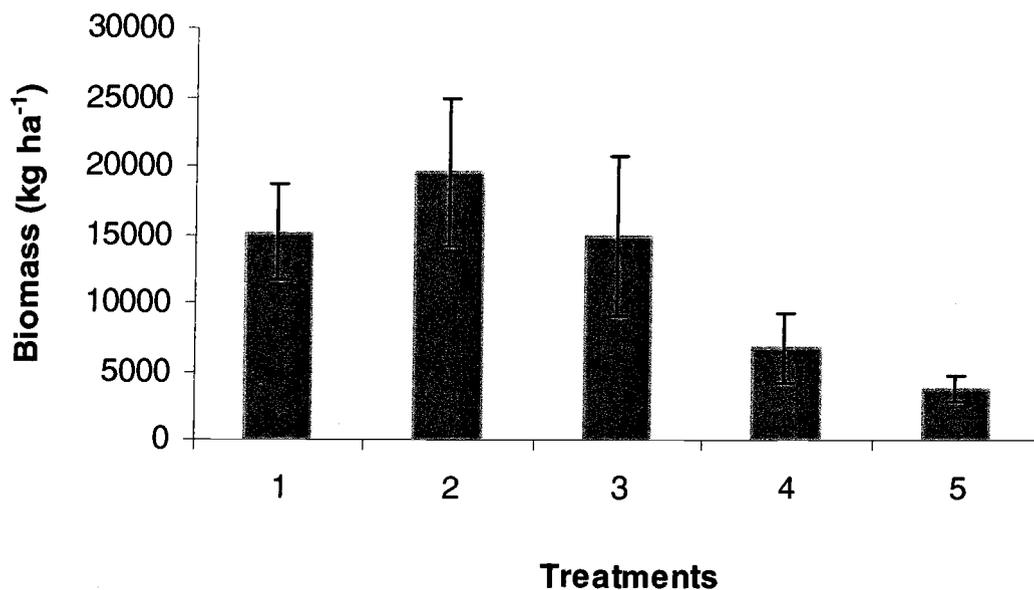
At age 5 yr, even though total understory removal increased tree biomass 12-fold over that of the trees on DFC sites, the presence of shrubs and herbs offset the total aboveground biomass differences among sites (Figure 2.6).

Figure 2.6. Aboveground plant biomass (kg ha^{-1}) in 5 yr old Douglas-fir plantations. Mean and SE shown for each vegetation component.
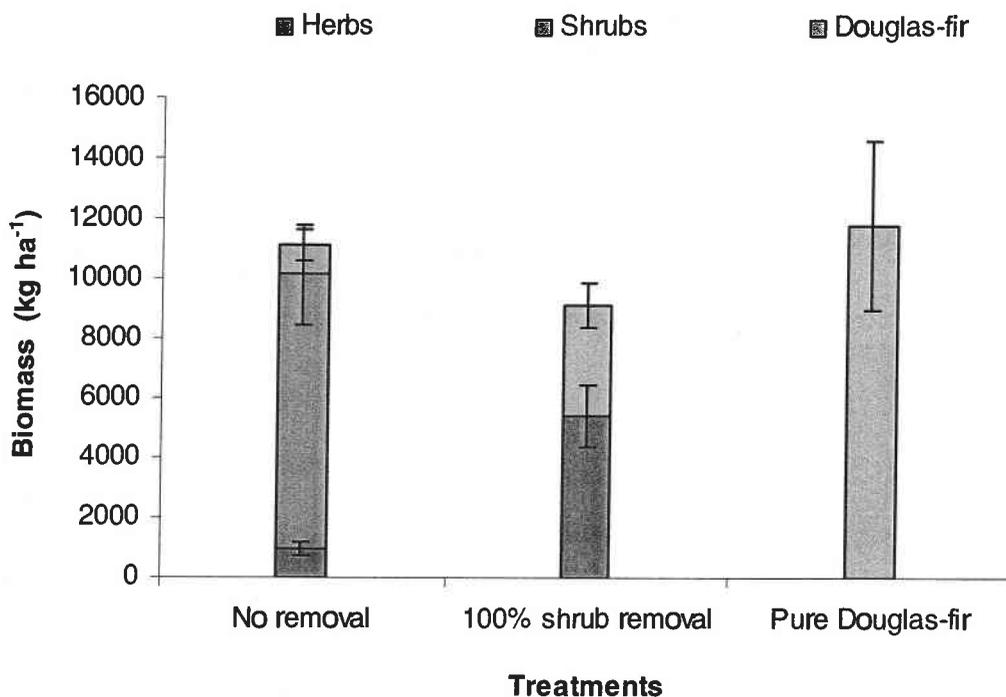
By age 15 yr, total aboveground plant biomass was similar between DFH and DFO plots, but significantly lower on DFC plots (P < 0.0001). Total aboveground biomass was about 58% lower on DFC plots compared to DFO stands. Trees accounted for only 54% of the aboveground biomass on DFC plots (Figure 2.7).

At plantation age 5 yr, herb biomass was 9% and 60% of total aboveground plant biomass on DFC and DFH plots, respectively (Figure 2.6). However, at plantation age 15 yr, the contribution of herb biomass to total aboveground plant biomass was negligible in all of the plots (Figure 2.7).

Figure 2.7. Aboveground plant biomass (kg ha⁻¹) in 15 yr old Douglas-fir plantations. Mean and SE shown for each vegetation component.
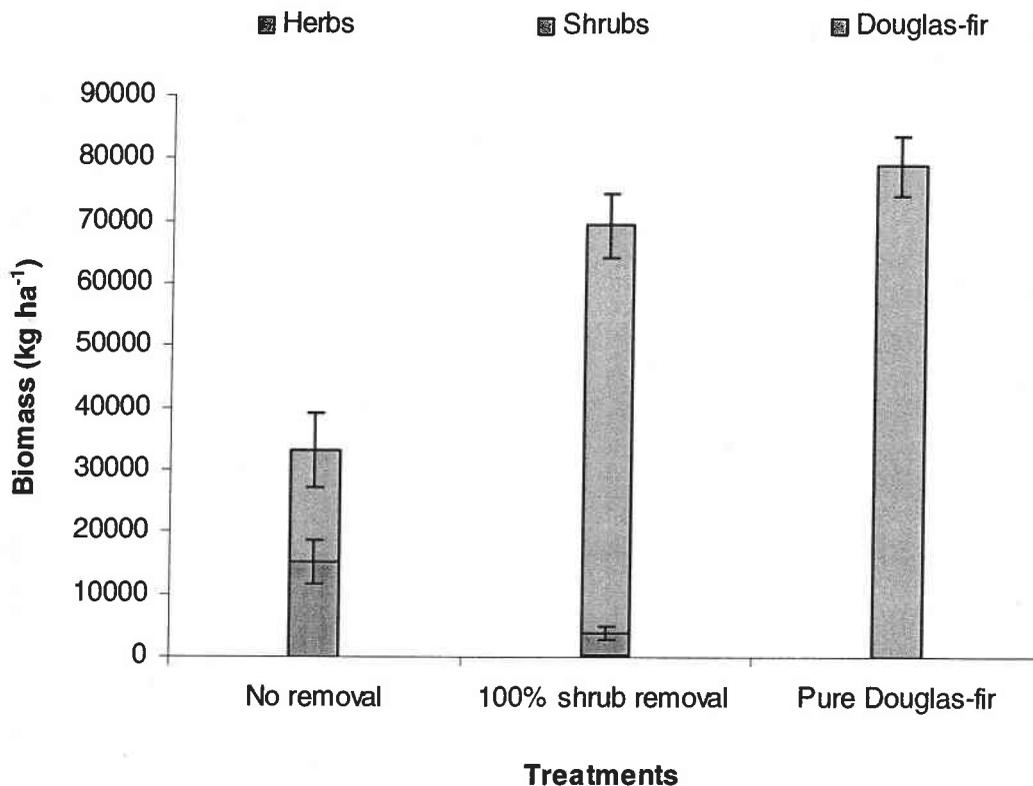
Nutrients

Douglas-fir needle C concentration was significantly lower on DFC plots than in other treatments (P < 0.03). On DFC sites, needle C concentration was significantly reduced from age 5 yr to 15 yr (P < 0.01) (Table 2.5). Needle N concentration was 13% higher on DFC plots than on DFO plots (Table 2.3) at age 5 yr (P < 0.01), but needle N concentration significantly decreased from age 5 yr to 15 yr (P < 0.0018) on all treatments. Needle Ca concentration was similar among treatments at 5 yr and 15 yr. However, from age 5 yr to 15 yr, needle Ca concentration

decreased at all sites ($P < 0.0002$) (Table 2.5). For 5 yr old seedlings, needle Al concentration was 60% higher on DFH plots than on DFO plots. By age 15 yr, needle Al concentration was 43% higher on DFO plots than on DFH plots (Table 2.6).

Table 2.5. Mean and SE of macronutrient concentrations of Douglas-fir needles collected at age 5 and 15 yr.

	C (%)	N (%)	S (%)	P (%)	K (%)	Ca (%)	Mg (%)
			1989				
No removal	52 (2.0) a	1.8 (0.04) b	0.1 (0.009) a	0.15 (0.03) a	0.55 (0.08) a	0.36 (0.06) a	0.09 (0.020) a
100% shrub removal	48 (2.0) a	1.4 (0.10) a	0.1 (0.005) a	0.13 (0.01) a	0.47 (0.03) a	0.36 (0.02) a	0.07 (0.006) a
Pure Douglas-fir	49 (0.5) a	1.6 (0.04) a	0.1 (0.010) a	0.11 (0.01) a	0.44 (0.03) a	0.30 (0.04) a	0.07 (0.003) a
			1999				
	C (%)	N (%)	S (%)	P (%)	K (%)	Ca (%)	Mg (%)
No removal	47 (0.6) a	1.4 (0.10) a	0.08 (0.006) a	0.14 (0.01) a	0.57 (0.04) a	0.2 (0.03) a	0.10 (0.008) a
100% shrub removal	48 (0.6) b	1.3 (0.06) a	0.08 (0.004) a	0.13 (0.01) a	0.55 (0.06) a	0.2 (0.02) a	0.09 (0.007) a
Pure Douglas-fir	48 (0.5) b	1.4 (0.06) a	0.09 (0.007) a	0.13 (0.01) a	0.57 (0.06) a	0.2 (0.03) a	0.09 (0.006) a

Note: Within a column, means with a common lowercase letter are not significantly different at $P = 0.05$.

Table 2.6. Mean and SE of micronutrient concentrations of Douglas-fir needles collected at age 5 and 15 yr.

	1989					
	Mn (ppm)	Fe (ppm)	Cu (ppm)	B (ppm)	Zn (ppm)	*Al (ppm)
No removal	582 (135) a	149 (27) a	7.97 (0.9) a	20.1 (4.4) a	57.3 (28) a	309 (35) b
100% shrub removal	279 (27) a	180 (11) a	8.06 (1.1) a	18.6 (3.5) a	32.2 (9.3) a	437 (49) a
Pure Douglas-fir	740 (209) a	173 (29) a	7.50 (1.0) a	17.4 (1.6) a	24.8 (5.3) a	272 (43) b
	1999					
	Mn (ppm)	Fe (ppm)	Cu (ppm)	B (ppm)	Zn (ppm)	*Al (ppm)
No removal	167 (29) a	53 (30) a	5.4 (1.3) a	10 (1.6) a	15.2 (2.0) a	131 (7) ab
100% shrub removal	171 (4) a	49 (7) a	4.1 (0.4) a	8.9 (0.4) a	13.0 (0.9) a	114 (12) b
Pure Douglas-fir	199 (32) a	65 (14) a	4.3 (0.5) a	8.6 (1.0) a	12.0 (1.1) a	163 (17) a

Note: Within a column, means with a common lowercase letter are not significantly different at $P = 0.05$.
*Aluminum is not an essential plant nutrient (Waring and Running 1998).

The total aboveground C pool was similar among treatments at age 5 yr. However, 82% of C on DFC plots was attributed to shrub species on these plots (Table 2.7). At age 15 yr, the aboveground C pool was 56% lower on DFC plots than on DFO plots (Table 2.8). Aboveground N content was 165% higher on DFC plots than on DFO plots at age 5 yr. But on DFC plots, 85% of total aboveground N was contained in shrub species (Table 2.7). The total aboveground N pool dramatically increased from age 5 yr to 15 yr on all plots. Even though tree N content was more than 3 times greater on DFO plots than on DFC plots, the presence of an understory offset the difference in the aboveground N pool among treatments at age 15 yr (Table 2.8). At age 5 yr, aboveground P content was similar among plots. However, herbs on DFH sites contributed 74% of P on these plots (Table 2.7). By age 15 yr, aboveground P content was 88% higher on DFO plots than on DFC plots (Table 2.8).

Table 2.7. Mean and SE of aboveground nutrient distribution among vegetation components collected from 5 yr old Douglas-fir plantations.

		No removal	100% shrub removal	Pure Douglas-fir
Carbon (kg ha^{-1})	**Herb**	485 (122) a	2700 (504) b	0
	Shrub	4571 (817)	0	0
	Tree	505 (274) a	1805 (357) a	5805 (1388) b
	Total C	5561 (935) a	4505 (833) a	5805 (1388) a
Nitrogen (kg ha^{-1})	**Herb**	14.9 (3) a	73.9 (17.7) b	0
	Shrub	86.8 (19)	0	0
	Tree	4.1 (2.1) a	12 (1.9) a	40 (9) b
	Total N	106 (21) a	86 (19) a	40 (9) b
Phosphorus (kg ha^{-1})	**Herb**	1.8 (0.38) a	9.2 (2.1) b	0
	Shrub	4.64 (1.4)	0	0
	Tree	0.9 (0.4) a	3.3 (0.7) a	10.1 (2.3) b
	Total P	7.3 (1.5) a	12.5 (2.6) a	10.1 (2.3) a

Note: Within a row, means with a common lowercase letter are not significantly different at $P = 0.05$.

