AN ABSTRACT OF THE THESIS OF

David R. Woodruff for the degree of Master of Science in Forest Science presented on March 8, 2000. Title: The Effects of Stand Density on the Growth and Microclimate of Young Douglas-fir Stands.

Abstract Approved: ___________________________  Signature redacted for privacy.
Barbara J. Bond

My objectives were to investigate the correlation of height and diameter growth in young Douglas-fir (Pseudotsuga menziesii) plantations with stand density, and to determine the effects of stand density on the canopy boundary layer conductance ($g_{sc}$) and microclimate characteristics of young Douglas-fir plantations. I measured annual height (h) and diameter (d) growth (retrospectively) of trees on three sites in southwestern Washington. Each site consisted of test plantations of eight- and twelve-year-old Douglas-fir in initial planting densities of 300, 1359, and 2960 trees hectare$^{-1}$. Both height and diameter growth increased with initial seedling density through the fifth year after planting. I used $d^2h$ as an index of seedling volume. Mean annual increase in $d^2h$ was greatest in the high-density treatment and lowest in the low-density treatment through the fifth year after planting. By the seventh year after planting, this trend was reversed (presumably due to the effects of competition from neighboring
trees). The greatest observed difference in annual increase in $d^2h$ between high- and low-density treatments occurred in the second year after planting. Mean $d^2h$ of the high-density treatment was 3 times that in the low-density treatment for that year.

Measurements to determine the effects of stand density on the $g_{ac}$ and microclimate characteristics were conducted in stands of 5-year-old Douglas-fir trees in densities of 300 and 1360 trees hectare$^{-1}$. $[CO_2]$, relative humidity, air temperature and wind speed were measured in a vertical profile at three heights in canopies (one, three and five meters) to gain information about how environmental conditions are affected by stand density. To quantify $g_{ac}$ for stands of different densities, evaporation rate of water from canopy foliage was measured. $g_{ac}$ was calculated using a form of the Penman equation for evaporation. Differences in all parameters between density treatments decreased with height in the canopy. $g_{ac}$ in the low-density treatment for individual trees was 1.5 times that in the high-density stand ($p = 0.0038$). Canopy boundary layers may reduce atmospheric mixing, resulting in different concentrations of gases within than above the canopy. The higher morning $[CO_2]$ around plant foliage may function to increase morning photosynthetic rates. Stomata may respond to increased humidity by opening more and/or remaining open longer throughout the day, resulting in increased photosynthesis as well as increased photosynthetic water use efficiency.
The Effects of Stand Density on the Growth and Microclimate of Young Douglas-fir Stands.

By

David R. Woodruff

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Dean of Graduate School

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

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David R. Woodruff, Author
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The successful completion of this project would not have been possible without the generous assistance of a number of people and organizations. I will always be indebted to my advisor, Dr. Barbara Bond, for her constant support, encouragement and patience. I would also like to express my appreciation to the National Center for Air and Stream Improvement (NCASI) for providing the funding for this study. To Dr. Bill Scott, Dr. Gary Ritchie and the Weyerhauser Corporation for giving us access to their research sites where they allowed us to conduct measurements. To Dr. Jim Ehleringer who provided the generous use of a CO₂ profile manifold. To Dr. Nathan Phillips who was the source of frequent advice, key ideas and assistance in field data collection. A special thanks to Gonzalo Leon, Eric Watrud, and Jeremy Coate for their critical assistance in field data collection, as well as good company and lots of laughs. I am especially grateful for the love and support I have received from my family.
# TABLE OF CONTENTS

**INTRODUCTION**

1

**CHAPTER ONE**
The Effects of Stand Density on the Growth of Young Douglas-fir Stands

6

Abstract 7
Introduction 8
Methods 24
Results 30
Discussion 44

**CHAPTER TWO**
The Effects of Stand Density on the Canopy Boundary Layer and Microclimate of Young Douglas-fir Stands

50

Abstract 51
Introduction 52
Methods 57
Results 64
Discussion 79

Conclusion 83

Bibliography 84
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Map indicating locations of three field sites: Doty (site 1), Fall River (site 2), and A6000 (site 3)</td>
<td>26</td>
</tr>
<tr>
<td>1.2</td>
<td>Annual height growth for trees in the low-, mid-, and high-density treatments</td>
<td>33</td>
</tr>
<tr>
<td>1.3</td>
<td>Annual diameter growth for trees in the low-, mid-, and high-density treatments</td>
<td>36</td>
</tr>
<tr>
<td>1.4</td>
<td>Annual increase in d²h for trees in the low-, mid-, and high-density treatments</td>
<td>39</td>
</tr>
<tr>
<td>1.5</td>
<td>δ¹³C of cellulose extracted from 2nd and 3rd years of stem growth from low-, mid-, and high-density treatment seedlings</td>
<td>43</td>
</tr>
<tr>
<td>2.1</td>
<td>Map indicating location of Marcusson Creek field site</td>
<td>57</td>
</tr>
<tr>
<td>2.2</td>
<td>Evaporation of water and first derivative of evaporation from foliage for one evaporation session in a high-density plot</td>
<td>62</td>
</tr>
<tr>
<td>2.3</td>
<td>[CO₂] for high- and low-density stands at heights of one-, three- and wind speed at five-meters for block 2</td>
<td>65</td>
</tr>
<tr>
<td>2.4</td>
<td>[CO₂] for high- and low-density stands at heights of one-, three- and wind speed at five-meters for block 3</td>
<td>66</td>
</tr>
<tr>
<td>2.5</td>
<td>Differences in mean relative humidity between weather station values and measurement plots at one-, three- and five-m heights</td>
<td>69</td>
</tr>
<tr>
<td>2.6</td>
<td>Differences in mean air temperature between weather station values and measurement plots at one-, three- and five-m heights</td>
<td>71</td>
</tr>
<tr>
<td>2.7</td>
<td>Differences in mean wind speed between weather station values and measurement plots at one-, three- and five-m heights</td>
<td>74</td>
</tr>
</tbody>
</table>
LIST OF FIGURES (continued)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.8</td>
<td>Evaporation of water from foliage in high- and low-density Stands</td>
<td>76</td>
</tr>
<tr>
<td>2.9</td>
<td>Mean $g_{ac}$ for blocks one, two and three</td>
<td>78</td>
</tr>
</tbody>
</table>


# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Predicted differences in $\delta^{13}C$ of cellulose resulting from the proposed hypotheses</td>
<td>23</td>
</tr>
<tr>
<td>1.2</td>
<td>ANOVA statistics for comparisons of mean annual height increment in the low-, mid-, and high-density treatments</td>
<td>32</td>
</tr>
<tr>
<td>1.3</td>
<td>ANOVA statistics for comparisons of mean annual diameter increment in the low-, mid-, and high-density treatments</td>
<td>35</td>
</tr>
<tr>
<td>1.4</td>
<td>ANOVA statistics (back-transformed) for comparison of median annual $d^2h$ increment in the low-, mid-, and high-density treatments</td>
<td>38</td>
</tr>
<tr>
<td>1.5</td>
<td>Comparison of mean annual increase in $d^2h$ for 300 largest trees from low-, mid- and high-density treatments</td>
<td>41</td>
</tr>
<tr>
<td>1.6</td>
<td>ANOVA statistics for comparison of treatments for $\delta^{13}C$ isotopic composition for sites one and two</td>
<td>42</td>
</tr>
<tr>
<td>2.1</td>
<td>Differences in mean relative humidity between weather station values and low-, and high-density measurement plots at one-, three- and five-m heights</td>
<td>68</td>
</tr>
<tr>
<td>2.2</td>
<td>Differences in mean air temperature between weather station values and low-, and high-density measurement plots at one-, three- and five-m heights</td>
<td>70</td>
</tr>
<tr>
<td>2.3</td>
<td>Differences in mean wind speed between weather station values and low-, and high-density measurement plots at one-, three- and five-m heights</td>
<td>73</td>
</tr>
<tr>
<td>2.4</td>
<td>ANOVA statistics for comparisons of mean evaporation rates for low-, and high-density treatments</td>
<td>75</td>
</tr>
<tr>
<td>2.5</td>
<td>ANOVA statistics for comparisons of mean boundary layer conductance for low-, and high-density treatments</td>
<td>76</td>
</tr>
</tbody>
</table>
THE EFFECTS OF STAND DENSITY ON THE GROWTH AND
MICROCLIMATE OF YOUNG DOUGLAS-FIR STANDS

INTRODUCTION

Silvicultural prescriptions involving stand density are often made based on the assumption that at higher stocking levels, individual tree productivity is inversely related to stand density (Evert, 1971; Clark et al., 1994; Smith et al., 1997). Many sources indicate that height growth is insensitive to density, and that radial growth increases with increased spacing (e.g.: Hiley, 1959; Sjolte-Jorgensen, 1967; Dahms, 1973; Schmidt et al., 1976; Seidel, 1984; Lanner, 1985). However, a few detailed studies show that in very young forest plantations, seedlings planted at high densities show more rapid growth than those planted at lower densities (Helmers, 1948; Cameron et al., 1989; DeBell & Giordano, 1994; Gilbert et al., 1995; Knowe and Hibbs, 1996; Ritchie, 1997, Scott et al., 1998).

These detailed studies indicate that, over time, annual growth in the higher stocking densities decreases to a level below that of the lower densities. This shift is presumably caused by intraspecific competition increasing over time, and suppressing growth in the higher density stands. Some studies have shown greater annual tree growth for seedlings in mid-densities than in high- and low-densities (Belanger and Pepper, 1978; Bormann and Gordon, 1984; Cole and Newton, 1987; Giordano and Hibbs, 1993; Pienaar and Shiver, 1993).

These studies, in which the mid-density treatments were found to have the highest growth, involve initial measurements taken several years after planting (initial
measurements: 3 to 6 years after planting), and therefore may have missed an early phase in which annual growth was greatest in the highest density. A possible explanation for the contradiction in the literature of the effects of density on tree growth is that those studies indicating only a negative growth response to density may not have growth measurements for the first several years after planting. It is during this early stage of the growth of seedlings that a positive growth response to density is often observed. This contradiction highlights the importance of investigating the temporal dynamics involved in the responses of growth to stand density.

Because the positive growth response to density is somewhat counterintuitive, it is possible that it has been noted in even more studies but not reported. Where it has been noted, it is a short-lived phenomenon, typically lasting only a few years. Although it has been observed in several hardwood and coniferous species, the mechanisms that cause it, as well as its temporal dynamics, are still not fully known.

The purpose of the study presented in chapter one was to investigate the positive growth response of young conifers to density, to determine the temporal dynamics of this growth response, and to test general hypotheses concerning mechanisms responsible for its occurrence. Knowledge of the temporal dynamics involved in the positive growth response to density could allow foresters to develop thinning and silvicultural prescriptions to maintain ideal stocking densities for maximum tree growth. In addition, increased knowledge of this phenomenon could
lead to new ways of thinking about the biology and physiology of plant interaction and competition.

Forest processes such as photosynthesis and transpiration, plant and soil respiration, and soil evaporation produce or deplete CO₂ and water vapor in the canopy atmosphere relative to the bulk atmosphere. Canopy boundary layers may reduce atmospheric mixing, resulting in different concentrations of gases within than above the canopy (Brooks et al., 1997). An even canopy surface, low wind speed, small plant stature, and increased plant density are all factors affecting boundary layer conductance (Monteith and Unsworth, 1990). Calm wind conditions at night result in minimal atmospheric mixing. CO₂ concentrations within a forest are highest at night due to soil and plant respiration, the lack of photosynthesis and low atmospheric mixing (Buchmann et al., 1996, 1998; Brooks et al., 1997; Anthoni et al., 1999). This condition may result in substantially higher CO₂ levels around plant foliage in short canopies with low canopy roughness and a low degree of coupling with the bulk atmosphere (Jarvis, 1976). A low boundary layer conductance could result in the maintenance of elevated CO₂ concentrations in the morning hours, before atmospheric mixing increases with increasing radiation and wind speed.

A low canopy boundary layer conductance can also increase humidity levels within a stand due to the decrease in loss of water vapor from plant transpiration and soil evaporation to above the canopy. Stomata may respond to increased humidity by opening more and or remaining open longer throughout the day, resulting in
increased photosynthesis and/or increased photosynthetic water use efficiency (Waring and Winner, 1996; Harrington et al., 1994; Hall et al., 1993).

The purpose of the study presented in chapter two was to investigate the effects of stand density on the micro-climate and boundary layer of young conifer forests. My hypothesis was that stands of higher density generally have lower boundary layer conductance, especially during the night and morning. This lower canopy boundary layer conductance functions to “trap” morning high levels of respired CO$_2$ and transpired water vapor within the stand. The higher concentrations of CO$_2$ and H$_2$O may enhance photosynthesis within the higher density stands.

