AN ABSTRACT OF THE THESIS OF

Heidi J. Renninger for the degree of Master of Science in Wood Science and Forest Science presented on November 11, 2005.

Title: Effects of Release from Suppression on Hydraulic Architecture, Photosynthetic Capacity and Functional Wood Characteristics in Douglas-fir and Western Hemlock.

Abstract approved:

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Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a shade intolerant species, and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), a shade tolerant species, were compared to learn more about the temporal pattern of release from suppression in both species, whether hydraulic architecture or photosynthetic capacity constrain release and how wood functional properties change after release from suppression. The study was conducted in 10-20 year old Douglas-fir and western hemlocks, either in a site that had been thinned to release suppressed trees or in a site that remained unthinned. Douglas-fir had lower height growth (from 1998-2003) and lower relative height growth (height growth from 1998-2003/height in 1998) than western hemlock. However, the relative height growth of released vs. suppressed trees was much higher in Douglas-fir (130%) than western hemlock (65%), suggesting that although height growth was lower, Douglas-fir did indeed release from suppression.

Release seems to be constrained initially by photosynthetic capacity in Douglas-fir and western hemlock. In Douglas-fir released trees had 14 times the leaf

area and 1.5 times the nitrogen per unit leaf area (N_{area}) as suppressed trees. Needles

on released western hemlock trees had approximately twice the maximum assimilation

rate (A_{max}) at ambient [CO_2] as suppressed trees and did not exhibit photoinhibition at

the highest light levels. Hydraulic architecture appears to constrain further release

from suppression in Douglas-fir more so than western hemlock after the increase in

leaf area, leaf N content and overall photosynthetic capacity. Released trees had

significantly less negative foliar $\delta^{13}C$ values and there was also a positive relationship

between leaf area:sapwood area ratios and $\delta^{13}C$ suggesting that trees with more leaf

area for a given sapwood area experienced a stomatal limitation on carbon gain.

Growth of released trees, thus, may have been limited by stomatal constraints on

carbon gain despite a doubling of A_{max} after release. Nonetheless, trees exhibited no

significant differences between the leaf-specific conductivities (K_L) of suppressed vs.

released trees of either species. However, leaf-specific root conductance (k_{RL}) was

significantly greater in suppressed Douglas-fir compared to released trees.

Functional wood characteristics were also much different in trees released

from suppression and those that remained suppressed. Growth ring widths in released

trees increased by 370% for Douglas-fir and 300% for western hemlock, while

specific conductivity (K_s) increased by 182% for Douglas-fir and 42% for western

hemlock compared to suppressed trees. Earlywood width was approximately four

times greater in released than suppressed trees of both species, whereas the relative

increase in latewood width between suppressed and released trees was much greater in

Douglas-fir than in western hemlock. Latewood proportion decreased by 21% in

released Douglas-fir and by 47% released western hemlock compared to suppressed

trees. Tracheids were 25% wider and 11% longer in released Douglas-fir saplings than suppressed saplings, whereas in western hemlock released saplings had 19% wider tracheids that were approximately the same length as suppressed saplings. Wood moisture content was 66% higher in released Douglas-fir compared to suppressed Douglas-fir and 41% higher in released western hemlock compared to suppressed western hemlock. Wood density decreased from 0.57 to 0.47 g cm^{-3} in Douglas-fir trees released from suppression and from 0.50 to 0.45 g cm^{-3} in western hemlock trees released from suppression. Therefore, it appears that as management patterns switch from even-age systems to uneven-age systems, both Douglas-fir and western hemlock will be able to release from suppression and the wood of released trees will be of good quality for most applications.

Effects of Release from Suppression on Hydraulic Architecture, Photosynthetic
Capacity and Functional Wood Characteristics in Douglas-fir and Western Hemlock

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

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CONTRIBUTION OF AUTHORS

Barbara L. Gartner and Frederick C. Meinzer assisted with design, interpretation of

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CHAPTER 1: INTRODUCTION

RELEASE FROM SUPPRESSION

Saplings growing in the shade of the overstory are said to be suppressed and, when exposed to increased light by removal of part of the overstory, are released from suppression. Suppressed trees have been shown to grow more slowly and erratically in the understory than dominant trees (Kozlowski and Peterson, 1962). Suppressed trees can be a very important source of potential regeneration within a natural forest because, as gaps are created, these saplings can eventually become a part of the overstory. The ability of suppressed trees to release quickly is important because recent canopy gaps are rare in a natural forest (Canham, 1989). In the Pacific Northwest, recently formed gaps represent 0.7% of the forest in mature stands and 0.2% in old growth stands (Spies et al., 1990). Therefore, the ability of a particular tree species to survive in a suppressed state and, in turn, release quickly enough to outcompete its neighbors increases the probability that these species will be more successful as the forest matures. However, some suppressed trees are unable to release immediately and may take several years before they show signs of increased growth. Van Pelt and Franklin (1999) found that branch growth actually decreased immediately following release: it was not until three years following release that trees finally began growing more rapidly. Also, less shade tolerant species show a lag in response to release, particularly if they had been suppressed for a long period of time (Wright et al., 2000).

Because gaps are not common in natural forests, trees may need to spend prolonged periods in a suppressed state. Silver fir (*Abies alba* Miller) and Norway spruce (*Picea abies* (L.) Karst.) have been shown to withstand periods of suppression of 150 years or more and still retain the ability to release from suppression (Ferlin, 2002). However, the ability to tolerate shade and remain in a suppressed state has been shown to decrease as a tree gets older because the ratio of photosynthetic to nonphotosynthetic tissues declines as trees age (Canham, 1989). Furthermore, suppressed trees may not reach the top of the canopy immediately following suppression. For example, in sugar maple (*Acer saccharum* Marsh.) forests, it may take several release events in order for once suppressed trees to reach the upper canopy position (Canham, 1985). Therefore, trees in a natural forest may need to withstand multiple periods of suppression before they reach the top of the canopy.

Understanding suppression and release is also important in managed forests. Social, political and ecological concerns about even-aged, plantation forests have made uneven-aged, two-story stands increasingly important in the Pacific Northwest. These stands will make periods of suppression and release more prevalent in canopy recruitment (Wright et al., 2000). Likewise, differences between tree species in their ability to release from suppression are important. Species composition in uneven-aged systems may shift toward species that are able to more quickly release from suppression (Tesch and Korpela, 1993).

Trees released from suppression may have differing wood properties compared to those grown in open conditions during the beginning of their lives. This will be

important if these trees comprise the future crop potential of the stand. For example, trees that are suppressed during the period in which they are producing juvenile wood in their lower stem will have a much smaller juvenile core and a reduced proportion of juvenile wood at harvest compared with trees grown in open conditions (Cregg et al., 1988, Watson et al., 2003). Also, because suppressed trees have grown slowly, they exhibit tight growth rings, small knots and straight stems which could make them suitable for use in value-added products (LeVan-Green and Livingston, 2001). However after trees are released from suppression and their growth rates are increased, wood properties may change making trees less desirable for wood utilization purposes. For example, Dutilleul et al. (1998) found that fast-growing spruces exhibited a negative correlation between ring width and fiber length and between ring width and wood density, especially in juvenile wood. Zahner and Oliver (1962) also found that the transition from earlywood (less dense) to latewood (more dense) was delayed by thinning by about two to three weeks, meaning wood produced in these growth rings was less dense. Wood density is highly correlated with many important wood quality properties.

COMPARISON OF DOUGLAS-FIR AND WESTERN HEMLOCK

In this study, release from suppression was compared in both Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees. Douglas-fir/western hemlock forests dominate many regions of Oregon west of the Cascade Mountains. Western hemlock is likely to be found in codominant, intermediate, or suppressed forms (making up the regeneration potential

for the stand), while Douglas-fir is likely to be the dominant species in the forest (Spies et al., 1990, Huff, 1995). This relationship can, however, be reversed if disturbance is reduced in the system. Douglas-fir is losing dominance to western hemlock in some old-growth stands where Douglas-fir accounts for one third of the growth and one half of the mortality as compared to western hemlock which accounts for one half of the growth and about one fourth of the mortality (DeBell and Franklin, 1987). Munger (1940) also found that in stands under 70 years of age, there were more than twice as many Douglas-fir trees as western hemlock, whereas this relationship was reversed in stands over 110 years of age. Since Douglas-fir, an early-successional species, and western hemlock, a late-successional species, have differing roles in the forest ecosystem, one might expect them to exhibit differing growth rates following partial removal of the overstory and release from suppression.

Traditionally, Douglas-fir is considered less shade tolerant than western hemlock (Minore, 1979). Pioneer species (like Douglas-fir) tend to be most successful in large gaps while climax, shade tolerant species (like western hemlock) can regenerate and grow under the forest canopy (Whitmore, 1989). Because Douglas-fir and western hemlock differ in shade tolerance, their ability to grow in a suppressed state and successfully release from suppression should also differ. Shade tolerant species can grow for extended periods of time with a marginal carbon balance compared with less shade tolerant species (Kobe and Coates, 1997). Conversely, less shade tolerant species may be better able to release from suppression. Wright et al. (2000) found that less shade tolerant species exhibited declines in growth rate during

suppression, the effects of suppression eventually disappeared after release. Likewise, growth rate during suppression does not decline in the most shade tolerant species, but these species also did not show increases in growth rate after release.

Comparison of Rooting Characteristics

Because water uptake and nutrient acquisition are primarily performed by the root system of trees, differences in the root systems of Douglas-fir and western hemlock may affect their abilities to grow in a suppressed state and to release from suppression. Western hemlock and Douglas-fir seedlings both initially exhibit a single well-developed taproot (Eis, 1974). However, Douglas-fir develops a deeper rooting depth than western hemlock, making it more drought tolerant (Minore, 1979). Although Douglas-fir tolerates drought better, western hemlock can tolerate excess moisture better (Minore, 1979). Western hemlock also tends to have more fine roots than Douglas-fir, while Douglas-fir tends to have roots of larger diameter and proportionally greater weight than western hemlock (Eis, 1974). Differences in root weight could also correspond to differences in storage capacity of the root systems. DeLucia et al. (1998) found that black cherry (*Prunus serotina* Ehrh.) had higher than average stores of carbohydrates in its taproot and that these stores of carbohydrates allowed the trees to better take advantage of sudden gaps in the understory.

Comparison of Photosynthetic Characteristics

Light provides energy that is used by plants to perform photosynthesis, a process that transforms light energy into chemical energy. However, light may be very limiting for trees growing in suppressed form in the forest understory. Douglas-

fir and western hemlock may have differing abilities to take advantage of limited light. Douglas-fir has greater needle volume and weight and a higher concentration of nitrogen in its needles than western hemlock (Minore, 1979, Bond et al., 1999). Douglas-fir also has higher maximum assimilation rates per unit leaf area (A_{max}), higher dark respiration rates, a higher light compensation point and higher leaf mass per unit leaf area (LMA) than western hemlock (Bond et al., 1999, Lewis et al., 2000). All of these characteristics should make Douglas-fir more successful in well-lit environments compared to shaded environments. Lewis et al. (2000) also found that western hemlock had higher net photosynthetic rates at lower photosynthetically active radiation (PAR) levels, while Douglas-fir had higher net photosynthetic rates at higher PAR levels.

Shade tolerant species also seem to show more plasticity in their photosynthetic apparatus under differing light environments than shade intolerant species (Teskey and Shrestha, 1985, Kubriske and Pregitzer, 1996). Bond et al. (1999) found that LMA increased by 100% in western hemlock in branches exposed to sun vs. shade whereas LMA in Douglas-fir increased by 86%. However, they also found that leaf properties most sensitive to PAR responded similarly in both species in that relationships were similar even though absolute values differed. This would lead to the conclusion that the two species have a similar plasticity in terms of photosynthetic apparatus. Differences in species ability to tolerate shade differ in different periods of their development. For example, Khan et al. (2000) found that

Douglas-fir and western hemlock seedlings growing under four different levels of shade responded similarly.

Comparison of Hydraulic Architecture and Wood Properties

Hydraulic architecture describes the movement of water from the roots to the leaves and the relationship between the water-conducting conduits (both below and aboveground) within a tree and the amount of water required to support a given quantity of foliage (Tyree and Ewers, 1991, Cruiziat et al., 2002). Therefore, hydraulic architecture should be important as trees released from suppression increase their leaf areas to take advantage of the increased light. Douglas-fir and western hemlock tend to differ in their amounts of sapwood relative to the total basal area of their stems. Marshall and Waring (1986) found that sapwood area for Douglas-fir trees that were larger than 100 cm in diameter ranged from 5-22 % of the total basal area compared to 34-67 % of the total basal area for western hemlock at 1.37 meters from the ground. However, Waring et al. (1982) also noted that Douglas-fir and western hemlock had very similar leaf area:sapwood area ratios (A_L/A_S)(0.54 m^2 cm^{-2} and 0.46 $m^2 cm^{-2}$ respectively).   During suppression, however, A_L/A_S could be altered. For example, Douglas-fir has been found to respond to low light levels by limiting the number of branches in its live crown (Williams et al., 1999). This implies that A_L/A_S would be lower in suppressed Douglas-fir trees than in trees grown in open conditions.

Although the ratio of leaf area to sapwood area is an important component of hydraulic architecture, the conductivity of the sapwood is also important. Bond and Kavanagh (1999) reported that western hemlock had slightly lower leaf-specific

conductivity (K_L) than Douglas-fir (0.7 and 1.1 mmol H_2O m^{-2} s^{-1} MPa^{-1} respectively), but similar minimum water potentials (-2.1 MPa). Because of the K_L and the equivalent minimum water potential, stomatal conductance of western hemlock was found to be more sensitive to humidity than Douglas-fir (Bond and Kavanagh, 1999). Western hemlock seedlings were also found to be more vulnerable to embolism than Douglas-fir (Kavanagh and Zaerr, 1997).

Changes in wood properties with cambial age also differ between Douglas-fir and western hemlock. For example, Douglas-fir density is high in the first few growth rings, decreases sharply, then begins to climb steadily until reaching a relatively constant value at age 20-25, which corresponds to the transition from juvenile wood to mature wood (Megraw, 1985, Kennedy, 1995). DeBell et al. (2004) found that western hemlock density was also highest near the pith (about 0.49 g cm^{-3}), declined to 0.4 g cm^{-3} at age 10, remained stable to age 25, then increased gradually and remained between 0.43 g cm^{-3} and 0.44 g cm^{-3} from age 38 and beyond.   Douglas-fir tracheid diameter increases for approximately the first 10 years then remains relatively constant (Spicer and Gartner, 2001), while tracheid length increases for approximately the first 30 to 40 years before becoming relatively constant (Megraw, 1985, Fabris, 2000).

RESEARCH QUESTIONS AND HYPOTHESES

The first research question in this study addresses whether Douglas-fir can release from suppression as effectively as western hemlock. There are several lines of evidence showing that Douglas-fir trees experience a lag between the time of thinning

and when the residual trees exhibit increased growth rates (Staebler, 1956, Van Pelt and Franklin, 1999, Kneeshaw et al., 2002). For example, Kneeshaw et al. (2002) found that stem growth did not significantly increase until two years after the thinning treatment, while height growth decreased the first year after thinning and did not increase until two years after the thinning treatment. Also, Van Pelt and Franklin (1999) found that the number of years needles were retained decreased for Douglas-fir trees recently released from suppression. There is also some evidence that Douglas-fir growth rate increases after a thinning intended to release suppressed trees. Chen et al. (1992) found that Douglas-fir exhibited increased growth rates following release from suppression, although growth was not as pronounced as in similarly released western hemlock trees.

