AN ABSTRACT OF THE DISSERTATION OF

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Title: Size-related variation in tree growth and physiology.

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Barbara J. Bond

The goal of this dissertation was to improve our understanding of age-related constraints on aboveground production of forest trees. Previous research suggesting that carbon uptake of old trees is hydraulically constrained by tree size was used as the springboard for this research. Three specific working hypotheses were investigated: 1) compensation for height via decreasing the ratio of leaf area to sapwood area as trees become taller occurs for all tree species, 2) compensation via both physiological and structural mechanisms is insufficient to prevent age- or height-related reductions in stomatal conductance and photosynthesis of Douglas-fir, and 3) removal of competition via stand density reductions allows old ponderosa pine to increase growth via increased stomatal conductance.

I found that, for most species in which data were available, the ratio of leaf area to sapwood area declines as trees become taller. This response should act to maintain leaf-specific hydraulic sufficiency as trees become taller. This decline was observed both within- and between-species growing in wet vs. dry climates, and for broadleaf and needleleaf species. Two species (Norway spruce and Balsam fir)

increased the ratio with height, showing that compensation for hydraulic constraints via reducing leaf area per unit sapwood area is not a universal response.

In Douglas-fir trees ranging in height from 15 m to 60 m, hydraulic limitation and compensation co-occur. Growth efficiency, stomatal conductance as indexed using stable carbon isotopes, and leaf-specific hydraulic conductance declined as trees became taller. A simple model based on Darcy's Law showed that the observed 44% decline in hydraulic conductance with increasing tree height would have been greater than 70% had the leaf area to sapwood area ratio and the soil-to-leaf water potential not changed in concert with height.

I observed that growth and carbon isotope discrimination of ≥ 250-year-old ponderosa pine are very sensitive to increasing moisture availability after stand density reductions. The assumptions that old trees are unable to respond to increased growing space, or that they are genetically predisposed to grow slowly, were shown to be false.

Together, these results support the theory that hydraulic constraints to tree height exist. Furthermore, these studies show that resource availability and hydraulic compensation can mitigate size-induced changes in hydraulic conductance and stomatal conductance. Future research on the mechanisms of age-related growth decline should focus on testing multiple hypotheses within the same set of forests. Incorporation of model predictions of each hypothesis will allow estimation of the relative role of each potential mechanism. Future research on the hydraulic limitation hypothesis should investigate the consequences of compensation for hydraulic driving forces-such as height-induced reductions in liquid phase conductance-on gas exchange and carbon allocation.

SIZE-RELATED VARIATION IN TREE GROWTH AND PHYSIOLOGY

by

Nate G. McDowell

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APPROVED:

Major Professor, representing Forest Science

Chair of Department of Forest Science

Dean of Graduate School

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

Nate G. McDowell, Author

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CHAPTER 1.

INTRODUCTION

1.1 WHY STUDY AGE-RELATED TRENDS IN CARBON ASSIMILATION?

The importance of understanding the limitations of carbon assimilation by forests has grown immensely in the last few decades, and is certain to become more important in the upcoming centuries. Carbon assimilation sets the upper limit on the amount of carbon that may be sequestered in forest biomass, which has implications for forest management and biology. Because forests, particularly temperate forests, are thought to be sinks for atmospheric CO_2, they provide a method to balance the global carbon budget (Tans et al. 1990, Keeling et al. 1996). The Kyoto protocol, which was designed to mitigate the current rise in atmospheric CO_2, suggested managing forests to maximize carbon uptake and sequestration and that nations be responsible for quantifying their carbon sequestration. Thus, the role of forests in sequestering CO_2 has become a political issue of global importance (Schulze et al. 2000). Another aspect of carbon assimilation that is of importance to forest managers is stemwood yield, the amount of which can have large impacts on regional economies (Sedjo et al. 1999, USDA-GCP 2001). Stemwood yield depends on carbon assimilation, and factors that reduce assimilation will also reduce yields (Davis and Johnson, 1987). From an ecological perspective, carbon assimilation provides the mechanism by which the energy available from solar radiation is converted into substrates useable for all other forms of life. Within forest ecosystems, changes in carbon assimilation can have drastic effects on ecosystem metabolism (Waring and Running 1998). Therefore, constraints on carbon assimilation are important to understand from the perspectives of politics, management, and basic biology and ecology.

Carbon assimilation of "old-growth" forests, defined here in the Pacific Northwest as forests older than 195-years (Spies and Franklin 1991), is also of paramount importance. One theory suggests that old forests should be replaced by rapidly growing young forest in order to sequester more carbon (Kershaw et al. 1993). This theory is based on well-documented fact that young stands grow faster than old stands. However, this approach actually leads to net carbon emissions due to the removal and eventual release of carbon stored in the old forests (Harmon et al. 1990, Janisch and Harmon 2002). The replacement of old trees with young, shade-tolerant trees and shrubs via succession may also mitigate ecosystem-scale decline in carbon assimilation and growth associated with age (Waring and McDowell 2002). Furthermore, there is little direct evidence that old forests assimilate less carbon than young forests. This makes model-based predictions of carbon sequestration suspect, as most physiological process models predict carbon assimilation based on measurements of photosynthesis on young trees (Ryan et al. 1996). Therefore, it is important that we understand the constraints on carbon assimilation of old trees if we are to manage old forests wisely in the future.

1.2 CONSTRAINTS ON CARBON ASSIMILATION

Young and old trees share a number of constraints on carbon assimilation. At the ecosystem scale, the amount of leaf area per unit ground area has a large effect on canopy-scale carbon assimilation (Waring and Running 1998). This is an emergent property of the ecosystem, dependent on constraints on the amount of leaf area each tree can sustain and the number of trees the ecosystem can support. At the leaf- and individual tree-scales, which are the scales of focus for this dissertation, numerous variables constrain photosynthesis, the effects of which are observed at scales much larger (ecosystem to globe). In C_3 plants under optimal environmental conditions, the carboxylation of CO_2 and ribulose 1,5-bisphosphate (RuBP) by the enzyme ribulose 1,5 bisphosphate carboxylase-oxygenase (Rubisco) is typically a rate-limiting step in photosynthesis due to the slow regeneration of Rubisco (Taiz and Zeiger 1998). The rates of electron transport and triose phosphate availability can also become limiting to photosynthesis, such as at low light or high CO_2 levels, respectively (Harley et al. 1992).

Nutrient availability, particularly nitrogen, is important to carbon fixation by young and old trees due to the strong relationship between carboxylation capacity, electron transport, and leaf nitrogen concentration (Field and Mooney 1986, Evans

1989, Harley et al. 1992, Mitchell and Hinckley 1993). Although excess nitrogen can also have deleterious effects (i.e. Aber et al. 1991), excess nitrogen it typically limited to areas of northeastern United States and Europe and, in general, nitrogen limitation, rather than nitrogen saturation is the standard condition in temperate forests (Ericsson 1994). In needle leaf trees, the typical response to nitrogen addition is an increase in leaf area per tree, whereas in broad leaf trees the nitrogen concentration usually rises (Brix and Mitchell 1983, Ericsson 1994). In either case, tree-scale carbon assimilation usually increases in response to nutrient addition.

Light availability is another constraint on carbon assimilation. Light energy is absorbed by pigments within the chloroplasts of leaves and converted into chemical energy (ATP and NADPH). Reductions in light interception and hence photosynthesis can occur due to shading or due to changes in needle structure associated with pathogens (Manter 2000). Clouds or airborne particles can reduce the availability of direct light but may also increase carbon uptake by increasing diffuse light penetration into canopies, thereby increasing total carbon assimilation (Roderick et al. 2001). Reductions in chlorophyll content can reduce light absorption and electron transfer, and may occur due to nutrient limitations (particularly nitrogen), or due to down-regulation of chlorophyll synthesis due to reduced light levels.

Carbon assimilation is also constrained by both high and low temperatures (Berry and Björkman 1980). Quantum yield (the amount of carbon assimilated per unit absorbed light) is reduced at high temperatures because of the increased affinity of Rubisco for O_2 relative to CO_2 (Ehleringer and Björkman 1977). Because of the exponential relationship between respiration and temperature, high temperatures can cause high respiration rates, leading to reduced net photosynthesis. At very high temperatures, enzymes and pigments can denature, leading to reduced photosynthetic capacity. Very low temperatures can suppress Calvin cycle enzymes, electron transport, and reduce stomatal conductance (Stenberg et al. 1995).

Perhaps the most common constraint on carbon assimilation is that associated with low conductance of CO_2 from the atmosphere to the site of reduction in the chloroplast. The transfer of CO_2 into foliage is mediated by stomata and associated guard cells, which balance CO_2 diffusion into foliage with water loss out of the foliage via regulation of stomatal aperture (Hinckley and Braatne, 1994). The optimal balance between water loss and carbon uptake is thought to be that which maximizes carbon uptake relative to water availability per unit time (Cowan and Farquhar 1977). Too much water loss via high conductance can lead to tissue desiccation, which initiates loss of RuBP and chlorophyll (Gimenez et al. 1992), down regulation of photosynthetic capacity (Tezara et al. 1999), and eventually to mortality. Too little carbon uptake via low conductance can lead to reduced carbon storage and, therefore, less carbon availability for growth, reproduction, and defense.

Soil and atmospheric water contents are primary constraints on photosynthesis because reductions in either lead to reduced stomatal conductance. Low soil water content constrains the amount of water that may be supplied to the canopy. Adaptations to low soil water availability include, but are not limited to, development of deep roots (Jackson et al. 1996, Sperry et al. 1998), reduced leaf area (White et al. 1998), increased water storage (Goldstein et al. 1998), increased cavitation resistance (Ewers et al. 2000), increased leaf pubescence or decreased area per unit weight, and alterations in leaf-level carbon-water balance via reduced stomatal conductance (Cowan and Farquhar 1977, Ehleringer 1993) or via alternative photosynthetic pathways (i.e. C_4, CAM, Taiz and Zeiger 1998). Low atmospheric water content in association with warm air temperatures causes a large driving force for evaporation of water from the stomatal cavities. To prevent excessive evaporation, stomatal conductance declines as the air around the foliage becomes warmer and drier (Grieu et al. 1988, Hinckley and Braatne 1994). Other adaptations to atmospheric drought include, but are not limited to, those listed above for low soil water availability.

1.3 CONSTRAINTS ON CARBON ASSIMILATION: THE OLD TREE

Mature and old trees are subject to the same constraints upon carbon assimilation as young trees; however, other constraints may also exist. Among these potential constraints are nutrient based limitation of photosynthetic capacity, genetic down-regulation of photosynthesis, reductions in whole-tree leaf area per unit live biomass, reductions in mesophyll conductance, and reductions in hydraulic conductance per unit leaf area. These are a few of the mechanisms that may be responsible for the globally-consistent observation of age-related growth decline in trees (reviewed in section 1.4). Next, I will review the first four potential constraints to assimilation listed above, and will then review the fifth (reduced hydraulic conductance) in section 1.5.

As forests age, nutrients, and nitrogen in particular, may become scarce due to sequestration in biomass and necromass (Gower et al. 1996, Ryan et al. 1997). Such scarcity may lead to reductions in nitrogen allocation to thylakoid membranes and enzymes, thereby reducing photosynthetic capacity. However, very little supporting evidence for this hypothesis exists. Some forests exhibit increases in nitrogen availability, some show no change, and some show declines with stand age (Ryan et al. 1997). Schoettle (1994) and Kull and Koppel (1987) observed declines in leaf nitrogen and photosynthetic capacity as trees aged, although most other studies have seen no change in nitrogen concentration or photosynthetic capacity with tree age (Ryan et al. 1992, Mencuccini and Grace 1996, Olsson et al. 1998, Hubbard et al. 1999, Barnard 2001, McDowell et al. 2002a, Ryan and Whitehead *unpublished data,*).

Genetic down-regulation of photosynthesis has not been specifically proposed in the literature, nor are there data testing this hypothesis. However, genetic limitation of growth of old trees has been proposed (Becker et al. 2000, Bond 2000), and therefore, a potential hypothesis is that carbon assimilation is genetically regulated to decrease with age. However unlikely this seems from an adaptive viewpoint, this hypothesis merits testing. Such a test would ideally be conducted on trees of similar size but different age, thereby separating the confounding factors of size and age. However, trees that have similar sizes but different ages (hence different growth rates) are likely to have another confounding factor involved that led to the differences in growth (i.e. growing in shade or on nutrient- or water-limited sites). An alternative is to graft scions of old twigs onto young trees and vice versa, and then measure carbon assimilation after the grafts have adjusted to the new hosts.

An alternative mechanism of genetic regulation of carbon assimilation could be indirect: if trees are genetically programmed to reduce growth (i.e. Greenwood et al. 1989, Day et al. *in press*), then this may reduce sink strength. Sink strength can be important in regulating photosynthetic rates (Luxmoore 1991, Kozlowski 1992, Shishido et al 1999).

Reductions in whole-tree leaf area can also reduce carbon assimilation at the whole-tree scale. Such reductions may occur due to physical damage and loss of branches due to storms (wind, ice) or abrasion against neighboring trees (Ryan et al. 1997, Smith and Long 2000). Alternatively, reductions in leaf area may occur as a mechanism to maintain leaf-specific hydraulic sufficiency (Meinzer et al. 1997, Ryan and Yoder 1997). Further examination of this rationale will be provided in section 1.5.

Whatever the mechanism, if the photosynthetic surface area (leaf area) declines on a whole-tree basis, then this may reduce total carbon assimilation if carbon assimilation per unit leaf area does not increase proportionately (Whitehead et al. 1996).

Reduced mesophyll conductance to CO_2 causes lower CO_2 concentration at the site of carboxylation, which subsequently may reduce photosynthetic rates (Vitousek et al. 1990, Gillon and Yakir 2000). Mesophyll conductance is strongly correlated with specific leaf area (area per unit mass) because thicker leaves tend to have more distance through which CO_2 must diffuse from the sub-stomatal cavity to the mean site of carboxylation (Hanba et al. 1999). Because specific leaf area declines (i.e. leaves become thicker) with height above the ground (Bond et al. 1999, Thomas and Winner 2002), it is logical that mesophyll conductance will also decline with tree size. Mesophyll conductance may be further reduced in old trees because foliage from tall, old trees has a lower proportional area of internal leaf-volume allocated to mesophyll compared to young trees (Apple et al. 2001). In place of the photosynthetic mesophyll tissue, non-photosynthetic and presumably non-conductive tissues such as asterosclereoids become more prominent in foliage of old trees (Apple et al. 2001). The driving force for the increased presence of asteroscleroids is not known.

1.4 AGE-RELATED GROWTH DECLINE

A pattern universally observed in chronosequence studies is that trees and stands grow quickly until they reach peak leaf area index (m^2 leaf area per m^2 ground area), after which growth begins a slight but steady decline for the remainder of the trees' life (Ryan et al. 1997). Growth decline per unit leaf area has been observed at both the individual- and stand-scales (Mencuccini and Grace 1996a, Ryan et al. 1997, McDowell et al. 2002a). The mechanism causing this age-related growth decline has yet to be explained, but many promising theories exist. In this section, I will briefly review the hypotheses that have been proposed to explain age-related growth decline.

In section 1.3 I detailed potential mechanisms by which carbon assimilation of old trees may be constrained beyond that of young trees. Genetic, nutrient, and leaf area reduction constraints may all occur in some circumstances, but evidence supporting these is currently limited. Before reviewing another potential constraint on assimilation, that of hydraulic constraints, I will first review non-photosynthetic based hypotheses for growth decline.

Carbon assimilation of old trees may not differ from that of young trees at the leaf- to whole-tree scale. If this were true, the age-related decline in growth must be due to changes in carbon allocation. Carbon may be allocated away from aboveground growth and toward respiration (Yoda et al. 1965), to defense against pathogens or insects, reproduction (Ryan et al. 1997, Becker et al. 2000) or belowground growth (Grier et al. 1981, Gower et al. 1996, Magnani et al. 2000). However, tests of the respiration hypothesis in lodgepole pine (Ryan and Waring 1992) and eucalyptus (M.G. Ryan *unpublished data*) have failed to support it, and it is only weakly supported by modeling studies (Magnani et al. 2000, Mäkelä and Valentine 2001). Allocation to defense against insects and pathogens has not been quantified in relation to tree age or size. Therefore, it is not known if allocation to defense can consume sufficient carbon to explain the large decline in growth with age. Likewise, the reproduction hypothesis has not been tested. Although studies in gymnosperms have found that cone respiration is not a large component of gross primary production (Linder and Troeng 1981, Dicks et al. 1990, McDowell et al. 2000), large cone crops have been correlated with reduced diameter increment (Eis et al. 1965, Tappeiner 1969, El-Kassaby and Barclay 1992). Becker et al. (2000) argued that trees are genetically programmed to increase carbon allocation to reproduction at the expense of stemwood. However they provide no evidence in support of this theory beyond the strong evolutionary logic that increasing reproduction at the expense of stemwood is likely to increase the fitness of a species. Further work on this hypothesis is merited. Increased carbon allocation belowground has also been poorly tested, but indirect evidence from measurements (Grier et al. 1981) and from model theory (Magnani et al. 2000) supports this theory. Gower et al. (1996) proposed that increased allocation to fine roots may occur with increasing age in response to increased nutrient limitation, and Magnani et al. (2000) proposed that increased belowground allocation may act to minimize age-related reductions in hydraulic conductance. However, Smith and Resh (1999) and Giardina and Ryan (*in review*) found no increase in belowground carbon allocation with age. In summary, there is currently no strong evidence in support of the hypothesis that carbon allocation away from stem growth increases as trees age.

Hypotheses also exist that suggest age-related growth decline is a stand-level phenomenon rather than an individual tree phenomenon. Binkley et al. (2002) suggested the "single-tree hypothesis" that proposes that as stands age and become less even-aged, suppressed trees use resources (light, nutrients, carbon) less efficiently than dominant trees, causing a net decline in stand level growth per unit resource consumption. Smith and Long (2000) argue that the decline in stand level leaf area is completely responsible for stand level growth decline. However, neither of these hypotheses explain why height growth ceases in open-grown trees, such as those found in metropolitan parks (Ryan and Yoder 1997).

1.5 THE HYDRAULIC LIMITATION HYPOTHESIS

A mechanism that may explain age-related growth decline and the ultimate limits to tree height is the hydraulic limitation hypothesis (Ryan and Yoder 1997). This hypothesis suggests that stomatal conductance to CO_2 diffusion declines with increasing tree size because the resistance to water transport from the soil to leaves increases as trees grow larger. As water transport sufficiency declines, stomatal conductance declines to prevent xylem cavitation and leaf desiccation. The net effect of reduced stomatal conductance is reduced carbon assimilation, therefore less carbon is available for growth.

The hydraulic limitation hypothesis is based on interactions between cavitation avoidance and water transport capacity. Foliage tends to have minimum water potentials beyond which cavitation (the filling of transport elements with air, thus blocking water transport) will occur. Stomatal closure prevents leaf water potential from dropping below this minimum. The minimum leaf water potential tends to be species-specific and usually does not vary with tree height (Hinckley et al. 1978, Tyree & Sperry 1988, Tyree & Ewers 1991, Sperry & Pockman 1993, Saliendra et al. 1995, Hubbard et al. 1999, Bond & Kavanagh 1999, but see Yoder et al. 1994, Barnard 2001, McDowell et al. 2002a). Cavitation avoidance via regulation of vapor phase water loss from stomata is coordinated with the liquid phase transport of water from the soil to the guard-cell complexes (Meinzer et al. 2001b). Hydraulic conductance, which is the inverse of hydraulic resistance, is therefore an important regulator of stomatal conductance via a supply-and-demand relationship. That is, if the supply is reduced (reduced hydraulic conductance), then the internal demand is reduced via a proportional reduction in stomatal conductance. This supply-and-demand relationship is well-documented in the literature (Sperry and Pockman 1993, Sperry et al. 1993, Saliendra et al. 1995, Whitehead et al. 1996, Pataki et al. 1998, Hubbard et al. 1999, Hubbard et al. 2001). Hydraulic conductance is expected to decline as trees grow taller due to increased pathlength associated with increased height and longer branches (Waring and Sylvester 1994, Panek and Waring 1995, Walcroft et al. 1996, Warren and Adams 2000, Bond and Panek *unpublished data*), and increased tortuosity associated with changes in wood density particularly at branch/bole junctions (Gartner 1995). Evidence showing reduced hydraulic conductance with increasing tree size has been observed in numerous species (Mencuccini and Grace 1996b, Hubbard et al. 1999, Ryan et al. 2000, Schäfer et al. 2000, but see Barnard 2001, Phillips et al. 2002). Therefore, reduced hydraulic conductance associated with increasing tree size can induce reduced stomatal conductance per unit leaf area. Reductions in stomatal conductance force reductions in carbon assimilation despite flexibility in water-use efficiency with tree height (Fessenden and Ehleringer 2002, McDowell et al. 2002a), leading to reduced carbon assimilation (Yoder et al. 1994, Hubbard et al. 1999, Kolb et al. 2000). See the appendix for a detailed example of how the above-described theory can explain the maximum heights trees can achieve.

1.6 HYDRAULIC COMPENSATION FOR TREE SIZE

Critics of the hydraulic limitation hypothesis have pointed to the numerous mechanisms by which plants compensate for hydraulic constraints as evidence that the increased height and structural complexity of old trees are unlikely to constrain hydraulic conductance and hence assimilation. While these compensating mechanisms were briefly addressed in Ryan and Yoder (1997) and more fully described by Becker et al. (2000), Bond and Ryan (2000), Mencuccini and Magnani (2000), and Meinzer et al. (2001a), they have not been fully reviewed even yet.

Hydraulic compensation is a term that broadly encompasses any mechanism by which woody plants may mitigate the *potential* age-related changes in hydraulic conductance, including structural and physiological changes. An underlying premise is that increasing tree size induces a hydraulic driving force for maintenance of hydraulic conductance. In other words, the hypothesis of hydraulic compensation assumes that increased tree size will lead to reduced hydraulic conductance if no compensating mechanisms exist.

Some of the potential mechanisms of hydraulic compensation are included in a hydraulic model based on Darcy's Law:

$$g_s = \frac{k_s A_s \Delta\Psi}{h \eta A_l D} \tag{1}$$

where g_s is stomatal conductance, k_s is specific conductivity of the xylem, A_s is sapwood area, $\Delta\Psi$ is the soil-to-leaf water potential difference, h is soil-to-leaf pathlength, η is the viscosity of water, A_l is leaf area, and D is the leaf-to-air vapor pressure deficit. It can be seen that g_s will decline as h increases if no other parameters change concurrently. Certainly, there may be other compensating mechanisms beyond those explicit in equation (1). However, from this equation, hypotheses can be made as to what parameters may change in order to maintain g_s as h increases.

The ratio of leaf area to sapwood area (A_l:A_s) is usually lower for individuals located on dry sites or in dry climates. This observation conforms to equation (1), which predicts that as D increases, A_l:A_s will decline. This occurs both across species (Waring et al. 1982), and more importantly for our discussion, within species (White et al. 1998). This results in an increase in the transport capacity of the liquid-phase conducting system per unit leaf area, thereby increasing water flow per guard-cell complex. Similar to the effects of D, equation (1) predicts that increasing h should cause a decline in A_l:A_s. A literature review showed that such changes do occur as trees become larger, partially compensating for the potential increased hydraulic resistance (McDowell et al. 2002b).

Equation (1) predicts that k_s should increase with tree height. This has been observed for balsam fir trees (Pothier et al. 1989). Factors important in controlling k_s include tracheid or vessel diameter and length, the number of tracheids or vessels per unit sapwood area, the permeability of pit membranes (Mencuccini et al. 1997), tracheid tapering (West et al. 1999), and at the whole-tree level, changes in conductivity throughout the continuum of sapwood from root to shoot (Spicer and Gartner 2001, Domec and Gartner 2001).

Equation (1) predicts that increasing $\Delta\Psi$ as h increases can maintain g_s at a constant level. If foliage can tolerate lower water potential (by whatever mechanism) while maintaining g_s at a given level, then this may allow tall trees to spend a greater period of the daylight period prior to stomatal closure. Indeed, this has been observed (Yoder et al. 1994, Kolb et al. 2000, Barnard 2001, McDowell et al. 2002a). Another benefit of a reduced minimum water potential threshold is that stomatal conductance may stay high for longer periods of time during the day, allowing increased carbon assimilation prior to stomatal closure. However, this requires that either 1) the minimum leaf water potential at which damaging cavitation occurs is reduced with tree size, or 2) an increase in the capacity of xylem to refill cavitated elements. Neither of these requirements have been tested. McDowell et al. (2002a) did observe an increase in apparent cavitation and a decrease in potential conductivity of shoots of large vs. small Douglas-fir trees. Repeated cavitation can weaken cavitation resistance of xylem (Hacke et al. 2001). However, the implications of cavitation in question, particularly for trees of different sizes. Finally, reduced minimum leaf water potential has been shown to reduce photosynthetic capacity (Tezara et al., 1999). This has yet to be thoroughly investigated in trees near their maximum height.

Schäfer et al. (2000) observed that g_s per unit D increased with tree height in *Fagus sylvatica*, and they argue that this is a mechanism that allows tall trees with low hydraulic conductance increased opportunity to assimilate carbon. This follows the theory of Oren et al. (1999) that trees with relatively low g_s will have less sensitivity to D, thus buffering g_s from D to some degree. Similar to the $\Delta\Psi$ question above, the mechanisms and implications of reduced stomatal sensitivity to D remain an open question. See the appendix for further explanation of how reduced stomatal sensitivity to D can alleviate hydraulic constraints imposed by tree height.