Aboveground Ca pool size was 41% higher on DFO plots than on DFC plots at plantation age 15 yr (Table 2.8).

Table 2.8. Mean and SE of aboveground nutrient pools on 15 yr old Douglas-fir plantations.

		No removal	100% shrub removal	Pure Douglas-fir
Douglas-fir (kg ha^{-1})	**Carbon**	9062 (2944) a	33003 (2019) b	37126 (2438) b
	Nitrogen	92 (31) a	261 (27) b	290 (23) b
	Phosphorus	18 (5.8) a	62.1 (4.9) b	69 (5.5) b
	Potassium	53 (18) a	177 (19) b	197 (15) b
	Calcium	39 (13) a	146 (6.8) b	162 (12) b
	Magnesium	10.2 (3.5) a	34.1 (2.6) b	38.2 (2.9) b
Shrub (kg ha^{-1})	**Carbon**	7202 (1689) a	1708 (525) b	0
	Nitrogen	202 (49) a	36 (13) b	0
	Phosphorus	18 (4.8) a	4 (1.2) b	0
	Potassium	124 (31) a	32 (9.8) b	0
	Calcium	48 (11) a	10.7 (2) b	0
	Magnesium	38 (11) a	9.1 (2.5) b	0
Herb (kg ha^{-1})	**Carbon**	73.3 (34) a	116 (60) a	0
	Nitrogen	3.41 (1.45) a	4.95 (1.5) a	0
	Phosphorus	0.4 (0.18) a	0.41 (0.14) a	0
	Potassium	3.9 (2) a	5.4 (2.2) a	0
	Calcium	0.86 (0.3) a	0.93 (0.5) a	0
	Magnesium	0.46 (0.19) a	0.86 (0.4) a	0
Total (kg ha^{-1})	**Carbon**	16337 (2143) a	34826 (2392) b	37126 (2438) b
	Nitrogen	297 (41) a	303 (37) a	290 (23) a
	Phosphorus	36.6 (6.6) a	66.5 (5.5) b	69 (5.5) b
	Potassium	181 (24) a	215 (23) a	197 (15) a
	Calcium	87 (9) a	158 (7) b	162 (12) b
	Magnesium	49 (9) a	44 (4) a	38 (2.9) a

Note: Within a row, means with a common lowercase letter are not significantly different at P = 0.05.

Isotopes

At plantation age 5 yr, needles on DFH plots had significantly lower negative $\delta^{15}N$ than needles on DFC plots (P < 0.07). Salmonberry branches on DFH plots were significantly enriched in ^{13}C (P < 0.05) at plantation age 15 yr. In the same plots, the herb ^{13}C value was also higher compared to herbs on DFC plots (Table 2.9).

Table 2.9. Mean and SE of $\delta^{13}C$ and $\delta^{15}N$ in Douglas-fir needles, salmonberry branches (SBB), salmonberry leaves (SBL), and herbs collected at plantation age 5 yr and 15 yr.

	Isotope abundance (‰)	No removal	100% shrub removal	Pure Douglas-fir
1989	**Needle $\delta^{13}C$ (‰)**	-29.1 (0.30) a	-28.56 (0.26) a	-28.71 (0.07) a
	Needle $\delta^{15}N$ (‰)	-1.54 (0.28) ab	-2.32 (0.22) b	-1.14 (0.33) a
1999	**Needle $\delta^{13}C$ (‰)**	-27.6 (0.30) a	-27.72 (0.09) a	-27.57 (0.34) a
	Needle $\delta^{15}N$ (‰)	-1.64 (0.35) a	-2.19 (0.29) a	-1.23 (0.11) a
	SBB $\delta^{13}C$ (‰)	-28.6 (0.47) a	-30.4 (0.47) b	
	SBL $\delta^{13}C$ (‰)	-29.16 (0.60) a	-30.04 (0.37) a	
	SBL $\delta^{15}N$	-2.2 (0.42) a	-2.61 (0.32) a	
	Herb $\delta^{13}C$ (‰)	-29.31 (0.34) a	-31.69 (0.60) b	
	Herb $\delta^{15}N$ (‰)	-2.51 (0.30) a	-1.87 (0.48) a	

Note: Within a row, means with a common lowercase letter are not significantly different at $P = 0.10$.

Belowground

Physical properties

At plantation age 15 yr of, the forest floor biomass on DFO stands was 2.5 times greater than that on DFC plots (Table 2.10). Soil bulk density at plantation age 5 yr was 29% higher on DFO plots than on DFC plots (Table 2.10). At plantation age 15 yr, bulk density on DFO plots was 22% higher than on DFC plots. About 50% of the soil from every treatment was < 2 mm in particle size (fine) at age 5 yr. Due to wet sieving at age 15 yr, < 2 mm particles comprised about 70% of the soil at 15 cm soil depth. The light density fraction of fine soil (< 2 mm) (1.7 g cm^{-3} NPT solution) ranged from 5 – 7.5% of soil mass at age 15 yr (Table 2.10). Root densities in the

upper 15 cm soil depth were 10 times higher on DFC plots than on DFO

stands (Table 2.10).

Table 2.10. Mean and SE of some soil properties at 0-15 cm depth in 5 yr and 15 yr old Douglas-fir plantations.

	No removal	100% shrub removal	Pure Douglas-fir
		1989	
Soil bulk density (g cm^{-3})	0.49 (0.035) a	0.59 (0.025) ab	0.63 (0.020) b
< 2mm (fine) soil fraction (%)	54 (7) a	51 (8) a	49.2 (5) a
Root density (kg ha^{-1}) in 0-15 cm	8550 (1550) a	11400 (1443) a	870 (255) b
		1999	
Soil bulk density (g cm^{-3})	0.47 (0.028) a	0.54 (0.027) ab	0.57 (0.019) b
< 2mm (fine) soil fraction (%)	68 (5) a	68 (4) a	71 (2) a
% Light fraction in < 2 mm soil	7.5 (2) a	5 (1) a	7 (2) a
Forest floor (kg ha^{-1})	5924 (952) a	10295 (1127) ab	15163 (2290) b

Note: Within a row, means with a common lowercase letter are not significantly different at P = 0.05.

Nutrients

At age 5 yr, C concentration in the < 2 mm soil fraction (Table 2.11)

was significantly affected by understory vegetation removal (P < 0.02).

Total understory vegetation removal reduced the soil C concentration in the

fine fraction by about 27%. Concentrations of some soil cations were also

influenced by the presence of understory vegetation. The soil fine fraction

on DFC plots had 15%, 25% and 32% lower Fe, Al and Ca concentrations,

respectively, than the same soil fraction on DFO plots (Table 2.11).

Table 2.11. Mean and SE of mineral concentrations in the < 2 mm mineral soil fraction from 0-15 cm depth on 5 yr and 15 yr old Douglas-fir plantations.

	Macronutrients						
1989	**C (%)**	**N (%)**	**S (%)**	**P (%)**	**K (%)**	**Ca (%)**	**Mg (%)**
No removal	13.6 (1.2) a	0.72 (0.04) a	0.065 (0.009) a	0.12 (0.03) a	0.70 (0.04) a	0.20 (0.030) a	0.40 (0.15) a
100% shrub removal	10.7 (0.4) ab	0.62 (0.05) a	0.060 (0.006) a	0.12 (0.03) a	0.84 (0.10) a	0.25 (0.004) ab	0.49 (0.10) a
Pure Douglas-fir	10.0 (0.9) b	0.55 (0.04) a	0.055 (0.006) a	0.11 (0.03) a	0.85 (0.10) a	0.28 (0.040) b	0.55 (0.10) a
1999	**C (%)**	**N (%)**					
No removal	11.5 (1.3) a	0.62 (0.07) a					
100% shrub removal	10.7 (0.6) a	0.61 (0.07) a					
Pure Douglas-fir	10.8 (1.3) a	0.57 (0.08) a					

	Micronutrients				
1989	**Mn (ppm)**	**Fe (%)**	**Cu (ppm)**	**Zn (ppm)**	***Al (%)**
No removal	1270 (697) a	3.98 (0.9) a	33 (9.7) a	78 (10) a	5.0 (0.60) a
100% shrub removal	1099 (361) a	4.45 (1.0) ab	37 (13) a	90 (11) a	6.3 (0.42) b
Pure Douglas-fir	1105 (455) a	4.70 (1.0) b	36 (12) a	95 (12) a	6.7 (0.26) b

Note: Within a column, means with a common lowercase letter are not significantly different at P = 0.05.
*Aluminum is not an essential plant nutrient (Waring and Running 1998).

Table 2.12. Mean and SE of mineral concentrations in the ≥ 2 mm soil fraction from 0-15 cm depth on 5 yr and 15 yr old Douglas-fir plantations.

		1989	
	C (%)	N (%)	S (%)
No removal	5.89 (1.2) a	0.27 (0.04) a	0.027 (0.007) a
100% shrub removal	4.99 (0.5) a	0.28 (0.02) a	0.023 (0.002) a
Pure Douglas-fir	4.67 (0.6) a	0.24 (0.02) a	0.023 (0.003) a
		1999	
	C (%)	N (%)	S (%)
No removal	7.8 (1.8) a	0.32 (0.04) a	0.027 (0.005) a
100% shrub removal	5.7 (0.5) a	0.27 (0.01) a	0.022 (0.002) a
Pure Douglas-fir	5.9 (1.2) a	0.25 (0.03) a	0.022 (0.003) a

Note: Within a column, means with a common lowercase letter are not significantly different at $P = 0.05$.

Total soil C content (kg ha^{-1}) in the ecosystem was affected by the removal of understory vegetation at plantation age 5 yr. Effects of treatments on the soil total C pool were not significant at $P = 0.05$. However, they were significant at $P = 0.10$ ($P < 0.09$), suggesting a possible change developing in the amount of soil C associated with the presence of understory vegetation in the ecosystem (Table 2.13).

Table 2.13. Mean and SE of C and N in mineral soil from 0-15 cm depth on 5 yr and 15 yr old Douglas-fir plantations.

	1989	
	C (kg ha^{-1})	N (kg ha^{-1})
No removal	69938 (3890) a	3628 (87) a
100% shrub removal	57505 (7735) a	3374 (533) a
Pure Douglas-fir	52452 (3687) a	2892 (257) a
	1999	
	C (kg ha^{-1})	N (kg ha^{-1})
No removal	69610 (3504) a	3590 (336) a
100% shrub removal	63776 (6889) a	3630 (612) a
Pure Douglas-fir	66198 (11299) a	3407 (584) a

Note: Within a column, means with a common lowercase letter are not significantly different at $P = 0.05$.

At age 5 yr, total inorganic N ($NH_4^+ + NO_3^-$) collected from resin bags was significantly affected by vegetation cover and also by proximity to trees (Table 2.14). On DFO plots, resin bags placed at 5 cm depth collected twice as much N leachate as those on DFC sites. Initial NO_3^- in DFO plots soil was also 5 times higher than in DFC plots soil. However, net mineralizable NH_4^+ was almost 3 times higher on DFC plots than on DFO plots (Table 2.14).

Table 2.14. Mean and SE of physical and chemical properties of mineral soil from 0-15 cm depth in 5 yr old Douglas-fir plantations with partial to complete understory vegetation removal.

Variables	No removal	100 % shrub removal	Pure Douglas-fir
Total inorganic N (μg g^{-1})	296 (100) a	125 (75) a	675.6 (160) b*
			553.6 (122) ab**
Percent of fine soil in 0-15 cm	54 (7) a	51 (8) a	49.2 (5) a
Soil (< 2 mm) dry weight (g cm^{-3}) in 0-15 cm	0.38 (0.04) a	0.44 (0.05) a	0.47 (0.04) a
Net mineralizable NH$_4^+$ (μg g^{-1})	61 (12) a	43 (12) ab	21 (6) b
Incubated NH$_4^+$ (μg g^{-1})	173 (22) a	122 (16) a	90 (11) a
Initial NH$_4^+$ (μg g^{-1})	112 (16) a	79 (12) a	69 (6) a
Initial NO$_3^-$ (μg g^{-1})	6.45 (1.2) a	3.4 (0.6) a	30.4 (7) b
Soil bulk density (g cm^{-3}) in 0-15 cm	0.49 (0.035) a	0.59 (0.025) ab	0.63 (0.02) b
Soil moisture (%) in 0-7 cm	39.6 (2.6) a	37.1 (2.2) a	35.5 (1.9) a
Soil moisture (%) in 7-15 cm	38.4 (3.9) a	35.7 (2.9) a	37.8 (1) a

Note: Within a row, means with a common lowercase letter are not significantly different at P = 0.05.
* Data were collected between Douglas-fir trees.
** Data were collected next to Douglas-fir trees.

Total K, Ca and Mg (kg ha^{-1}) at the 0-15 cm soil depth were 53%,

94%, and 85% higher on DFO plots than on DFC plots, respectively.

Exchangeable K and Mg were <3% of the total amounts of these nutrients

at 15 cm soil depth. However, understory removal did not have significant

effects on the exchangeable forms of these nutrients. On the other hand,

even though DFC plots had 48% less total soil Ca than DFO plots, 13% of

this total Ca was in the exchangeable form on DFC plots. The amount of

this exchangeable Ca on DFC plots was 95% higher than on DFO plots

(Table 2.15).