The second research question addressed in this study was whether photosynthetic capacity or hydraulic architecture (both below- and above-ground) constrain release from suppression. Several lines of evidence suggest that photosynthetic capacity could constrain release. For example, delays in release following suppression may relate to the fact that suppressed trees growing in the understory of a forest have shade needles instead of sun needles. Tucker and Emmingham (1977) studied western hemlock trees released from suppression, and found that needles made while the trees were suppressed abscised prematurely, while needles formed in the two years after the release clearcut were thicker and had more stomates per surface area. Brooks et al. (1996) found that Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) foliage produced in the sun had higher A_{max} values, dark

respiration rates, nitrogen content and chlorophyll content than foliage produced in the shade. However, Palmroth and Hari (2001) found that although nitrogen concentration did not vary in needles on sun and shade branches in Scots pine (*Pinus sylvestris* L.), LMA increased and dark respiration rate decreased with increasing PAR. Not only will trees released from suppression need to change their leaf structure to take advantage of the increased light, they may also need to dissipate excess heat caused by the overstory removal. For example, seedlings of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) grown under high and low light conditions actually showed a decrease in their capacity to capture light under increasing light conditions due to decreased chlorophyll and an increase in their thermal dissipation mechanisms, particularly the xanthophyll cycle (McKinnon and Mitchell, 2003). Elevated temperatures were also shown to increase nitrogen concentration by 26% and light saturated net photosynthetic rates by 17% in Douglas-fir seedlings (Lewis et al., 2004).

An alternative hypothesis to the one that photosynthetic capacity constrains release was that hydraulic architecture constrains release. Hydraulic architecture could constrain release if the root systems of suppressed trees are not equipped to transport water to an increased leaf area after release from suppression. Seedlings grown in light to moderate shade were shown to allocate less biomass to roots than to shoots compared with seedlings grown in open conditions (St. Clair and Sniezko, 1999). However, Mailly and Kimmins (1997) found that both Douglas-fir and western hemlock reduced their allocation to roots with increasing relative light intensity.

Therefore, it is uncertain whether allocation to root systems will increase or decrease when trees are released from suppression. Newton and Cole (1991) compared root to shoot ratios in different size classes of Douglas-fir and found that the average root to shoot ratio of trees was 4:1 in dominant and codominant tree classes while the ratio in severely suppressed trees was 1:1. Therefore, suppressed trees had about one fourth the amount of roots as other trees of their species. This could greatly affect their ability to release from suppression because not only are roots important in nutrient acquisition, but also in water absorption and hydraulic architecture.

Hydraulic architecture could also constrain release if the above-ground shoot system was not equipped to transport water to an increased amount of leaf area. Dominant trees had significantly more leaf area per unit sapwood area (A_L/A_S) than other crown classes, while no significant differences were found between codominant, intermediate and suppressed classes (Thompson, 1989). Margolis et al. (1988) found that Balsam fir (*Abies balsamea* (L.) Mill.) trees adjusted their sapwood area to correspond closely with their leaf area. They pruned trees to 20 and 40 percent of their live crown ratio and found that the trees responded by adjusting their breast height sapwood area. This correlation between leaf area and sapwood area could be important in a tree's ability to release from suppression because leaf area and sapwood area will need to increase proportionally for release to occur.

In addition to the A_L/A_S response after release, wood produced after release will also need to be able to transport water more efficiently. Suppressed trees have wood that is more resistant to water flow than open grown trees (Reid et al., 2003).

Keane and Weetman (1987) found A_L/A_S decreased from 0.30 m^2 cm^{-2} to 0.15 m^2 cm^{-2}, wood density increased from 0.52 g cm^{-3} to 0.70 g cm^{-3} as lodgepole pine (*Pinus contorta* Dougl. ex Loud.) trees became increasingly suppressed. The proportion of earlywood in the growth rings also decreased, leading to reductions in the specific conductivity (K_s) of the wood. Reid et al. (2003) found that K_s of sapwood of dominant lodgepole pines was 2.7 times greater than that of suppressed lodgepole pines. Although these dominant trees had never been suppressed, their growing conditions would be similar to trees that had been released from suppression. Sellin (1993) also found that the relative conductivity of open-grown Norway spruce (*Picea abies* (L.) Karst.) was 1.4 to 3.1 times greater than shade-grown trees.

Hydraulic architecture affects the amount of water delivered to leaves, thereby influencing stomatal conductance and carbon gain because open stomata allow carbon dioxide to enter the leaf so that photosynthesis can occur. Hubbard et al. (2001) found that if trees maintain a constant minimum midday water potential, then reductions in leaf specific conductivity (K_L) will cause stomatal conductance to decrease and presumably increases in K_L will cause stomatal conductance to increase. Whitehead et al. (1996) found that *Pinus radiata* D. Don shade needles had decreased stomatal conductance compared to sun needles. McDowell et al. (2003) found that reductions in stand density increased rates of stomatal conductance even in old-growth Ponderosa pine (*Pinus ponderosa* P.& C. Lawson).

The third research question addressed in this study was how functional wood characteristics will be affected in Douglas-fir and western hemlock after release from

suppression. Trees releasing from suppression will either need to make a greater volume of wood than when suppressed, make wood that is more conductive than when suppressed, or some combination of both. To transport water more efficiently, tracheids produced after release could be larger in diameter than the tracheids produced before release. According to the Hagen-Poiseuille law, the flow through tracheids is related to the radius of the tracheid raised to the fourth power (Zimmermann, 1983). Longer tracheids would also be more efficient at water transport, since bordered pits between tracheids are the main region of resistance to water flow in the pathway (Lancashire and Ennos, 2002) and longer tracheids would reduce the number of bordered pits that need to be crossed in the overall path from the ground to the leaves (Comstock and Sperry, 2000).

Changes in either the volume of wood produced after release or the efficiency of water transport of wood produced after release could also alter wood density. Wood density is a composite of the density of the earlywood, the density of the latewood, and the proportion of each in the growth ring. This proportion could be altered after release if wood that is produced transports water more efficiently. For example, earlywood is 11 times more conductive, but less dense than latewood (Domec and Gartner, 2002). Keane and Weetman (1987) found that earlywood proportions were reduced in suppressed trees of lodgepole pine, while Reid et al. (2003) found that dominant trees had a greater proportion of earlywood in outer rings than suppressed trees in lodgepole pine. Therefore, increases in the proportion of

earlywood to latewood in growth rings produced after release could decrease wood density in response to the need to transport water more efficiently.

The characteristic changes in wood properties that occur with age may also be altered by suppression and subsequent release. For example, trees grown in open conditions tend to exhibit very high wood densities in the growth rings near the pith, a sharp decrease in wood density, then a steady increase until reaching a fairly constant value between 20 and 30 years (Abdel-Gadir and Krahmer, 1993, Kennedy, 1995). The point at which wood density becomes fairly constant also coincides with the transition from juvenile wood to mature wood, which in addition to differences in wood density also exhibits increases in tracheid length and decreases in microfibril angle (Mencuccini et al., 1997). As the cambium continues to age, tracheids with larger lumens are produced, making wood that is more conductive to water flow, and the growth rings contain a greater proportion of latewood (Pothier et al., 1989, Spicer and Gartner, 2001). However during suppression, growth rates would be altered and would possibly diverge from these normal patterns of cambial maturation. Subsequent release could also cause significant changes in wood properties that would be more dramatic than the gradual changes that normally occur during cambial maturation.

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CHAPTER 2: HYDRAULIC ARCHITECTURE AND PHOTOSYNTHETIC CAPACITY AS CONSTRAINTS ON RELEASE FROM SUPPRESSION IN DOUGLAS-FIR AND WESTERN HEMLOCK

ABSTRACT

We compared hydraulic architecture, photosynthesis and growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a shade intolerant species, with that of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), a shade tolerant species, to learn more about the temporal pattern of release in both species, and particularly to determine if hydraulic architecture or photosynthetic capacity constrains release. The study was conducted in 10-20 year old Douglas-fir and western hemlocks, either in a site that had been thinned to release suppressed trees or that remained unthinned. Douglas-fir had lower height growth (from 1998-2003) and lower relative height growth (height growth from 1998-2003/height in 1998) than western hemlock. However, the relative height growth of released vs. suppressed trees was much higher in Douglas-fir (130%) than western hemlock (65%), suggesting that although height growth was lower, Douglas-fir did indeed release from suppression. Release seemed to be constrained initially by photosynthetic capacity in both species. Douglas-fir released trees had 14 times the leaf area and 1.5 times the N_{area} as suppressed trees. Needles on released western hemlock trees had approximately twice the A_{max} at ambient $[CO_2]$ as suppressed and did not exhibit photoinhibition at the highest PAR levels. After released trees increased their leaf area, leaf N content and overall photosynthetic capacity, hydraulic architecture appeared to constrain further release from suppression in Douglas-fir and, to a lesser extent, western hemlock. Released

trees had significantly less negative foliar $\delta^{13}C$ values and there was also a positive relationship between leaf area:sapwood area ratios (A_L/A_S) and $\delta^{13}C$ suggesting that trees with more leaf area for a given sapwood area experienced a stomatal limitation on carbon gain. Growth of released trees thus may have been limited by stomatal constraints on carbon gain despite a doubling of A_{max} after release. Nonetheless, these changes had no significant effects on leaf-specific conductivities (K_L) of suppressed vs. released trees of either species. However, leaf specific root conductance (k_{RL}) was significantly greater in suppressed Douglas-fir compared to released Douglas-fir.

INTRODUCTION

Understanding the mechanisms that allow understory saplings to release from suppression is important both ecologically and silviculturally because suppressed saplings comprise an important part of the gap regeneration potential of natural forests. However, recent gaps are rare in most natural forests (Canham, 1989). For example, recently formed gaps in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Pacific Northwest make up about 0.7% of mature forests and 0.2% of old-growth forests (Spies et al., 1990). Nevertheless, understanding the mechanisms by which trees release from suppression is becoming increasingly important in places like the Pacific Northwest where forestry practices are shifting from even-aged to uneven-aged stand management. Uneven-aged stand management systems favor partial cutting over clearcutting of stands. Therefore, regeneration is more likely to develop under an overstory, making periods of suppression and eventual release more common. Species

able to quickly take advantage of gaps formed by thinning will outcompete slower responding neighbors and become part of the upper canopy.

There is some uncertainty about how a moderately shade intolerant, but commercially important species like Douglas-fir will be affected by a shift in forestry practices from even- to uneven-aged systems. Douglas-fir has intermediate shade tolerance (Minore, 1979) and normally regenerates in large gaps such as those created by a fire or by clearcutting practices (Franklin et al., 2002). Shade tolerant species like western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Minore, 1979) are frequently found to regenerate under a canopy of mature trees, making suppression and release more common occurrences (Munger, 1940, Gray and Spies, 1997, Franklin et al., 2002). There is some concern that uneven-aged stand management could shift species composition from less shade tolerant, but high-value, species like Douglas-fir toward more shade tolerant lower-value tree species like western hemlock (Tesch and Korpela, 1993). Therefore, comparison of Douglas-fir and western hemlock growing in both suppressed and released states will help evaluate how effectively Douglas-fir can release from suppression and if concerns about shifts in species composition are warranted.

In addition to determining how effectively both Douglas-fir and western hemlock release from suppression, another objective of this study was to identify structural and physiological constraints on release. This is important because Douglas-fir exhibits some delays before showing signs of release after thinning and these delays could be the result of structural or physiological changes that need to

occur before trees can increase growth rates to effectively release from suppression (Staebler, 1956, Van Pelt and Franklin, 1999, Kneeshaw et al., 2002). This study addressed two competing hypotheses about the relative importance of hydraulic architecture and photosynthetic capacity in constraining release from suppression.

In the first hypothesis, release of trees from suppression following thinning of the overstory is initially constrained by the inability of the vascular system to compensate for increased water demand by the leaves. As a result, trees will not show signs of release until they change their hydraulic architecture. Hydraulic architecture describes the movement of water from the roots to the leaves and the relationship between the water-conducting conduits (both below- and above-ground) within a tree and the amount of foliage they need to supply with water (Tyree and Ewers, 1991, Cruiziat et al., 2002). Therefore, in order to release from suppression, trees may need to increase their sapwood area and/or specific conductivity (K_s) relative to their leaf area. Several studies have found that faster growing trees have more leaf area for a given unit of sapwood area than slower growing trees (Espinosa Bancalari et al., 1987, Thompson, 1989, Mencuccini and Grace, 1994). In addition to having greater leaf area for a given amount of sapwood area, leaves of released trees may also have a greater demand for water than those of suppressed trees. Whitehead et al. (1996) found that sun needles of *Pinus radiata* D. Don had higher stomatal conductance, and therefore transpiration, than did shade needles. If this is also true for Douglas-fir and western hemlock, then water will need to be transported more efficiently to sun needles than to shade needles in order maintain the same leaf water potentials.

Finally, Kneeshaw et al. (2002) found that lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and Douglas-fir saplings showed moisture stress after overstory removal and they predicted that reduced height growth was not the result of insufficient carbon but rather the result of an insufficient capacity of the tree to transport water to its leaves.

Trees could also be constrained by hydraulic architecture if their root area and the conductivity of their root systems were insufficient to meet the transpirational needs of their leaves. Newton and Cole (1991) compared root to shoot ratios in different size classes of Douglas-fir and found that the average root to shoot ratio of trees was 4:1 in dominant and codominant classes, but was 1:1 in severely suppressed trees. Eis (1974) also found that dominant trees had more symmetrical and well-developed root systems than either intermediate and suppressed individuals. Therefore, suppressed trees could be severely lacking in root area needed to acquire and transport water to their leaves after release.

An alternative hypothesis is that photosynthetic capacity constrains release. This hypothesis states that delays in release in Douglas-fir (if any) result from the time required for the tree to replace existing needles with ones that have a higher photosynthetic capacity (i.e. replacing shade needles with sun needles). This hypothesis makes a comparison of Douglas-fir and western hemlock especially interesting given that they exhibit different photosynthetic efficiencies depending on light levels. For example, western hemlock has a lower mean light-saturated photosynthetic rate, light compensation point and dark respiration rate than Douglas-fir (Bond et al., 1999, Lewis et al., 2000). Lewis et al. (2000) also found that western

hemlock had higher net photosynthetic rates at lower photosynthetically active radiation (PAR) levels while Douglas-fir had higher net photosynthetic rates at higher PAR levels. Douglas-fir and western hemlock also differ in the amount of carbon they allocate to different tissues. Douglas-fir allocates more carbon to stem biomass and less to foliage biomass than western hemlock (Mailly and Kimmins, 1997). This means that at the time of release, western hemlock could have a more appropriate leaf area than Douglas-fir for the post-release light conditions. Douglas-fir would then experience delays in release while developing its appropriate leaf area relative to western hemlock. Such a delay was reported in sapwood growth in white spruce (*Picea glauca* (Moench) Voss) following release because of a temporary reallocation of carbon to producing new foliage and roots (Lieffers et al., 1993).