Water storage, or capacitance, can increase daily transpiration and g_s by providing increased water availability per guard-cell complex. Although this is not explicit within equation (1), the increase in daily water availability would act similarly to increasing $\Delta\Psi$ because it would increase the length of time that leaves could freely assimilate carbon prior to stomatal closure. This can occur via increased sapwood volume per unit leaf area (Waring and Running 1978, Mencuccini and Grace 1996a, Goldstein et al. 1998, Phillips et al. *unpublished data*), via cavitation of tracheids or vessels (Tyree and Yang 1990, Zwieniecki and Holbrook 1998), via consumption and recharge of water in the upper soil volume via hydraulic-lift (Caldwell et al. 1998), or via increased nocturnal condensation of water on the tall, complex canopies of old forests. If hydraulic lift increases soil water availability for taller trees, this may also interact with the $\Delta\Psi$ hypothesis described above.

Changing the root-to-shoot ratio with increasing tree size may also act similarly to increasing capacitance or $\Delta\Psi$, via increasing whole-tree hydraulic conductance per unit leaf area. Both model and measurement results have shown that root-to-shoot ratios increase for *Pinus taeda* in response to experimental and natural reductions in soil water availability (Sperry et al. 1998, Ewers et al 2000, Hacke et al. 2000). Magnani et al. (2000) suggested that as hydraulic conductance decreases with tree height, so should the root:shoot ratios increase to minimize reductions in hydraulic conductance. However, no observational evidence comparing tall and short trees exists (Smith and Resh 1999, Giardina and Ryan *in review*).

1.7 OBJECTIVES

There are three primary objectives of this dissertation: 1) determine if increasing tree size is associated with reduced leaf area per unit sapwood area for trees regardless of species or climate, 2) test the hydraulic limitation hypothesis and the hydraulic compensation hypothesis in Douglas-fir, and 3) determine if large, old ponderosa pine are genetically constrained to have slow growth, or if they are able to increase growth if site resource availability is increased via management. Douglas-fir was used for study two because a construction crane located in a 60 m tall forest of Douglas-fir made access to foliage of tall trees possible. Ponderosa pine was used in study three because forest managers are conducting thinning studies in old pine stands with the objective or returning these forests to their pre-fire exclusion condition. These objectives correspond to chapters two, three, and four.

CHAPTER 2

THE RELATIONSHIP BETWEEN TREE HEIGHT AND LEAF AREA:SAPWOOD AREA RATIO

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2.1 ABSTRACT

The leaf area to sapwood area ratio (A_l:A_s) of trees has been hypothesized to decrease as trees become older and taller. Theory suggests that A_l:A_s must decrease to maintain leaf-specific hydraulic sufficiency as pathlength, gravity, and tortuosity constrain whole-plant hydraulic conductance. We tested the hypothesis that A_l:A_s declines with tree height. Whole-tree A_l:A_s was measured on 15 individuals of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) ranging in height from 13 to 62 m (aged 20 to 450 years). A_l:A_s declined substantially as height increased ($p = 0.03$).

Our test of the hypothesis that A_l:A_s declines with tree height was extended using a combination of original and published data on nine species across a range of maximum heights and climates. Meta-analysis of 13 whole-tree studies revealed a consistent and significant reduction in A_l:A_s with increasing height ($p < 0.05$). However, two species (*Picea abies* and *Abies balsamea*) exhibited an increase in A_l:A_s with height, although the reason for this is not clear. The slope of the relationship between A_l:A_s and tree height (ΔA_l:$A_s/\Delta h$) was unrelated to mean annual precipitation. Maximum potential height was positively correlated with ΔA_l:$A_s/\Delta h$. The decrease in A_l:A_s with increasing tree size that we found in the majority of species may be a homeostatic mechanism that partially compensates for decreased hydraulic conductance as trees grow in height.

2.2 INTRODUCTION

The allometric relationship between stem basal- or sapwood area and whole-tree leaf area has been recognized since the original work by Huber (Huber 1928, Waring et al. 1982). This relationship was conceptualized into the pipe model (Shinozaki et al. 1964a, 1964b), which proposes that a given unit of leaf area is supplied with water from a constant quantity of conducting pipes. Implicit in the model is the assumption that the ratio of leaf area to sapwood area is a constant throughout plant development (Shinozaki et al. 1964a). Consistent with the model, it should be possible to estimate the leaf area of trees if the sapwood area and the ratio of whole-tree leaf area to sapwood area (A_l:A_s) are known (Waring et al. 1982). The pipe model has been widely employed in studies that require knowledge of tree- or stand leaf area (e.g. Gholz et al. 1976, Waring et al. 1982, Turner et al. 2000).

Investigation of the pipe model over the last two decades has revealed that A_l:A_s is often dependent on site water balance. Whole-tree A_l:A_s declined with decreasing soil water availability at constant evaporative demand for a study on *Eucalyptus* (White et al. 1998). Furthermore, A_l:A_s declined along gradients of low to high evaporative demand (Waring et al. 1982, Mencuccini and Grace 1995). These observations can be explained using a simple model based on Darcy's Law showing that reductions in A_l:A_s may compensate for increased evaporative demand, thus preventing the development of damaging water potential gradients and minimizing reductions in canopy conductance.

This hydraulic model was described by Whitehead and Jarvis (1981) and Whitehead et al. (1984) as:

$$\frac{A_l}{A_s} = \frac{k_s \Delta\psi}{h \eta g_s D} \qquad (1)$$

where D is atmospheric vapor pressure deficit (a net radiation term should be added for poorly coupled canopies), g_s is canopy conductance to water vapor, k_s is sapwood permeability of the hydraulic pathway, $\Delta\psi$ is the soil-to-leaf water potential difference including the effect of gravity, η is the viscosity of water at a given temperature and h is tree height. We note that this model is most appropriately applied to cylinders of uniform material, and it is an oversimplification of tree hydraulics in several respects. The pathlength from bulk soil to leaf, rather than height *per se*, is the most appropriate term. However, because height is a significant fraction of total pathlength and is much more commonly measured, we use it here as a surrogate. This model does not include the effects of changing root surface area (Sperry et al. 1998, Magnani et al. 2000) or variation in k_s, due to, for example, partial cavitation or tapering of conducting elements (West et al. 1999). $\Delta\psi$ in our application of this model includes the effect of gravity because physiological and architectural behavior responds to the *net* effect of the soil-to-leaf water potential difference as regulated by leaf and soil water potential and the gravitational constraint on minimum leaf water potential. This model is consistent with both the cohesion-tension theory (Dixon and Joly 1895, Zimmermann 1983) and the concept of the development of a homeostatic mechanism to reduce the occurrence of cavitation and avoid runaway embolism (Tyree and Sperry, 1988). Such a homeostatic response may occur via short-term (i.e. minutes to days) adjustment of g_s and leaf water potential, or long-term (i.e. days to generations) adjustment of k_s, h, and A_l:A_s. This hydraulic model provides a framework to develop and test hypotheses regarding the interaction between hydraulic architecture, stomatal conductance, and climate.

One hypothesis derived from the hydraulic model is that A_l:A_s will decline with increases in height. This hypothesis assumes that other variables within the hydraulic model are constant with increasing height, or that any changes in these variables with increasing height do not oppose or exceed concurrent changes in A_l:A_s. This hypothesis is supported by observations and predictions of a decline in A_l:A_s with increasing tree height or age (Mencuccini and Grace 1996a, 1996b, Grace 1997, Becker et al. 2000, Bond and Ryan 2000, Mencuccini and Magnani, 2000, Schäfer et al. 2000). A potential advantage of decreasing A_l:A_s with increasing h is that hydraulic compensation for h may occur, in which g_s is maintained, or reductions in g_s are minimized, as h increases.

An important distinction about compensation of hydraulic constraints must be made to avoid confusion about leaf- vs. whole-plant physiology. While a decline in A_l:A_s with increasing tree height may mitigate hydraulic constraints to canopy conductance, this does not mean that hydraulic constraints to whole-tree transpiration will also be mitigated. Reduced A_l:A_s may maintain stomatal conductance per unit leaf area while simultaneously reducing the transpiring leaf area per plant relative to whole-plant biomass. Because photosynthesis is closely tied to transpiration, whole-plant carbon assimilation may also decline depending on how light interception is affected. Note that these declines could occur even though leaf-specific stomatal conductance is maintained. The critical distinction is that a change in one parameter *per unit leaf area* does not translate directly into an equal change in another parameter at the *whole-tree scale*. In this paper, we will discuss the role of A_l:A_s vs. height only in relation to leaf-specific stomatal conductance.

In light of the recent debate regarding the role of compensatory mechanisms to alleviate hydraulic limitations to water transport (Becker et al. 2000, Bond and Ryan 2000, Mencuccini and Magnani 2000), it is necessary to examine the generality of evidence supporting such mechanisms. The objective of this study was to determine if evidence for the age- or size-related reduction in A_l:A_s is consistent across species and climates. We tested two primary hypotheses: 1) that A_l:A_s declines with increasing height over the lifetime of a species, and 2) that the direction of change or lack of change in A_l:A_s with plant development is consistent across a range of species, maximum heights, and environments. Hypothesis 1 was tested using measurements of *Pseudotsuga menziesii* var. *menziesii*, a long-lived, large-statured conifer native to North America. Hypothesis 2 was tested using data derived from a review of original and published data for a variety of species spanning a broad range of maximum height.

To further explore relationships between A_l:A_s vs. height and climate or species, we tested relationships between the rate of change of A_l:A_s vs. height and a) annual precipitation and b) maximum tree height.

2.3 METHODS

Study site We tested hypothesis (1) in three even-aged *Pseudotsuga menziesii* var. *menziesii* stands located in the Wind River basin of the Cascade Mountains near Carson, Washington (45°49' N Lat., 121°57' W. Long). The climate of this region is maritime, with cool, wet winters and warm, dry summers. Site elevation is approximately 355 m. Annual precipitation is approximately 2500 mm, with less than 10% of that falling in summer (June through September ~120 mm). The soils are loamy sands and sandy loams developed from two to three meters of volcanic tephra over a basalt flow. Stand ages were determined using increment cores taken at breast height from five or more trees per site. The three sample stands were approximately 20-, 40-, and 450-years-old. Both the 20- and 40-year-old stands originated after clearcuts, whereas the 450-year-old originated after a stand-replacing forest fire (Franklin and DeBell 1988). Average tree heights for the 20-, 40-, and 450-year-old stands were 15 m (14-16), 33 m (29-36), and 57 m (51-62), respectively.

Leaf area and sapwood area measurements Whole-tree leaf area of *Pseudotsuga menziesii* var. *menziesii* was estimated by scaling branch estimates of leaf area to the canopy (Maguire and Batista, 1996, Monserud and Marshall 1999). Branch-scale allometric equations were developed through branch harvest and analysis at each of the three stands. For the 20- and 40- year old stands, scaffolding towers were erected to allow access to harvest branches. Six branches were harvested from each of five trees for a total of thirty branches per stand in July 1998. For each tree, branches were harvested from the lower, middle and upper crown on the northeast and southwest facing aspects. Leaves from each branch were immediately sub-sampled and used to determine specific leaf area (*S*, cm^2 g^{-1}). Four twigs for measuring *S* were collected systematically from along the axis of each branch, located at the second twig from each end of the foliated length, and from two twigs in the middle of the foliated length. The remaining leaves were collected in paper bags, dried at 65°C and weighed. Leaf area was determined using a video image recorder and AgVision software (Decagon Devices, Pullman Wash.). In late-August 1998, another 30 branches were harvested from the 20- and 40-year-old stands using a sampling scheme identical to the July sample. These branches were measured for whole-branch leaf weight only.

Branches were harvested from six, 450-year-old trees. A total of 17 branches from the old trees were analyzed to develop branch-level allometric relationships. Branches were accessed by climbing the trees using fixed ropes. After cutting, branches were lowered to the ground using a second rope. We randomly collected 10% of the foliated shoots from each branch as measured by visual cluster measurements (Ishii 2000). Leaf samples were collected from each of these shoots and analyzed for *S*. Both *S* and total branch leaf weight were measured using identical methods to those used for the younger stands.

Independent variables measured at all three stands included branch diameter (twenty mm distal from the swollen branch-stem juncture), branch length, foliated length, height above ground, distance from top of tree, and aspect at the position of branch origin. Suitability of these variables was tested using both stepwise and independent regression analysis (Systat 9.0). Only branch diameter (*d*) was a significant factor for branches from the 20- and 40-year-old stands, and branch length (*L*) was the only important factor for branches from the 450-year-old stand. For the 450-year-old trees, branch length was a better predictor of branch leaf area than diameter because diameter continues to increase even after breakage (e.g. during wind and ice storms); however, the length of a branch is sensitive to such stochastic events (Ishii and McDowell 2001). Scatterplots of branch leaf area vs. *d* or *L* revealed that variance in leaf area increased with larger values of the predictive variable, a violation of an assumption of linear regression. We therefore developed predictive equations using weighted regression (Monserud and Marshall, 1999), a technique that homogenizes variances. The equations for estimating *P. menziesii* branch leaf area (A_l, projected, cm^2) from branch d (cm) and L (m) are:

20-year-old trees $A_l = 2958(d)^{1.67}$ (44% variation explained) (2)

40-year-old trees $A_l = 4221(d)^{1.60}$ (70% variation explained) (3)

450-year-old trees $A_l = 1.032(L)^{1.66}$ (55% variation explained) (4)

Whole-tree estimates of leaf area were obtained via application of the stand-specific branch models (equations 2-4) to measurements of branch d (20- and 40-year-old trees) or branch L (450-year-old trees). For the 20- and 40-year-old trees, trees were climbed using the towers for rope anchors and each branch's diameter was measured in two perpendicular directions. The average diameter for each branch was recorded and used to estimate branch leaf area. Leaf areas for each branch were then summed to give total leaf area for the tree. Five 20-year-old and six 40-year-old trees were climbed. For the 450-year old trees, five trees were climbed using the trees as rope anchors and L was measured for every branch using an extendable measuring tape. Branch leaf area was estimated for each branch using the stand-specific equations (2-4), and then branch leaf area was summed for each tree. Sapwood area was estimated from four increment cores per tree taken at a height of 1.4 m. The sapwood-heartwood boundary was discerned by holding the core up to the sunlight and marking the position of the inner boundary of the translucent section, indicating a decrease in water content. This boundary was verified on a subset of cores (>30 cores) using multiple stains known to be absorbed by living cells. In all cores the boundary indicated by staining matched that from the method using visual examination.

Meta-analysis Published and original data sets that included whole-tree A_l:A_s and tree height were used in a meta-analysis test of hypothesis (2) using the study-specific slopes and associated variances from linear regression of A_l:A_s versus tree height (MetaWin 2.0, Rosenberg et al. 2000, also see Hedges et al. 1999). Slopes of linear regression (ΔA_l:$A_s/\Delta h$) were selected as the effect metric because most data sets with samples distributed throughout the height continuum showed that A_l:A_s changed linearly with height, and the majority of data sets included measurements throughout the height continuum rather than clusters of measurements for short and tall trees. On a theoretical note, however, A_l:A_s should decline non-linearly with height, as predicted from equation (1). Data sets were excluded from the analysis if they confounded tree height with other variables known to affect A_l:A_s, such as light environment (Kaufmann and Troendle 1981, O'Hara and Valappil 1995), nutrient availability or silvicultural manipulation (Brix and Mitchell 1983), site quality (Dean and Long 1986), vapor pressure deficit (Mencuccini and Grace, 1995), groundwater access (Zimmermann et al. 2000), soil waterlogging (Santiago et al. 2000) or stand density (Keane and Weetman 1987, Long and Smith 1988). Although this reduced the inference population from which we may draw conclusions, the restricted data set is necessary to test the relationship between tree height and A_l:A_s. Variability due to effects of site and species was further reduced by standardizing each data set relative to the largest values of A_l:A_s and height within each respective data set. This should remove differences associated with site and species, while allowing the regression slopes to be used to indicate the effect of height on A_l:A_s. The slopes of the regressions both before and after standardization are presented and included in the meta-analysis. Three outliers were excluded from the *Pseudotsuga menziesii* var. *glauca* data set. One of these trees was a suppressed individual and the other two were grown in stands with wide spacing and had larger-than-average crowns (J.D. Marshall *personal observation*). Stand spacing (or "density") has been shown to dramatically change A_l:A_s in conifers (Oren et al. 1986a, Keane and Weetman 1987, Long and Smith 1988). In a few studies the sample trees did not include trees that had reached maximum height for that site. In these cases, we used empirically-based estimates of potential maximum height based on local site index curves or observations. Two data sets for *Pinus sylvestris* included foliar weight rather than area; for these studies we converted weight to area using S measured at nearby sites. Sapwood area measured at breast height (1.4 m) was used for all studies. Verification of accuracy of sapwood estimates was impossible from the published data sets. Although both age and height may interact with A_l:A_s, we have used only height as the independent variable in statistical analysis for this study.

We used a subset of data from the meta-analysis to test the null hypotheses that the slope of A_l:A_s vs. height and maximum potential height were independent of climate. Mean annual precipitation data was used from each published study to investigate the relationship between A_l:A_s vs. height and climate. Precipitation was used in place of other environmental variables such as D or temperature because it was the most widely available and most consistently measured. We used only studies in which the p-value of the slope was <0.10 and in which documented maximum potential height was available. For maximum potential height we used either the height of the tallest individual if sampled trees included the tallest trees in the study area, or estimates of potential height based on local observations if sampled trees did not include the tallest individuals in the study area.

The meta-analysis includes multiple cases from the same species (Table 2.1); however, meta-analysis techniques are not currently able to evaluate the impact of non independence associated with replication within species (Gurevitch et al. 1999). We determined if replication within species affected our overall result in two ways. First, the meta-analysis was repeated 16 times using a unique combination of cases each time

Legend for Table 2.1

Table 2.1 Summary of studies and results of regressions of leaf area:sapwood area (A_l:A_s) vs. tree height. Values include range of tree heights, diameter at breast height (DBH), and study-level mean A_l:A_s. The slopes, p-values and r^2 from regressions of raw data (A_l:A_s in m^2 cm^{-2}, tree height in meters) as well as standardized data are presented. Slope p-values and r^2 are identical for raw and normalized data for all cases. All studies presented were used in the meta-analysis except for *Abies balsamea,* which was excluded due to lack of information regarding variance about the regression slope. Citations include studies from which data was obtained or studies that may be used for further reference. 1) this study (Pseudotsgua menziesii var. menziesii), 2) Monserud and Marshall 1999 (Pseudotsgua menziesii var. glauca), 3) Ryan et al. 2000, 4) Mencuccini and Grace 1996a, 5) van Hees and Bartelink 1993, 6) Vanninen et al. 1996, 7) Albrektson 1984, 8) Barnard 2000, 9) Bartelink 1997, 10) Ryan and Whitehead *unpublished,* 11) Köstner et al. *in review*, and 12) Coyea and Margolis 1992.

Table 2.1

Species (citation)	n	Height(m)	DBH(m)	A_l:A_s	Raw slope	Std. slope	r^2	P
Negative slopes, Tracheid bearing species								
Pseudotsuga menziesii (1)	15	13-62	0.15-1.53	0.46	-0.003	-0.24	0.36	0.024
Pseudotsuga menziesii (2)	23	5-33	0.05-0.81	0.33	-0.004	-0.22	0.20	0.046
Pinus ponderosa (3)	5	9-34	0.19-0.98	0.12	-0.002	-0.05	0.91	0.011
Pinus ponderosa (2)	19	4-41	0.05-0.71	0.09	-0.003	-0.62	0.40	0.004
Pinus monticola (2)	21	4-44	0.05-0.74	0.22	-0.004	-0.42	0.44	0.001
Pinus sylvestris (4)	8	8-24	0.70-0.35	0.09	-0.002	-0.56	0.85	0.001
Pinus sylvestris (5)	4	3-22	0.40-0.23	0.13	-0.006	-0.93	0.89	0.057
Pinus sylvestris (6)	9	5-33	0.90-0.45	0.20	-0.007	-0.67	0.74	0.003
Pinus sylvestris (7)	14	5-25	n/a	0.19	-0.008	-0.55	0.32	0.036
Negative slopes, Vessel bearing species								
Eucalyptus saligna (8)	37	6-26	0.06-0.30	0.25	-0.044	-0.48	0.34	<0.001
Fagus sylvatica (9)	6	3-23	0.31-0.28	0.54	-0.041	-0.83	0.53	0.103
Nothofagus solandrii (10)	11	5-14	0.39-0.67	0.13	-0.013	-0.64	0.42	0.033
Positive slopes								
Picea abies (11)	28	7-31	0.07-0.45	0.36	+0.017	+0.79	0.46	<0.001
Abies balsamea (12)	~50	n/a	0.02-0.21	0.71	+0.031	n/a	n/a	0.001

and never including more than one case per species. If the results of these 16 analyses were the same as the overall meta-analysis, we concluded that replication within species did not affect the overall result. The second approach was to group the cases by species and repeat the analysis; if species were not significantly different from each other then we concluded that replication within species did not skew the overall result (J. Gurevitch, *pers. comm.*).

2.4 RESULTS

Whole-tree A_l:A_s varied with tree height for *Pseudotsuga menziesii* var. *menziesii* (ANOVA, p=0.03, n=14, Figure 2.1). Orthogonal polynomial contrasts in the ANOVA showed that A_l:A_s varied linearly with tree height ($p < 0.01$). Regression analysis verified that linear regression provided the best fit to the data, with a slope of -0.003 $m^2\ cm^{-2}\ m^{-1}$ ($r^2 = 0.36$, $p = 0.02$, Figure 2.1).

A_l:A_s declined with increasing tree height for nearly all studies in the meta-analysis (Table 2.1). Meta-analysis of the whole-tree studies revealed a common negative slope of A_l:A_s vs. height ($p<0.05$, n=13 whole-tree studies, Table 2.2). The significant decline in A_l:A_s vs. height was evident when analyzed using either standardized or absolute values of A_l:A_s and height (Table 2.2). There was no effect of replication within species on the overall outcome. A negative slope of ΔA_l:$A_s/\Delta h$ resulted from each of the 16 unique analyses of the meta-data that had no replication of species. In no case did the 95% confidence intervals overlap zero.

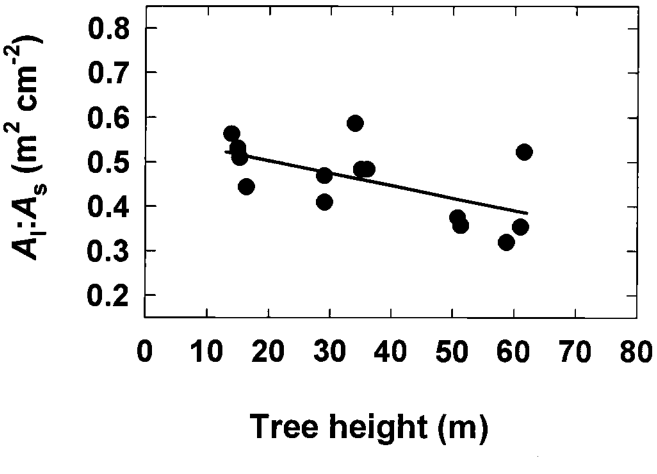


Figure 2.1 Leaf area:sapwood area (A_l:A_s) vs. tree height for *Pseudotsuga menziesii* var. *menziesii* trees in Wind River Experimental Forest, Washington. The regression line is: A_l:A_s = -0.003+0.559·(height), $R^2 = 0.36$, $p=0.02$.

Table 2.2 Meta-analysis results of the slope of leaf area:sapwood area ($A_l{:}A_s$, m^2 cm^{-2}) vs. tree height (m). Slopes were used as the "effect size" and were generated separately for each study via regression of $A_l{:}A_s$ vs. tree height (Table 1). The within-study variance estimate was the variance about the slope of each regression. The significance (p-value) of model heterogeneity is Q(p); a non-significant Q indicates homogeneity within the data set.

	n	Mean slope	Q(p)	95% confidence interval
Raw data	13	-0.0027	0.64	-0.0044 to -0.0010
Standardized data	13	-0.3594	0.76	-0.5974 to -0.1215

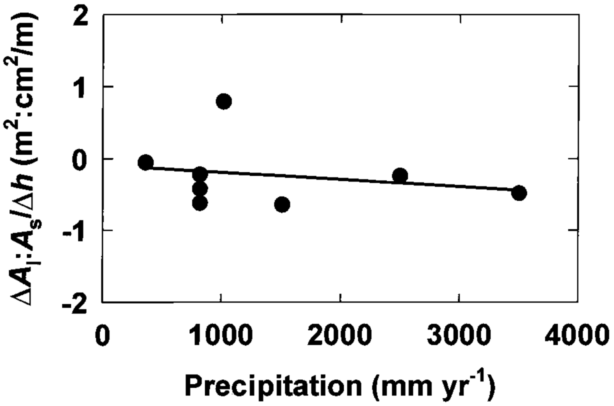
Likewise, replicated species (species with more than one data set in the meta-analysis, *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Pinus sylvestris*) were not significantly different from each other (n=3, p = 0.99).