The purpose of the study presented in chapter two was originally to investigate a hypothesis presented in the first chapter as an explanation for enhanced growth with density in young Douglas-fir stands. This hypothesis proposes that the observed positive growth response to density may be associated with enhanced microclimate, brought about by decreased canopy boundary layer conductance. This enhanced microclimate would, in turn result in greater growth at the individual tree level. Results of stable isotope analyses conducted for the study presented in chapter one indicate that the positive correlation of growth with density is not likely to be associated with canopy boundary layer. At the time these results were obtained, a substantial amount of preparation had been conducted for this hypothesis test. It was therefore decided that for chapter two, a study would be conducted investigating the canopy boundary layer and microclimate of young Douglas-fir stands, but that it
would not be a test of the hypothesis presented in chapter one. We decided to look at
stands which were older than the stands for which we were seeing the greatest
enhancement of growth with density, because stands of this very young age are not
likely to exhibit any significant differences in canopy boundary layer or microclimate
with density.
CHAPTER ONE

The Effects of Stand Density on the Growth of Young Douglas-fir Stands.
ABSTRACT

My objectives were to 1) determine whether initial tree density is positively correlated with height and diameter growth in young Douglas-fir (Pseudotsuga menziesii) plantations, 2) if so, determine at what point after planting the positive growth response occurs and how long it lasts, and 3) use stable isotopes of carbon to test whether the mechanism(s) responsible for the positive growth response to density are related to variables affecting photosynthesis such as nutrient or moisture availability. I hypothesized that high stand density in the first several years of growth results in environmental conditions favorable to growth. I measured annual height (h) and diameter (d) growth (retrospectively) of trees on three sites in southwestern Washington. Each site consisted of test plantations of eight- and twelve-year-old Douglas-fir in initial planting densities of 300, 1360, and 2960 trees hectare$^{-1}$. Both height and diameter growth increased with initial seedling density through the fifth year after planting. I used $d^2h$ as an index of seedling volume. Mean annual increase in $d^2h$ was greatest in the high-density treatment and lowest in the low-density treatment through the fifth year after planting. By the seventh year after planting, this trend was reversed (presumably due to the effects of competition from neighboring trees). The greatest observed difference in annual increase in $d^2h$ between high- and low-density treatments occurred in the second year after planting. Mean $d^2h$ of the high-density treatment was 309% of that in the low-density treatment for that year. $\delta^{13}C$ values of wood cellulose from core samples of the 2$^{nd}$ and 3$^{rd}$ were not
significantly different among densities of either site. These results suggest either no significant differences in the effects of water availability, nutrient availability, or source air on photosynthesis in the three density treatments; or differences that produced no net effect on δ^{13}C.

INTRODUCTION

Silvicultural prescriptions involving stand density are often made based on the assumption that at higher stocking levels, individual tree productivity is inversely related to stand density (Evert, 1971; Clark et al., 1994; Smith et al., 1997). Many sources indicate that height growth is insensitive to density, and that radial growth increases with increased spacing (e.g.: Hiley, 1959; Sjolte-Jorgensen, 1967; Dahms, 1973; Schmidt et al., 1976; Seidel, 1984; Lanner, 1985). However, a few detailed studies show that in very young forest plantations, seedlings planted at high densities show more rapid growth than those planted at lower densities. For example, annual height growth has been shown to be positively correlated with stocking density at a young age for several species of broad-leaved and coniferous trees (Helmers, 1948; DeBell & Giordano, 1994; Gilbert et al., 1995; Knowe and Hibbs, 1996; Ritchie, 1997). Helmers (1948) showed that the taller seedlings of western white pine (Pinus monticola) were growing in seed spots (area of approximately 30.5 cm^2) that had the most seedlings 9 years after sowing. In red alder (Alnus rubra), the mean height of
five-year-old seedlings was 41% greater in 1.9 m² spacing than those at 6.5 m² spacing (DeBell and Giordano, 1994). Gilbert et al. (1995) found that, one year after planting, the mean height of black cottonwood (Populus trichocarpa) seedlings at the highest density (8 trees m⁻¹) was 119% of that of the seedlings in the lowest density (1 tree m⁻¹). In the following year of the same study (after increasing treatments) seedlings in the highest density (12 trees m⁻¹) had a mean height 136% of that of the seedlings in the lowest density (0.5 tree m⁻¹) (Gilbert et al, 1995). In a study conducted by Knowe and Hibbs (1996), mean height growth of red alder seedlings in the first year after planting was greatest for those planted at the highest density (64672 trees hectare⁻¹) and lowest for those planted at the widest spacing (345 trees hectare⁻¹). Ritchie (1997) found increased height growth and increased branch number with increased density for Douglas-fir after one growing season.

In addition to height growth being positively correlated with density, there are also reports of greater annual diameter growth occurring at higher density at an early age (Cameron et al., 1989; Scott et al., 1998). Cameron et al. (1989) found increased diameter growth with increased stocking density in their study of Eucalyptus (Eucalyptus grandis). In this study, one and a half years after planting, trees in the highest density (3580 trees hectare⁻¹) were 163% taller, and 137% larger in diameter, than those in the lowest density (42 trees hectare⁻¹). In a study of five- to six-year-old Douglas-fir planted at variable densities, height growth in the highest density (2960 trees hectare⁻¹) was 133%, and diameter growth was 149% of that in the lowest density (300 trees hectare⁻¹) (Scott et al, 1998).
All of these studies indicate that, over time, annual growth in the higher stocking densities decreases to a level below that of the lower densities. This shift is presumably caused by intraspecific competition increasing over time, and suppressing growth in the higher density stands.

Some studies have shown greater annual tree growth for seedlings in mid-densities than in high- and low-densities (Belanger and Pepper, 1978; Bormann and Gordon, 1984; Cole and Newton, 1987; Giordano and Hibbs, 1993; Pienaar and Shiver, 1993). Belanger and Pepper (1978) conducted a study analyzing the growth of American Sycamore (*Plantanus occidentalis*) grown at seven densities ranging between 200 and 27,000 trees hectare\(^{-1}\). Total height at three and four years of age was significantly greater at the high and intermediate densities than at the two lowest densities. For the first year that diameter measurements were conducted (age five) the greatest mean stem diameter was found in the intermediate density of 1050 trees hectare\(^{-1}\), which was 112% of that in the lowest density of 200 trees hectare\(^{-1}\). Measurements conducted during the following year (the final year of measurements for this study) indicate that the greatest mean stem diameter was still in the 1050 trees hectare\(^{-1}\) density. However, it was down to 108% of that in the lowest density. This study by Belanger and Pepper (1978) indicates a trend of low stand density becoming more correlated with growth after an initial period in which low density is not most favorable.

Bormann and Gordon (1984) found that mid-density stands (initially spaced at 1.22 x 1.82 m) of five-year-old red alder had greater total height than those of a lower
density (2.74 x 2.74 m) and a higher density (0.61 x 1.22 m). Mean height of trees in
the mid-density stand were 112% of those in the low-density stand. Mean height of
trees at age five in the high-density stand were slightly greater than those in the low-
density stand. The fifth year of growth was the first and only year for which
measurements were reported for this study.

Cole and Newton (1987) conducted measurements of Douglas-fir spaced
variably from 17 to 123 cm apart in Nelder plots. Tree height at the end of the fifth
year of growth ranged from 1.6 to 2.0 m in the high densities, from 2.4 to 2.9 m in the
intermediate densities, and from 2.2 to 2.3 m in the lowest densities. Age five was the
only year for which measurements were reported for this study.

Giordanno and Hibbs (1993) found that biomass, height and diameter of red
alder planted in spacings ranging from 0.1 to 41.99 m² tree⁻¹ were greatest in
intermediate densities and smaller in spacings that had not yet achieved crown
closure (from 3.7 to 14.13 m²). At the end of the fourth year of growth, the greatest
mean height was found in the intermediate density of 0.73 m² tree⁻¹. The mean height
in this density was 165% of that in the lowest density. For this same year the greatest
mean diameter was found in the intermediate density of 3.57 m² tree⁻¹. Maximum tree
height for this year in the 3.57 m² tree⁻¹ density was 121% of that in the lowest
density. Greatest above-ground biomass was also found in the 0.73 m² tree⁻¹ density
which was 189% of that in the lowest density. The fourth year of growth was the first
year for which measurements were reported for this study.
Pienaar and Shiver (1993) conducted growth measurements of three-, five- and eight-year-old loblolly pine (*Pinus taeda*) planted in variable densities of 100, 200, 400, 600, 800 and 1000 trees acre\(^{-1}\). At the end of the 3\(^{rd}\), 5\(^{th}\) and 8\(^{th}\) years of growth they found the greatest mean tree height for all three years in the intermediate density of 400 trees acre\(^{-1}\). The greatest mean diameter for year five was also found in the 400 trees acre\(^{-1}\) density. By year eight the greatest diameter was in the lowest density of 100 trees acre\(^{-1}\). Diameter measurements for year three were not reported.

These studies, in which the mid-density treatments were found to have the highest growth, involve initial measurements taken several years after planting (initial measurements: 3 to 6 years after planting), and therefore may have missed an early phase in which annual growth was greatest in the highest density. A possible explanation for the contradiction in the literature of the effects of density on tree growth is that those studies indicating only a negative growth response to density may not have growth measurements for the first several years after planting. It is during this early stage of the growth of seedlings that a positive growth response to density is often observed. This contradiction highlights the importance of investigating the temporal dynamics involved in the responses of growth to stand density.

Because the positive growth response to density is somewhat counterintuitive, it is possible that it has been noted in even more studies but not reported. Where it has been noted, it is a short-lived phenomenon, typically lasting only a few years.
Although it has been observed in several hardwood and coniferous species, the mechanisms that cause it, as well as its temporal dynamics, are still not fully known.

**Hypotheses for positive growth response to density**

Plant growth can be influenced by several environmental and ecological variables that directly or indirectly affect tree physiology. These include light, humidity, soil moisture and nutrient availability, ambient CO₂ concentrations, temperature, wind, herbivory, and changes in light quality. Enhanced growth at higher densities could result from situations involving any one or a combination of these factors.

1. Control of interspecific competition

Understory plants compete with trees in a stand for resources. Plant responses to competition are similar to those for coping with water and nutrient deficiency in the soil (Price et al., 1986; Nambiar and Sands, 1993). Increased planting densities and rapid canopy closure can be used to improve weed control (Mohler, 1996). The greater number of trees in a higher density stand are likely to achieve canopy closure at an earlier time than trees in a stand of lower density (Smith et al., 1997). Trees planted in higher initial stocking density could therefore quickly exclude understory competing shrubs and herbs.
2) Reduced browse damage

Browsing animals can have significant negative effects on the growth of young trees (Gill, 1992). Tighter tree spacing may restrict access for browsing animals, resulting in reduced browse damage and greater growth in higher density stands (Welch et al., 1991; Heikkila, 1992). Additionally, a greater number of seedlings should result in a lower ratio of browsing animals to seedlings. Hence, it may be possible to enhance tree growth through an increase in stand density and a subsequent reduction of browse damage.

3) Increased mycorrhizal linkages

Mycorrhizal fungi form close associations with roots, allowing plants to capture and absorb significantly more nutrients. Individual trees can be physically linked by the hyphae of mycorrhizal fungi that allow carbon and nutrients to pass between them (Perry et al., 1992; Amaranthus and Perry, 1994). Mycorrhizal linkages between trees in a stand may reduce competition between trees by 1) the ability of mycorrhizal fungi to exploit spatially distinct substrates such as humus vs. mineral soil, 2) the ability of fungi to be active during temporally changing conditions of moisture and temperature, and 3) a more even distribution of nutrients between individuals via hyphal connections (Perry et al., 1992; Amaranthus and Perry, 1994). Due to the closer proximity of tree roots in higher density stands, a dense stand is likely to form a greater number of linkages among mycorrhizal hyphae more rapidly than a sparse one.
4) Phytochrome response

Increased stand density can cause a change in the spectral composition of the canopy interception by individual trees within a stand. Radiation reflected from green foliage is depleted in the red (R, $\lambda \sim 660$ nm) region of the spectrum due to the preferential absorption of red light by chlorophyll. Far-red light (FR, $\lambda \sim 730$ nm) is not depleted because virtually all FR received by foliage is reflected or transmitted. Subsequently, the ratio of red to far-red light (R:FR) reflected from green foliage is reduced relative to direct sunlight (Holmes & Smith, 1975, 1977). As stand density is increased, R:FR decreases due to the increase in reflected light. Plants are able to sense this change in quality of light through phytochrome pigments. Phytochromes are chromoproteins that exist in two, photoconvertible, stable forms: Pr, which absorbs maximally $\lambda \sim 600$ nm, and Pfr, which absorbs maximally $\lambda \sim 730$ nm. The absorption of red light causes a phytochrome shift to the Pfr form, and the absorption of far-red light causes a shift to the Pr form. This equilibrium is typically denoted by Pfr/P, where P is total phytochrome. A characteristic response to a phytochrome shift from Pfr to Pr is accelerated stem elongation (Ballare et al., 1987; Gilbert et al., 1995). This response may result in increased height growth in stands of higher density.