MATERIALS AND METHODS

Site Description

The approximately 30 hectare site for this study was located in the Coast Range near Falls City, Oregon (latitude 44.82 ^{o}N, longitude 123.62 ^{o}W, elevation 350 m) and had a site index (SI_{50}) of 128. The site was thinned from 415 trees per hectare (trees/ha) to 289 trees/ha in 1978 to allow self-seeding of Douglas-fir and western hemlock that were to function as advance regeneration. In 1998, a portion of the site (approximately 20 hectares) was thinned again to a density of 99 to 148 trees/ha releasing the Douglas-fir and western hemlock advance regeneration from suppression while an adjacent portion of the site (approximately 10 hectares) remained unthinned and contained Douglas-fir and western hemlock trees still suppressed in the

understory. Herbaceous vegetation in the understory consisted of bracken fern

(*Pteridium aquilinum* (L.) Kuhn), sword fern (*Polystichum munitum* (Kaulf.) Presl.),

Oregon grape (*Berberis nervosa* Pursh), salal (*Gaultheria shallon* Pursh), trailing

blackberry (*Rubus hispidus* L.) and foxglove (*Digitalis purpurea* L.).

Tree Selection and Measurement

     In June and July 2004, we non-randomly chose 10 trees of each species

(Douglas-fir and western hemlock) in each stand (thinned and unthinned). We chose

trees that we estimated to be 1-2 m tall in 1998, exhibited no signs of damage to the

bark, had no branches strongly competing with the terminal shoot for dominance and

were distributed across the entire range of the stand. For each of the 40 trees, we

measured current height and estimated height in 1998, the year of the release thinning.

In Douglas-fir the 1998 height was estimated as the point five branch whorls below

the top, not including the current year's growth. In western hemlock the 1998 height

was estimated by finding the point on the stem that had branches that appeared to be

five years old based on annual changes in the color and texture of their bark. Height

growth was calculated as the change in height in the five-year period from 1998 to

2003 and relative height growth was calculated as height growth in a five year

period/height in 1998.

     After the height was measured, we harvested trees and cut two disks from each

tree: the reference disk (about 2 cm tall, from near ground level), and a disk for

specific conductivity (about 15 cm tall, from about 10 cm above ground level). The

reference disk was used in the field to measure bark thickness and estimate the radius

of heartwood and sapwood by painting them along two perpendicular diameters with each of two sapwood/heartwood differentiation stains, alizarine red and methyl orange (Kutscha and Sachs, 1962). None of the samples had heartwood, therefore sapwood area was calculated by measuring two diameters on the reference disk, taking the average and calculating the area of a circle. Additionally, growth rings were counted in order to determine age of the trees.

Leaf-specific Root Conductance

Immediately after trees were felled, we measured root conductance using a high-pressure flow meter (Tyree et al., 1995) and filtered tap water as the liquid. Trees were felled with a handsaw, leaving about 5 cm of stump. We then used a razorblade to make a cleaner stump surface to allow maximum water penetration to the root system. Next, a tight-fitting rubber collar was placed around the stump and a plastic chamber was sealed to the top of the rubber collar. The water in the pressurized reservoir of the high-pressure flowmeter could then be forced to flow through one of six capillary tubes of varying size before flowing into the cut stump via the plastic chamber. The pressure at both ends of the chosen capillary tube was recorded and the flow rate ($kg\ s^{-1}$) was calculated from the difference in pressure across the capillary tube using a predetermined regression equation for the relationship between the pressure difference and flow. The pressure head (MPa) driving water through the root system was then defined as the pressure observed at the downstream end of the capillary tube. The temperature of a beaker of water located in close

proximity to the high pressure flow meter was also recorded so that a viscosity correction could be made. Root conductance (k_R) was then calculated as follows:

$$k_R = \frac{Q}{\Delta P}$$

where Q is the volume flow rate (kg s^{-1}) and ΔP is the pressure difference (MPa). k_R was normalized by leaf area by dividing by the leaf area of the tree giving a measure of leaf-specific root conductance (k_{RL}; kg m^{-2} s^{-1} MPa^{-1}).

Leaf Area

As each tree was harvested, it was placed on a tarp and all its branches containing leaves were cut into pieces approximately 10 cm long. The mass of the fresh branches and leaves was obtained. Next, a random subsample of the cut branches and leaves was placed in each of three paper bags and weighed. The bags were placed in a 50 $^{\circ}$C drying oven for approximately 48 hours and a dry mass of the branches and leaves was obtained. We separated leaves from branches, reweighed samples, and calculated the ratio of dry leaf mass to dry leaf and branch mass.

Additionally, approximately 20 to 30 fresh leaves were randomly selected from each tree, taken back to the lab and kept in the freezer until their total area could be determined. Briefly, the leaves were placed face down on the glass of the scanner along with an image of a reference square with an area of 1 cm^2. The leaves and the square were scanned and imported into an image analysis system (Scion Image, version 4.0.2, Scion Corp., Frederick, MD, USA) and leaf areas were converted from pixels to cm^2. These leaf samples were then dried so that a ratio of fresh leaf area to leaf dry mass could be calculated. Using the ratios of subsample leaf dry weight/leaf

and branch dry weight, subsample fresh weight of leaves and branches/ dry weight of leaves and branches, and fresh weight of all leaves and branches, we were able to estimate fresh leaf area for the whole tree.

Leaf-specific Conductivity

Upon return from the field site, specific conductivity samples were submerged in water and placed in a cold room (5 $^{\circ}$C) until they could be processed the next morning. We prepared two subsamples (1 cm x 1 cm x 10 cm, tangential x radial x longitudinal) from each sample. Subsamples were first cut roughly to size using a band saw and were then refined to their final size using a chisel making sure to follow the grain along the length of the sample. Samples included the outer growth ring, and usually two to three other rings interior to that in released trees and five to six rings in suppressed trees, depending on ring width. To the extent possible, we avoided compression wood and branch junctions in the samples. After the samples were cut to their final dimensions, they were vacuum infiltrated in tap water for approximately one hour.

Specific conductivity (K_s) was measured using a pressure sleeve apparatus where the sample is placed in a chamber containing a latex membrane (Spicer and Gartner, 1998). A very low pressure was applied to the chamber to press the membrane against the sample to prevent water leakage from its cut sides. For flow measurements, filtered water at pH 2 was placed in an Erlenmeyer flask at a height of 0.48 m above the sample creating a pressure head of 0.0048 MPa. Tubing was connected from the flask to the upstream end of the sample. Tubing also connected

the downstream end of the sample to a pipette, marked in graduations of 0.01 ml. The

time required for the meniscus to pass consecutive units of 0.05 ml was tracked using

a stopwatch making certain that a fairly constant rate was achieved. Flow rate was

corrected to the rate it would have been at 20 $^{\circ}$C and then used in this equation to

calculate K_s.

$$K_s = \frac{Ql}{A_{sample}\Delta P}$$

where Q is the volume flow rate (kg s^{-1}), l is the length of the sample (m), A_{sample} is

the cross-sectional area of the sample (m^2) and ΔP is the pressure difference between

the two ends of the sample (MPa). Leaf-specific conductivity (K_L) was then calculated

as follows:

$$K_L = \frac{A_S}{A_L} K_s$$

where A_S is sapwood area (m^2), A_L is leaf area (m^2) and K_s is specific conductivity (kg

m^{-1} s^{-1} MPa^{-1}).

Leaf Water Potential

During August and September 2004, 24 trees, consisting of six trees of each

species in each stand were chosen from across the entire range of the stand and used to

measure predawn and midday leaf water potential. During three separate days, two

branch samples from two trees of each species in each stand were used to measure

predawn water potential using a pressure bomb (PMS Corvallis, Oregon) before

sunrise. Likewise, two branch samples from the same trees used for the predawn

measurements were used to take midday water potentials between 11:00 and 12:00 solar time.

Photosynthesis

During a two-week period in July 2005, light-response curves and A/C_i curves were obtained from four trees of each species in each stand. Curves were generated between 9:00 and 13:00 solar time using a portable photosynthesis system (Li-Cor 6400, Li-Cor Inc., Lincoln, NE) equipped with a red/blue LED light source and a CO_2 injector. Leaf temperature matched closely with air temperature and ranged from 20-30 ^{o}C. Current year leaves were measured on branches approximately one meter above ground level. Additionally, the amount of photosynthetically active radiation (PAR) was determined at eight different locations per stand over a period of two weeks using the quantum sensor mounted outside of the cuvette and oriented parallel to the ground as the data used to construct the curves were being obtained. In order to produce the light-response curves, CO_2 was held at a constant ambient concentration of 400 µmol mol^{-1} while PAR was progressively lowered from 1500 µmol m^{-2} s^{-1} to 50 µmol m^{-2} s^{-1} in 200 µmol m^{-2} s^{-1} intervals. PAR was graphed vs. assimilation rate (µmol CO_2 fixed m^{-2} s^{-1}) individually for each tree as well as averaged over all trees in a given category. Graphs from individual trees were used to estimate quantum yield from the initial slope, light compensation point (τ) from the x-intercept, dark respiration rate (R_d) from the y-intercept, and maximum assimilation rate (A_{max}) at ambient [CO_2].

To obtain the A/Ci curves, PAR was held at 1200 μmol m^{-2} s^{-1} while the cuvette CO_2 concentration was set near ambient (400 μmol mol^{-1}) then lowered in 100 μmol mol^{-1} increments until a reading was taken at 50 μmol mol^{-1}. Cuvette CO_2 concentration was then increased directly back to 400 μmol mol^{-1} and then increased in 200 μmol mol^{-1} increments until further increases no longer elicited increases in assimilation rate. Concentration of CO_2 inside the leaf (Ci) was plotted vs. assimilation rate to construct A/Ci curves for each tree separately as well as values for all trees with the same species/stand combined on one graph. Graphs from individual trees were used to estimate CO_2 compensation point (Γ) from the x-intercept, and A_{max} at saturating [CO_2].

δ^{13}C and Leaf Nitrogen Content

During late June 2004, we chose five trees of each species in each stand from the entire range of the stand for leaf collection. We then collected about 100 mg of leaf sample from each of the 20 trees from all sides and heights of the tree in each of the following four foliage age classes: one-, two- , three- and four-year-old leaf samples. The 80 leaf samples were then dried at 60 ^{o}C in a drying oven for at least 48 hours, ground to a fine powder using a ball mill, and sent to the University of Idaho Stable Isotopes Laboratory where measurement of δ^{13}C and % leaf nitrogen were performed on each sample. The amount of ^{13}C relative to ^{12}C in leaf tissue provides an indication of the intrinsic water use efficiency (assimilation/stomatal conductance), and therefore relative stomatal limitation of photosynthesis, when the leaf was being formed

(Farquhar et al., 1989). Nitrogen content was normalized by leaf area (N_{area}) using leaf mass per area ratios for each category of foliage.

Statistical analyses

Means, 95 % confidence intervals and p-values for comparisons of means were calculated for all variables in Tables 2.1 and 2.2 using PROC MIXED SAS version 9.1 (SAS Institute Inc., Cary, NC, USA). If needed, log transformations on the data were made to meet assumptions of normality and constant variance. If log transformations were made, the means and confidence intervals were backtransformed and reported on the original scale. Species and stand were used as indicator variables and comparisons of means were made between each category. Differences in means with a p-value of 0.05 or smaller were deemed significant. P-values for all regressions were also calculated using PROC MIXED SAS version 9.1. Values of r^2 for all regressions were obtained using SigmaPlot (version 9.01 Systat software Inc., Richmond, CA).

RESULTS

Site Conditions

As expected, the thinned stand with its lower density of overstory trees received higher daily mean values of PAR compared to the unthinned stand (approximately 1400 and 400 μmol m^{-2} s^{-1} respectively). The unthinned site did experience some sun flecks but, in general, PAR was much lower than in the thinned stand. Soil water potentials were similar in both stands as estimated by predawn water potential measurements on both species (Table 2.1).

Table 2.1: Means and 95 % confidence intervals for variables relating to hydraulic architecture in suppressed and released Douglas-fir and western hemlock trees. Different superscript letters signify a statistically significant difference (p-value <0.05) between the four mean values.

	Douglas-fir		western hemlock	
	suppressed	released	suppressed	released
total height (m)	2.34 (1.99-2.68) [a]	3.62 (3.28-4.00) [b]	2.62 (2.28-2.97) [a]	3.74 (3.39-4.08) [b]
age (years)	17.6 (15.8-19.4) [a]	18.0 (16.2-19.8) [a]	13.9 (12.1-15.7) [b]	12.1 (10.3-13.9) [b]
height growth (m)	0.80 (0.54-1.07) [a]	1.99 (1.73-2.25) [b]	1.37 (1.11-1.63) [c]	2.36 (2.10-2.63) [d]
relative height growth (m m^{-1})	0.51 (0.42-0.63) [a]	1.22 (1.00-1.49) [b]	1.03 (0.84-1.25) [b]	1.74 (1.42-2.12) [c]
k_{RL} x 10^{-4} (kg m^{-2} s^{-1} MPa^{-1})	4.51 (2.53-8.02) [a]	1.00 (0.54-1.83) [b]	1.47 (0.82-2.61) [b]	1.04 (0.52-2.07) [b]
leaf area (m^2)	0.69 (0.54-0.89) [a]	9.77 (7.59-12.56) [b]	2.07 (1.61-2.66) [c]	9.90 (7.70-12.74) [b]
sapwood area x 10^{-4} (m^2)	2.57 (2.1-3.1) [a]	9.79 (8.1-11.8) [b]	3.35 (2.8-4.0) [a]	10.95 (9.1-13.2) [b]
A_L/A_S (m^2 cm^{-2})	0.27 (0.23-0.31) [a]	1.00 (0.87-1.14) [b]	0.62 (0.54-0.71) [c]	0.90 (0.79-1.03) [b]
K_s (kg m^{-1} s^{-1} MPa^{-1})	0.38 (0.28-0.51) [a]	1.07 (0.80-1.45) [b]	0.59 (0.44-0.80) [a]	0.84 (0.62-1.13) [b]
K_L x10^{-4} (kg m^{-1} s^{-1} MPa^{-1})	1.48 (1.15-1.81) [a]	1.16 (0.83-1.50) [a]	1.06 (0.73-1.39) [a]	1.09 (0.75-1.42) [a]
predawn Ψ (MPa)	-0.53 (-0.43--0.63) [a]	-0.54 (-0.43--0.64) [a]	-0.34 (-0.24--0.45) [b]	-0.35 (-0.25--0.46) [b]
midday Ψ (MPa)	-1.22 (-1.09--1.35) [a]	-1.28 (-1.16--1.41) [a]	-1.16 (-1.03--1.28) [ab]	-1.07 (-0.95--1.20) [b]

Relative Height Growth

The current height of Douglas-fir and western hemlock released trees was not significantly different nor was the current height of suppressed Douglas-fir and western hemlock (Table 2.1). However, height growth did differ significantly between all categories. Suppressed western hemlock had 71% greater height growth than suppressed Douglas-fir and released western hemlock had 19% greater height growth than released Douglas fir. Relative height growth (height growth from 1998 to 2003/ height in 1998) was significantly lower in Douglas-fir than in western hemlock in both released and suppressed trees (Table 2.1).

Leaf-specific Root Conductance

Leaf-specific root conductance (k_{RL}) was not significantly different between released Douglas-fir and western hemlock (Table 2.1), but did differ substantially between suppressed Douglas-fir and western hemlock. k_{RL} was 4.5 times larger in suppressed than in released Douglas-fir, whereas k_{RL} was not significantly different between suppressed and released western hemlock.