Table 2.15. Mean and SE of total and exchangeable cations in the < 2 mm
soil fraction on 15 yr old Douglas-fir plantations.

| | **Total** | | | |
	K (kg ha^{-1})	**Na (kg ha^{-1})**	**Ca (kg ha^{-1})**	**Mg (kg ha^{-1})**
No removal	3369 (379) a	1625 (256) a	881 (94) a	1812 (446) a
100% shrub removal	4664 (658) ab	2148 (171) a	1374 (59) ab	2675 (535) b
Pure Douglas-fir	5171 (686) b	2506 (245) a	1710 (212) b	3368 (649) c
	K (kg ha^{-1})	**Exchangeable** **Na (kg ha^{-1})**	**Ca (kg ha^{-1})**	**Mg (kg ha^{-1})**
No removal	90.5 (9) a	30 (2) a	113 (15) a	65 (15) a
100% shrub removal	140 (57) a	29 (3) a	115 (34) a	74 (34) a
Pure Douglas-fir	96 (15) a	32 (5) a	58 (13) b	58 (23) a

Note: Within a column, means with a common lowercase letter are not significantly
different at P = 0.05

Isotopes

Total understory vegetation removal significantly enriched soil δ^{15}N

on DFO plots (P < 0.09) at age 5 yr. Soil on DFO plots had the highest

δ^{15}N values (about 1 per mil higher than in DFC stand soil) (Table 2.16).

δ^{13}C signatures of < 2 mm soil light (LF) and heavy fractions (HF) were not

different between plots, but the differences between LF and HF were

significantly affected by understory removal (P < 0.04).

Table 2.16. Mean and SE of δ^{13}C and δ^{15}N in < 2 mm light, heavy, and total soil fractions on Douglas-fir plots at plantation age 5 yr and 15 yr.

		No removal	100% shrub removal	Pure Douglas-fir
1989	**Total soil δ^{13}C**	-26.1 (0.10) a	-26.3 (0.07) a	-26.2 (0.12) a
	Total soil δ^{15}N	1.54 (0.27) a	1.83 (0.12) ab	2.31 (0.14) b
1999	**Total soil δ^{13}C**	-26.2 (0.10) a	-26.5 (0.10) a	-26.3 (0.20) a
	Total soil δ^{15}N	1.78 (0.21) a	1.75 (0.15) a	2.31 (0.22) a
	Light fraction δ^{13}C	-25.8 (0.26) a	-26.65 (0.26) a	-26.4 (0.26) a
	Heavy fraction δ^{3}C	-25.7 (0.26) a	-26.1 (0.26) a	-25.8 (0.26) a
	LF-HF δ^{13}C	-0.09 (0.29) a	-0.57 (0.31) ab	-0.61 (0.44) b

Note: Within a row, means with a common lowercase letter are not significantly different at P = 0.10.

Discussion

Survival

Douglas-fir survival was not affected by the presence of understory at plantation age 5 yr. Average tree survival was between 92% and 98%. Wagner (1989) reported that during the first 3 yr of the experiment, a total of 4.7% of the seedlings died, with 1.7% of the mortality attributed to animal damage. Results from the maximum-likelihood logistic regression indicate that the percentage of surviving seedlings was not correlated with the abundance of woody or herbaceous vegetation during the first 3 yr after planting (Wagner 1989). Tesch and Hobbs (1989) also did not find a significant difference in the survival of 3 yr old Douglas-fir trees grown under different levels of shrub competition in southern Oregon; even after 5 yr, Douglas-fir seedling survival was not significantly different among the same treatments (Tesch et al. 1993). On a similar site to our study area, Rose et al. (1999) also did not find any influence of woody and herbaceous species on the survival of 3 yr old Douglas-fir seedlings. White and Newton (1990), however, reported survival differences among 2 yr old Douglas-fir seedlings under different weed control treatments with varying kinds and rates of herbicides and fertilizers.

Seedling growth and survival are affected by several factors. Douglas-fir seedlings are expected to grow well when they are released from overtopping weeds and planted far enough apart to avoid intraspecific

competition. Good stock and large seedlings at the beginning of planting also favor survival and growth (Newton et al. 1993). In another study, Roth and Newton (1996) found a nearly 60% increase in Douglas-fir seedling survival (2nd yr) with total weed control on 2 of 3 sites after planting plug-1 transplant seedlings at 0.5 m to 1 m spacing in the Oregon Coast Range. They concluded that from three of their experimental treatments (weed control, N fertilization, and seed source), weed control was the dominant factor influencing seedling survival and growth. They also stated that weed control in conjunction with large planting stock is the silvicultural treatment that most contributes to Douglas-fir growth. In the White and Newton (1990) study, 1 m spacing was used to plant 2-0 bare-root seedlings. In our study and in Rose et al. (1999), spacing was 3 m. In our research, average seedling height was 30 cm during planting. Basal area increment at the end of the first year of planting was not influenced by basal area at the beginning of planting. However, during the following 2 yr, basal area and growth increment were affected by basal area and height at the start of each growing season (Wagner 1989).

At age 15 yr, tree survival was significantly different among plots ($P < 0.01$). The vegetation zone, which may be interacting with aspect, appears to have an effect on Douglas-fir survival at age 15 yr. The southern spruce zone site has the highest percent survival, with 30% higher survival than the southern hemlock zone.

Growth

Douglas-fir seedling growth at age 5 yr was strongly affected by the presence of understory vegetation on the sites. Several possibilities of resource limitation could be responsible for the observed patterns: Light availability, water availability, and nutrient availability.

First, light availability for Douglas-fir seedlings can be different among treatments. Wagner (1989) suggested that woody species cover was strongly correlated with available sky ($P < 0.001$) following 3 yr of planting, but herbaceous vegetation was not correlated with it. Leaves in a full sunlight environment have a lower specific leaf area than those in shade due to additional layers of mesophyll in leaves exposed to sunlight (Stenberg et al. 1995). Thus, significantly higher specific leaf areas of Douglas-fir needles on DFC plots relative to other plots indicated that seedlings were shaded by shrubs at age 5 yr. Larger trees with more extensive crowns would develop closed stands more rapidly on DFO plots than on DFH plots. As a result, needles in lower crown positions became increasingly more shaded and exhibited higher average specific leaf areas on DFO plots than needles from DFH sites. Therefore, light affects seedling performance, and its availability for seedling growth was influenced by the amount of shrub coverage on the site.

Secondly, available soil water can be a limiting factor on seedling growth. After the third year of the experiment, the cumulative soil water potential was negatively correlated ($P < 0.01$) with the abundance of woody

neighbors (Wagner 1989). Soil water depletion by woody and herbaceous vegetation decreased with increasing soil depth. Herbaceous vegetation decreased cumulative water potentials at 30 and 60 cm soil depth. Even though cumulative water potential decreased with increasing abundance of understory vegetation, soil water stresses were relatively low. Daily potentials rarely fell under −0.1 Mpa during any of the growing seasons in the first 3 yr of the plantations (Wagner 1989). Our data indicate that soil moisture concentration was not significantly different between treatments, and $\delta^{13}C$ values of Douglas-fir needles also did not indicate moisture stress at any of the plots at age 5 yr.

Thirdly, nutrient availability can also be an important factor in tree growth. Although DFH plots had total shrub removal and full sun exposure, trees on DFO plots had more than 3 times the average tree biomass than those on DFH plots after 5 yr. Therefore, the big difference in seedling growth is likely attributable to soil nutrient availability. Shrub and herb removal between and under seedlings disturbed the soil and may have accelerated decomposition and mineralization through mixing the upper organic layer with the lower mineral soil. On DFH plots, only shrubs were removed, and therefore soil disturbance was not as severe as on DFO plots. Inorganic N collected in resin bags on DFH plots was only one-fifth of that from DFO plots after 5 yr which may indicate higher decomposition on DFO plots due to incorporation of soil organic matter with mineral soil. The presence of herbs alone also may result in competition with seedlings for

nutrients (DFH). Rose et al. (1999) found that 3 yr old coastal Oregon Douglas-fir seedlings had a 70% greater diameter (at 15 cm) and 27% greater height on herbaceous control plots than on plots with no herbaceous control. They speculated that herbs competed with seedlings for water, but did not discuss nutrient competition. On DFH plots, 74% of aboveground P content was taken up by herbs. Kimmins (1997) suggested that competition for light may result in the death of some individuals in the plant community, while nutrient competition usually does not cause plant death. However, nutrient deficiencies may prevent plants from competing effectively for water and light. Our data show that light is a limiting factor in young seedling growth on these sites, and shrub removal during the early stages of stand development increases tree growth. In addition, nutrients also are an important limiting factor in determining seedling growth in these soils.

At age 5 yr, tree biomass was significantly reduced in the presence of understory vegetation ($P < 0.0001$). Total understory removal increased tree biomass 12-fold over that of Douglas-firs on DFC plots. However, the presence of shrubs and herbs offsets the total aboveground biomass difference among sites at age 5 years. Understory vegetation removal made a significant difference in biomass accumulation of Douglas-fir trees through age 15 yr ($P < 0.0001$). The difference in tree biomass among plots at age 15 was not as large as it was at stand age 5 yr. Nonetheless, trees on DFO plots had 336% more average standing biomass ha^{-1} than

trees on control plots (DFC). These differences in tree biomass per hectare can mostly be accounted for by survival differences among plots. On the average, 59% of the trees survived on DFC plots, but this value was 89% on DFO plots. Performance of trees by treatments also showed that tree diameter (dbh) on DFC plots averaged 10.3 cm, which was 41% lower than that of trees on DFO plots. An average tree on DFO plots had 3 times greater biomass than average trees on DFC plots after 15 years. Differences in tree growth among plots may be attributed to the significant variation in tree leaf area (LA). Trees on DFO plots had about 80% higher LA per tree than trees on DFC plots. Thus, the presence of understory vegetation significantly reduced the standing biomass of Douglas-firs on a per tree basis ($P < 0.0001$) by age 15 yr. However, after 50% shrub removal, any increase in understory removal did not significantly contribute to tree growth by the end of the fifteenth growing season. Differences in specific leaf area (SLA) of Douglas-fir needles among treatments at age 5 yr disappeared by stand age 15 yr, since trees on every plot had already established themselves in the overstory and were equally exposed to sunlight.

Removing understory biomass from some of the plots during the five years following tree planting in 1985, secured successful tree establishment in those treatments with an indication of a higher overall survival rate and biomass accumulation for Douglas-firs on the plots. After understory removal was completed in 1989, some of the shrubs and herbs

reestablished themselves on the plots during the following years. However, at plantation age 15 yr, there was a significant difference in the amount of understory biomass between plots (P < 0.0005). Plots that received total shrub removal each year from 1985 through 1989 (DFH) had accumulated about 25% of the understory biomass present on DFC plots. Plots that received 50% and 25% shrub removal 10 yr before, had about the same amount of understory biomass (~ 16000 kg ha^{-1}) present on DFC plots at the end of plantation year 15. More than 95% of the understory biomass on each plot was accounted for by salmonberry.

At plantation age 15 yr, total aboveground plant biomass was similar between DFH and DFO plots, but significantly lower on DFC plots (P < 0.0001). Even though tree biomass ha^{-1} on DFO plots was more than 4 times higher than on DFC plots, total aboveground biomass was only about 58% lower on DFC plots than in DFO stands. Therefore, trees accounted for only 54% of the aboveground biomass on DFC sites.

At plantation age 5 yr, herb biomass was 9% and 60% of total aboveground plant biomass on DFC and DFH plots, respectively. However, at plantation age 15 yr, the contribution of herb biomass to total aboveground plant biomass was negligible in all of the plots.

In order to investigate water limitation, Douglas-fir needles, shrub branches, shrub leaves, and also herbs (sword fern) were analyzed for δ^{13}C isotopic composition. We did not detect differences in Douglas-fir needle δ^{13}C composition. But, salmonberry branches showed a 2‰ enrichment in

$\delta^{13}C$ on DFC plots compared to DFH plots. There are two possible explanations for this difference in shrub $\delta^{13}C$ isotope composition:

The first is that lower light intensity in the understory on DFH plots might lead to a lower ratio of internal to atmospheric CO_2 concentration in plants, and increasing irradiation may limit stomatal photosynthesis due to reduced stomatal conductance under high light levels (Zimmerman and Ehleringer 1990). Thus, understory plants in shade (DFH) may have more negative $\delta^{13}C$ values compared to plants that are more exposed to light (DFC) (Ehleringer et al. 1987; Lajtha and Marshall 1994). On DFH plots, 99% of the light was intercepted by the Douglas-fir canopy. However, due to tree mortality (40%) on DFC plots, most of the understory shrub species were exposed to sunlight. Thus, reduced $\delta^{13}C$ in shrub branches on DFH sites can be attributable to lower light intensity on these plots.

The second possibility is that the recycling of lighter CO_2 (depleted in ^{13}C) generated by forest litter decomposition, decreases ^{13}C composition of the source CO_2 with depth in the canopy, resulting in lower $\delta^{13}C$ values in understory plants compared to plants which rely on atmospheric CO_2 in the open canopy (Ehleringer et al. 1986; Lajtha and Marshall 1994). Since herb species on every plot were shaded by trees, shrubs, or a combination of both, herbs on every plot may potentially rely on decomposition derived CO_2 sources. If source effects were the environmental parameter responsible for these variations, then we would expect the most negative isotope ratios in the herb layer, and the least negative values in trees, but

no differences in the herbs' isotopic composition among sites. Thus, CO_2 source or shading effects on decreased $\delta^{13}C$ values can be distinguished by comparing ^{13}C isotopic composition of herbs, which was 2.4 ‰ lower on DFH plots than on DFC plots. This implies that water limitation was primarily responsible for the observed isotopic differences between plots. This leads us to conclude that plants on DFC plots had more water competition than those on DFH plots in at least the upper part of the soil profile. Since we did not detect any fractionation differences in DF needles, we assume that these trees probably access water from the deeper soil profile. Further investigation is needed to determine the source of water for different species on the plots.