Although the meta-analysis revealed a significant and consistent negative relationship between A_l:A_s and h, there were two significant exceptions (Table 2.1). *Abies balsamea* and *Picea abies* both exhibited positive relationships between A_l:A_s and h. A similar increase in A_l:A_s with height has been observed for *Picea abies* (Oren et al. 1986a). We note that the *Abies balsamea* data set could not be included in the meta-analysis due to lack of variance estimates (only the slope was available from Coyea and Margolis, 1992). *Fagus sylvatica* exhibited a negative slope of marginal significance (p=0.103, Table 2.1). We note that this is not an attribute particular to this species, because Schäfer et al. (2000) observed a large and significant reduction in A_l:A_s with h in *Fagus sylvatica.*

Climate does not appear to regulate the slope of ΔA_l:$A_s/\Delta h$ for the studies included in this analysis. The lack of significant heterogeneity among all studies (Q in Table 2.2) is evidence that ΔA_l:$A_s/\Delta h$ is independent of the large differences in climate across these studies (J. Gurevitch, *pers. comm.*). Plotting ΔA_l:$A_s/\Delta h$ vs. mean annual precipitation for the subset of studies that had precipitation data supports the conclusion that climate (as indexed by precipitation) does not regulate ΔA_l:$A_s/\Delta h$ (Figure 2.2). The

Legend for Figure 2.2

Figure 2.2. The slope of A_l:A_s vs. tree height (ΔA_l:$A_s/\Delta h$) as a function of mean annual precipitation (mm yr^{-1}). Annual precipitation was available for *Nothofagus* in New Zealand, *Pinus ponderosa*, *Pinus monticola*, and *Pseudotsuga menziesii* var. *glauca* sites in Priest River, ID, the *Pseudotsuga menziesii* var. *menziesii* site in Wind River Experimental Forest, WA, the *Pinus ponderosa* site in Oregon, the *Picea abies* site in Germany, and the *Eucalyptus saligna* site in Hawaii. The regression line is: ΔA_l:$A_s/\Delta h$ = -0.087-0.001•(precipitation), $R^2 = 0.06$, p=0.57.



$\Delta A_l:A_s/\Delta h$ (m^2:cm^2/m)
2
1
0
-1
-2
0
1000
2000
3000
4000
Precipitation (mm yr^{-1})

Figure 2.2

independence of $\Delta A_l{:}A_s/\Delta h$ from site water availability can also be seen by comparing $\Delta A_l{:}A_s/\Delta h$ for *Pinus ponderosa* trees growing on a site of relatively high precipitation (817 mm year^{-1}, Priest River Idaho) and low precipitation (360 mm year^{-1}, Metolius Oregon, Figure 2.3). Neither the slope nor the intercept was significantly different between these two locations ($p > 0.54$) despite the two-fold difference in precipitation. To investigate the potential relationship between tree size and the sensitivity of $A_l{:}A_s$ to height, we plotted $\Delta A_l{:}A_s/\Delta h$ vs. maximum potential tree height (Figure 2.4). A positive relationship was found (Figure 2.4). For this analysis we used data sets from the meta-analysis with significant ($p < 0.1$), negative slopes and that had accurate documentation of maximum potential height. The equation for the best fit line is:

$$\text{Maximum height} = 53.4\exp(87.5 \bullet \Delta A_l{:}A_s/\Delta h),\ n=10,\ R^2 = 0.45 \qquad (5)$$

2.5 DISCUSSION

The meta-analysis revealed similar responses of $A_l{:}A_s$ to increasing tree height across a broad range of species (Table 1, Table 2). The common decrease in $A_l{:}A_s$ with increasing height supports the hypothesis that trees may respond to increasing hydraulic constrictions by maintaining a lower ratio of $A_l{:}A_s$ (Meinzer et al. 1997, Becker et al. 2000, Schäfer et al. 2000). However, a number of unanswered questions arise from the

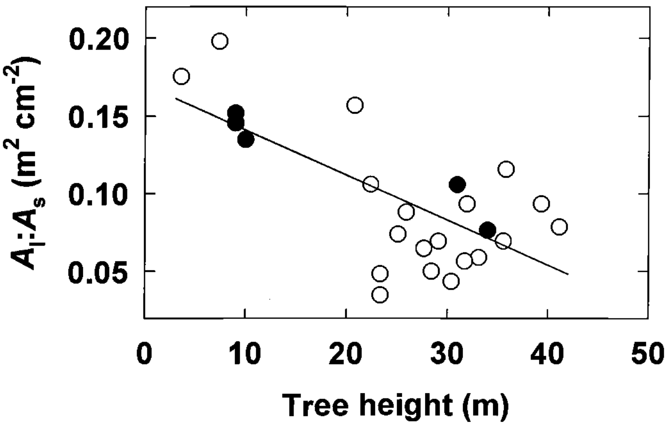


Figure 2.3. A_l:A_s vs. tree height for two *Pinus ponderosa* stands. The site in Oregon (shaded circles) received 360 mm of precipitation annually, and the Idaho site (open circles) received 817 mm annually. The pooled regression line for both data sets is: A_l:A_s = -0.003+0.171•(height), R^2=0.47, $p<0.001$.

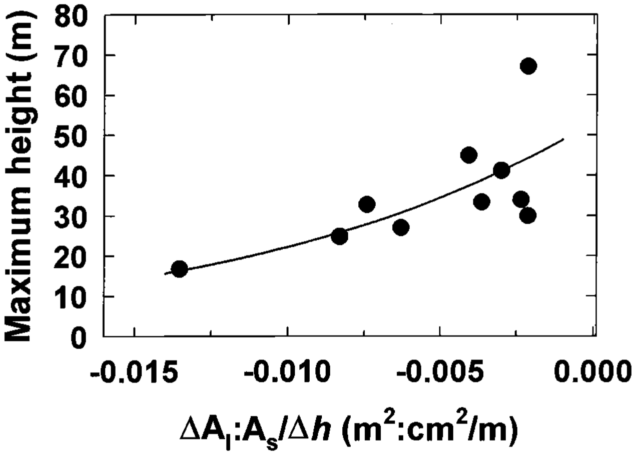


Figure 2.4. Whole-tree $\Delta A_l{:}A_s/\Delta h$ vs. maximum tree height. $\Delta A_l{:}A_s/\Delta h$ is the regression slope from table 1 for each study. Studies were included only if the p-value of the slope was <0.10 and if well-documented maximum tree heights were available.

meta-analysis. These include: 1) why was $\Delta A_l{:}A_s/\Delta h$ positive for *Abies balsamea* and *Picea abies*, and 2) what mechanism(s) may regulate the species specific differences $\Delta A_l{:}A_s/\Delta h$? We will focus the remainder of the discussion on these questions.

The positive relationship between $A_l{:}A_s$ and tree height for *Abies balsamea* and *Picea abies* must be rationalized in light of equation (1). If equation (1) is applicable to describe the system then, to maintain homeostasis with no increase in the water potential gradient, an increase in $A_l{:}A_s$ with tree height will require a decrease in canopy conductance or an increase in k_s in conditions where D and η remain constant. Indeed, in *Abies balsamea*, Coyea and Margolis (1992) found that k_s of stemwood increased more rapidly than tree height such that $A_l{:}(A_s{\bullet}k_s)$ declined with tree height. They concluded that the *Abies balsamea* data conformed to the hydraulic model (equation 1) because the increased k_s more than offset the increase in $A_l{:}A_s$ with height. Although increasing k_s with tree height has been documented for many species, it is typically insufficient to prevent height related reductions in hydraulic conductance (Mencuccini and Magnani 2000). An alternative hypothesis is that the fraction of leaf area that is actively transpiring is reduced with height, or the hydro-active sapwood area increases, such that the functional $A_l{:}A_s$ decreases with height. Köstner et al. (*in review*) found that standardizing the leaf area by light interception resulted in constant $A_l{:}A_s$ values across a range of heights. However, Oren et al. (1986b) observed that 92% of the leaf area actively transpired for *Picea abies* and concluded that the functional $A_l{:}A_s$ increased with height. It is possible that another variable in equation (1) such as $\Delta\psi$ changed with tree size for *Picea abies* and *Abies balsamea* and we were unaware of it. Barnard (2000) and McDowell et al. (2002) both found increases in $\Delta\psi$ via declines in mid-day leaf water potential with increasing tree size. Likewise, a parameter not even included in equation (1) may have changed for *Picea abies* and *Abies balsamea.* For example, increasing root surface area may act to increase the capacity of trees to supply foliage with water (Sperry et al. 1998, Magnani et al. 2000). Further work on these species with positive $\Delta A_l{:}A_s/\Delta h$ values is needed, with an emphasis on understanding the trade-offs between $A_l{:}A_s$, height, and other important characteristics of the hydraulic system.

The advantage of an increase in $A_l{:}A_s$ with height for *Picea abies* and *Abies balsamea* is unknown. Increasing $A_l{:}A_s$ does increase the photosynthetic area relative to respiring sapwood biomass, which could act to increase net carbon uptake if canopy conductance remains constant. However, if canopy conductance declines in an equal and opposite fashion to the increased leaf area, then whole-tree carbon gain will remain unchanged or will even decrease due to higher respiration costs associated with the high leaf area. Alternatively, retaining leaves may provide a mechanism to recycle nutrients more efficiently. Both *Picea abies* and *Abies balsamea* grow in cold, nutrient poor ecosystems where nutrients may be more limiting than water. Retention of nutrients within leaves can allow greater retranslocation of nutrients to growing canopy (Waring and Ludlow 1998; Waring and Running 1998). However, Oren and Schulze (1989) found that retranslocation of nutrients to new leaves in *Picea abies* came from leaves on the same upper-canopy branches rather than from lower canopy leaves. Therefore, holding lower canopy branches is unlikely to provide an advantage for nutrient retention. Retaining lower canopy branches may act to shade out competing vegetation, making soil resources more available (Waring and Major 1964). We conclude that the mechanisms and advantages of increasing A_l:A_s with tree height for *Picea abies* and *Abies balsamea* remain unknown.

Providing a mechanistic explanation for differences in species-specific ΔA_l:$A_s/\Delta h$ is impossible given the lack of controlled investigations where ΔA_l:$A_s/\Delta h$ is measured within a given species growing in different climatic and edaphic conditions. Furthermore, the lack of studies that matched our criteria for inclusion in the meta-analysis hampers our ability to interpret patterns. For example, among the studies with negative ΔA_l:$A_s/\Delta h$, the vessel-bearing species had an average ΔA_l:$A_s/\Delta h$ of -0.0326, nearly one order of magnitude greater than the tracheid bearing species average slope of -0.0042. However, the limited sample size of vessel bearing species makes statistical comparisons impossible. Despite the limited sample size, we can examine patterns from the meta-analysis data set that allow us to generate testable hypotheses as to the controls over ΔA_l:$A_s/\Delta h$.

We expected that site water availability would be negatively related to ΔA_l:$A_s/\Delta h$ because forests with greater precipitation or greater soil moisture availability tend to hold more leaf area per unit sapwood area (Waring et al. 1982, White et al. 1998). If this hypothesis were true it would indicate that the driving force for a decline in $A_l:A_s$ with increasing height was sensitive to water availability. However, the decline in $A_l:A_s$ with increasing height occurred independently of precipitation. This lack of change in $\Delta A_l:A_s/\Delta h$ with precipitation was true when compared across species (Figure 2.2) and within species (*Pinus ponderosa*, Figure 2.3). It is possible that another, more physiologically meaningful parameter such as soil water potential or atmospheric vapor pressure deficit during the growing season is a better predictive parameter than mean annual precipitation. However, it seems likely that mean annual precipitation was strongly correlated with these more direct measures of water availability. Therefore, it appears that water availability has no effect on the decline in $A_l:A_s$ as height increases among the sites investigated in this study.

The independence of $\Delta A_l:A_s/\Delta h$ from precipitation indicates homeostasis between water availability, hydraulic pathlength and $A_l:A_s$. This is because mean annual precipitation is positively correlated with both $A_l:A_s$ and maximum tree height. Small trees in wet environments have greater $A_l:A_s$ values than trees of similar size in drier environments (Waring et al. 1982). Likewise, trees in wetter environments tend to grow to greater maximum heights. So although trees in wet environments have greater $A_l:A_s$ at small heights and greater maximum heights than dry site trees, the change in $A_l:A_s$ with a unit increase in height is invariant with water availability. This suggests that another variable, such as hydraulic pathlength, exerts stronger regulation over $\Delta A_l{:}A_s/\Delta h$ than site water availability.

There is a trend for trees with greater maximum potential heights to have less negative values of $\Delta A_l{:}A_s/\Delta h$ (Figure 2.4). The relationship shown in Figure 2.4 is derived from the significant, negative slopes from studies used in the meta-analysis where accurate measurements of maximum potential height were available. This positive relationship suggests trees able to maintain high $A_l{:}A_s$ as they grow taller are able to grow to greater final heights. However, the regression equation is of little predictive value for trees with small $\Delta A_l{:}A_s/\Delta h$ values due to increased scatter in this range. Nonetheless, the positive relationship between maximum potential height and $\Delta A_l{:}A_s/\Delta h$ may account for some of the variation observed in $\Delta A_l{:}A_s/\Delta h$ among species and sites.

A decline in $A_l{:}A_s$ with increasing tree height has been hypothesized to prevent reductions in stomatal conductance associated with hydraulic constraints (Becker et al. 2000). McDowell et al. (2002) investigated this hypothesis by comparing measured values of leaf-specific g_s for *Pseudotsuga menziesii* var. *menziesii* trees in this study to values modelled with equation (1) using either a) measured values of $A_l{:}A_s$ for each tree height, or b) $A_l{:}A_s$ set at the value for 15 m trees (0.51 m^2 cm^{-2}) for all tree heights. $\Delta\psi$ (including the effect of gravity) and g_s values are from McDowell et al. (2002). This analysis is nearly identical to that performed by Schäfer et al. (2000) on individual

Fagus sylvatica trees within one stand except that in this case trees from different aged stands were compared. Modelled and measured g_s were within 10% of each other when A_l:A_s was allowed to vary. However, when A_l:A_s was held constant, modelled and measured g_s deviated from each other. Measured g_s for the 32-m-trees was only 5% lower than modelled g_s, but for the 60-m-trees the modelled g_s was 45% lower than the measured g_s. This large difference between measured and modelled g_s for the 60 m trees suggests that adjusting A_l:A_s becomes more critical in regulating g_s as trees become taller. This result for trees from different aged stands is similar to that found for individual *Fagus sylvatica* trees within one stand (Schäfer et al. 2000). However, in both the analysis by McDowell et al. (2002) and the one by Schäfer et al. (2000), the decline in A_l:A_s with increasing tree height did not prevent a reduction in g_s, it only minimized the reduction. Other studies of whole-tree A_l:A_s and stomatal conductance also show evidence that conductance declines despite declining A_l:A_s with increasing tree height (Mencuccini and Grace 1996a, Ryan et al. 2000, Ryan and Whitehead *unpublished data*, Mencuccini and Magnani 2000). It is important to point out that Barnard (2000) found that A_l:A_s reduction with tree height fully mitigated hydraulic limitations to stomatal conductance in *Eucalyptus saligna*; however, these trees were only at half of their maximum height. It remains to be seen if these *Eucalyptus* trees can maintain complete compensation through the rest of their height development. Therefore, the overwhelming majority of studies suggest that the decline in A_l:A_s with increasing tree height acts to minimize, but not eliminate, size related reductions in canopy conductance.

A reduction of the leaf area:sapwood area ratio of trees with increasing height has been proposed as a homeostatic mechanism that may alleviate decreasing hydraulic conductance, thereby allowing canopy conductance to be maintained throughout height development (Becker et al. 2000). Nearly all of the cases included in this study support the idea that A_l:A_s decreases in response to increasing tree height. However, these compensatory shifts in A_l:A_s do not appear to fully mitigate the observed decline in stomatal conductance with tree height.

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CHAPTER 3

AN INVESTIGATION OF HYDRAULIC LIMITATION AND COPMENSATION IN LARGE, OLD DOUGLAS-FIR TREES

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3.1 ABSTRACT

The hydraulic limitation hypothesis (Ryan and Yoder 1997) proposes that leaf-specific hydraulic conductance (K_l) and stomatal conductance (g_s) decline for trees as they grow taller, resulting in decreased carbon assimilation. We tested the hydraulic limitation hypothesis through comparison of canopy-dominant Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) trees in stands that were approximately 15 m (20 year), 32 m (40 year), and 60 m (450 year) tall in Wind River, Washington, USA. Carbon isotope discrimination (Δ) declined with tree height (18.6, 17.6, and 15.9 ‰, respectively) indicating that g_s may have declined proportionally with tree height in the spring months when carbon used for new foliage is assimilated. Hydraulic conductance decreased by 44% as tree height increased from 15 to above 32m and showed a 6% further decline with increasing height. The general non-linear pattern of K_l vs. height was predicted by a model based on Darcy's Law. Growth efficiency also declined non-linearly with height (60, 35, and 28 gC stemwood per m^2 leaf area, respectively). Unlike K_l and growth efficiency, g_s and A during summer drought did not decrease monotonically with height. The lack of decline in cuvette-based A means that reduced A, at least during summer months, is not responsible for the decline in growth efficiency. The inconsistency between g_s and A results and the K_l and Δ results may indicate temporal changes (spring vs. summer) in the response of gas exchange to height-related changes in K_l, or may be due to measurement inadequacies. The formal hydraulic limitation

hypothesis was not supported by our mid-summer g_s and A data. Future tests of the hydraulic limitation hypothesis in this forest should be conducted in the spring months, when carbon uptake is greatest.

We applied a model based on Darcy's Law to quantify the extent to which compensating mechanisms buffer hydraulic limitations to gas exchange. Sensitivity analyses indicated that without the observed increases in the soil-to-leaf water potential differential ($\Delta\Psi$) and decreases of leaf area:sapwood area ratio (A_l:A_s), K_l would have decreased by more than 70% rather than the observed 44% reduction between the 15m and 60m trees. However, compensation may have come at a cost; for example, the greater $\Delta\Psi$ of the largest trees was associated with smaller tracheid diameters and increased sapwood cavitation, which may have a negative feedback on K_l and g_s.

3.2 INTRODUCTION

A size- or age-related reduction in leaf-specific hydraulic conductance (K_l) has been suggested as a mechanism that constrains stomatal conductance (g_s) of tall trees, causing reduced photosynthesis (A) and subsequent reductions in primary productivity (Yoder et al. 1994). K_l may decrease with tree size due to greater pathlength from soil to stomata, sapwood density and tortuosity, and the gravitational pull on water columns of large trees. Stomatal conductance is expected to decline concurrently with reduced K_l because of the fundamental inter-dependence of these two variables (Sperry et al. 1993, Hubbard et al. 2000). Reductions in g_s will reduce leaf conductance to CO_2 and therefore A should decline, and subsequently annual gross primary production should also decline (Gower et al. 1996, Ryan et al. 1997). This theory was formalized into the "hydraulic limitation hypothesis" (Ryan and Yoder 1997), which requires the tenets described above be met in order for hydraulic limitation *per se* to be responsible for the age-related growth decline. Specifically, these tenets are: 1) reduced K_l must occur with increasing tree size, 2) reduced g_s and A must occur concurrent with decreased K_l, and 3) the reduction in A must be sufficient to account for reduced growth (Ryan and Yoder 1997).

However, accumulating size associated with growth may provide a driving force for physiological and structural changes that act to minimize size-related constraints on leaf-specific gas exchange. These "compensation" mechanisms could increase the water transport capacity of the tree relative to the total leaf area (Ryan and Yoder 1997, Becker et al. 2000). Potential changes include, but are not limited to: 1) increasing sapwood specific conductivity (Pothier et al. 1989), 2) increasing sapwood area relative to leaf area (McDowell et al. 2002), 3) increasing driving force for water transport (the water potential difference between soil and leaf, Hacke et al. 2000), 4) increasing amount of root surface area (Sperry et al. 1998, Magnani et al. 2000), and 5) increasing water storage (Goldstein et al. 1998, Phillips et al. 2002). There is evidence for the above-mentioned changes from both theoretical and experimental analyses (Becker et al. 2000, Bond and Ryan 2000, Mencuccini and Magnani 2000).

The objective of our study was to test the hydraulic limitation hypothesis and examine potential compensations to hydraulic limitations using three age/size classes of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) stands located at the Wind River Experimental Forest in southwestern Washington, USA.

3.3 THEORY

Hydraulic limitation

Leaf-specific hydraulic conductance can be expressed as:

$$K_l = \frac{E_l}{(\Psi_{soil} - \rho g h - \Psi_{leaf})} \qquad (1)$$

where E_l is vapor-phase water flux (transpiration), Ψ_{leaf} and Ψ_{soil} are the water potentials of the leaf and the soil, ρgh is the effect of gravity (g is the acceleration due to gravity) at a given height (h) and water density (ρ) (symbols and units are provided in Table 3.1). Vapor-phase water flux equals liquid-phase water flux at times when water storage is zero (i.e. steady-state), such as during mid-day (Phillips et al. 2002). Stomatal

Table 3.1. Symbols, definitions and units for terms used in this paper.

Symbol	Description	Units
$\delta^{13}C$	Stable carbon isotope ratio: foliage	‰
$\delta^{13}C_a$	Stable carbon isotope ratio: CO_2	‰
Δ	Carbon isotope discrimination	‰
ψ_{leaf}	Leaf water potential	MPa
ψ_{soil}	Soil water potential	MPa
$\Delta\psi$	$\psi_{soil} - \psi_{leaf}$	MPa
η	Dynamic viscosity	$kg\ m^{-1}\ s^{-1}$
A	Net carbon assimilation	$\mu mol\ m^{-2}\ s^{-1}$
A_t	Lumen area	μm^2
A_l:A_s	leaf area:sapwood area ratio	$m^2\ cm^{-2}$
C_i	Foliar internal CO_2 concentration	Pa
D	Vapor pressure deficit	kPa
D_a	Mean (arithmetic) tracheid diameter	μm^2
D_{95}	95% flow mean tracheid diameter	μm^2
D_h	Hydraulic mean diameter of tracheids	μm^2
g_s	Stomatal conductance	$mol\ m^{-2}\ s^{-1}$
k_{sp}	Potential saturated hydraulic conductivity	$kg\ m^{-1}\ s^{-1}\ MPa^{-1}$
K_l	Hydraulic conductance	$mmol\ m^{-2}\ s^{-1}\ MPa^{-1}$
LAI	Leaf area index	$m^2\ m^{-2}$
[N]	Nitrogen concentration	$g\ g^{-1}$
SLA	Specific leaf area	$cm^2\ g^{-1}$
HLH	Hydraulic Limitation Hypothesis (Ryan and Yoder, 1997)	

conductance is related to K_l because the following expression can replace E_l in equation (1):

$$E_l = g_s \bullet D \qquad (2),$$

where D is vapor pressure deficit from leaf to air. Equation (2) holds if leaves are well-coupled to the atmosphere. From equations (1) and (2), we predict that if K_l declines due to increases in pathlength, tortuosity, or other reasons, then g_s should also decline proportionally. This direct relationship between K_l and g_s assumes that D is constant and that mid-day minimum leaf water potential does not change with tree height, as has been found for ponderosa pine but not for lodgepole pine (Yoder et al. 1994). Assuming no change in leaf water potential or D, then from equations (1) and (2) we see that a decline in K_l will result in a proportional declines in g_s (Ryan and Yoder 1997).

Having three height classes of trees gave us the opportunity to test the prediction that the relationship between height and K_l would be inversely proportional (Mencuccini and Grace, 1996a). The specific relationship between height and K_l has been found to be non-linear, with a steep initial drop in K_l as height increases, leading to a plateau in which K_l becomes nearly constant with any further increases in height (Mencuccini and Grace 1996a). This pattern is predicted by a hydraulic corollary of Darcy's Law applied to trees (Whitehead et al. 1984, Whitehead 1998):

$$K_l = \frac{k_s A_s}{h \eta A_l} \qquad (3)$$

where k_s is specific conductivity of the xylem, A_s is sapwood area, A_l is leaf area, and η is the viscosity of water. If all components are constant except for h, then equation (3) reduces to $K_l = 1/h$, which takes the shape of a non-linear decline similar to that found by Mencuccini and Grace (1996a).

Our specific hypotheses used to test the hydraulic limitation hypothesis are derived from Ryan and Yoder (1997) and Hubbard et al. (1999) and are modified to include three height-classes using equations (3-4). The hypothesis tests are as follows: 1) K_l will be inversely proportional to h, 2) g_s and A decline with increasing h, and 3) the decline in tree growth efficiency (see definition below) is proportional to the decline in A.

Hydraulic compensation

The theoretical basis for hydraulic compensation is presented in equation (3). A similar derivation of Darcy's Law for g_s can be written in which the soil-to-leaf water potential difference ($\Delta\Psi$) is explicit (Whitehead and Hinckley 1991):

$$g_s = \frac{k_s A_s \Delta\Psi}{h \eta A_l D} \qquad (4).$$

In this case the numerator from equation (1) is expressed as $\Delta\Psi/h$, the soil-to-leaf water potential gradient, and all other variables are defined as above. This derivation shows that similar to K_l, g_s will also show an inverse relationship with increasing height, if all other variables remain constant.

However, if all other variables do *not* remain constant, then compensation for h may occur. Decreasing the leaf area to sapwood area ratio (A_l:A_s) or increasing k_s may balance the effect of h on K_l; additionally, increasing $\Delta\Psi$ may balance the effect of h on g_s. If compensation is complete via changes in these variables then there will be no decline in g_s or K_l with increasing h. Our specific tests for hydraulic compensation are 1) for compensation to exist, we must observe a decrease in A_l:A_s, or an increase in k_s or $\Delta\Psi$ with increasing h, 2) for compensation to be complete, we must observe no decline in K_l with increasing h. To further test for compensation of hydraulic limitations, we compared measured K_l and g_s to that predicted by equations (3) and (4) with and without changes in compensating variables.

A few additional points must be made regarding the use of equations (1-4) for development of the hydraulic limitation and hydraulic compensation hypotheses. If the mid-day maximum $\Delta\Psi$ changes, this will violate an assumption of the hydraulic limitation hypothesis by disrupting the linear relationship between K_l and g_s.