Aboveground Hydraulic Architecture

Released Douglas-fir had 14 times the leaf area of suppressed Douglas-fir, whereas released western hemlock had about 5 times the leaf area of suppressed western hemlock (Table 2.1). Differences in sapwood area were less pronounced: released Douglas-fir had 3.8 times the sapwood area of suppressed Douglas-fir, while released western hemlock had almost 3.3 times the sapwood area as suppressed western hemlock (Table 2.1).

Leaf area:sapwood area ratios (A_L/A_S) also differed significantly between suppressed and released trees, although the differences were more substantial in Douglas-fir than in western hemlock. For example, the A_L/A_S in released Douglas-fir was 3.7 times larger than that of suppressed Douglas-fir whereas the A_L/A_S in released western hemlock was only 1.45 times greater than in suppressed western hemlock (Table 2.1).

The relationship between relative height growth and A_L/A_S was not significant for suppressed Douglas-fir, whereas relative height growth decreased slightly as A_L/A_S increased ($r^2 = 0.2$, p-value = 0.036, Figure 2.1) for released Douglas-fir. The scenario was reversed for western hemlock. The relationship between relative height growth and A_L/A_S was not significant, whereas relative height growth decreased sharply as A_L/A_S increased ($r^2 = 0.6$, p-value=0.009) in suppressed western hemlock.
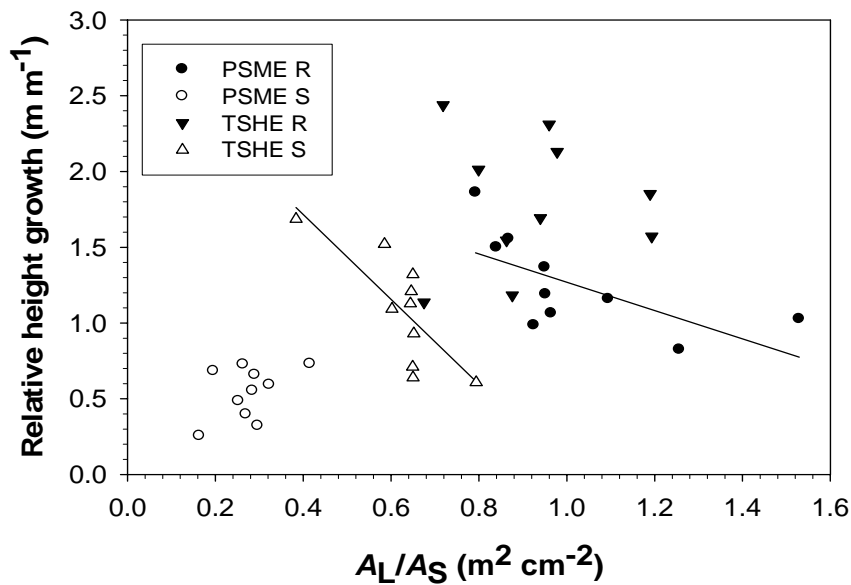
Figure 2.1: Relationship between relative height growth and leaf area-sapwood area ratio (A_L/A_S) for the 40 trees measured. Relationships between species/stand categories differ so separate regressions were done for each and only significant regression are shown. Circles: Douglas-fir; triangles: western hemlock; open symbols: suppressed trees; closed symbols: released trees.

Specific conductivity (K_s) was significantly higher in released trees than in suppressed trees, but the magnitude of difference was greater in Douglas-fir than in western hemlock (Table 2.1). Despite differences in leaf area, sapwood area, and K_s in suppressed and released trees, leaf-specific conductivities (K_L) were not significantly different in suppressed and released trees in either Douglas-fir or western hemlock. However, although not significantly different with 95% confidence, K_L of suppressed Douglas-fir was 28% lower than released Douglas-fir (p-value = 0.183) suggesting some difference that may become more pronounced with a larger sample size.

Leaf Water Potentials

Both Douglas-fir and western hemlock exhibited isohydric behavior in that their midday water potentials were similar whether they were growing in a suppressed or a released state (Table 2.1).

Photosynthesis

N_{area} in released Douglas-fir trees was on average 48% greater than in suppressed Douglas-fir, whereas released western hemlock needles had only 29% more nitrogen than suppressed western hemlock needles (Table 2.2). Suppressed Douglas-fir had on average 59% greater N_{area} than suppressed western hemlock (but 1/3 the leaf area), whereas released Douglas-fir had on average 83% greater N_{area} than released western hemlock and approximately the same leaf area (Table 2.2).

Table 2.2: Means and 95 % confidence intervals for variables relating to photosynthesis in suppressed and released Douglas-fir and western hemlock trees. Different superscript letters signify a statistically significant difference (p-value <0.05) between the four mean values.

	Douglas-fir		western hemlock	
	suppressed	released	suppressed	released
N_{area} (mmol N m^{-2})	87.6 (82.29-92.82) [a]	129.9 (124.59-135.12) [b]	55.2 (49.93-60.46) [d]	71.0 (65.74-76.27) [c]
quant. yield (μmol CO$_2$ μmol PAR^{-1})	0.015 (0.011-0.018) [ac]	0.018 (0.015-0.021) [a]	0.015 (0.011-0.019) [a]	0.020 (0.016-0.023) [c]
light comp. pt. (τ)(μmol m^{-2} s^{-1})	49 (40.52-58.28) [a]	47 (35.85-58.77) [a]	33 (23.56-43.41) [b]	42 (33.51-51.27) [ab]
dark resp. rate (R_d)(μmol m^{-2} s^{-1})	-0.7 (-0.93--0.55) [ab]	-1.0 (-1.22--0.73) [a]	-0.5 (-0.71--0.29) [b]	-0.8 (-1.02--0.64) [a]
A_{max} (ambient CO$_2$)(μmol m^{-2} s^{-1})	1.6 (0.978-2.30) [a]	2.6 (1.95-3.15) [b]	1.5 (0.76-2.24) [a]	3.1 (2.42-3.75) [b]
A_{max} (saturating CO$_2$)(μmol m^{-2} s^{-1})	4.1 (2.94-5.25) [a]	9.7 (8.59-10.90) [b]	4.9 (3.70-6.01) [a]	8.2 (7.07-9.38) [c]
CO$_2$ comp. pt. (Γ) (μmol m^{-2} s^{-1})	20 (7.49-53.67) [a]	28 (13.79-55.48) [a]	38 (21.74-67.76) [a]	23 (13.14-40.96) [a]
δ^{13}C (‰)	-31.78 (-32.27--31.28) [a]	-30.56 (-31.06--30.07) [b]	-31.62 (-32.11--31.13) [a]	-30.97 (-31.47--30.48) [b]

In both suppressed and released Douglas-fir, N_{area} was not significantly different in

needles of different ages (Figure 2.2). However, in both suppressed and released

western hemlock, N_{area} decreased with increasing needle age (p-values <0.0001 and

0.008 respectively) (Figure 2.2).
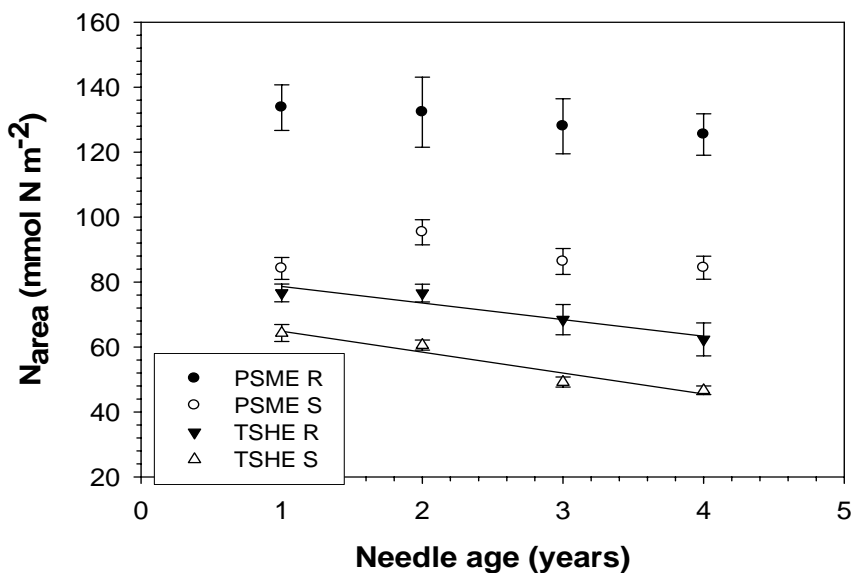
Figure 2.2: Relationship between N_{area} and needle age for the 20 trees measured. Only significant regressions are shown and r^2 for suppressed and released western hemlock were 0.94 and 0.90 respectively. Symbols correspond to those in Figure 2.1.

Light-response curves for suppressed and released trees were consistent with

the differences in light environment (Figure 2.3).

Figure 2.3: Light response curves for suppressed and released Douglas-fir and western hemlock trees. Symbols correspond to those in Figure 2.1.

A_{max} values differed significantly between suppressed and released trees, although differences between species were not significant. For Douglas-fir, A_{max} of released trees was 55% higher than in suppressed trees. For western hemlock, A_{max} of released trees was approximately 100% higher than that of suppressed trees. Released western hemlock also had a 21% higher A_{max} value than released Douglas-fir, however, this difference was not significant. Dark respiration rates (R_d) did not differ significantly in Douglas-fir suppressed and released trees, but they did differ significantly in western hemlock suppressed and released trees. Released western hemlock trees had 66% higher R_d than suppressed trees. Although released western hemlock showed no photoinhibition at the highest light levels, released Douglas-fir showed slight

photoinhibition at the highest light level. Suppressed trees of both species showed

some photoinhibition, which was more pronounced in western hemlock than in

Douglas-fir. Additionally, there was a significantly positive relationship between

relative height growth and A_{max} at saturating light and ambient $[CO_2]$ ($r^2= 0.40$, p-

value= 0.0032) (Figure 2.4).
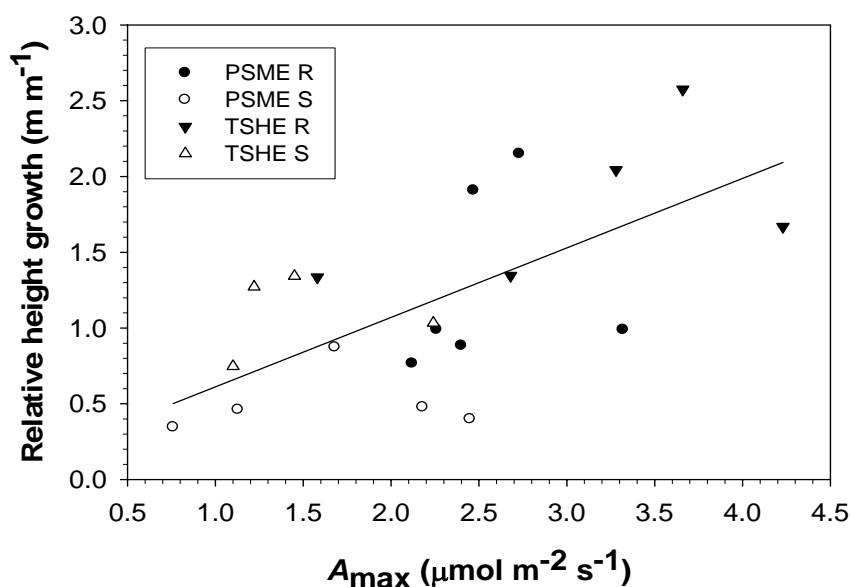
Figure 2.4: Relationship between relative height growth and A_{max} at ambient $[CO_2]$.
Symbols correspond to those in Figure 2.1.

Although released western hemlock had higher assimilation when light was

increased and $[CO_2]$ was held constant, a different pattern emerged when light levels

were held constant and $[CO_2]$ was increased. Released Douglas-fir had 18% higher

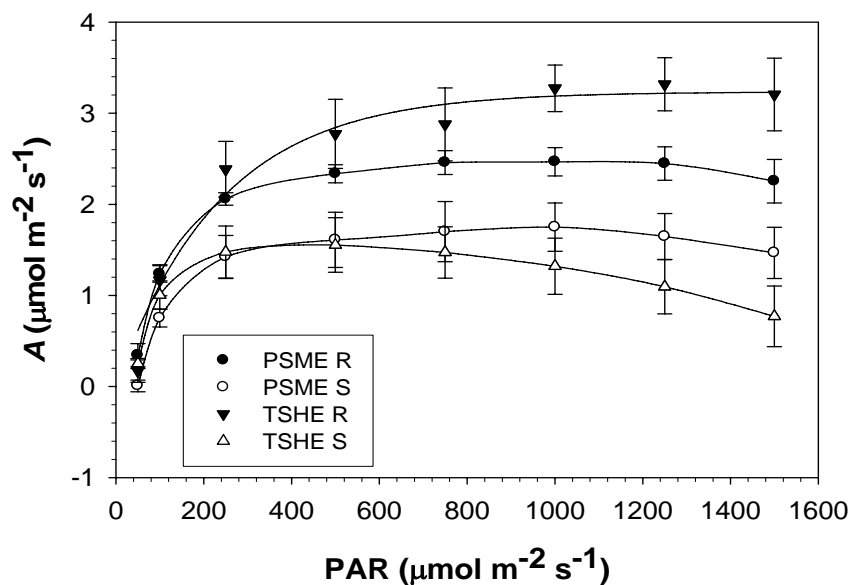A_{max} at saturating $[CO_2]$ than released western hemlock (Table 2.2, Figure 2.5).
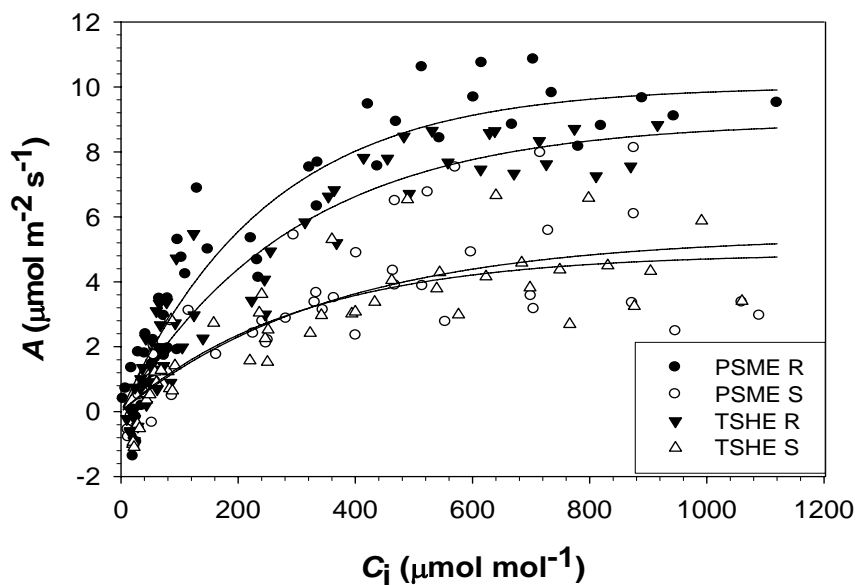
Figure 2.5: A/C_i curves for suppressed and released Douglas-fir and western hemlock trees. Symbols correspond to those in Figure 2.1.