5) Decreased boundary layer conductance

When air flows over a surface, the flow velocity decreases towards that surface as a consequence of the friction between the surface and the air and of the viscous forces
of the air. A boundary layer is the area adjacent to a surface where the flow rate is greatly reduced below that of the free air stream. Conductance is the property of a system that relates flux to concentration difference, where flux equals conductance times the difference in concentration. Boundary layer conductance is inversely proportional to its thickness, which is determined primarily by wind speed. The boundary layer conductance of a forest canopy \( (g_{sc}) \) is also strongly determined by properties of the canopy (Jarvis et al., 1976). When wind speed is high, the drag of the moving air reduces the thickness of the boundary layer and therefore effectively increases the conductance of this layer. Plant density is one of the determinant factors of canopy boundary layer conductance (Monteith and Unsworth, 1990; Landsberg and Gower, 1997). Canopy boundary layers reduce atmospheric mixing, resulting in different concentrations of gases within the canopy compared with that above the canopy (Brooks et al., 1997). Calm wind conditions at night result in minimal atmospheric mixing. \( \text{CO}_2 \) concentrations within a forest are highest at night in response to soil and plant respiration, the lack of photosynthesis, and low atmospheric mixing (Buchmann et al., 1996; Brooks et al., 1997, Anthoni et al. 1999). This condition may result in substantially higher \( \text{CO}_2 \) levels around plant foliage in short canopies with low canopy roughness and low coupling with the atmosphere. A low boundary layer conductance could result in the maintenance of elevated \( \text{CO}_2 \) concentrations in the morning hours before atmospheric mixing increases with increasing radiation and wind speed. This would increase morning photosynthetic rates. A low canopy boundary layer conductance may also increase humidity levels.
within a stand in response to the trapping of water vapor from plant transpiration and soil evaporation. Stomata may respond to increased humidity by opening more and/or remaining open longer throughout the day, resulting in increased photosynthesis as well as increased photosynthetic water use efficiency (Waring and Winner, 1996; Harrington et al., 1994; Hall et al., 1993). Hence, increased stocking density may enhance the microclimate of the seedlings within a stand at least until shading becomes limiting, resulting in greater growth at the individual tree level. A more thorough analysis of the effects of increased stand density on boundary layer conductance is presented in chapter two.

**Using stable carbon isotopes to test hypotheses**

Analysis of stable carbon isotopes ($^{12}$C and $^{13}$C) can provide a means to investigate a variety of issues in plant physiology (O’Leary, 1981, 1988). As the isotopic signal for any given year of tree growth is contained within the wood cellulose of annual rings, one way to evaluate some of the hypotheses previously presented is to examine the stable isotope ratios of plant carbon.

Atmospheric CO$_2$ contains the naturally occurring carbon isotopes $^{12}$C, $^{13}$C, and $^{14}$C in the proportions 98.9%, 1.1%, and $10^{-10}$%, respectively. The chemical properties of $^{13}$CO$_2$ are identical to those of $^{12}$CO$_2$, but because of the slight difference in mass (2.3%), the heavier $^{13}$CO$_2$ behaves differently in physical and biological processes involved in plant growth. The same applies to a greater extent to
$^{14}\text{CO}_2$; however, the $^{14}\text{C}$ isotope occurs naturally in such small quantities as to make measuring it impractical.

The $^{13}\text{C}$ content of $\text{CO}_2$ is represented by the ratio ($R$) of the heavier $^{13}\text{C}$ isotope to the lighter $^{12}\text{C}$ isotope.

$$R = \frac{^{13}\text{CO}_2}{^{12}\text{CO}_2} \quad (1.1)$$

For convenience, ratios are typically expressed as values of $\delta^{13}\text{C}$. This eliminates the need for numbers extending to several decimal points.

$$\delta^{13}\text{C} = \left[ \frac{R(\text{sample})}{R(\text{standard})} - 1 \right] \times 10000/_{oo} \quad (1.2)$$

This value is in the dimensionless units of per thousand ($^_/oo$). The standard is carbon dioxide obtained from “PDB” a limestone from the Pee Dee belemnite formation in South Carolina for which $^{13}\text{C}/^{12}\text{C} = 0.01124$ (Craig, 1957). The carbon dioxide in air has a $\delta^{13}\text{C}$ value of about -8$^_/oo$ ($^{13}\text{C}/^{12}\text{C} = 0.01115008$), and this value becomes slightly more negative each year as a result of deforestation and combustion of fossil fuels (Keeling et al., 1979).

To reflect the effect of biological activity on isotopic composition, a fractionation scale is used indicating the difference in $\delta^{13}\text{C}$ between source and product,
\[ \Delta = \left( \delta^{13}C_a - \delta^{13}C_p \right) / 1 + \delta^{13}C_p \]  

(1.3)

where \( \delta^{13}C_a \) is the \( \delta^{13}C \) value of air and \( \delta^{13}C_p \) is that of the plant.

The photosynthetic process of C\(_3\) plants discriminates against the heavier \( ^{13}C \) isotope (Farquhar et al., 1982). There are two processes that contribute to discrimination in the photosynthetic process: diffusion and carboxylation.

\[ \text{CO}_2(\text{external}) \xrightarrow{\text{diffusion}} \text{CO}_2(\text{internal}) \xrightarrow{\text{carboxylation}} \text{CO}_2(\text{assimilated}) \]  

(1.4)

"a"                                "b"

External \( \text{CO}_2 \) diffuses from the atmosphere to the site of carboxylation first through the stomata, then through the intercellular air spaces, and ultimately into the chloroplasts. The process of diffusion discriminates against the heavier \( ^{13}C \) isotope resulting in a change in the isotopic ratio of the \( \text{CO}_2 \) available for carboxylation. The isotopic composition of internal \( \text{CO}_2 \) is then altered further as it undergoes discrimination due to carboxylation (Farquhar and Richards, 1984). The total discrimination (\( \Delta \)) for C\(_3\) plants then ranges between that of discrimination associated with diffusion (\( 4.4^\circ/oo \)), and that associated with carboxylation (\( 29^\circ/oo \)) represented in equation 1.5 by \( a \) and \( b \) respectively (as indicated in equation 1.4).

\[ \Delta = a + (b - a) * \frac{C_f}{C_a} \]  

(1.5)
where $C_i$ is the intercellular concentration of CO$_2$ and $C_a$ is the concentration of CO$_2$ in the ambient air. When stomatal conductance is high and carboxylation is low, $C_i/C_a$ approaches 1 and discrimination approaches $b$ ($29\,^\circ/oo$). When stomatal conductance is low and carboxylation is high, $C_i/C_a$ approaches 0 and overall discrimination approaches $a$ ($4.4\,^\circ/oo$).

The hypotheses for the cause of a positive growth response to density that involve changes in moisture availability, nutrient availability, and boundary layer effects can all be examined through stable isotope analysis. Trees will decrease stomatal conductance ($g_s$) when the vapor pressure deficit (VPD) is high and/or when soil moisture is limited (Tyree and Sperry, 1988; Jones and Sutherland, 1991). $C_i$ is strongly dependent on $g_s$.

\[
C_i = C_a - 1.6 \frac{AP}{(g_s + g_b)}
\]  

(1.6)

where $C_a = $ ambient CO$_2$ concentration, $A = $ assimilation net photosynthesis of leaves during daylight hours), $P = $ atmospheric pressure, and $g_b = $ boundary layer conductance. Rearranging this equation to solve for $C_i/C_a$ gives:

\[
\frac{C_i}{C_a} = 1 - \frac{1.6 \frac{AP}{(g_s + g_b)}}{C_a}
\]  

(1.7)

Decreased VPD and/or increased soil moisture availability will result in increased $g_s$ and an increased ratio of $C_i/C_a$. This in turn will result in an increase in
the level of discrimination against the heavier $^{13}$C isotope (Equation 1.5), and a decrease in the $^{13}$C/$^{12}$C ratio in wood cellulose.

A greater availability of nutrients can result in a reduction in carbon isotopic discrimination (Sparks and Ehleringer, 1997; Livingston et al., 1998; 1999). Aside from the availability of CO$_2$, the efficiency of carboxylation is limited mainly by the quantity and activity of the enzyme carboxylase. Quantity and activity of carboxylase is highly dependent on the availability of nutrients, especially nitrogen. Enhanced carboxylation efficiency can reduce C$_i$/C$_a$ by increasing the plant’s ability to assimilate intracellular CO$_2$. This reduction in C$_i$/C$_a$ can result in a decrease in discrimination against the heavier $^{13}$C isotope because as C$_i$/C$_a$ approaches 0, discrimination decreases towards the minimum level of 4.4°/oo (Equation 1.5).

Several of the factors involved in the hypotheses presented including decreased interspecific competition, increased mycorrhizal linkage, and increased boundary layer resistance could have an effect on the $^{13}$C/$^{12}$C ratio in wood cellulose. These factors could affect either moisture availability, nutrient availability, or a combination of effects. Elimination of foliage, for example from browse damage, could result in an increase in the ratio of available soil moisture to leaf area. Because g$_s$ is limited by availability of soil moisture, browse damage could result in an increase in g$_s$ per unit leaf area (Meinzer et al., 1990). However, the level of foliage reduction may need to be significant to show a noticeable increase in g$_s$. Increased development of mycorrhizal linkages could result in increased nutrient or soil moisture availability.
The phytochrome-induced mechanisms caused by shifts in Pfr/Pr, result in adjustments in growth allometry (Ballare et al., 1987; Gilbert et al., 1995). Because this is not expected to affect the photosynthetic apparatus, it should not alter isotope discrimination. Hence, it is difficult to make a prediction of stable carbon isotope ratios of wood cellulose from trees grown in different stand densities as it pertains to a phytochrome response.

A greater boundary layer resistance could lead to changes in $^{13}$C/$^{12}$C ratio in two ways. Higher water vapor pressure will result in increased $g_s$, causing an increase in $C_i/C_a$, and a reduction in $^{13}$C/$^{12}$C (Equation 1.5). Further depletion of $^{13}$C is expected if CO$_2$ from overnight respiration is “re-fixed”, because it is derived from plant material that has already gone through a photosynthetic discrimination process (Sternberg, 1989). The following table summarizes the predicted differences in $\delta^{13}$C of cellulose resulting from the different proposed hypotheses (Table 1.1).
Table 1.1 Predicted differences in $\delta^{13}$C of cellulose resulting from the proposed hypotheses.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Predicted change in $\delta^{13}$C of cellulose (low to high density)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a Reduced interspecific competition (increased nutrient availability)</td>
<td>↑</td>
</tr>
<tr>
<td>1b Reduced interspecific competition (increased soil-moisture availability)</td>
<td>↓</td>
</tr>
<tr>
<td>2 Reduced browse damage (decreased soil-moisture availability)</td>
<td>↑</td>
</tr>
<tr>
<td>3a Increased mycorrhizal development (increased nutrient availability)</td>
<td>↑</td>
</tr>
<tr>
<td>3b Increased mycorrhizal development (increased soil-moisture availability)</td>
<td>↓</td>
</tr>
<tr>
<td>4 Phytochrome response</td>
<td>No prediction</td>
</tr>
<tr>
<td>5a Decreased boundary layer conductance (decreased VPD)</td>
<td>↓</td>
</tr>
<tr>
<td>5b Decreased boundary layer conductance (re-fixation of respired CO$_2$)</td>
<td>↓</td>
</tr>
</tbody>
</table>
The purpose of the study was to investigate the positive growth response of young conifers to density, to determine the temporal dynamics of this growth response, and to test general hypotheses concerning mechanisms responsible for its occurrence. Knowledge of the temporal dynamics involved in the positive growth response to density could allow foresters to develop thinning and silvicultural prescriptions to maintain ideal stocking densities for maximum tree growth. In addition, increased knowledge of this phenomenon could lead to new ways of thinking about the biology and physiology of plant interaction and competition.

METHODS

Site Location and Description

Study plots were located on Weyerhauser Co. land at Twin Harbors Tree Farm South, (sites one and two) near Doty, Washington; and Twin Harbors Tree Farm North, (site three) near Oakville, Washington (Figure 1.1). Site 1 “Doty Site” is located at latitude 46° 38', and longitude 123° 21’, at an elevation of 61 m. Site 2 “Fall River Site” is located at latitude 46° 42’, and longitude 123° 29’, at an elevation of 183 m. Site 3 “A 6000 Site” is located at latitude 46° 51’, and longitude 123° 26’, at an elevation of 122 m. All three sites are located within an area of a 13.15 km radius. All three locations are site index 43 m (50 yr.), with third-growth Douglas-fir plantations (Bill Scott, personal communication).
The maritime Pacific climate of the region is characterized by a wet winter and dry summer. The mean annual precipitation in Centralia WA, (32 - 42 km from the field sites) is 1200 mm. Approximately 90% of the precipitation falls between October and May, and the small amount of precipitation between June and September (~150 mm) creates potential summer drought conditions. The mean annual snowfall is 170 mm. Mean minimum temperature for January is 0.8° C, mean maximum temperature for July is 26° C (Western Regional Climate Center, 1998).