Furthermore, increasing $\Delta\Psi$ via lowering of Ψ_{leaf} (if Ψ_{soil} is relatively constant) may cause embolism of xylem and effectively reduce k_s. Embolism probably does occur routinely in these trees (Domec and Gartner 2001), making the assumption that resistance increases linearly with h probably invalid. Lastly, hydraulic resistance and compensation may also occur in branches (Waring and Silvester 1994), belowground (Sperry et al. 1998, Magnani et al. 2000), or via other mechanisms. However, we use h as a surrogate for the many resistances from root to leaf for these equations and for the remainder of this paper because h is a significant fraction of total path length and because measurements of total path length were not available. Similarly, compensating mechanisms may exist besides those presented here. Therefore, failure to observe changes in the variables listed under test #1 of the hydraulic compensation hypotheses would not necessarily mean that compensation at the whole-tree level does not exist.

3.4 METHODS

Site description Our study sites were three stands of Douglas-fir located within the Wind River basin of the Cascade Mountains near Carson, Washington (45°49' N Lat., 121°57' W. Long.). Climate of this region is maritime, with cool, wet winters and warm, dry summers. Annual precipitation is approximately 2500 mm, with less than

10% of that falling between June and September (~120 mm). The soils are loamy sands and sandy loams developing over two to three meters of volcanic tephra. The three stands we used were within 10 km and 200 m elevation of each other and are described in greater detail in Phillips et al. (2002). The average height and age were 15, 32, and 60 m and 20, 40, and 450 years, respectively. Both the 20- and 40-year old stands originated after clearcuts, whereas the 450-year old originated after a stand-replacing fire (Franklin and DeBell 1988). Canopy access towers were erected in the center of the 15 and 32 m tall stands, and a construction crane was used for crown access in the 60 m tall stand. Four to five trees and their subtending branches were selected that were typical of each stand. Foliage was measured from three branches per tree in each stand. The same trees were measured for sapflow (Phillips et al. 2002). Further stand and tree data are provided in Table 3.2.

Growth efficiency Growth efficiency, defined as stemwood carbon production per unit leaf area per year (Waring et al. 1980), was measured to determine if the Douglas-fir trees were growing more slowly as they aged, and to determine whether growth declined concurrently with reductions in A. Growth efficiency is a useful measure because it standardizes stemwood growth to the amount of leaf area held by each tree, allowing inter-comparison across trees of different sizes with different amounts of leaf

Table 3.2. Site and tree characteristics

Ht./age (m/year)	Density >5cm (# ha^{-1})	LAI_s[d] (m^2m^{-2})	LAI_i[e] (m^2m^{-2})	SLA[f] ($cm^2\ g^{-1}$)	Foliar [N][g] ($g\ g^{-1}$) (se)	Ring widths (mm)	Leader height[h] (m)
15/20	21250[a]	6.1	10.6	60/44	1.03 (0.02)	4.4	0.96
32/40	1420[b]	5.6	na	71/47	1.48 (0.03)	2.3	0.93
60/450	448[c]	8.6	na	69/39	0.76 (0.08)	0.8	0.06

[a] Data from 12, 10x10m plots, all trees >2.5cm DBH

[b] Data from Chen et al. (2000)

[c] Data from Wind River Canopy Crane Research Facility

[d] Stand level leaf area index. LAI of the entire stand. Note that LAI of Douglas-fir in the 32m stand is approximately 5, and in the 60m stand is only 2.5. The remaining leaf area is dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and understory plants.

[e] Patch level leaf area index. LAI in the immediate vicinity of the sample trees, approximately 100 m^2 ground area.

[f] Mean specific leaf area of foliage from the entire canopy and mean specific leaf area of foliage from gas exchange, nitrogen and carbon isotope measurements (i.e. entire canopy/canopy top). The canopy mean SLA is from branch harvests throughout the vertical profile of the canopy and includes all age classes (McDowell et al. 2002). Canopy top SLA is for foliage that elongated in 1998.

[g] Foliar [N] from one year old foliage that elongated in 1998.

[h] Average heights of 1998 leaders of Douglas-fir at the 60m site from Ishii et al. (2000).

area (Waring et al. 1980, Yoder et al. 1994, Ryan et al. 1997). Although stemwood growth per unit ground area has often been shown to decline with stand age, this is an inappropriate measure for individual tree-level tests, particularly in old forests of the Pacific Northwest in which Douglas-fir is replaced by other, late-successional, species (Franklin and DeBell 1988; for example, Douglas-fir comprises < 30% of the basal area in the 450 year old forest included in our study). Growth efficiency was determined on five or six trees per stand. Increment cores were taken from the four cardinal directions of each tree for measurement of ring widths (Table 2). Tree average ring widths from 1994 through 1999 were used to calculate stemwood production using an allometric equation for Douglas-fir (Gholz et al. 1979) and assuming that stemwood dry matter was 50% carbon. Whole-tree leaf area was determined for each of the cored trees using site and age-specific allometric equations that predict whole-tree leaf area from sapwood area at 1.3m (McDowell et al. 2002). The individual tree was the sample unit for growth efficiency.

Gas exchange Diurnal gas exchange (g_s and A) was measured at each stand in July, August and September 1999. Gas exchange was measured with a Li-Cor 6400 portable photosynthesis system (Li-Cor, Lincoln, NE) equipped with a blue-red artificial light source. Cuvette irradiance was 1400 μmol photons m^{-2} s^{-1}; photosynthesis saturates by 1000 μmol photons m^{-2} s^{-1} in the upper crown of Douglas-fir (Lewis et al. 1999).

Cuvette [CO_2] was set to 40 Pa. Hourly measurements were made using one-year-old foliage within the top 10% of the live crown and from all aspects of the trees from ~7:00 am until mid- or late-afternoon unless excessive winds made use of the canopy crane impossible. One shoot was repeatedly measured per branch per day, and all three branches per tree were pooled for tree-specific averages. Because of the distance between sites and the logistics of working in tall towers or the crane, it was not possible to measure all sites on a single day. Therefore, trees at different sites were measured on successive days of similar weather to minimize confounding site comparisons with time. Foliage was not measured unless it had been in full sunlight for at least 20 minutes prior to measurement. D near the same canopy height as the gas exchange measurements was calculated using air temperature and humidity (Phillips et al. 2002) measured concurrently with the gas exchange measurements.

To determine if A and g_s declined with increasing size, we compared the slopes of A and g_s vs. D for each site using analysis of covariance. Comparing the slopes rather than comparing mean daily values of g_s and A is necessary due to the strong affect of D on g_s, transpiration and A. (Monteith 1995, Hubbard et al. 1999). Stomatal conductance should be non-linearly, negatively related to tree D as predicted by equation (4). However, we observed a linear rather than non-linear relationship, and so used linear analysis of covariance for analysis. We used individual shoots as our sampling unit for A and g_s.

Water potential We measured Ψ_{leaf} concurrently with each gas exchange measurement with a Scholander-type pressure chamber (PMS, Corvallis, OR). Small shoots neighboring the shoot measured for gas exchange were used. We estimated soil water potential (Ψ_{soil}) in the root zone using gravity-corrected pre-dawn measurements of Ψ_{leaf} of western hemlock (*Tsuga heterophylla*) saplings located at the 15 and 32 m stands and of *T. heterophylla* trees at the 60 m stand. Bauerle et al. (1999) found that these small trees represented gravity-adjusted predawn water potential for the 60 m Douglas-fir trees. We duplicated the test of Bauerle et al. (1999) and similarly found that pre-dawn water potential of hemlocks was identical to that of overstory trees after correction for the gravitational gradient (0.01 MPa m^{-1}, $P = 0.27$, $n = 3$). We assumed that nighttime transpiration was negligible. We used shoots from individual trees as our sampling unit for ψ_{leaf}.

Hydraulic conductance Leaf-specific hydraulic conductance was calculated using equation (1). Measurements for calculating K_l included g_s, Ψ_{leaf} and Ψ_{soil}, along with estimates of foliage height above the ground. Measurements were made over one daylight period at each of the three stands in July, August and September 1999. In some cases K_l was positively related to D at very low values of D (< 1.0 kPa, results not shown). Therefore we present mean values of K_l from periods of equal sample size (36 leaf-level measurements per site) and similar D: 0.5 to 1.0 kPa, 1.25 to 1.75 kPa, and 2.25 to 2.75 kPa. We used individual shoots as our sampling unit for K_l. Similar estimates of K_l on the whole-tree scale using sapflow measurements are described in a related study by Phillips et al. (2002).

Carbon isotopes We utilized carbon isotope discrimination from canopy-top foliage as an independent test of the hypothesis that g_s declined with height. Discrimination, which we calculated from the stable carbon isotope ratio ($\delta^{13}C$) of foliar cellulose, is an assimilation-weighted index of stomatal conductance if photosynthetic capacity, light availability, and source air $\delta^{13}C$ are similar or known. Cellulose was extracted from foliage that elongated in 1998 using the method described by Wise et al. (1945). Cellulose $\delta^{13}C$ was analyzed using an isotope ratio mass spectrometer at the Idaho Stable Isotope Laboratory (Moscow, ID). Standard deviations around the in-lab $\delta^{13}C$ flour standards average 0.10‰ (n = 17), and around a separate $\delta^{13}C$ pine standard was 0.09‰ (n = 6). Because this foliage was extracted from well-ventilated, sun-exposed branches near the tops of each tree, we assumed that light availability was similar across sites. Independent measurements of atmospheric $\delta^{13}CO_2$ ($\delta^{13}C_a$) at the canopy top showed no difference among stands (Fessenden and Ehleringer, 2002). Therefore, we calculated Δ using site-specific values for cellulose $\delta^{13}C$ and a $\delta^{13}C_a$ value of -8.00‰ (Farquhar et al. 1989):

$$\Delta = (\delta^{13}C_a - \delta^{13}C)/(1 + \delta^{13}C/1000) \quad (‰) \qquad (5)$$

Δ should show a negative, non-linear relationship with tree height if photosynthetic capacity is constant and stomatal conductance declines with height as predicted by the hydraulic limitation hypothesis and equation (4). We used foliage from individual trees as our sampling unit for Δ.

Photosynthetic capacity We estimated foliar photosynthetic capacity two ways. Foliar nitrogen concentration [N] was measured because foliar [N] is strongly related to photosynthetic capacity (Field and Mooney 1986, Livingston et al. 1998). Second, photosynthetic capacity was assessed using response curves of photosynthesis to internal [CO_2] (A/C_i curves). Foliar [N] was obtained from a subset of whole-foliage samples collected after gas exchange measurements. Samples were dried at 65 °C for 48 hours, ground with a mortar and pestle, and analyzed with a LECO CNS 2000. A/C_i curves were measured on five 32 m tall trees and four 60 m tall trees on overcast days between June 22 and 29, 1999, and on five 15 m tall trees on July 21, 1999. Cuvette conditions were the same as those described above for gas exchange measurements. A/C_i curves were generated by changing the cuvette [CO_2] in the following order: 40, 30, 20, 10, 40, 60, 80, 100, 120, 160, 200 Pa. After each exposure to a new [CO_2] level, foliar *A* was allowed to reach steady state (cuvette [CO_2] coefficient of variation < 2%) prior to measurement. Six measurements were made per sample per [CO_2]-level over a 60 second period after steady-state had been reached. The maximum carboxylation rate and maximum electron transport rate were calculated from the A/C_i curves using non-linear least squares regression to fit the values of these parameters to the best fit equations of von Caemmerer and Farquhar (1981) photosynthesis model (Harley et al. 1992).

Sapwood-specific hydraulic conductivity Measurements of sapwood anatomy for estimation of k_{sp} were done on shoots from the 15 m and 60 m trees, and from boles of the 15, 32, and 60 m trees. Five shoots were harvested, one per tree, from upper canopy branches at sunrise (typically before 7:00) and again at 15:00 to 17:00. Shoots were typically 0.5 to 2.0 cm in diameter. We placed the samples under a gravitational pressure potential of 0.01 MPa with 0.22 μm filtered, 0.5% safranin dye and allowed the dye to perfuse for 30 minutes. Three cross-sectional samples were sectioned with a sliding microtome and fixed on glass slides with a 70% ethyl alcohol solution. Stained sapwood and tracheid lumen areas were determined using a digital imaging and analysis system (Sony CCD/RGB Color Video Camera with a Nikon Labophot-2 compound microscope, with a NIH Image v. 1.59 public domain-image processing and analysis program). Lumen areas were measured on three sub-samples per cross section distributed across the outside-pith radius of the shoot. For the 60 m trees, the three sub-samples were typically located on the 2nd, 5th, and 9th ring from the pith, and for the 15 m tall trees, the sub-samples were located on the 1st, 2nd and occasionally the 3rd ring from the pith. Stained sapwood and vessel density were determined as a proportion of total sapwood-area. We estimated native cavitation as the percentage differences between stained sapwood area and total sapwood area, not including the pith area (Panek and Waring 1995). Shoots from the 60 m stand were, on average, 10 years old, whereas the shoots from the 15 m stand were typically three years old.

Anatomy of bole-sapwood was examined using a similar technique as described above for shoots. Sapwood cores were collected at approximately 1.4 m height on five trees per site using increment borers. One core was collected per tree. Lumen areas were typically measured on two or three of the outermost rings on each core, and were distributed approximately evenly between earlywood and latewood.

Tracheid density and lumen areas within the sapwood were used to estimate potential saturated hydraulic conductivity (k_{sp}, kg m^{-1} s^{-1} MPa^{-1}) according to Poiseuille's law:

$$k_{\mathrm{sp}} = [\pi/8\eta\ (\Sigma\, r^4)]/A_{\mathrm{s}} \qquad (6)$$

where r is the radius of a circle having the same area as the corresponding tracheid, and A_s is sapwood area. This is considered an estimate of maximum potential conductivity because it assumes no differences in tracheid length or friction due to bordered pits, tracheid tapering or xylem cavitation.

Leaf area:sapwood area Shoot level A_l:A_s was measured on shoots collected in July 2000. Shoots that were at least 0.5 cm in diameter were collected from five trees per site at the 15 and 60 m tall sites. Shoots were obtained from the upper 10% of the crowns of each tree, from all aspects. Leaf area was measured on all foliage from the shoots. Whole-tree A_l:A_s was obtained from five or six trees per site as described by McDowell et al. (2002).

Statistics All data used to test the hydraulic limitation and hydraulic compensation hypotheses were collected between June and September 1999, with the following exceptions: Ψ_{soil} and Ψ_{leaf} data were collected in both 1998 and 1999, and shoot level vascular anatomy, A_l:A_s, and cavitation were measured between June and September 2000. All statistical analyses were done with Systat 9.0, using an alpha level of 0.05. Post-hoc analyses were done after detection of significant differences using a Tukey's HSD test for pairwise differences (Neter et al. 1990). Analysis of covariance was used to compare if the slopes of A and g_s vs. D. Repeated measures analysis of covariance was used for data collected from the same trees repeatedly throughout time. Data met the assumptions of normality and homogeneity of variance as examined using scatterplots and histograms of the residuals.

3.5 RESULTS

Stemwood growth efficiency declined in a non-linear fashion with increasing tree height ($R^2 = 0.68$, Figure 3.1). Stemwood growth efficiency averaged 59.8, 34.7, and 27.9 gC m^{-2} leaf area year^{-1} for the 15, 32, and 60 m tall trees, respectively. Height growth averaged nearly 1 m year^{-1} for the 15 and 32 m tall trees, and only 0.06 m year^{-1} for the 60 m tall trees (Table 2).

There was no statistical difference in the slope of A vs. D between stands ($P = 0.08$, Figure 3.2a). Similarly, there was no statistical difference in the slope of g_s vs. D between stands ($P = 0.32$, Figure 3.2b).

The $\delta^{13}C$ values of cellulose extracted from canopy top foliage increased (became less negative) with increasing tree size. $\delta^{13}C$ differed significantly with height class (polynomial contrast $P < 0.001$). Carbon isotope discrimination calculated from equation (5), averaged 18.6‰, 17.6‰, and 15.9‰ for the 15, 32 and 60 m tall trees, respectively (polynomial contrast $P < 0.001$, Figure 3.3). Foliar [N] was highest at the 32 m stand (1.48 %), intermediate at the 15 m tall stand (1.03 %), and lowest at the 60 m stand (0.76 %, Table 3.2). Foliar [N] at canopy tops was different between each size

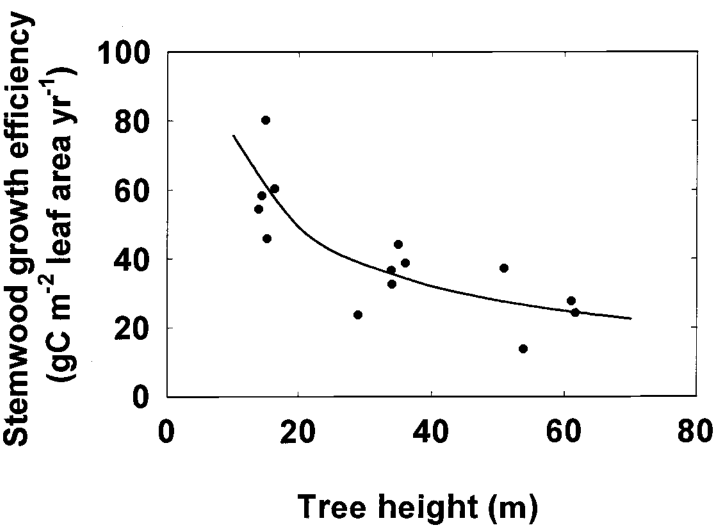
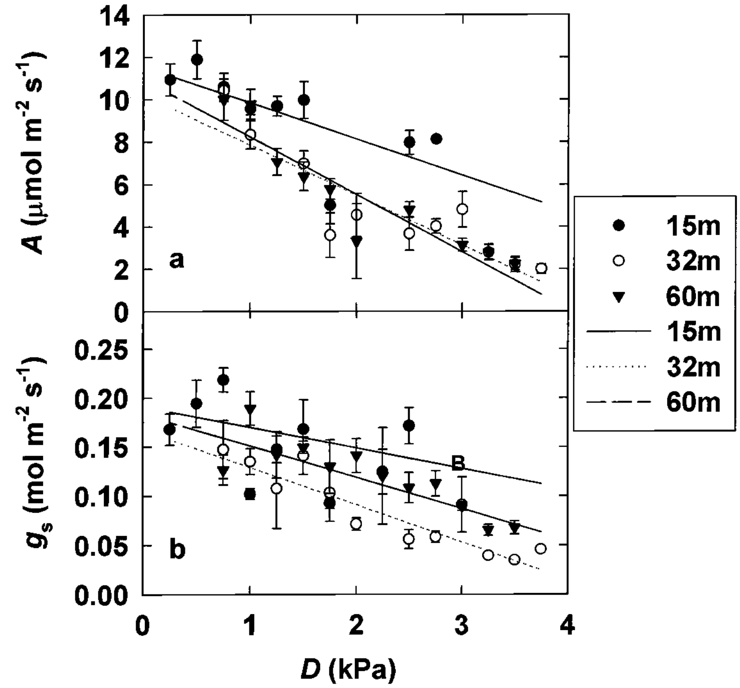


Figure 3.1 Stemwood growth efficiency, defined as stemwood growth per whole-tree leaf area, vs. tree size. Individual trees are plotted. The equation is: growth efficiency = 317.34•height$^{-0.62}$, r^2=0.68.

Legend for figure 3.2

Figure 3.2 (a) Stomatal conductance (g_s) and (b) net photosynthesis (*A*) vs. vapor pressure deficit (*D*) for Douglas-fir trees. Values were binned by 0.25 kPa classes of *D* for presentation. Regression lines were not significantly different from each other, and are shown only to aid in identifying data from each height class. Foliage was the sample unit. Bars are standard errors.


A (μmol m^{-2} s^{-1})
14
12
10
8
6
4
2
0
a
g_s (mol m^{-2} s^{-1})
0.25
0.20
0.15
0.10
0.05
0.00
b
B
0
1
2
3
4
D (kPa)
15m
32m
60m
15m
32m
60m

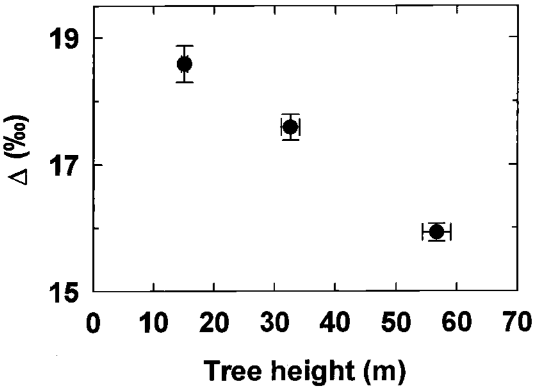


Figure 3.3. Carbon isotope discrimination (Δ) of upper canopy foliage vs. tree height for Douglas-fir trees. Values are the mean of ten or more foliage samples per stand. Bars are standard errors.

class ($P < 0.001$) but was not correlated with height. The maximum carboxylation rates, calculated from the A/C_i curves, were 27.5, 47.9 and 38.9 μmol m^{-2} s^{-1} for the 15, 32 and 60 m tall trees, respectively ($P = 0.01$). The maximum electron transport rates were 97.9, 147.4 and 128.7 μmol m^{-2} s^{-1} for the 15, 32 and 60 m tall trees, respectively ($P = 0.03$). There was no relationship between Δ and photosynthetic capacity as indexed with foliar [N] ($P = 0.56$). Likewise, there was no relationship between Δ and carboxylation rates or electron transport rates ($P = 0.82$ and 0.90, respectively).

Leaf specific hydraulic conductance calculated from equation (1) was not statistically related to D for any of the height classes ($P > 0.1$). Mean K_l of the 32 and 60 m tall trees equaled 0.87 and 0.82 mmol m^{-2} s^{-1} MPa^{-1}, respectively, and were statistically identical ($P = 0.79$). Hydraulic conductance of the 15 m tall trees averaged 1.56 mmol m^{-2} s^{-1} MPa^{-1} and was approximately 44% higher than K_l of the 32 m trees and 50% higher than that of the 60 m trees ($P < 0.01$, Figure 3.4).

Pre-dawn Ψ_{soil} was not significantly different across tree size classes (repeated measures ANOVA, $P = 0.54$ and 0.87 for 1998 and for 1998-1999 combined) except for September 1999, at which time Ψ_{soil} in the 15 m site became significantly more negative than the other two stands ($P < 0.01$). The trees at all sites showed a characteristic threshold minimum mid-day Ψ_{leaf}, and for the 15 and 32 m tall trees this minimum was approximately -2.1 MPa. However, the 60 m trees had significantly more negative mid-

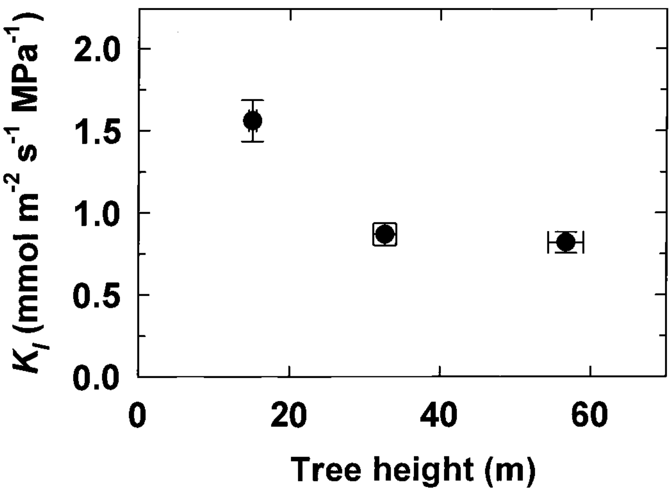


Figure 3.4. Leaf-specific hydraulic conductance (K_l) vs. tree height for Douglas-fir trees. The filled circles are mean measured K_l averaged between July, August, and September 1999. Foliage was the sample unit and bars are standard errors.

day Ψ_{leaf} than the 15 or 32 m tall trees in both 1998 and 1999, reaching daily mean values of –2.6 MPa (repeated measures ANOVA, $P < 0.001$ for both, Figure 3.5a,b). The soil-to-leaf water potential range estimated as mean Ψ_{soil} minus Ψ_{leaf} for the corresponding days, was consistently larger for the 60 m stand (repeated measures ANOVA, $P < 0.01$, Figure 3.5c,d). $\Delta\Psi$ did not differ between the 15 and 32 m tall trees when compared over the entire season ($P = 0.29$).

Shoot-level A_l:A_s decreased with increasing size, averaging 1.21 and 0.97 $m^2\ cm^{-2}$ for the 15 and 60 m trees, respectively (t-test, $P = 0.02$, Table 3.3). This 20% decline in shoot-level A_l:A_s was similar in magnitude to that found for whole-trees. Whole-tree A_l:A_s declined by 25% between the 15 and 60 m trees (from 0.51 to 0.39 $m^2\ cm^{-2}$, McDowell et al. 2002). Mean lumen area of shoot xylem from the 60 m trees was significantly lower than for the 15 m trees (53.3 and 75.1 μm^2, respectively, $P = 0.02$, Table 3). Lumen diameters were smaller for the 60 m shoots in comparison to the 15 m shoots, independent of the method of calculation ($P < 0.02$, Table 3.3). The average number of tracheids per unit sapwood area was also significantly higher for the 60 m shoots compared to the 15 m shoots ($P = 0.001$, Table 3.3). Despite the substantial differences in vascular anatomy between tree size classes, calculated shoot k_{sp} (equation (6)) was not significantly different between 15 m tall trees ($1.17 * 10^{-12}\ m^2$) and 60 m trees ($0.84 * 10^{-12}\ m^2$, $P = 0.11$, Table 3.3). At the bole level, the number of tracheids per unit sapwood area was the only anatomical measurement that differed significantly

Legend for Figure 3.5

Figure 3.5. Water potential (MPa) results for the 15, 32 and 60 m Douglas-fir trees. (a,b) Mid-day water potential (Ψ_{leaf}) for 1998 and 1999. (c,d) The soil-to-leaf water potential difference ($\Delta\Psi$) calculated as Ψ_{soil}-Ψ_{leaf}, for 1998 and 1999. Soil water potential are provided in Phillips et al. (2002). The shoot is the sample unit. Error bars are standard errors of shoot-level measurements for Ψ_{leaf}. Ψ_{leaf} measurements were averaged between 12:00 and 15:00 on each date.