Additionally, A_{max} at saturating $[CO_2]$ was 2.4 times higher for released than for suppressed Douglas-fir, whereas A_{max} at saturating $[CO_2]$ was 1.7 times higher for released than suppressed western hemlock (Table 2.2). Both suppressed Douglas-fir and western hemlock had similar assimilation rates at any given internal $[CO_2]$. All A/C_i curves yielded similar estimates of CO_2 compensation points.

$\delta^{13}C$

Foliar $\delta^{13}C$ was significantly less negative in released trees of both species than in to suppressed trees (Table 2.2). Foliar $\delta^{13}C$ values were positively correlated with height growth (r^2= 0.33, p-value=0.0086) (Figure 2.6).
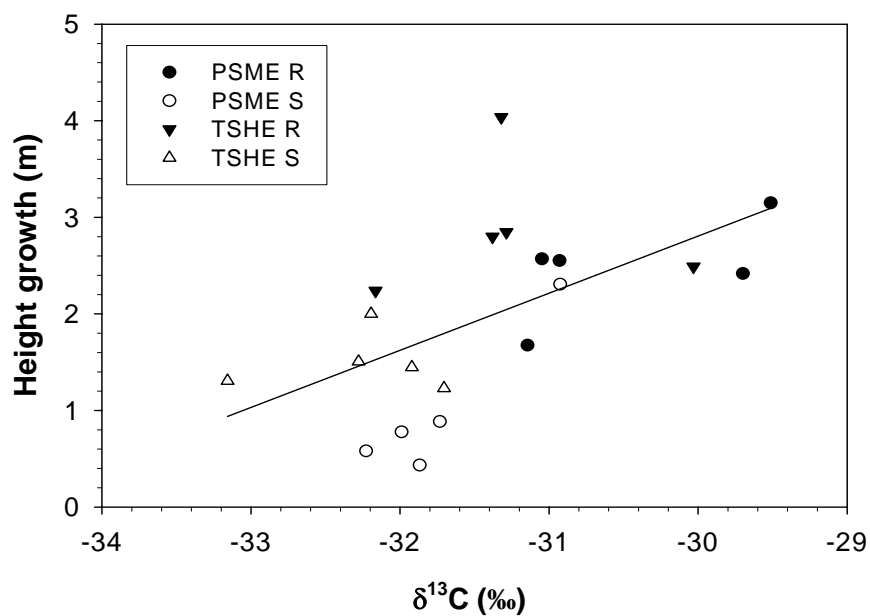
Figure 2.6: Relationship between absolute height growth and mean $\delta^{13}C$ of the four foliage age classes. Symbols correspond to those in Figure 2.1.

Height growth increased as mean $\delta^{13}C$ for the four foliar age classes became less negative (more enriched). As A_L/A_S increased, $\delta^{13}C$ of the one year old foliage became linearly less negative (r^2=0.49, p-value= 0.01) (Figure 2.7).
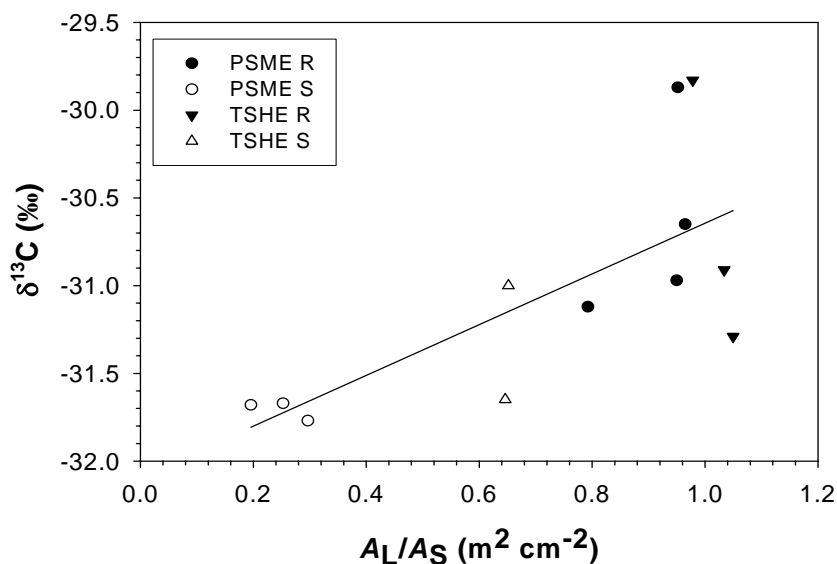
Figure 2.7: Relationship between leaf area-sapwood area ratio (A_L/A_S) and $\delta^{13}C$ of the one year old foliage. Symbols correspond to those in Figure 2.1.

DISCUSSION

Our first conclusion was that the Douglas-fir trees in this study were indeed able to release from suppression. Although released western hemlock had higher relative height growth than released Douglas-fir, Douglas-fir had a larger increase in relative height growth after thinning. The much lower relative growth rates of suppressed Douglas-fir than of suppressed western hemlock, indicate that Douglas-fir trees were more suppressed when growing in the shade and therefore overcame a larger degree of suppression when released. Consistent with these results, Tesch and Korpela (1993) found that average annual height growth of Douglas-fir almost

doubled five years after release and continued to increase as the trees adjusted to their new environment.

One of the reasons for the perceived lack of response of Douglas-fir to release treatments is the delayed increase in its growth rates relative to rapidly responding species like western hemlock. However, delayed response to release in Douglas-fir could result simply from differences in growth patterns between these species. Western hemlock has indeterminate growth, whereas Douglas-fir has determinate shoot growth, meaning that the shoot growth in Douglas-fir depends to a larger extent on the amount of cell division that occurred in the bud during the previous year (Cannell et al., 1976, Kneeshaw et al., 2002). This is further illustrated by a study reporting that the previous year's competition explained 65% of the current year's shoot growth in Douglas-fir whereas the current year's competition only explained 6% of the shoot growth (Harrington and Tappeiner, 1991). Therefore, Douglas-fir may not show increases in growth rate the year after release because its buds were formed during the previous year's suppression.

We also asked whether hydraulic architecture or photosynthetic capacity constrained release from suppression in Douglas-fir and western hemlock. There was evidence from this study to support the conclusion that both hydraulic architecture and photosynthetic capacity constrained release from suppression. It appeared that photosynthetic capacity was the larger constraint initially after release and that hydraulic architecture became a constraint later. It appeared that initially after release, both species shifted allocation towards increasing leaf tissue, and therefore,

photosynthetic capacity. This shift increased the leaf area on trees relative to the sapwood area which was likely to cause hydraulic architecture to become a limitation to increased carbon gain and further release. Released trees also had substantially more N_{area} than suppressed trees and, in turn, higher A_{max} at saturating $[CO_2]$ than suppressed trees. This suggests that released trees needed to construct needles with greater photosynthetic capacity after release from suppression. Released western hemlock trees also produced needles that were acclimated to the higher PAR levels and did not exhibit the same photoinhibition as suppressed western hemlock needles (Figure 2.3).

There were several lines of evidence that led to the conclusion that hydraulic architecture further limited carbon gain after release from suppression, more so in Douglas-fir than western hemlock. First, there were differences in leaf-specific root conductance (k_{RL}) between suppressed and released trees. k_{RL} was 4.5 times larger and K_L was 1.3 times larger (although the difference was not significant at $p<0.05$) in suppressed than released Douglas-fir trees. This can be compared to western hemlock, in which k_{RL} was only 1.4 times larger in suppressed than released trees (although the difference was not significant at $p<0.05$), and K_L was about the same in both conditions. Because the root system and the tree stem are in series, their resistances to water flow can be thought of as being additive. Although both species had lower whole-tree conductances in their released state than in their suppressed state, the differences for Douglas-fir were much greater than for western hemlock. Hubbard et al. (2001) found that if trees maintain a constant minimum midday water potential,

then reductions in K_L (and presumably k_{RL}) will cause stomatal conductance to decrease and in turn assimilation to decline. In the present study, photosynthetic capacity increased and whole-plant leaf-specific conductance decreased upon release while minimum leaf water potentials remained constant. Stomatal restriction of transpiration to maintain constant minimum leaf water potential despite reduced leaf-specific hydraulic conductance therefore led to increased relative stomatal limitation of photosynthesis in released trees. Douglas-fir probably experienced more hydraulic limitation after release from suppression than did western hemlock due to the greater differences in k_{RL} between suppressed and released trees.

The second piece of evidence that hydraulic architecture limited release in Douglas-fir was the relationship between relative height growth and A_L/A_S. There was no relationship between relative height growth and A_L/A_S for either suppressed Douglas-fir or released western hemlock (Figure 2.1). However, in released Douglas-fir and suppressed western hemlock relative height growth decreased as A_L/A_S increased. This pattern suggests that relative height growth in released Douglas-fir (and suppressed western hemlock) was constrained by stomatal closure and trees exhibited greater amounts of relative height growth when they had less leaf area that needed to be supplied with water. Additionally, leaves became more enriched in ^{13}C as A_L/A_S increased, suggesting a greater stomatal limitation on photosynthesis as a greater leaf area needed to be supplied by a given sapwood area (Figure 2.7).

A third piece of evidence that hydraulic architecture limited release to a greater extent in Douglas-fir than in western hemlock relates to differences in A_{max} estimated

from the light-response curves and the A/C_i curves. For both species, A_{max} observed at saturating [CO_2] levels was significantly higher than when [CO_2] was held constant at ambient conditions and PAR was increased. However, the ratio of A_{max} at saturating [CO_2] to A_{max} at ambient [CO_2] in Douglas-fir increased from 2.5 in suppressed trees to 3.8 in released trees, whereas in western hemlock this ratio decreased from 3.2 in suppressed trees to 2.7 in released trees. These results imply that relative stomatal limitation on carbon gain increased upon release in Douglas-fir and decreased in western hemlock. This interpretation is also consistent with the relationships between relative height growth and A_L/A_S in which both released Douglas-fir and suppressed western hemlock exhibited decreased relative height growth with increased A_L/A_S and presumably increased stomatal limitation on carbon gain.

Even though released Douglas-fir needles had 83% more N_{area} than released western hemlock needles, they had slightly lower A_{max} values at ambient [CO_2]. This again leads to the conclusion that released Douglas-fir trees were not able to take full advantage of their increased photosynthetic capacity associated with increased nitrogen content because photosynthesis was stomatally limited. Likewise, trees with greater height growth also exhibited less negative $\delta^{13}C$ values implying that the increases in photosynthetic capacity were greater than the ability of the tree to supply water to the needles causing a stomatal limitation on assimilation.

One final note in comparison of Douglas-fir and western hemlock and their abilities to release from suppression deals with the plasticity of each species. It seems that Douglas-fir showed a greater plasticity in hydraulic architecture than western

hemlock. Although it is commonly thought that more shade tolerant species exhibit greater plasticity, Douglas-fir tended to show much more variation in A_L/A_S, k_{RL} and K_L than western hemlock in that these parameters varied substantially depending on the environment in which the trees were growing. However, western hemlock seemed to show more plasticity than Douglas-fir in terms of leaf functional traits. For example, western hemlock also appeared to reallocate nitrogen from older needles to younger ones (Figure 2.2) which may furnish it with an advantage over Douglas-fir in releasing from suppression. Although there are costs associated with nitrogen redistribution, in the long run, these costs are reported to be smaller than the benefits that can be realized by redistributing nitrogen to leaves receiving more sunlight (Field, 1983). Also, quantum yield, R_d and A_{max} were all significantly different in suppressed and released western hemlock trees whereas for Douglas-fir only A_{max} was significantly different. It seems that Douglas-fir did not have the ability to make leaves that were suited for shaded conditions, and therefore had as little leaf area as possible when shaded, cutting down on the amount of maintenance respiration needed and maintaining a positive carbon balance.

Based on the results of this study, although Douglas-fir was able to release from suppression, it appears that hydraulic architecture and photosynthetic capacity both constrained release, possibly at different periods after thinning. However, it is important to note that this research was conducted on one site in the relatively humid central Oregon Coast Range on one age class of trees, and therefore, these results may not be applicable to other sites where drier conditions may prevail. However, results

on the constraint on release could provide guidance on how best to release trees from suppression. For example, because photosynthetic capacity was found to initially constrain release, initial thinnings could be light as not to cause photoinhibition and increased stress on Douglas-fir and western hemlock trees that have been suppressed in the understory. After photosynthetic capacity has increased, more intense thinnings could be performed to further release trees. Additionally, soil water content could be monitored, because Douglas-fir seems to allocate much more carbon to increased leaf area relative to root area, leaving trees vulnerable if soils become dried. Also, because released western hemlock had greater height growth than released Douglas-fir, thinning of the western hemlock advance regeneration may be needed in the future to ensure that the released Douglas-fir is not overtopped. This will maintain a mix of tree species that is often desired in uneven-aged stands.

ACKNOWLEDGMENTS

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CHAPTER 3: EFFECTS OF RELEASE FROM SUPPRESSION ON FUNCTIONAL WOOD CHARACTERISTICS IN DOUGLAS-FIR AND WESTERN HEMLOCK

ABSTRACT

Little is known of the wood properties in trees that were initially suppressed and subsequently released from suppression. The purpose of this study was to assess differences in growth ring width, specific conductivity (K_s), tracheid dimensions, moisture content, and wood density, in suppressed Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) saplings and saplings released from suppression. Growth ring width in released trees compared to suppressed trees increased by 370% for Douglas-fir and 300% for western hemlock and K_s increased by 182% for Douglas-fir and 42% for western hemlock. Although relative increases in growth ring width and K_s were both correlated with increased height growth (a measure of release from suppression), growth ring width was more strongly correlated with height growth than was K_s. Earlywood width was approximately four times greater in released than suppressed trees of both species whereas the relative increase in latewood width between suppressed and released trees was much greater in Douglas-fir than in western hemlock and thus latewood proportion decreased by 21% in released Douglas-fir and by 47% in released western hemlock compared to suppressed trees. Tracheids were 25% wider and 11% longer in released Douglas-fir saplings compared to suppressed saplings, whereas released western hemlock saplings had 19% wider tracheids that were approximately the same length as suppressed saplings.

Moisture content was 66% higher in released compared to suppressed Douglas-fir and 41% higher in released compared to suppressed western hemlock. Wood density decreased from 0.57 to 0.47 g cm^{-3} in Douglas-fir trees released from suppression and from 0.50 to 0.45 g cm^{-3} in western hemlock trees released from suppression. Height growth, growth ring width and K_s upon release from suppression were all negatively correlated with wood density. However, wood density of released trees did not differ from average reported values, implying that wood from released trees may be suitable for many of its traditional applications.

INTRODUCTION

Forestry practices in the Pacific Northwest are beginning to shift from even-aged to uneven-aged stand management, and therefore the regeneration that will replace these stands is changing. Regeneration in uneven-aged stands comes from saplings that were suppressed under the canopy of mature trees. Through selection thinnings that remove selected mature trees with the purpose of opening up the canopy, these saplings can be released from suppression and grow to become a part of the overstory (Miller and Emmingham, 2001). Trees that have spent the beginning of their lives suppressed in the understory may also make better crop trees (from a wood quality perspective) compared with seedlings that are grown in open conditions because their core of juvenile wood and branch size on the first log are likely to be smaller (Cregg et al., 1988, Watson et al., 2003).

Additionally, trees that are suppressed during the beginning of their lives exhibit recession of their crown earlier than trees growing in open conditions.

