University of Alberta

Sapwood hydraulic characteristics of lodgepole pine, defined using Darcy's law, in relation to competitive position, height repression, and tree water use following thinning

Spine title: Darcy's Law competition and water use of lodgepole pine

by

Douglas Edward Boyd Reid ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Fall 2004

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-96009-9
Our file Notre référence
ISBN: 0-612-96009-9

The author has granted a non-exclusive license allowing the Library and Archives Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Dedication

To Kelly Marie Sharp
who only ever asked that I try to change the world for the better
and to Emma, Ruby and Violet
who gave me the inspiration to try.

Abstract

In this dissertation, I investigated the relationship between the water conducting properties of lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) stems and the phenomenon of height repression in high-density fire-origin stands. The literature dealing with the physical limitations on water movement through trees uses inconsistent terminology, symbols and units to describe the water conducting properties of wood, due to application of either an Ohm's law analogy and/or Darcy's law. Explanations of Ohm's law and Darcy's law are provided to clarify this confusion. A proposal for a unified nomenclature based on Darcy's law to define hydraulic conductivity (K_Ψ), permeability (k), hydraulic capacity (Q_h) and leaf specific hydraulic capacity (Q_L) is presented. Hydraulic properties of excised dominant (D), co-dominant (CD), and suppressed (SP) tree stem segments from low (height repressed) and medium sites were measured. Leaf area, crown projection area and growth over the last five years were measured to assess growth efficiency (GE) and crown efficiency (CE). Leaf area index (LAI) was also measured. Faster growing trees from medium sites were more permeable to water, as were D ($k = 1.97 \times 10^{-12}$ m^2) and CD ($k = 1.79 \times 10^{-12}$ m^2) trees compared to SP ($k = 0.71 \times 10^{-12}$ m^2) due, in part, to a greater proportion of early-wood. The leaf/sapwood area ratio (S) varied with crown dominance position (D>CD>SP), but not by site type. Volume growth was closely associated with both hydraulic capacity (Q_h) and leaf area, but LAI and Q_L did not differ between sites. Height repression was not associated with lower GE, but was associated with lower CE. SP tree needles had the highest concentration of N and P in their needles, allowing them to maintain higher GE for a given Q_L. Height repression on low sites may be a result of total leaf area being distributed among too many small trees, capable of supplying sufficient water to small crowns. Finally, water use in thinned and un-thinned trees was examined using thermal dissipation sap flow sensors. Declines in k of thinned trees did not result in declines in tree water use, suggesting that soil water availability is more important than sapwood hydraulic properties in determining stomatal behavior.

Acknowledgements

I am grateful to my supervisors, Victor Lieffers and Uldis Sillins, who provided me with an appropriate mix of excited optimism and well grounded skepticism. My colleagues in the silviculture research group also provided valuable discussion when I needed input, as well as inspiration and insight through their own work. In particular, I would like to thank Mark Rudnicki for sharing his passion to seek 'the truth', Ken Stadt for rekindling my interest in physics and assistance with all things electronic, and Erin Fraser, Issac Amponsah, Simon Landhausser, Brent Frey and Annie Derosches for many spirited discussions. My work involved many hours in the field and lab, and would not have been possible without the excellent assistance of Wei (Wolf) Liu, Ben Seaman, Todd Baiden, Cam MacLean, Eric Paton, Kevin Bladon, Brendan Brabender, Xiaodong (Mike) Liu, and Bryn Jonzon.

I would also like to thank the entire Faculty and Staff of the Department of Renewable Resources who have helped make it possible for me to support my family while pursuing my studies. My days spent pounding the keyboard were made all the more enjoyable by my fellow HEB residents, Jon Hornung and Darcy Henderson who listened to me ramble on about hydraulic conductivity and exposed me to the wonderful worlds of invertebrate zoology and grassland ecology.

I have had great support from my family through the last 5 and ½ years of work. My parents, Charles and Elizabeth Reid were always there for me when things got difficult, and were always keen to expose my daughters to the many wonders of the natural world, just as they did for me when I was young. My In-Laws, Joe and Lorraine Sharp, were also always there for us, whether the van needed a new rack and pinion, or Kelly needed a little nudge to take the plunge. Without the constant encouragement and support I have received from all of my extended family, I doubt I would have had the fortitude to stay the course.

Project Funding was provided through the NSERC Weldwood/Weyerhauser Industrial Research Chair in Silviculture in Enhanced Forest Management. Personal Support was provided through the Des Crosley Memorial Scholarship and the West Fraser Timber Scholarship.

Table of Contents

List of Figures

List of Tables

List of Symbols and Abbreviations

K_Ψ	hydraulic conductivity ($m^2\ Pa^{-1}\ s^{-1}$)
K	hydraulic conductivity ($m\ s^{-1}$)
k	permeability (m^2)
Q	volumetric flow ($m^3\ s^{-1}$)
q	water flux ($m^3\ m^{-2}\ s^{-1}$)
Q_h	hydraulic capacity ($m^4\ Pa^{-1}\ s^{-1}$) under a unit hydraulic gradient
Q_L	leaf specific hydraulic capacity ($m^2\ Pa^{-1}\ s^{-1}$)
$\Delta\Psi$	water potential difference across a sample (Pa)
ΔH	hydraulic head difference across a sample (m)
G	volumetric conductance ($m^3\ s^{-1}\ Pa^{-1}$)
G_c	whole tree canopy averaged stomatal conductance ($mm\ s^{-1}$)
I	electrical current (amperes; A)
V	electrical potential (volts; V)
R	electrical resistance (ohms; Ω)
r	electrical resistivity (Ω m)
L	length (m)
A	cross-sectional area (m^2)
A_s	sapwood cross-sectional area (cm^2)
A_L	leaf area (m^2)
S	leaf area per unit sapwood area ($m^2\ cm^{-2}$)
GE	growth efficiency; volume growth per unit projected leaf area ($cm^3\ m^{-2}\ y^{-1}$)
CE	crown efficiency; volume growth per unit crown projection area ($cm^3\ m^{-2}\ y^{-1}$)
η	dynamic fluid viscosity (Pa s)
ρ	density ($kg\ m^{-3}$)
g	acceleration due to gravity ($m\ s^{-2}$)
A_n	needle specific area ($m^2\ g^{-1}$)
w_n	dry weight of needles from a representative branch (g)
w_b	fresh weight of needles from a representative branch (g)
w_B	fresh weight of all branches in crown section which representative branch was taken from(g)
N	Nitrogen
P	Phosphorous
P	probability
Q_l	leaf related sap flow from thermal dissipation sap flow measurements ($mmol\ m^{-2}\ s^{-1}$)
Q^*	net radiation ($W\ m^{-2}$)
ΔT	temperature difference between heated and un-heated sap flow probes (°C)
ΔT_max	maximum daily temperature difference (°C)
v_s	mean sap flux density ($m\ s^{-1}$)
Q_d	volumetric water use from thermal dissipation sap flow measurements ($m^3\ day^{-1}$)
W_a	relative humidity
T_a	air temperature (K)
e_s	saturation vapour pressure (kPa)
e_a	ambient vapour pressure (kPa)
u	wind speed ($m\ s^{-1}$)

E_o	potential evaporation (mm day^{-1})
Γ	slope of the saturation vapor pressure vs. temperature curve (kPa K^{-1})
Π	net radiation expressed as an equivalent water depth (mm day^{-1})
γ	the psychrometric constant (0.067 kPa K^{-1})
D	vapor pressure deficit of the air (e_s - e_a; kPa)
ρ_a	density of air (kg m^{-3})
c_a	heat capacity of air (1.0×10^{-3} MJ kg^{-1} K^{-1})
M	medium (re: stand site quality)
L	low (re: stand site quality)
D	dominant crown class
CD	co-dominant crown class
SP	suppressed crown class
LAI	leaf area index (m^2 m^{-2})
%E	percent earlywood
SI_{50}	Site Index, predicted height of dominant trees at age 50 (m)
dbh	diameter at breast height
ht.	height
LCR	live crown ratio
SDI	stand density index
BA	stand basal area (m^2 ha^{-1})
JT	just thinned one month prior to the measurement period, thinned in 2002
5T	thinned 5 years prior to the measurement period, thinned in 1998
C	un-thinned control
tpha	trees per hectare
CT	copper-constantan thermocouple
DOY	day of year

Chapter 1
Introduction

Water is essential for all plant life. It is the main constituent of most plant cells, and has a variety of unique chemical, thermal, and physical properties that make it essential for plant physiological functions. Water is the medium in which diffusion of solutes within plant cells occurs, and is particularly suited for dissolving ions. The mineral nutrients needed for photosynthesis and metabolism (N P K etc.) are typically transported in aqueous solutions, as are the organic products of photosynthesis. Because it has a high heat of vaporization, high heat capacity and high thermal conductivity, water is ideal for maintaining temperature uniformity (Nobel 1983), thus minimizing temperature effects on plant physiological processes. The strong intermolecular forces resulting from hydrogen bonds between water molecules make water very cohesive (Fiscus & Kaufmann 1990). Liquid water at 25°C has a tensile strength of 1,800 MPa (Nobel 1974), enabling trees to lift water to extreme heights. The growth of plant tissues requires the simultaneous uptake of water, extension of cell walls, and accumulation of water (Boyer 1985). Innovative techniques developed over the last two decades (Booker & Kininmonth 1978; Zimmermann 1978; Sperry et al. 1988; Tyree et al. 1995; Spicer & Gartner 1998; Holbrook et al. 2001) have enabled the movement of water in tree xylem to be studied in great detail.

The movement of water from roots to leaves in long-lived and potentially very tall trees occurs in the sapwood xylem. Sapwood is found in the outer portion of stem and branch cross-sectional area, and can be distinguished from heartwood by a variety of methods (Blanche et al. 1984; David et al. 1993; Fromm et al. 2001). Sapwood xylem is wet, and contains three types of dead cells (fibres, tracheids, and/or vessel elements), as well as living ray parenchyma cells (Fiscus & Kaufmann 1990). Vessel elements are arranged end to end, and during the final stages of development the end walls may disappear altogether, or are modified to allow the passage of water. A contiguous string of vessel elements forms a hollow tube called a vessel. Between tracheids (and along the side walls of vessel elements) are short and narrow bordered pits which minimize air entry and the passage of air from one cell to the next (Zwieniecki & Holbrook 2000), but are also the point of greatest resistance to water flow within sapwood xylem (Tyree & Ewers 1991). Bulk flow of water in sapwood xylem occurs in the lumens of tracheids, which can be as short as a millimetre, and vessels, which can be as long as a metre (Sperry et al. 2003). The flow through an ideal capillary increases by the fourth power of its radius (Zimmermann,1983;

Tyree & Zimmermann 2002), and water flows along the path of least resistance. Thus, water flow in xylem occurs primarily in large diameter vessels (up to 1 mm) in angiosperms, and earlywood tracheids (10-20 μm) in gymnosperms (Fiscus & Kaufmann 1990). The variability that has evolved in sapwood hydraulic architecture enables trees to deliver water from roots to leaves in a wide range of environments (Eagleson 2002).

How water moves from roots to leaves continues to be a source of debate among tree physiologists. The cohesion-tension (CT) theory, first proposed by Dixon and Joly (1895), relies on the thermodynamic properties of water to explain how water moves from roots to leaves (Zimmermann,1983). There is a preponderance of evidence in support of the CT theory (Tyree 1997; Richter 1997; Sperry et al. 2003; Tyree 2003), and results from direct measurements of internal xylem pressures which appear contradictory (Zimmermann et al. 1994) have been explained as largely due to the limitations of the measurement technique (Wei et al. 1999a; Wei et al. 1999b; Wei et al. 2000; Steudle 2001). The CT theory states that reductions in the potential energy per unit volume of water within leaf mesophyll cells occur as water evaporates from cell wall surfaces into intercellular air spaces. This drop in water potential is transferred down through the continuous water column from the leaves to the root apices and throughout all parts of the apoplast in every organ of the plant (Tyree 1997). The narrow conduits within the water conducting tissues of the tree allow the column of water to withstand very low water potentials (e.g. -20 MPa, Koch et al. 2004). Provided the force is great enough to overcome frictional resistance and gravitational force, trees can move water over 110 m up to leaves (Koch et al. 2004). For the purpose of this dissertation, the essential feature of the CT theory is that water flow through xylem is a passive process driven by a decline in water potential in the direction of flow, and limited by the characteristics of the xylem which impart resistance. Examination of water movement through trees requires a detailed explanation of the nature and quantity of the limitation to flow imposed by sapwood xylem.

The Need for a Unified Nomenclature

The physical limitations on water movement through xylem (hereafter "hydraulic properties of xylem") have important implications for tree growth and associated ecosystem function. The hydraulic properties of xylem in stems, branches and roots of trees have been the focus of a large number of recent investigations (see reviews by (Tyree & Ewers 1991; Sperry 1995; Gartner

1995; Whitehead 1998; Comstock & Sperry 2000; Meinzer et al. 2001; Tyree & Zimmermann 2002; Tyree 2003). Stomatal behaviour and transpiration in trees subject to boundary layer and soil moisture constraints (Meinzer et al. 1995), stand level productivity (Mencuccini & Grace 1996a), and the growth of large old trees (Hubbard et al. 1999) are influenced by the physical limitations on water movement imposed by sapwood xylem. When soil water availability is not limiting, there is a direct relationship between xylem hydraulic properties and stomatal behaviour of trees (Hubbard et al. 2001) and the maximum height attainable by trees is ultimately limited by the hydraulic properties of xylem (Ryan & Yoder 1997; Koch et al. 2004). Hydraulic properties of sapwood xylem clearly are important in determining the structure and function of forest ecosystems.

The theoretical framework, nomenclature and mathematical formulations used to describe xylem hydraulic properties are unfortunately inconsistent. Two approaches have been used, one based on an analogy to Ohm's law (Tyree & Ewers 1991), and another based on Darcy's law (Whitehead & Jarvis 1981). The inconsistent nomenclature and mathematical formulations used to describe hydraulic properties of xylem have hampered understanding within the discipline of tree physiology (Aumann & Ford 2002), made work in tree hydraulic architecture unnecessarily difficult (Fiscus & Kaufmann 1990), and limited the accessibility of findings to the broader scientific community. A desire to better understand the movement of water through ecosystems has spawned the new field of ecohydrology (Baird & Wilby 1999; Eagleson 2002), which integrates tree and plant physiology, physical hydrology, and hydrogeology. It will thus become increasingly important for physiologists, hydrologists, soil scientists, and geomorphologists to understand one another. A unified nomenclature to describe the hydraulic properties of xylem is needed so that the results presented in this dissertation and elsewhere are understandable to researchers studying tree physiology, as well as to the broader scientific community.

Competition, Height Repression and Hydraulic Limitation

Plant growth, development, and survival depend on the availability of light, water and nutrients to photosynthesizing leaves. In forest stands experiencing competition for limited resources, individual trees grow at differing rates resulting in differentiation into crown dominance classes (Oliver & Larson 1990). One-sided competition, where larger dominant individuals are able to secure proportionally more resources and improve their growth rate at the expense of smaller individuals, typically results in self-thinning as dominant trees survive and suppressed trees die (Peet & Christensen 1987). It has been suggested that "one-sided" competition is primarily due to the fact that larger dominant trees have better access to light (Weiner & Thomas 1986). Even-aged conifer stands like those that typically emerge following natural regeneration of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud.) forests provide an excellent venue to explore the relationship between intraspecific competitive interactions and sapwood hydraulic characteristics.

Another unique characteristic of lodgepole pine is that it can establish at extremely high densities, resulting in intense competition and lower than expected height growth, or height repression (Farnden & Herring 2002). These stands can grow for decades without apparent differentiation, which would in theory prevent self thinning and result in cessation of growth (Oliver & Larson 1990). Though small differences in growth rate between individuals are always present (Oliver & Larson 1990), high density lodgepole pine stands can, nevertheless, experience much lower than expected growth rates (Worall et al. 1985). Height repression appears to be common in naturally established high density lodgepole pine stands (Huang et al. 2004), and is hypothesized to be related to limitation on water supply to leaves imposed by the hydraulic properties of sapwood (Keane & Weetman 1987). This hypothesis has not been tested.

Gas exchange in response to dynamic water stress is thought to be influenced by the limitation on water movement imposed by sapwood hydraulic characteristics (Whitehead 1998), thus influencing productivity. Sapwood hydraulic characteristics are also thought to influence ecological processes governing tree growth and forest stand dynamics (Mencuccini & Grace 1996a; Mencuccini & Grace 1996b; Mencuccini et al. 1997; Ryan & Yoder 1997; Hubbard et al. 1999; Magnani et al. 2000). Sapwood hydraulic characteristics are known to be positively associated with above-ground site productivity (Pothier et al. 1989a; Pothier et al. 1989b). Differences in the hydraulic properties of sapwood between crown dominance classes in self-thinning stands, and any interaction with site quality has not been investigated.

Growing Space Efficiency and Height Repression

Individual trees that are successful under one-sided competition are thought to occupy more growing space relative to their less successful neighbours. The growing space occupied by individual trees has been quantified by measurement of crown projection area (Assmann 1970), or by measurement of photosynthetic leaf area (O'Hara 1988). Crown projection area was the primary measure of growing space prior to the development of techniques to estimate leaf area from sapwood basal area, and has long been used by foresters to make silvicultural decisions (Assmann 1970). With the application of the pipe model theory (Shinozaki et al. 1964a; Shinozaki et al. 1964b) to trees (Grier & Waring 1974; Waring et al. 1977) and subsequent development of techniques to accurately estimate leaf area in conifers from more easily measured parameters (Dean & Long 1986), leaf area has become the most common measure of growing space. Measurement of stemwood growth per unit of occupied growing space can be thought of as a measure of the efficiency with which growing space is utilized, because allocation to stemwood is thought to have lower priority relative to other tissues and biochemical compounds (Waring & Pitman 1983; Waring and Schlesinger,1985). Stem volume growth per unit of leaf area is generally referred to as growth efficiency (*GE*; Waring et al. 1980), and stem volume growth per unit crown projection area is referred to as crown efficiency (*CE*; Assmann 1970).

Both *GE* (Waring et al. 1980) and *CE* (Assmann 1970) have been suggested as measures of tree vigour. Investigations into the relationship between crown dominance and *GE* and *CE*, however, suggest that the fastest growing (most vigorous) trees are not always the most efficient in terms of stemwood production. Both dominant (Kollenberg & O'Hara 1999) and suppressed (Kaufmann & Ryan 1986) lodgepole pine trees have been reported to have highest *GE*, and there is no consistent trend of *GE* between crown classes in published results for a variety of conifer species (O'Hara 1988; Kaufmann & Ryan 1986; Gilmore & Seymour 1996). Recently, Sterba and Amateis (1998) showed that dominant loblolly pine trees have the highest *CE,* but large dominants have lower *CE* than small co-dominants. These apparently contradictory results call into question the utility of *GE* and *CE* as indicators of individual and stand level tree vigour.

There is nevertheless evidence to suggest that *GE* and *CE* may be useful in understanding how sapwood hydraulic properties contribute to the phenomenon of height repression. Measures of efficiency, particularly *GE*, have been useful in understanding how environmental stress affects the growth rate of trees (Waring et al. 1980; Kaufmann & Ryan 1986), and differences in the ability of trees to survive insect outbreaks (Waring & Pitman 1983; Coyea & Margolis 1994). Declining *GE* with age has been associated with the universal phenomenon of declining stand level productivity following crown closure (Long & Smith 1992; Ryan & Waring 1992; Yoder et al. 1994; Mencuccini & Grace 1996b; Gower et al. 1996), possibly due to hydraulic limitation

(Hubbard et al. 2001). Measurement of the hydraulic properties of sapwood across a Scots pine chronosequence wherein *GE* declined with age (Mencuccini & Grace 1996b), suggest the limitation on water availability to leaves imposed by sapwood is a key factor in the determination of *GE*. Examination of the relationship between *GE* and hydraulic properties of xylem should therefore be useful in testing the hypothesis that height repression in lodgepole pine is due to a hydraulic limitation (Keane & Weetman 1987).