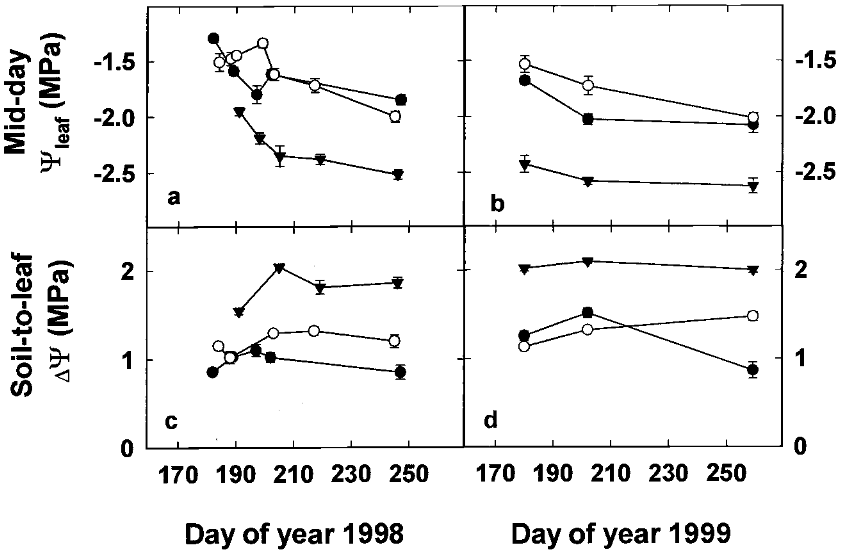

Mid-day
Ψ leaf (MPa)
-1.5
-2.0
-2.5
a
b
Soil-to-leaf
ΔΨ (MPa)
2
1
0
c
d
170 190 210 230 250
Day of year 1998
Day of year 1999

Figure 3.5

Table 3.3. Anatomical and structural characteristics. Within the subheadings Shoot and Bole, variables labeled with the same letter are not significantly different between height classes at $\alpha = 0.05$. k_{sp} is potential saturated hydraulic conductivity calculated from equation (5), A_t is measured lumen area, and D is diameter calculated from the A_t measurements. Tracheid number is provided per unit sapwood area, and A_l:A_s is leaf area:sapwood area ratio.

Height (m)	Sample	k_{sp} (kg m^{-1} s^{-1} MPa^{-1})	A_t (μm^2)	D_a° (μm)	D_h• (μm)	Tracheid number (# mm^{-2})	A_l:A_s* (m^2 cm^{-2})
15m	Shoot	1.17^a	75.1^a	9.4^a	11.29^a	4280^a	1.21^a
60m	Shoot	0.84^a	53.3^b	7.9^b	10.46^b	6048^b	0.97^b
15m	Bole	11.70^a	520.2^a	25.3^a	29.6^a	1025.1^a	0.51^a
32m	Bole	16.95^a	565.1^a	24.6^a	31.9^a	947.5^a	0.49^a
60m	Bole	14.51^a	716.3^a	27.0^a	36.6^a	650.4^b	0.39^b

°Mean diameter of tracheids calculated as the arithmetic mean.

•Hydraulic mean diameter, equivalent to $\sum \text{diameter}^4 / \sum \text{diameter}^5$, (Pockman and Sperry 2000).

*Whole-tree A_l:A_s from McDowell et al. (2002).

with height, with the 60 m trees having significantly lower values compared to the 15 and 32 m trees ($P = 0.01$, Table 3.3). The number of tracheids per unit sapwood area did not differ between 15 and 32 m tall trees ($P = 0.77$, Table 3.3). The lower number of tracheids per unit sapwood area in the bole sapwood of the 60m trees counteracted the slightly larger lumen areas (Table 3.3), resulting in similar estimates of k_{sp} of bole sapwood between size classes ($P = 0.33$, Table 3.3).

The proportion of sapwood that was conductive to water was consistently less for shoots of the 60 m than the 15 m tall trees throughout summer 2000 ($P < 0.001$, Figure 3.6). The proportion of functional sapwood did not differ between shoots collected at dawn and those collected in the late afternoon ($P = 0.37$). Likewise, there were no differences in the proportion functional sapwood of shoots across months ($P = 0.19$).

We modeled K_l from equation (2) using measured whole-tree A_l:A_s and $\Delta\Psi$ values for all tree height classes (Figure 3.7a, solid line). The model predictions were within 9% of the measured values when A_l:A_s and $\Delta\Psi$ were allowed to vary with tree size ($R^2 = 0.99$, $P = 0.03$). To examine the effect of compensating mechanisms on K_l, we re-modeled K_l, but either held A_l:A_s constant at the mean value of the 15 m tall trees (maximum A_l:A_s, dotted line), held $\Delta\Psi$ constant at the mean value of the 15 m tall trees (minimum $\Delta\Psi$, dashed line), or held both A_l:A_s and $\Delta\Psi$ constant at the mean value of the 15 m tall trees (maximum A_l:A_s, minimum $\Delta\Psi$, dashed and dotted line). We chose

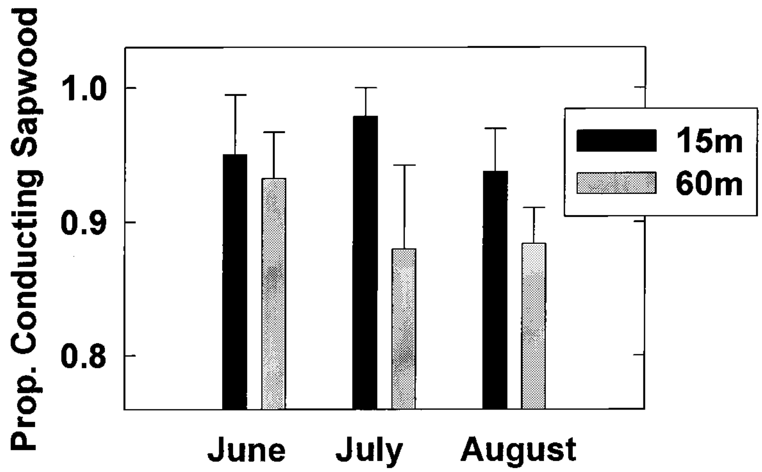


Figure 3.6. The proportion of conducting sapwood of shoots from the 15 and 60 m Douglas-fir trees. Functional sapwood was measured with dye perfusion. The individual shoot is the sampling unit. Bars are standard errors.

Legend for Figure 3.7

Figure 3.7. (a) Leaf-specific hydraulic conductance (K_l) vs. tree height. (b) Stomatal conductance (g_s) vs. tree height. For (7a) the filled circles are mean measured K_l averaged over the year. For (7b) the filled circles are mean g_s measured in July. July g_s data was used because this is the only sample period when D was similar. Standard error bars are provided for measured data in both panels. The solid trace (variable) is the hydraulic model (equation 1) using measured values for A_l:A_s and $\Delta\Psi$ for all trees. The dot trace is the same model but holding A_l:A_s constant at the mean value of the 15m tall trees. The dash trace is the same model but holding $\Delta\Psi$ constant at the mean value of the 15m tall trees. The dash/dot trace is the same model assuming no compensation by A_l:A_s or $\Delta\Psi$. The dashed line at the top of the figure is the hypothesize relationship between K_l and tree height if compensation fully balances hydraulic constraints.

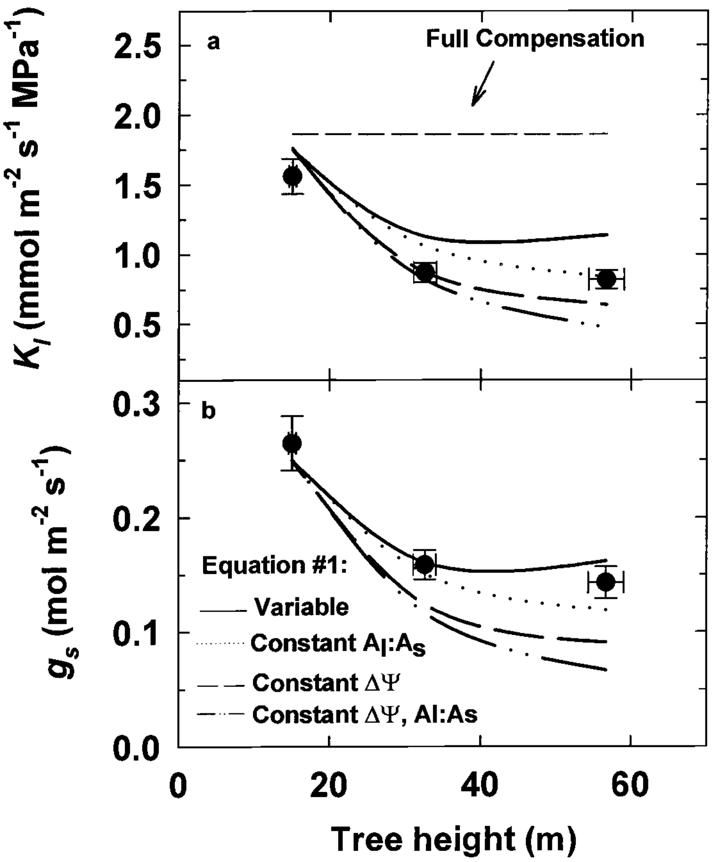

K_l (mmol m^{-2} s^{-1} MPa^{-1})
2.5
2.0
1.5
1.0
0.5
a
Full Compensation
0.3
0.2
0.1
0.0
b
g_s (mol m^{-2} s^{-1})
Equation #1:
Variable
Constant A_l:A_s
Constant $\Delta\Psi$
Constant $\Delta\Psi$, Al:As
0
20
40
60
Tree height (m)

Figure 3.7

not to model the effect of changing k_{sp} because no statistical differences were found between k_{sp} of 15 and 60 m tall trees. K_l values for each individual tree obtained from equation (2) were divided by the value of the shortest tree and then multiplied by K_l of that tree (as in Schäfer et al. 2000). Assuming that A_l:A_s does not vary with height causes the model to underestimate K_l by 6% and 18% for the 32 and 60 m tall trees, respectively. Assuming $\Delta\Psi$ does not change with height caused the model to underestimate K_l by 22% and 38% for the 32 and 60 m tall trees, respectively. Finally, assuming that both A_l:A_s and $\Delta\Psi$ do not change with height causes the model to underestimate K_l by 27%- and 54% for the 32 and 60 m tall trees, respectively.

Equation (4) was used to predict g_s (Figure 3.7b) because measured and modeled K_l are not fully independent (they share $\Delta\Psi$), whereas measured and modeled g_s are fully independent. This model was run identically to that presented in Figure 3.7a, except mean cuvette-based g_s measured in July was used as the dependent variable. July g_s measurements were used because similar environmental conditions existed across the three sites only for this months samples. When A_l:A_s and $\Delta\Psi$ were allowed to vary with tree size, model predictions were within 5% of measured g_s for the 15 and 32 m trees, and within 13% of measured g_s for the 60 m trees ($R^2 = 0.97$, $P = 0.08$). Assuming that A_l:A_s does not vary with height causes the model to underestimate g_s by 17% for the 60 m trees. Assuming $\Delta\Psi$ does not change with height caused the model to underestimate

g_s by 36% for the 60 m tall trees. Finally, assuming that both A_l:A_s and $\Delta\Psi$ do not change with height causes the model to underestimate g_s by 53% for the 60 m tall trees.

3.7 DISCUSSION

Evidence for and against the hydraulic limitation hypothesis

Contrary to predictions of size related hydraulic limitation to gas exchange, we found that: 1) cuvette-based g_s and A did not differ with height when compared across a range of D (Figure 3.2a,b), and 2) the lack of difference in cuvette-based A (Figure 3.2a) means that the decline in growth efficiency (Figure 3.1) cannot be explained by a decline in A. On the other hand, the K_l and Δ results conformed to predictions of the hydraulic limitation hypothesis. We suspect that the cause for these mixed results is due to one of the following scenarios: 1) the important period for manifestation of hydraulic constraints to carbon gain occurs in the pre-drought months (before July) and thus the appropriate time to test for hydraulic limitation is in the spring months, or 2) hydraulic limitations to gas exchange are not operating in this system, and Δ is controlled by some factor other than g_s.

In reconciling our cuvette-based g_s measurements with g_s inferred from Δ results we have been led to hypothesize that hydraulic limitations to gas exchange may be manifest in the spring months but not during summer drought. Eddy covariance measurements have shown that April and May are the months of maximal carbon uptake at the 60 m forest (Paw U et al. *in review*). Because $\delta^{13}C$ of foliar cellulose is an assimilation-weighted measure of Δ during leaf elongation (Brugnoli et al. 1998), we know that Δ must have varied linearly with height during April and May, 1998 (Figure 3.3). In turn, the Δ results suggest that g_s declines linearly with height because variation in Δ was not due to photosynthetic capacity or light availability (Farquhar et al. 1989, Livingston et al. 1998). Because spring is the time of maximum carbon assimilation in this forest (Paw U et al. *in review*), then any height-related reductions in g_s may translate into height related reductions in gross carbon uptake.

We must reconcile our cuvette-based g_s measurements from July, August and September 1999 with g_s inferred from the Δ results. As stated above, a temporal mismatch between years and seasons likely exists between the $\delta^{13}C$ and cuvette data because the cellulose-carbon from which $\delta^{13}C$ was measured was laid down in May 1998, whereas the cuvette data were collected 14-16 months later. In support of this theory, cuvette-based g_s and C_i from July was more similar to that predicted by cellulose $\delta^{13}C$ than the cuvette data from August or September. For example, cuvette-based C_i measured in July shares a similar trend with height as that predicted by $\delta^{13}C$ ($r^2= 0.87$) but cuvette-based C_i measured in later in the summer does not ($r^2<0.05$). Both cuvette and Δ data were derived from the same foliage near the top of the trees, so spatial variation cannot be responsible for the discrepancy between Δ and cuvette-g_s. Bauerle et al. (1999) made a similar comparison of $\delta^{13}C$ and cuvette-based g_s and concluded that cuvette-based g_s was a poor measure in comparison to $\delta^{13}C$ data because of the limited temporal integration of gas exchange instruments. Similar to our study, Bauerle et al. (1999) found no difference in cuvette-based g_s between sapling and old Douglas-fir trees, but a large $\delta^{13}C$ difference (4.5‰). Alternatively, if both measurements are accurate, then a change in the relationship between g_s and height must occur between spring and summer.

Fessenden and Ehleringer (2002) also found that cuvette-based g_s did not exactly match $\delta^{13}C$ of leaf isotopes; however, they did find evidence that g_s is lower in older stands. Ecosystem-respired $\delta^{13}C$ was most negative in the 15 m stand, intermediate in the 32m stand, and most enriched in the 60 m stand. Because soil and ecosystem-respired $\delta^{13}C$ has been strongly linked to g_s (Ekblad and Hogberg 2001, Bowling et al. 2002), the data of Fessenden and Ehleringer (2002) suggest that cuvette-based g_s may be missing height-related patterns of g_s that are manifest at the canopy scale.

Alternatively, the height-related foliar Δ patterns may be caused by a factor other than stomatal conductance. Although we can only speculate on these mechanisms, they may include differences in 1) the occurrence of freezing between sites, 2) stomatal sensitivity to freezing, 3) differences in photosynthetic capacity during the period prior to- and during leaf elongation, or 4) differences in mesophyll resistance.

We must consider the quality of our gas exchange data. Despite conducting gas exchange measurements on subsequent days, we obtained relatively little g_s and A data at D greater than 2 kPa at the 15m site (Figure 3.2a,b, 3.2a shows this most clearly). At D less than 2 kPa it appears that g_s and A are generally higher in the 15m trees than the taller trees (Figure 3.2a,b). However, the poor distribution of data across the range of D may have hampered our statistical ability to discern differences between the 15m tall trees and the taller trees. We note that sapflow estimates of crown conductance also did not support the hydraulic limitation hypothesis; however, caution interpreting sapflow estimates in these sites has also been acknowledged (Phillips et al. 2002).

Hydraulic conductance declined with tree height in a pattern similar to that predicted by equation (3) (Figure 3.4). This supports the hypothesis that height is an important factor governing K_l. Interestingly, the decline in K_l parallels the decline in growth efficiency (Figure 3.1). However, K_l declined less for the tall trees than was predicted by equation (3) (Figure 3.7a), suggesting that hydraulic compensation occurred.

Evidence for and against the hydraulic compensation hypothesis

Evidence for hydraulic compensation is found in the fit, or lack thereof, of predictions from equations (3) and (4) to the measured K_l and g_s data under the four different scenarios presented in Figure 3.7a and 3.7b. The model under-predicted K_l and g_s for the 60 m trees by 18 to 61% when A_l:A_s or $\Delta\Psi$ were not allowed to vary with height. A similar result was found in *Fagus sylvatica* by Schäfer et al. (2000), where height-related reductions in crown conductance were minimized by concurrent reductions in A_l:A_s. This clear evidence for the existence of hydraulic compensation supports the ideas proposed by Mencuccini and Grace (1996*b*), Meinzer et al. (1997), Ryan and Yoder (1997) and Becker et al. (2000). However, because K_l declined with increasing tree height, it is also clear that hydraulic compensation is insufficient to fully mitigate size-related constraints on hydraulic and stomatal conductance (Bond and Ryan 2000, Mencuccini and Magnani 2000).

The results of Figure 3.7a and 3.7b suggest that increasing $\Delta\Psi$ had a greater effect on maintaining conductance than decreasing A_l:A_s. The concept of increasing $\Delta\Psi$ as a compensating mechanism for tree size has not been suggested previously. This is due in part to evidence for species-specific values for threshold mid-day Ψ_{leaf} (e.g. Bond and Kavanagh 1999). Mid-day minimum Ψ_{leaf} does not vary for large and small ponderosa pine (Yoder et al. 1994, Ryan et al. 2000). However, more negative minimum Ψ_{leaf} was observed with increasing tree height in lodgepole pine (Yoder et al.

1994) and *Eucalyptus saligna* (Barnard 2001). Using loblolly pine trees, Hacke et al. (2000) found that Ψ_{leaf} decreased as soil texture became more course, and suggested that this maintains the trees capacity to extract sufficient water for transpiration. Therefore, a height-related decline in minimum Ψ_{leaf} may be a mechanism of maintaining transpiration and thereby minimizing reductions in K_l and g_s as trees become larger.

The more negative mid-day Ψ_{leaf} found in tall trees (Figure 3.5a,b) may act to minimize height related reductions in g_s by increasing the range of Ψ_{leaf}. The Ψ_{leaf} required to hold a vertical water column is equal to 0.01 MPa per meter above the ground. Therefore, the most positive water potential a leaf can have at the top of a 60 m tree is -0.60 MPa. If the minimum mid-day Ψ_{leaf} were invariant with tree height, say – 2.1 MPa for example, and since g_s declines at a threshold Ψ_{leaf} (Tyree and Sperry 1988, Bond and Kavanaugh 1999), then the maximum range of Ψ_{leaf} over which foliage at the top of 60m trees may operate at is only 1.5 MPa (-0.6 minus -2.1), whereas for a 10 m tree the Ψ_{leaf} range is 2.0 MPa (-0.10 minus -2.1). The smaller Ψ_{leaf} range for the large trees should result in a relative reduction in daily g_s because the foliage will reach the threshold Ψ_{leaf} earlier in the day (assuming maximum g_s is invariant with height). However, given the observed Ψ_{leaf} values of -2.6 MPa for the 60 m trees and -2.1 MPa for the 15 and 32 m tall trees, the potential range over which foliage may operate is actually greatest for the tallest trees, with a range of 2.0 MPa (-0.6 minus -2.6 MPa) vs. 1.95 MPa for the 15 m tall trees (-0.15 minus -2.1) and 1.78 MPa for the 32 m tall trees

(-0.32 minus -2.1 MPa). Decreasing the mid-day Ψ_{leaf} may mitigate the cost of gravity on water transport.

The consequences of decreasing Ψ_{leaf} below tensions at which xylem cavitation occurs are well established (Tyree and Sperry 1988). If increased $\Delta\Psi$ in taller trees compensates for increased path length, it may be at the cost of increased cavitation. We observed significantly less functional sapwood, as indexed by dye perfusion, in the shoots of the 60 m trees (Figure 3.6). The loss of functional sapwood in the 15 m tall trees was similar to that observed in Douglas-fir in cool, wet coastal locations while that of the 60 m trees was similar to Douglas-fir located in hot, dry inland locations (Panek and Waring 1995). This large difference in conducting sapwood may be partially responsible for the relatively low K_l in the 60 m trees. However, we found a decrease in A_l:A_s in shoots, which may act as a mechanism to maintain K_l during times of cavitation (Phillips et al. 2000).

We expected k_{sp} to increase with tree size as a compensation for tree size (Pothier et al. 1989, Ryan and Yoder 1997, Becker et al. 2000). Increasing tracheid size is one of the components of cellular anatomy that can increase k_{sp} (Mencuccini et al. 1997). However, we observed no significant change in tracheid area of bole sapwood with tree height, and a decrease in tracheid area of shoot sapwood with increased height (Table 3). Hydraulic conductivity was statistically unrelated to height for both shoot and bole sapwood (Table 3). The decreasing tracheid diameter of shoots may increase xylem resistance to cavitation (e.g. Pockman and Sperry 2000). The greater water tensions experienced in the 60 m trees (Figure 3.5) and the lower percentage of functional sapwood (Figure 3.6) may provide the driving force for declining tracheid diameter in the shoots of taller trees. Despite reductions in tracheid size of shoots, whole-tree k_s may have remained constant or even increased with tree size (Phillips et al. 2002). Other factors are important in controlling k_s, including tracheid length and the permeability of pit membranes (Mencuccini et al. 1997), tracheid tapering (West et al. 1999), as well as changes in k_{sp} throughout the continuum of sapwood from root to shoot (Spicer and Gartner 2001, Domec and Gartner 2001).

3.8 CONCLUSION

The hydraulic limitation hypothesis did not pass all of the tests in Douglas-fir trees in Wind River, Washington. However, strong evidence of hydraulic constraints to water transport were observed. Hydraulic compensation was also observed, but was insufficient to fully alleviate height-related reductions in hydraulic conductance. We have demonstrated that constraints to hydraulic conductance occur in conjunction with hydraulic compensation. Indeed, the simultaneous co-occurrence of hydraulic constraints with compensation suggests that compensation itself may be a response to a hydraulic driving force. The notion that hydraulic systems of trees interact to balance the benefits and costs of height growth is not new (e.g. Whitehead et al. 1984; Magnani et al. 2000).

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CHAPTER 5

CARBON ISOTOPE DISCRIMINATION AND GROWTH RESPONSE OF OLD *PINUS PONDEROSA* TREES TO STAND DENSITY REDUCTIONS

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4.1 ABSTRACT

Stand density reductions have been proposed as a method by which old-growth ponderosa pine (*Pinus ponderosa*) forests of North America can be converted back to pre-1900 conditions. These management techniques are expected to reduce the danger of catastrophic forest fires and insect attacks while increasing productivity of the remaining old-growth trees. However, the duration of this productivity response, and the physiological mechanisms underlying the response remain speculative issues in old ponderosa pine. Carbon isotope ratios ($\delta^{13}C$) of tree rings are commonly used for inferring intrinsic water-use efficiency (the ratio of photosynthesis, A to stomatal conductance, g) and may provide insight into the mechanisms and temporal patterns regulating the response of trees to stand density manipulation. We examined the response of growth and isotope discrimination (Δ) in >250-year-old ponderosa pine trees to stand density manipulations in Oregon, USA. We hypothesized that reductions in stand density increase soil moisture availability, thus altering canopy A/g and Δ. We measured cellulose-$\delta^{13}C$ of annual tree rings, soil water availability, photosynthetic capacity, stem basal growth and xylem anatomy in three pairs of thinned and un-thinned stands. The thinned stands were treated seven to 15 years prior to measurement. Carbon isotope discrimination of thinned trees increased by 0.89 ‰ (± 0.15‰), whereas Δ did not change for un-thinned trees (0.00‰ ± 0.04‰). Significant differences were observed in the first growing season after the thinning took place but it took 6 years

before the full 0.89 ‰ difference was observed. Basal area increment (*BAI*) doubled or tripled after disturbance, depending on the stand, and the growth response lasted up to 15 years after thinning. The *BAI* response did not begin until three years after the Δ response, peaked one year after the Δ peak, and then *BAI* and Δ oscillated in unison. The variable lag of *BAI* behind Δ is possibly due to changes in whole-tree hydraulic conductance associated with growth of roots, sapwood and foliage. The lag between *BAI* and Δ was not due to slow changes in anatomical properties of the sapwood, because tracheid dimensions and sapwood specific conductivity remained unchanged after disturbance. The Δ response of thinned trees indicated that A/g decreased after thinning. Photosynthetic capacity, as indexed by foliar nitrogen ([N]) and by the relationship between photosynthesis and internal CO_2 (A-C_i curves), was unchanged by thinning, suggesting that the A/g decline was due to a greater increase in g relative to A. Soil water availability is positively correlated with stomatal conductance in many forests, and we found soil water availability was greater at the thinned stands. Pre-dawn soil water potential averaged 0.11 MPa (± 0.03 MPa) less negative for the thinned compared to the un-thinned stands, and was strongly correlated with Δ post-thinning ($R^2 = 0.91$). Model estimates agreed with the indirect evidence, predicting that g increased by nearly 25% after thinning relative to a smaller 15% increase in A. There was a strong relationship between stem basal growth and modeled A, suggesting that changes in water availability and g have a significant effect on carbon assimilation and growth of these old trees. We conclude that stand density reductions result in increased growth via increased stomatal conductance and that this response can last for up to 15 years in old ponderosa pines if stand leaf area is not fully re-established.