Therefore, changes in crown architecture caused by periods of suppression could also change wood properties. For example, Larson (1969) found in red pine (*Pinus resinosa* Soland.) that tracheid diameter and percent earlywood were higher and cell walls thinner in stemwood formed within the crown than in wood formed below the crown. Also, crown length and branch longevity affect the location, and size of knots. Because suppressed trees have been growing slowly, they exhibit tight growth rings, small knots and straight stems making them suitable for use in value-added products (LeVan-Green and Livingston, 2001). Green et al. (2005) found that 70 to 90 year old suppressed Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) had very good grade recovery with 68% qualifying for Select Structural lumber.

It is usually assumed that seedlings growing in the understory are suppressed, even though it is likely that they first germinated in understory gaps (Spies et al., 1990). The patterns of wood development in open- and plantation-grown trees are generally well-characterized (e.g., Zobel and van Buijtenen, 1989, DeBell et al., 2004), but the properties of shade-grown, suppressed trees could be different. For example, age-related changes in growth ring width, earlywood width and latewood width were much less dramatic in suppressed Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) than in dominant trees in the same age ranges (Fabris, 2000).

Although few studies have examined wood anatomy in saplings released from suppression, perhaps insight can be gained by characterizing the changes that occur when trees are released by a thinning treatment. In fast-growing spruces, Dutilleul et

al. (1998) found negative correlations between ring width and fiber length and between ring width and wood density, especially in juvenile wood. Zahner and Oliver (1962) also found that thinning delayed the transition from earlywood (less dense) to latewood (more dense) by about two to three weeks in red pine and jack pine (*Pinus banksiana* Lamb.) implying that wood produced in these growth rings could have a decreased density. However, Markstrom et al. (1983) found that although radial growth increased in ponderosa pine (*Pinus ponderosa* P.& C. Lawson) after thinning, wood density, latewood percentage, tracheid length and microfibril angle were not significantly different. Therefore, there is some uncertainty with regard to the changes in wood properties that will occur in trees that are released from suppression.

One would expect changes in the wood because trees tend to balance their leaf area with the area and permeability of their sapwood (Margolis et al., 1988). We already reported that these released trees have much greater leaf area, photosynthetic capacity, and leaf area:sapwood area ratio (A_L/A_S) in than suppressed trees (Chapter 2 and Table 3.1), both of which should create a higher demand for water transport, which, in turn, could be associated with changes in stem wood properties. Trees could increase their water transport by any of the following changes: increasing sapwood area by increasing new growth ring width and/or by decreasing the rate at which sapwood is changed to heartwood, or by changing the anatomical features of the wood produced to make it more conductive (increase K_s) (Ewers, 1985). Trees could potentially produce less dense wood after suppression for two reasons: to make a greater volume increment of wood in the form of wider growth rings, they may be

constrained to make "cheaper wood" that is not as dense as that made previously; and to make more conductive wood they may need to make wood that has a lower latewood proportion (Dome and Gartner, 2002) and thus is less dense. Because of the great importance of wood density and uniformity in wood utilization, changes in silviculture could affect the suitability of wood for various uses. However, in species like Douglas-fir that exhibit strong pith to bark trends in density, trees released from suppression may actually have wood that is more uniform in wood density and therefore better suited for certain applications.

This study addresses the changes in wood anatomy that are most closely associated with release from suppression. Douglas-fir and western hemlock were compared because they are commercially important species in the Pacific Northwest and have differing levels of shade tolerance (with western hemlock being more shade tolerant than Douglas-fir (Minore, 1979)), that could lead to contrasting responses upon release. We already reported that suppressed trees were shorter than released trees in both Douglas-fir and western hemlock (Chapter 2 and Table 3.1), and that height growth in the most recent five-year period was lowest in suppressed Douglas-fir trees, followed by suppressed western hemlock, released Douglas-fir, and then released western hemlock. Our interpretation of these data along with data on hydraulic architecture was that both species showed release from suppression. Both species appeared to be initially constrained by photosynthetic capacity then, as leaf area increased, became constrained by hydraulic architecture; Douglas-fir more so than western hemlock.

The first research question thus addresses whether Douglas-fir and western hemlock respond more strongly to release from suppression with increases in growth ring width or increases in K_s. We hypothesize that trees released from suppression will increase the width of their growth rings as well as the proportion of earlywood to latewood within individual growth rings. Furthermore, trees released from suppression will produce more conductive wood with higher K_s through the production of tracheids that are longer and wider. Our second research question asks how wood density is affected after trees release from suppression. We hypothesize that wood density will decrease in trees released from suppression because of decreased latewood proportion and increases in tracheid diameter. MATERIALS AND METHODS

Site Description

The approximately 30 hectare site for this study was located in the Coast Range near Falls City, Oregon (latitude 44.82 ^{o}N, longitude 123.62 ^{o}W, elevation 350 m) and had a site index (SI_{50}) of 128. The site was thinned from 415 trees per hectare (trees/ha) to 289 trees/ha in 1978 to allow self-seeding of Douglas-fir and western hemlock that were to function as advance regeneration. In 1998, a portion of the site (approximately 20 hectares) was thinned again to a density of 99 to 148 trees/ha releasing the Douglas-fir and western hemlock advance regeneration from suppression while an adjacent portion of the site (approximately 10 hectares) remained unthinned and contained Douglas-fir and western hemlock trees still suppressed in the understory. Herbaceous vegetation in the understory consisted of bracken fern

(*Pteridium aquilinum* (L.) Kuhn), sword fern (*Polystichum munitum* (Kaulf.) Presl.),

Oregon grape (*Berberis nervosa* Pursh), salal (*Gaultheria shallon* Pursh), trailing

blackberry (*Rubus hispidus* L.) and foxglove (*Digitalis purpurea* L.).

Tree Selection and Measurement

In June and July 2004, we non-randomly chose 10 trees of each species

(Douglas-fir and western hemlock) in each stand (thinned and unthinned). We chose

trees that we estimated to be 1-2 m tall in 1998, exhibited no signs of damage to the

bark, had no branches strongly competing with the terminal shoot for dominance and

were distributed across the entire range of the stand.   Height and height growth since

1998 for these trees were reported in Chapter 2. Briefly, in Douglas-fir the 1998

height was estimated as the point five branch whorls below the top, not including the

current year's growth. In western hemlock the 1998 height was estimated by finding

the point on the stem that had branches that appeared to be five years old based on

annual changes in the color and texture of their bark. Height growth was calculated as

the change in height in the five-year period from 1998 to 2003.

After the height was measured, we harvested trees and took two disks for this

study: a disk for moisture content (about 2 cm tall, from about 5 cm above ground

level) and a disk for specific conductivity (about 15 cm tall, from about 10 cm above

ground level). In the field we removed the bark from the moisture content disks then

obtained fresh mass (M_f). Both the moisture content disks and the specific

conductivity disks were placed in a plastic bag with wet paper towels and then

transported to the laboratory within several hours. Sapwood area, tree leaf area and age were also estimated, as described and reported in Chapter 2.

Specific Conductivity

Upon return from the field site, specific conductivity samples were submerged in water and placed in a cold room (5 ^{o}C) until they could be processed the next morning. We prepared two subsamples (1 cm x 1 cm x 10 cm, tangential x radial x longitudinal) from each sample. Subsamples were first cut roughly to size using a band saw and were then refined to their final size using a chisel making sure to follow the grain along the length of the sample. Samples included the outer growth ring, and usually two to three other rings interior to that in released trees and five to six rings in suppressed trees, depending on ring width. To the extent possible, we avoided compression wood and branch junctions in the samples. After the samples were cut to their final dimensions, they were vacuum infiltrated in tap water for approximately one hour.

Specific conductivity (K_s) was measured using a pressure sleeve apparatus where the sample is placed in a chamber containing a latex membrane (Spicer and Gartner, 1998). A very low pressure was applied to the chamber to press the membrane against the sample to prevent water leakage from its cut sides. For flow measurements, filtered water at pH 2 was placed in an Erlenmeyer flask at a height of 0.48 m above the sample creating a pressure head of 0.0048 MPa. Tubing was connected from the flask to the upstream end of the sample. Tubing also connected the downstream end of the sample to a pipette, marked in graduations of 0.01 ml. The

time required for the meniscus to pass consecutive units of 0.05 ml was tracked using a stopwatch making certain that a fairly constant rate was achieved. Flow rate was corrected to the rate it would have been at 20 $^\circ$C and then used in this equation to calculate K_s.

$$K_s = \frac{Ql}{A_{sample}\Delta P}$$

where Q is the volume flow rate (kg s^{-1}) l is the length of the sample (m), A_{sample} is the cross-sectional area of the sample (m^2) and ΔP is the pressure difference between the two ends of the sample (MPa).

Wood Anatomical Analyses

After K_s was measured, we made 30 to 40 μm thick transverse sections of each sample with a sliding microtome. We stained the sections with safranin and mounted them on slides with glycerine. We viewed the slides using a compound microscope (Eclipse E400, Nikon Inc., Melville NY USA) fitted with a camera (CoolSnap, Roper Scientific Photometric, Tucson, Arizona, USA) and made measurements using image software (version 4.0.2, Scion Corp., Frederick, MD, USA).

For each sample we measured growth ring width, earlywood width and latewood width on all growth rings that were fully formed within the approximately 1 cm^2 conductivity sample. We estimated the transition from earlywood to latewood visually as a distinct difference in cell wall thickness which approximated Mork's definition of a latewood tracheid as one in which the width of the common cell wall multiplied by two is equal to or greater than the width of an individual lumen (Denne,

1988). Average latewood proportion in each sample was estimated as the average of the latewood proportion of each growth ring in the sample.

To obtain an estimate of tracheid diameter, we used two random rows of earlywood tracheids per growth ring and avoiding the first or last several tracheids within the earlywood zone. Tracheids were measured in the radial direction. Measurement included the lumen and the single cell wall on either side of the lumen.

In order to measure tracheid length, we made macerations of wood from each of the K_s samples taking care to sample only from the earlywood. Macerations were made by taking matchstick-sized pieces of the earlywood and putting them into a test-tube with a solution of sodium chlorite and acetic acid. The test-tubes were then placed in a waterbath at 80°C for 2 to 3 hours or until the wood looked bleached and frayed. The wood was then rinsed with water and a small portion of the now separated tracheids were mounted in glycerine on glass slides. We measured tracheid length using a stereoscopic zoom microscope (SMZ-2T, Nikon Inc., Melville, NY, USA) fitted with a camera (Pulnix, Motion Analysis Inc., Eugene, OR, USA). Using image software (version 1.60, NIH, Bethesda, MD, USA) we measured 50 tracheids per slide and three slides for each K_s sample for a total of 150 tracheids per sample. Additionally, we made sure that we only measured tracheids that had two tapered ends to avoid including tracheids that had been cut or broken.

Moisture Content, Wood density, Relative Water Content

After obtaining a fresh mass of the moisture content disks in the field (M_f), we obtained each disk's volume (V_f) using the water submersion method. We then placed

the disks in a drying oven at 50 $^{\circ}$C for approximately one week so that a dry mass (M_d) could be measured. We used the sample fresh and dry masses to calculate moisture content as follows:

$$MC = \frac{M_f - M_d}{M_d} \times 100$$

Then we used dry mass and fresh volume to calculate wood density (D_w) as follows:

$$D_w = \frac{M_d}{V_f \rho}$$

where ρ is the density of water at 4 $^{\circ}$C (g cm^{-3}).

After we calculated moisture content and wood density, we then calculated relative water content of each disk as follows:

$$RWC = \frac{M_f - M_d}{(V_f - V_s)\rho}$$

where V_s is the volume of solid material calculated as dry mass divided by the density of cell wall material (1.53 g cm^{-3}) (Siau, 1984) and ρ is the density of water at 4 $^{\circ}$C (g cm^{-3}).

Statistical Analyses

Means, 95% confidence intervals and p-values were calculated for all variables in Table 3.1 using PROC MIXED SAS version 9.1(SAS Institute Inc., Cary, NC, USA). If needed, log transformations on the data were made to meet assumptions of normality and constant variance. If log transformations were made, the means and confidence intervals were backtransformed and reported on the original scale. Species and stand were used as indicator variables and comparisons of means were made

between each category. Differences in means with a p-value of 0.05 or smaller were deemed significant. Relationships for regression were chosen based on the research questions in this study and significance in the relationships ($r^2 > 0.30$). Values of r^2 were obtained using SigmaPlot (version 9.01 Systat software Inc., Richmond, CA).

RESULTS

The ages of suppressed and released trees did not differ significantly within either species, but western hemlock trees were younger on average than Douglas-fir trees (Table 3.1). Average width of the outer growth rings increased significantly in both Douglas-fir and western hemlock after release from suppression (Table 3.1), and was 3.7 and 3.0 times larger in released vs. suppressed Douglas-fir and western hemlock, respectively (Table 3.1).

Table 3.1: Means and 95% confidence intervals for morphological, anatomical, and physiological characteristics in suppressed and released Douglas-fir and western hemlock trees. Different superscript letters signify a statistically significant difference (p-value <0.05) between the four mean values.