Nutrients

At plantation age 15 yr of, Douglas-fir needle C concentration was significantly lower on DFC plots than those in other treatments ($P < 0.03$). On DFC plots, needle C concentration was significantly reduced from age 5 yr to 15 yr ($P < 0.01$). Needle N concentration was significantly higher on DFC plots at age 5 yr ($P < 0.03$). Control plots (DFC) had about 13% higher needle N concentration than DFO plots. After conducting an experiment on a clearcut site in a Quebec boreal forest, Jobidon (2000) reported that hardwood competition significantly reduced N (24%) and Ca (29%), and increased K (49%) concentrations in 3 yr old white spruce foliage (*Picea glauca* (Moerch) Vass) compared to the pure stand. In our

study, at stand age 5 yr, shrubs on DFC plots probably shaded out Douglas-fir seedlings, resulting in a higher needle N content on DFC plots than on other treatments with more light. Needles on DFO plots had the lowest N concentrations. This may be explained by dilution as a result of the vigorous tree growth. Needle isotopic composition indicated that needles on DFH plots had more negative $\delta^{15}N$ values than those on other treatments at age 5 yr. Apparently, removing all of the shrubs reduced the total demand for N in the system and, additionally, herbs had taken up excess N and prevented leaching from the system. Thus, trees in the DFH treatment may rely on nitrate more than ammonium at plantation age 5 yr. Most soil N is bound in forms not immediately available for plant uptake, thus the soil inorganic N pool may be more appropriate for a good approximation of the $\delta^{15}N$ of plant available N. Overall needle N concentration significantly decreased from age 5 yr to 15 yr ($P < 0.0018$), but there were no differences in N concentration among sites at age 15 yr. Needle Ca concentration was similar among treatments at 5 yr and 15 yr. However, from age 5 yr to 15 yr, needle Ca concentrations decreased at all sites ($P < 0.0002$). For 5 yr old seedlings, needle Al concentrations were 60% higher on DFH plots than on DFO plots. But, at age 15 yr, needle Al concentrations were 43% higher on DFO plots than on DFH plots.

At age 5 yr, the total aboveground C pool was similar among treatments. However, 82% of C on DFC plots was attributed to shrub species on these plots. At age 15 yr, the aboveground C pool was 56%

lower on DFC plots than on DFO plots. At age 5 yr, the aboveground N content was 165% higher on DFC plots than on DFO plots. But, on DFC plots, 85% of total aboveground N was in shrub biomass. The total aboveground N pool dramatically increased from age 5 yr to 15 yr on all sites. Even though tree N content was more than 3 times greater on DFO plots than on DFC plots, the presence of understory offset the differences in aboveground N pools among treatments at age 15 yr. At age 5 yr, aboveground P content was similar among plots. However, herbs on DFH plots contributed 74% of P mass on these plots. At age 15 yr, the aboveground P content was 88% higher on DFO plots than on DFC plots. The aboveground Ca pool size was 41% higher on DFO plots than on DFC plots at plantation age 15 yr.

Needle nutrient concentrations were compared with data that were assumed to be the normal range of macronutrients in Douglas-fir foliage provided by Ericsson (1994). We adjusted the normal range of nutrient ratios in Douglas-fir foliage, using 100 units for N to compare Ericsson's nutrient ratios with the data in the current study. The N:P:K:Mg:Ca ratios in his report were: 100:22:34:9:23, respectively. In the current study at age 5 yr, DFC had 100:9:31:5:20, DFH had 100:9:33:5:26 and DFO had 100:7:28:5:19 ratios for the same order of nutrients. According to these ratios, P was about 60% lower and Mg was about 40% lower in the needles than expected for optimal nutritional balance. At stand age 15 yr, DFC had 100:10:41:7:14, DFH had 100:10:42:7:15, and DFO had 100:9:41:6:14

ratios for the same order of nutrients. According to these ratios, K was 17% higher, P was 55% lower, Ca was about 39% lower, and Mg was 22% lower in the needles than expected for optimal nutritional balance at all sites.

Belowground

The forest floor mass on DFO plots was 2.5 times greater than that on DFC plots after 15 yr, reflecting relatively less decomposable needle accumulation on the soil surface in the pure stand. Soil bulk density at plantation age 5 yr was 29% higher on DFO plots than on DFC plots due to compaction during understory vegetation removal on DFO plots at that time. At plantation age 15 yr, bulk density on DFO plots was 22% higher than on DFC plots. After 5 yr, about 50% of the soil from every treatment was < 2 mm in particle size (fine). At stand age 15 yr, < 2 mm particles comprised about 70% of the soil at 15 cm soil depth. This difference between years was attributed to sieving methods (dry sieving in 1989 vs. wet sieving in 1999).

Carbon concentration in the < 2 mm soil fraction was significantly affected by understory vegetation removal (P < 0.02). Total understory vegetation removal reduced the soil C concentration in the fine fraction about 27% through age 5 yr. Total soil C content (kg ha^{-1}) in the ecosystem was affected by the removal of understory vegetation at plantation age 5 yr. Soil C pools were not significantly different at P < 0.05 among plots. However, significance at P < 0.09 suggests a possible change developing

in the amount of soil C associated with the presence of understory vegetation in the ecosystem at age 5 yr. Total C and nutrient pool sizes in soil were not significantly changed by the presence or absence of understory vegetation at age 15 yr. However, total nutrients in the soil represent a long-term reservoir that is generally relatively unavailable to plants (Kimmins 1997). Thus, a large nutrient pool that cycles slowly may provide fewer nutritional benefits than a smaller pool of rapidly cycling nutrients. Having extensive rooting, shrubs and herbs may have greater root turnover than conifers.

Busse et al. (1996) reported that the presence of understory vegetation in a ponderosa pine ecosystem (*Pinus ponderosa* Dougl.) increased soil C content 50% over the adjacent soil in a central Oregon 35 year old pure ponderosa pine stand. Nitrogen content was also increased by 46%. In our study, DFC plots had 33% higher soil C than DFO plots at age 5 yr. However, there was no difference in soil C among plots at age 15 yr. In the present research, overall decomposition probably was faster and more complete than in the study by Busse et al. (1996), due to different climatic conditions. Our study plots are located in coastal Oregon with annual precipitation nearly 3-fold that of Busse et al.'s central Oregon site (180 cm vs. 61 cm). This may lead to increased soil C in the stand with an understory in their study due to faster understory leaf and root turnover, but probably with less complete decomposition than in our work.

Herb and shrub substrate quality could contribute to faster decomposition and nutrient turnover, both above and belowground. Root biomass in the upper 15 cm of soil was nearly 10 times higher on DFC plots than on DFO plots at age 5 yr. On the other hand, with relatively higher lignin, the needle dominated forest floor may retard the decomposition rate. The forest floor on DFO stands was 2.5 times greater in biomass than that on DFC plots at age 15 yr. Since turnover of different soil organic matter components varies due to complex interactions of biological, chemical, and physical processes in soil, further investigation is needed to determine the microorganisms dominating organic matter decomposition on different sites. Our data imply that organic matter on DFC plots decomposed faster at age 5 yr due to the fact that these sites were dominated by shrubs and herbs. In contrast, the forest floor on DFO plots decomposed slowly due to the more recalcitrant properties of needles. Residual lignin is the C fraction most likely to be preserved during organic matter (humus) decay, since lignin decomposes relatively slowly in the early stages of litter decay (Nadelhoffer and Fry 1988). Soil C was higher on the DFC plots at this early age of stand establishment. At age 15 yr, we did not detect soil C differences among treatmentss. A possible explanation of this is that after leaf litter reaches a well-decomposed state, lignin and other residual fractions decompose at similar rates. Thus, during later stages of litter decay, lignin has also begun decomposing (Nadelhoffer and Fry 1988). This then resulted in similar soil C content among treatments. To test this

hypothesis, we investigated the isotopic composition of the < 2 mm soil fraction. The light fraction (LF) is taken to be less decomposed plant and animal residues with a relatively high C:N ratio and rapid turnover. The heavy fraction is considered to be organomineral complexed soil organic matter which is taken to have comparatively more advanced or humified decomposition products, with a narrower C:N ratio, slower turnover rate, and a higher specific density due to its intimate association with soil minerals (Sollins et al. 1984; Christensen 1992). Light fraction soil organic matter is likely to be affected by vegetation type, litter production and decomposition. Plant materials have lower ^{13}C than soil.

Plant litter and roots are both depleted in ^{13}C relative to soil (Sollins et al. 1984; Christensen 1992). As ^{13}C depleted inorganic C is released via decomposition to the soil solution and to the atmosphere, organic matter particles gradually decrease in size and in C:N ratio, and become relatively enriched in ^{13}C (Nadelhoffer and Fry 1988). Thus, more highly decomposed organic matter is relatively enriched in ^{13}C compared to new litter inputs. In our study, the light density fraction of the fine soil (< 2 mm) ranged from 5 – 7.5% of soil mass at all treatments. But, DFO soil was relatively more depleted in ^{13}C than DFC soil, possibly due to discrimination against ^{13}C during rapid plant material decomposition on DFC plots, resulting in ^{13}C enrichment in the remaining organic matter. Continual replacement of needle driven organic matter, which is relatively higher in lignin, may also lower the soil ^{13}C on DFO plots, since undecomposed lignin

has an isotopic composition similar to fresh plant material (Nadelhoffer and Fry 1988).

Concentrations of some of the soil cations were also influenced by the presence of understory vegetation. The soil fine fraction on DFC plots had 15%, 25% and 32% lower Fe, Al and Ca concentrations, respectively, than the same soil fraction on DFO plots at age 5 yr. Total K, Ca and Mg (kg ha^{-1}) at the 0-15 cm soil depth were 53%, 94%, and 85% higher on DFO plots than on DFC plots, respectively. At age 15 yr, exchangeable K and Mg were < 3% of the total amounts of these nutrients at 15 cm soil depth. However, understory removal did not have significant effects on the exchangeable forms of these nutrients. On the other hand, even though DFC plots had 48% less total soil Ca than DFO plots, 13% of this total Ca was in the exchangeable form on DFC plots. The amount of this exchangeable Ca on DFC plots was 95% higher than on DFO plots.

Soil organic matter (SOM) plays a key role in soil fertility (Wild 1988; Tiessen et al. 1994). Cation exchange capacity of soil is influenced by humus content (Wild 1988). Highly mobile ions that are poorly buffered can be lost through disturbance (Ehleringer et al. 1986). Soil pH is one of the major factors in determining soil nutrient availability. High concentrations of H^+ ions may increase the loss of base cations. Higher amounts of nitrate leaching in soil may indicate: 1) a limitation of energy source (C) for soil microorganisms, 2) increased acidity due to production of H^+ ions during nitrification, and 3) higher removal of cations from the upper soil horizon via

nitrate leaching due to negative electrical charges and a high diffusion coefficient of this nutrient in soil (Paul and Clark 1996).

Soil on DFO plots had 5 times more nitrate than DFC soil at age 5 yr. When the substrate NH_4^+ pool is too large to be consumed by nitrifiers, then NO_3^- becomes depleted in ^{15}N values (Nadelhoffer and Fry 1994). Since nitrification discriminates against ^{15}N in the substrate (NH_4^+) more than mineralization does (Hogberg 1997), the loss of ^{15}N depleted N (leaching NO_3^-) would result in ^{15}N enrichment on DFO plots. Our data showed that $\delta^{15}N$ values of soil were different between the sites ($P < 0.09$), with the highest values being found on DFO plots at age 5 yr. This would help to explain the lower exchangeable Ca on DFO plots. Data collected 10 years later (1999) did not show the same trend in soil N isotopic composition, possibly due to higher nutrient uptake and less nitrate leaching because of a more extended nutrient depletion zone by growing Douglas-fir roots.

At plantation age 5 yr, the data suggested that the most intensive level of vegetation control would permit a similar harvest level on less than a tenth of the area required without any control. Even with shrub control alone, a nearly 4-fold gain in wood yield ha^{-1} was obtained over no vegetation control. However, at stand age 15 yr, after 50% shrub removal, any increase in the degree of understory removal did not significantly contribute to tree growth. Apparently, management can harvest similar amounts of merchantable wood by not exceeding the limits of an ecosystem's ability to accommodate stressors. Thus, ecological and

commodity benefits can be achieved by maintaining a desired set of ecological conditions (Perry 1988; Chapin et al. 2000; McCann 2000).

Organic matter is a major source for soil macro- and micronutrients, and is an important component of the global C cycle. The amount of C stored in soil organic matter exceeds by a factor of two or three the amount stored in living vegetation on most of the earth's land surface, and this large pool plays a dynamic part in the geochemical C cycle (Schlesinger 1990). Terrestrial biomass can act as a sink or source of atmospheric CO_2, depending on changes in the biomass of terrestrial vegetation. Forest ecosystems store 86% of terrestrial C (Krankina and Harmon 1994). Thus, forest management largely determines if forest ecosystems are sources or sinks for atmospheric CO_2.

Annual plant nutrient requirements are mostly met by nutrient release from organic matter decomposition. Nutrient availability is largely determined by the activity of decomposers, which release the nutrients captured in the dead biomass. Nutrients, such as N and P, can accumulate under pure stands due to changes in decomposer activity induced by litter quality, and nutrient cycles can thereby be altered. Depletion of readily available nutrients due to slow cycling induced by accretion in trees or recalcitrant soil organic matter may create conditions which provide advantages for Douglas-fir that are more nutrient preservative. These conditions may eliminate other species through competitive exclusion. Future productivity can be jeopardized by excessive nutrient removal from

sites during tree harvesting. For example, nutrients, especially Ca, can be removed from sites by harvesting (Fisher and Binkley 2000). If sufficient time is not allowed between rotations, nutrient replacement rates may be inadequate. Management can create more ecologically stable, structurally heterogeneous ecosystems by leaving some of the understory vegetation as functional ecosystem components. In addition, nutrient management regimes can be more nutrient retentive by changing effects on soil microbial components through fertilization practices such as Ca to decrease mineral N losses and increase N storage in soil organic matter (Richards 1987), and a better understanding of both abiotic and biotic mechanism of soil N retention (Johnson et al. 2000).