4.2 INTRODUCTION

Ponderosa pine is a conifer with a widespread range in North America, occurring from central Mexico to southern Canada, and is an economically important species on both public and private forests. Prior to 1900, frequent ground fires removed competing understory vegetation and maintained park-like stand structure in ponderosa pine forests. However, with the advent of fire exclusion circa 1900, stand density (the number of individuals per unit ground area) has increased dramatically (McCune 1988, Agee 1993). Fire exclusion has resulted in increased regeneration of understory plants as well as invasion of shade-tolerant conifers, resulting in increased competition and reduced productivity of overstory trees (Parsons and DeBendetti 1979). Reductions in growth capacity of individual trees results in increased susceptibility to attack from insects such as the mountain pine beetle (*Dendroctonus ponderosae*) (Larrson et al. 1983, Waring and Pitman 1985). Of particular relevance to the public is the increased danger of catastrophic forest fires associated with the large fuel loads in the dense forests. Concern is mounting that old-growth pine forests of western North America are in danger of disappearing due to fire and insect attack unless intervention via management techniques is employed.

Thinning of understory competition to reduce stand density is a popular new management method because it effectively reduces within-stand competition while maintaining the presence, and increasing the vigor of old-growth trees (Newton and Cole 1987, Waring and Pitman 1985). However, the duration of the growth response is variable. Oren et al. (1987) observed that the thinning induced growth response of young pine trees lasted for only a few years. Growth decline after the initial peak was associated with re-establishment of canopy leaf area index (*LAI*, m^2 leaf area per m^2 ground area) to pre-thinning levels. However, if a sufficiently large reduction in *LAI* occurs via thinning, stands may potentially respond for as long as 15 years (Latham and Tappeiner 2002).

The mechanism of growth response is also variable. In relatively dry ecosystems it seems likely that soil moisture availability should increase after partial removal of transpiring leaf area via thinning, thereby increasing water availability to the remaining trees. Some previous investigations support this theory. Selective cutting resulted in increased soil water availability for *Pinus resinosa* (Sucoff and Hong 1974) and *Pinus contorta* (Donner and Running 1986). However, Waring and Pitman (1985) found large increases in growth efficiency in sub-alpine lodgepole pine (*Pinus contorta*) stands after thinning despite no changes in soil moisture availability. In some circumstances, increases in nitrogen or light availability with thinning are responsible for the growth response (Warren et al. 2001). In other situations, no thinning response has been observed at all (Leavitt and Long 1986).

If thinning results in increased soil water availability then crown-scale stomatal conductance (*g*) and photosynthetic carbon assimilation (*A*) should also increase. Such an increase in *A* may be a proximal mechanism of increased growth after thinning. If this is the mechanism of growth response, it should be recorded in the stable carbon isotope ratio ($\delta^{13}C$) record of tree rings. Photosynthesis by terrestrial C_3 plants discriminates against CO_2 with ^{13}C relative to CO_2 with ^{12}C because ^{13}C has a lower diffusivity through the stomatal pore and lower reactivity with the photosynthetic enzyme Rubisco. This discrimination results in a decrease in $\delta^{13}C$ of plant matter of approximately 20‰ below that of atmospheric CO_2. Discrimination can be expressed mathematically as (Farquhar et al. 1989):

$$\Delta = a + (b - a) \bullet \frac{C_i}{C_a} \qquad (1)$$

where *a* is the fractionation associated with diffusion in air (4.4‰) and *b* is the net fractionation associated with carboxylation by Rubisco (27-29‰), and C_i and C_a are the intercellular and atmospheric partial pressures of CO_2, respectively. Discrimination is physiologically linked to gas-exchange because *g* and *A* regulate C_i:

$$C_i = C_a - \frac{A}{g} \tag{2}$$

A/g is also referred to as the intrinsic water use efficiency. Changes in A/g cause a proportional change in Δ. This will result in a change in $\delta^{13}C$ because $\delta^{13}C$ is related to Δ as (Farquhar et al. 1982):

$$\Delta = \frac{\delta^{13}C_p - \delta^{13}C_a}{1 + \delta^{13}C_p / 1000} \tag{3}$$

where $\delta^{13}C_a$ and $\delta^{13}C_p$ are the isotope compositions of the source air used for photosynthesis and from tree ring cellulose, respectively. Because cellulose is immobile within tree rings once it has been deposited within the cell walls (Tans et al. 1978), it can be analyzed to provide an isotopic record at the annual timestep. Therefore, tree ring cellulose can be used as a record of crown-scale A/g.

A/g is negatively correlated with water availability (Dupouey et al. 1993, Livingston and Spittlehouse 1996, Ehleringer 1993) because g increases more in response to increasing water availability than the concomitant increase in A (Meinzer et al. 1993). However, in thinned forests this response may be mediated or even overwhelmed by a simultaneous increase in nutrient or light availability associated with disturbance (Warren et al. 2001). Alternatively, there may be no response of A/g to thinning (Leavitt and Long 1986), potentially due to a balancing effect of increased light or nitrogen (which should increase A/g) against the effect of increased soil moisture (which should decrease A/g).

The primary objectives of our study were to 1) determine if growth responds to thinning in old ponderosa pines, 2) determine if canopy gas exchange responds to thinning, and 3) if responses are observed, to determine if such responses could be maintained if *LAI* remained below pre-thinning levels. We also investigated the relationship between canopy gas exchange and sapwood anatomy (Ponton et al. 2001) before and after stand density reductions. We used three independent stands of ≥ 250 year old ponderosa pine trees, each of which had a section thinned with ≥ 61% of the basal area removed in the last two decades. Because this is a relatively dry region with low leaf area indices (Law et al. 2001), we expected that reductions in stand density would result in increased soil water availability and therefore increased Δ.

4.3 METHODS

Experimental design Three separate stands of ≥ 250 years-old ponderosa pine (stands A, B and C) were selected to test the hypothesis that stand density reductions affect Δ. Each stand had a pair of thinned and control plots located within a few hundred meters of each other. Plots were located randomly but with a minimum of 100 meters between each plot and the edge of the treatment (the forest edge). Plots were made large enough to ensure that a minimum of five overstory trees were present within the plot. This resulted in plot sizes of 706 m^2 to 2153 m^2. Five trees per plot were selected for assessment of Δ and other sapwood characteristics. Detailed measurements of leaf gas exchange and further detail measurements of the tree ring record (described below) were done at Stand A only.

Study stands Ponderosa pine stands were selected near Black Butte, OR (between 44°25' N and 121°40' W, and 44°30' N and 121°37' W). The three stands are located along an 18 km transect that runs from north to south. They are located at elevations between 960 m and 1035 m and are on deep, sandy loam soils derived from volcanic ash. Ponderosa pine is the dominant overstory tree species, comprising over 80% of the basal area at each stand. The area receives approximately 360 mm annual precipitation. Nearly all of the annual precipitation falls during the winter, with the summers characterized as warm and dry. The average leaf area index for forests in this area is 1.5 m^2 m^{-2} ground area (Law et al. 2001). This region has experienced fire exclusion since

Table 4.1. Stand characteristics.

Stand	Plot	*B.A.* cut (m^2 ha^{-1})	*B.A.* left (m^2 ha^{-1})	% *B.A.* removed	Sample trees *DBH* (mean, range, cm)	Plot mean *DBH* (cm)	LAI (m^2 m^{-2})	Leaf area per tree (m^2)
A	Control	0	31.47	0	58.4 (45.5 - 84.1)	58.4	1.56	200.5
	Thinned	18.49	11.45	61	74.8 (53.7 – 87.6)	74.8	0.49	191.2
B	Control	0	60.00	0	79.2 (70.2 - 87.4)	43.6	3.17	210.0
	Thinned	39.14	8.45	82	72.0 (65.0 - 78.1)	72.0	0.37	74.95
C	Control	0	43.19	0	63.0 (56.8 to 69.4)	46.6	2.06	137.3
	Thinned	34.85	12.23	74	69.4 (61.8 - 85.2)	69.4	0.53	165.4

Basal area is presented per unit ground area. The amount of basal area removed from each plot (*B.A.* cut) was assessed by measuring the mean diameter of every stump within the plot and then correcting stump basal area to basal area at 1.3m using stand-specific relationships of basal area at stump height to basal area at 1.3 m height.

Mean *DBH* is from all trees within plot ≥ six cm *DBH.* Differs from sample trees mean *DBH* only when there were more trees within the plot than were sampled. *DBH* of trees ≤ six cm *DBH* provided in text when applicable.

Leaf area per tree is for the five-cored trees per plot. Leaf area and leaf area index are calculated using the allometric equations to predict sapwood area from *DBH* from Grier and Waring (1974) and leaf area from sapwood area from McDowell et al. 2002, and assumes no change in the allometric relationships associated with thinning.

approximately 1910 and as a result, most forests are more heavily stocked with regenerating trees than was typical of pre-settlement conditions (Weaver 1943, Agee 1993).

Treatments Details on tree sizes and the treatment sizes are given in Table 4.1. In each stand, the thinning treatments selectively left the largest trees with a wide spacing. Stand A was selectively harvested in 1987. Regenerating ponderosa pines were present at low density in the thinned plot. In the un-harvested control stand, small ponderosa pines with $DBH \leq 6$ cm comprised 12% of the basal area and 91% of the number of stems. Stand B was selectively harvested in 1993. The understory was sparsely covered by regenerating ponderosa pine. The un-harvested control forest was heavily stocked with large ponderosa pines and grand fir trees (*Abies grandis*), but very few saplings or seedlings. Stand C was selectively harvested in 1985. Regenerating ponderosa pines were present at low density. Ponderosa pines comprised nearly all of the trees in the un-harvested control forest. Also presented in Table 4.1 are estimates of whole-tree leaf area from the cored trees on each plot and plot level leaf area index (LAI). Leaf area and leaf area index were calculated using the allometric equations to predict sapwood area from *DBH* from Grier and Waring (1974) and leaf area from sapwood area from McDowell et al. (2002). Because these allometric equations are from trees in stands that were not thinned, application of them to our study assumes no change in the allometric relationships associated with thinning and therefore, they should be used for reference only.

Growth measurements One five-mm diameter core was removed from each of the five sampled trees at 1.3 m height to measure ring widths and basal area increment (*BAI*). Cores were dated and ring widths were measured to the nearest 0.001 mm under 40X magnification (Olympus SZ-4045, Japan) with a linear-encoded measurement stage (Velmex, Bloomfield, NY). The instrument was calibrated daily. Ring widths were converted to *BAI* over the last 20 years using tree-specific *DBH* (inside bark).

Carbon isotope composition We focus on Δ as a measure of canopy gas exchange rather than $\delta^{13}C$ because the $\delta^{13}C$ of atmospheric CO_2 has become progressively depleted during the last century due to fossil fuel burning (Keeling 1989) thus complicating the isotope record. Because Δ accounts for changing $\delta^{13}C_a$ (equation 3), we are able to examine directly how disturbance affected tree physiology without confounding of $\delta^{13}C_a$. One 12-mm diameter core was removed from each of the five trees on all six plots for carbon isotope analyses. After drying, annual rings (including both late and earlywood) were carefully dated for the period of 1980 to 1999 and separated with a sharp blade. Because our focus was on the annual response of Δ to reductions in stand density, we did not attempt to separate earlywood from latewood (i.e. Livingston and Spittlehouse 1996). Samples were ground using a Wiley mill to pass a 0.2 mm mesh. Cellulose was extracted from the ground tree rings using the method described by Leavitt and Danzer (1993). Cellulose $\delta^{13}C$ was analyzed using an isotope ratio mass spectrometer (Delta Plus, Finnigan, Bremen, Germany) at the Integrated Stable Isotope Research Facility (ISIRF) at Environmental Protection Agency in Corvallis, OR. Precision for $\delta^{13}C$ was assessed using a NIST certified standard, with an average standard deviation of 0.08‰ (n = 36). We calculated Δ with equation (3) using tree-ring $\delta^{13}C$ and $\delta^{13}C_a$ from Moana Loa, Hawaii (Keeling et al. 1989)

Photosynthetic capacity Photosynthetic capacity can influence Δ by increasing or decreasing A, and therefore C_i/C_a. We used two approaches to determine whether thinning affected photosynthetic capacity. First, we used foliar nitrogen concentration [N] as an indicator of photosynthetic capacity (Field and Mooney 1986, Livingston et al. 1998). Second, photosynthetic capacity was assessed using response curves of photosynthesis to internal [CO_2] (A/C_i curves). Foliar [N] was measured on foliage from three trees in each of the control and thinned plots in each stand (total of 18 samples). Year 2000 foliage was collected with a shotgun in the autumn of 2000 from relatively exposed, south facing branches located in the middle or upper third of the crown. Samples were dried at 65 °C for 48 hours, ground with a mortar and pestle, and analyzed with a elemental analyzer (Carlo Erba 1108EA, Milan, Italy). Precision was better than 0.1% around a NIST standard. A/C_i curves were measured at Stand A on five trees in the control and five trees in the thinned stand on overcast days in June 2000. Branches were severed with a shotgun and the cut ends were submerged immediately into water and re-cut. A/C_i curves were measured with a Li-Cor 6400 portable photosynthesis system (Li-Cor, Lincoln, NE) equipped with a blue-red artificial light source. Cuvette irradiance was 1400 μmol photons m^{-2} s^{-1}; photosynthesis of ponderosa pine A saturates at irradiance levels near 800 μmol photons m^{-2} s^{-1} (Hadley 1969). A/C_i curves were generated by changing the cuvette CO_2 in the following order: 40, 30, 20, 10, 40, 60, 80, 100, 120, 160, 200 Pa. After each exposure to a new CO_2 level, foliar A was allowed to reach steady state (cuvette CO_2 coefficient of variation < 2%) prior to measurement. Six measurements were made per sample per CO_2-level over a 60 second period after steady-state had been reached. The maximum catalytic activity of Rubisco (V_{cmax}) and the maximum electron transport rate (J_{max}) were calculated from the A/C_i curves using non-linear, least-squares regression to fit the values of these parameters to the equations of the Farquhar et al. (1980) photosynthesis model (Harley et al. 1992). Parameters were temperature-corrected to 25 °C using the equations of Leuning (1997), and the activation energies measured for *Pinus taeda* (Ellsworth 2000).

Water potential We estimated soil water availability in the root zone using pre-dawn measurements of leaf water potential ($\Psi_{\text{pre-dawn}}$) of five overstory ponderosa pines per plot on all six plots. Foliage amples were removed from the lower branches of each crown using a shotgun and measured within three minutes with a Scholander-type pressure chamber (PMS, Corvallis, OR). These leaf water potential measurements were corrected for gravitational potential (0.01 MPa per meter). We assumed that nighttime transpiration was negligible. Measurements were made on June 10, July 9, and August 13, 2000.

Sapwood anatomy At stand A, two 12-mm diameter cores were removed per tree at 1.4 m height in winter 2001 for analysis of tracheid lumen dimensions, earlywood/latewood ratios, and wood density. One core was used for tracheid anatomy measurements to be used for calculation of potential hydraulic conductivity; the other core was used for the earlywood/latewood ratio and wood density measurements. For tracheid lumen dimensions, cross-sectional samples including all annual rings from year 2000 back through 1980 were removed with a sliding microtome and fixed on glass slides with a 70% ethyl alcohol solution. Tracheid lumen areas were determined using a digital imaging and analysis system (Roper Scientific Coolsnap camera v 1.7.3 with a Nikon Eclipse 400 compound microscope, with Scion Image 1998 public domain-image processing and analysis program). Lumen areas were measured across the entire earlywood section of each ring from 1980 through 1999. Tracheid densities were determined as a proportion of total earlywood sapwood area.

Tracheid density and lumen areas within the sapwood were used to estimate potential saturated hydraulic conductivity (k_{sp}, $\bullet 10^{-12}$ m^2) according to Poiseuille's law:

$$k_{sp} = \frac{\left[\frac{\pi}{8\eta} \bullet \left(\sum r^4\right)\right]}{A_s} \tag{4}$$

where r is the radius of a circle having the same area as the corresponding tracheid, and A_{s} is sapwood area. This is considered an estimate of maximum potential conductivity because it assumes no differences in tracheid length or friction due to bordered pits, tracheid tapering or xylem cavitation.

Annual ring density and earlywood/latewood ratios were measured using an X-ray densitometer (Enraf-Nonius FR-590, 545). Prior to density measurement, one core per tree was oven dried at 40 °C for three days. Density was measured every millimeter along the length of each core, and then converted to whole-ring densities with DendroScan software (UBC Press, Vancouver BC).

Modeling A from Δ and A/C_{i} functions Assimilation-weighted A was estimated from tree-ring calculations of Δ and A/C_{i} relationships. Equation (2) can be solved for C_{i}

using cellulose-derived Δ. Using the equations of Farquhar (1980), A in the carboxylation-limited region of the A/C_i curve is:

$$A = V_{c\max} \bullet \left(\frac{C_i}{C_i + K_c \bullet (1 + O_x / K_o)} \right) \bullet \left(1 - \frac{0.5 \bullet O_x}{\tau \bullet C_i} \right) - R_d \qquad (5),$$

where V_cmax is derived from the measured A/C_i curves and C_i is obtained from tree ring δ^{13}C:

$$C_i = C_a \bullet \left(\frac{\delta^{13}C - \delta^{13}C_a - a}{b - a} \right) \qquad (6)$$

All parameters used in these equations are described in Table 4.2. We assumed that electron transport-limited A occurs only over C_i of 25 Pa (Harley et al. 1992), and examination of our A/C_i curves verified that, at the low C_i levels recorded in the tree rings (< 20 Pa), electron transport was less limiting than carboxylation capacity. Triose phosphate utilization may also limit A, but we found no evidence of such limitation in

Table 4.2 List of symbols, definitions, and sources used in this paper.

Symbol	Definition	Units	Source
A	net photosynthesis	μmol m^{-2} s^{-1}	This study
A_s	Sapwood area	μm^{2}	This study
a	fractionation due to diffusion	‰	(1)
b	enzymatic fractionation	‰	(1)
BAI	basal area index	cm^{2}	This study
C_i	leaf-internal CO_2	μmol mol^{-1}	This study
DBH	diameter at breast height	meters	This study
g	stomatal conductance	mol m^{-2} s^{-1}	This study
g_w	stomatal conductance to water vapor	mol m^{-2} s^{-1}	This study
g_C	stomatal conductance to CO_2	μmol m^{-2} s^{-1}	This study
J_{max}	electron transport limited A	μmol m^{-2} s^{-1}	This study
K_c	Michaelis-Menton constant: CO_2	Pa	(2), (3)
K_o	Michaelis-Menton constant: O_2	kPa	(2), (3)
k_{sp}	Sapwood hydraulic conductivity	$\bullet 10^{-12}$ m^{-2}	This study
[N]	nitrogen concentration	%	This study
O_x	Oxygen concentration	kPa	(2)
P_i	leaf-internal CO_2	Pa	This study
r	lumen radii	μm	This study
R_d	respiration	μmol m^{-2} s^{-1}	This study
T_{air}	air temperature	C°	This study
T_{max}	air temperature (maximum)	C°	(4)
V_{cmax}	Carboxylation limited A	μmol m^{-2} s^{-1}	This study
WUE_i	Intrinsic water-use efficiency (A/g)	μmol mol^{-1}	This study
Δ	Carbon isotope discrimination	‰	This study
$\delta^{13}C$	Carbon isotope ratio	‰	This study
$\delta^{13}C_a$	$\delta^{13}C$ of atmospheric CO_2	‰	(5)^{1}
τ	Specificity of rubisco for O_2/CO_2	μmol m^{-2} s^{-1}	(2)
Ψ_{soil}	Soil water potential	MPa	This study

Sources are (1): Farquhar et al. (1989), (2) Harley et al. (1992), (3) Ellsworth (2000), (4) Oregon Climate Service, WEBSTAND. (5) Keeling et al. (1989). $^{1}\delta^{13}C_a$ data obtained from the Institute of Arctic and Alpine Research (INSTAAR) at the University of Colorado (CU), and the National Oceanic and Atmospheric Administration (NOAA), Climate Monitoring and Diagnostics Laboratory (CMDL), Carbon Cycle Group the analysis of our A/C_i curves, therefore we did not incorporate this limitation into our calculations.

We assumed that V_{cmax} was invariant among thinning treatments or years because we found no difference in V_{cmax} or leaf [N] between treatments (see results) and because our values were very similar to estimates from A/C_i curves measured on old ponderosa pines in a nearby region in the early 1990's (B.J. Bond, *unpublished data*). However, modeling A and g over varying temperature conditions requires correction ofV_{cmax} to the average air temperature during photosynthesis. We corrected V_{cmax} for each year from 1980 to 1999 using a relationship between air temperature measured at mid-canopy height at an Ameriflux stand near our forests (Law et al. 2001) and maximum temperature measured at the Sisters Ranger Station (15 km distant) from day of year 110 to 243, 1997. This is the period in which stem growth occurs in this region (Cleary and Waring 1969, R.H. Waring, *personal communication*). Daily average air temperature in the forest from 9 am to 3 pm (T_{air}, the period of maximum photosynthesis, Law et al. 2000) was related to maximum air temperature at the Ranger Station (T_{max}) as:

$$T_{air}\ (\mathrm{C}°) = 0.44 * T_{max} - 13.93,\ \mathrm{R}^2 = 0.66 \qquad (7)$$

Relationships between T_{air} and Ranger Station average temperature or minimum temperature were not as strong (R^2 values of 0.51 and 0.19, respectively). We then modeled T_{air} from 1980 to 1999 using daily T_{max} records from the Ranger Station. We assumed that needle temperature equaled air temperature.

We also modeled g for the sake of completeness. Stomatal conductance for each year was modeled by combining and re-arranging equations (1), (2) and (5):

$$g_w = \left[\frac{A}{C_a - \left(C_a \bullet \left(\frac{\Delta - a}{b - a} \right) \right)} \right] \bullet 1.6 \qquad (8)$$

Our estimate of g is derived from CO_2 variables expressed as mol fractions, therefore the factor 1.6 is necessary to convert g for CO_2 (g_c) to g for water vapor (g_w). In this model, g_w is not independent of A and therefore inferences on the interaction between A and g_w are impossible. However, the model allows us to examine retrospectively how A or g_w varied after thinning.

Statistics The response of Δ to stand density reduction at Stand A was tested using a blocked analysis of variance with repeated measures, where the three stands make up the blocks and average pre-and post-thinning BAI, Δ or tracheid anatomy of annual tree rings from 1980 to 1999 is the repeated measure. Ψ_{soil} was analyzed as a blocked, repeated-measures analysis of variance. Foliar [N] was analyzed as a blocked analysis of variance and A/C_i parameters were compared using a paired t-test. Relationships between *BAI*, Δ, g_w, and *A* were examined via non-linear regression, including exponential, power, and polynomial functions. Our statistical criteria for selecting equations included 95% confidence intervals, correlation coefficients, and mean square error. If these criteria were similar, we chose the simplest model. Autocorrelations were not examined explicitly because of our limited time-series (Monserud and Marshall, 2001); however, correlations between lagged parameters including *BAI*, Δ, g_w, and *A* were examined using linear regression.

4.4 RESULTS

Overall response to stand density reduction

Average tree *BAI* exhibited a large increase in response to stand density reductions in each forest (Figure 4.1, Figure 4.2a). The pre-thinning *BAI* did not differ between control and thinned stands for any forest ($p = 0.98, 0.57, 0.99$ for stands A, B and C, respectively, $n=5$ trees per treatment and stand), but increased dramatically after thinning in all three forests ($p < 0.01$ for each stand). At stand A, *BAI* of the trees remaining after thinning increased by 124%, at stand B by 109%, and at stand C by

Legend for Figure 4.1

Figure 4.1. Basal area index (*BAI*, cm^2) of trees from the control stand (open circles) and the thinned stand (filled circles) from Site B (upper panel) and Site C (lower panel) from before and after the thinning. Carbon isotope discrimination (Δ, ‰) for the same trees is shown in the upper portion of each figure, with open triangles representing control trees and filled triangles representing thinned trees. Δ values for Site B are averages of five trees for tree rings from 1990-1992 and 1996-1998. Δ values for Site C are averages of five trees for tree rings from 1978-1980 and 1990-1992. The date of thinning for Site B is 1993, and for Site C is 1985 (indicated by dashed lines). Bars are standard errors, and the sample size equaled five trees per plot.