	Douglas-fir		western hemlock	
	suppressed	released	suppressed	released
leaf area (m^2)	0.69 (0.54-0.89)[a]	9.77 (7.59-12.56)[b]	2.07 (1.61-2.66)[c]	9.90 (7.70-12.74)[b]
A_L/A_S (m^2 cm^{-2})	0.27 (0.23-0.31)[a]	1.00 (0.87-1.14)[b]	0.62 (0.54-0.71)[c]	0.90 (0.79-1.03)[b]
height (m)	2.34 (1.99-2.68)[a]	3.62 (3.28-4.00)[b]	2.62 (2.28-2.97)[a]	3.74 (3.39-4.08)[b]
height growth (m)	0.80 (0.54-1.07)[a]	1.99 (1.73-2.25)[b]	1.37 (1.11-1.63)[c]	2.36 (2.10-2.63)[d]
age (years)	17.6 (15.8-19.4)[a]	18.0 (16.2-19.8)[a]	13.9 (12.1-15.7)[b]	12.1 (10.3-13.9)[b]
growth ring width (mm)	0.54 (0.45-0.64)[a]	1.99 (1.68-2.35)[b]	0.94 (0.79-1.11)[c]	2.91 (2.46-3.44)[d]
earlywood width (mm)	0.31 (0.26-0.38)[a]	1.32 (1.08-1.61)[b]	0.65 (0.54-0.80)[c]	2.46 (2.02-3.00)[d]
latewood width (mm)	0.22 (0.18-0.27)[a]	0.65 (0.53-0.80)[b]	0.26 (0.21-0.32)[a]	0.41 (0.33-0.50)[c]
percent latewood (%)	43.2 (38.4-47.9)[a]	34.0 (29.3-38.7)[b]	30.0 (25.1-34.6)[b]	15.9 (11.2-20.6)[c]
K_s (kg m^{-1} s^{-1} MPa^{-1})	0.38 (0.28-0.51)[a]	1.07 (0.80-1.45)[b]	0.59 (0.44-0.80)[a]	0.84 (0.62-1.13)[b]
tracheid diameter (µm)	24.3 (22.8-25.7)[a]	30.4 (28.9-31.9)[b]	22.7 (21.2-24.2)[a]	27.1 (25.6-28.5)[c]
tracheid length (mm)	1.69 (1.61-1.77)[a]	1.87 (1.79-1.96)[b]	1.75 (1.67-1.83)[a]	1.64 (1.56-1.72)[a]
wood density	0.57 (0.55-0.59)[a]	0.47 (0.45-0.49)[b]	0.50 (0.49-0.52)[c]	0.45 (0.44-0.47)[b]
moisture content (%)	66.5 (55.5-77.6)[a]	110.3 (99.2-121.3)[b]	96.6 (85.5-107.6)[b]	136.2 (125.2-147.3)[c]
relative water content (%)	0.60 (0.54-0.67)[a]	0.75 (0.68-0.82)[b]	0.73 (0.66-0.80)[b]	0.87 (0.80-0.94)[c]

Similarly, there was a positive relationship between growth ring width and height growth for both species (Figure 3.1). However, the relationship was non-linear in that as growth ring width increased, height growth became independent of ring width.
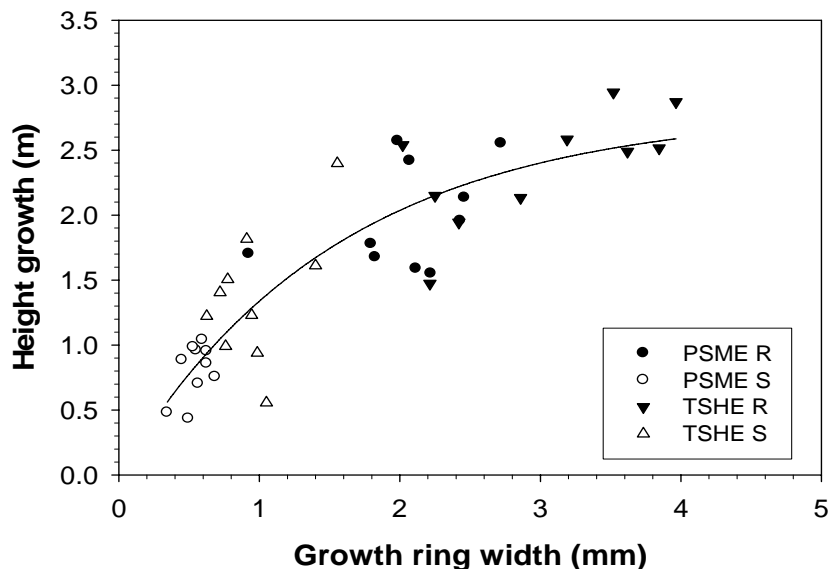
Figure 3.1: Relationship between height growth and growth ring width (r^2= 0.76, p-value <0.0001) Circles: Douglas-fir; triangles: western hemlock; open symbols: suppressed trees; closed symbols: released trees.

Earlywood width was approximately four times greater in released than suppressed trees of both species. The relative increase in latewood width between suppressed and released trees was much greater in Douglas-fir than in western hemlock (Table 3.1). Therefore, latewood proportion decreased by 21% in released compared to suppressed Douglas-fir trees, and by 47% in released compared to suppressed western hemlock trees.

The relationship between earlywood width and growth ring width was very strong for both Douglas-fir and western hemlock (Figure 3.2A). In Douglas-fir, the relationship between latewood width and growth ring width was also very strong. Although the relationship between latewood width and growth ring width for western hemlock was significant, it was much weaker than that of Douglas-fir (Figure 3.2B).
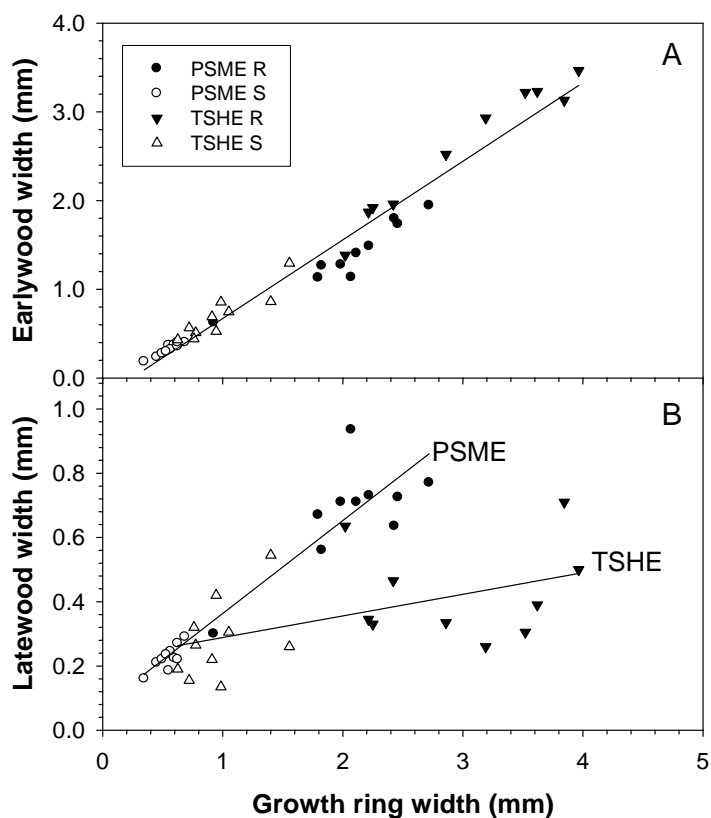
Figure 3.2.   Relationship between growth ring width and A) earlywood width (r^2= 0.97, p-value<0.0001) or B) latewood width for Douglas-fir (r^2=0.90, p-value<0.0001) and western hemlock (r^2=0.26, p-value= 0.02). Symbols correspond to those in Figure 3.1.

In both Douglas-fir and western hemlock, released trees had significantly higher K_s than did suppressed trees although the relative differences were larger in Douglas-fir (Table 3.1). There was also a significant positive relationship between K_s and height growth (Figure 3.3), but it was weaker than the relationship between growth ring width and height growth (Figure 3.1). Again, as with growth ring width, the relationship between height growth and K_s was non-linear in that as K_s increased, differences in height growth became independent of K_s.
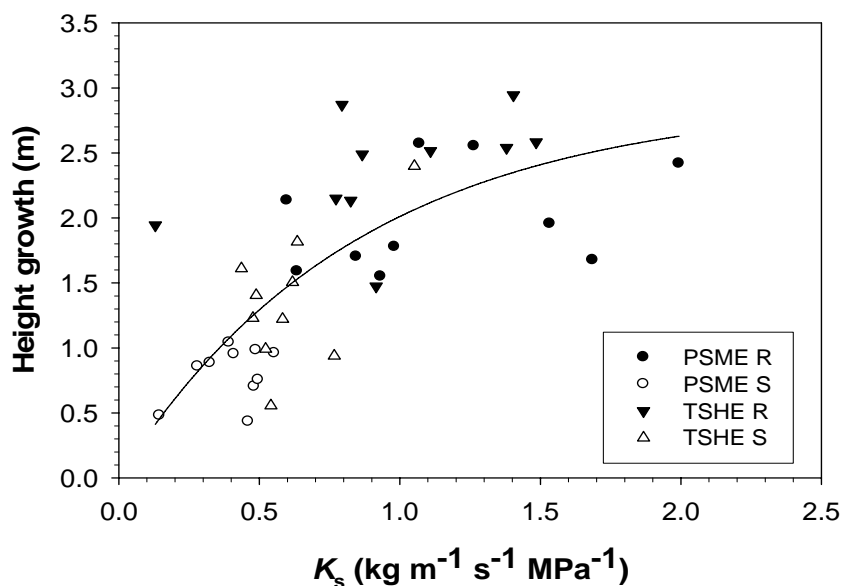
Figure 3.3: Relationship between height growth and specific conductivity (K_s) ($r^2=0.49$, p-value<0.0001). Symbols correspond to those in Figure 3.1.

Both tracheid diameter and tracheid length were significantly greater in released Douglas-fir trees than in suppressed trees (Table 3.1). For western hemlock, however, only tracheid diameter increased significantly when trees were released from

suppression. Although both tracheid diameter and length were positively correlated

with K_s in both species (Figures 3.4A and B), K_s was more closely associated with

tracheid diameter than tracheid length (r^2=0.54 and 0.30 respectively).
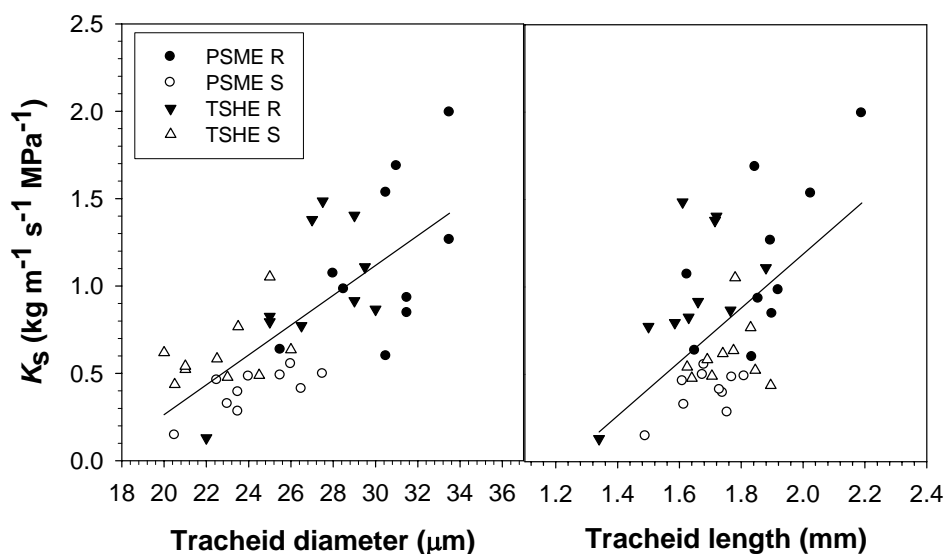
Figure 3.4. Relationship between specific conductivity (K_s) and A) tracheid diameter (r^2= 0.54, p-value<0.0001) or B) tracheid length (r^2= 0.30, p-value =0.0003). Symbols correspond to those in Figure 3.1.

In both Douglas-fir and western hemlock, wood density was significantly

lower after release from suppression (Table 3.1). There were significant negative

relationships between wood density and all of the following factors: height growth,

growth ring width and K_s for both species (Figures 3.5A, B, and C).
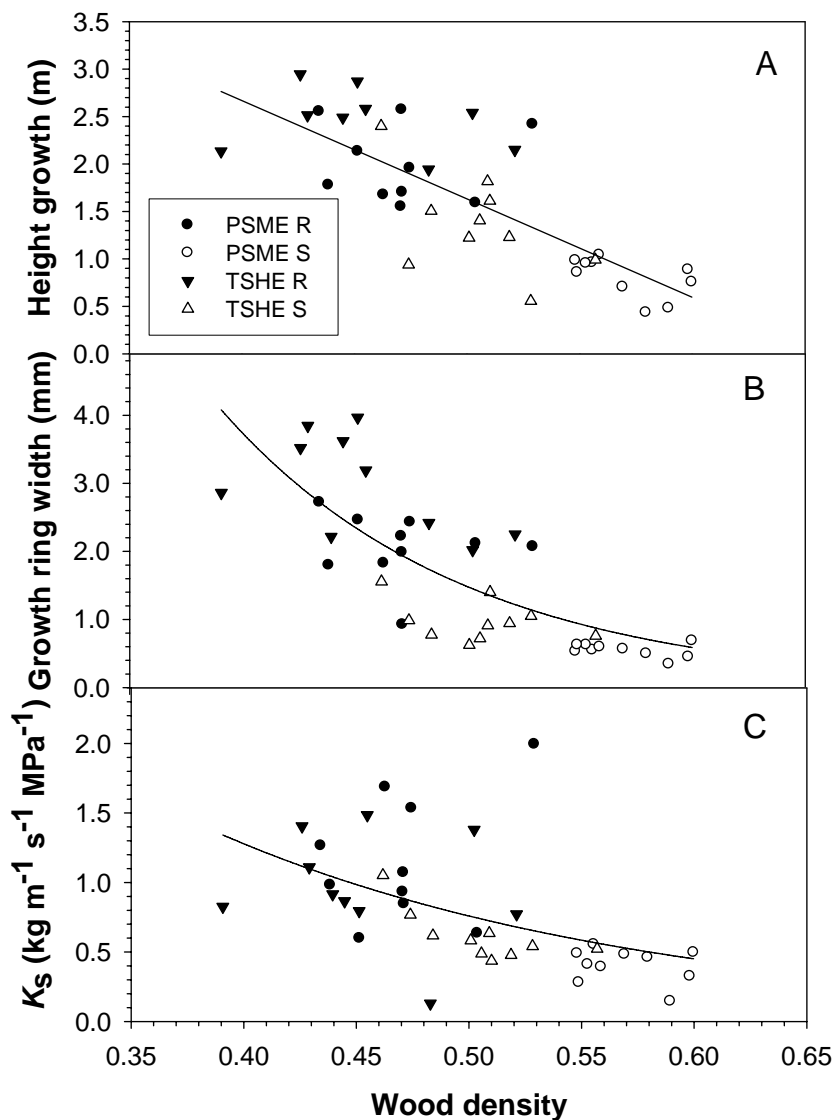
Figure 3.5:   Relationship between wood density and A) height growth ($r^2 = 0.59$, p-value <0.0001), B) growth ring width ($r^2 = 0.61$, p-value<0.0001) or C) specific conductivity (K_s) ($r^2 = 0.35$, p-value= 0.0005). Symbols correspond to those in Figure 3.1.

The relationships between wood density and both growth ring width and K_s were non-linear in that as wood density increased, the rate of decline in growth ring width and K_s diminished. For both Douglas-fir and western hemlock moisture content and

relative water content increased significantly after trees release from suppression

(Table 3.1).

DISCUSSION

Anatomical Changes that Occur with Release

Both Douglas-fir and western hemlock appear to release from suppression by

making more wood, as shown by growth ring width, and by making wood with much

higher K_s by increasing earlywood tracheid length and diameter and decreasing

latewood proportion, compared to trees that remained suppressed. Similar responses

have been observed in other studies. For example, Reid et al. (2003) found that K_s of

sapwood of dominant lodgepole pines (*Pinus contorta* Dougl. ex Loud.) was 2.7 times

greater than that of suppressed lodgepole pines, and although these dominant trees had

never been suppressed, their growing conditions would be similar to trees that had

been released from suppression. Sellin (1993) also found that the relative conductivity

of open-grown Norway spruce (*Picea abies* (L.) Karst.) was 1.4 to 3.1 times greater

than shade-grown trees.

K_s was positively related to both tracheid diameter and length. The

relationship between K_s and tracheid diameter is expected, given the Hagen-Poiseuille

equation which states that flow through conduits is related to the radius of the conduits

raised to the fourth power (Zimmermann, 1983). However, the strength of the

relationship between K_s and tracheid diameter is variable. Pothier et al. (1989) found

that K_s was positively correlated with tracheid diameter in trees between the ages of 15

and 35 yr, but not in older trees. They also found that K_s was never more than 60% of

that predicted by the Hagen-Poiseuille equation. This discrepancy was reconciled by Lancashire and Ennos (2002) who found that resistance to flow through bordered pits made up a significant proportion of the total resistance of flow through tracheids, and that the proportion of the total resistance that was caused by pits increased with tracheid diameter. Therefore, wider tracheids also need to be longer with more bordered pits connecting their overlapping portions in order to minimize resistance in the pathway. Models by Hacke et al. (2004) also show that short tracheids have low conductivity because they are limited by the conductivity of the bordered pits, and as tracheids increase in length, they become limited by their lumen diameter.