Soils of all three sites are derived from parent material of sedimentary sandstone. The soils are classified as Haplohumults (reddish brown lateritic soils) (Franklin and Dyrness, 1988), and “Astoria series” by Weyerhauser Co. All three sites were planted with 2-0 seedlings that were randomly assigned to densities. Planting occurred in the spring of 1989 at sites one and two, and in the spring of 1985 at site three. Seed source for sites one and three was a ten-family custom mix selected for volume. Site two seed source was 030 seed zone at 150 m.
Experimental design

Trees were planted by the Weyerhauser Co. in a randomized block design, with a single replicate of density treatments at each site. Weyerhauser Co. randomly assigned treatment densities to plots. All plots were approximately 2 hectares (five acres) in size with variable dimensions. For this analysis, measurements were blocked by site for a total of three blocks. Within each block, three different treatments of stocking densities were examined, 300, 1360 and 2960 trees hectare$^{-1}$ (120, 550, and 1200 trees acre$^{-1}$), referred to hereafter as low-, mid- and high-density treatments. Within each plot, I randomly selected 50 measurement trees using plot maps.
superimposed by a 1cm x 1cm grid (scale: 1 cm = 1 m). From a list of random 
numbers, points on each plot map’s grid were chosen for 50 measuring locations. The 
tree nearest to these points was chosen in the field for measurement by pacing and the 
use of a compass. Trees within 10 meters of plot boundaries were not considered in 
order to avoid edge effects. Dead trees were not considered suitable for measurement 
and were dropped.

Measurements

Measurements were conducted during the summer of 1997. Stem diameter was 
measured at breast height and at 30 cm above ground using diameter tapes. A core 
sample was taken from each tree using an 8" increment corer 30 cm above ground on 
the north side of seedlings. If the pith was missed, additional samples were taken until 
the core included pith. From the cores, annual diameter growth was measured using a 
Metronics Quick Chek QC-1000-M-AR digital readout unit, a 0.001 mm resolution 
Accu-Rite linear encoder and a Velmex Unislide measuring stage. Heights were 
measured with a height pole to a 0.1 m resolution. Retrospective annual height 
measurements were determined by measuring the distance between branch whorls for 
each year of growth. Trees in site three were four years older than those in sites one 
and two and were therefore significantly larger. Due to the larger tree size, the upper 
branch whorls of trees in the mid- and high-density treatment at site three were 
completely obscured by those of neighboring trees. This prohibited identifying the 
locations of branch whorls indicating the start of annual height growth. Because of
this, height measurements were not conducted at site three for this study. Height measurements for site three were conducted by Weyerhauser Co. commencing at 6 years after planting. These data were used to present height growth increment commencing at year seven (Figure 1.2). These data were not included in the analysis of height growth because they were collected separately from those of sites one and two, and because they represent different years of growth. A tree biomass index was calculated as \((\text{stem diameter at } 30 \text{ cm above ground})^2 \times \text{ height} \ (d^2h)\). An analysis of \(d^2h\) could not be conducted for site three because of the absence of height growth data coinciding with diameter growth data for this site.

In determining diameter growth of annual rings, I began measuring from the current year and counted inward. For some trees, the number of growth rings was less than the total number of years since planting because the end of the first or second year of growth occurred below the sampling height of 30 cm. Consequently, several of the plots contained very few diameter growth measurements for the first year after planting, or none at all. Similarly, I measured height increments from the top whorl (current year) down, and for some trees, the number of internodes was less than the number of years since planting. Nodes for years at or prior to the first year after planting were often indeterminable. For these reasons, the sample size of measurements during early growth years was less than the 50 trees per plot that I measured. Additionally, height growth measurements from the first year after planting were inflated due to the inclusion of growth in years prior to planting for which nodes were not found. For these reasons measurements of the first year of
diameter and height growth were either entirely absent from a given plot, extremely limited or unreliable, and were therefore not used in this analysis.

**Relative growth analyses**

Analyses of relative growth rates indicated little differences between density treatments. Since differences in relative growth precede those in absolute growth, significant differences in relative growth rates were likely to occur in the first year after planting. Since this year was not available for analysis, relative growth rates were not reported.

**Growth analyses**

Data were analyzed by analysis of variance (SAS, 1996) to determine the effect of initial stocking density on diameter, height and volume ($d^2h$) of seedlings for all ages from year two on. Data for the analysis of $d^2h$ were transformed (ln) after determining that they violated assumptions of constant variance and normal distribution. Reports of "significance" refer to the $\alpha$ level of 0.1.

**Stable isotope analysis**

The growth rings for the second and third years after planting were excised from the core samples using a razorblade. These years were chosen for stable isotope analysis because height and diameter growth was greater in high-density compared with low-density treatments in both of these years. The excised xylem was dried at 70° C for at
least 72 hours. It was then ground with a coffee grinder and pulverized in liquid nitrogen using a mortar and pestle. Cellulose was extracted from pulverized xylem samples following the procedures described by Wise (1945). Stable carbon isotope ratios of the extracted cellulose were determined at the SIRFER laboratory (Stable Isotope Ratio Facility for Environmental Research) at the Biology Department of the University of Utah. All isotope data are expressed in delta notation (δ) and are presented relative to the Pee Dee belemnite standard for δ13C.

**RESULTS**

**Analyses of height, diameter and d2h growth**

In the comparison of growth measurements between the three different density treatments, the null hypothesis is that there is no effect of planting density on annual growth. For growth measurements from each year analyzed, a separate ANOVA was conducted (SAS, 1996) to determine if there were differences among the three density treatments for that year. Data for the analysis of d2h were transformed (LN) after determining that they violated assumptions of constant variance and normal distribution.

Significant differences in mean annual height increment were observed among the three density treatments with the most significant differences consistently occurring between the low- and high-density treatments (Table 1.2). Greater mean
annual height increment consistently occurred in the high-density treatment than the low-density treatment, and that of the mid-density treatment typically occurred at a level between that of the low- and high-density treatments. The greatest observed difference in mean annual height increment occurred between the low- and high-density treatments in the second year after planting. Mean second-year height increment averaged across sites one and two in the high-density treatment was 135% of that in the low-density treatment. Significantly greater growth in the high-density treatment occurred for the comparison between high- and low-density treatments in the second, fifth and sixth years after planting. This positive growth response to density declined over time such that by the eighth year after planting, height growth in the high-density treatment was less than 104% of that in the low-density treatment.

Differences in mean annual height increment between mid- and high-density treatments were typically greater than those between mid- and low-density treatments. No significant differences in mean annual height increment occurred between the low- and mid-density treatments for any of the years after planting. (Table 1.2 & Figure 1.2).
Table 1.2 ANOVA statistics for comparisons of mean annual height increment in the low-, mid-, and high-density treatments. P-values are indicated and significance levels are highlighted by *** $P < 0.01$; ** $P < 0.05$; * $P < 0.1$ where growth is greater in the higher density treatment; and are $\infty\infty\infty P < 0.01$; $\infty\infty P < 0.05$; $\infty P < 0.1$ where growth is greater in the lower density treatment.

<table>
<thead>
<tr>
<th>YR 2</th>
<th>stand density</th>
<th>mean ht. growth (m)</th>
<th>SE (mean)</th>
<th>degrees of freedom</th>
<th>treatment comparisons</th>
<th>difference in treatments (cm)</th>
<th>SE (treatment difference)</th>
<th>p-value for treatment comparisons</th>
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<tbody>
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<td>0.05</td>
<td>low vs. mid</td>
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<td>mid vs. high</td>
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<td>0.043**</td>
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<td>low vs. high</td>
<td>0.13</td>
<td>0.03</td>
<td>0.024**</td>
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<td>YR 7</td>
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<td>0.04</td>
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<td>0.02</td>
<td>0.163</td>
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</table>
Figure 1.2 Annual height growth for trees in the low-, mid-, and high-density treatments. Error bars are standard errors of the estimate of the mean for 50 trees for sites one and two, and between 28 and 323 trees for site three.
Significant differences in mean annual diameter increment were observed between the three density treatments as well. For the second through sixth years after planting greater mean annual diameter increment consistently occurred in the high-density treatment than the low-density treatment. Mean annual diameter increment of the mid-density treatment consistently occurred at a level between that of the low- and high-density treatments. The greatest observed difference in mean annual diameter increment occurred between the low- and high-density treatments in the second year after planting. Averaged across sites one, two and three, mean diameter increment in the second-year after planting in the high-density treatment was 165% of that in the low-density treatment. Significantly greater growth in the high-density treatment occurred for the comparison between high- and low-density treatments in the second, third, fourth, and fifth years after planting. This positive growth response to density declined over time such that by the seventh and eighth years after planting significantly greater annual diameter increment was occurring in the low-density treatment as compared to other treatments. Averaged across all three sites, mean diameter increment for the eighth year after planting in the low-density treatment was 138% of that in the high-density treatment. The shift in this relationship illustrates a more dramatic reversal over time in the effect of density on diameter growth than what was observed for height growth (Table 1.3 & Figure 1.3).
Table 1.3 ANOVA statistics for comparisons of mean annual diameter increment in the low-, mid-, and high-density treatments. P-values are indicated and significance levels are highlighted by *** $P < 0.01$; ** $P < 0.05$; * $P < 0.1$ where growth is greater in the higher density treatment; and are °°° $P < 0.01$; °° $P < 0.05$; ° $P < 0.1$ where growth is greater in the lower density treatment.

<table>
<thead>
<tr>
<th>Year</th>
<th>Stand Density</th>
<th>Mean Diam. Growth (cm)</th>
<th>SE (mean)</th>
<th>Degrees of Freedom</th>
<th>Treatment Comparisons</th>
<th>Difference in Treatments (cm)</th>
<th>SE (Treatment Difference)</th>
<th>P-value for Treatment Comparisons</th>
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<td></td>
<td>2960 tph</td>
<td>0.51</td>
<td>0.046</td>
<td>4</td>
<td>low vs. high</td>
<td>0.21</td>
<td>0.07</td>
<td>0.035**</td>
</tr>
<tr>
<td>YR 3</td>
<td>300 tph</td>
<td>0.49</td>
<td>0.057</td>
<td>4</td>
<td>low vs. mid</td>
<td>0.08</td>
<td>0.080</td>
<td>0.370</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
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<td>0.057</td>
<td>4</td>
<td>mid vs. high</td>
<td>0.13</td>
<td>0.080</td>
<td>0.074*</td>
</tr>
<tr>
<td></td>
<td>2960 tph</td>
<td>0.77</td>
<td>0.057</td>
<td>4</td>
<td>low vs. high</td>
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<td>0.080</td>
<td>0.027**</td>
</tr>
<tr>
<td>YR 4</td>
<td>300 tph</td>
<td>0.69</td>
<td>0.10</td>
<td>4</td>
<td>low vs. mid</td>
<td>0.11</td>
<td>0.104</td>
<td>0.362</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
<td>0.80</td>
<td>0.10</td>
<td>4</td>
<td>mid vs. high</td>
<td>0.19</td>
<td>0.104</td>
<td>0.140</td>
</tr>
<tr>
<td></td>
<td>2960 tph</td>
<td>0.99</td>
<td>0.10</td>
<td>4</td>
<td>low vs. high</td>
<td>0.30</td>
<td>0.104</td>
<td>0.046**</td>
</tr>
<tr>
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<td>4</td>
<td>low vs. mid</td>
<td>0.120</td>
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<td>0.092</td>
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<td>mid vs. high</td>
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<td>0.113</td>
<td>0.451</td>
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<td>1.42</td>
<td>0.092</td>
<td>4</td>
<td>low vs. high</td>
<td>0.29</td>
<td>0.113</td>
<td>0.061*</td>
</tr>
<tr>
<td>YR 6</td>
<td>300 tph</td>
<td>1.37</td>
<td>0.172</td>
<td>4</td>
<td>low vs. mid</td>
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<td>0.17</td>
<td>0.395</td>
</tr>
<tr>
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<td>1.53</td>
<td>0.172</td>
<td>4</td>
<td>mid vs. high</td>
<td>0.01</td>
<td>0.17</td>
<td>0.968</td>
</tr>
<tr>
<td></td>
<td>2960 tph</td>
<td>1.54</td>
<td>0.172</td>
<td>4</td>
<td>low vs. high</td>
<td>0.17</td>
<td>0.17</td>
<td>0.376</td>
</tr>
<tr>
<td>YR 7</td>
<td>300 tph</td>
<td>1.78</td>
<td>0.187</td>
<td>4</td>
<td>low vs. mid</td>
<td>-0.06</td>
<td>0.17</td>
<td>0.732</td>
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<tr>
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<td>1.71</td>
<td>0.187</td>
<td>4</td>
<td>mid vs. high</td>
<td>-0.19</td>
<td>0.17</td>
<td>0.343</td>
</tr>
<tr>
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<td>2960 tph</td>
<td>1.53</td>
<td>0.187</td>
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<td>low vs. high</td>
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<td>0.223</td>
</tr>
<tr>
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<td>low vs. mid</td>
<td>-0.22</td>
<td>0.063</td>
<td>0.352</td>
</tr>
<tr>
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<td>1.90</td>
<td>0.21</td>
<td>4</td>
<td>mid vs. high</td>
<td>-0.37</td>
<td>0.063</td>
<td>0.146</td>
</tr>
<tr>
<td></td>
<td>2960 tph</td>
<td>1.53</td>
<td>0.21</td>
<td>4</td>
<td>low vs. high</td>
<td>-0.58</td>
<td>0.063</td>
<td>0.046°°</td>
</tr>
</tbody>
</table>
Figure 1.3 Annual diameter growth for trees in the low-, mid-, and high-density treatments. Error bars are standard errors of the estimate of the mean for 50 trees.
For the second through fifth years after planting, greater median annual $d^2h$ increment consistently occurred in the high-density treatment than the low-density treatment (Table 1.4 & Figure 1.4). The greatest observed difference in median annual $d^2h$ increment occurred between the low- and high-density treatments in the second year after planting. Median second-year $d^2h$ increment averaged across sites one and two in the high-density treatment was 309% of that in the low-density treatment. A decline in this positive growth response to density, similar to that which took place for diameter increment, occurred over time. By the seventh and eighth years after planting significantly greater median $d^2h$ increment was occurring in the low-density treatment than in the high-density treatment. Median eighth-year $d^2h$ increment averaged across all sites one and two in the low-density treatment was 222% of that in the high-density treatment.
Table 1.4 ANOVA statistics (back-transformed) for comparison of median annual $d^2h$ increment in the low-, mid-, and high-density treatments. P-values are indicated and significance levels are highlighted by *** P < 0.01; ** P < 0.05; * P < 0.1 where growth is greater in the higher density treatment; and are °°° P < 0.01; °° P < 0.05; ° P < 0.1 where growth is greater in the lower density treatment.