Management Implications

The results described above have several implications for forest ecosystem management in the Oregon Coast Range:

A) The presence of shrubs and herbs did not appear to affect Douglas-fir seedling survival in the first five years following plantation establishment. However, removing understory biomass from some of the plots during the five years following tree planting secured successful tree establishment in those treatments, with a high overall survival rate and biomass accumulation for Douglas-firs on the sites at the end of 15 yr. Variables, such as dbh, height, and tree biomass, measured at early plantation ages (5 yr for this study), may not be good indicators of a stand's future

properties. At plantation age 5 yr, the data suggested that the most intensive level of vegetation control, the pure stand, would permit a similar harvest level on less than a tenth of the area required without any vegetation control. Even with shrub control alone, a nearly 4-fold gain in wood yield ha^{-1} would be obtained compared to no vegetation control. However, at stand age 15 yr, after 50% shrub removal, any increase in the degree of understory removal did not contribute significantly to additional tree survival and growth. Furthermore, the relative tree growth rate, calculated by dividing the tree biomass increase between age 5 yr and 15 yr by biomass of the same tree at age 5 yr (Hunt 1982), was 3 times greater on DFH plots than on DFO plots between plantation age 5 yr and 15 yr (Figure 2.8). Assuming adequate light is available from thinning, trees maintaining their current growth rate on DFH plots may surpass Douglas-firs on DFO plots.

Figure 2.8. Mean and SE of average tree biomass at age 5 yr and 15 yr for each treatment. DFC: Control, DFH: 100% shrub removal, and DFO: pure Douglas-fir stand.
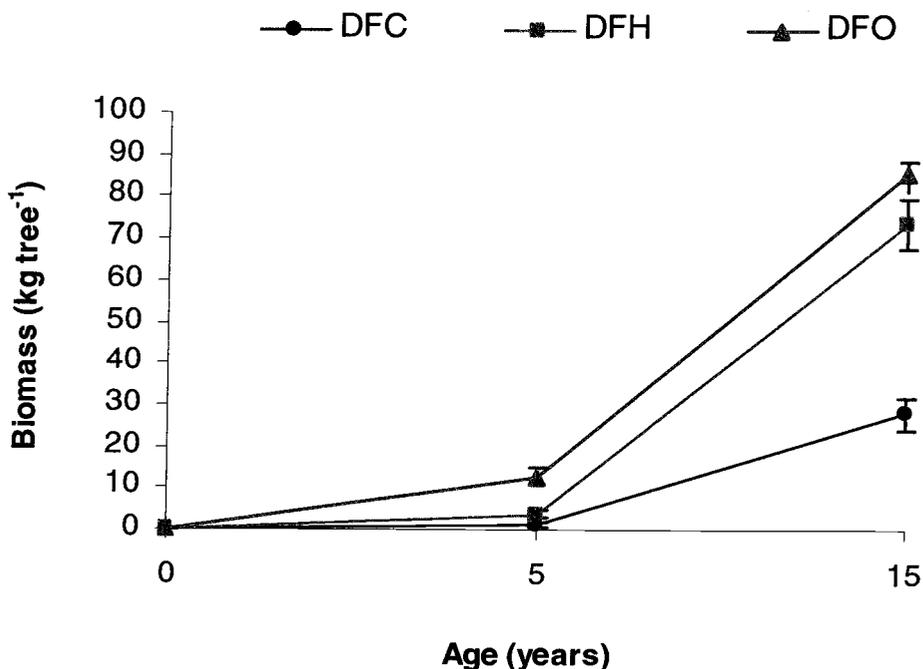
B) Several possible resource limitations could be responsible for the observed results: 1) More light was available to seedlings where shrub cover was reduced, as indicated by significantly lower specific leaf areas of Douglas-fir needles collected from DFO plots as compared to DFC plots. 2) Although soil moisture was not significantly different among treatments, $\delta^{13}C$ values of Douglas-fir needles indicated no moisture stress at any of the plots by age 5 yr. However at age 15 yr, plants on DFC plots had more competition for water, in at least the upper part of the soil profile, than those on DFH plots. Since Douglas-fir needle C isotopic composition did not vary among sites, these trees may have accessed to water from the deeper soil

profile. Further investigation is needed to determine the water source for different species on the plots. Nutrients also are important limiting factors in determining seedling growth in these soils. The presence of herbs alone may result in competition with seedlings for nutrients, especially for P at early ages.

C) Douglas-fir needle nutrient concentrations were compared with data that were assumed to be the normal range of macronutrients in Douglas-fir foliage provided by Ericsson (1994). Our data indicate that P was 55% lower, Ca was about 39% lower, and Mg was 22% lower in the needles than expected for optimal nutritional balance at all sites by age 15 yr. If available N is too high, it can be leached, volatilized, or taken up and stored as amino acids that are likely to make trees more susceptible to attack from defoliating insects and pathogens (Waring and Running 1998). Soil C:N ratio can be increased by leaving boles and branches after thinning the stands, thereby reducing the availability of mineral N to plant uptake. Using fertilizers, especially cations, including micronutrients, on these sites may help to establish nutritional balance of the trees. For example, liming can help to increase Ca availability. However, once the stand approaches its maximum leaf area (index), many of the nutrients required for annual growth are available in the canopy, and recycling makes only a modest contribution to annual needs (Waring 2000). Having data only from 15 yr old plantations may not be enough to give solid management

recommendation. Therefore further research is needed to monitor nutritional changes in tree and soil pools as plantations age.

D) The total aboveground C pool was similar among treatments at age 5 yr. Even though DFO plots had almost 12 times the C sequestered in trees as did DFC plots, the presence of shrubs and herbs contributed significantly to the total C pool in aboveground biomass and eliminated differences in total aboveground C. Shrub species on DFC plots contained 82% of C on these plots at age 5 yr. By age 15 yr, the aboveground C pool was 56% lower on DFC plots than on DFO plots. Understory removal also significantly affected the total N pool in aboveground biomass. At age 5 yr, trees in the DFO stands had 10 times more N than trees on DFC plots. However, the presence of understory vegetation increased the N pool in aboveground biomass to 2.6 times over that of DFO plots. In addition, at age 5 yr on DFC plots, 85% of total aboveground N was contained in shrub species. The total aboveground N pool substantially increased from age 5 yr to 15 yr on all plots. Even though tree N content was more than 3 times greater on DFO plots than on DFC plots, the presence of an understory offset the differences in aboveground N pools among treatments at age 15 yr. At age 5 yr, aboveground P content was similar among plots. However, herbs on DFH plots contributed 74% of abovegound P. By age 15 yr, aboveground P content was 88% higher on DFO plots than on DFC sites. At this same age, the aboveground Ca pool size was 41% higher on DFO plots than on DFC plots. As one consequence, however, the soil

exchangeable Ca was 49% lower on DFO plots at age 15 yr than on DFC plots.

E) The presence of understory vegetation had significant effects on soil physical properties. The forest floor on DFO stands had 2.5 times greater biomass than on DFC plots due to accumulation of recalcitrant needles on the soil surface of the pure stand. Soil bulk density at plantation age 5 yr was 29% higher on DFO plots than on DFC plots. At plantation age 15 yr, bulk density on DFO plots was 22% higher than on DFC plots. Although relatively large changes in bulk densities and surface moisture conditions were recorded in association with treatments, since bulk density values are so low (ranging between $0.47 - 0.63$ g cm^{-3}) they are not likely to be critical with regard to altering soil drainage properties or exerting water stress on these sites.

F) Total understory vegetation removal reduced the soil C concentration in the fine fraction by about 27% through age 5 yr. Concentrations of some soil cations were also influenced by the presence of understory vegetation. The soil fine fraction on DFC plots had 15%, 25% and 32% lower Fe, Al and Ca concentrations, respectively, than the same fraction on DFO plots at age 5 yr.

G) Total soil C content (kg ha^{-1}) in the ecosystem was affected by understory vegetation removal at plantation age 5 yr. Soil C pool data suggested a possible change developing in the amount of soil C associated with the presence of understory vegetation in the ecosystem at this same

age. Control plots had 33% higher soil C than DFO plots at age 5 yr.

However, by age 15 yr, there was no difference in soil C among plots.

Isotopic composition of light and heavy soil fractions suggests that organic

matter decomposition may differ between plots. Continual replacement of

needle driven organic matter, with relatively higher lignin concentrations,

may lower the decomposition rate in pure stands. Busse et al. (1996)

reported that the presence of understory vegetation in a ponderosa pine

ecosystem (*Pinus ponderosa* Dougl.) increased soil C content 50% over the

adjacent soil in a central Oregon 35-year-old pure ponderosa pine stand. It

may be too early to speculate about the effects of the presence of an

understory on soil C. Further research is needed to investigate soil C and

nutrient changes due to the presence or absence of an understory as an

ecosystem component.

At age 15 yr, total K, Ca and Mg (kg ha^{-1}) at the 0-15 cm soil depth

were 53%, 94%, and 85% higher on DFO plots than on DFC plots,

respectively. Exchangeable K and Mg were <3% of the total amounts of

these nutrients at 15 cm soil depth. However, understory removal did not

have significant effects on the exchangeable forms of these nutrients. On

the other hand, even though DFO plots had 94% more total soil Ca than

DFC plots, only 3% of the total Ca was in the exchangeable form on DFO

plots. The amount of this exchangeable Ca on DFO plots was 49% lower

than on DFC plots.

H) There may be benefits in encouraging a mixture of tree and shrub species on these sites; 1) to create a more favorable substrate for decomposition and mineralization. For example, western red cedar with high Ca levels and ability to moderate soil pH, can be considered as part of the ecosystem (Kiilsgaard et al. 1987). Slash disposal by burning was shown to increase Douglas-fir foliar Ca and K concentrations from 5 to 15 yr after burning relative to unburned sites (Vihnaneck and Ballard 1988). Leaving logging or thinning residues to decompose would promote release of base cations, with consumption of H^+ and an increase in soil alkalinity (Nykvist and Rosen 1985). 2) to create suitable wildlife habitat. Having highly palatable leaves and fruits, salmonberry provides an important source of food and cover for bears, elk, deer, raccoons, beavers, mountain beavers, rabbits, chipmunks, deer mice, and various birds (Jensen et al. 1995).

Literature Cited

Bailey, J.D., Mayrsohn, C., Doescher, P.S., Pierre, E.S., and Tappeiner, J.C., II. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. For. Ecol. and Manage. **112**: 289-302.

Barnes, B. V., Zak, D. R., Denton, S. R., and Spurr, S.H. 1998. Forest ecology. 4th ed. John Wiley & Sons, Inc. New York.

Berendse, F., and Elberse, W. T. 1990. Competition and nutrient availability in heathland and grassland ecosystems. *In* Perspectives on plant competition. *Edited by* J.B. Grace and D.Tilman. Academic Press, Inc. San Diego. pp. 93-116.

Binkley, D., and Giardina, C. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry, **42**: 89-106.

Binkley, D., and Matson, P. A. 1983. Ion-exchange resin bag method for assessing forest soil nitrogen availability. Soil Sci. Soc. Amer. J. **47**: 1050-1052.

Blake, J. R., and Hartge, K. H. 1986. Bulk density. *In* Methods of soil analysis. Part 1. *Edited by* A. Klute. SSSA book series. 5. ASA and SSSA, Madison, WI. pp. 363-375.

Bormann, B.T., Cromack, K.,Jr., and Russell, W.O., III. 1994. The influence of red alder on soils and long-term ecosystem productivity. *In* The biology and management of red alder. *Edited by* D.E. Hibbs, D.S. DeBell and R.F. Tarrant. Oregon State University Press, Corvallis.

Bormann, F.H., and Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Brady, N.C., and Weil, R.R. 1996. The nature and property of soils. 11th ed. Prentice-Hall, Upper Saddle River, New Jersey.

Busse, M.D., Cochran, P.H., and Barrett, J.W. 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. Soil Sci. Soc. Amer. J. **60**: 614-1621.

Chapin, F.S., III., Zaveleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sal, O.E., Hobbie, S.E., Mack, M. C., and Diaz, S. 2000. Consequences of changing biodiversity. Nature, **405**: 234-242.

Christensen, B.T. 1992. Physical fractionation of soil and organic matter in primary particle size and density separates. Springer-Verlag, New York. Adv. Soil Sci. **20**: 1-90.

Cole, C. E., and Newton, M. 1986. Nutrient, moisture, and light relations in 5 year-old Douglas-fir plantations under variable competitions. Can. J. For. Res. **16**: 727-732.

Cole, D.W., and Rapp, M. 1981. Elemental cycling in forest ecosystems. *In* Dynamic properties of forest ecosystems. *Edited by* D.E. Reichle. Cambridge University Press, New York, pp. 341-409.

Cromack, K., Jr., Miller, R. E., Helgerson, O. T., Smith, R.B., and Anderson, H.W. 1999. Soil carbon and nutrients in a coastal Oregon Douglas-fir plantation with red alder. Soil Sci. Soc. Amer. J. **63**: 232-239.

Drinkwater, L. E., Wagoner, P., and Sarrantonio, M. 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. Nature, **396**: 262-265.

Ehleringer, J.R., Field, C.B., Lin, Z., and Kuo, C. 1986. Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. Oecologia, **70**: 520-526.

Ehleringer, J.R., Field, C.B., Lin, Z., and Kuo, C. 1987. Leaf carbon isotope ratios of plants from a subtropical monsoon forest. Oecologia, **72**: 109-114.

Ericsson,T. 1994. Nutrient dynamics and requirements of forest crops. New Zealand J. For. Sci. **24:** 133-168.

Fisher, R.F., and Binkley, D. 2000. Ecology and management of forest soils. 3rd ed. John Wiley and Sons, New York.

Franklin, J. F. 1993. The fundamentals of ecosystem management with applications in the Pacific Northwest. *In* Defining sustainable forestry. *Edited by* G. Aplet et al. The Wilderness Society. Island Press. Washington, D.C., pp. 127-144.

Harlow, W. M., Harror, E. S., and White, F. M. 1979. Textbook of dendrology: Covering the important forests of the United States and Canada. 6th ed. McGraw-Hill Book Co., New York.