The Effect of Thinning on Water Use of Lodgepole Pine Trees

Lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud.) forests of western Canada contribute significantly towards the production of high-quality structural lumber, and other forest products. To date, management of these forests has been primarily focused on clear-cut harvesting of even-aged stands that are generally >120 years old, followed by site preparation and planting. Stands currently under this management regime were primarily established naturally following stand replacing wildfires. Despite fire-suppression efforts, wildfires have continued to disturb large areas of lodgepole pine forests, resulting in natural stands of varying ages. These stands can occupy significant portions of managed forests, but are often considered largely 'non-productive' because of high density and associated height repression. Relative to managed stands established using silvicultural techniques, high density fire-origin stands tend to be less productive (Huang et al. 2004), suggesting there may be an opportunity to improve productivity through thinning.

Thinning increases the available growing space for retained trees by removing competing neighbors, but does not always result in immediate improvements in growth. In many cases improved growth rates are not observed for several years (Yang 1988; Youngblood 1991), particularly in fire origin lodgepole pine stands (Worall 1995). Height repressed lodgepole pine stands have responded to density management, combined with fertilization to achieve dramatic increases in height growth and yield (Farnden & Herring 2002).

Within thinned stands, retained trees experience changes in their environment that are likely to cause an increase in water stress following thinning because leaf water potentials must decline in order to produce increases in transpiration (Jarvis 1975) typically observed in thinned stands (Morikawa et al. 1986; Bréda et al. 1995; Medhurst et al. 2002). Declining leaf water potential is transferred down through the water column in the plant. If xylem water potential becomes low enough cavitation of the water column occurs (Sperry et al. 2003), resulting in changes in the hydraulic properties of xylem that limit flow. Greater wind loading on individual crowns in thinned lodgepole pine stands results in greater crown sway (Rudnicki et al. 2003), which can also negatively affect sapwood hydraulic properties (Silins et al. unpublished). Despite greater leaf area, sapwood area, and diameter growth, damage to conducting sapwood has been observed in retained lodgepole pine trees four growing seasons after thinning (Liu et al. 2003). How this damage influences transpiration and stomatal behavior under field conditions is unclear.

Measurement of Transpiration and Stomatal Behavior *in situ*

Transpiration and stomatal behavior can be assessed under field conditions using techniques that quantify water movement through sapwood xylem from measurable dissipation of heat. The heat pulse method uses carefully timed pulses of heat as markers in the sap stream (Huber & Schmidt 1937; Marshall 1958a; Marshall 1958b; Swanson & Whitfield 1981). A variety of heat balance methods measure the transfer of heat from a constant heat input (Daum 1967; Cermak et al. 1976; Sakuratani T. 1981; Granier 1987; Granier 1985). With appropriate recognition of the limitations of the various methods employed (Phillips et al. 1996; Smith & Allen 1996; Kostner et al. 1998; Clearwater et al. 1999; Ewers & Oren 2000) these techniques offer a means by which the dynamic response of stomata to changes in environmental variables driving transpiration can be evaluated.

Most of the water that moves through trees is lost by evaporation through leaf stomata as atmospheric carbon is taken in. Changes in sap flow rates can reflect stomatal behavior under evaporative demand (Martínez-Vilalta et al. 2003), because trees close their stomata to limit water losses (Jarvis & McNaughton 1986). When the rate of transpiration can be measured, stomatal behavior can be quantified by inversion of the Pennman-Monteith equation (Whitehead & Jarvis 1981). Changes in tree water use in response to thinning have been successfully measured using heat balance sap flow technology in other conifer species (Lagergren & Lindroth 2002; Lagergren & Lindroth 2004). Whole tree transpiration and stomatal behavior following thinning in lodgepole pine have not been observed.

Research Objectives

The principle objective of this dissertation is to explore how competition, and management practices designed to reduce competition, influence the hydraulic properties of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. Ex Loud.) trees. A secondary objective is to test the hypothesis that there is a hydraulic basis for height repression.

In Chapter 2, I have proposed adoption of consistent terminology and symbols to describe the hydraulic properties of sapwood xylem based on the theoretical framework of Darcy's law. The foundation of this proposal is a definition of hydraulic conductivity (K_Ψ) as a property of sapwood xylem that is independent of its length and surface area perpendicular to the direction of flow. I have also defined the related terms permeability (k), hydraulic capacity (Q_h), and leaf specific hydraulic capacity (Q_L), and provided discussion of the concepts of water potential (Ψ) and conductance (G) in relation to water flow through sapwood xylem. The symbols and units I have proposed are consistent with those used in other hydrological fields to describe volumetric water flow through porous media.

The objective of Chapter 3 is to explore how leaf area and sapwood hydraulic properties (specifically k, Q_h, and Q_L) vary among dominant, codominant and suppressed trees lodgepole pine trees from height repressed and normally developed stands. I studied trees of similar age from stands that had established south of Hinton, Alberta, following a large stand replacing wildfire in 1957. The area of the fire was large enough to include a number of low quality sites wherein height repression was evident, as well as a number of medium quality sites which did not appear to be height repressed. I hypothesized that faster growing trees (i.e. dominant and/or from medium sites), would have more permeable sapwood, and that the hydraulic properties of slow growing trees (i.e. suppressed and/or from height repressed stands) would limit the water available to leaves.

The objective of Chapter 4 is to compare measures of growing space efficiency between dominant, codominant and suppressed trees from height repressed and normally developing stands. Using data collected from the same trees studied in Chapter 3, I examined the relationship between growth efficiency (*GE*) and leaf specific hydraulic capacity (Q_L) to test the hypothesis that height repression is due to a hydraulic limitation on leaf area imposed by sapwood. I hypothesized that site quality and dominance would be positively related to *GE* and crown efficiency (*CE*), and that these differences would be related to differences in Q_L.

In Chapter 5, I discuss measurements of the water use of thinned and un-thinned lodgepole trees using thermal dissipation sap flow sensors in one of three stands used to examine the effects of thinning and bending stress on sapwood hydraulic properties (Liu et al. 2003). In these stands, the most dramatic effect on sapwood permeability (*k*) was associated with thinning treatment (Liu et al. 2003), suggesting that damage to conducting xylem may result from the change in environment for retained trees. I also instrumented a number of trees in an adjacent stand where thinning treatment had been applied just one month before measurements began to determine whether damage to sapwood was experienced immediately following thinning. I anticipated that thinned trees would experience greater transpiration, and that they would be more likely to reduce stomatal conductance during hot dry weather due to water stress.

References

Assmann, E. 1970. The principles of forest yield study studies in the organic production, structure, increment, and yield of forest stands. 1st English ed. ed. Pergamon Press, Oxford, New York.

Aumann, C.A. and Ford, E.D. 2002. Modeling tree water flow as an unsaturated flow through a porous medium. Journal of Theoretical Biology 219: 415-429.

Baird, A.J. and Wilby, R.L. 1999. Eco-hydrology: Plants and water in terrestrial and aquatic environments. New York. Routledge , London.

Blanche, C.A., Nebeker, T.E., Schmitt, J.J., and Hodges, J.D. 1984. Techniques for distinguishing the sapwood-heartwood boundary in living loblolly pine (*Pinus taeda* L). Forest Science 30: 756-760.

Booker, R.E. and Kininmonth, J.A. 1978. Variation in longitudinal permeability of green radiata pine wood. New Zealand Journal of Forest Science 8(2), 295-308.

Boyer, J.S. 1985. Water transport. Annual Review of Plant Physiology and Plant Molecular Biology 36: 473-516.

Breda, N., Granier, A., and Aussenac, G. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt) Liebl). Tree Physiology 15: 295-306.

Cermak, J., Kucera, J., and Penka, M. 1976. Improvement of method of sap flow-rate determination in full-grown trees based on heat balance with direct electric-heating of xylem. Biologia Plantarum 18: 105-110.

Clearwater, M.J., Meinzer, F.C., Andrade, J.L., Goldstein, G., and Holbrook, N.M. 1999. Potential errors in measurement of non-uniform sap flow using heat dissipation probes. Tree Physiology 19: 681-687.

Comstock, J.P. and Sperry, J.S. 2000. Theoretical considerations of optimal conduit length for water transport in vascular plants. New Phytologist 148: 195-218.

Coyea, M.R. and Margolis, H.A. 1994. The historical reconstruction of growth efficiency and its relationship to tree mortality in balsam fir ecosystems affected by spruce budworm. Canadian Journal of Forest Research 24: 2208-2221.

Daum, C.R. 1967. A method for determining water transport in trees. Ecology 48: 425-431.

David, A.J., Karasek, T.S., and Ramm, C.W. 1993. A comparison of ultraviolet-light and benzidine stain for determining heartwood sapwood boundaries in red pine. Canadian Journal of Forest Research 23: 1242-1243.

Dean, T.J. and Long, J.N. 1986. Variation in sapwood area leaf-area relations within 2 stands of lodgepole pine. Forest Science 32: 749-758.

Dixon, H.H. and Joly, J. 1895. On the ascent of sap. Philosophical Transactions of the Royal Society of London. B 186: 563-576.

Eagleson, P.S. 2002. Ecohydrology: Darwinian expression of vegetation form and function . Cambridge University Press, Cambridge, New York.

Ewers, B.E. and Oren, R. 2000. Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. Tree Physiology 20: 579-589.

Farnden, C. and Herring, L. 2002. Severely repressed lodgepole pine responds to thinning and fertilization: 19-year results. Forestry Chronicle 78: 404-414.

Fiscus, E.L. and Kaufmann, M.R. 1990. The nature and movement of water in plants. Agronomy Monograph No. 30, pp.191-241.

Fromm, J.H., Sautter, I., Matthies, D., Kremer, J., Schumacher, P., and Ganter, C. 2001. Xylem water content and wood density in spruce and oak trees detected by high-resolution computed tomography. Plant Physiology 127: 416-425.

Gartner, B.L. 1995. Patterns of xylem variation within a tree and their mechanical consequences. *In* Plant Stems: Physiology and Functional Morphology. Academic Press, New York. pp. 125-149.

Gilmore, D.W. and Seymour, R.S. 1996. Alternative measures of stem growth efficiency applied to *Abies balsamea* from four canopy positions in central Maine, USA. Forest Ecology and Management 84: 209-218.

Gower, S.T., McMurtrie, R.E., and Murty, D. 1996. Aboveground net primary production decline with stand age: potential causes. Trends in Ecology & Evolution 11: 378-382.

Granier, A. 1985. A New Method of Sap Flow Measurement in Tree Stems. Annales Des Sciences Forestieres 42: 193-200.

Granier, A. 1987. Evaluation of Transpiration in a Douglas-Fir Stand by Means of Sap Flow Measurements. Tree Physiology 3: 309-319.

Grier, C.C. and Waring, R.H. 1974. Conifer Foliage Mass Related to Sapwood Area. Forest Science 20: 205-206.

Holbrook, N.M., Ahrens, E.T., Burns, M.J., and Zwieniecki, M.A. 2001. In vivo observation of cavitation and embolism repair using magnetic resonance imaging. Plant Physiology 126: 27-31.

Huang, S., Monserud, R.A., Braun, T., Lougheed, H., and Bakowsky, O. Comparing site productivity of mature fire-origin and post-harvest juvenile lodgepole pine stands in Alberta. Canadian Journal of Forest Research 34, 1181-1191. 2004.

Hubbard, R.M., Bond, B.J., and Ryan, M.G. 1999. evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiology 19: 165-172.

Hubbard, R.M., Ryan, M.G., Stiller, V., and Sperry, J.S. 2001. stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. Plant Cell and Environment 24: 113-121.

Huber, B. and Schmidt, E. 1937. Eine Kompensationmethode zur thermoelektrischen Messung langsamer Safströme. Ber. Dtsch. Bot. Ges. 55: 514-529.

Jarvis, P.G. 1975. Water transfer in plants. *In* Heat and Mass Transfer in the Plant Environment. Part 1. Scripta Book Co., Washington D.C. pp. 369-394.

Jarvis, P.G. and McNaughton, K.G. 1986. Stomatal control of transpiration - scaling up from leaf to region. Advances in Ecological Research 15: 1-49.

Kaufmann, M.R. and Ryan, M.G. 1986. Environmental, physiographic, and stand effects on individual tree growth in sub-alpine forests. Tree Physiology 2: 47-59.

Keane, M.G. and Weetman, G.F. 1987. Leaf-Area - Sapwood cross-sectional area relationships in repressed stands of lodgepole pine. Canadian Journal of Forest Research 17: 205-209.

Koch, G.W., Sillett, S.C., Jennings, G.M., and Davis, S.D. 2004. The limits to tree height. Nature 428: 851-854.

Kollenberg, C.L. and O'Hara, K.L. 1999. Leaf area and tree increment dynamics of even-aged and multi-aged lodgepole pine stands in Montana. Canadian Journal of Forest Research 29: 687-695.

Köstner, B., Granier, A., and Cermak, J. 1998. Sapflow measurements in forest stands: methods and uncertainties. Annales Des Sciences Forestieres 55: 13-27.

Lagergren, F. and Lindroth, A. 2002. Transpiration response to soil moisture in pine and spruce trees in Sweden. Agricultural and Forest Meteorology 112: 67-85.

Lagergren, F. and Lindroth, A. 2004. Variation in sapflow and stem growth in relation to tree size, competition and thinning in a mixed forest of pine and spruce in Sweden. Forest Ecology and Management 188: 51-63.

Liu, X.D., Silins, U., Lieffers, V.J., and Man, R.Z. 2003. Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. Canadian Journal of Forest Research 33: 1295-1303.

Long, J.N. and Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia* - the influence of stand development and crown dynamics. Forest Ecology and Management 53: 53-64.

Magnani, F., Mencuccini, M., and Grace, J. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant Cell and Environment 23: 251-263.

Marshall, D.C. 1958a. Measurement of Sap Flow by Heat Transfer. Nature 182: 878-879.

Marshall, D.C. 1958b. Measurement of sap flow in conifers by heat transport. Plant Physiology 33: 385-396.

Martínez-Vilalta, J., Mangirón, M., Ogaya, R., Sauret, M., Serrano, L., Peñuelas, J. and Piñol, J. 2003. Sap flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. Tyree Physiology 23:747-758.

Medhurst, J.L., Battaglia, M., and Beadle, C.L. 2002. Measured and predicted changes in tree and stand water use following high-intensity thinning of an 8-year-old *Eucalyptus nitens* plantation. Tree Physiology 22: 775-784.

Meinzer, F.C., Clearwater, M.J., and Goldstein, G. 2001. Water transport in trees: current perspectives, new insights and some controversies. Environmental and Experimental Botany 45: 239-262.

Meinzer, F.C., Goldstein, G., Jackson, P., Holbrook, N.M., Gutierrez, M.V., and Cavelier, J. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species - the influence of boundary-layer and hydraulic-properties. Oecologia 101: 514-522.

Mencuccini, M. and Grace, J. 1996a. Hydraulic conductance, light interception and needle nutrient concentration in scots pine stands and their relations with net primary productivity. Tree Physiology 16: 459-468.

Mencuccini, M. and Grace, J. 1996b. Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus Sylvestris* L.) age sequence. Plant Cell and Environment 19: 939-948.

Mencuccini, M., Grace, J., and Fioravanti, M. 1997. Biomechanical and hydraulic determinants of tree structure in scots pine: anatomical characteristics. Tree Physiology 17: 105-113.

Morikawa, Y., Hattori, S., and Kiyono, Y. 1986. Transpiration of a 31-year-old *Chamaecyparis obtusa* Endl. stand before and after thinning. Tree Physiology 2: 105-114.

Nobel, P.S. 1974. Introduction to biophysical plant physiology. W. H. Freeman, San Francisco.

Nobel, P.S. 1983. Biophysical plant physiology and ecology. W.H. Freeman, San Francisco.

O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Canadian Journal of Forest Research 18: 859-866.

Oliver, C.D. and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill Pub. Co, New York.

Peet, R.K. and Christensen, N.L. 1987. Competition and tree death. Bioscience 37: 586-595.

Phillips, N., Oren, R., and Zimmermann, R. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. Plant Cell and Environment 19: 983-990.

Pothier, D., Margolis, H.A., Poliquin, J., and Waring, R.H. 1989a. Relation between the permeability and the anatomy of jack pine sapwood with stand development. Canadian Journal of Forest Research 19: 1564-1570.

Pothier, D., Margolis, H.A., and Waring, R.H. 1989b. Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. Canadian Journal of Forest Research 19: 432-439.

Richter, H. 1997. Water relations of plants in the field: some comments on the measurement of selected parameters. Journal of Experimental Botany 48: 1-7.

Rudnicki, M., Lieffers, V.J., and Silins, U. 2003. Stand structure governs the crown collisions of lodgepole pine. Canadian Journal of Forest Research 33: 1238-1244.

Ryan, M.G. and Waring, R.H. 1992. Maintenance respiration and stand development in a sub-alpine lodgepole pine forest. Ecology 73: 2100-2108.

Ryan, M.G. and Yoder, B.J. 1997. Hydraulic limits to tree height and tree growth. Bioscience 47: 235-242.

Sakuratani T. 1981. A heat balance method for measuring water flux in the stems of intact plants. Journal of Agricultural Meteorology 37: 9-17.

Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. 1964a. A quantitative analysis of plant form - the unit pipe model theory. I. Basic Analyses. Japanese Journal of Ecology 14: 97-105.

Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. 1964b. A quantitative analysis of plant form - the unit pipe model theory. II. Further evidence of the theory and its application in forest ecology. Japanese Journal of Ecology 14: 133-139.

Smith, D.M. and Allen, S.J. 1996. Measurement of sap flow in plant stems. Journal of Experimental Botany 47: 1833-1844.

Sperry, J.S. 1995. Limitations on stem water transport and their consequences. *In* Plant Stems: Physiology and Functional Morphology. Academic Press , New York. pp. 105-124.

Sperry, J.S., Donnelly, J.R., and Tyree, M.T. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell and Environment 11: 35-40.

Sperry, J.S., Stiller, V., and Hacke, U.G. 2003. Xylem hydraulics and the soil-plant-atmosphere continuum: opportunities and unresolved issues. Agronomy Journal 95: 1362-1370.

Spicer, R. and Gartner, B.L. 1998. Hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) branches and branch halves with reference to compression wood. Tree Physiology 18: 777-784.

Sterba, H. and Amateis, R.L. 1998. Crown efficiency in a loblolly pine (pinus taeda) spacing experiment. Canadian Journal of Forest Research 28: 1344-1351.

Steudle, E. 2001. The cohesion-tension mechanism and the acquisition of water by plant roots. Annual Review of Plant Physiology and Plant Molecular Biology 52: 847-875.

Swanson, R.H. and Whitfield, D.W.A. 1981. A numerical-analysis of heat pulse velocity theory and practice. Journal of Experimental Botany 32: 221-239.

Tyree, M.T. 1997. The cohesion-tension theory of sap ascent: current controversies. Journal of Experimental Botany 48: 1753-1765.

Tyree, M.T. 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees-Structure and Function 17: 95-100.

Tyree, M.T. and Ewers, F.W. 1991. The hydraulic architecture of trees and other woody-plants. New Phytologist 119: 345-360.