<table>
<thead>
<tr>
<th>Stand density</th>
<th>Median increase in $d^2h$ (cm$^3$)</th>
<th>$\alpha = 0.05$ lower 95% con. limit (mean)</th>
<th>$\alpha = 0.05$ upper 95% con. limit (mean)</th>
<th>Degrees of freedom</th>
<th>Treatment comparisons</th>
<th>Ratio of treatments</th>
<th>$\alpha = 0.05$ lower 95% con. limit (treatment ratio)</th>
<th>$\alpha = 0.05$ upper 95% con. limit (treatment ratio)</th>
<th>P-value for treatment comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>YR 2 300 tph</td>
<td>4.75</td>
<td>1.57</td>
<td>14.34</td>
<td>2</td>
<td>low vs. mid</td>
<td>.80</td>
<td>.26</td>
<td>5.97</td>
<td>0.598</td>
</tr>
<tr>
<td>1360 tph</td>
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<td>1.97</td>
<td>17.96</td>
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<td>mid vs. high</td>
<td>.42</td>
<td>.09</td>
<td>1.99</td>
<td>0.138</td>
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<tr>
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<td>14.24</td>
<td>4.71</td>
<td>42.95</td>
<td>2</td>
<td>low vs. high</td>
<td>.33</td>
<td>.07</td>
<td>1.58</td>
<td>0.094*</td>
</tr>
<tr>
<td>YR 3 300 tph</td>
<td>17.03</td>
<td>5.4</td>
<td>53.69</td>
<td>2</td>
<td>low vs. mid</td>
<td>.91</td>
<td>.18</td>
<td>4.60</td>
<td>0.819</td>
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<tr>
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<td>5.95</td>
<td>59.23</td>
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<td>mid vs. high</td>
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<td>.09</td>
<td>2.30</td>
<td>0.171</td>
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<tr>
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<td>41.68</td>
<td>13.2</td>
<td>130.32</td>
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<td>low vs. high</td>
<td>.41</td>
<td>.08</td>
<td>2.08</td>
<td>0.142</td>
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<tr>
<td>YR 4 300 tph</td>
<td>43.38</td>
<td>6.61</td>
<td>286.29</td>
<td>2</td>
<td>low vs. mid</td>
<td>.86</td>
<td>.37</td>
<td>3.54</td>
<td>0.700</td>
</tr>
<tr>
<td>1360 tph</td>
<td>50.4</td>
<td>7.64</td>
<td>330.3</td>
<td>2</td>
<td>mid vs. high</td>
<td>.67</td>
<td>.16</td>
<td>4.73</td>
<td>0.340</td>
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<td>75.49</td>
<td>11.47</td>
<td>497.7</td>
<td>2</td>
<td>low vs. high</td>
<td>.57</td>
<td>.14</td>
<td>2.36</td>
<td>0.234</td>
</tr>
<tr>
<td>YR 5 300 tph</td>
<td>181.64</td>
<td>120.76</td>
<td>159.08</td>
<td>2</td>
<td>low vs. mid</td>
<td>.95</td>
<td>.88</td>
<td>1.83</td>
<td>0.627</td>
</tr>
<tr>
<td>1360 tph</td>
<td>190.51</td>
<td>126.71</td>
<td>286.43</td>
<td>2</td>
<td>mid vs. high</td>
<td>.79</td>
<td>.55</td>
<td>1.51</td>
<td>0.107</td>
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<tr>
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<td>241.58</td>
<td>160.68</td>
<td>363.22</td>
<td>2</td>
<td>low vs. high</td>
<td>.75</td>
<td>.52</td>
<td>1.08</td>
<td>0.078*</td>
</tr>
<tr>
<td>YR 6 300 tph</td>
<td>272.82</td>
<td>82.8</td>
<td>898.93</td>
<td>2</td>
<td>low vs. mid</td>
<td>1.03</td>
<td>.70</td>
<td>1.52</td>
<td>0.754</td>
</tr>
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<td>264.16</td>
<td>80.17</td>
<td>870.44</td>
<td>2</td>
<td>mid vs. high</td>
<td>.92</td>
<td>.62</td>
<td>1.35</td>
<td>0.446</td>
</tr>
<tr>
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<td>287.44</td>
<td>87.23</td>
<td>947.1</td>
<td>2</td>
<td>low vs. high</td>
<td>.95</td>
<td>.64</td>
<td>1.40</td>
<td>0.620</td>
</tr>
<tr>
<td>YR 7 300 tph</td>
<td>445.32</td>
<td>243.72</td>
<td>813.71</td>
<td>2</td>
<td>low vs. mid</td>
<td>1.21</td>
<td>.59</td>
<td>2.10</td>
<td>0.062°</td>
</tr>
<tr>
<td>1360 tph</td>
<td>367.42</td>
<td>201.08</td>
<td>671.36</td>
<td>2</td>
<td>mid vs. high</td>
<td>1.36</td>
<td>.98</td>
<td>1.51</td>
<td>0.025°°°</td>
</tr>
<tr>
<td>2960 tph</td>
<td>269.43</td>
<td>147.45</td>
<td>492.31</td>
<td>2</td>
<td>low vs. high</td>
<td>1.65</td>
<td>1.33</td>
<td>2.05</td>
<td>0.010°°°</td>
</tr>
<tr>
<td>YR 8 300 tph</td>
<td>659.64</td>
<td>433.59</td>
<td>1003.65</td>
<td>2</td>
<td>low vs. mid</td>
<td>1.4</td>
<td>1.00</td>
<td>1.95</td>
<td>0.050°</td>
</tr>
<tr>
<td>1360 tph</td>
<td>472.48</td>
<td>310.44</td>
<td>718.6</td>
<td>2</td>
<td>mid vs. high</td>
<td>1.59</td>
<td>1.14</td>
<td>2.23</td>
<td>0.027°°°</td>
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<tr>
<td>2960 tph</td>
<td>296.78</td>
<td>195.08</td>
<td>452.01</td>
<td>2</td>
<td>low vs. high</td>
<td>2.22</td>
<td>1.59</td>
<td>3.11</td>
<td>0.009°°°</td>
</tr>
</tbody>
</table>
Figure 1.4. Annual increase in $d^2h$ for trees in the low-, mid-, and high-density treatments. Error bars are standard errors of the estimate of the mean for 50 trees.
Analysis of $d^2h$ for trees representing largest 300 trees hectare$^{-1}$

To gain a better understanding of the potential benefits of increasing initial stocking density, an analysis was conducted of the trees representing the largest 300 trees hectare$^{-1}$ for each density treatment. At the 300 trees hectare$^{-1}$ thinning retention level, 100% of the trees in the low density treatment, 22% of the trees in the mid-density treatment, and 10% of the trees in the high-density treatment would be available for analysis. These respective retention levels will be referred to as post-thinning levels. This analysis is hypothetical since data are from stands in which thinning was not actually conducted. The following analysis was conducted by comparing increase in $d^2h$ of trees in the different density treatments represented by their upper post-thinning level percentages. Averaged across sites one and two, post-thinning increase in $d^2h$ in the high-density treatment was greater than that in the low-density treatment for all years analyzed (Table 1.5). The level of post-thinning increase in $d^2h$ for the mid-density treatment consistently occurred between that of the low- and high-density treatments, with the exception of the eighth year after planting in which post-thinning increase in $d^2h$ of the low-density treatment was greater than that of the mid-density treatment. The greatest observed difference in post-thinning increase in $d^2h$ occurred between the low- and high-density treatments in the second year after planting. Post-thinning increase in $d^2h$ for the high-density treatment in the second year after planting was 15 times that in the low-density treatment. Differences in post-thinning increase in $d^2h$ between the low- and high-
density treatments declined steadily over time since planting such that by the eighth year after planting, the post-thinning increase in $d^2h$ in the high-density treatment was only 10% greater than that of the low-density treatment (Table 1.5).

Table 1.5 Comparison of mean annual increase in $d^2h$ for 300 largest trees from low-, mid- and high-density treatments. Data are from trees in sites 1 and 2.

<table>
<thead>
<tr>
<th>Year</th>
<th>Stand Density</th>
<th>Trees Analyzed</th>
<th>% of Original Trees</th>
<th>Mean Increase in $d^2h$ (cm$^3$)</th>
<th>Treatment Comparisons</th>
<th>Difference in Treatments (cm$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>YR 2</td>
<td>300 tph</td>
<td>300</td>
<td>100</td>
<td>4.75</td>
<td>low vs. mid</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
<td>300</td>
<td>22</td>
<td>17.70</td>
<td>low vs. high</td>
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<tr>
<td></td>
<td>2960 tph</td>
<td>300</td>
<td>10</td>
<td>72.80</td>
<td>mid vs. high</td>
<td>55</td>
</tr>
<tr>
<td>YR 3</td>
<td>300 tph</td>
<td>300</td>
<td>100</td>
<td>17.55</td>
<td>low vs. mid</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
<td>300</td>
<td>22</td>
<td>49.59</td>
<td>low vs. high</td>
<td>128</td>
</tr>
<tr>
<td></td>
<td>2960 tph</td>
<td>300</td>
<td>10</td>
<td>145.53</td>
<td>mid vs. high</td>
<td>96</td>
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<tr>
<td>YR 4</td>
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<td>300</td>
<td>100</td>
<td>48.69</td>
<td>low vs. mid</td>
<td>134</td>
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<tr>
<td></td>
<td>1360 tph</td>
<td>300</td>
<td>22</td>
<td>182.62</td>
<td>low vs. high</td>
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<td>2960 tph</td>
<td>300</td>
<td>10</td>
<td>303.61</td>
<td>mid vs. high</td>
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<tr>
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<td>100</td>
<td>182.42</td>
<td>low vs. mid</td>
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<tr>
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<td>100</td>
<td>287.49</td>
<td>low vs. mid</td>
<td>243</td>
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<td>22</td>
<td>530.00</td>
<td>low vs. high</td>
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<td>300</td>
<td>10</td>
<td>719.00</td>
<td>mid vs. high</td>
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<tr>
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<td>100</td>
<td>451.04</td>
<td>low vs. mid</td>
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<td>300</td>
<td>22</td>
<td>721.78</td>
<td>low vs. high</td>
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<tr>
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<td>300</td>
<td>10</td>
<td>736.30</td>
<td>mid vs. high</td>
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<td>300</td>
<td>100</td>
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<td>low vs. mid</td>
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<tr>
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<td>22</td>
<td>519.00</td>
<td>low vs. high</td>
<td>65</td>
</tr>
<tr>
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<td>2960 tph</td>
<td>300</td>
<td>10</td>
<td>726.00</td>
<td>mid vs. high</td>
<td>207</td>
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</tbody>
</table>
Stable isotope analysis

An analysis of variance was conducted (SAS, 1996) to determine if there was a significant difference in stable carbon isotope ratios between the three density treatments for wood from the third and fourth years after planting. Carbon isotope analysis was not conducted on core samples from site three due to cost considerations and conclusive results from sites one and two. Data conformed to assumptions of constant variance and normal distribution. There were no significant differences in carbon isotopic composition among the three density treatments among sites one and two (Table 1.6 & Figure 1.5).

Table 1.6 ANOVA statistics for comparison of treatments for $\delta^{13}C$ isotopic composition for sites one and two.