Harrington, T.B., and Tappeiner, J.C.,II. 1997. Growth responses of young Douglas-fir and tanoak 11 years after various levels of hardwood removal and understory suppression in southwestern Oregon, USA. For. Ecol. Manage. **96**: 1-11.

Haynes, R. W., Adams, D. M., and Mills, J. R. 1995. The 1993 RPA timber assessment update. USDA For. Serv. Gen. Tech. Rep. RM-GTR-259.

Helgerson, O. T., Cromack, K., Jr., Stafford, S., Miller, R. E., and Slagle, R. 1988. Equations for estimating aboveground components of young Douglas-fir and red alder in a coastal Oregon plantation. Can. J. For. Res. **18**: 1082-1085.

Hillel, D. 1998. Environmental soil physics. Academic Press, New York.

Hogberg, P. 1997. ^{15}N natural abundance in soil-plant systems. New Phytol. **137**: 179-203.

Hosner, L.R. 1996. Dissolation for total elemental analysis. *In* Methods of soil analysis- Chemical methods. *Edited by* D.L. Sparks. Soil Science Society of America, Madison, Wisconsin. Pp. 49-64.

Hughes, T.F., Tappeiner, J.C., II.,and Newton, M. 1990. Relationship of Pacific madrone sprouts to productivity of Douglas-fir seedlings and understory vegetation. West. J. Appl. For. **5**: 20-24.

Hunt, R. 1982. The functional approach to plant growth analysis. University Park Press. Baltimore.

Ingestad, T. 1979. Nitrogen stress in birch seedlings. II. N, K, P, Ca and Mg nutrition. Physiol. Plant., **45**: 149-157.

Jensen, E.C., and Anderson, D.J. 1995. The reproductive ecology of broadleaved trees and shrubs: An overview. Forest Research Laboratory, Oregon State University, Corvallis. Res. Publ. 9a. 10p.

Jensen, E.C., and Anderson, D.J., Zasada, J.C., and Tappeiner, J.C.,II 1995. The reproductive ecology of broadleaved trees and shrubs: Salmonberry (*Rubus spectabilis* Pursh). Forest Research Laboratory, Oregon State University, Corvallis. Res. Publ. 9e. 7p.

Jobidon, R. 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition, and stand structural development - a 5-year study. For. Ecol. Manage. **130**: 77-97

Johnson, D.W. 1992. Nitrogen retention in forest soils. J. Environ. Qual. **21**: 1-12.

Johnson, D.W., Cheng, W., and Burke, I.C. 2000. Biotic and abiotic nitrogen retention in a variety of forest soils. Soil Sci. Soc. Amer. J. **64**: 1503-1514.

Jones, J.B, Jr., and Case, V.W. 1990. Sampling, handling, and analyzing plant tissue samples. *In* Soil testing and plant analysis. *Edited by* R.L.Weiterman. Third edition. Soil Science Society of America, Madison, Wisconsin. Pp.389-427.

Keeney, D. R., and Bremner, J. M. 1966. Comparison of laboratory methods of obtaining an index of soil nitrogen availability. Agron. J. **58**: 498-503.

Kiilsgaard, C.W., Greene, S.E., and Stafford, S.G. 1987. Nutrient concentrations in litterfall from some western conifers with special reference to calcium. Plant and Soil, **102**: 223-227.

Killham, K. 1994. Soil ecology. Cambridge University Press.

Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. Soil Sci. Soc. Amer. J. **60**: 1643-1654.

Kimmins, J.P. 1997. Forest ecology: A foundation for sustainable management. 2nd ed. Prentice-Hall, Upper Saddle River, New Jersey.

Knowe, S.A., Harrington, T.B., and Shula, R.G. 1992. Incorporating the effects of interspecific competition and vegetation management treatments in diameter distribution for Douglas-fir saplings. Can. J. For. Res. **22**: 1255-1262.

Krankina, O.N., and Harmon, M.E. 1994. The impact of intensive forest management on carbon stores in forest ecosystems. World Resource Review, **6**: 161-177.

Kuo, S. 1996. Phosphorus. *In* Methods of soil analysis. Part 3. *Edited by* D. L. Sparks et al. SSSA book series. 5. ASA and SSSA. Madison, WI. pp. 869-919.

Lajtha, K. and Marshall, J.D. 1994. Source of variation in stable isotopic composition of plants. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific Publications. Boston.

Mao, D.M., Min, Y.W., Yu, L. L., Martens, R., and Insam, H. 1992. Effects of afforestation on microbial biomass and activity in soils of tropical China. Soil Biol. Biochem. **24**: 865-877.

Marks, P.L., and Bormann, F.H. 1972. Revegetation following forest cutting: mechanisms for the return to steady state nutrient cycling. Science, **176**: 914-915.

McCann, K.S. 2000. The diversity-stability debate. Nature, **405**: 228-233.

McComb, W.C., Spies, T.A., and Emmingham, W.H. 1993. Douglas-fir forest. Managing for timber and mature-forest habitat. J. For. **91**: 3-42.

McNabb, D.H., Cromack, K. Jr., and Fredriksen, R.L. 1986. Variability of nitrogen and carbon in surface soils of six forest types in the Oregon Cascades. Soil Sci. Soc. Am. J. **50**: 1037-1041.

Nadelhoffer, K.J., and Fry, B. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Sci. Soc. Am. J. **52**: 1633-1640.

Nadelhoffer, K.J., and Fry, B. 1994. Nitrogen isotope studies in forest ecosystems. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific Publications. Boston. pp. 22-44.

Nambiar, E. K. S., and Sands, R. 1993. Competition for water and nutrients in forests. Can. J. For. Res. **23**: 1955-1968.

Nasholm, T., Ekblad, A., Nordin, A., Giesler, R., Hogberg, M., and Hogberg, P. 1998. Boreal forest plants take up organic nitrogen. Nature, **392**: 914-916.

Nelson, D.W., and Sommers, L. E. 1980. Total nitrogen analysis for soil and plant tissues. J. Assoc. Off. Anal. Chem. **63**: 770-778.

Nelson, D.W., and Sommers, L. E. 1996. Total carbon, organic carbon and organic matter. *In* Methods of soil analysis. *Edited by* D. L. Sparks et al. Part 3. SSSA book series. 5. ASA and SSSA, Madison, WI. pp. 961-1010.

Newton, M., and Preest, D. S. 1988. Growth and water relations of Douglas-fir seedlings under different weed control regimes. Weed Sci. **36**: 653-662.

Newton, M., Cole, E.C., and White, D.E. 1993. Tall planting stock for enhanced growth and domination of brush in the Douglas-fir region. New Forests, **7**: 107-121.

Nykvist, N., and Rosen, K. 1985. Effect of clear-felling and slash removal on the acidity of northern coniferous soils. For. Ecol. Manage. **11**: 157-169.

Paul, E.A., and Clark, F.E. 1996. Soil microbiology and biochemistry. Academic Press, 2nd ed., New York.

Perry, D. A. 1988. An overview of sustainable forestry. J. Pesticide Reform, **8**: 8-12.

Perry, D. A. 1994. Forest ecosystems. Johns Hopkins University Press. Baltimore, Maryland.

Philip, M.S. 1994. Measuring trees and forests. CAB International. 2nd ed. University Press. Cambridge.

Radosevich, S. 1998a. My view. Weed Sci. **46**: 149.

Radosevich, S. 1998b. Weed ecology and ethics. Weed Sci. **46**: 642-646.

Radosevich, S., Halt, J., and Ghersa, C. 1997. Weed ecology. Implications for management. John Wiley & Sons, Inc. 2nd ed., New York.

Richards, B.N. 1987. The microbiology of terrestrial ecosystems. Longman Scientific and Technical, Essex, England.

Rose, R., Ketchum, J.S., and Hanson, D.E. 1999. Three-year survival and growth of Douglas-fir seedlings under various vegetation-free regimes. For. Sci. **45**: 117-126.

Roth, B.E., and Newton, M. 1996. Survival and growth of Douglas-fir relating to weeding, fertilization, and seed source. West. J. Appl. For. **11**: 62-69.

Russell, E.W. 1973. Soil conditions and plant growth. 10th ed., Longman, London.

SAS systems for windows™. 1996. Release 6.12. SAS Institute Inc. Cary, North Carolina.

Schlesinger, W. H. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature, **348**: 232-234.

Schlesinger, W. H. 1997. Biogeochemistry: An analysis of global change. 2nd ed., Academic Press. San Diego.

Sea, D. S., and Whitlock, C. 1995. Postglacial vegetation and climate of the Cascade Range, Central Oregon. Quaternary Research, **43**: 370-81.

Sollins, P., Spycher, G., and Glassman, C.A. 1984. Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. Soil Biol. Biochem. **16**: 31-37.

Soltanpour, P.N., Johnson, G.W., Wolkman, S. M., Jones, J.B., Jr., and Miller, R.Q. 1996. Inductively coupled plasma emission spectrometry and inductively coupled plasma-mass spectrometry. *In* Methods of soil analysis. *Edited by* D.L. Sparks et al. SSSA book series. 5. ASA and SSSA. Madison, WI. Pp. 91-139.

Spies, T.A., Ripple, W.J., and Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. **4**: 555 -568.

Stenberg, P., DeLucia, E.H., Schoettle, A.W., and Smolander, H. 1995. Photosynthetic light capture and processing from cell to canopy. *In* Resource physiology of conifers: Acquisition, allocation and utilization. *Edited by* W. K. Smith and T. M. Hickley. Academic Press. San Diego. pp.3-38.

Stevenson, F.J. 1986. Cycles of soil, carbon, nitrogen, phosphorus, sulfur, and micronutrients. John Wiley and Sons, Inc. New York.

Stiling, P. 1999. Ecology. Theories and applications. 3rd ed. Prentice-Hall, New Jersey.

Strickland, T.C., and Sollins, P. 1987. Improved method for separating light- and heavy-fraction organic material from soil. Soil Sci. Soc. Am. J. **51**: 1390-1393.

Tesch, S.D., and Hobbs, S.D. 1989. Impact of shrub sprout competition on Douglas-fir seedling development. West. J. Appl. For. **4**: 89-92.

Tesch, S.D., Korpela, E.J., and Hobbs, S.D. 1993. Effects of sclerophyllous shrub competition and root and shoot development and biomass partitioning of Douglas-fir seedlings. Can. J. For. Res. **23**: 1415-1426.

Tiessen, H., Cueva, E., and Chacon, P. 1994. The role of soil organic matter in soil fertility. Nature, **371**: 783-785.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. Amer. Nat. **129**: 766-774.

Tilman, D., Lehman, C. L., and Thomson, K. T. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Nat. Acad. Sci. USA, **94**: 1857-1861.

Vihnaneck, R., and Ballard, T. 1988. Slashburning effects on stocking, growth, and nutrition of young Douglas-fir plantations in salal-dominated ecosystems of eastern Vancouver Island. Can. J. For. Res. **18**: 718-722.

Vitousek, P.M., and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience, **25**: 376-381

Wagner, R.G. 1989. Interspecific competition in young Douglas-fir plantations of the Oregon Coast Range, Ph.D. Dissertation, Oregon State University, Corvallis.

Wagner, R.G., and Radosevich, S. R. 1989. Neighborhood predictors of interspecific competition in young Douglas-fir plantations. Can. J. For. Res. **21**: 821-828.

Wagner, R.G., and Radosevich, S. R. 1998. Neighborhood approach for quantifying interspecific competition in a coastal Oregon forest. Ecol. Appl. **8**: 779-794.

Walstad, J.D., and Kuch, P.J. 1987. Introduction to forest vegetation management. *In* Forest vegetation management for conifer production. *Edited by* J.D. Walstad and P.J. Kuch. John Wiley and Sons, New York. pp. 3-14.

Walstad, J.D., Newton, M., and Boyd, R.J. 1987. Forest vegetation problems in the Northwest. *In* Forest vegetation management for conifer production. *Edited by* J.D. Walstad and P.J. Kuch. John Wiley and Sons, New York. pp. 15-53.

Waring, R. H. 1986. The ecological foundation for forestry in the Northwest- limits and opportunities. *In* Forests of the Northwest: A time for reflection. 1986 Starker Lectures. Oregon State University, Corvallis. pp. 1-8.

Waring, R.H. 2000. A process model analysis of environmental limitations on the growth of Sitka spruce plantations in Great Britain. Forestry, **73**: 65-79.

Waring, R. H., and Franklin, J. F. 1979. Evergreen coniferous forests of the Pacific Northwest. Science, **204**: 1380-1386.

Waring, R. H., and Running, S. W. 1998. Forest ecosystems: Analysis at multiple scales. 2nd ed. Academic Press. San Diego .

Waring, R. H., Schroeder, P. E., and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. **121**: 556-560.

Waring, R.H., Cromack, K. Jr., Matson, P.A., Boone, R.D., and Stafford, S.H. 1987. Responses to pathogen-induced disturbance: decomposition, nutrient availability, and tree vigor. Forestry, **60**: 219–227.

White, D.E. and Newton, M. 1990. Herbaceous weed control in young conifer plantations with formulations of nitrogen and simazine. Can. J. For. Res. **20**: 1685-1689.

Wild, A. 1988. Russell's soil conditions and plant growth. 11th ed. Longman Scientific and Technical, Essex, England.

Zimmerman, J.K., and Ehleringer, J.R. 1990. Carbon isotope ratios are correlated with irradiance levels in the Panamanian orchid *Catasetum viridiflavum*. Oecologia, 83: 247-249.

CHAPTER 3

Management Implications

The results described above have several implications for forest ecosystem management in the Oregon Coast Range:

A) The presence of shrubs and herbs did not appear to affect Douglas-fir seedling survival in the first five years following plantation establishment. At the end of the fifth growing season (1989), about 93% of the seedlings had survived in all treatments. However, shrub and herb removal significantly increased Douglas-fir tree growth. Douglas-fir seedlings were almost twice as tall, and had diameters 3.5 times larger in pure stands (DFO) than on control plots (DFC). With total understory removal, tree biomass was 12 times that of the control after 5 years. However, with the presence of shrubs and herbs (DFC), the total aboveground biomass was not significantly different among treatments.