Tyree, M.T., Patino, S., Bennink, J., and Alexander, J. 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. Journal of Experimental Botany 46: 83-94.

Tyree, M.T. and Zimmermann, M.H. 2002. Xylem structure and the ascent of sap. 2nd ed. Springer, Berlin, New York.

Waring, R.H., Gholz, H.L., Grier, C.C., and Plummer, M.L. 1977. evaluating stem conducting tissue as an estimator of leaf area in 4 woody angiosperms. Canadian Journal of Botany 55: 1474-1477.

Waring, R.H. and Pitman, G.B. 1983. Physiological stress in lodgepole pine as a precursor for mountain pine-beetle attack. Journal of Applied Entomology 96: 265-270.

Waring, R.H., Thies, W.G., and Muscato, D. 1980. Stem growth per unit of leaf-area - a measure of tree vigor. Forest Science 26: 112-117.

Waring, R.H. and Schlesinger, W.H. 1985. Forest ecosystems concepts and management. Academic Press, Orlando.

Wei, C., Tyree, M.T., and Bennink, J.P. 2000. The transmission of gas pressure to xylem fluid pressure when plants are inside a pressure bomb. Journal of Experimental Botany 51: 309-316.

Wei, C.F., Steudle, E., and Tyree, M.T. 1999a. Water ascent in plants: do ongoing controversies have a sound basis? Trends in Plant Science 4: 372-375.

Wei, C.F., Steudle, E., and Tyree, M.T. 2000. Reply ... Water ascent in plants. Trends in Plant Science 5: 146-147.

Wei, C.F., Tyree, M.T., and Steudle, E. 1999b. Direct measurement of xylem pressure in leaves of intact maize plants: a test of the cohesion-tension theory taking hydraulic architecture into consideration. Plant Physiology 121: 1191-1205.

Weiner, J. and Thomas, S.C. 1986. Size variability and competition in plant monocultures. Oikos 47: 211-222.

Whitehead, D. 1998. Regulation of stomatal conductance and transpiration in forest canopies. Tree Physiology 18: 633-644.

Whitehead, D. and Jarvis, P.G. 1981. Coniferous forests and plantations: water uptake and movement. Water Deficits and Plant Growth 6, 50-152.

Worall, J. 1995. Height growth stagnation in lodgepole pine: all (well almost all) is revealed. Branchlines 6: 5.

Worall, J., Draper, D.A., and Anderson, S.A. 1985. Shoot characteristics of stagnant and vigorous lodgepole pines, and their growth after reciprocal grafting. Canadian Journal of Forest Research. 15(2): 365-370.

Yang, R.C. 1988. Growth response of white spruce to release from trembling aspen. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-302.

Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., and Kaufmann, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. Forest Science 40: 513-527.

Youngblood, A.P. 1991. Radial growth after a shelterwood seed cut in a mature stand of white spruce in interior alaska. Canadian Journal of Forest Research 21: 410-413.

Zimmermann, M.H. 1978. Hydraulic architecture of some diffuse-porous trees. Canadian Journal of Botany 56: 2286-2295.

Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, New York.

Zimmermann, U., Meinzer, F.C., Benkert, R., Zhu, J.J., Schneider, H., Goldstein, G., Kuchenbrod, E., and Haase, A. 1994. Xylem water transport - is the available evidence consistent with the cohesion theory. Plant Cell and Environment 17: 1169-1181.

Zwieniecki, M.A. and Holbrook, N.M. 2000. Bordered pit structure and vessel wall surface properties. implications for embolism repair. Plant Physiology 123: 1015-1020.

Chapter 2

A unified nomenclature for quantification and description of water conducting properties of sapwood xylem based on Darcy's law[1]

Introduction

The movement of water from roots to leaves in long-lived and potentially very tall trees occurs in the sapwood xylem. Physical limitations on water movement through xylem have important implications for tree growth and associated ecosystem function. In the last two decades there has been an explosion of new and important work regarding the hydraulic properties of xylem in stems, branches and roots of trees (see reviews by Tyree and Ewers 1991, Sperry 1995, Gartner 1995, Whitehead 1998, Comstock and Sperry 2000, Meinzer et al. 2001, Tyree and Zimmerman 2002, and Tyree 2003). This work has been possible thanks to the development of innovative techniques for measuring water flow through xylem (Booker and Kinninmonth 1978, Zimmerman 1978, Sperry et al. 1988, Tyree et al. 1995, Spicer and Gartner 1998). The physical limitations on water movement imposed by sapwood xylem has been shown to influence stomatal behavior and transpiration in trees subject to boundary layer and soil moisture constraints (Meinzer et al. 1995), stand level productivity (Mencuccini and Grace 1996), and the growth of large old trees (Hubbard et al. 1999). Others have shown a direct relationship between xylem hydraulic properties and stomatal behavior of trees under well watered conditions (Hubbard et al. 2001) and that the maximum height attainable by trees is ultimately limited by the hydraulic properties of xylem (Ryan and Yoder 1997, Koch et al. 2004). Research in this field has greatly enhanced our understanding of how different species and genotypes have adapted to deliver water from the soil to the leaves, under different growing conditions.

There are, however, substantial inconsistencies in the theoretical framework and associated nomenclature and mathematical formulations used to quantify the hydraulic properties of xylem present in the literature. An analogy to Ohm's law has long been used to describe the resistance to CO_2 and water vapour transfer in photosynthesis and transpiration (Larcher 1980), and has

---

[1] A version of this Chapter has been submitted to Tree Physiology

been applied widely to describe water movement through trees (Tyree and Ewers 1991). Darcy's law has also been used for many years to quantify the liquid and gas conducting properties of sapwood (Siau 1971, 1983). As early as 1975 Jarvis observed that a "plethora of often misleading definitions of resistance, conductance, conductivity and permeability, with various combinations of units" had made its way into the physiological literature. In the intervening quarter century, this problem has become worse.

Inconsistent nomenclature and mathematical formulations of hydraulic characteristics of xylem have hampered understanding within the discipline of tree physiology (Aumann and Ford 2002), and have made work in tree hydraulic architecture unnecessarily difficult (Fiscus and Kaufmann 1990). Indeed, there is an ongoing drift in terminology in this field. For example, within my research group, as a result of changes in views or pressure from referees, varying terminology and formulations have been used to quantify the hydraulic properties of sapwood (Protz et al 1999, Reid et al. 2003, Liu et al. 2003, Reid et al. 2004). Furthermore, emergence of the new field of ecohydrology (Baird and Wilby 2001, Eagleson 2002) is likely to provide new insights into the movement of water through ecosystems by integrating tree and plant physiology, physical hydrology, and hydrogeology. It will thus become increasingly important for physiologists, hydrologists, soil scientists, and geomorphologists to understand one another through use of common nomenclature. To minimize confusion I propose that plant physiologists adopt a definition of hydraulic conductivity that is consistent with Darcy's law, which is widely used to describe the flow of water through other porous media (Freeze and Cherry 1979, Hillel, 1982, Rawls et al. 1983, Smith and Wheatcraft 1983, Chow et al. 1988, Zaitchick et al. 2003). Darcy's law is also the foundation of complex models that describe unsaturated, three-dimensional flow (see discussion of Richards equation in Rawls et al. 1983) and the contribution of stored water to transpirational flow in woody xylem of large trees (Aumann and Ford 2002).

My objective is to clarify the physical meaning of hydraulic conductivity, and clearly distinguish this term from both conductance and permeability when describing the flow of water through the porous matrix of sapwood xylem. To that end, I discuss how both Ohm's law and Darcy's law have been used to describe hydraulic properties of sapwood xylem. I then suggest that a single unifying nomenclature, based on the widely understood and physically meaningful Darcy's law, be used to quantify the hydraulic properties of woody xylem (Table 1).

Ohm's law

The use of a mathematical model, now known as Ohm's law, to describe the flow of electrical current was first suggested by Ohm (1827). Strictly speaking, Ohm's law is limited to the statement, "the current through a metal conductor is proportional to the applied voltage, $I \alpha V$" (Giancoli 1995). Electrical current (I, Amperes) is the quantity of charge per unit time, which provides an analogue to the flow rate of water through plants. Ohm's law is most frequently presented as a means to quantify the amount of electrical current flowing through a device of known resistance (R, ohms) driven by a difference in electrical potential (V, volts). Thus, current (i.e., flow of electrons) is described by:

Equation 2-1

$$I = \frac{V}{R}$$

Conductance is the inverse of resistance. If the device is a metal conductor (e.g. a wire), its physical size is not explicitly included in this common expression of Ohm's law. However, the size of the conducting element is implicit in the calculation of R, which is directly proportional to its length (L) and inversely proportional to its cross-sectional area (A).

Equation 2-2

$$R = r\frac{L}{A}$$

Resistivity (r) is a property of the material used which describes its ability to conduct electricity (Giancoli 1995). The quantity of electric current (I) flowing under a given electrical potential (V) can thus be quantified by combining Equations 1 & 2 to explicitly account for both the conducting property and geometry of a conductor:

Equation 2-3

$$I = A\frac{1}{r}\frac{V}{L}$$

Wires or other conductors are generally made of pure metals or alloys for which resistivity and cross-sectional area are constant at stable temperature, so the property that is commonly measured is resistance. Electrical current is quantified using Amperes, which are base SI units (Nelson 1999). Thus, electrical current can only be compared to mass or volume flow of water by analogy.

Darcy's law

Not long after Ohm published his experiments on electrical current and voltage, Darcy (1856) investigated the rate of infiltration of water through saturated sand, resulting in his discovery of the "laws of water flow through sand", commonly known as Darcy's law. Under conditions of laminar, viscous flow, the volumetric flow of water is described by:

Equation 2-4
$$Q = A\,K\,\frac{\Delta H}{L}$$

where Q is the flow or volumetric discharge per unit time (m^3 s^{-1}) through a soil column of cross sectional area A (m^2) and length L (m), ΔH is the hydraulic head difference across the column, and K is the hydraulic conductivity (m s^{-1}) using a head-based measure of the hydraulic gradient. The driving force causing water to flow is described by the drop in hydraulic head per unit distance in the direction of flow, or the hydraulic gradient ($\Delta H/L$). Hydraulic head is potential energy per unit weight (J N^{-1}) (Hubbert 1940). It is the preferred measure of water potential for hydrogeologists and hydrologists because it can be equated to the elevation of the top of a water column, and thus easily measured using piezometers. Darcy's law is mathematically equivalent to the classic linear transport equations of Fourier, Ohm, and Fick (Hillel 1982), and is used as the basis for more complex models that describe unsaturated flow in soils (Hillel 1982, Ryel et al. 2002) and plants (Aumann and Ford 2002). Darcy's Law is typically presented in pedological and geophysical texts (Freeze and Cherry 1979, Rawls et al. 1983, Smith and Wheatcraft 1983, Chow et al. 1988) in the form:

Equation 2-5
$$q = \frac{Q}{A} = K\frac{\Delta H}{L}$$

where q is the water flux (m^3 m^{-2} s^{-1}).

Total water potential is the sum of hydrostatic potential (pressure or tension), osmotic potential and gravitational potential (Nobel 1983). The influence of osmosis on sap flow is generally very low however, since plants transport nearly pure water in xylem (Tyree 1999). Water potential is generally defined as a measure of the potential energy (capacity to do work) of a unit quantity of water (e.g., Hanks 1992), and this driving force can have different dimensions depending on how the unit quantity of water is defined. The use of unit quantities of mass, volume or weight to define water potential is possible because liquid water is a near incompressible fluid (Narasimhan 2003).

Water potential is the term most frequently used by plant physiologists to describe the potential energy per unit volume of water (Niklas 1992). When the unit quantity of water is defined as a volume, water potential has units of pressure (Pa = J m^{-3}) (Tyree 1999), and Darcy's law is expressed as:

Equation 2-6

$$Q = A\,K_{\Psi}\,\frac{\Delta\Psi}{L}$$

where K_{Ψ} is the hydraulic conductivity (m^2 Pa^{-1} s^{-1}) using a pressure-based measure of the hydraulic gradient. I use the symbol K_{Ψ} simply to distinguish between hydraulic conductivity measured using head-based and pressure-based expressions of water potential. Both K and K_{Ψ} have identical physical meaning, only the units differ. Pressure units are the preferred units of measurement for physiologists since leaf or shoot water potential is easily and accurately measured using the pressure chamber technique (Scholander et al. 1964., Richter 1997, Cochard et al. 2001), and stem hygrometers are becoming more reliable (Stöhr and Lösch 2004).

Hydraulic conductivity as described by Darcy's law (Equations 4 or 6) is mathematically equivalent to the inverse of resistivity in Ohm's law (Equation 3). Conductivity is a property of a conductor which describes its ability to conduct either electricity or water and is independent of its geometry, particularly cross-sectional area (A) and length (L). Hydraulic conductivity reflects the combined effects of the properties of the porous medium and the properties of the liquid (Hillel 1982) on the instantaneous bulk flow. When dynamic fluid viscosity (η; Pa s) (Whitehead et al. 1984*a*, Whitehead 1998) is accounted for, the property of the porous medium is permeability (k; m^2). When water potential is expressed using head units (m), permeability can be calculated from:

Equation 2-7

$$k = \frac{Q}{A}\,\frac{L}{\Delta H}\,\frac{\eta}{\rho g}$$

where ρ is density (kg m^{-3}) and g is the acceleration due to gravity (m s^{-2}). When water potential is expressed using units of pressure (Pa or kg m^{-1} s^{-2}), permeability is expressed as:

Equation 2-8 $$k = \frac{Q}{A}\frac{L}{\Delta\Psi}\eta$$

These two expressions are equivalent because the product of head, density and acceleration due to gravity has units of pressure (M L^{-1} T^{-2}).

Hydraulic Properties in Tree Physiology

Early Works

Tree physiologists have applied both an Ohm's law analogy and Darcy's law to the study of plant-water relations. I present the following brief historical discussion in order to provide a context specific to the measurement of the hydraulic properties of woody xylem. Farmer (1918) may have been the first to measure the "water-conductivity" of a variety of species of woody plants to explore the "limitation which the structure of wood" imposes on the flow of water through sapwood xylem. Measurement of the amount of water that transpires from leaves and the water potential (analogous to electrical potential in Equations 1 & 3) of soil and leaves was possible long before reliable techniques existed to measure flow through living stems. In such situations the total resistance to water flow through the plant can be reasonably quantified using an Ohm's law analogy without explicitly quantifying the physical dimensions of stems and branches. An analogy to Ohm's law (Gradman 1928, Huber 1928 (cited in Van den Honert 1948)) was used by early physiologists to quantify the passive resistances to movement of water in plants. Huber (1956) reported on the "specific conductivity" of a variety of species, defined by Kramer and Kozlowski (1960) as the "volume of water moved per unit of time under a given pressure through a segment of given length and cross section". Heine (1971) presented a survey of published values, encouraged the use of "relative conductivity" as opposed to "specific conductivity", and attempted to clarify confusion between different expressions of conductivity. Siau (1971) expanded this discussion to introduce Darcy's law and the terms "permeability" and "specific permeability" to physiologists. Richter (1973) provided a theoretical examination of the Ohm's law analogy with particular attention to the choice of dimensions for "fluxes" and resistances.

Application of Ohm's law analogies

Richter's (1973) detailed account of the dimensions of water flow through trees under an Ohm's law analogy has provided the theoretical basis for many advances in our understanding of the hydraulic architecture of trees. Tyree and Sperry (1988) demonstrated that "hydraulic conductance" (k_h) (i.e. the mass flow rate of water (kg s^{-1}) per unit pressure gradient (dP/dl)) is positively related to stem diameter. In a related paper, Tyree (1988) defined "hydraulic conductivity" and used an electrical analogue to develop a dynamic model for water flow in a single tree. The models of Tyree and Sperry (1988) and Tyree (1988) have, until very recently, represented the state-of-the-art in tree water flow modeling because of their ability to link the functional aspects of the hydraulic system to its branched structure (Fruh and Kurth, 1999).

Tyree and Ewers (1991), in a thorough and heuristic examination of the hydraulic architecture of trees, presented an Ohm's law analogy using the following terms:

Equation 2-9

$$F_{AB} = k_{AB}(\Psi_A - \Psi_B)$$

Where F_{AB} is the "water flux" (kg s^{-1}), k_{AB} is the "hydraulic conductance" (kg s^{-1} MPa^{-1}), and $\Psi_A - \Psi_B$ is the "water potential drop across the structure" (MPa). This formulation is consistent with the quantification of electrical "flux", "conductance" and "potential". "Hydraulic conductivity" (k_h; kg m s^{-1} MPa^{-1}) was defined as:

Equation 2-10

$$k_h = F/(dP/dx)$$

where F is the "water flux" (kg s^{-1}), and (dP/dx) is the "pressure gradient causing the flow" (MPa m^{-1}). However, this formulation of conductivity is not analogous to the inverse of resistivity ($\frac{1}{r}$ in Equation 2-3), nor is it equivalent to K of Darcy's law (Equation 2-4). The effect of cross sectional area on flow is not accounted for in Equation 2-10. Increases in conducting cross-sectional area with increasing stem diameter will result in higher flow that does not necessarily reflect a change in the hydraulic conductivity of the sapwood xylem through which flow occurs.

Hydraulically, an Ohm's law analogy as presented in Equations 2-9 and 2-10 describes a flow of water (volume per unit time) rather than a flux (volume per unit time per unit area). In soil physics (Hillel 1982) and hydrology (Freeze and Cherry 1979, Rawls et al. 1983, Smith and Wheatcraft 1983, Chow et al. 1988) flux is consistently defined as the flow per unit conducting surface area. This confusion is understandable since "flux" is a term with a variety of physical definitions, and the physical size of the metal conductor is not explicitly included in the common expressions of Ohm's law (Equation 2-1). Indeed, in Slayter's (1967) textbook devoted to plant-water relations, a mass per time and a mass per time per unit area are both referred to as a "flux", despite clear differences in physical meaning.

Applications of Darcy's law

Darcy's law is used in a number of fields to quantify the conducting properties of porous media to liquids and gasses, and is the foundation upon which more complicated three-dimensional models of saturated and unsaturated flow through porous media have been developed (Hillel 1982, Aumann and Ford 2003). Zimmerman (1978), in his investigation into the hydraulic architecture of trees, defined "hydraulic conductivity" consistent with Siau's (1971, 1984) definition of "permeability" and Jarvis's (1975) "conductivity" but did not cite either author. Darcy's law has been invoked more than 30 times[2] in publications wherein sapwood hydraulic properties are quantified (e.g. Reid et al. 2004), or when modeling the relationship between bulk flow of water through saturated woody xylem and the water potential gradient driving flow (e.g. Whitehead 1998). Some authors who cite Darcy have used the term permeability, presented as Equation 2-8 (e.g. Pothier et al. 1989*a*, 1989*b*), but this definition has also been referred to by a variety of other names (see Table 1). In all cases where bulk flow through woody xylem is measured, the area term is calculated from sapwood area (A_s), since heartwood is not involved with water transport (Tyree and Ewers 1991). Despite these numerous references, terminology, units, and symbols are not always consistent with standard formulations of Darcy's law in related hydrologic fields. Furthermore, definitions of "hydraulic conductivity" (similar to k_h; Equation 2-10) have incorrectly been referred to as Darcy's law.

---

[2] Including Booker (1977), Whitehead and Jarvis (1981), Edwards and Jarvis (1982), Whitehead et al. (1984*a* & 1984*b*), Edwards et al. (1986), Whitehead and Hinkley (1991), Mencuccini and Grace (1995), Mencuccini et al. (1997), Ewers et al. (2000), Mencuccini and Bonosi (2001), McDowell et al. (2002), and Mencuccini (2002) in addition to others referenced directly in the text.