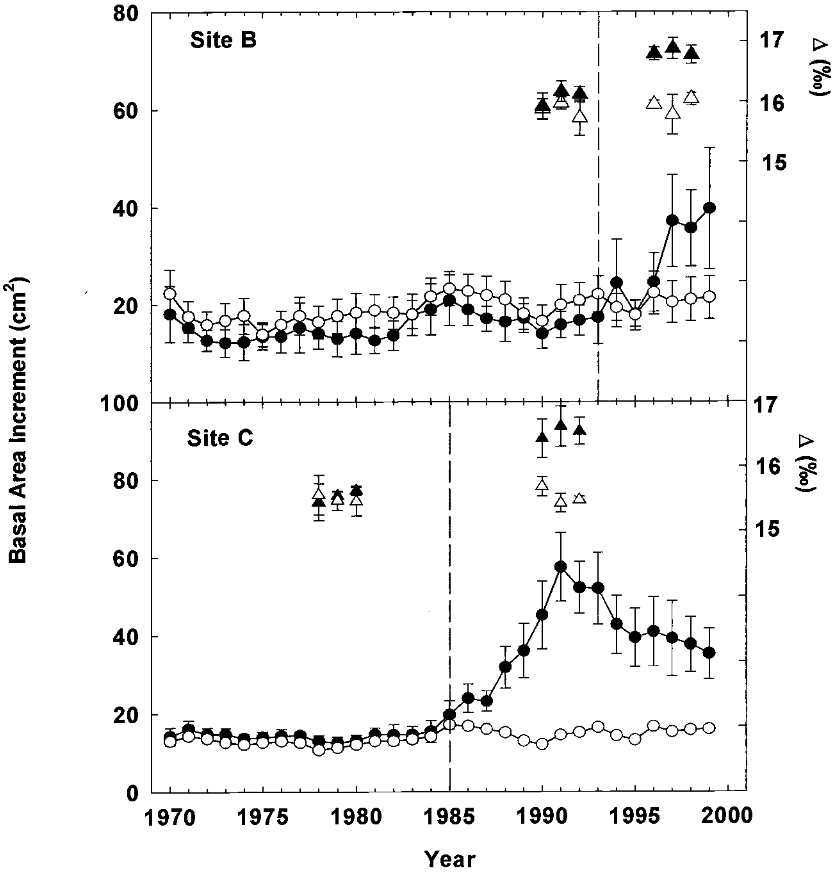

Site B
Site C
Basal Area Increment (cm^2)
Year
Δ (‰)
0
20
40
60
80
100
15
16
17
1970
1975
1980
1985
1990
1995
2000

Figure 4.1

Legend for Figure 4.2

Figure 4.2. A) *BAI* and B) Δ of trees from the paired thinned and control portions of stand A. Trees from the thinned stand are indicated by closed symbols and from the control stand are indicated by open symbols. The date of thinning is indicated by the dashed line. Values are means with standard errors.

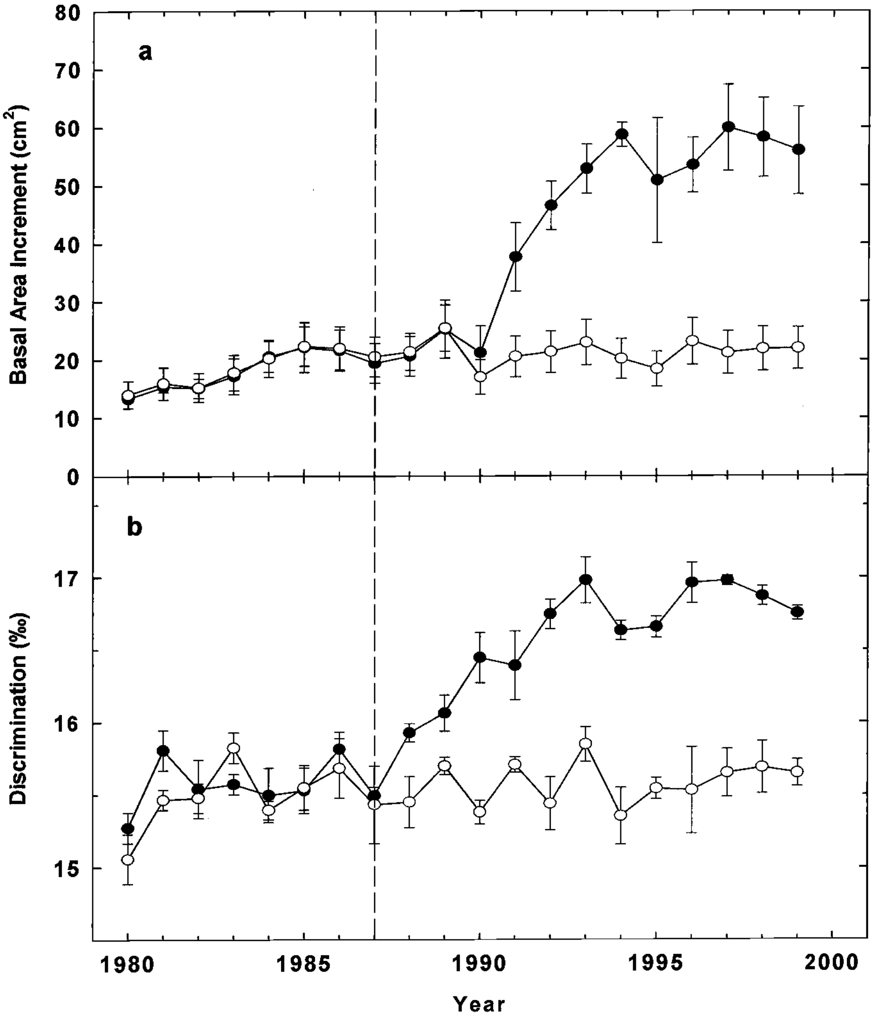

a
Basal Area Increment (cm^2)
0
10
20
30
40
50
60
70
80
b
Discrimination (‰)
15
16
17
1980
1985
1990
1995
2000
Year

Figure 4.2

303%. When analyzed as a blocked analysis of variance with repeated measures, the increase in average tree *BAI* was significant for all three thinned stands ($p < 0.01$), but the effect of stand (block) was not significant ($p = 0.54$).

The growth responses to stand density reductions were associated with significant increases in Δ (Figure 4.1). At stand B, Δ of the thinned trees increased from 16.25 to 16.86 ‰ after thinning ($p < 0.01$), whereas no change occurred in the control trees. At stand C, Δ of the thinned trees increased from 15.46 to 16.43 ‰ after thinning ($p < 0.01$), whereas no change in Δ occurred in the control trees.

At stand A, where we measured average tree *BAI* and Δ for 20 consecutive years, both parameters increased after thinning (Figure 4.2). As mentioned above, *BAI* more than doubled after thinning; however, the growth response did not begin until four years after the thinning occurred, and did not peak until seven years after thinning (Figure 4.2a). The temporal dynamics were different for Δ. A slight response in Δ is apparent one year after the thinning took place, followed by peak Δ six years after the thinning (Figure 4.2b). There was no significant decline in Δ 12 years after the thinning. No apparent change in Δ of control trees was detected during the two decades. The Δ response was a common and significant response of all three forests when analyzed as a blocked analysis of variance ($p < 0.01$), but there was no difference among stands ($p = 0.11$).

Table 4.3. Foliar nitrogen concentration ([N], percent dry mass) from old ponderosa pine trees in three paired thinned and unthinned stands, and the parameters V_{cmax} and J_{max} from A-C_i curves from trees located at the paired thinned and unthinned plots at stand *A*. V_{cmax} and J_{max} are presented in μmol m^{-2} s^{-1}, and are temperature corrected to 25°C (Leuning 1997). Values in parentheses are standard errors (n=3 trees)

Stand	Treatment	[N]	V_{cmax}	J_{max}
A	Control	1.11 (0.04)	42.8 (2.6)	100.7 (6.8)
	Thinned	1.12 (0.10)	42.7 (3.0)	104.6 (9.8)
B	Control	1.11 (0.02)		
	Thinned	1.12 (0.07)		
C	Control	1.13 (0.06)		
	Thinned	1.09 (0.04)		

Photosynthetic capacity and water availability Photosynthetic capacity as assessed using foliar [N] and A/C_i curves was unchanged by thinning (Table 4.3). Foliar [N] values averaged 1.11%, and did not vary with thinning or stand (blocked ANOVA, $p = 0.41$ and $p = 0.26$, respectively). The A/C_i parameters V_{cmax} and J_{max} were also unresponsive to thinning at stand A (paired t-test, $p = 0.97$ and $p = 0.51$, respectively).

$\Psi_{pre\text{-}dawn}$ was significantly less negative at the thinned stands throughout the summer of 2000 (repeated measures blocked ANOVA, $p < 0.01$, Table 4.4). $\Psi_{pre\text{-}dawn}$ became more negative at both control and thinned stands as summer drought progressed, but the relative rankings between treatments did not change at any date or stand. There was a strong relationship between stand- average $\Psi_{pre\text{-}dawn}$ and stand-average Δ after thinning (Figure 4.3).

Sapwood anatomy Sapwood anatomy was unresponsive to stand density reductions (Table 4.5). There was no response of tracheid lumen diameters calculated as the straight mean or the "hydraulic" mean (equivalent to $\Sigma \text{diameter}^4/\Sigma \text{ diameter}^5$, Pockman and Sperry 2000) between the thinned and control trees after thinning ($p = 0.50$ and 0.60, respectively). Potential hydraulic conductivity of sapwood calculated from equation (4) also did not respond to thinning ($p = 0.72$), nor did the ratio of earlywood to latewood ($p = 0.94$). The lumen surface area per unit sapwood area was invariant with stand density reduction ($p = 0.93$). Wood density did not respond to thinning (p =

Table 4.4. Pre-dawn water potential ($\Psi_{pre\text{-}dawn}$, MPa) of foliage collected from old ponderosa pine trees at three thinned and control stands. $\Psi_{pre\text{-}dawn}$ is gravity corrected (0.01 MPa m^{-1}) and therefore represents soil water potential in the vicinity of the roots. The difference between $\Psi_{pre\text{-}dawn}$ of trees in the thinned and control stands is given in italics. Values in parentheses are standard errors (n=5 trees).

Stand	Treatment	June 2000	July 2000	August 2000
A	Control	-0.92 (0.03)	-0.95 (0.04)	-1.03 (0.03)
	Thinned	-0.74 (0.05)	-0.78 (0.02)	-0.87 (0.03)
	Difference	*0.18*	*0.17*	*0.16*
B	Control	-0.71 (0.03)	-0.82 (0.03)	-1.04 (0.06)
	Thinned	-0.66 (0.04)	-0.76 (0.04)	-0.96 (0.02)
	Difference	*0.05*	*0.06*	*0.08*
C	Control	N/A	-0.93 (0.05)	-1.01 (0.05)
	Thinned	N/A	-0.82 (0.03)	-0.91 (0.05)
	Difference		*0.11*	*0.10*

Legend for Figure 4.3

Figure 4.3. Mean Δ vs. mean $\Psi_{\text{pre-dawn}}$ for trees in the thinned and controls stands at sites A, B and C. Δ is calculated as the mean for a given stand for all years post-thinning, and Ψ_{soil} is calculated as the mean of all measurements for a given stand in 2000. Controls stands are indicated by open symbols and thinned stands are indicated by closed symbols. Bars are standard errors. The equation is: $\Delta = 7.38 \bullet \Psi_{\text{soil}} + 22.63$, $R^2 = 0.91$, $p = 0.003$.

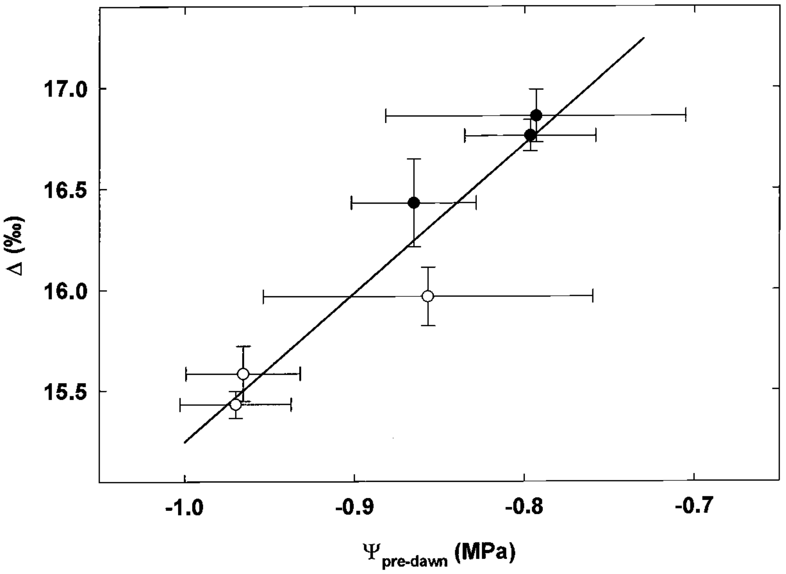


Figure 4.3

Table 4.5. Sapwood anatomical parameters from Stand A. Mean values pre- and post-thin are presented for the control and thinned trees, with standard errors in parentheses. Estimates of significance from repeated measures analysis of variance gave p-values > 0.10 for all parameters.

Parameter	Control Pre-thin	Control Post-thin	Thinned Pre-thin	Thinned Post-thin
Diameter[1] (μm)	18.57 (0.42)	18.86 (0.44)	20.99 (0.69)	19.26 (0.57)
Diameter[2] (μm)	22.82 (0.42)	22.88 (0.50)	25.12 (0.70)	24.11 (0.70)
k_{sp} (10^{-12} m^2)	3.08 (0.23)	3.13 (0.22)	4.6 (0.48)	3.5 (0.34)
EW/*LW*	2.23 (0.67)	2.12 (0.34)	1.68 (0.17)	1.77 (0.12)
$A_{\text{lumen}}/A_{\text{sapwood}}$	0.21 (0.01)	0.20 (0.01)	0.24 (0.01)	0.20 (0.01)
Density (g/cm^3)	0.37 (0.01)	0.38 (0.01)	0.40 (0.01)	0.43 (0.01)

[1] Mean lumen diameter

[2] Hydraulic mean diameter. See text for calculation details.

0.12). Correlations between anatomical parameters and Δ were not examined due to the lack of variation in anatomical parameters.

Modeled A and g_w At stand A, A and g_w for each tree were modeled for the period of 1980 to 1999 using equations (5) and (8), respectively. A/g_w calculated from the model, which equals eq. 5/(eq. 8•1.6) was identical to A/g_w from the traditional equations of Farquhar et al. (1989). A significant response of A/g_w occurred the year after the thinning (Figure 4.4). A/g_w decreased from approximately 112 μmol mol^{-1} to 97 μmol mol^{-1} over six years, and stayed at this low level through 1999, 12 years after thinning. This response was associated with increases in both A and g (Figure 4.5a,b). A peaked five years after thinning and stayed at that peak through the sixth year, whereas g_w did not peak until year six. The decrease in A/g_w after thinning was associated with a 25% increase in g_w relative to the 15% increase in A (Figure 4.5c).

The increase in A after thinning preceded the increase in average tree *BAI* by approximately three years (Figure 4.6). *BAI* did not begin increasing generally until four years after the thinning occurred, and peaked one year after A. It appears that after 1996 (nine years after the harvest at forest A), A and *BAI* oscillated in unison. To quantify the lag between average tree *BAI* and A, we regressed *BAI* against A using A from concurrent years or lagged one to four years behind *BAI,* i.e. *BAI* from year X was regressed against A at year X_{-0}, X_{-1}…X_{-4}. Pearson correlation coefficients for

Legend for Figure 4.4

Figure 4.4. *A*/*g*, where g is conductance to water vapor rather than CO_2, for trees from the control stands (open symbols) and thinned stands (closed symbols) trees at Site A. Bars are standard errors, and the year of thinning is indicated by the dashed line.

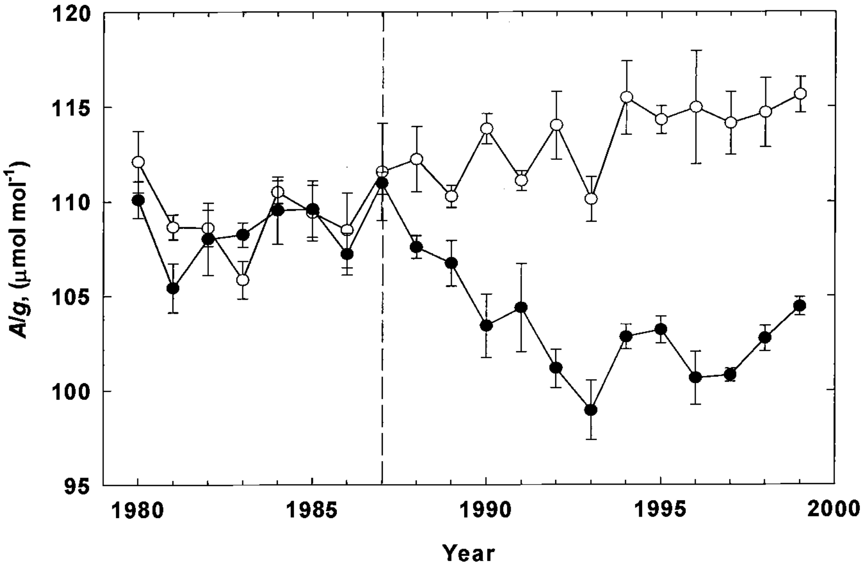

A/g, (μmol mol^{-1})
120
115
110
105
100
95
1980
1985
1990
1995
2000
Year

Figure 4.4

Legend for Figure 4.5

Figure 4.5. A) *A* and B) *g* calculated from equations (5) and (8) for the trees from the control stands (open symbols) and thinned stands (closed symbols). C) The percent change in *A* (open symbols) and *g* (closed symbols) for trees in the thinned plot at Site A. The percent change is calculated as: (pre-thin mean - post thin mean)/pre-thin mean, where the pre-thin mean is the mean of *A* or *g* from 1980-1986. The date of thinning is indicated by the dashed line. Bars are standard errors.

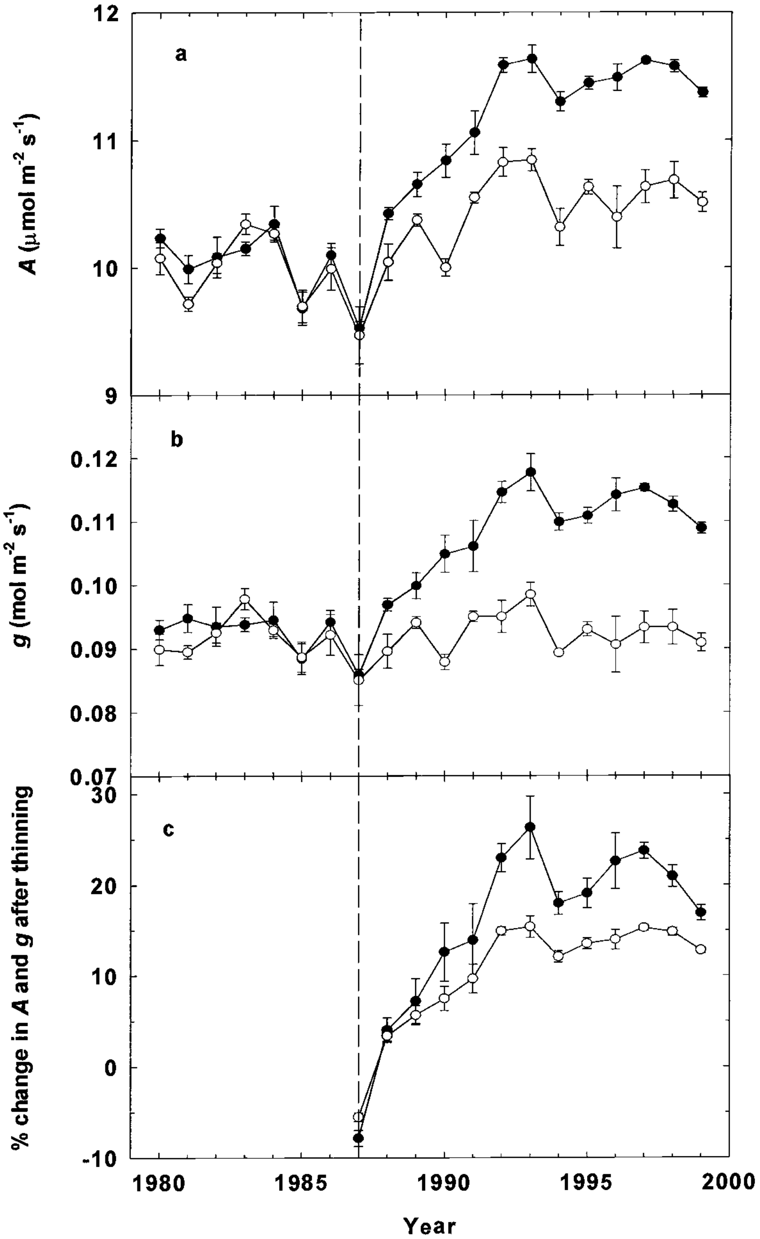

a
b
c
A (μmol m^{-2} s^{-1})
12
11
10
9
g (mol m^{-2} s^{-1})
0.12
0.11
0.10
0.09
0.08
0.07
% change in A and g after thinning
30
20
10
0
-10
1980
1985
1990
1995
2000
Year

Figure 4.5

Legend for Figure 4.6

Figure 4.6. *BAI* (open symbols) and *A* (filled symbols) from the control and thinned trees at Site A. The stand was thinned in 1987. Bars are standard errors.

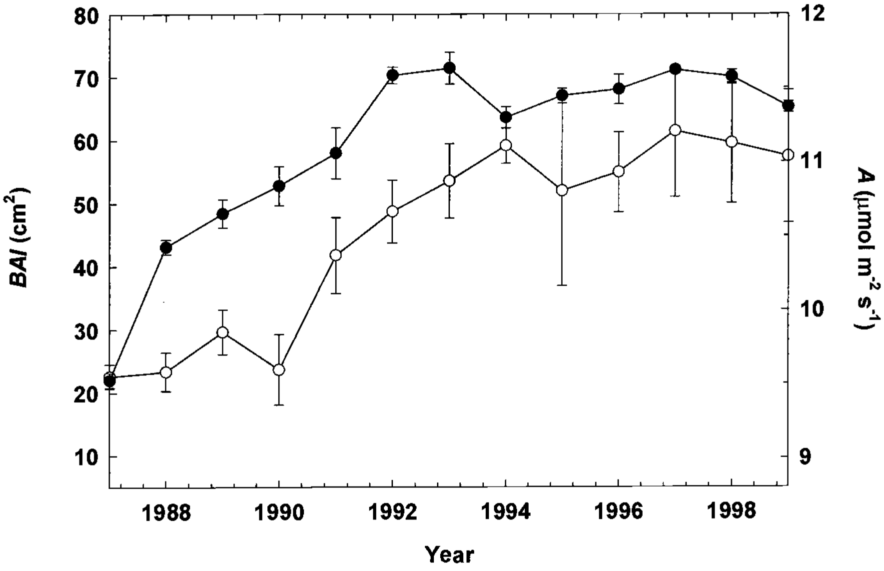

80
70
60
50
40
30
20
10
BAI (cm^2)
12
11
10
9
A (μmol m^{-2} s^{-1})
1988
1990
1992
1994
1996
1998
Year

Figure 4.6

regressions of BAI vs. A were 0.86, 0.92, 0.87, 0.89, and 0.86, with time lags of 0, 1, 2, 3, and 4 years, respectively. This indicated that BAI was best correlated with A in the previous year. However, analysis of the 95% confidence intervals about each correlation indicated that the correlations were not statistically different (Sokal and Rohlf 1987). The lack of significant differences is due in part to variation in the length of the lag period, i.e. a three year lag between A and BAI in the late 1980's, a one year lag between 1993 and 1995, and a zero-year lag between 1996 and 1999 (Figure 4.6).

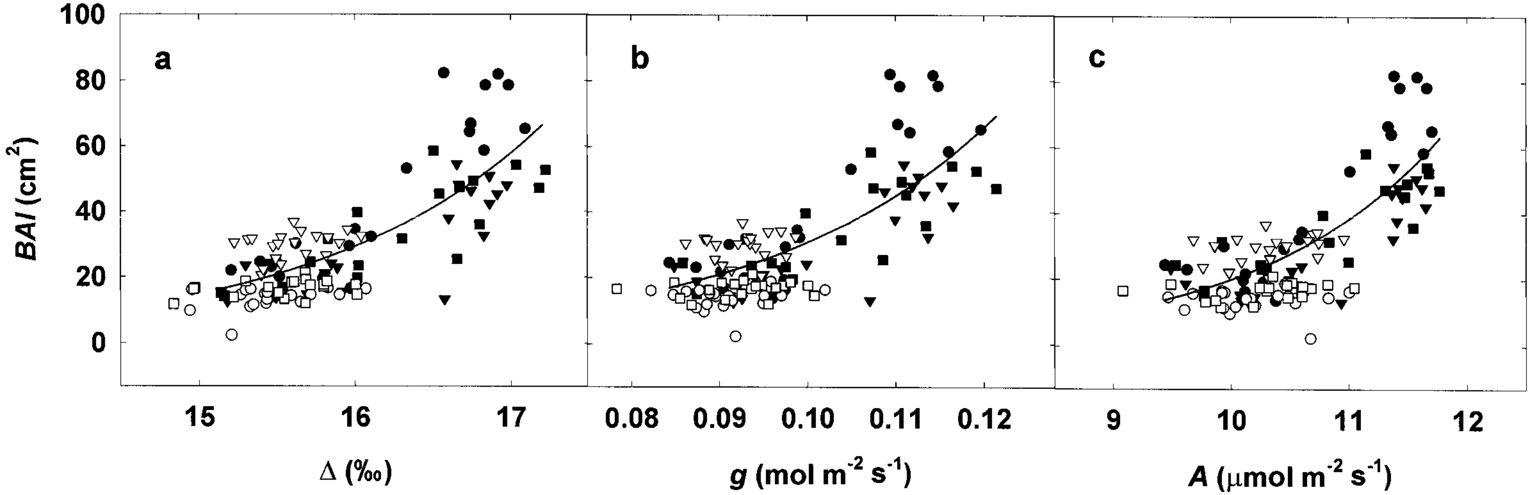
The lag between canopy-scale physiological parameters and growth was also examined through plots of Δ, g_w and A vs. BAI (Figure 4.7). There was no relationship between BAI and Δ, g_w, or A for the control trees (regression p-values > 0.05 for all comparisons, Figure 4.7). However, the thinned trees showed a significant ($\alpha = 0.05$ non-linear increase in BAI as Δ, g, or A increased (Figure 4.7a, b, c).