Understory vegetation removal significantly increased Douglas-fir tree survival through age 15 yr. The two different vegetation zones, which may be interacting with aspect, appear to have an effect on Douglas-fir survival. The southern spruce zone site exhibited 30% higher survival than the southern hemlock site. On the average, 59% of the trees survived on DFC plots, compared to 89% on the DFO plots. Douglas-fir tree biomass accumulation at the end of 15 yr also was affected by understory removal. Trees in the pure Douglas-fir stands (DFO) had 336% more average standing biomass ha^{-1} than trees on control plots at the end of the fifteenth

season. Tree diameter (dbh) on DFO plots averaged 17.5 cm, which was 70% greater than that of Douglas-firs on DFC plots. On DFO plots, Douglas-fir biomass ha^{-1} was more than 4 times higher than on DFC plots. Total aboveground plant biomass was similar between DFH and DFO plots, and 42% higher than on DFC plots, where trees accounted for only 54% of the aboveground biomass.

Differences in tree growth among plots may be attributed to the significant variation in tree leaf area (LA). Douglas-firs on DFO plots had about 80% higher LA per tree than those on DFC plots. Thus, the presence of understory vegetation significantly reduced Douglas-fir standing biomass on a per tree basis. An average tree on DFO plots had 3 times greater biomass than those on DFC plots.

Removing understory biomass from some of the plots during the five years following tree planting secured successful tree establishment in those treatments, with a high overall survival rate and biomass accumulation for Douglas-firs on the sites at the end of 15 yr. Variables, such as dbh, height, and tree biomass, measured at early plantation ages (5 yr for this study), may not be good indicators of a stand's future properties. At plantation age 5 yr, the data suggested that the most intensive level of vegetation control, the pure stand, would permit a similar harvest level on less than a tenth of the area required without any vegetation control. Even with shrub control alone, a nearly 4-fold gain in wood yield ha^{-1} would be obtained compared to no vegetation control. However, at stand age 15 yr, after 50% shrub

removal, any increase in the degree of understory removal did not contribute significantly to additional tree survival and growth. Furthermore, the relative tree growth rate was 3 times greater on DFH plots than on DFO plots during the last 10 yr. Assuming adequate light is available from thinning, trees maintaining their current growth rate on DFH plots may surpass Douglas-firs on DFO plots

B) Several possible resource limitations could be responsible for the observed results: 1) More light was available to seedlings where shrub cover was reduced, as indicated by significantly lower specific leaf areas of Douglas-fir needles collected from DFO plots as compared to DFC plots. 2) Although soil moisture was not significantly different among treatments, $\delta^{13}C$ values of Douglas-fir needles indicated no moisture stress at any of the sites by age 5 yr. However, at age 15 yr, plants on DFC plots had more competition for water, in at least the upper part of the soil profile, than those on DFH plots. Since Douglas-fir needle C isotopic composition did not vary among sites, these trees may have accessed water from the deeper soil profile. Further investigation is needed to determine the water source for different species on the sites. Nutrients also are important limiting factors in determining seedling growth in these soils. The presence of herbs alone may result in competition with seedlings for nutrients, especially for P at early ages.

C) Douglas-fir needle C concentration was significantly lower on DFC plots than on other plots at age 5 yr. On DFC plots, needle C concentration was significantly reduced from age 5 yr to 15 yr. Needle N concentration was significantly higher on DFC plots at age 5 yr. Trees on control plots had 13% higher needle N concentrations than needles from trees on DFO plots. From age 5 yr to 15 yr, needle N concentration significantly decreased. Needle Ca concentration was similar among treatments at 5 yr and 15 yr. However, from age 5 yr to 15 yr, needle Ca concentration decreased significantly at all sites. For 5 yr old seedlings, needle Al concentration was 60% higher on DFH plots than on DFO plots. But at age 15 yr, needle Al concentration was 43% higher on DFO plots than on DFH plots.

Needle nutrient concentrations were compared with data that were assumed to be the normal range of macronutrients in Douglas-fir foliage provided by Ericsson (1994). Our data indicate that K was 17% higher, P was 55% lower, Ca was about 39% lower, and Mg was 22% lower in the needles than expected for optimal nutritional balance at all sites by age 15 yr. If available N is too high, it can be leached, volatilized, or taken up and stored as amino acids that are likely to make trees more susceptible to attack from defoliating insects and pathogens (Waring and Running 1998). Soil C:N ratio can be increased by leaving boles and branches after thinning the stands, thereby reducing the availability of mineral N to plant uptake. Using fertilizers, especially cations including micronutrients, on

these sites may help to establish nutritional balance of the trees. For example, liming can help to increase Ca availability. However, once the stand approaches its maximum leaf area (index), many of the nutrients required for annual growth are available in the canopy, and recycling makes only a modest contribution to annual needs (Waring 2000). Having data only from 15 yr old plantations may not be enough to give solid management recommendations. Therefore, further research is needed to monitor nutritional changes in tree and soil pools as plantations age.

D) The total aboveground C pool was similar among treatments at age 5 yr. Even though DFO plots had almost 12 times the C sequestered in trees as did DFC plots, the presence of shrubs and herbs contributed significantly to the total C pool in aboveground biomass and eliminated differences in total aboveground C. Shrub species on DFC plots contained 82% of C on these plots at age 5 yr. By age 15 yr, the aboveground C pool was 56% lower on DFC plots than on DFO plots. Understory removal also significantly affected the total N pool in aboveground biomass. At age 5 yr, trees in the DFO stands had 10 times more N than trees on DFC plots. However, the presence of understory vegetation increased the N pool in aboveground biomass to 2.6 times over that of DFO plots. In addition, at age 5 yr on DFC plots, 85% of total aboveground N was contained in shrub species. The total aboveground N pool substantially increased from age 5 yr to 15 yr on all plots. Even though tree N content was more than 3 times greater on DFO plots than on DFC plots, the presence of an

understory offset the differences in aboveground N pools among treatments by age 15 yr. At age 5 yr, aboveground P content was similar among plots. However, herbs on DFH plots contributed 74% of abovegound P. By age 15 yr, aboveground P content was 88% higher on DFO plots than on DFC plots. At this same age, the aboveground Ca pool size was 41% higher on DFO plots than on DFC plots. As one consequence, however, the soil exchangeable Ca was 49% lower on DFO plots at age 15 yr than on DFC plots.

E) The presence of understory vegetation had significant effects on soil physical properties. The forest floor in DFO stands had 2.5 times greater biomass than on DFC plots. Soil bulk density at plantation age 5 yr was 29% higher on DFO plots than on DFC plots. By plantation age 15 yr, bulk density on DFO plots was 22% higher than on DFC plots. Although relatively large changes in bulk densities and surface moisture conditions were recorded in association with treatments, since bulk density values are so low (ranging between $0.47 - 0.63$ g cm^{-3}) they are not likely to be critical with regard to altering soil drainage properties or exerting water stress on these sites.

F) Total understory vegetation removal reduced the soil C concentration in the fine fraction by about 27% through age 5 yr. Concentrations of some soil cations were also influenced by the presence of understory vegetation. The soil fine fraction on DFC plots had 15%, 25%

and 32% lower Fe, Al and Ca concentrations, respectively, than the same fraction on DFO plots at age 5 yr.

G) Total soil C content (kg ha^{-1}) in the ecosystem was affected by understory vegetation removal at plantation age 5 yr. Soil C pool data suggested a possible change developing in the amount of soil C associated with the presence of understory vegetation in the ecosystem at this same age. Control plots had 33% higher soil C than DFO plots at age 5 yr. However, by age 15 yr, there was no difference in soil C among treatments. Isotopic composition of light and heavy soil fractions suggests that organic matter decomposition may differ among sites. Continual replacement of needle driven organic matter, with relatively higher lignin concentrations, may lower the decomposition rate in pure stands. Busse et al. (1996) reported that the presence of understory vegetation in a ponderosa pine ecosystem (*Pinus ponderosa* Dougl.) increased soil C content 50% over the adjacent soil in a central Oregon 35 year old pure ponderosa pine stand. It may be too early to speculate about the effects of the presence of an understory on soil C. Further research is needed to investigate soil C and nutrient changes due to the presence or absence of an understory ecosystem component.

At age 15 yr, total K, Ca and Mg (kg ha^{-1}) at the 0-15 cm soil depth were 53%, 94%, and 85% higher on DFO plots than on DFC plots, respectively. Exchangeable K and Mg were <3% of the total amounts of these nutrients at 15 cm soil depth. However, understory removal did not

have significant effects on the exchangeable forms of these nutrients. On the other hand, even though DFO plots had 94% more total soil Ca than DFC plots, only 3% of the total Ca was in the exchangeable form on DFO plots. The amount of exchangeable Ca on DFO plots was 49% lower than on DFC plots.

H) There may be benefits in encouraging a mixture of tree and shrub species on these sites to: 1) create a more favorable substrate for decomposition and mineralization. For example, western red cedar with high Ca levels and the ability to moderate soil pH, can be considered as part of the ecosystem (Kiilsgaard et al. 1987). Slash disposal by burning was shown to increase Douglas-fir foliar Ca and K concentrations from 5 to 15 yr after burning relative to unburned sites (Vihnaneck and Ballard 1988). Leaving logging or thinning residues to decompose would promote release of base cations, with consumption of H^+ and an increase in soil alkalinity (Nykvist and Rosen 1985). 2) to create suitable wildlife habitat. Having highly palatable leaves and fruits, salmonberry provides an important source of food and cover for bears, elk, deer, raccoons, beavers, mountain beavers, rabbits, chipmunks, deer mice, and various birds (Jensen et al. 1995).

Bibliography

Bailey, J.D., Mayrsohn, C., Doescher, P.S., Pierre, E.S., and Tappeiner, J.C., II. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. For. Ecol. and Manage. **112**: 289-302.

Barnes, B. V., Zak, D. R., Denton, S. R., and Spurr, S.H. 1998. Forest ecology. 4th ed. John Wiley & Sons, Inc. New York.

Berendse, F., and Elberse, W. T. 1990. Competition and nutrient availability in heathland and grassland ecosystems. *In* Perspectives on plant competition. *Edited by* J.B. Grace and D.Tilman. Academic Press, Inc. San Diego. pp. 93-116.

Binkley, D., and Giardina, C. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry, **42**: 89-106.

Binkley, D., and Matson, P. A. 1983. Ion-exchange resin bag method for assessing forest soil nitrogen availability. Soil Sci. Soc. Amer. J. **47**: 1050-1052.

Blake, J. R., and Hartge, K. H. 1986. Bulk density. *In* Methods of soil analysis. Part 1. *Edited by* A. Klute. SSSA book series. 5. ASA and SSSA, Madison, WI. pp. 363-375.

Bormann, B.T., Cromack, K.,Jr., and Russell, W.O., III. 1994. The influence of red alder on soils and long-term ecosystem productivity. *In* The biology and management of red alder. *Edited by* D.E. Hibbs, D.S. DeBell and R.F. Tarrant. Oregon State University Press, Corvallis.

Bormann, F.H., and Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Brady, N.C., and Weil, R.R. 1996. The nature and property of soils. 11th ed. Prentice-Hall, Upper Saddle River, New Jersey.

Busse, M.D., Cochran, P.H., and Barrett, J.W. 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. Soil Sci. Soc. Amer. J. **60**: 614-1621.

Chapin, F.S., III., Zaveleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sal, O.E., Hobbie, S.E., Mack, M. C., and Diaz, S. 2000. Consequences of changing biodiversity. Nature, **405**: 234-242.

Christensen, B.T. 1992. Physical fractionation of soil and organic matter in primary particle size and density separates. Springer-Verlag, New York. Adv. Soil Sci. **20**: 1-90.

Cole, C. E., and Newton, M. 1986. Nutrient, moisture, and light relations in 5 year-old Douglas-fir plantations under variable competitions. Can. J. For. Res. **16**: 727-732.

Cole, D.W., and Rapp, M. 1981. Elemental cycling in forest ecosystems. *In* Dynamic properties of forest ecosystems. *Edited by* D.E. Reichle. Cambridge University Press, New York, pp. 341-409.

Cromack, K., Jr., Miller, R. E., Helgerson, O. T., Smith, R.B., and Anderson, H.W. 1999. Soil carbon and nutrients in a coastal Oregon Douglas-fir plantation with red alder. Soil Sci. Soc. Amer. J. **63**: 232-239.

Drinkwater, L. E., Wagoner, P., and Sarrantonio, M. 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. Nature, **396**: 262-265.

Ehleringer, J.R., Field, C.B., Lin, Z., and Kuo, C. 1986. Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. Oecologia, **70**: 520-526.

Ehleringer, J.R., Field, C.B., Lin, Z., and Kuo, C. 1987. Leaf carbon isotope ratios of plants from a subtropical monsoon forest. Oecologia, **72**: 109-114.

Ericsson,T. 1994. Nutrient dynamics and requirements of forest crops. New Zealand J. For. Sci. **24:** 133-168.

Fisher, R.F., and Binkley, D. 2000. Ecology and management of forest soils. 3rd ed. John Wiley and Sons, New York.

Franklin, J. F. 1993. The fundamentals of ecosystem management with applications in the Pacific Northwest. *In* Defining sustainable forestry. *Edited by* G. Aplet et al. The Wilderness Society. Island Press. Washington, D.C., pp. 127-144.

Harlow, W. M., Harror, E. S., and White, F. M. 1979. Textbook of dendrology: Covering the important forests of the United States and Canada. 6th ed. McGraw-Hill Book Co., New York.

Harrington, T.B., and Tappeiner, J.C.,II. 1997. Growth responses of young Douglas-fir and tanoak 11 years after various levels of hardwood removal and understory suppression in southwestern Oregon, USA. For. Ecol. Manage. **96**: 1-11.