A Proposal for a Unified Nomenclature

Ohm's law and Darcy's law are mathematically equivalent; therefore, the use of an analogy to Ohm's law is not needed to describe water flow through xylem of stems or branches where the dimensions of the conducting tissues are quantifiable. The use of an analogy is justified when the analogy is easier to understand and/or more complete than a proper theory, or when students and researchers are more familiar with the properties of an analog than with the proper theory (Fiscus and Kaufmann 1990). Darcy's law is an explicit hydraulic theory that can account for fluid viscosity, and offers greater potential to address issues of water storage, and transient flow in unsaturated sapwood xylem. It therefore serves as a robust theoretical framework for describing the flow of water through woody xylem. The Ohm's law analogy may be familiar, but it is not a more complete theory for describing the hydraulic properties of porous media, nor is it easier to understand than Darcy's law. I therefore propose that tree physiologists adopt the units, nomenclature, and terminology used to quantify water conducting properties of sapwood xylem typically used in the context of Darcy's law (Table 1). Darcy's law provides a means by which the water conducting property of sapwood xylem can be quantified, and easily described and understood by scientists from all hydrologic disciplines.

The foundation of my proposal is that hydraulic conductivity (K_Ψ; Equation 6), be defined as the constant of proportionality between volume flow rate of water per unit conducting surface area and the hydraulic gradient. A flow (amount per time) per conducting surface area is a flux, and a hydraulic gradient is the difference in water potential per unit of length across which the difference exists. I advocate the adoption of the terms and SI units defined in Table 1 to quantify hydraulic properties of sapwood xylem, consistent with terms used by most other physical earth sciences to quantify hydraulic properties of other porous media. Measurement of water potential of living trees and woody plants can be done using a variety of instruments which measure pressure, or potential energy per unit volume (Cochard et al. 2001). Tree physiologists are thus likely to be more comfortable using K_Ψ ($m^2\ Pa^{-1}\ s^{-1}$) to quantify hydraulic conductivity, though using K ($m\ s^{-1}$) is also correct (see Table 1 for conversion).

I discourage the use of the term "specific conductivity", to describe K_Ψ since 'specific' has a variety of meanings and for this reason could be a source of confusion for readers from different backgrounds. As was pointed out by Heine (1971) and Jarvis (1975) some have suggested that the term 'specific' only be used where 'divided by mass' is the intended meaning (Symbols

Committee of the Royal Society 1975), though it can also mean 'per area'. The phrase "specific conductivity" is also sometimes used synonymously with temperature compensated electrical conductivity in describing water quality (Stuart et al. 1995, Patni et al. 1996) or the chemical composition of soil amendments (Bouranis et. al. 1997). To minimize confusion, I suggest hydraulic conductivity be adopted as the standard term to describe K_Ψ.

An advantage of using Darcy's law and hydraulic conductivity (K_Ψ) is that permeability (k) can also be directly determined. Permeability (k) allows researchers to disentangle the combined effects of the dynamic fluid viscosity of the liquid and the conducting property of the porous medium. Permeability (k) can be correctly quantified using either head or pressure units for water potential (Equation 2-7 or 2-8) and substituting sapwood area (A_s) for the area term. Since most measurements are made under laboratory conditions, where temperature effects on the viscosity of water are negligible, k and K_Ψ are likely to show strongly similar patterns of variability between samples. Determination of k in the field requires measurement of the fluid temperature (Whitehead et al. 1984*b*). In research reporting "specific conductivity", flow measurements are sometimes corrected to what would be expected at 20°C (e.g. Spicer and Gartner 1998, Spicer and Gartner 2001, Gartner et al. 2003, Liu et al. 2003), but not always (Stout and Sala 2003, Pitterman and Sperry 2003). The intent of correcting "specific conductivity" to a standard temperature reflects a desire to standardize hydraulic measurements by accounting for slight differences in the viscosity of the flowing liquid. I suggest that this unnecessarily complicates the literature as permeability (k) specifically accounts for the effect of viscosity, and new terms are not required where well established terms for hydraulic properties already exist. Hydraulic conductivity and permeability are sufficient as long as there is a clear understanding of the difference between K_Ψ and k.

If K_Ψ or k is known, the capacity of a stem segment to pass water or the hydraulic capacity (Q_h) can be defined using the symbols presented in Table 1 as:

Equation 2-11

$$Q_h = K_\Psi \ A_s = \frac{k}{\eta} A_s$$

where Q_h describes the flow (volume per unit time) that would occur under a unit hydraulic gradient. This parameter is very useful to describe the combined effects of hydraulic conductivity and conducting sapwood area in regulating flow through stems or in modeling saturated flow through whole trees under a known hydraulic gradient. While the phrase and symbol are new to the literature, the idea is not. This term is equivalent to "hydraulic conductivity (k_{h})" as defined by Tyree and Ewers (1991) (Equation 2-9) and to the definition published elsewhere using the symbol Q^* (Reid et al. 2003, Liu et al. 2003, Reid et al. 2004). I propose that physiologists use the symbol Q_{h} in an effort to limit confusion because Q^* is generally used as the symbol for net radiation in descriptions of bulk transfer of water to the atmosphere (Oke 1987).

Because leaves are dependent on the conducting xylem for water, the water conducting properties of xylem can influence photosynthetic efficiency. Zimmerman (1978) first recognized the functional biological importance of this physiological relationship in his formulation of "leaf specific conductivity". Zimmerman calculated this parameter by substituting leaf area distal to the stem segment measured in place of the sapwood area term (A_{s}) in Equation 2-6. While I recognize the utility of this measure, I believe that the term "leaf specific conductivity" is inappropriate because this formulation does not describe a property of the conducting tissue (i.e., a measure of conductivity per unit area or mass), but describes a functional relationship between the flow capacity of a stem or branch and the distal leaf area it supports. Further, the use of a similar symbol (typically k_{L} or K_{L}) incorrectly implies that it is a hydraulic property of xylem analogous to K_{Ψ} or k.

The relationship between the water conducting property of xylem and leaf area can be appropriately quantified by dividing Q_{h} by the leaf area distal to the stem segment measured (i.e. $Q_{\mathrm{h}}/A_{\mathrm{l}}$). Again, although this idea is not new to the literature, I propose using leaf specific hydraulic capacity as the standard term, and Q_{L} as the standard symbol, to describe this important functional relationship. I suggest the use of a capital 'L' for a sub-script to distinguish this term from leaf-related sap flow (Q_{l}) measured using thermal dissipation methods (Edwards et al. 1996). Leaf specific hydraulic capacity is mathematically equivalent to the formulations of "leaf specific conductivity" presented by Zimmerman (1978) and Tyree and Ewers (1991).

Comment on Conductance

Conductance is not analogous to any of the terms I am suggesting be adopted to describe sapwood xylem hydraulic properties since the length of the sapwood xylem is explicit in defining the hydraulic gradient and the conducting sapwood surface area is explicit in defining the water flux. Conductance integrates the influences of length, cross sectional area, and conductivity of the porous medium on the instantaneous flow of water at any point in the flow path. Strictly speaking, hydraulic conductance is the constant of proportionality between the rate of flow (volume or mass per time) and the water potential or hydraulic head difference that is producing the flow in a saturated porous medium. Using a symbol proposed by Jarvis (1975), conductance (G, $m^3\ s^{-1}\ Pa^{-1}$) can be defined as:

Equation 2-12 $$G = Q / \Delta\Psi$$

In the tree physiology literature, conductance in the context of whole tree water movement is often presented using the letter 'G' or 'g' with various subscripts depending on how it is employed (e.g. Rayment et al. 2000, Martínez-Vilalta et al. 2003). Division of Q_h by the length of a sample is also mathematically analogous to G, but I suggest that G only be used to describe the limitation on water flow through sapwood xylem when the dimensions of the tissues that water is flowing through are accounted for (e.g. Mencuccini and Grace 1996*b*) or unknown (Tyree et al. 1995), and K_Ψ can reasonably be expected to remain more or less constant along the entire path length.

It is sometimes very useful, to calculate leaf specific hydraulic conductance (or conductance per unit leaf area) when investigating canopy water relations of trees or stands. When Q, $\Delta\Psi$, and A_l are quantifiable, leaf specific hydraulic conductance can be used to better understand dynamic water stress in the canopy caused by transpiration (e.g. Phillips et al. 2002). I strongly suggest researchers examining this issue use the symbol 'G_L' to denote leaf specific hydraulic conductance since conductance is both qualitatively and quantitatively different from hydraulic conductivity (K_Ψ) and permeability (k).

Conclusion

Adoption of Darcy's law as a framework to describe the water conducting properties of woody xylem in no way minimizes the insights in published works which have utilized the Ohm's law analogy. Understanding of the biophysical factors which influence water transport through trees has been greatly advanced by work which has employed the Ohm's law analogy. Darcy's law similarly provides a defensible and theoretically sound framework within which changes in the water conducting properties of sapwood xylem can be effectively quantified. I hope that this manuscript will inspire researchers studying tree physiology to consistently use terminology and units that are familiar to the broader scientific community as they continue to investigate the ecological factors which influence water movement through trees.

Table 2-1: Symbols and Definitions for quantification of hydraulic characteristics of sapwood xylem.

Symbol	*Definition*	SI Units	*Not Recommended*
Q	volume[*] flow per unit time at any point	$m^3 s^{-1}$	flux, F, q, v, J
A_s	sapwood conducting surface area	m^2	
q	water flux	$m^3 m^{-2} s^{-1}$	Flow
L	length of sample through which water is flowing	m	
ΔH	hydraulic head difference across a sample	m	
$\Delta\Psi$	water potential difference across a sample	Pa	diffusion pressure deficit (D.P.D.), ΔP
η	dynamic fluid viscosity	Pa s	
ρ_w	density of water	$kg\ m^{-3}$	
g	acceleration due to gravity	$m\ s^{-2}$	
K_Ψ	hydraulic conductivity (equation 2-6)	[**] $m^2 Pa^{-1} s^{-1}$	specific conductivity, conductance, permeability, k_s, σ, K_s, L
k	permeability (equations 2-7 & 2-8)	m^2	relative conductivity, specific conductivity, specific permeability, permeability constant, k value, K, k_s
Q_h	hydraulic capacity under a unit hydraulic gradient (equation 2-11)	$m^4 Pa^{-1} s^{-1}$	hydraulic conductivity, conductivity, hydraulic conductance, K, k, k_h, K_h, Q^*, $\hat{K}$, COND
Q_L	leaf specific hydraulic capacity (Q_h/A_L)	$m^2 Pa^{-1} s^{-1}$	leaf specific conductivity, leaf specific conductance, K_L, k_L LSC

---

[*] unit volume of water can be easily converted to unit mass of water by multiplying by ρ_w

[**] $K = K_\Psi \times \rho_w g$; generally one m of head is equivalent to about 9.8 kPa (Horvath 1986)

References

Aumann, C.A. and E.D. Ford. 2002. Modeling tree water flow as an unsaturated flow through a porous medium. J. Theor. Biol. 219: 415-429.

Baird, A.J. and R. Wilby (eds.). 2001. Eco-Hydrology: Plants and Water in Terrestrial and Aquatic Environments. Routledge, New York.

Booker, R.E. 1977. Problems in the measurement of longitudinal sapwood permeability and hydraulic conductivity. N.Z. J. For. Sci. 7(3): 297-304.

Booker, R.E. and J.A. Kinninmonth. 1978. Variation in longitudinal permeability of green radiata pine wood. N.Z. J. For. Sci. 8(2): 295-308.

Bouranis, D.L., A.G. Vlyssides, J.B. Drossopoulos, D.G. Economides, B. Mourafeti and D.G. Drissis. 1997. Physicochemical characteristics of a new organic soil conditioner from composted sludges from a pulp deinking process. Commun. Soil Sci. Plan. 28 (17-18): 1549-1564.

Chow, V.T., D.R. Maidment and L.W. Mays. 1988. Applied Hydrology. McGraw-Hill Inc. New York.

Comstock, J.P. and J.S. Sperry. 2000. Theoretical considerations of optimal conduit length for water transport in vascular plants. New Phytol. 148: 195-218.

Cochard, H., S. Forestier and T. Ameglio. 2001. A new validation of the Scholander pressure chamber technique based on stem diameter variations. J. Exp. Bot. 52(359): 1361-1365.

Darcy, H. 1856. Determination of the laws of flow of water through sand (in French). *In*: Les Fontaines Publiques de la Ville de Dijon pp.590-594. Paris: Victor (available at http://biosystems.okstate.edu/darcy)

Eagleson, P.S. 2002. Ecohydrology. Cambridge University Press, Cambridge UK. 443p.

Edwards, W.R.N. and P.G. Jarvis. 1982. Relations between water content, potential and permeability in stems of conifers. Plant Cell Environ. 5:271-277.

Edwards, W.R.N., P.G. Jarvis, J.J. Landsberg and H. Talbot. 1986. A dynamic model for studying flow of water in single trees. Tree Phys. 1:309-324.

Ewers, B.E., R. Oren and J.S. Sperry. 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda.* Plant Cell Environ. 23(10): 1055-1066.

Farmer, J.B. 1918. On the quantitative differences in the water-conductivity of the wood in trees and shrubs. Proc. R. Soc. B 90: 218-250.

Freeze, R.A. and J.A. Cherry. 1979. Groundwater. Prentice Hall, Englewood Cliffs, NJ.

Fiscus, E.L. and M.R. Kaufmann. 1990. The nature and movement of water in plants. *In*: Irrigation of Agricultural Crops. Eds. B.A. Stewart and D.R. Nielsen. Vol.30 Agronomy Chap.8 pp.191 –241.American Society of Agronomy, Madison, WI.

Fruh T. and W. Kurth. 1999. The hydraulic system of trees: Theoretical framework and numerical simulation. J. Theor. Biol. 201 (4): 251-270.

Gartner, B.L. 1995. Patterns of xylem variation within a tree and their mechanical consequences. *In*: Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, New York, pp 125-149.

Gartner, B.L., J. Roy and R. Huc. 2003. Effects of tension wood on specific conductivity and vulnerability to embolism of Quercus ilex seedlings grown at two atmospheric CO2 concentrations. Tree Physiol. 23(6): 387-395

Giancoli, D.C. 1995. Physics: principles with applications 4th Ed. Prentice Hall, Englewood Cliffs, NJ.

Hanks, R.J. 1992. Applied Soil Physics: Soil Water and Temperature Applications 2nd Ed. Springer-Verlag, New York.

Heine, R.W. 1971. Hydraulic conductivity in trees. J. Exp. Bot. 22:503-511.

Hillel, D. 1982. Introduction to Soil Physics. Academic Press Inc., Orlando.

Horvath, A.L. 1986. Conversion tables of units in science & engineering. Macmillan, London. 147 p.

Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old Pinus ponderosa trees. Tree Physiol. 19: 165-172.

Hubbard, R.M., V. Stiller, M.G. Ryan and J.S. Sperry. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. Plant Cell Environ. 24:113–121.

Hubbert, M.K. 1940. The theory of ground-water motion. J. Geol. 48(8): 785-944.

Huber, B. 1928. Weitere quantitative untersuchungen uber das wasserletiungssystem der pflanzen. Jb. wiss. Bot. 67: 877-859.

Huber, B. 1956. Die Saftstrome der pflanzen. Springer-Verlag, Berlin.

Jarvis, P.G. 1975. Water transfer in plants. *In*: Heat and Mass Transfer in the Plant Environment. Part 1. Eds. D.A. deVries and N.G. Afgan. Scripta Book Co., Washington D.C. pp 369-394.

Koch, G.W., S.C Sillet, G.M. Jennings and S.D. Davis. 2004. The limits to tree height. Nature 428:851-854.

Kramer, P.J. and T.T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill, New York

Larcher, W. 1980. Physiological Plant Ecology. Springer-Verlag, Berlin.

Liu, X., U. Silins, V.J. Lieffers and R. Man. 2003. Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. Can. J. For. Res. 33: 1295-1303.

Martínez-Vilalta, J., M Mangirón, R. Ogaya, M. Sauret, L. Serrano, J. Penuelas and J. Pinol. 2003. Sap-flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. Tree Phys. 23:747-758.

McDowell, N.G., N. Phillips, C. Lunch, B.J. Bond and M.G. Ryan. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiol. 22 (11): 763-774.

Meinzer, F.C. G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Gutierrez and J. Cavelier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species – the influence of boundary-layer and hydraulic properties. Oecologia 101: 514-522.

Meinzer, F.C., M.J. Clearwater and G. Goldstein. 2001. Water transport in trees: current perspectives, new insights and some controversies. Environmental and Experimental Botany 45: 239-262.

Mencuccini, M. 2002. Hydraulic constraints in the functional scaling of trees. Tree Phys. 22:553-565.

Mencuccini, M. and J. Grace. 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Phys. 15:1-10.

Mencuccini, M. and J. Grace. 1996*a*. Hydraulic conductance, light interception and needle nutrient concentration in Scots pine stands and their relations with net primary productivity. Tree Phys. 16:459-468.

Mencuccini, M. and J. Grace. 1996*b*. Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. Plant Cell Environ. 19:939-948.

Mencuccini, M., J. Grace., and M. Fioravanti. 1997. Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. Tree Phys. 17:105-113.

Mencuccini, M. and L. Bonosi. 2001. Leaf area/sapwood area ratios in Scots pine show acclimation across Europe. Plant Cell Environ. 19:939-948.

Narasimhan, T.N. 2003. "Maxwell, Electromagnetism, and Fluid Flow in Resistive Media". EOS 84(44): 469, 474-475.

Nelson, R.A. 1999. Guide for metric practice. Physics Today 52: 11-12.

Ohm, G.S. 1827. Die galvanische Kette, mathematisch bearbeitet. Berlin.

Oke, T.R. 1987. Boundary layer climates. 2nd ed., Routledge, New York.

Patni, N.K., L. Masse, and P.Y. Jui. 1996. Tile effluent quality and chemical losses under conventional and no-tillage. 1. Flow and nitrate. Trans. ASAE. 39(5): 1665-1672.

Phillips, N., B.J. Bond, N.G. McDowell and M.G. Ryan. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. Tree Phys. 22:205-211.

Pitterman, J. and J. Sperry. 2003. Tracheid diameter is the key trait determining the extent of freezing-induced embolism in conifers. Tree Physiol. 23: 907-914.

Pothier D., Margolis, H.A., and Waring, R.H. 1989*a*. Patterns of change in saturated sapwood permeability and conductance with stand development. Can. J. For. Res. 19: 432-439.

Pothier D., Margolis, H.A., Poliquin, J., and Waring, R.H. 1989*b*. Relation between the permeability and the anatomy of jack pine sapwood with stand development. Can. J. For. Res. 19: 1564-1570.

Protz, C.G., Silins, U., and Lieffers, V.J. 1999. Reduction in branch sapwood hydraulic permeability as a factor limiting survival of lower branches of lodgepole pine. Can. J. For. Res. 30: 1088-1095.

Rawls, W.J., L.R. Ahuja, D.L. Brakensiek and A. Shirmohammadi. 1983. Infiltration and soil water movement. *In*: Handbook of Hydrology. Ed. D.R. Maidment. McGraw-Hill, New York. pp 5.1-5.51.

Rayment, M.B., D. Loustau and P.G. Jarvis. 2000. Measuring and modeling conductances of black spruce at three organizational scales: shoot, branch and canopy. Tree Phys. 20:713-723.

Reid, D.E.B., U. Silins and V.J. Lieffers. 2003. Stem sapwood permeability in relation to crown dominance and site quality in self-thinning fire-origin lodgepole pine stands. Tree Phys. 23: 833-840.