<table>
<thead>
<tr>
<th>stand density</th>
<th>mean $\delta^{13}C$</th>
<th>SE</th>
<th>degrees of freedom</th>
<th>treatment comparisons</th>
<th>difference in treatments</th>
<th>SE</th>
<th>p-value for treatment comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 tph</td>
<td>-23.84</td>
<td>0.45</td>
<td>2</td>
<td>low vs.mid</td>
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<td>0.17</td>
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<tr>
<td>1360 tph</td>
<td>-23.78</td>
<td>0.45</td>
<td>2</td>
<td>mid vs.high</td>
<td>0.09</td>
<td>0.17</td>
<td>0.67</td>
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<td>2</td>
<td>low vs.high</td>
<td>0.03</td>
<td>0.17</td>
<td>0.92</td>
</tr>
</tbody>
</table>
Figure 1.5 $\delta^{13}$C of cellulose extracted from 2nd and 3rd years of stem growth from low-, mid-, and high-density treatment seedlings. Error bars are standard errors for mean fractionation values for 50 samples.
DISCUSSION

The results from the growth analyses indicate that initial stocking density had a significant effect on the growth of seedlings. Traditional ideas of the relationships between stand density and individual tree growth would lead one to expect a decrease in individual tree growth with higher stand density (e.g.: Hiley, 1959; Sjolte-Jorgensen, 1967; Evert, 1971; Dahms, 1973; Schmidt et al., 1976; Seidel, 1984; Lanner, 1985; Clark et al., 1994; Smith et al., 1997). Studies of single-species plant populations have shown a relationship between the maximum number of individuals that can occupy a site and the average size of the individuals. In these studies, the maximum number of plants of any given size that can exist on a site is correlated to the average individual plant biomass raised to the power of \(^{3/2} \) (Westoby, 1984). This relation has been termed the “self-thinning rule”.

This rule suggests that as trees grow larger, the competition for resources increases, and this level of competition will increase with increasing stand density. Once trees of a given density reach an average biomass of a certain level, the competition for resources is so intense that mortality ensues. Measurements conducted for this study, however, indicate that in early years of seedling growth not only was height growth positively correlated with initial stocking density, but diameter growth was as well. This trend reversed in later years resulting in decreased growth in stands of higher initial stocking density. The positive growth response to density occurred early. The greatest positive correlation between growth and density
occurred in the second year after planting. As time progressed, high initial density became less advantageous to growth, such that by the eighth year after planting diameter growth and increase in d²h was significantly lower in the high- and mid-density treatments than in the low-density treatment. This suggests two possible scenarios: the positive growth response to density is caused by a mechanism that only functions early on in the growth of seedlings, or the effects of greater competition from neighboring seedlings in the higher stocking densities negates any growth benefits derived from the still-functioning mechanism.

The lack of any significant differences in stable isotope signals from the three density treatments suggest that the observed differences in growth are probably not caused by any mechanism that operates primarily through changes in photosynthetic performance or availability of water or nutrients. This raises doubts about individual components of the various hypotheses proposed as main causes of a positive growth response to density. However, because the effects of nutrient availability would have the opposite effect of water availability on isotopic discrimination, situations involving a combination of these may have canceling effects on isotopic discrimination. This could result in a scenario in which increased moisture availability and increased nutrient availability are enhancing growth, yet their effects are not evident through stable isotope analysis. Another question that arises is whether the stable isotope analysis has the resolution required to pick up differences in past gas-exchange activity that could lead to differences in growth equivalent to what was found in my measurements.
A greenhouse study conducted on individually potted seedlings suggests that growth enhancement could be associated with above-ground allocation (Ritchie, 1997). Height, crown biomass, and branch number of Douglas-fir seedlings increased with decreasing growing space. Plant height was inversely correlated with estimated phytochrome photoequilibrium values. This study by Ritchie showed support for the hypothesis that the quality of light, altered due to reflectance from green leaves of neighboring individuals, may cause a phytochrome response, resulting in an adjustment of growth allometry in a way that reduces the possibility of being over-topped by adjacent competitors. However, a question arises from the phytochrome hypothesis that casts serious doubt upon it as the cause of enhanced growth with increased seedling density. How would seedlings be able to discriminate between trees and interspecific competition? Presumably such plants would also affect the R:FR ratio of light around trees, causing a phytochrome response in the adjacent seedlings. Ritchie suggests that seedlings may be able to identify different species as potential competitors or non-competitors due to variations in leaf reflectance properties and respond accordingly. Because the study was conducted in a greenhouse and involved individually potted and hand-weeded seedlings, it provides evidence of a positive growth response to density without differences in interspecific competition, browse damage, or mycorrhizal linkages. These interactions may still affect growth in the field. However, an unpublished study conducted by researchers at Weyerhauser Co. showed a positive growth response to stocking density even when
both understory vegetation was controlled, and fences were installed to restrict
browsing animals (Bill Scott, personal communication).

Observations soon after planting of seedling plots with variable stocking
densities make it difficult to imagine the true cause of positive growth response to
density in the first one to three years of growth. At one year after planting, the mean
seedling height of the trees measured for this study was less than one meter. At the
highest stocking density in which measurements were conducted (2960 trees hecare$^{-1}$),
seedling stems were at a distance of two meters apart from each other. The large
distance between trees relative to height illustrates that the observed positive growth
response to density is not a simple response to shading, even in the high stocking
density of 2960 trees hectare$^{-1}$.

Potential benefits of increasing stocking density are better understood when
considering pre-commercial thinning. Taking advantage of enhanced growth of
seedlings through increased density would necessitate a high initial stocking density.
If initial stocking density is high then a thinning is often desirable (Randall, 1971;
Smith et al, 1997). Planting a greater number of trees and a thinning both require
added expense. However, to obtain a single density following a thinning, the different
number of trees in the high- and low-density treatments results in the retention of a
different percentage of the originally planted trees. Pre-commercial thinning
applications often emphasize the retention of the larger and higher quality trees
(Smith et al., 1997). The high-density treatment will retain a lower percentage of the
originally planted trees, allowing for a greater level of selection of larger and higher-quality trees to retain for future harvest.

Tree mortality and spatial constraints of thinning are factors affecting post-thinning growth estimates that were not possible to incorporate in this analysis. The importance of relatively even spacing following thinning could force the removal of some of the larger trees during thinning. Scott et al. (1997) found slightly higher survival rates for five-year-old Douglas-fir in the highest of six different planting densities (300-, 590-, 890-, 1360-, and 2869-tree hectare\(^{-1}\)). However, depending on the time at which thinning is implemented, a significant amount of mortality could occur in a high-density treatment prior to thinning. For these reasons, actual differences in post-thinning growth between different stocking densities could vary from those levels determined here. However, it is important to realize that the differences in mean growth values between treatments presented earlier in this study are lower than what would be realized following the implementation of thinning simply because there are a greater number of trees in the higher density treatments.

The question arises as to whether the added expense of planting more trees and conducting a thinning is worth the benefits derived from enhanced growth through a positive response in seedlings to density in early years of growth. It is clear that the benefits of increasing initial stocking density are greater when considering pre-commercial thinning than when not taking this prescription into consideration.

For seedlings in an exponential growth phase, small changes in biomass partitioning or net carbon gain can lead to large differences in time-integrated growth.
However, if foresters are to take advantage of the positive growth response to density, it is important to understand what causes it and how plants respond to it physiologically. Increases in stocking density are already being implemented in certain areas of the coastal Pacific Northwest as a result of research indicating a positive growth response to density (Bill Scott, personal communication). These prescribed densities are based entirely on empirical information. Improved understanding of the mechanisms behind enhanced growth associated with increased density should allow more thoughtful analysis of the most cost-efficient approach for maximizing early growth. Additionally, a greater understanding of this phenomenon could lead to new ways of thinking about the physiology and biology of plant competition and interaction.
CHAPTER TWO

The Effects of Stand Density on the Canopy Boundary Layer and Microclimate
of Young Douglas-fir Stands.
ABSTRACT

My objectives were to determine the effects of stand density on the canopy boundary layer and microclimate characteristics of young Douglas-fir \textit{(Pseudotsuga menziesii)} stands. Measurements were conducted in stands of 5-year-old Douglas-fir trees in densities of 300 and 1360 trees hectare\(^{-1}\). \([\text{CO}_2]\), relative humidity, air temperature and wind speed were measured in a vertical profile at three heights in canopies (one, three and five meters) in order to gain information about how environmental conditions are affected by stand density. In order to quantify canopy boundary layer conductance \((g_{ac})\) for stands of different densities, evaporation rate of water from canopy foliage was measured. \(g_{ac}\) was calculated using a form of the Penman equation for evaporation. At one hour after sunrise, \([\text{CO}_2]\) in the high-density stand was 32.8 ppm greater than that in the low-density stand at the one-m height, 23.74 ppm greater at the three-m height, and 23.2 ppm greater at the five-m height. At one meter above ground, mean relative humidity, air temperature and wind speed were 143\%, 67\% and 13\% of that in the low-density treatment, respectively. Differences in all parameters between density treatments decreased with height in the canopy. \(g_{ac}\) in the low-density treatment for individual trees was 146\% of that in the high-density stand \((p = 0.0038)\). Canopy boundary layers may reduce atmospheric mixing, resulting in different concentrations of gases within than above the canopy. The higher morning \([\text{CO}_2]\) around plant foliage may function to increase morning photosynthetic rates. Stomata may respond to increased humidity by opening more
INTRODUCTION

Effects of Canopy Boundary Layer on Photosynthesis

Forest processes such as photosynthesis and transpiration, plant and soil respiration, and soil evaporation produce or deplete CO₂ and water vapor in the canopy atmosphere relative to the bulk atmosphere. Canopy boundary layers may reduce atmospheric mixing, resulting in different concentrations of gases within than above the canopy (Brooks et al., 1997). An even canopy surface, low wind speed, small plant stature, and increased plant density are all factors affecting boundary layer conductance (Monteith and Unsworth, 1990). Calm wind conditions at night result in minimal atmospheric mixing. CO₂ concentrations within a forest are highest at night due to soil and plant respiration, the lack of photosynthesis and low atmospheric mixing (Buchmann et al., 1996, 1998; Brooks et al., 1997; Anthoni et al., 1999). This condition may result in substantially higher CO₂ levels around plant foliage in short canopies with low canopy roughness and a low degree of coupling with the bulk atmosphere (Jarvis, 1976). A low boundary layer conductance could result in the maintenance of elevated CO₂ concentrations in the morning hours, before atmospheric mixing increases with increasing radiation and wind speed.
A low canopy boundary layer conductance can also increase humidity levels within a stand due to the decrease in loss of water vapor from plant transpiration and soil evaporation to above the canopy. Stomata may respond to increased humidity by opening more and or remaining open longer throughout the day, resulting in increased photosynthesis and/or increased photosynthetic water use efficiency (Waring and Winner, 1996; Harrington et al., 1994; Hall et al., 1993).

**Hypothesis**

The purpose of the study was to investigate the effects of stand density on the micro-climate and boundary layer of young conifer forests. My hypothesis was that stands of higher density generally have lower boundary layer conductance, especially during the night and morning. This lower canopy boundary layer conductance functions to “trap” morning high levels of respired CO₂ and transpired water vapor within the stand. The higher concentrations of CO₂ and H₂O may enhance photosynthesis within the higher density stands.

**Background: Canopy Boundary Layer**

When a fluid, such as air, flows over a surface the flow rate decreases towards that surface. The reduction in flow rate is caused by the friction between the fluid and the surface, as well as the viscous forces within the fluid (Monteith and Unsworth, 1990). A boundary layer is the area adjacent to a surface where the flow rate is greatly reduced below that of the free air stream. Conductance is the property of a system
which relates flux to concentration difference:

\[
\text{flux} = \text{conductance} \times (\Delta \text{concentration})
\]  \hspace{1cm} (2.1)

Boundary layer conductance is inversely proportional to its thickness, which is determined primarily by wind speed. The boundary layer conductance of a forest canopy \((g_{ac})\) is also strongly determined by properties of the canopy (Jarvis et al., 1976). When wind speed is high, the drag of the moving air reduces the thickness of the boundary layer and therefore effectively increases the conductance of this layer.

The pattern of fluid movement within a boundary layer may either be laminar, where all the fluid movement is parallel to the surface, or it may be turbulent. Transfer within laminar flow is primarily diffusional and thus driven by a concentration gradient; and transfer within turbulent flow is driven by random eddies and thus materials are transported directly in the moving air currents. A canopy boundary layer is generally turbulent (Jones, 1992).

Canopy boundary layer conductance is typically calculated from the momentum transfer equation (Monteith, 1965):

\[
g_{ac} = k^2 u_z / (\ln(z - d) / z_o)^2
\]  \hspace{1cm} (2.2)

Where: \(k\) = Von Karman's constant, \(u_z\) = wind speed at reference height \(z\), \(z\) = the reference height above the forest canopy where wind speed is measured, \(d\) = zero plane displacement height of the forest (0.78 x stand height), \(z_o\) = aerodynamic roughness length of the underlying forest canopy surface (0.075 x stand height), (empirical coefficients from Jarvis et al. 1976).
Wind speed and properties of the canopy are the primary determinants of canopy boundary layer conductance. The canopy parameters \( z_0 \) and \( d \) required to solve the above momentum transfer equation are only easily estimated for a closed canopy and even then they are quite variable (Jarvis et al., 1976). Very little research has been done on the effects of stand density on boundary layer conductance, and different estimates of \( d \) and \( z_0 \) have not been made for stands of variable stand density. There is therefore a great deal of uncertainty about the validity of the momentum transfer equation for trees in stands of lower density. As a result, this approach to the determination of \( g_{ac} \) has been regarded as impractical for stands of lower densities (Teklehaimanot et al., 1991).