A relationship between K_s and tracheid length was also found in this study. However, whereas tracheid diameters were evenly scattered throughout the range of data (Figure 3.4A), tracheid lengths for most of the trees seemed to be clustered between 1.6 and 2 mm (Figure 3.4B) with the few trees with significantly longer or shorter tracheids making the linear relationship discernable. These patterns make sense given the tradeoffs of conductivity against safety where tracheid length is concerned. Although increases in tracheid length reduce the number of bordered pits that need to be crossed in the overall path from the ground to the leaves, longer tracheids also mean that a proportionally larger region of the conducting pathway will be lost if cavitation of these longer tracheids occurs (Comstock and Sperry, 2000). Therefore, whereas tracheid length is probably not an important variable for most trees that tend to have an average tracheid length, when length is shifted above or below an average

value it can have major impacts on specific conductivity and redundancy in the conducting pathway.

Although height growth was correlated with both growth ring width and K_s, the relationship between height growth and growth ring width was stronger than the one between height growth and K_s. Larger increases in the number of tracheids as opposed to the efficiency of individual tracheids may thus be an important safety mechanism for trees that release from suppression. Larger tracheids that would be more efficient at water transport are also more vulnerable to embolism (Sperry and Tyree, 1990). Therefore, making a greater number of tracheids with lower water conducting efficiency may prove less risky than making fewer, more efficient tracheids because it would result in decreased vulnerability to embolism and a greater redundancy in the system in the event that some tracheids are lost to embolism (Cruiziat et al., 2002).

The relationships of height growth with either growth ring width or K_s also appeared to be asymptotic. This pattern implies that water transport capacity of the main stem limits height growth in trees with narrow growth rings and low K_s, but as growth ring width and K_s increase, other factors begin to limit height growth. This limitation could result from an insufficient increase in the water transport capacity of the root system in released trees, or limitations on increasing the photosynthetic capacity of the leaf tissue, thereby limiting whole-tree carbon fixation (see Chapter 2).

Effects of release on wood density

The other main question addressed in this study was how wood density is affected by changes in growth rate that occur after trees release from suppression.

Wood density was negatively related to height growth, growth ring width and K_s. Therefore, increases in either growth ring width or K_s led to decreases in wood density. This is in agreement with Johnson et al. (2005) who found that wood density was positively correlated with the number of growth rings per cm in Douglas-fir trees affected by a foliar pathogen, but other studies in Douglas-fir are less conclusive (McKimmy, 1959, Cown, 1976, Abdel-Gadir et al., 1993).

The relationship between wood density and growth ring width will depend on how earlywood density, latewood density, and latewood proportion change as growth ring width changes. Several species of southern pine trees under moisture stress have been found to initiate latewood formation sooner than trees that are well-watered (Zahner et al., 1964, Cregg et al., 1988). Therefore, due to increased competition by overstory trees, the suppressed trees in this study could be under more moisture stress than the released trees and would initiate latewood formation sooner and therefore have a larger proportion of latewood per growth ring. This would give suppressed trees higher wood densities and greater water storage capacities given that latewood has a higher water storage capacity than earlywood (Domec and Gartner, 2002). If earlywood width is driven by the leaf area the tree will develop, then the larger leaf areas of the released trees could be the driver for wider earlywood and thus lower latewood proportion. Because earlywood has 11 times the K_s of latewood in Douglas-fir, growth rings with a higher proportion of earlywood will be more conductive and have lower wood density (Domec and Gartner, 2002).

Douglas-fir exhibited a strong linear relationship between both earlywood and latewood width with growth ring width. However, for western hemlock, growth ring width was more strongly related to earlywood width than latewood width. This means that increases in growth ring width in western hemlock will correspond to increases in earlywood width but not necessarily with increases in latewood width. DeBell et al. (1994) found that wood density was negatively correlated with ring width in western hemlock and that latewood percentage dropped significantly with increasing ring width. However, Watson et al. (2003) found that wood density of 38-year-old western hemlock trees planted at different spacings (and with presumably different growth rates) was not significantly different. Some of this discrepancy can be reconciled by considering the age of the trees in that the negative relationship between growth rate and wood density was strongest in young western hemlock trees and decreases with time becoming insignificant in trees after age 30 (DeBell et al., 2004). Therefore, relationships in this study between growth ring width and earlywood and latewood width in relatively young western hemlock trees may change as the trees age.

One aspect that could be a confounding factor in this research is the difference in ages between the Douglas-fir and western hemlock trees studied. The age of the western hemlock samples could have been underestimated because of missing rings in the suppressed region of the wood. However, it is more likely that the age difference was caused by our design of choosing trees on the basis of height: younger western hemlock trees would be of a similar height to older Douglas-fir trees given that western hemlock grew faster than Douglas-fir in both suppressed and released

conditions (Chapter 2). The differences in age could be a problem when comparing wood characteristics between the two species because the samples would be coming from different positions within the juvenile zone. However, Fabris (2000) found that changes in wood properties in the juvenile zone of western hemlock were more gradual than for Douglas-fir. Therefore, age of the wood in western hemlock should not be as much of an issue as it could be in other species.

Although wood density has been shown to decrease after release from suppression, values of wood density for released Douglas-fir and western hemlock in the present study are only slightly lower than those reported for open-grown trees (Simpson and TeaWolde, 1999). Therefore, if maintenance of some threshold wood density is an important determinant for the way the wood will be utilized, then release from suppression should not have deleterious effects on wood quality for these species. Furthermore, trees that have experienced suppression during the beginning of their lives may be better from a wood utilization standpoint because they will have a smaller core of juvenile wood in their lower log, increased wood density in their core wood, and fewer knots because of self-pruning of the lower branches that has occurred when trees were suppressed. However, if more subtle characteristics should prove to be important, such as the homogeneity of growth ring width, wood density or moisture content, then released trees may have wood with very different value than trees that were never suppressed.

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CHAPTER 4: CONCLUSIONS

DOUGLAS-FIR WAS ABLE TO SUCCESSFULLY RELEASE

One of the first conclusions from this study is that Douglas-fir was able to successfully release from suppression. Although relative height growth in released western hemlock was substantially higher than in released Douglas-fir, the relative differences between relative height growth between suppressed and released trees were more substantial for Douglas-fir than for western hemlock. Therefore Douglas-fir can release from suppression. However, the question now becomes: Will released Douglas-fir be able to keep up with released western hemlock, or will it again become suppressed by the released western hemlock? It would be interesting to visit this site in another five to ten years, measure height growth and relative height growth again, to see if Douglas-fir has made gains at catching up to western hemlock in height. This could conceivably happen because released Douglas-fir was found to have more N_{area} than released western hemlock and approximately the same leaf area. This would give Douglas-fir a higher photosynthetic capacity than western hemlock, and assuming Douglas-fir simply needs more time to overcome its hydraulic limitation, Douglas-fir has the capacity for higher carbon gain than western hemlock.

PHOTOSYNTHETIC CAPACITY AND HYDRAULIC ARCHITECTURE
CONSTRAIN RELEASE

The second and third conclusions of this study are that photosynthetic capacity initially limited release in Douglas-fir and western hemlock, and that hydraulic architecture limited further release in Douglas-fir more so than western hemlock. These conclusions were drawn from comparison of root conductance (k_{RL}), leaf

specific conductivity (K_L), leaf area:sapwood area ratios (A_L/A_S), N content of leaves, A_{max}, and $\delta^{13}C$ between suppressed and released trees. However differences between suppressed and released trees can only reveal a certain amount of information and comparison of released trees with trees that have never been suppressed would be fruitful, especially in Douglas-fir.   Because Douglas-fir is less shade tolerant than western hemlock, differences between the open-grown and the suppressed condition are likely to be more substantial. For example, if another plot of land had been clearcut when the first thinning occurred, then Douglas-fir could have regenerated in gaps in a forest understory (this study) as well as in a clearcut situation. This would have also provided trees that were approximately the same age but grown in open conditions (assuming the natural regeneration was not too dense) to compare with trees released from suppression. It would also shed some light on how far the released Douglas-fir trees have come in changing their hydraulic architecture to grow successfully in a well-lit environment as opposed to a shaded environment. For example, are the A_L/A_S, K_L, and k_{RL} of released Douglas-fir trees similar to trees that have always been growing in an open condition, or are released Douglas-fir trees still adjusting their hydraulic architecture to better take advantage of their current growing situation? A_L/A_S, K_L and k_{RL} in suppressed and released western hemlock were fairly similar suggesting that little more adjustment in hydraulic architecture will be made in western hemlock.

Data from this study may also shed light on the shade tolerance of Douglas-fir in sites with contrasting soil moisture. There is conflicting evidence in the literature

suggesting that Douglas-fir is either more or less shade tolerant on drier sites as opposed to wetter soil sites. Atzet and Waring (1970) found that the minimum light requirement for Douglas-fir increased when moisture was limiting in the site compared to when moisture was adequate, suggesting Douglas-fir is less shade tolerant on drier sites. However, other studies have found that Douglas-fir is more shade tolerant on drier sites (Carter and Klinka, 1992, Williams et al., 1999). This decrepancy in the literature could be the result of differences in the interpretation of shade tolerance. If, for example, shade tolerance is defined as the ability of a species to tolerate deep shade, then results of Atzet and Waring (1970) make sense in that when moisture is adequate, Douglas-fir needs to allocate less carbon belowground and therefore has a lower minimum light requirement. However, if the definition of shade tolerance is the ability of a species to persist for long periods of time in a shaded environment, then Douglas-fir would appear to be more shade tolerant on drier sites because, on drier sites, Douglas-fir would allocate more carbon belowground and be able to survive a season where rainfall was below-average (Williams et al., 1999). In our study, which was conducted in a rather wet environment, released Douglas-fir allocated much less carbon to roots than to leaf structure and in turn had a much lower k_{RL} when released than trees that were still suppressed. If these trees faced an unusually dry season, they may not have been able to survive and release as well as they had.

SUGGESTIONS FOR STAND MANAGEMENT

This research may also give some insight into some stand management techniques that may help Douglas-fir trees release and grow successfully after being suppressed. Because photosynthetic capacity was found to initially constrain release, care should be taken when performing thinnings to release Douglas-fir. Thinnings should not be too heavy as this may cause photoinhibition and increased stress on Douglas-fir trees that have been suppressed in the understory. Gray and Spies (1996) studied saplings exposed to high light levels after growing in a shaded environment and found that high light levels led to stress and in some cases sapling mortality. Nitrogen fertilization may also be beneficial to allow needles on released trees to have increased photosynthetic capacity. However, fertilizations should only be performed once hydraulic architecture has increased and is no longer limiting carbon gain because, as found in this study, the increased N_{area} of Douglas-fir was not being utilized optimally because hydraulic architecture was limiting. Also, fertilization may make trees less drought tolerant. Ewers et al. (2000) found that soil fertilization caused lowered root area to leaf area ratios, although roots were more resistant to embolism than roots of trees in an unfertilized soil. Also, in our study released Douglas-fir allocated much less carbon to roots than leaves (given the large increases in A_L/A_S relative to the decrease in k_{RL}), therefore water supply should be monitored because released Douglas-fir trees could be vulnerable if soils become dried. Finally, care could be taken when choosing which overstory trees to remove. Cline et al. (2005) found that Douglas-fir seedlings growing near mature trees had higher species

richness and diversity of ectomycorrhizal fungi than did seedlings located far from trees. Therefore, it may be beneficial to keep some of the large overstory trees growing near the advance regeneration in an effort to maintain the mycorrhizal community and protect the advance regeneration from too much direct sunlight.

CHANGES IN FUNCTIONAL WOOD CHARACTERISTICS

The remaining conclusions of this study deal with how the functional wood characteristics differ between suppressed trees and trees released from suppression in Douglas-fir and western hemlock. We found that growth ring width, specific conductivity, earlywood tracheid diameter, moisture content and relative water content were higher in both released Douglas-fir and western hemlock than in suppressed trees. Tracheid length was higher in released Douglas-fir but not in released western hemlock compared to suppressed trees of the same species. Latewood proportion and wood density were lower in both released Douglas-fir and western hemlock compared to suppressed trees.

Because latewood proportion decreased in released trees compared to suppressed trees, it would be interesting to see how wood formation differs throughout the growing season in suppressed vs. released trees. For example, Antonova and Stasova (1993) found that nocturnal temperature was the main influence on cambial activity in the beginning of the growing season. If this is the case, then it would seem reasonable that suppressed trees would begin wood formation sooner than released trees given that they are growing under an overstory that would be providing some protection from heat loss at night. Cregg et al. (1988) found that the transition from

earlywood to latewood was related to soil moisture and evaporative demand.

However, in our study both released and suppressed trees had approximately the same

predawn water potentials, implying that soil moisture did not differ between the two

sites and that they should have approximately the same date of transition from

earlywood to latewood. One way to determine whether the transition from earlywood

to latewood occurs at a similar date in suppressed and released trees would be to

perform a cambial pinning study (Wolter, 1968) whereby small pins would pierce the

cambium of the trees weekly, creating callus tissue in the wood that could then be

used to track the process of wood formation throughout the growing season.

One of the interesting differences between Douglas-fir and western hemlock in

this study was the fact that tracheids were longer in released Douglas-fir trees but not

western hemlock trees compared to suppressed trees. Longer tracheids should provide

greater conductivity because they reduce the number of bordered pit crossings in the

pathway from roots to leaves, with bordered pits representing the main resistance to

water flow in wood (Comstock and Sperry, 2000, Lancashire and Ennos, 2002). This

can be seen in Douglas-fir in that released trees had longer tracheids as well as higher

specific conductivity (K_s). However, released western hemlock also had higher K_s

with tracheids that were approximately the same length as suppressed trees.

Therefore, it would be interesting to take a closer look at the pit structure in

suppressed and released western hemlock to determine if the pits themselves were

different in released vs. suppressed trees conferring higher K_s to the wood of released

trees. For example, Domec et al. (submitted) found that hydraulic conductivity can be

explained by the amount of tracheid radial wall that contains pits, the flexibility of pit membranes and pit porosity. Therefore, even though western hemlock tracheids were the same length in released vs. suppressed trees, differences in pit structure and frequency in tracheids could confer released trees with higher K_s than suppressed trees.

One of the final questions that still remain in this study deals with juvenile wood and if the patterns of cambial maturation seen in open-grown trees would also apply to trees released from suppression. In the juvenile zone of open-grown trees, wood density increases, tracheid length and diameter increases, microfibril angle decreases and latewood proportion increases until the transition to mature wood when these characteristics become relatively constant (Zobel and van Buijtenen, 1989). However, many of these qualities (wood density, tracheid length and diameter, latewood proportion) also change with environment, as seen in our study. Therefore, is cambial maturation simply a function of cambial age or is it also affected by environmental factors that change as trees grow and mature? One way to address this question would be to look at the relatively environment-independent variable of microfibril angle in the wood of trees released from suppression to determine if the changes in microfibril angle with age that characterize the transition from juvenile wood to mature wood are also seen in these trees. Identification of microfibril angle would also be important in determining the quality of trees released from suppression in terms of strength, longitudinal shrinkage and warp.

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