Reid D.E.B., V.J. Lieffers and U. Silins. 2004. Growth and crown efficiency of height repressed lodgepole pine; are suppressed trees more efficient? Trees 18(4): 390-398.

Richter, H. 1973. Frictional potential losses and total water potential in plants: a re-evaluation. J. Exp. Bot. 24: 983-994.

Richter, H. 1997. Water relations of plants in the field: some comments on the measurement of selected parameters. Journal of Experimental Botany. 48(306): 1-7.

Ryan, M. J. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. Bioscience 47:235–242.

Ryel, R.J., M.M. Caldwell, C.K. Yoder, D. Or, and A.J. Leffler. 2002. Hydraulic redistribution in a stand of Artemisia tridentata: evaluation of benefits to transpiration assessed with a simulation model. Oecologia 130:173–184.

Scholander, P.F., H.T. Hammel, E.A. Hemmingsen and E.D. Bradstreet. 1964. Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proceedings of the National Academy of Sciences, USA. 52: 119-125.

Siau, J.F. 1971. Flow in Wood. Syracuse University Press, Syracuse, New York.

Siau, J.F. 1983. Transport Processes in Wood. Springer-Verlag, Berlin Heidelberg New York.

Slayter, R.O. 1967. Plat-Water Relations. Academic Press, London and New York.

Smith, L. and S.W. Wheatcraft. 1983. Groundwater flow. *In*: Handbook of Hydrology Ed. D.R. Maidment. McGraw-Hill, New York. pp 6.1-6.58.

Sperry, J.S. 1995. Limitations on Stem water transport and their consequences *In*: Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, New York, pp 105-124.

Sperry, J.S., J.R. Donnelly and M.T. Tyree. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ. 11: 35-40.

Spicer, R. and B.L. Gartner. 1998. Hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) branches and branch halves with reference to compression wood. Tree Phys. 18: 777-784.

Spicer, R. and B.L. Gartner. 2001. The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. Trees 15: 222-229.

Stöhr, A. and R. Lösch. 2004. Xylem sap flow and drought stress of *Fraxinus excelsior* saplings. Tree Phys. 24: 169-180.

Stout, D.L. and A. Sala. 2003. Xylem vulnerability to cavitation in Pseudotsuga menziesii and Pinus ponderosa from contrasting habitats. Tree Physiol. 23: 43–50

Stuart, M.A., F.J. Rich and G.A. Bishop. 1995. Survey of nitrate contamination in shallow domestic drinking water wells of the Inner Coastal Plain of Georgia. Ground Water. 33(2):284-290.

Symbols Committee of the Royal Society. 1975. Quantities, Units, and Symbols 2nd Ed. The Royal Society, London.

Tyree, M.T. 1988. A dynamic model for water flow in a single tree: evidence that models must account for hydraulic architecture. Tree Phys. 4:195-217.

Tyree, M.T. 1997. The cohesion-tension theory of sap ascent: current controversies. J. Exp. Bot. 48:1753-1765.

Tyree, M.T. 1999. Water relations of plants. *In*: Eco-hydrology. Eds. A.J. Baird and R.L. Wilby. Routledge, New York, pp 11-38.

Tyree, M.T. 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees. 17:95-100.

Tyree, M.T. and F.W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119: 345-360.

Tyree, M.T., S. Patino, J. Bennink and J. Alexander. 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. Journal of Experimental Botany. 46: 83-94.

Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers form a model. Plant Pysiol. 88: 574-580.

Tyree, M.T. and M.H. Zimmerman. 2002. Xylem structure and the ascent of sap, 2nd edn. Springer-Verlag, Berlin Heidelberg New York.

van den Honert, T.H. 1948. Water transport in plants as a catenary process. Discuss. Faraday Soc. 3: 146-153.

Whitehead, D. 1998. Regulation of stomatal conductance and transpiration in forest canopies. Tree Physiol. 18:633–644.

Whitehead, D and P.G. Jarvis. 1981. Coniferous Forests and Plantations *In*: Water Deficits and Plant Growth Vol. 6. Ed. T.T. Kozlowski. Academic Press, New York, pp. 49-52.

Whitehead, D., Edwards, W.R.N., and Jarvis, P.G. 1984*a*. Conducting sapwood area, foliage area, and permeability in mature trees of Picea sitchensis and Pinus contorta. Can. J. For. Res. 14: 940-947.

Whitehead, D., P.G. Jarvis and R.H. Waring. 1984*b*. Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment. Can. J. For. Res. 14: 692-700.

Whitehead, D. and T.M. Hinkley. 1991. Models of water flux through forest stands: critical leaf and stand parameters. Tree Phys. 9:35-57.

Ziatchick, B.F., H.M. van Es and P.J. Sullivan. 2003. Modeling slope stability in Honduras: parameter sensitivity and scale of aggregation. Soil Sci. Soc. Am. J. 67:268-278.

Zimmerman, M.H. 1978. Hydraulic architecture of some diffuse-porous trees. Can. J. Bot. 56:2286-2295.

Chapter 3

Stem sapwood permeability in relation to crown dominance and site quality in self-thinning fire origin lodgepole pine stands[5]

Introduction

Differentiation of individual trees into dominance classes is a result of competitive interactions between individuals building upon inherent factors affecting growth rates such as differences in genotype or microsite. Size differences are expanded by one-sided competition (Weiner and Thomas 1986), wherein larger individuals secure proportionally more resources and improve their growth rate at the expense of smaller individuals (Oliver and Larsen 1990). This eventually results in self-thinning (Peet and Christansen 1987). These interactions among trees of different competitive rank result in changes in phenotype, crown size and arrangement of foliage (Xu and Harrington 1998), and leaf physiology. In addition, the rate of stand development and self-thinning varies considerably among sites of differing site quality or site index (Oliver and Larson 1990). For this reason, stand density and site quality covary in unmanaged stands, which can result in differences in density between similar aged stands of different site quality (Pothier et al. 1989a, 1989b).

Sapwood permeability can influence photosynthesis and productivity by affecting stomatal conductance in response to dynamic water stress (Whitehead 1998). I suspect that competitive rank would also influence hydraulic properties of sapwood, which would have a long-term impact on growth and competitive processes. Recent exploration of sapwood hydraulic characteristics has focused on the climatic factors that affect the hydraulic architecture of trees (Mencuccini and Grace 1995, DeLucia et al. 2000, Mencuccini and Bonosi 2001) and the influence of hydraulic architecture on ecological processes governing forest stand dynamics (Mencuccini and Grace 1996a, Mencuccini and Grace 1996b, Mencuccini et al. 1997, Ryan and Yoder 1997, Hubbard et al. 1999, Magnani et al. 2000). Growth rate is positively associated with sapwood permeability,

---

[5] A slightly different version of this chapter has been published.

Reid, D.E.B., U. Silins and V.J. Lieffers. 2003. Stem sapwood permeability in relation to crown dominance and site quality in self-thinning fire origin lodgepole pine stands. Tree Physiology. 23:833–840. © 2003 Heron Publishing -Victoria, Canada since trees from better quality sites (as measured by site index) have more permeable sapwood (Pothier et al. 1989a, Pothier et al. 1989b). To date, there have been no studies that have explored differences in sapwood hydraulic characteristics between dominant, co-dominant, and suppressed trees in self-thinning stands, or how these differences may interact with differences in site quality.

The principal objective of this study was to explore how leaf area, sapwood area, and sapwood permeability varies between dominant, co-dominant, and suppressed lodgepole pine trees from medium and low sites. Since the flow rate through an ideal capillary increases by the fourth power of its radius (Zimmerman 1983), and earlywood tracheids have larger lumen diameters than latewood (Saranpaa 1984), I hypothesized that competitive dominants or faster growing individuals from better site conditions would have more permeable stem sapwood owing to a greater proportion of earlywood. I was also interested in how crown class differentiation might be related to differences in radial variation of sapwood conductivity (Shelburne and Hedden 1996). Ultimately, my intention was to explore the balance between leaf area and the ability of the stem to supply water to leaves, and what role this balance may play in competitive dynamics of these stands.

Materials and Methods

Site Selection and Sample Tree Characteristics

All plots were located within the Gregg River Burn (56,000 ha, burned in 1956), *ca.* 50 km south of Hinton, Alberta. The terrain is hilly, with soils derived from glaciofluvial, glaciolacusterine and eolian deposits. All trees were sampled from plots established between 53°8' and 53°17'N and 117°15' and 117°27'W and between 1200-1300 m elevation. Normal annual precipitation (1962-1992) is 452 mm, with almost half (197mm) falling as snow (Environment Canada 1993). Sample trees were taken from fully occupied even aged lodgepole pine stands showing signs of mortality and crown class differentiation, which were free of disease and not subject to a permanent or periodic high water table (no mottling or evidence of gleying observed in a 75cm soil pit). Sites were identified as Medium (M) or Low (L) based on ecological association and density (Table 3-1). Sites of each type were also similar in terms of site index, calculated based upon heights of dominants using a locally derived height-site index-age model (Huang et al. 1997). All sites were fully occupied since Reineke's (1933) stand density index (SDI) was greater than 600 (Long, 1985) and spacing factors were below 15% (Day, 1997). The SDI for a stand is the number of trees per hectare as if the diameter of a tree of average basal area were 25 cm (see footnote to Table 3-1 for formula).

Plots were randomly located during the summer of 1999 in each of six M sites and six L sites; circular plot radius varied from 5.64 m to 2 m depending on density and included 28-54 trees. Age of all stands, determined from basal disks, was 37 - 46 years, except for stand M-5 that was 63 years old. Three healthy sample trees from each plot were selected for harvesting, one each from dominant (D), co-dominant (CD) and suppressed (SP) categories according to Oliver and Larson (1990). A total of 36 trees were harvested. Canopy trees (D&CD), while interacting on all sides with neighbours were not physically restricted from above; D trees were taller than their immediate neighbours. Suppressed trees (SP) were overtopped. In each plot, the D tended to be one of the largest trees, the CD was generally an average sized tree, and the SP tended to be one of the smallest (Table 3-2). Only SP trees with healthy leaders, and showing no sign of damage or disease were sampled; as a result, in some plots the SP tree was selected from just outside of the plot. I measured diameter at breast height (dbh) of all trees within each plot, and trees with regular cylindrical stem form (for measurement of conductivity) were selected. Standing dead trees in sampled plots were common on M sites (3100 ± 1369 per ha), but almost completely absent from L site plots.

Field Sampling

To account for differences in branch morphology and specific weight of needles growing in different degrees of shade, crowns of all D and CD trees were divided into three sections of equal length. For each of three crown sections, all branches were cut at their base, and weighed fresh. The fresh weight of a representative (median) branch from each section of each tree was also measured using a calibrated (10 g accuracy) spring balance, and all needles from this branch were collected and taken to the lab in sealed plastic bags and stored at 5 °C until processed. All live needles from the crowns of SP trees were harvested, sealed in plastic bags, transported under ice and stored at 5 °C until processed.

Stem samples used to measure hydraulic characteristics were approximately 1 m long and centered on 1.3 m height. All samples were placed in moistened, airtight plastic bags in the field, stored in an insulated box covered with ice, and transported to the lab. Samples were then double bagged and frozen at –15 °C within 12 hours of harvest.

While freeze thaw cycles in stems under tension is known to cause cavitation and loss of conductivity (Sperry and Sullivan 1992, Sparks et al. 2001), small diameter conifer tracheids are relatively resistant to cavitation by freezing (Davis et. al. 1999, Sperry and Robinson 2001) and the water columns in my frozen stem samples were not under tension. In order to test whether freezing and thawing of excised stem sections caused cavitation, eight similar-sized (dbh 5-8 cm) lodgepole pine trees were harvested and two sample sections (below the live crown) from each tree collected. Permeability (*k*) was measured immediately after transport to the lab on half the sections collected (4 upper sections and 4 lower sections). The remaining eight sections from the same trees were frozen and thawed as described below prior to measurement of *k*. There were no significant differences ($P = 0.63$) in mean *k* between fresh ($k = 2.53 \pm 0.01 \times 10^{-12}$ m^2) and frozen ($k = 2.73 \pm 0.25 \times 10^{-12}$ m^2) samples.

Laboratory Processing

Projected leaf area of foliage was measured from scanned images of a sub-sample of needles from each representative branch (or whole crown in the case of suppressed trees), using Sigma Scan-Pro® image analysis software. Needle specific area (cm^2 g^{-1}) was determined from the dry weight (measured to the nearest 0.1 g) of the scanned sub-sample. The dry weight of all needles from each branch was also measured. The leaf area of each crown section (A_l; m^2) was calculated by:

Equation 3-1 $$A_l = A_n * (w_n/w_b) * w_B$$

Where; A_n is needle specific area (m^2 g^{-1}), w_n is the dry weight of needles from the representative branch, w_b is the fresh weight of the representative branch, and w_B is the fresh weight of all branches in the section. All leaves of suppressed crowns were taken to the lab, and leaf area was determined by multiplying needle specific area by the dry weight of all live needles.

From each stem section harvested, a 1 cm disk cut at breast height (1.3 m) was used to measure sapwood area. The sapwood heartwood boundary was determined from apparent differences in water content on freshly cut, frozen samples. Where the sapwood-heartwood boundary was unclear, the disk was held up to a light, and opaque heartwood marked with a pencil. Each disk was scanned, and sapwood area (A_s) measured digitally from the image. The leaf area / sapwood area ratio (S, m^2 cm^{-2}) was determined for each sample from these measurements.

Sapwood Hydraulic Characteristics

Permeability measurements were made on a 12-20 cm long sub-section of the stem sample collected; re-cut immediately above or below breast height (1.3 m) depending on the position of branch nodes. Sample position was adjusted so that there were no branch nodes near the cut ends to facilitate attachment to the permeability apparatus. Samples were cut while frozen to prevent the introduction of embolism to the end cut. Samples were thawed overnight, submerged in water to prevent drying, with 10 mmol L^{-1} oxalic acid to suppress growth of bacteria and fungi. Once completely thawed, the remainder of the bark was peeled off, and the ends were planed with a sharp low angle (20°) block plane. All measurements were completed within 1 month of collection.

Each sample was installed into a constant head permeability apparatus using a hanging water column to generate 16.75 kPa of pressure head ($\Delta\Psi$) (after Protz et al. 1999). Samples were attached to the water column using plastic caps fitted with rubber tubing clamped to the sample. Permeability measurements were made using degassed water at room temperature, and outflow was constantly recorded using an electronic balance. Once flow stabilized (usually within 5 minutes), the average flow rate over the next 20 minute period was used to calculate permeability. Because the flow rate through some of the suppressed tree samples was very slow, outflow of water was measured for a longer period of time (up to 200 minutes). In all cases the reservoir on the scale was covered to prevent evaporation from the pan during measurement of flow rate.

Hydraulic conductivity (K_Ψ; m^2 Pa^{-1} s^{-1}) was determined using Darcy's Law after Hillel (1982):

Equation 3-2

$$K = \frac{Q}{A_s}\frac{L}{\Delta\Psi}$$

where Q is the flow rate (m^3 s^{-1}) of water through a stem sample of length (l, m), and conducting area of sapwood (A_s, m^2), under a water potential difference ($\Delta\Psi$, Pa) along it's length. Sapwood permeability (k, m^2), which accounts for the effect of viscosity of the permeate on flow, was determined after Whitehead et al. (1984) and Pothier et al. (1989*a*, 1989*b*):

Equation 3-3

$$k = \frac{Q}{A_s}\frac{L}{\Delta\Psi}\eta$$

where η is the viscosity of water (Pa s). In addition to changes in $\Delta\Psi$, water flow rate to tree crowns is sensitive to differences in both K_Ψ and A_s. Whitehead et al. (1984) utilized this relationship to demonstrate that leaf area was more closely related to the product of sapwood area × permeability than to sapwood area alone. Though hydraulic conductivity and permeability are very closely related, dimensional analysis indicates that hydraulic conductivity (L T^{-1}), rather than permeability (L^2) is the appropriate expression of the combined effect of sapwood area and hydraulic conductivity on stem flow capacity (L^3 T^{-1}). Hydraulic conductivity multiplied by sapwood area can therefore be thought of as a measure of the capacity of the stem to transmit water under a unit hydraulic gradient (Q_h, m^4 Pa^{-1} s^{-1}).

Equation 3-4 $$Q_h = K_\Psi \times A_s$$

Leaf specific hydraulic capacity (Q_L) (a.k.a. LSC *sensu* Zimmerman 1978) was calculated by dividing Q_h by leaf area (A_L, m^2).

Percent Earlywood

On the discs taken from the inflow side of each section used to measure permeability, the width of earlywood and latewood from the last five years of growth (1994-1998) was measured on 4 perpendicular axes using a dissecting microscope and stage micrometer. The four measurements were averaged and percent earlywood (%E) for each sample was calculated by dividing the average cumulative width of earlywood by the total width.

Radial Flow Profiles

Once permeability measurements were completed, degassed water in the inflow connector was replaced with non-binding, 10% (w:v) acid fuchsin dye. The dye solution was run through the sample under the same constant hydraulic head, just long enough to begin flowing out of the stem section. The time the dye was run was recorded for each sample, and samples were immediately frozen to preserve the staining pattern. Each sample was cut frozen, longitudinally along four perpendicular radii, and the cut surfaces planed and digitally scanned. In order to compare radial patterns from samples of different sizes, the sapwood radius on each image was divided into five equal sections, and the mean distance of dye penetration for each section measured (Figure 3-1). The flow velocity for any given section was calculated from the mean distance of penetration of dye, divided by time. The flow profile for each sample was determined from the average of the four radial surfaces measured. The flow velocity of the dye under constant pressure was used as a surrogate measure of radial variation in sapwood permeability. The number of rings stained along each radius in all sample trees were counted, and averaged. In some cases, particularly among trees from L sites, there was significant outflow of dye from the sample. As a result, the entire length of more than one radial section of the sample was stained and differences in flow velocity between sections could not be distinguished. These samples were discarded and not used in the analysis. Thus, only data collected from trees from M sites were analysed for radial flow variation, with n = 6 for D, and n = 4 for both CD and SP.

Statistical Analysis

Crown class, site quality, and interaction effects on all hydraulic variables were analyzed using the GLM procedure for mixed models in release 8.1 of SAS® (SAS Institute Inc. Carey N.C.) for a split plot design (with sites nested within site quality). Post hoc comparisons between means where effects of crown class or site quality were significant were made using the Student-Newman-Keuls test. The leaf area estimate of one dominant tree from an M site was exceedingly high (20.5 m^2). This tree had the longest and heaviest crown, total fresh weight was above the 99% confidence interval of the sample mean, and was from the older site (M-5, Table 3-1). This tree was thus identified as an outlier, and dropped from the analyses related to leaf area.

Linear regressions of the relationship between stem hydraulic capacity (Q_h) and leaf area were calculated and compared using analysis of covariance in the form of an F-test of the appropriate sums of squares (Zar 1996).

Because the number of repeated measures (5 radial sections) exceeded the number of experimental units for some treatments, radial dye flow patterns were analyzed first by determining if there were linear (or higher order) trends, then comparing the slopes of any significant trends (Meredith and Stehman 1991). The GLM procedure of SAS was used to determine if the relationships between radial position and sap flow velocity represented significant linear, or higher order polynomial trends. Only linear trends were significant. Differences in slope between the linear trends of D, CD, and SP were tested using the univariate procedure.