An alternative method for calculating \( g_{ac} \) is with the use of the Penman equation for evaporation (Penman, 1948). The Penman equation can be represented by a linear equation of the form:

\[
E_t = \left[ \frac{\varepsilon (Q_n - S)/(\varepsilon + 1) \lambda}{(\varepsilon + 1) P_a} \right] + g_{ac} VPD/(\varepsilon + 1) P_a
\]

(2.3)

Where \( E_t \) is evaporation of intercepted water, \( \varepsilon \) is a coefficient for change in the ratio of sensible and latent heat contents of air with respect to temperature, \( Q_n \) is the net radiation absorbed, \( S \) is soil heat flux, \( \lambda \) is the molar latent heat of vaporization of water, \( VPD \) is water-vapor pressure deficit of the air, and \( P_a \) is atmospheric pressure.

Net radiation can be very difficult to measure or estimate in situations where trees are widely spaced. During evaporation of intercepted water from wet canopies, the available net radiation is typically small (Stewart, 1977) and evaporation is driven by
the saturation deficit (McNaughton and Jarvis, 1983). Teklehaimanot et al. (1991) showed only a small dependence of evaporation on the net radiation term of the Penman equation in a stand of Sitka spruce (*Picea sitchensis*). They found a much stronger dependence on the term containing the saturation deficit and boundary layer conductance. The exclusion of the radiation term in equation 2.3 leads to a simpler version of the Penman equation:

\[ E_t = \frac{g_{ac} \text{VPD}}{(\varepsilon + 1)\text{Pa}} \] 

We can rearrange this equation to solve for \( g_{ac} \):

\[ g_{ac} = \frac{(\varepsilon + 1)\text{Pa}E_t}{\text{VPD}} \] 

A mass exchange method was designed by Teklehaimanot et al. (1991) to measure evaporation rate directly by weighing a cut tree, suspended from a load cell, as water evaporated from the tree’s surface. The use of this method enables a direct calculation of canopy boundary layer conductance for stands of varying densities. This method was derived from three mass balance approaches previously developed. Roberts (1977, 1978) measured transpiration directly from large pine and spruce trees in the forest by cutting a tree trunk under water, suspending the tree, and measuring the amount of water being depleted from the reservoir in which the trunk was placed. Storage capacity of small trees was determined by Aston (1979) by measuring the increase in mass when the trees were sprayed with water in a laboratory. Hancock and Crowther (1979) measured the cantilever deflection of wetted branches with displacement transducers in order to measure the amount of water held by branches in a closed Sitka spruce canopy. These three methods combined led to the development
of the system used for this study to measure evaporation from foliage, thereby enabling one to quantify $E_1$.

METHODS

Site Location and Description

The study plot was located on Weyerhauser Co. land at Marcusson Creek, near Dryad, Washington (Figure 2.1), (latitude 46° 54' N, longitude 123° 25' W, elevation 125 m).

Figure 2.1 Map indicating location of Marcusson Creek field site.
The site is on parent material of sedimentary sandstone. The soils are classified as Haplohumults (reddish brown lateritic soils) (Franklin and Dyrness, 1988). The site was established in the spring of 1993 by Weyerhauser Co. with randomly selected two-year-old Douglas-fir (transplanted (1+1) nursery stock) planted at densities of 300, 1360, and 3000 trees hectare\(^{-1}\) (120, 550, and 1200 trees acre\(^{-1}\)). Seed source was an orchard mix of 50 families. Prior to planting, the site was sprayed to eliminate competition from brush and fenced to prevent browse damage. Brush control was conducted by hand cutting during the first three growing seasons following planting. All plots are approximately 0.4 hectares (one acre) in size. Site index (50 yr. height) is approximately 43 m (Bill Scott, personal communication). At time of measurements, trees were approximately five meters tall.

The maritime Pacific climate of the region is characterized by a wet winter and dry summer. The mean annual precipitation in Centralia WA, (32 - 42 km from the field sites) is 1200 mm. Approximately 90% of the precipitation falls between October and May, and the small amount of precipitation between June and September (~150 mm) creates potential summer drought conditions. The mean annual snowfall is 170 mm. Mean minimum temperature for January is 0.8°C, mean maximum temperature for July is 26°C (Western Regional Climate Center, 1998).

**Experimental design**

Measurements were blocked at the site for a total of three blocks. Within each block, two plots of different stocking densities were examined: 300 and 1360 trees hectare\(^{-1}\)
(120 and 550 trees acre\(^{-1}\)), referred to hereafter as low-, and high-density treatments. Measurements were conducted in one plot at a time due to logistical limitations. Different-density treatments were initially measured on separate half-days, and then on separate whole days.

Variations in weather conditions between measuring periods of different densities were accounted for by analyzing the differences in climatic variables relative to local weather station values. The weather station from which data was used for comparison with treatments was located at the Olympia airport (OLM, Lat: 46° 58'N, Long: 122° 54’W; Elevation: 60 m), located south of Olympia, WA, approximately 30 km from the nearest, and 40 kilometers from the most distant study site. Climatic conditions at the Olympia weather station were not identical to those at the research sites. The Olympia weather station was used as a reference, the offset of which was used to normalize for day-to-day differences in weather.

**Measurements**

*Evaporation from foliage*

Measurements were conducted during the summer of 1998. Low-density plots were measured on July 28th (morning), 29th (evening), and 30th (evening); August 25th, and 28th; and September 9th. High-density plots were measured on July 28th (evening), 29th (morning); August 26th, and 27th; and September 10th. Evaporation was measured directly using the mass exchange method designed by Teklehaimanot et al. (1991). In this method, rate of evaporation from foliage is measured directly by
weighing a saturated tree over the course of its drying. From plot center a location was selected at a random azimuth and a random distance between ¼ and ¾ of the distance from plot center to the plot boundary. These distance constraints were imposed in order to have a sufficient distance from plot center and the plot boundary. This was done to ensure sampling of a large portion of the plot, to avoid influencing relative humidity and temperature measurements being conducted at the center of the plot and to avoid edge effects. A complete tree was cut from a nearby stand and suspended with a 5-m tripod from a load cell (Futek model L1900 mini-beam load cell), and water was sprayed onto the tree from a fine spray nozzle. Water was supplied from a 121 liter tank using a 12 volt electric pump (Shurflo model 8000-943-236 diaphragm pump). Spraying was continued until the weight of the tree reached a maximum and remained constant for at least 60 seconds. Saturation typically required approximately ten minutes of continual spraying of all sides of the tree. The wetting process was then stopped and the tree was allowed to dry. The weight of the tree was recorded at 1-min intervals on a CR21X Datalogger (Campbell Scientific, Logan Utah).

The rate of evaporation was calculated over a time period that commenced ten minutes after spraying stopped, continuing until 75% of the total amount of water on the foliage had evaporated. In order to avoid recording water loss from dripping as evaporation, it was important to start recording evaporation at a time when water loss was from dripping was negligible. I chose a period of ten minutes after spraying stopped as a starting time for evaporation by observing graphs of the derivative of the
water loss from foliage (Figure 2.2). On the graph of the derivative of water loss against time, the point where the slope becomes level is the point where water loss is constant. Prior to this point the slope is steep, indicating rapid water loss from dripping. I monitored saturation and drying in real time using PC208W software on a laptop connected to the CR21X field recorder during measurements. The total wetting and drying procedure was conducted 4 times per day on a single cut tree. The same procedure was carried out in both the high- and low-density treatments in the three blocks. Evaporation from foliage was normalized by leaf area on an individual tree basis, as opposed to leaf area index.
Figure 2.2 Evaporation of water and first derivative of evaporation from foliage for one evaporation session in a high-density plot.
**Stomatal conductance measurements**

Stomatal conductance on five trees was measured in each density in each block. Stomatal conductance measurements were conducted concurrently with evaporation measurements. One-year-old foliage was measured from one branch in each cardinal direction for each tree with a Li-Cor 1600 porometer, for a total of four measurements per tree per evaporation measurement. After all measurements were complete for a plot, needles used for stomatal conductance measurements were harvested. Projected surface area of foliage was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Wash.).

**Microclimate measurements**

Air temperature, relative humidity, wind speed, and [CO$_2$] were recorded at three elevations within the canopy: one meter above soil surface, $\frac{1}{2}$ of the distance from the ground to the tree tops (three meters), and one above tree tops (five meters). The sampling equipment was secured to a mast placed at the center of each plot. Air temperature and relative humidity were recorded with Onset Hobo dataloggers at one-minute intervals. Wind velocity was measured with R.M. Young Wind Sentry anemometers at 15-second intervals and averaged and recorded at ten-minute intervals. CO$_2$ concentrations were measured with Li-Cor 6262 gas analyzers and recorded at ten-minute intervals. These micro-meteorological measurements were recorded continually for the 24-hour periods during which evaporation measurements were conducted with the suspended tree. However, I restricted my comparative
analyses to a one-hour average commencing two hours after sunrise. This time was selected because it occurred both during daylight when photosynthesis could take place and during a period when atmospheric mixing was still low.

RESULTS

CO₂ Concentration

Measurements of [CO₂] were conducted during two of the three measurement sessions. Averaged over two measurement sessions and over the time between two and three hours after sunrise, mean [CO₂] in the high-density stand was 8.89, 7.84, and 10.22 ppm greater than that in the low-density stand at one, three and five meters respectively. For the same two measurement sessions, averaged over the time between one and two hours after sunrise, mean [CO₂] in the high-density stand was 32.8, 23.74, and 23.2 ppm greater than that in the low-density stand at one, three and five meters respectively (Figures 2.3 & 2.4). Due to the limited sampling size statistical analysis was not possible for [CO₂].
Figure 2.3 [CO$_2$] for high- and low-density stands at heights of one, three and five meters and wind speed at five meters for block 2. Vertical line indicates time of sunrise.
Figure 2.4 [CO$_2$] for high- and low-density stands at heights of one, three and five meters and wind speed at five meters for block 3. Vertical line indicates time of sunrise.
The effects of stocking density on environmental parameters such as relative humidity, temperature, and wind speed were assessed by analyzing the differences in these variables between the study plots and values from a local weather station. In the comparison of climatic parameters between the two different density treatments, the null hypothesis is that there is no effect of planting density on conditions. For measurements of climatic parameters for each height analyzed, a separate t-test was conducted (SAS, 1996) to determine if there were differences among the two density treatments for each height within the canopy, and the average of the values from all heights. Reports of “significance” refer to the $\alpha$ level of 0.1.

**Relative Humidity**

Significant differences in mean relative humidity were observed among the two density treatments between two and three hours after sunrise. The greatest observed difference in relative humidity occurred at the one-m height. Mean relative humidity at the one-m height in the high-density treatment was 143% of that in the low-density treatment. Relative humidity was 8.96% greater within the high-density treatment, and 15.66% lower in the low-density treatment when compared to station values for concurrent days.

Significantly greater mean relative humidity in the high-density treatment occurred at the one- and three-m heights; as well as the average of all heights. This
positive humidity response to density declined with height such that at the five-m height no significant difference occurred between low- and high-density treatments (Table 2.1, Figure 2.5).

<table>
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<tr>
<th>height within canopy</th>
<th>stand density</th>
<th>relative humidity (plot-station)</th>
<th>SE (mean)</th>
<th>Degrees of freedom</th>
<th>difference in treatments (%)</th>
<th>SE (treatment difference)</th>
<th>p-value for treatment comparisons</th>
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<td>3.73</td>
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Table 2.1. Differences in mean relative humidity between weather station values and low-, and high-density measurement plots at one-, three- and five-m heights. Measurements are mean values between two and three hours after sunrise. P-values are indicated and significance levels are highlighted by *** P < 0.01; ** P < 0.05; * P < 0.1.
Figure 2.5 Differences in mean relative humidity between weather station values and measurement plots at one-, three- and five-m heights. Measurements are mean values between two and three hours after sunrise. Error bars are standard errors for three sampling sessions per density.
Temperature

Mean air temperature was significantly greater at one-m height in the low-density stand compared with the high-density stand between two and three hours after sunrise. The greatest observed difference in temperature occurred at the one-m height. Mean temperature at the one-m height in the high-density treatment was 67% of that in the low-density treatment. Compared with the Olympia weather station for concurrent times, temperature was 0.56° greater within the high-density treatment and 4.22° greater in the low-density treatment. There were no significant temperature differences at three and five m heights, nor for the average of all heights (Table 2.2, Figure 2.6).