Haynes, R. W., Adams, D. M., and Mills, J. R. 1995. The 1993 RPA timber assessment update. USDA For. Serv. Gen. Tech. Rep. RM-GTR-259.

Helgerson, O. T., Cromack, K., Jr., Stafford, S., Miller, R. E., and Slagle, R. 1988. Equations for estimating aboveground components of young Douglas-fir and red alder in a coastal Oregon plantation. Can. J. For. Res. **18**: 1082-1085.

Hillel, D. 1998. Environmental soil physics. Academic Press, New York.

Hogberg, P. 1997. ^{15}N natural abundance in soil-plant systems. New Phytol. **137**: 179-203.

Hosner, L.R. 1996. Dissolation for total elemental analysis. *In* Methods of soil analysis- Chemical methods. *Edited by* D.L. Sparks. Soil Science Society of America, Madison, Wisconsin. Pp. 49-64.

Hughes, T.F., Tappeiner, J.C., II.,and Newton, M. 1990. Relationship of Pacific madrone sprouts to productivity of Douglas-fir seedlings and understory vegetation. West. J. Appl. For. **5**: 20-24.

Hunt, R. 1982. The functional approach to plant growth analysis. University Park Press. Baltimore.

Ingestad, T. 1979. Nitrogen stress in birch seedlings. II. N, K, P, Ca and Mg nutrition. Physiol. Plant., **45**: 149-157.

Jensen, E.C., and Anderson, D.J. 1995. The reproductive ecology of broadleaved trees and shrubs: An overview. Forest Research Laboratory, Oregon State University, Corvallis. Res. Publ. 9a. 10p.

Jensen, E.C., and Anderson, D.J., Zasada, J.C., and Tappeiner, J.C.,II 1995. The reproductive ecology of broadleaved trees and shrubs: Salmonberry (*Rubus spectabilis* Pursh). Forest Research Laboratory, Oregon State University, Corvallis. Res. Publ. 9e. 7p.

Jobidon, R. 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition, and stand structural development - a 5-year study. For. Ecol. Manage. **130**: 77-97

Johnson, D.W. 1992. Nitrogen retention in forest soils. J. Environ. Qual. **21**: 1-12.

Johnson, D.W., Cheng, W., and Burke, I.C. 2000. Biotic and abiotic nitrogen retention in a variety of forest soils. Soil Sci. Soc. Amer. J. **64**: 1503-1514.

Jones, J.B, Jr., and Case, V.W. 1990. Sampling, handling, and analyzing plant tissue samples. *In* Soil testing and plant analysis. *Edited by* R.L.Weiterman. Third edition. Soil Science Society of America, Madison, Wisconsin. Pp.389-427.

Keeney, D. R., and Bremner, J. M. 1966. Comparison of laboratory methods of obtaining an index of soil nitrogen availability. Agron. J. **58**: 498-503.

Killham, K. 1994. Soil ecology. Cambridge University Press.

Kiilsgaard, C.W., Greene, S.E., and Stafford, S.G. 1987. Nutrient concentrations in litterfall from some western conifers with special reference to calcium. Plant and Soil, **102**: 223-227.

Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. Soil Sci. Soc. Amer. J. **60**: 1643-1654.

Kimmins, J.P. 1997. Forest ecology: A foundation for sustainable management. 2nd ed. Prentice-Hall, Upper Saddle River, New Jersey.

Knowe, S.A., Harrington, T.B., and Shula, R.G. 1992. Incorporating the effects of interspecific competition and vegetation management treatments in diameter distribution for Douglas-fir saplings. Can. J. For. Res. **22**: 1255-1262.

Krankina, O.N., and Harmon, M.E. 1994. The impact of intensive forest management on carbon stores in forest ecosystems. World Resource Review, **6**: 161-177.

Kuo, S. 1996. Phosphorus. *In* Methods of soil analysis. Part 3. *Edited by* D. L. Sparks et al. SSSA book series. 5. ASA and SSSA. Madison, WI. pp. 869-919.

Lajtha, K. and Marshall, J.D. 1994. Source of variation in stable isotopic composition of plants. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific Publications. Boston.

Mao, D.M., Min, Y.W., Yu, L. L., Martens, R., and Insam, H. 1992. Effects of afforestation on microbial biomass and activity in soils of tropical China. Soil Biol. Biochem. **24**: 865-877.

Marks, P.L., and Bormann, F.H. 1972. Revegetation following forest cutting: mechanisms for the return to steady state nutrient cycling. Science, **176**: 914-915.

McCann, K.S. 2000. The diversity-stability debate. Nature, **405**: 228-233.

McComb, W.C., Spies, T.A., and Emmingham, W.H. 1993. Douglas-fir forest. Managing for timber and mature-forest habitat. J. For. **91**: 3-42.

McNabb, D.H., Cromack, K. Jr., and Fredriksen, R.L. 1986. Variability of nitrogen and carbon in surface soils of six forest types in the Oregon Cascades. Soil Sci. Soc. Am. J. **50**: 1037-1041.

Nadelhoffer, K.J., and Fry, B. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Sci. Soc. Am. J. **52**: 1633-1640.

Nadelhoffer, K.J., and Fry, B. 1994. Nitrogen isotope studies in forest ecosystems. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific Publications. Boston. pp. 22-44.

Nadelhoffer, K.J., Emmett, B.A., Gundersen, P., Kjonaas, O.J., Koopmans, C.J., Schleppi, P., Tietema, A., and Wright, R.F. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature, **398**: 145-148.

Nambiar, E. K. S., and Sands, R. 1993. Competition for water and nutrients in forests. Can. J. For. Res. **23**: 1955-1968.

Nashholm, T., Ekblad, A., Nordin, A., Giesler, R., Hogberg, M., and Hogberg, P. 1998. Boreal forest plants take up organic nitrogen. Nature, **392**: 914-916.

Nelson, D.W., and Sommers, L. E. 1980. Total nitrogen analysis for soil and plant tissues. J. Assoc. Off. Anal. Chem. **63**: 770-778.

Nelson, D.W., and Sommers, L. E. 1982. Total carbon, organic carbon and organic matter. *In* Methods of soil analysis. *Edited by* A. L. Page et al. Part 2. SSSA book series. 5. ASA and SSSA, Madison, WI. pp. 539-579.

Nelson, D.W., and Sommers, L. E. 1996. Total carbon, organic carbon and organic matter. *In* Methods of soil analysis. *Edited by* D. L. Sparks et al. Part 3. SSSA book series. 5. ASA and SSSA, Madison, WI. pp. 961-1010.

Newton, M., and Preest, D. S. 1988. Growth and water relations of Douglas-fir seedlings under different weed control regimes. Weed Sci. **36**: 653-662.

Newton, M., Cole, E.C., and White, D.E. 1993. Tall planting stock for enhanced growth and domination of brush in the Douglas-fir region. New Forests, **7**: 107-121.

Nykvist, N., and Rosen, K. 1985. Effect of clear-felling and slash removal on the acidity of northern coniferous soils. For. Ecol. Manage. **11**: 157-169.

Olson, S. R., and Sommers, L. E. 1982. Phosphorus. *In* Methods of soil analysis. Part 2. *Edited by* A. L. Page et al. SSSA book series. 5. ASA and SSSA. Madison, WI. pp. 403-430.

Paul, E.A., and Clark, F.E. 1996. Soil microbiology and biochemistry. Academic Press, 2nd ed., New York.

Perry, D. A. 1988. An overview of sustainable forestry. J. Pesticide Reform, **8**: 8-12.

Perry, D. A. 1994. Forest ecosystems. Johns Hopkins University Press. Baltimore, Maryland.

Philip, M.S. 1994. Measuring trees and forests. CAB International. 2nd ed. University Press. Cambridge.

Radosevich, S. 1998a. My view. Weed Sci. **46**: 149.

Radosevich, S. 1998b. Weed ecology and ethics. Weed Sci. **46**: 642-646.

Radosevich, S., Halt, J., and Ghersa, C. 1997. Weed ecology. Implications for management. John Wiley & Sons, Inc. 2nd ed., New York.

Richards, B.N. 1987. The microbiology of terrestrial ecosystems. Longman Scientific and Technical, Essex, England.

Rose, R., Ketchum, J.S., and Hanson, D.E. 1999. Three-year survival and growth of Douglas-fir seedlings under various vegetation-free regimes. For. Sci. **45**: 117-126.

Roth, B.E., and Newton, M. 1996. Survival and growth of Douglas-fir relating to weeding, fertilization, and seed source. West. J. Appl. For. **11**: 62-69.

Russell, E.W. 1973. Soil conditions and plant growth. 10th ed., Longman, London.

SAS systems for windows™. 1996. Release 6.12. SAS Institute Inc. Cary, North Carolina.

Schlesinger, W. H. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature, **348**: 232-234.

Schlesinger, W. H. 1997. Biogeochemistry: An analysis of global change. 2nd ed., Academic Press. San Diego.

Sea, D. S., and Whitlock, C. 1995. Postglacial vegetation and climate of the Cascade Range, Central Oregon. Quaternary Research, **43**: 370-81.

Sollins, P., Spycher, G., and Glassman, C.A. 1984. Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. Soil Biol. Biochem. **16**: 31-37.

Soltanpour, P.N., Johnson, G.W., Wolkman, S. M., Jones, J.B., Jr., and Miller, R.Q. 1996. Inductively coupled plasma emission spectrometry and inductively coupled plasma-mass spectrometry. *In* Methods of soil analysis. *Edited by* D.L. Sparks et al. SSSA book series. 5. ASA and SSSA. Madison, WI. Pp. 91-139.

Spies, T.A., Ripple, W.J., and Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. **4**: 555 -568.

Stenberg, P., DeLucia, E.H., Schoettle, A.W., and Smolander, H. 1995. Photosynthetic light capture and processing from cell to canopy. *In* Resource physiology of conifers: Acquisition, allocation and utilization. *Edited by* W. K. Smith and T. M. Hickley. Academic Press. San Diego. pp.3-38.

Stevenson, F.J. 1986. Cycles of soil, carbon, nitrogen, phosphorus, sulfur, and micronutrients. John Wiley and Sons, Inc. New York.

Stiling, P. 1999. Ecology. Theories and applications. 3rd ed. Prentice-Hall, New Jersey.

Strickland, T.C., and Sollins, P. 1987. Improved method for separating light- and heavy-fraction organic material from soil. Soil Sci. Soc. Am. J. **51**: 1390-1393.

Tesch, S.D., and Hobbs, S.D. 1989. Impact of shrub sprout competition on Douglas-fir seedling development. West. J. Appl. For. **4**: 89-92.

Tesch, S.D., Korpela, E.J., and Hobbs, S.D. 1993. Effects of sclerophyllous shrub competition and root and shoot development and biomass partitioning of Douglas-fir seedlings. Can. J. For. Res. **23**: 1415-1426.

Tiessen, H., Cueva, E., and Chacon, P. 1994. The role of soil organic matter in soil fertility. Nature, **371**: 783-785.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. Amer. Nat. **129**: 766-774.

Tilman, D., Lehman, C. L., and Thomson, K. T. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Nat. Acad. Sci. USA, **94**: 1857-1861.

Vihnaneck, R., and Ballard, T. 1988. Slashburning effects on stocking, growth, and nutrition of young Douglas-fir plantations in salal-dominated ecosystems of eastern Vancouver Island. Can. J. For. Res. **18**: 718-722.

Vitousek, P.M., and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience, **25**: 376-381

Wagner, R.G. 1989. Interspecific competition in young Douglas-fir plantations of the Oregon Coast Range, Ph.D. Dissertation, Oregon State University, Corvallis.

Wagner, R.G., and Radosevich, S. R. 1989. Neighborhood predictors of interspecific competition in young Douglas-fir plantations. Can. J. For. Res. **21**: 821-828.

Wagner, R.G., and Radosevich, S. R. 1998. Neighborhood approach for quantifying interspecific competition in a coastal Oregon forest. Ecol. Appl. **8**: 779-794.

Walstad, J.D., and Kuch, P.J. 1987. Introduction to forest vegetation management. *In* Forest vegetation management for conifer production. *Edited by* J.D. Walstad and P.J. Kuch. John Wiley and Sons, New York. pp. 3-14.

Walstad, J.D., Newton, M., and Boyd, R.J. 1987. Forest vegetation problems in the Northwest. *In* Forest vegetation management for conifer production. *Edited by* J.D. Walstad and P.J. Kuch. John Wiley and Sons, New York. pp. 15-53.

Waring, R. H. 1986. The ecological foundation for forestry in the Northwest- limits and opportunities. *In* Forests of the Northwest: A time for reflection. 1986 Starker Lectures. Oregon State University, Corvallis. pp. 1-8.

Waring, R.H. 2000. A process model analysis of environmental limitations on the growth of Sitka spruce plantations in Great Britain. Forestry, **73**: 65-79.

Waring, R. H., and Franklin, J. F. 1979. Evergreen coniferous forests of the Pacific Northwest. Science, **204**: 1380-1386.

Waring, R. H., and Running, S. W. 1998. Forest ecosystems: Analysis at multiple scales. 2nd ed. Academic Press. San Diego .

Waring, R. H., Schroeder, P. E., and Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. **121**: 556-560.

Waring, R.H., Cromack, K. Jr., Matson, P.A., Boone, R.D., and Stafford, S.H. 1987. Responses to pathogen-induced disturbance: decomposition, nutrient availability, and tree vigor. Forestry, **60**: 219–227.

White, D.E and Newton, M. 1990. Herbaceous weed control in young conifer plantations with formulations of nitrogen and simazine. Can. J. For. Res. **20**: 1685-1689.

Wild, A. 1988. Russell's soil conditions and plant growth. 11th ed. Longman Scientific and Technical, Essex, England.

Zimmerman, J.K., and Ehleringer, J.R. 1990. Carbon isotope ratios are correlated with irradiance levels in the Panamanian orchid *Catasetum viridiflavum*. Oecologia, 83: 247-249.