Results

Measures of Conductivity

Sapwood permeability (*k*) was related to crown class ($P<0.001$); the average *k* of dominant (D) and co-dominant (CD) trees was 2.65 times greater than that of suppressed (SP) trees regardless of site quality (Table 3-3; Figure 3-2a). In terms of site quality, *k* of trees from medium sites was 1.4 times that of trees from low sites ($P = 0.033$). There was no interaction between crown class and site quality ($P = 0.382$). The effect of crown class and site quality on hydraulic conductivity (K_Ψ) mirrored those of *k* and, in this case can be considered to be equivalent, because there was little variation in viscosity of the permeate in our samples. Leaf specific hydraulic capacity (Q_L) did not vary significantly between sites ($P = 0.1613$), nor were the effect of crown class ($P = 0.2830$) or interaction ($P = 0.5083$) significant.

Leaf/Sapwood Area Ratio (*S*)

Crown dominance was positively related to *S* ($P < 0.0001$) (Figure 3-2b) and mean *S* for the D trees was 38% greater than that of CD, and 212% greater than for SP trees (Table 3-3). The slopes of regressions forced through the origin also differed among crown dominance classes (D = 0.10, CD = 0.08, SP = 0.05) ($P < 0.05$), and were very similar to the mean values of *S* for each class. There was no significant effect of site quality, or interaction between site quality and crown position.

Percent Earlywood

There was a strong effect of crown dominance position ($P = 0.008$), and site quality ($P < 0.001$) on percent earlywood in xylem produced between 1994 and 1998 (Figure 3-3). Trees from M sites had 8.6% more earlywood within the last 5 years of growth than trees from L sites, and dominant trees had a greater proportion of earlywood than other crown classes.

Radial Variation in Flow Velocity

Dye flow velocity declined linearly from a maximum in the exterior sapwood to a minimum at the sapwood heartwood boundary ($P = 0.047$), and these trends differed between crown classes ($P = 0.013$). Dominant (D) trees had the most gradual decline (least negative slope) ($P > |t| < 0.001$) (Figure 3-4a), across a wider sapwood radius relative to CD and SP trees (Figure 3-4b).

Note that D and CD trees, however, had more annual rings in their sapwood compared to SP trees, and there were more annual rings in sapwood of trees from M sites (Figure 3-5). Both the effects of crown class ($P < 0.001$) and site quality ($P = 0.041$) on the number of annual rings in sapwood were significant but there was no interaction. There was no penetration of dye into the heartwood.

Stem hydraulic capacity (Q_h) vs. Crown Leaf Area (A_L)

There were large differences in Q_h among trees from different crown classes (Table 3-3). For all crown dominance classes, and for both site qualities, tree leaf area was linearly and positively related to Q_h (Figure 3-6). Pair-wise comparison indicated there were no differences in slope ($P = 0.569$), but there were differences in intercept ($P = 0.007$) among crown classes. The relationship between leaf area and Q_h for D trees had a higher intercept than the same relationships for CD ($P = 0.016$) and SP ($P = 0.043$). There were no significant differences due to site quality.

Discussion

My study shows that stem sapwood of suppressed (SP) trees had, inferior hydraulic characteristics compared to dominant (D) trees. (Figure 3-2a, Table 3-3). Canopy D and CD trees were superior to SP trees in terms of sapwood permeability (k), confirming the non-replicated study of Shelburne and Hedden (1996). I also observed a similar trend in leaf/sapwood area ratio (S) with crown class; D had more leaf area per unit of sapwood basal area than SP trees (Figure 3-2b). Furthermore, the D trees with their large stem size and high hydraulic conductivity (K) had much greater hydraulic capacity (Q_h) than SP trees (Table 3-3), which was reflected in large differences in leaf area (A_L, Table 3-2) between D and SP trees. Dominant trees had more leaf area for a given Q_h than subdominant trees (Figure 3-6); this may reflect increased capacitance of larger D stems, superior water and nutrient foraging capability (larger root biomass), better access to light, and/or genotypic differences. Conversely, the reduction in leaf area relative to Q_h in the subdominant trees might be interpreted as being related to factors other than the ability of the stem to deliver water to crowns. Lastly and in contrast to the findings of Coyea et al. (1990) on balsam fir, SP trees had fewer annual rings of sapwood than D trees (Figure 3-5). Overall, the slow growing, suppressed trees developed sapwood that was more resistant to water flow. Somewhat surprisingly, no differences in Q_L were evident between crown classes (Table 3-3).

Lower *S* associated with reduced *k* suggests that SP trees reduced their leaf area in response to decline in sapwood permeability.

The decline in *k* and *S* from dominant to suppressed trees was related to reduced percent earlywood (% E) in suppressed trees compared to canopy trees (Figure 3-3). Keane and Weetman (1987) suggested a similar decline in earlywood production related to lower *S* in trees from high density stands. Another factor related to the decline in *S* in SP trees is the steep decline in conductivity from outer sapwood to inner sapwood compared to D trees (Figure 3-4). This effect was also observed in loblolly pine by Shelburne and Hedden (1996). Thus, on an area basis, inner sapwood contributed less than outer sapwood to the supply of water to leaves. Therefore, the effective sapwood area of SP trees was probably less than that of D trees, which had more conductive inner sapwood. Surprisingly, the decline in *S* I observed from D to CD trees was not associated with a concurrent decline in *k* between D and CD trees on medium (M) sites (Figure 3-2a). This unexpected observation might relate to two factors: a) Conductivity declined more rapidly from outer to inner sapwood in CD trees from M sites (Figure 3-4) which may reduce effective sapwood area, while more conductive outer sapwood may have been able to compensate, resulting in equivalent *k*. b) It is possible that the co-dominants on M sites might have lost some of their leaves from crown friction with neighbouring trees. The tall but slender stems of co-dominants (Table 3-2) would likely have allowed crowns to sway more in wind and collide with neighbours with greater intensity (Rudnicki et. al. 2001) thereby abrading leaf area, which might have lowered the leaf area component in the calculation of *S*.

The reduced permeability of stems from L sites I observed is similar to the findings of Pothier et al. (1989*a*, 1989*b*) who found low *k* of jack pine on poor sites. Reduced % E and reduced numbers of annual rings in the sapwood (Figure 3-5) of trees on the L sites likely contributed to lower permeability. Despite differences in *k*, the lack of difference in Q_L between sites does not support the hypothesis of hydraulic limitation on leaf area related to site type (Keane and Weetman 1987). Nevertheless, there were large differences in the rate of self-thinning between these two site types; there were very few standing dead trees in the L site stands and they had a much greater proportion of SP trees. The fact that the site index measured on trees from L sites, (mean = 9.5 Table 3-1) was well below that of reported values for UF d ecosites ($SI_{50} = 12.9 \pm 0.2$, Beckingham et al. 1996), suggests that the L sites from which I selected sample trees were displaying repression of height growth (Farnden and Herring 2002), likely related to high stem density interacting with low site quality.

My observations of differences in sapwood hydraulic characteristics between trees from differing crown classes may provide insights into the lack of self-thinning mortality I encountered in the height repressed L sites. I hypothesize that greater stem hydraulic supply capacity in relation to leaf area of sub-dominant trees (Figure 3-6) improves their ability to survive short-term water stress. While it is clear that subdominant trees, especially SP trees, had stems that are more resistant to water flow (Figure 3-2a), subdominants actually had proportionately fewer leaves and thus likely suffered less water stress than dominants. Also, SP trees likely have less water demand per unit leaf area since they are shaded much of the time and lodgepole pine stomata are very responsive to changes in light (Lopushinsky 1975). Furthermore, less earlywood in subdominant trees means they are less likely to cavitate during freeze-thaw events since the likelihood of cavitation increases in tracheids with larger lumen diameters (Sperry and Sullivan 1992, Davis et al. 1999). Thus, CD and SP trees (and trees from L sites in general) are more likely to resist cavitation during periodic freeze-thaw events. Small differences in cavitation related mortality, compounded over many cycles may eventually contribute to the differences in self-thinning noted between site types. This hypothesis for reduced self-thinning in low sites requires further physiological measures under dynamic water stress, and measurement of freeze-thaw induced cavitation from high-density stands on medium and low sites.

Table 3-1. Site description and mean stand characteristics of the medium (M) and low (P) sites from which sample trees were collected.

Site	Ecosite[a]	SI_{50} (m)	Density (trees ha^{-1})	SDI[b] (trees ha^{-1})	Spacing[c] Factor (%)	dbh (cm)	ht. (m)
M-1	UF e	14.8	6000	840	11.6	7.5 ± 0.2	11.1 ± 0.5
M-2	UF e	13.4	5659	1140	12.9	8.5 ± 0.3	10.3 ± 0.4
M-3	UF e	14.6	5602	1000	13.4	8.5 ± 0.2	9.9 ± 0.7
M-4	UF e	14.5	7198	950	14.0	6.5 ± 0.2	8.4 ± 0.4
M-5	UF e	12.5	5857	817	10.8	8.0 ± 0.2	12.1 ± 0.4
M-6	UF c	14.4	3803	798	10.7	9.3 ± 0.3	15.1 ± 0.5
L-1	UF d	11.5	10197	1225	13.2	5.4 ± 0.2	7.5 ± 0.3
L-2	UF d	7.4	22282	1134	12.9	3.2 ± 0.1	5.2 ± 0.1
L-3	UF d	8.7	27502	2015	9.4	3.8 ± 0.1	6.4 ± 1.1
L-4	UF d	8.5	27852	962	11.7	3.3 ± 0.1	5.1 ± 0.5
L-5	UF d	9.6	22282	1258	12.6	3.5 ± 0.1	5.3 ± 0.3
L-6	UF d	11.5	30239	1501	11.5	3.3 ± 0.1	5.0 ± 0.2

[a](as per Beckingham et. al., 1996; UF = upper foothills; e = mesic moisture class (MC)/ medium nutrient class (NC); c = submesic MC/medium NC; d = mesic MC/poor NC)

[b] SDI = tpha $(DBH_q/25)^{1.6}$; where tpha = trees per hectare, and DBH_q = quadratic mean diameter.

[c] $$Spacing\ Factor = \left(\sqrt{10000/Density}\Big/ht\right)*100$$

Table 3-2 Mean attributes of dominant (D), co-dominant (CD), and suppressed (SP) sample trees from medium and low sites (LCR = live crown ratio).

	Medium Sites					
Crown Class	dbh (cm)	ht. (m)	A_L (m^2)	Crown width(cm)	LCR	ht. / dbh
D[a]	13.3a	11.2a	10.2a	175.0a	0.47ab	84.9a
C	8.9b	10.8a	3.2bc	125.8b	0.40ab	120.8b
S	4.5c	6.1b	0.4c	78.3c	0.38b	139.6b
	Low Sites					
D	8.7b	8.1b	4.9b	123.3b	0.54a	93.7a
C	5.4c	6.3b	1.2c	88.3bc	0.48ab	118.9b
S	2.4d	3.0c	0.1c	48.3c	0.42ab	127.7b

Note: Means within columns (by variable) followed by the same letter are not significantly different at the 0.05 level according to the Student-Newman-Keuls test.

[a] n=5, n=6 for all other groups

Table 3-3 Means for leaf area sapwood area ratio (S), sapwood permeability (k), sapwood hydraulic conductivity (K_Ψ), leaf specific capacity (Q_L), and hydraulic capacity (Q_h) for dominant (D), co-dominant (CD) and suppressed (SP) trees from all sites combined.

	D (n=11)	CD (n=12)	SP (n=12)
S (m^2 cm^{-2})	0.11a	0.08b	0.05c
k (m^2*10^{-12})	1.97a	1.79a	0.71b
K (m^2 Pa^{-1} $s^{-1}\times10^{-9}$)	2.07a	1.87a	0.74b
Q_L (m^2 Pa^{-1} $s^{-1}\times10^{-12}$)	1.98a	2.45a	1.95a
Q_h (m^4 Pa^{-1} $s^{-1}\times10^{-12}$)	14.8a	5.4b	0.5c

Note. Means within rows (by variable) followed by the same letter are not significantly different at the 0.05 level according to the Student-Newman-Keuls test.

Figure 3-1 Example drawing of an image used to measure distance of dye penetration across sapwood radial axis showing 5 sections of equal width. For the outermost section (radial position 1); dye flow velocity (m s^{-1}) = ((a + b)/2) / time.

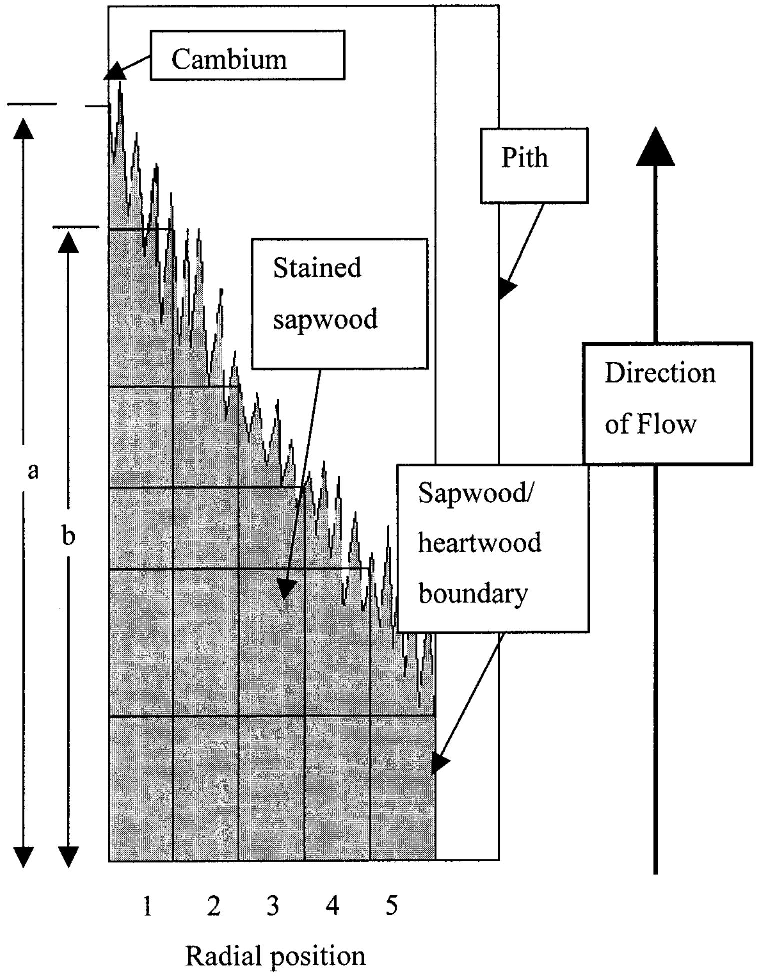


Figure 3-2 Means and standard errors across crown dominance classes and site qualities in terms of a) Saturated sapwood permeability (*k*), and b) Leaf area sapwood area ratio (*S*). (n = 5 for Dominants from Medium sites, n = 6 for all other groups).

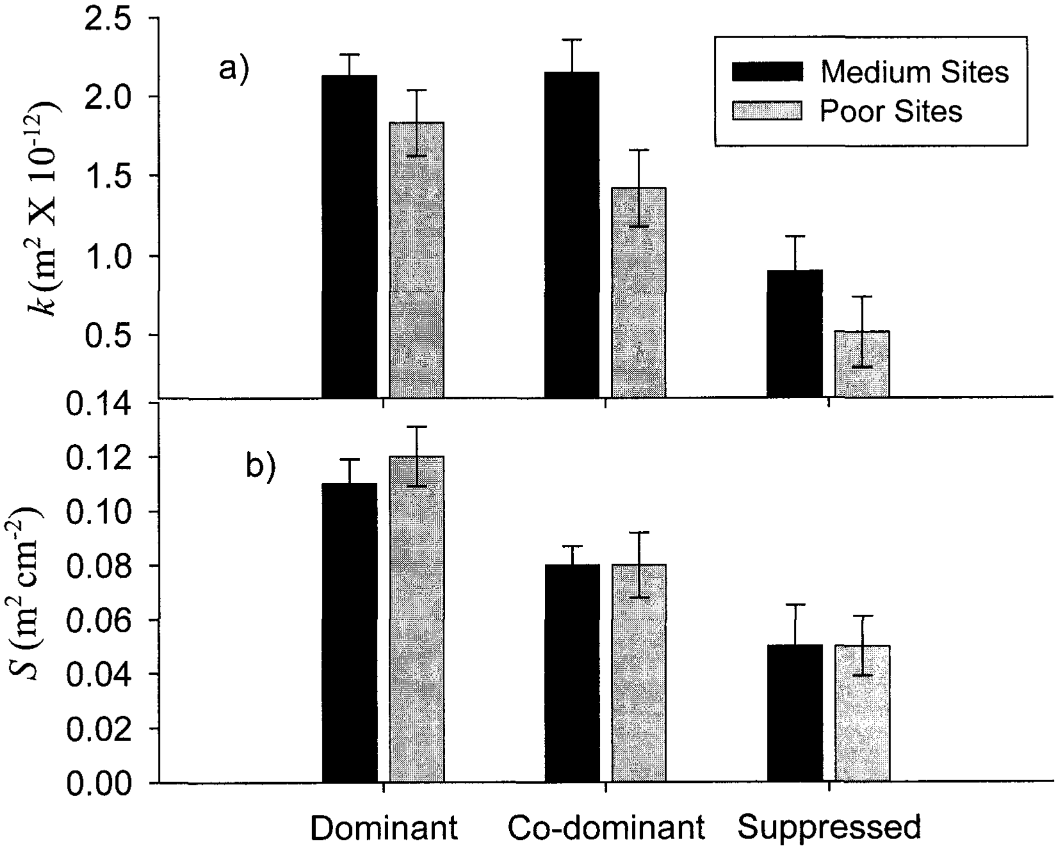


Figure 3-3 Percent earlywood in annual rings at breast height from 1994-1998. Error bars are standard error. Bars with the same letter are not significantly different at the 0.05 level according to the Student-Newman-Keuls test. (n = 6 for all groups)

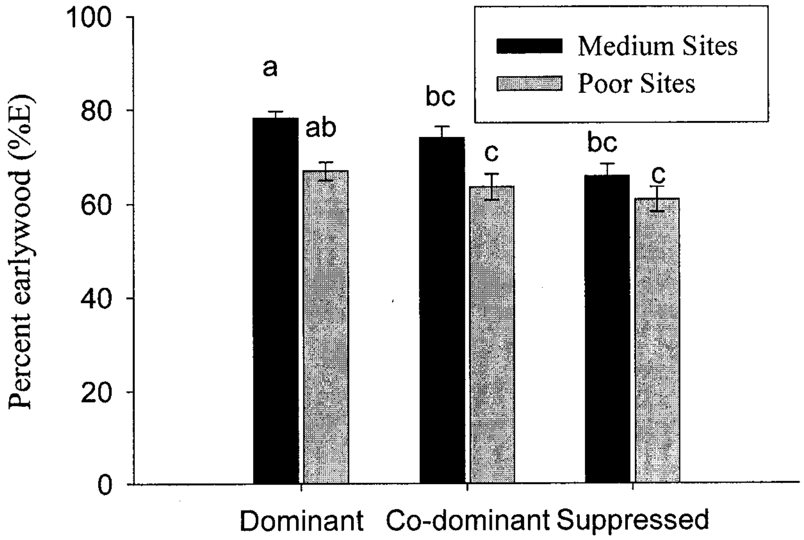


Figure 3-4 Radial dye flow velocity of Dominant (n = 6), Co-dominant (n = 4), and Suppressed trees (n = 4) from Medium sites. a) Symbols represent the mean flow velocity at each radial position; error bars represent standard error. Means are offset along x-axis for clarity. b) Symbols represent mean velocity vs. mean distance from cambium at each radial position for each sample used in the analysis.