Table 2.2 Differences in mean air temperature between weather station values and low-, and high-density measurement plots at one-, three- and five-m heights. Measurements are mean values between two and three hours after sunrise. P-values are indicated and significance levels are highlighted by ***(P < 0.01; **(P < 0.05; *P < 0.1.

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<th>degrees of freedom</th>
<th>difference in treatments (°C)</th>
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<td>0.97</td>
<td>1.73</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>AVG</td>
<td>300 tph</td>
<td>3.40</td>
<td>0.32</td>
<td>4</td>
<td>2.44</td>
<td>1.68</td>
<td>0.221</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
<td>0.95</td>
<td>1.65</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.6 Differences in mean air temperature between weather station values and measurement plots at one-, three- and five-m heights. Measurements are mean values between two and three hours after sunrise. Error bars are standard errors for three sampling sessions per density.
Wind speed

No statistically significant differences in wind speed were observed between the two densities. However, this lack of significance appears to be due to a high degree of variance within sample populations. Large differences were observed in mean wind speed between the two density treatments. The greatest contrast in wind speed occurred at the one-m height. Mean wind speed at the one-m height in the high-density treatment was 13% of that in the low-density treatment. Mean wind speed at the one-m height was 1.25 m s\(^{-1}\) lower within the high-density treatment and 0.26 m s\(^{-1}\) lower in the low-density treatment when compared to station values for concurrent days. The largest difference in wind speed occurred at the three-m height. Mean wind speed at the three-m height in the high-density treatment was 0.86 m s\(^{-1}\) lower within the high-density treatment, and 0.48 m s\(^{-1}\) greater in the low-density treatment when compared to station values for concurrent days (Table 2.3, Figure 2.7).
Table 2.3. Differences in mean wind speed between weather station values and low-, and high-density measurement plots at one-, three- and five-m heights. Measurements are mean values between two and three hours after sunrise.

<table>
<thead>
<tr>
<th>height within canopy</th>
<th>stand density</th>
<th>wind speed (plot - station)</th>
<th>SE (mean)</th>
<th>degrees of freedom</th>
<th>difference in treatments (m/s)</th>
<th>SE (treatment difference)</th>
<th>p-value for treatment comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 M</td>
<td>300 tph</td>
<td>-0.26</td>
<td>0.36</td>
<td>4</td>
<td>0.98</td>
<td>0.96</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
<td>-1.26</td>
<td>0.93</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 M</td>
<td>300 tph</td>
<td>0.48</td>
<td>0.19</td>
<td>4</td>
<td>1.33</td>
<td>1.06</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
<td>-0.86</td>
<td>1.05</td>
<td>4</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>5 M</td>
<td>300 tph</td>
<td>0.96</td>
<td>0.38</td>
<td>4</td>
<td>1.31</td>
<td>1.20</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>1360 tph</td>
<td>-0.35</td>
<td>1.13</td>
<td>4</td>
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<tr>
<td>AVG</td>
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<td>0.11</td>
<td>4</td>
<td>1.21</td>
<td>1.04</td>
<td>0.31</td>
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<tr>
<td></td>
<td>1360 tph</td>
<td>-0.82</td>
<td>1.04</td>
<td>4</td>
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<td></td>
</tr>
</tbody>
</table>
Figure 2.7 Differences in mean wind speed between weather station values and measurement plots at one-, three- and five-m heights. Measurements are mean values between two and three hours after sunrise. Error bars are standard errors for three sampling sessions per density.
Evaporation Rate

Significant differences in mean evaporation rates were observed between the two densities. Mean evaporation rate in the low-density treatment was 164% of that in the high-density treatment. (Table 2.4, Figure 2.8).

Table 2.4 ANOVA statistics for comparisons of mean evaporation rates for low-, and high-density treatments. *P*-values are indicated and significance levels are highlighted by *** *P* < 0.01; ** *P* < 0.05; * *P* < 0.1.

<table>
<thead>
<tr>
<th>stand density</th>
<th>evaporation rate (mmol m$^{-2}$ s$^{-1}$)</th>
<th>SE (mean)</th>
<th>degrees of freedom</th>
<th>difference in treatments (mmol m$^{-2}$ s$^{-1}$)</th>
<th>SE (treatment difference)</th>
<th><em>p</em>-value for treatment comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 tph</td>
<td>6.23</td>
<td>0.412</td>
<td>27</td>
<td>-1.99</td>
<td>0.59</td>
<td>0.0024***</td>
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<tr>
<td>1360 tph</td>
<td>4.24</td>
<td>0.426</td>
<td>27</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.7 Evaporation of water from foliage in high- and low-density stands.
Boundary Layer Conductance

Significant differences in mean boundary layer conductance were observed between the two densities. Mean boundary layer conductance in the high-density treatment was 68% of that in the low-density treatment. (Table 2.5, Figure 2.9).

Table 2.5 ANOVA statistics for comparisons of mean boundary layer conductance for low- and high-density treatments. P-values are indicated and significance levels are highlighted by *** P < 0.01; ** P < 0.05; * P < 0.1.

<table>
<thead>
<tr>
<th>stand density</th>
<th>$g_{bc}$ (mol m$^{-2}$ s$^{-1}$)</th>
<th>SE (mean)</th>
<th>degrees of freedom</th>
<th>difference in treatments (mol m$^{-2}$ s$^{-1}$)</th>
<th>SE (treatment difference)</th>
<th>p-value for treatment comparisons</th>
</tr>
</thead>
<tbody>
<tr>
<td>300 tph</td>
<td>1.686</td>
<td>0.116</td>
<td>27</td>
<td>-0.532</td>
<td>0.168</td>
<td>0.0038***</td>
</tr>
<tr>
<td>1360 tph</td>
<td>1.154</td>
<td>0.121</td>
<td>27</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Figure 2.9 Mean $g_{ac}$ for blocks one, two and three. Bars are standard errors for three, eight, and four sampling sessions per density for blocks one, two and three respectively.
DISCUSSION

Exchanges of water vapor and CO$_2$ between plant leaves and the atmosphere play a significant role in forest tree growth and physiology. The transfer of matter, heat and momentum between forests and the environment is strongly influenced by $g_{ac}$. Most analyses of the dynamics of transfer between forest canopies and the atmosphere have used the momentum transfer equation to solve for $g_{ac}$ (Monteith, 1965; Jarvis et al., 1976; Jones, 1992).

This method is unsuitable for forests of low density because key parameters are empirically derived from high-density stands and are difficult to determine for stands of widely spaced trees. When comparing stands of different densities, the ineffectiveness of determining $g_{ac}$ with the momentum transfer equation can be illustrated with the following example. A stand of trees, approximately five meters tall, in a density of 3000 trees hectare$^{-1}$ is adjacent to a stand of trees, roughly the same height, planted in a density of 300 trees hectare$^{-1}$. Wind speed is measured at a height of eight meters and is equal for both stands at 3 m s$^{-1}$. The momentum transfer equation yields a value of 1.4 mol m$^{-2}$ s$^{-1}$ for both stands. Direct measurements by ourselves and others (Whitehead et al., 1984; Teklehaimanot et al. 1991; Green, 1995; Asdak et al., 1998) indicate that $g_{ac}$ for the two different stands are typically not equal.

I found that free surface evaporation of individual trees per unit leaf area and $g_{ac}$ in the high-density stands were significantly lower than that in the low-density stands ($p = 0.0024$, and 0.0038, respectively). Evaporation from the high-density
stand was $4.24 \times 10^{-4}$ mol m$^{-2}$ s$^{-1}$, and $6.23 \times 10^{-4}$ mol m$^{-2}$ s$^{-1}$ from the low-density stand. $g_{ac}$ for the high-density stand was $1.15 \times 10^{-4}$ mol m$^{-2}$ s$^{-1}$, and $1.69 \times 10^{-4}$ mol m$^{-2}$ s$^{-1}$ from the low-density stand. This suggests that the capacity for vertical mixing and turbulent exchange between canopy and the atmosphere is decreased as density increases. Measurements of wind speed, relative humidity and [CO$_2$] support this finding. During morning measurement periods, [CO$_2$] and relative humidity in the high-density stands were substantially higher than in the low-density stands for all three measurement heights within the canopy. However, weather station data showed that the conditions in the bulk atmosphere were not significantly different between the times when I conducted measurements in the low- and high-density stands. The positive correlation of [CO$_2$] and water vapor with density overnight and in the morning are in accord with the hypothesis that $g_a$ decreases as canopy density increases. Morning wind speeds and temperatures within the low-density stands were greater than those in the high-density stands. Because wind speed is a key determinant of turbulence in a canopy, this is a further indicator of the enhancement of mass exchange from the canopy with decreased stand density.

Within the canopy of the high-density stands, CO$_2$ that was respired during the night did not immediately mix with the bulk atmosphere, allowing a substantial build-up. These concentrations were substantially larger than those within the low-density stands. Above-ambient [CO$_2$] (ambient ~360 ppm) persisted two and a half to three hours after sunrise within the high-density stands, potentially increasing photosynthesis. The decreased $g_{ac}$ of the high-density stands also resulted in significantly higher water-vapor concentrations than those in the low-density stand,
presumably in response to decreased loss of water vapor from plant transpiration and soil evaporation to the bulk air. This concentration of water vapor increased from top to bottom of the canopy, and the slope was steeper in higher density compared with low-density stands overnight and in the morning.

Few other studies have investigated the effect of tree spacing on \( g_{ac} \) (Teklehaimanot et al. (1991); Green et al. (1995); Asdak et al. (1998)). Two approaches have been used for determining canopy boundary layer conductance: per tree \( (g_{ac}) \), and per unit ground area \( (g_{acg}) \). Studies investigating \( g_{acg} \) typically indicate a decrease with an increase in tree spacing. Those using the individual tree approach typically find the opposite. Asdak et al. (1998) calculated \( g_{acg} \) for unlogged and logged stands of tropical rainforest. Mean \( g_{acg} \) for the unlogged stands was found to be 0.31 m s\(^{-1}\). In the logged stands, \( g_{acg} \) was calculated for the areas of closed canopy, partial canopy, and canopy gap. They found the average of \( g_{acg} \) to be 0.29 m s\(^{-1}\), 0.18 m s\(^{-1}\), and 0.13 m s\(^{-1}\) respectively. This study also found however, that thinning in tropical rain forests led to the creation of gaps, which allowed more wind to penetrate and resulted in an increase in turbulent flow. Green (1995) found that within-canopy wind speeds increased with spacing and that there were increases in turbulence parameters, such as tangential momentum stress \( (\mu/\nu^*) \) and turbulence velocity components \( (\nu/\nu^*) \) in stands of Sitka spruce. These are factors that would increase \( g_{ac} \). Teklehaimanot et al. (1991) used both approaches in their study of 18-m tall Sitka spruce. They found that \( g_{acg} \) declined from 0.24 m s\(^{-1}\) to 0.09 m s\(^{-1}\) as the density of trees decreased from 2-m spacing to 8-m spacing. However, \( g_{ac} \) increased with
spacing from 0.82 m$^3$ s$^{-1}$ in the 2-m spacing treatment to 5.92 m$^3$ s$^{-1}$ in the 8-m spacing. My study shows the same effect for stands of young Douglas-fir. Direct measurements of [CO$_2$] and [H$_2$O vapor] in stands of different densities support the results of my calculations of $g_{ac}$.

The distinction between $g_{ac}$ and $g_{sec}$ is important because the greater number of trees in a stand of higher density means a greater leaf surface area from which transpiration and evaporation may occur. Although the whole-stand level approach accurately reports the relative amount of moisture transfer from the stand to the bulk atmosphere, it over estimates the relative capacity of a high-density stand for aerodynamic momentum transfer.

The more even canopy surface and lower wind speeds in high stand-density decrease $g_{ac}$. A decrease in tree spacing may function to increase the aerodynamic roughness depth ($z_o$) of the stand. As the spacing between trees increases, the area where vertical free-flow of mass may occur increases as well. In other words, the gaps between trees provide areas where turbulent mixing with the above atmosphere may occur.
CONCLUSION

My objectives were to determine the effects of stocking density on growth of Douglas-fir seedlings, to examine how these effects changed over time and to determine the effects of stand density on $g_{ac}$ and micro-climate characteristics of young conifer forests. I found that substantially greater growth was initially associated with higher stocking levels. Over time, higher stocking levels were associated with lower growth, presumably in response to the effects of competition from neighboring trees in the higher density treatments. The analysis of stable isotopes suggests no significant differences in the effects of soil water content, or nutrient availability on photosynthesis in the three stocking densities, thus providing evidence against several environmental and ecological factors as likely causes of a positive growth response to density.

This study has shown both higher $g_{ac}$ and higher nighttime $[CO_2]$ around foliage for trees in high-density stands. Elevated $[CO_2]$ persisted into daylight, potentially increasing morning photosynthetic rates. Increased humidity levels were also observed in stands of high-density, presumably in response to the decrease in loss of water vapor from plant transpiration and soil evaporation to above the canopy. Stomata may respond to increased humidity by opening more and/or remaining open longer throughout the day, resulting in increased photosynthesis and/or increased photosynthetic water-use-efficiency.
BIBLIOGRAPHY