4.5 DISCUSSION

Our results show that growth and physiology of old ponderosa pine trees are responsive to stand density reductions. BAI and Δ showed large and consistent increases in response to disturbance (Figure 4.1, Figure 4.2). The observation that growth increased after thinning is not unique; in fact, foresters throughout the world rely on thinning-induced growth response for increasing stemwood yield of young to mature (< 100 year-old) forests. Although some foresters and biologists have assumed old trees

Legend for Figure 4.7

Figure 7. A) *BAI* vs. Δ, B) *BAI* vs. *g*, and C) *BAI* vs. *A* for control trees (open symbols) and thinned trees (closed symbols) from Site A. Both exponential and single parameter power regressions gave similar fits with significance at $\alpha = 0.05$, but for simplicity we present the exponential regressions: Figure A) $BAI = 0.000528 \bullet e(0.683 * \Delta)$, r = 0.91, Figure B) $BAI = 0.6838 \bullet e(38.065 * g)$, r = 0.91, and Figure C) $BAI = 0.031 \bullet e(0.647 * A)$, r = 0.92.


a
b
c
100
80
60
40
20
0
BAI (cm^2)
15
16
17
Δ (‰)
0.08
0.09
0.10
0.11
0.12
g (mol m^{-2} s^{-1})
9
10
11
12
A (μmol m^{-2} s^{-1})

are unable to respond to increases in resource availability, our data suggests that old trees do have the potential to increase growth dramatically after stand density reductions. Similar growth responses have been observed in 120-year-old lodgepole pine trees (Waring and Pitman 1985) and 160- to 650-year-old ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) trees (Latham and Tappeiner 2002). Likewise, dendrochronologists have long recognized that the growth of old trees is responsive to change in their environment (Fritz 1976). Most dendrochronology studies assume that ring widths of old trees respond to changes in resource availability associated with climatic variation, thereby allowing them to conduct retrospective analyses of climate change.

The observation that Δ of old trees responds to reductions in stand density is more unique. Leavitt and Long (1986) found no response of Δ or growth to thinning in old ponderosa pines. Few other studies have examined the response of crown gas exchange in old trees to thinning. For young *Pinus radiata* trees, Walcroft et al. (1996) and Warren et al. (2001) observed decreased Δ with reduced stand density -- the opposite of our observation. Both of these studies concluded that increased light and nitrogen availability in low-density stands caused a greater increase in A than g, resulting in reduced Δ. However, stands in those studies had much higher leaf area indices than those of our study, up to 4.7 m^2 leaf area per m^2 ground area in the case of Warren et al. (2001). Furthermore, in our study the trees remaining after thinning were canopy dominants prior to thinning, so, reductions in stand density caused only minor changes in light interception per tree. Therefore, reductions in leaf area were likely to have much larger effects on light interception per unit leaf area in their studies than in ours.

It appears that changes in water availability were the dominant control over the growth and gas exchange response in our study. Soil moisture increased after thinning for up to 15 years (Table 4.3), while photosynthetic capacity per unit leaf area remained unchanged (Table 4.4). The strong correlation between Δ and soil moisture ($R^2 = 0.91$, Figure 4.3) suggests that less than 10% of the variation in Δ is attributable to variables other than water availability.

Our application of the biochemistry model of Farquhar et al. (1980) to tree-ring $\delta^{13}C$ records provided estimates of A and g_w similar to those measured on 250-year-old trees at a stand approximately 3 km from Stand B (Hubbard et al. 1999). The model that we used is highly constrained by the $\delta^{13}C$ time-series along with independent measurements of photosynthesis and temperature. The model provided logical behavior of A and g_w, in response to increased water availability; that is, g_w responded more than A (Figure 4.5c), which both theory and leaf-level measurements have shown (Cowan 1985, Meinzer et al. 1993, Buckley et al. 1999). This application differs from other studies (i.e. Walcroft et al. 1997, Berninger et al. 2000), which utilized the Farquhar model as an independent method for interpreting the $\delta^{13}C$ time-series. These differences include: 1) our objective, which was to retrospectively examine the effects of A on Δ and stem growth, and 2) our approach, which was to combine together independent data to glean new information, rather than compare model output to the $\delta^{13}C$ data. An important point about our model is that the estimate of g_w is highly dependent on A, so they must be interpreted as dependent variables. This prevents us from making inferences about the separate roles of A and g_w on Δ. However, from a biological perspective, A and g_w truly are not physiologically independent (Wong et al. 1979, Meinzer et al. 1993). The estimates of A and g_w are independent of *BAI*, however, and thus can be used to examine relationships between carbon uptake and growth.

The lag between the date of thinning and the onset of changes in canopy gas exchange (g_w and A) and *BAI* (one- and four-years, respectively, Figure 4.6) resulted in non-linear relationships between *BAI* and A (Figure 4.7b) and *BAI* and g_w (Figure 4.7c). The one-year lag between canopy gas-exchange and the date of thinning in Figure 4.6 suggests that moisture availability increased one year after thinning and allowed greater canopy-scale g_w and therefore greater canopy-level A. However, the four-year delay in the onset of growth is puzzling, particularly in light of the immediate photosynthetic response. This is not an anomaly associated with Stand A, as Stand B also took four years to respond after thinning, and Stand C showed a small response the first year followed by a large response three years after thinning (Figure 4.1). There are several potential explanations for the time lag related including shifts in carbon allocation and changes in hydraulic architecture. In these regards, we speculated that with increased soil moisture availability, the thinned trees would produce sapwood rings with larger tracheid diameters, more tracheid area per unit sapwood area, and a greater ratio of earlywood to latewood, all of which should lead to greater k_{sp}. However, this hypothesis was rejected: none of the sapwood specific parameters changed after thinning (Table 4.5). Ponton et al. (2001) found a strong correlation between earlywood vessel surface area and Δ, however, they were studying ring-porous *Quercus* species that typically rely on the current year xylem for the majority of water transport. Ponderosa pine is the opposite: it has relatively deep sapwood, most of which is conductive to water transport (F.C. Meinzer *personal communication*), therefore the advantage gained by growing large tracheids is small. Furthermore, cavitation induced by freeze-thaw cycles is likely a determinant of tracheid diameter for temperate conifers (Sperry and Sullivan 1992), and the occurrence of freeze-thaw cycles is not likely to be altered by thinning.

We speculate that the lag between *A* and *BAI* (Figure 4.6) is associated with increased root growth. Conservation of mass requires that the “extra” carbon acquired during the three years between the increase in *A* and the increase in *BAI* must have been allocated somewhere. Leaf area typically increases dramatically after thinning; however, this response is usually associated with a concomitant increase in sapwood area (Brix and Mitchell 1983, Whitehead et al. 1984). While sapwood area and presumably leaf area increased dramatically after four years, they did not respond during the first three years. The potential carbon sinks remaining are reproductive tissues, respiration, insect and pathogen defense, and belowground. We have no information on reproduction or respiration from these stands, but we have no compelling reason to believe that carbon allocation to these sinks would change in response to thinning (until growth increased, at which time respiration would also increase). Carbon allocation to defense typically takes three years to respond to thinning (T. Schowalter, pers. comm.) similar to the lag in stemwood growth. However, Waring and Pitman (1985) found a large increase in bark beetle (*latin name*) resistance of old trees within one year after thinning. It remains unclear if carbon allocation to defense could explain the lag in growth. Carbon allocation to roots is typically thought to decrease with increasing water availability (Ryan et al. 1996, Waring and Running 1998, Ewers et al. 2000). However, we suspect that during the first few years after thinning, carbon allocation to roots actually increased for the thinned trees. Urban et al. (1994) found that trees along forest edges increased the growth of structural roots in the immediate years following harvest, but no increased growth was observed in the trunk (at breast height) until three to nine years later. This may aid in structural resistance to the increased wind load associated with forest clearing (Urban et al. 1994). From an adaptive standpoint, increasing root biomass during times of abundant moisture increases the soil volume that may be explored later during periods of scarce water supply. Furthermore, this would allow greater foraging for nutrients, thereby allowing an increase in leaf area without a dilution of foliar [N] (Table 4.3). Increased root growth in the immediate years after thinning would have resulted in increased whole-tree conductance (Sperry et al. 1998, Magnani et al. 2000). This may have caused a feed-forward response in which increased whole tree conductance leads to increased g_w and A, which feeds back into increased root growth. This is consistent with the rise in A in years 1989 and 1990, when sapwood growth had not yet responded (Figure 4.6). This cycle may still be continuing 15 years after thinning. The increased amount of sapwood from larger rings will also lead to increase whole-tree conductance; however, if leaf area increased concomitantly then whole-tree conductance should eventually plateau at a new level. Judging from Figure 4.6, this new level occurs between six and eight years after thinning. This theory deserves attention in future studies of physiological response to site disturbance.

Correlations and auto-correlations between ring width or $\delta^{13}C$ in year X with climate, ring widths, or $\delta^{13}C$ in year X_{+1} have been observed in many tree ring studies (Leavitt and Long 1988, Brooks et al. 1998, Monserud and Marshall 2001). These correlations are typically attributed to storage of photosynthate over winter or from photosynthate production by older foliage (Monserud and Marshall 2001). Alternatively, these correlations may also be due to structural changes in year X that carry over to effect physiological behavior in year X_{+1}. Such "carry-over effects" have been demonstrated in *Pseudotsuga menziesii* var. *glauca* forests (McDowell et al. 2001) and Pinus *taeda* forests (Ewers et al. 1999), in which fertilization or irrigation in early years leads to changes in coarse root biomass and water transport capacity in later years when treatment conditions have been removed. In our study, if the architectural components regulating whole-tree conductance are affected favorably by increased soil moisture in year X, such as through stand density reductions or increased precipitation, then canopy-scale g_w may be higher in year X_{+1}. This would lead to a correlation between the wet climate of year X and the $\delta^{13}C$ of year X_{+1}. Such a mechanism is supported by our observations of a feed-forward interaction between g_w, *A* and *BAI.*

There are important implications of these results. First, the observation that soil water availability, canopy gas exchange, and subsequent growth remain elevated as long as stand level *LAI* remains reduced (Table 4.1, and Oren et al. 1987) means that forest managers can effectively manipulate old-growth stands on an infrequent basis. The advantages to old-growth ecosystems are that susceptibility to fires, insects, and dought can be mitigated, and tree-level productivity can be enhanced with minimal mechanical damage associated with the harvest. Second, the strong growth and Δ response to stand density reductions re-affirms the caution that dendrochronologists have used in selecting trees that have not experienced substantial disturbance (Fritz 1976, Cook and Kairiukstis 1990, Fritz 1991). Stand density reductions cause patterns in tree-rings that appear similar to periods of wetter than normal climate, i.e. both cause increased Δ and growth. Therefore, site disturbances such as windthrow, fire, floods, insect induced mortality, and in recent centuries, harvest, may be misinterpreted in the tree-ring chronology as representative of cool, wet periods. Given this source of variation in the isotopic record, future research in paleo-gas exchange should consider methodologies to avoid mis-interpretation, including utilizing individual trees that are not subject to changes in stand density, examination of tree rings for abrasions or fire scars, and careful cross comparison to other chronologies when available (Fritts 1976). Also, the addition of $\delta^{18}O$ analysis of stem cellulose may allow us to separate the effects of disturbance vs. changes in the moisture regime, as $\delta^{18}O$ of cellulose is partially dependent on humidity (Roden and Ehleringer, 1999). Lastly, the variable lag between Δ and growth suggests that shifts in carbon allocation co-occur with changes in gas exchange after increases in soil water availability. Future work should quantify the interaction between resource availability, carbon assimilation, and carbon allocation.

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CHAPTER 5 SUMMARY

5.1 REVIEW OF RESULTS FROM THIS DISSERTATION

This dissertation research was conducted in hopes of increasing our society's knowledge of the constraints and compensations on growth of trees that are near their maximum heights. The foci of the three chapters were: (1) Does the ratio of leaf area to sapwood area decline as trees grow taller? (2) is there evidence for hydraulic limitation or hydraulic compensation in large, old Douglas-fir? and (3) can large, old ponderosa pine trees increase growth after stand density reductions?

In chapter two I observed a negative relationship between tree height and leaf area:sapwood area ratio (A_l:A_s) for 12 of 14 whole-tree studies found in the literature. This significant trend suggests that reducing A_l:A_s with increased tree height may indeed act as a compensation for potential reductions in hydraulic conductance. The change in A_l:A_s per meter of height (ΔA_l:$A_s/\Delta h$) provides a measure of how much a tree must compensate structurally for every meter of growth. ΔA_l:$A_s/\Delta h$ was not related to mean annual precipitation, suggesting that water availability does not influence the degree of compensation. However, maximum potential height was strongly correlated with ΔA_l:$A_s/\Delta h$, suggesting that trees able to maintain high A_l:A_s as they grow are able to attain greater maximum heights.

The data set was small (14 studies), due to the limited availability of whole-tree studies that did not confound other factors with tree height (i.e. water availability) and because reviewers required that we omit branch-level data. This caused there to be only three broad leaf studies (vessel-type xylem), making leaf-type or xylem anatomy-type comparisons impossible. However addition of two independent branch-level studies from Panama (Phillips et al. 2001, F.C. Meinzer *unpublished data*) shows consistency in the pattern; both of these broad leaf studies showed large declines in A_l:A_s with increasing tree height.

In chapter three I observed evidence of both hydraulic limitation and compensation in Douglas-fir trees. Carbon isotope discrimination declined linearly with increased height, indicative of reduced stomatal conductance during the period when carbon used for new foliage is assimilated. Hydraulic conductance declined non-linearly with height, as predicted by a model based on Darcy's Law (section 1.6, equation 1). Growth efficiency (stemwood growth per unit leaf area) also declined non-linearly with height. However, cuvette-based estimates of stomatal conductance and photosynthesis did not show strong size-related variation. I place more emphasis and belief on the carbon isotope data because: 1) the carbon isotope data is assimilation-weighted and integrates a much longer time frame than that of cuvette measurements, and 2) the potential for error (i.e. leaf area estimation) in cuvette based measurements is much larger than for isotope measurements. Future work on hydraulic limitation in Douglas-fir should focus on measurements when carbon assimilation is greatest, in the spring months, rather than when we focused our measurements, which was during the summer drought.

There was strong evidence of hydraulic compensation. Mid-day minimum leaf water potential was significantly more negative for the largest trees than the younger, shorter trees, resulting in a greater driving force -- the difference between soil and leaf water potential -- for liquid phase water flux. This increase in driving force, coupled with the reduced leaf area per unit sapwood area in larger trees, resulted in minimizing reductions in hydraulic conductance as the trees grew taller. These results have important implications for how we view the interactions between hydraulic compensation and limitation to growth.

In the fourth chapter I observed that large, old ponderosa pine are very sensitive to increases in resource availability. Stand density reductions resulted in significant increases in water availability. Stemwood growth (indexed by basal area increment) doubled or tripled after stand density reductions. This result, by itself, shows that trees near their maximum height *can* increase their growth rates, and therefore, are not genetically programmed to have a constant, low rate of growth after reaching old age.

However, much else was learned from the third chapter. The growth response after stand density reductions took four years for two of the stands. In all stands, carbon isotope discrimination increased significantly after stand density reduction. In the single stand where we closely examined the temporal dynamics of discrimination, we found that discrimination responded one year after thinning, peaked six years after thinning, and then maintained high discrimination through the remaining years (12 years after thinning). Growth lagged behind discrimination by three to zero years, depending on time since thinning. This has two implications for paleo-climate research: 1) site disturbance that results in increased water availability can appear similar to prolonged periods of wetter than normal climate, and 2) assuming a zero or single year lag between growth or carbon isotope ratios and climate may be incorrect in some circumstances.

5.2 INTEGRATION

When I began this research in 1998, the question of not only the generality but also the very existence of a hydraulic limitation to gas exchange was in question. The results of my research demonstrate substantial evidence in support of a hydraulic driving force for reduced gas exchange as trees become taller. A substantial advance in our knowledge has been the observation that vascular systems of woody plants can change as trees become taller and that these changes allow a partial compensation for pathlength effects on water transport capacity. Furthermore, I observed that the tolerance of reduced mid-day leaf water potential by foliage at the top of tall trees may also act to compensate for reduced hydraulic conductance in tall trees. Therefore, this research has shown that both structural and physiological changes occur in trees as they grow taller that act to minimize height-related reductions in gas exchange. As a result of these investigations, theories regarding hydraulic limitations and compensations to gas exchange in tall trees have made major advancements.

One unifying result of this dissertation research is the consistent observation that the simple hydraulic model (Chapter 1.6, equation 1) adequately represents the vascular system of trees. This suggests that we have some understanding of the constraints and compensating mechanisms on water movement within trees. This model can now be used to generate further hypotheses as to how the vascular system of plants operates to balance hydraulic constraints with evaporative demand. Future work should add more complexity to the model to incorporate other limitations and compensations, such as capacitance, temperature dependence of hydraulic conductance, cavitation, and carbon costs of structural changes.

While the research in this dissertation supports the idea that hydraulic compensation coexists with hydraulic limitation, it does not answer the question as to how compensation mechanisms may in themselves result in cost to aboveground growth. For example, increased carbon allocation to sapwood at the expense of leaf production can lead to a reduced carbon economy even if leaf-specific hydraulic conductance remains unchanged. Likewise, reductions in mid-day leaf water potential of tall trees may cause greater xylem cavitation, the consequences of which may cause a negative feedback on conductance. These costs and many more may increase as a result of hydraulic compensation. Exploration of these trade-offs will be an important avenue for future research.

CHAPTER 6. CONCLUSIONS AND SUGGESTION

6.1 CONCLUSIONS

Examination of the three chapters in this dissertation along with the previously published literature leads to the following conclusions about the hydraulic limitation hypothesis.

1. Although there is abundant evidence that woody plants regulate transpiration to maintain leaf water potential at a critical value, this minimum value may be reduced as trees grow in size. A tenet of the hypothesis is that trees maintain the threshold leaf water potential throughout the size continuum. Some studies have shown this to be the case, but not all studies. This calls into question the fundamental tenet that stomatal conductance will decline with tree size due to maintenance of leaf water potential. Further work to determine if reduced leaf water potential results in greater cavitation, if cavitated elements are refilled, and the potential feedbacks of cavitation upon stomatal conductance is needed.
2. Resistance to water flow does increase with tree size. While it is true that resistance is greatest in petioles (Yang and Tyree 1994), it is also true that increased pathlength, along with the other changes associated with age or size, is correlated with reduced hydraulic conductance (Waring and Sylvester 1994, Panek and Waring

1995, Walcroft et al. 1996, Hubbard et al. 1999, Ryan et al. 2000, Kolb et al. 2000, Schäfer et al. 2000, Warren and Adams 2000, Barnard 2001, McDowell et al. 2002a, Bond and Panek *unpublished data*). There are no published results showing that trees *near their maximum height* have hydraulic conductance similar to that of younger trees of the same species, growing in similar sites.

3. Stomatal conductance declines with reduced hydraulic conductance. This has been observed experimentally in small plants (Sperry and Pockman 1993, Sperry et al. 1993, Waring and Sylvester 1994, Saliendra et al. 1995, Walcroft et al. 1996, Whitehead et al. 1996, Pataki et al. 1998, Hubbard et al. 2001) and across chronosequences (Hubbard et al. 1999, Ryan et al. 2000, McDowell et al. 2002a). Schäfer et al. (2000) also found a decrease in canopy conductance with increasing tree size.
4. Reductions in stomatal conductance with increased tree size may or may not cause reduced carbon assimilation. With the exception of a Hawaiian Eucalyptus study (Barnard 2001), this question remains to be unambiguously tested. Cuvette-level measurements are inadequate for this test because of the large discrepancy in spatial scales (leaf to canopy), temporal scales (seconds to years) and because of potential measurement errors, such as errors in leaf area estimation. Furthermore, changes in water-use efficiency can cause small differences in carbon isotope discrimination without concomitant changes in total canopy carbon assimilation. In Hawaiian

Eucalyptus, whole-stand carbon assimilation was reduced without reductions in stomatal conductance, leaving the mechanisms of the decline in question (Barnard 2001).

5. Hydraulic compensation for *potential* increases in hydraulic resistance as trees grow taller occurs in nearly every case that has looked for it. However, in all cases hydraulic compensation was insufficient to prevent age-related constraints in hydraulic conductance, stomatal conductance or carbon assimilation (Mencuccini and Grace 1996a, 1996b, Hubbard et al. 1999, Schäfer et al. 2000, Ryan et al. 2000, Mencuccini and Magnani 2000, Barnard 2001, McDowell et al. 2002a, McDowell et al. 2002b, Ryan and Whitehead *unpublished data*).

6.2 SUGGESTION

The hydraulic limitation hypothesis, as proposed by Ryan and Yoder (1997) served as an enormous impetus behind research on age-related growth decline over the last five years. The eco-physiological community, however, still remains uncertain as to what the role of hydraulic limitation is in the age-related growth decline of forests. This may be due, in part, to the lack of clarity among scientists about what a "hydraulic limitation" really is. I propose a new way of looking at hydraulic limitation.

Critics of the hydraulic limitation hypothesis have focused on Ryan and Yoder's (1997) tenet that hydraulic conductance will decline due to increased resistance from soil-to-leaf. They argue that axial resistance is not likely to increase substantially as trees grow (Becker et al. 2000, Meinzer et al. 2001). This argument relies on two points: 1) hydraulic architecture studies have shown that within-tree resistance is greatest at the petioles (Yang and Tyree 1994) so increased axial resistance should have a minor effect on whole-tree resistance, and 2) compensation via numerous mechanisms should minimize if not completely remove any increases in axial resistance. These are good points regarding whole-tree water relations that deserve further testing. However, this focus on declines in hydraulic conductance *per se* also points to facets of the hydraulic limitation that were not explicitly stated in Ryan and Yoder (1997) and hence have been largely ignored. First of all, even if compensation for *potential* increases in hydraulic resistance is complete, it is still that *potential* that drove the compensation. This, in itself, is evidence that the potential increase in resistance associated with tree size was a driving force for structural (i.e. leaf area:sapwood area) or physiological (i.e. lower threshold leaf water potential) changes in trees as they grow. Second, if compensation occurs, it is likely at the expense of aboveground production. Increased carbon allocation to roots or sapwood and decreased leaf area are all likely to alter the carbon economy of trees such that carbon available for aboveground production is reduced. Therefore, if hydraulic conductance stayed constant with increasing tree size but these other factors change, and if these changes lead to reduced aboveground growth, then a *hydraulic driving force* is behind the reduction in stemwood growth.

This theory was not stated in Ryan and Yoder (1997), but it does adhere to the hydraulic limitation hypothesis. Importantly, this theory agrees with Becker et al. (2000) and Meinzer et al. (2001), that hydraulic conductance can be held constant with increased tree size, and yet simultaneously this theory can also explain age-related growth declines. If a hydraulic driving force increases as tree size increases, aboveground production can decline due to 1) reduced carbon assimilation, and/or 2) reduced carbon allocation aboveground. Either mechanism fits within the hydraulic driving force hypothesis.

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APPENDIX. GRAVITY AND LEAF WATER POTENTIAL

An example of the gravitational effects of tree height on leaf water potential and stomatal conductance follows. Gravity imposes a constant pull on water columns that is equivalent to 0.01 MPa per vertical meter (Zimmerman 1983, Bauerle 1999, McDowell et al. 2002a), therefore the nocturnal leaf water potential at the top of neighboring 30 m and 100m Coast Redwood trees can be no less than -0.3 MPa and -1.0 MPa, respectively. If both trees have a threshold mid-day water potential of -2.0 MPa, then the 30 m tree can have relatively open stomata, transpire, and assimilate carbon freely for the period equivalent to the change in water potential from -0.3 to -2.0 MPa, equivalent to a 1.7 MPa range. In contrast, if stomatal sensitivity to vapor pressure deficit is the same between the 30 m and 100 m trees (see section 1.6), then the 100 m tree must reduce stomatal conductance after a change of only 1.0 MPa (-1.0 to -2.0 MPa). If all else is equal between the two trees, this 41% reduction in daily leaf water potential range will force the taller tree to spend 41% less time per day with its stomata open. Therefore, daily integrated carbon assimilation will be 41% lower than that of the young tree. This is a conservative example because it assumes that hydraulic conductance is constant for the two sizes of tree, which is an unlikely assumption. Regardless of hydraulic conductance, this example shows that height itself imposes a limit on the maximum height a tree can attain. Taking this example to the extreme, if a tree were 200 m tall and maintained a minimum leaf water potential threshold of -2.0 MPa, then a tree could never assimilate enough carbon to survive. Leaf water potential would always be at the threshold and therefore, stomatal conductance would be extremely low at all times.