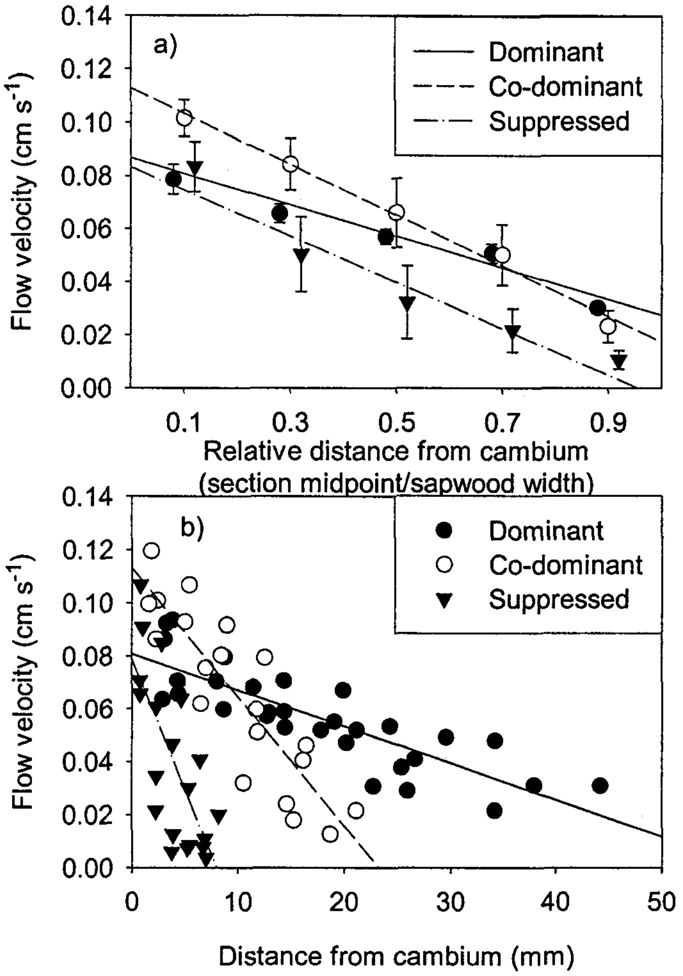


Figure 3-5 Number of annual rings within sapwood at breast height of Dominant, Co-dominant and Suppressed trees from Medium and Low Sites. Error bars are standard error. Bars with the same letter are not significantly different at the 0.05 level according to the Student-Newman-Keuls test. (n = 6 for all groups)

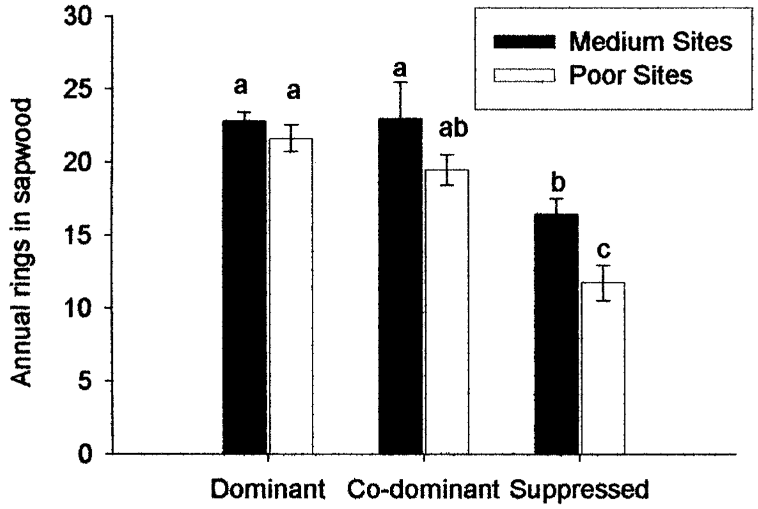
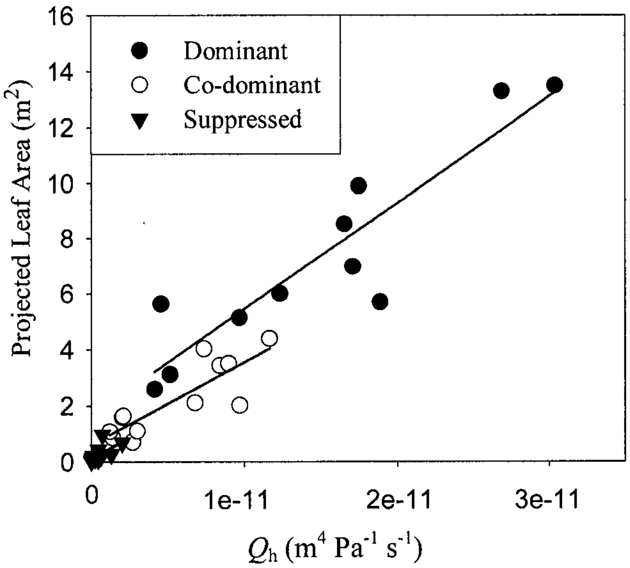


Figure 3-6 Projected leaf area vs. hydraulic capacity under a unit hydraulic gradient (Q_h) of the stem for Dominant ($r^2 = 0.84$; $P < 0.0001$; $n = 11$), Co-dominant ($r^2 = 0.72$; $P = 0.0005$; $n = 12$), and Suppressed ($r^2 = 0.41$; $P < 0.02$; $n = 12$) trees from both site types.



References

Beckingham, J.D., I.G.W. Corns and J.H. Archibald. 1996. Field guide to ecosites of west-central Alberta. Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 9.

Coyea, M.R., H.A. Margolis and R.R. Gagnon. 1990. A method for reconstructing the development of sapwood area and leaf area of balsam fir. Tree Physiol. 6:283-291.

Davis, S.D., J.S. Sperry and U.G. Hacke. 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. Am. J. Bot. 86(10):1367-1372.

Day, R.J. 1998. The ancient and orderly European discipline of thinning is now a reality in North America. *In* Stand Density Management: Planning and Implementation. Proceedings of a conference held November 6 & 7 in Edmonton, Alberta, Canada. Ed. C. Bamsey, Clear Lake Ltd., Edmonton, AB, pp 24-33.

DeLucia, E.H., H. Maherali and E.V. Carey. 2000. Climate driven changes in biomass allocation in pines. Global Change Biol. 6(5):587-593.

Environment Canada. 1993. Atmospheric Environment Service, Canadian Climate Normals 1961-1990 Prairie Provinces.

Farnden, C., and L. Herring. 2002. Severely repressed lodgepole pine responds to thinning and fertilization: 19-year results. For. Chron. 78 (3):404-414

Hillel, D. 1982. Introduction to Soil Physics. Academic Press. Pp.90-106.

Huang, S., S.J. Titus and G. Klappstein. 1997. Development of a sub-region based compatible height-site index-age model for young and mature lodgepole pine in Alberta. Land and Forest Service, For. Mgmt. Res. Note No. 6 Pub. No. T/353, Edmonton Alberta.

Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol. 19:165-172.

Keane, M.G., and G.F. Weetman. 1987. Leaf area – sapwood cross-sectional area relationships in repressed stands of lodgepole pine. Can. J. For. Res. 17:205-209.

Long, J.N. 1985. A practical approach to density management. For. Chron. 61(1):23-27.

Magnani, F., M. Mencuccini and J. Grace. 2000. Age related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant Cell Environ. 23:251-263.

Mencuccini, M., and L. Bonosi. 2001. Leaf/sapwood area ratios in Scots pine show acclimation across Europe. Can. J. For. Res. 31:442-456.

Mencuccini, M., J. Grace and M. Fioravanti. 1997. Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. Tree Physiol. 17:105-113.

Mencuccini, M., and J. Grace. 1995. Climate influences the leaf/sapwood area ratio in Scots pine. Tree Physiol. 15:1-10.

Mencuccini, M., and J. Grace. 1996*a*. Hydraulic conductance, light interception and needle nutrient concentration in Scots pine stands and their relations with net primary productivity. Tree Physiol. 16:459-468.

Mencuccini, M., and J. Grace. 1996*b*. Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. Plant Cell Environ. 19:939-948.

Meredith, M.P., and S.V. Stehman. 1991. Repeated measures experiments in forestry: focus on analysis of response curves. Can. J. For. Res. 21:957-965.

Oliver, C.D. and B.C. Larson. 1990. Forest Stand Dynamics. McGraw-Hill Inc., New York.

Peet R.K., and N.L. Christensen. 1987. Competition and tree death. Bioscience, 37:586-595.

Pothier, D., H.A. Margolis and R.H. Waring. 1989*a*. Patterns of change in saturated sapwood permeability and conductance with stand development. Can. J. For. Res. 19:432-439.

Pothier, D., H.A. Margolis, J. Poliquin and R.H. Waring. 1989*b*. Relation between the permeability and the anatomy of jack pine sapwood with stand development. Can. J. For. Res. 19:1564-1570.

Protz, C.G., U. Silins and V.J. Lieffers. 1999. Reduction in branch sapwood hydraulic permeability as a factor limiting survival of lower branches of lodgepole pine. Can. J. For. Res. 30:1088-1095.

Reineke, L.H. 1933. Perfecting a stand density index for even-aged forests. J. Agric. Res. 46: 627-638.

Rudnicki, M., U. Silins, V.J. Lieffers and G. Josi. 2001. Measure of simultaneous tree sways and estimation of crown interactions among a group of trees. Trees 15(2):83-90.

Ryan, M.G., and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. Bioscience, 47:235-242.Saranpaa, P. 1985. Length, diameter and cell wall thickness of tracheids in mature lodgepole pine bolewood. Silva Fennica, 19:21-32.

Shelburne, V.B., and R.L. Hedden. 1996. Effect of stem height, dominance class, and site quality on sapwood permeability of loblolly pine, (*Pinus taeda* L.). For. Ecol. Manage. 83:163-169.

Sparks, J.P., G.S. Campbell and R.A. Black. 2001. Water content, hydraulic conductivity, and ice formation in winter stems of *Pinus contorta*: a TDR case study. Oecologia 127:468-475.

Sperry, J.S., and D.J. Robinson. 2001. Xylem cavitation and freezing in conifers. *In* Conifer Cold Hardiness. Eds. F.J. Bigras and S.J. Colombo. Kluwer Academic Publishers, the Netherlands, pp 121-136.

Sperry, J.S., and J.M. Sullivan. 1992. Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. Plant Physiol. 100: 605-613.

Sperry, J.S., and M.T. Tyree. 1990. Water-stress-induced xylem embolism in 3 species of conifers. Plant Cell Environ. 13:427-436.

Steel, R.G., J.H. Torrie and D.A. Dickey. 1997. Principles and Procedures of Statistics: A Biometrical Approach. McGraw-Hill Inc., New York. p.26.

Weiner, J., and S.C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos, 47:211-222.

Whitehead, D. 1998. Regulation of stomatal conductance and transpiration in forest canopies. Tree Physiol. 18:633-644.

Whitehead, D., W.R.N. Edwards and P.G. Jarvis. 1984. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. Can. J. For. Res. 14:940-947.

Xu, M., and T.B. Harrington. 1998. Foliage biomass distribution of loblolly pine as affected by tree dominance, crown size, and stand characteristics. Can. J. For. Res. 28:887-892.

Zar, J.H. 1996. Biostatistical Analysis 3rd ed. Prentice Hall, Upper Saddle River NJ.

Zimmerman, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin.

Chapter 4

Growth and crown efficiency of height repressed lodgepole pine; are suppressed trees more efficient?[6]

Introduction

Growth efficiency (*GE*; stemwood volume growth per unit leaf area) is considered to be a measure of tree vigour (Waring et al. 1980) where leaf area is the measure of occupied growing space. It has been assumed that growth of stem volume is the best measure of the efficiency with which growing space is occupied because allocation to stemwood generally has a lower priority than allocation to shoots, roots, biochemical defensive and storage compounds (Waring and Schlesinger 1985, Waring and Pitman 1983). Several studies have shown that in conifers *GE* is sensitive to environmental stress (Waring et al. 1980, Kaufmann and Ryan 1986), and is positively associated with the ability of trees to survive insect outbreaks (Waring and Pitman 1985 Coyea and Margolis 1994). There are conflicting reports on which dominance classes have highest *GE*; dominant (Kollenberg and O'Hara 1999), codominant (O'Hara 1988), and suppressed (Kaufman and Ryan 1986; Gilmore and Seymore 1996) trees of various conifer species have all been identified as having superior *GE*. Prior to the development of simple methods for estimating leaf area in the early 1980s, crown efficiency (*CE*; volume growth per unit of crown projection area) was used to assess tree vigour (Assmann 1970). Recently, Sterba and Amateis (1998) showed that *CE* is positively related to crown dominance in plantation loblolly pine, but declines as crown size increases within a given crown class, e.g. large co-dominants were less efficient than small co-dominants. Because of these contrasting results concerning variation in *GE* and *CE* between crown classes, the utility of *GE* and *CE* as indicators of individual tree and stand level vigour remains unclear.

Within a species, differences in *GE* and *CE* should be explainable in terms of capture and utilization of growth limiting resources by individual trees, along with overall stand dynamics. For instance, growth of lodgepole pine can be negatively affected when stands establish at very

---

[6] A slightly different version of this chapter has been published.

Reid, D.E.B., V.J. Lieffers and U. Silins. Growth and crown efficiency of height repressed lodgepole pine; are suppressed trees more efficient? 2004. Trees 18:390-398. © 2004 Springer – Verlag.

high densities following wildfire. On nutrient poor sites, this species can experience slow self-thinning and repression of height growth (Farnden and Herring 2002) compared to the height growth observed on stands initiated at low stem density on the same site type (Huang et al. 2003). Where manual thinning has been attempted in height-repressed stands, a growth response may be delayed for more than 10 years (Worall, 1995). It has been suggested that height repression is related to increased allocation to root growth in response to poor site quality (Worall et al. 1985, Worall 1995), or an inability of stems to supply water to leaves (Keane and Weetman 1987). However, Reid et al. (2003) found that although trees from height repressed stands on low quality sites had sapwood of lower permeability, they did not appear to be experiencing a hydraulic limitation on existing leaf area. Within these height-repressed stands there were differences in crown size and growth rates of individual trees that suggest that one-sided competition (Weiner and Thomas 1986) will eventually result in self-thinning. An examination of the *GE* and *CE* of trees from differing social positions in height repressed and normally developing stands would be useful in explaining how intraspecific competition and resource limitations relate to height repression.

Hydraulic limitation (Hubbard et al. 2001, Mencuccini and Grace 1996) and differences in growth efficiency (Long and Smith 1992, Ryan and Waring 1992, Yoder et al. 1994, Gower et al. 1996) have also been used to explain the universal phenomenon of declining stand level growth following crown closure. Lower *GE* of larger trees combined with loss of leaf area through self-thinning provides one explanation for this phenomenon (Smith and Long 2001). Differences in *GE* between individual trees from height repressed and normally developing stands may therefore provide some insights into lower growth rates encountered in height-repressed stands. Declining *GE* with age is closely related to a reduction in hydraulic supply capacity per unit leaf area (Mencuccini and Grace 1996) suggesting water is probably a key limiting factor. Examination of the relationship between *GE* and hydraulic supply capacity per unit leaf area could therefore be useful in determining how hydraulic architecture is related to the lower productivity of individual trees typical of height repressed lodgepole pine stands.

The objectives of this study were to compare *GE* and *CE* of dominant, codominant and suppressed trees from height repressed and normally developing stands, and examine how *GE* is related to hydraulic supply capacity in this context. Specifically, I sought to test the hypotheses that site quality and dominance are positively related to *GE* and *CE*, and that differences in *GE* are related to differences in the ability of tree stems to supply water to crowns.

Materials and methods

Stand Measurements

Twelve study locations were located at 1200-1300 m elevation within even-aged, lodgepole pine stands in the Gregg river burn (56,000 ha, burned in 1956) located 50 km south of Hinton, Alberta. Crown class differentiation was apparent in all stands, and some stands appeared to be experiencing competition-induced mortality. Site occupancy can be assessed from measures that consider both the size and density of individuals in stands. Stand density index (SDI) increases as stem density and quadratic mean diameter increase (Long 1985) and spacing factor declines as stand height increases for equivalent density (Day 1997). All sites were fully occupied since stand density index was greater than 600 (Long, 1985) and spacing factors were below 15% (Day, 1997). Stand site quality was classified as Medium (M) or Low (L) based on ecological association (Beckingham et. al. 1996) and density (Table 4-1). Within these two site quality classes, all sites were similar in terms of site index (SI_{50}, height in m at age 50 years) calculated based upon heights of dominants using a locally derived height-site index-age model (Huang et al. 1997). Age of all stands, determined from basal disks, was 37-46 years, except for stand M-5 that was 63 years old. All L sites were experiencing height repression since site index measured from dominant trees (mean $SI_{50} = 9.5$) was well below that of reported values for their ecosite ($SI_{50} = 12.9 \pm 0.2$; Beckingham et al. 1996).

At each of twelve sites stem density, stand basal area and leaf area index were measured within randomly located circular fixed area plots established throughout the burn. Plot radius varied from 5.64 m in taller, more open stands, to 2 m in shorter, denser stands, and included 28-54 trees. Average density was 5,686 stems per hectare on M sites and 23,392 on L sites (Table 4-1). Standing dead trees were common on M sites (average of 3100 stems ha^{-1} +/- 1369 std.err.), but almost completely absent from L site plots. Basal area and diameter distribution of each stand were determined by measuring diameter at breast height (1.3 m) of all trees within each plot. The sample skewness of diameter class distributions within each stand (Table 4-1) was calculated from these measurements. Stand height was estimated from a random sub-sample of at least 4 co-dominant trees in the plot and surrounding forest measured with a height pole or clinometer.

Leaf area index (LAI) estimates were made from canopy photographs taken using a digital camera and a hemispherical 'fish-eye' lens. All photographs were taken in July, either early in the morning (04:00 - 06:00) or late in the day (19:00 - 22:00) to minimize errors caused by the presence of the solar disk and differential illumination of foliage. LAI was estimated from the digital images collected, using SLIM software (Comeau et al. 2002).

Tree Measurements

Three healthy sample trees with cylindrical stem form were selected from each plot: one each from dominant (D), co-dominant (CD) and suppressed (SP) crown dominance classes (Oliver and Larson 1990). A total of 36 trees were harvested. Crown classes were defined as follows: canopy trees (D&CD), while interacting on all sides with neighbours were not physically restricted from above; D trees were taller than their immediate neighbours (CD). SP trees were overtopped; the top of the crown was below the lower canopy of neighbouring trees. Only trees with healthy leaders and showing no sign of damage or disease were sampled.

Crown diameter and crown length were measured on felled trees. Crown projection area was estimated by assuming that the horizontal crown dimension was circular. Crown volume was estimated assuming an ellipsoid shape, appropriate for lodgepole pine undergoing self-pruning of lower branches (Stadt and Lieffers 2000). Leaf area density was determined by dividing projected leaf area by crown volume (Table 4-2).

Leaf area of each tree was determined by developing relationships between projected leaf area and dry weight of needles. Differences in branch morphology and specific weight of needles between crown positions on D and CD trees were accounted for by dividing crowns into upper, mid, and lower sections. Representative branches were sampled from each crown section, fresh weight of the representative branches, and the fresh weight of all branches from each crown section were measured. The needles from each representative branch, and all needles from the crowns of SP trees, were taken to the lab in moistened plastic bags in a cooler, and stored in the dark at 5°C until they were processed. A sub-sample of fresh needles from each representative branch (or each SP crown) were scanned and one-sided, projected leaf area measured using Sigma Scan-Pro® image analysis software. All needles were oven dried at 78°C until dry weight stabilized. Needle specific area was determined from the dry weight of the scanned sub-sample. The leaf area of each crown section (A_l; m^2) was calculated by:

Equation 4-1 $A_l = A_n * (w_n/w_b) * w_B$

where A_n is needle specific area (m^2 g^{-1}), w_n is the dry weight of needles from the representative branch, w_b is the fresh weight of the representative branch, and w_B is the fresh weight of all branches in the section. Crown section leaf areas were summed to determine total tree leaf area. The leaf area of each SP tree was determined from the dry weight of all needles and the needle specific area.

A random sample of dried needles was used to measure needle nitrogen and phosphorus concentrations. Samples were taken from the two uppermost representative branches of dominant and codominant trees, and from the whole crown of suppressed trees.

Tree Growth and Growth Efficiency

Tree height and dbh (outside bark at 1.3 m) were measured on all sample trees (Table 4-2). Height growth over the previous five years (1995-99) was also measured in the field based on distance between whorls. Basal area (inside bark; BA) of sample trees was measured with Sigma Scan-Pro® image analysis software on digitally scanned basal sections used for hydraulic measurements (below). From the same sections used to measure basal area, radial growth was estimated from the mean value of four perpendicular transects measured using a stage micrometer. To estimate changes in BA and volume from these radial measurements, the radius of a circle of equivalent area was calculated from the basal area (inside bark). The mean radial growth over the last five years was subtracted from this radius, and this was used to calculate the BA (inside bark) of the tree prior to the 1994 growing season. To estimate outside bark diameter (dbh) prior to the 1994 growing season, we used the following equation ($p=0.0001$, $r^2 = 0.9863$), developed from the sampled trees.

Equation 4-2 $\text{dbh} = 1.32905 * \text{BA}^{0.480559}$

Stem volume was calculated from dbh and height using a locally derived taper function, developed for upper foothills lodgepole pine (Huang, 1994).

Growth efficiency (*GE*) was calculated as the average change in total volume (m^3) over the last 5 years, per unit leaf area. Crown efficiency (*CE*) was calculated as the mean volume increment over the same five-year period per unit crown projection area. These measures assume that the crown leaf area and crown volume have not changed dramatically for a given tree over the period examined.

Sapwood Properties

Stem samples approximately 1 m long and centered on breast height (1.3 m) were used to measure hydraulic characteristics. Sample handling and preparation procedures are described in detail by Reid et al. (2003). Sapwood basal area was determined based on water content from 1 cm disks cut from frozen samples and immediately scanned for measurement. Where the sapwood-heartwood boundary was unclear, the disk was held up to a light, and the boundary between opaque heartwood and translucent sapwood marked with a pencil prior to scanning and measurement. Heartwood top height was assumed to be at the midpoint of the live crown based on independent observations of small amounts of heartwood at the base of the live crown (Reid unpublished), and reports that the distance to the center of the live crown is useful in accounting for sapwood taper (Long and Smith 1988). The volume of heartwood was calculated using estimated height and diameter (from scanned images) with the same taper function used to calculate total volume (Huang 1994). Sapwood volume was estimated by subtracting heartwood volume from total volume.

Water flow through stem samples was measured on 12-20 cm long sub-sections of each stem sample collected. The 1 m long sections collected in the field were wrapped in polyethylene, stored frozen at -18 °C for up to one month before measurements. Frozen samples were re-cut, centred on the breast height (1.3m) position; cuts were adjusted up or down so that there were no branch nodes near the cut ends to facilitate attachment to the permeability apparatus. Freezing samples has no apparent impact on conductivity measurements (Reid et al. 2003). Samples were thawed overnight prior to each measurement while submerged in 10 mmol l^{-1} oxalic acid to suppress growth of bacteria and fungi.

Each sample was installed into permeability apparatus that used a 167.5 cm hanging water column to generate a constant pressure head, and thus water potential difference across the sample ($\Delta\Psi$). Flow measurements were made using degassed water at room temperature, and outflow was constantly recorded using an electronic balance. Once flow stabilized (usually within 5 minutes), the average flow rate over the next 20-minute period was used. Because the flow rate through some of the suppressed tree samples was very slow, outflow of water was measured for a longer period of time (up to 200 minutes). In all cases the reservoir on the scale was covered to prevent evaporation from the pan during measurement of flow rate.

Saturated sapwood permeability (k; m^2) according to Darcy's Law was calculated from:

Equation 4-3

$$k = \frac{Q}{A_s} \frac{L}{\Delta\Psi} \eta$$

where Q is the flow rate (m^3 s^{-1}) of water, of viscosity (η, Pa s), through a stem sample of length (L, m) and conducting sapwood area (A_s, m^2), under a water potential difference ($\Delta\Psi$, Pa) along it's length. The pipe model theory suggests that a homeostatic balance exists between stem water supply and leaf area, which led to the historical application of constant A_l/A_s ratios for a given species (Waring et al. 1982). Across different species however, leaf area is more closely related to the combined effects of A_s and the water conducting properties of sapwood, than to A_s alone (Whitehead et al. 1984, Reid et al. 2003). The amount of water that can be delivered to leaves under a unit hydraulic gradient is thus affected by both the conducting properties of the sapwood and the amount of sapwood. Where k and A_s are known, the capacity of the stem to supply water to foliage under a unit hydraulic gradient (Q_h, m^4 Pa^{-1} s^{-1}) can be calculated (Chapter 2).

Equation 4-4

$$Q_h = \frac{k}{\eta} A_s$$

To test for the relationship between hydraulic supply capacity per unit leaf area and growth efficiency in the trees we studied, I calculated the leaf specific hydraulic capacity (Q_L, m^2 Pa^{-1} s^{-1} ; Chapter 2) for each tree, and plotted those values against *GE*.

Statistical Analysis

Crown class, site quality, and interaction effects on all dependent variables were analyzed using the GLM procedure for mixed models (SAS Institute Inc, release 8.1, Carey N.C.) for a split plot design (with sites nested within site quality). Where effects of crown class and/or site quality were significant, post hoc comparisons between means were made using the Tukey-Kramer test of the least square means. Since there was a log-linear relationship between the ratio of leaf area to sapwood volume and the ratio of sapwood volume to leaf area, these data were log transformed for statistical analysis. Regression lines were compared using an F-test for coincident regressions (Zar 1996). Two trees were identified as extreme outliers and dropped from the analysis.

Results

Tree volume growth was positively related to site quality ($P < 0.001$) and crown class ($P < 0.001$) (Figure 4-1a). We also observed a significant interaction between site quality and crown class ($P = 0.002$) since differences in growth between crown classes were greater in trees from medium (M) sites compared to trees from low (L) sites; low site D trees grew at a rate similar to good site CD trees. The same pattern of variation was observed for basal area growth. Mean annual height growth over the five year period examined varied between trees from different crown classes ($P < 0.001$), with dominants (D; 19.0 cm y^{-1}) > co-dominants (CD; 14.5) > suppressed (SP; 9.4). Average annual height growth of trees from M sites (15.3 ± 1.3 cm std. err.) tended to be higher than height growth of trees from L sites (13.4 ± 1.6 cm) but no effect of site quality was apparent ($P = 0.388$).

Strong variation in growth efficiency (*GE*; volume growth per unit leaf area) was observed between crown classes ($P < 0.001$). Average *GE* of dominant (D) and co-dominant (CD) trees was 28 % lower than that of suppressed (SP) trees regardless of site quality (Figure 4-1b). Though mean *GE* of M site trees tended to be greater than that of L site trees (544.7 vs. 417.7 cm^3 m^{-2} y^{-1}) the effect of site quality was not significant ($P = 0.261$).

Crown efficiency (*CE*), which considers crown projection area as the measure of growing space occupancy instead of leaf area, was also related to crown class, but the opposite trend was observed. Crown dominance was positively related to *CE* ($P < 0.001$) (Figure 4-1c) and mean *CE* for the D trees was 26% greater than that of CD, and 68% greater than for SP trees (Table 4-3). Trees from low sites had *CE* that was 28% lower than that of trees from medium sites ($P = 0.043$).

Stem hydraulic supply capacity (Q_h) was greater for trees from M than L sites ($P < 0.001$), and was greater for more dominant trees ($P < 0.001$). There was a relatively uniform decline in Q_h on the M sites compared to a sharp decline in Q_h between D and CD trees on the L sites resulting in interaction between site and crown class ($P = 0.002$; Figure 4-1d). I observed positive linear relationships between volume growth and both Q_h (Figure 4-2a, $P < 0.001$; $r^2 = 0.94$) and leaf area (Figure 4-2b, $P < 0.001$; $r^2 = 0.91$).

For all trees, *GE* was positively related to the leaf specific hydraulic capacity Q_L (Figure 4-3a, $P < 0.001$; $r^2 = 0.31$). Suppressed trees, which had higher overall *GE*, also had a higher intercept ($P < 0.001$) for the relationship between *GE* and Q_L, compared to D and CD trees (Figure 4-3a): this suggests a unit of leaf area of suppressed trees had higher productivity than dominant and co-dominant trees, relative to a unit of flow. There were no differences in slope between trees from differing crown classes ($P = 0.75$). There were no differences either in slope ($P = 0.47$) or intercept ($P = 0.82$) between M and L sites trees. There was also no effect of crown class ($P = 0.295$) or site quality ($P = 0.162$) on Q_L. However, we did observe a positive relationship between *k* and radial growth (Figure 4-3b, $P < 0.001$; $r^2 = 0.41$), where *k* increased more slowly as radial growth increased resulting in a log-linear relationship. No differences in this relationship between M and L site trees were observed.

Leaf area density differed between crown classes ($P < 0.001$) but not between trees from M and L sites ($P = 0.68$); post hoc comparisons revealed that D > CD > SP (Figure 4-4a). We observed differences in needle nutrient concentrations between crown classes, both in terms of nitrogen ($P = 0.001$) and phosphorus ($P < 0.001$). Needles from SP trees had higher concentrations of both N and P than D or CD trees (Table 4-3). Mean needle N concentration was higher in M site trees (10.9 g kg^{-1} vs. 10.1 g kg^{-1}; $P = 0.030$), but there was no significant site quality effect on needle P concentration ($P = 0.576$). Trees from M sites supported more sapwood volume per unit leaf area than did trees from L sites ($P = 0.024$) (Figure 4-4b). The ratio of sapwood volume to leaf area did not differ between crown classes ($P = 0.511$) nor was interaction between site quality and crown class observed ($P = 0.803$).

Leaf area indices within the sampled plots ranged from 2.3 to 3.9. Though the mean LAI for M sites (3.6) tended to be higher than that for L sites (3.1), the difference between site quality classes was weak ($P = 0.075$). Site Index was closely related to LAI on M sites ($P = 0.001$, $r^2 = 0.956$), but on L sites there was no relationship ($P = 0.49$) (Figure 4-5).

Discussion

Height repression in high density lodgepole pine stands growing on nutrient limited sites does not appear to be associated with reduced volume growth per unit leaf area (*GE*) of individual trees. Despite large differences in growth rates of individual trees (Figure 4-1a), *GE* was not significantly different between trees from M and L sites regardless of tree social status (Figure 4-

1b). Slower growing trees on height-repressed L sites, however, had lower volume growth per unit crown projection area (*CE*; Figure 4-1c), even though they had smaller crowns (Table 4-2). This is in contrast to findings of Sterba and Amateis (1998), who reported that smaller crowns had greater *CE* within a given crown class. In my study, the higher *CE* for the trees from the M sites was likely related to the higher photosynthetic efficiency because of their higher foliar N concentrations (Table 4-3), and more conductive stem sapwood (Reid et al. 2003). Despite lower than expected site indices (Beckingham et al. 1996), the stand level leaf areas of L sites were very close to those of M sites (Figure 4-5) suggesting that M and L sites had similar light transmission and competition for light among trees within the stands. This also suggests that height growth on L sites was substantially lower than expected given their leaf areas, and that LAI may not always be useful to quantify potential forest productivity.

My data show that there was a significant effect of crown class on *GE* for these self-thinning lodgepole pine stands. Superior *GE* of SP trees relative to D and CD trees (Figure 4-1b) might be interpreted as an adaptation that could potentially improve access to light for a SP tree through preferential allocation to stem growth. Suppressed loblolly pine trees in extensively managed plantations have been reported to allocate biomass preferentially to boles over needles and branches, compared to dominant trees (Naidu et al. 1998). My findings also call into question the notion that *GE* is a measure of tree vigour. Given that plants can change their allometry to counter resource deficiencies (Cannell and Dewar 1994), one might have expected an increased allocation to foliage rather than stem biomass in shaded SP trees. However, fewer needles in SP trees may be sufficient since smaller SP crowns have higher concentrations of N and P within needles (Table 4-3) and can thus be more photosynthetically efficient when illuminated. Given the relatively low leaf area indices (Table 4-1) and high gap fractions (55.8±1.5 %) in these stands, there is likely to be a moderate level of light available to the lower levels of the canopy as well as periodic sun flecks. Greater photosynthetic efficiency owing to higher needle nutrient concentrations explains the higher *GE* for a given Q_L that we observed for SP trees (Figure 4-3a). SP trees appear to be growing more for a given water supply.

My findings concerning *GE* are in contrast to several previous studies. O'Hara (1988) found that codominant Douglas fir trees with medium sized crowns had the highest *GE* across the same range of crown classes, however, his result was based on an assumption of a constant leaf area to sapwood area ratio. This ratio is now known to vary with length of live crown (Long and Smith

1988) and crown class (Reid et al. 2003). When I calculate *GE* as O'Hara did (growth per unit sapwood area), my results are very similar to his. Similarly, Binkley et al. (2002) demonstrated that crown dominance was positively related to *GE* in fast growing *Eucalyptus sp.* plantations. In contrast suppressed trees from high elevations/latitude (Kaufman and Ryan 1986; Gilmore and Seymour 1996; and this study) were found to have higher *GE.* This may be because the slow growth and lower leaf area of these kinds of temperate and boreal conifer stands allows more light penetration and generally allows suppressed trees to survive longer. SP trees in my study had very small crowns and low permeability sapwood (Reid et al. 2003), which suggests they will continue to grow slowly despite their greater *GE.*

The positive relationship I observed between crown dominance and *CE* (Figure 4-1c) is not surprising since taller canopy trees had better access to light within fully occupied stands. D trees had broad crowns with high leaf area density (Figure 4-4a) and because much of their crowns were positioned higher than neighbours' leaves, they would have been well illuminated, allowing them to maintain high *CE.* The contrasting trends between *GE* and *CE* in relation to crown class that we observed can be explained by differences in leaf area density. More densely foliated crowns of the D trees would have had higher photosynthetic efficiency per unit of crown projection area, and at the same time lower *GE* due to some self-shading. While CD trees would be less likely to experience self-shading since they had lower leaf area density, they would be more likely to be shaded for at least some portion of the day by taller, broader, and more densely foliated D neighbours. My observation of dominant crown positions with higher *CE* is consistent with the observations of Sterba and Amateis (1998) in loblolly pine and O'Hara (1988) in Douglas fir. I believe *CE* may be more useful for making management decisions in these types of lodgepole pine stands since it reflects the efficiency of production per unit of occupied land area. Desirable stand structure following thinning, based on crown projection area (*CE*), would be achieved by removing smaller diameter trees to retain the biggest trees, rather than retaining CD trees with medium sized crowns as has been suggested for Douglas fir (O'Hara 1988). It is important to note that O'Hara's (1988) inferences were based on much larger trees than the trees I studied; the un-thinned codominant trees he studied had an average crown projection area of 28.2 m^2 (10-20 times larger than those described here; Table 4-2).

The constant rate of increasing volume growth with increases in Q_h (Figure 4-2a) and leaf area (Figure 4-2b) suggests the larger trees I studied were able to utilize increases in available water and light equally as well as the smaller trees. This is somewhat surprising since increasing size of individual trees has been associated with declines in *GE* with age (Long and Smith 1990, Jack and Long 1992, Kollenberg and O'Hara 1999). The largest trees that I studied were younger and smaller than the large old trees examined in these other studies, and had not yet developed crowns with large non-photosynthetic components. Lower *GE* has been related to lower leaf area density in crowns of large old trees that have a significant non-foliated inner core (Long and Smith 1990), but the SP trees I studied had the lowest leaf area density, and were the most efficient. As stands age and trees become large, the ability to supply water to leaves in large old trees has been related to declines in *GE* (Magnani et al. 2000). While I did see a strong positive relationship between *GE* and Q_L (Figure 4-3a), this relationship does not appear to be affected by the differences in size between the trees I studied. Stomatal limitation due to differences in branch length (Walcroft et al. 1996, Waring and Silvester 1994) is also unlikely to have contributed to the differences I observed in *GE* (and *CE*) since branches were generally shorter than 1m. The lower *GE* I observed in D and CD trees were therefore likely not because they were the biggest trees, but rather because they had lower concentrations of N and P in their foliage than did SP trees.

Though I found no evidence to suggest that height repression is directly related to hydraulic limitation on existing leaf area, I did observe some important relationships between hydraulic characteristics and growth. My observation of a positive relationship between *GE* and Q_L (Figure 4-3a) is further evidence that the ability to supply water to leaves has an impact on gas exchange and carbon assimilation (Tyree 2003, Hubbard et al. 2001). I am the first to show that this relationship, previously applied to trees of differing ages (Mencuccini and Grace 1996), holds for trees of similar age. The correlation between k and radial growth (Figure 4-3b), suggests ring size and the production of new conducting tissue is important to maintain k. Growth of wide rings containing a greater proportion of earlywood should improve k, particularly since outer sapwood is generally more conductive (Reid et al. 2003). In trees experiencing very low radial growth rates, k is likely to remain low until sufficiently high radial growth rates are achieved to measurably affect Q_h and allow for development of new leaf area. Delays in growth response of height repressed lodgepole pine following thinning (Worall 1995; Farnden and Herring 2002) may be therefore be due to a hydraulic limitation on the development of new leaf area. Measurement of radial growth could provide a relatively easy index to assess the hydraulic status of trees. Thinning in stands where the average ring width in outer sapwood is less than 0.5 mm per year may not produce the desired 'release' effect since the reduced *k* of retained trees is likely to limit the development of new leaf area.

I suspect that the physiological differences I observed among trees of different crown classes and site qualities contribute to height repression by influencing stand structure and the resulting interactions between competing individuals within the stand's population. Low sites have positively skewed diameter distributions (Reid et al. 2003) reflecting a greater proportion of surviving SP trees. Though smaller SP trees do have higher *GE*, they grow very slowly. The lower ratio of sapwood volume to leaf area of L site trees (Figure 4-4b) suggests maintenance respiration costs are less of a drain on trees from L sites, which can therefore survive longer. Surviving trees reduce the area available for crown expansion of neighbouring trees, thereby limiting their growth rates. High *GE* of SP trees likely contributes to slow self-thinning, and too many small trees survive on L sites thereby suppressing growth rates, including height growth. Stands on L sites can thus develop LAI similar to those on M sites (Fig. 4-5), but this leaf area is allocated among too many small trees to achieve potential individual and stand level growth rates. Because regeneration at high densities following natural disturbance is unlikely to achieve potential growth rates (Huang et al. 2003), and SP trees have higher *GE* regardless of site quality, removal of SP trees through thinning may be very important to maintain productivity.

Table 4-1 Site and mean stand characteristics of the medium (M) and low (P) sites from which sample trees were collected.

Site	Age (yr.)	SI_{50}[1] (m)	Density (stems ha^{-1})	dbh[2] (cm)	Skewness of dbh distribution	BA[3] (m^2 ha^{-1})	height (m)	LAI[4] (m^2 m^{-2})
M-1	41	14.8	6000	7.5 ± 0.2	0.44	26.2	11.1 ± 0.5	3.9
M-2	40	13.4	5659	8.5 ± 0.3	0.29	37.5	10.3 ± 0.4	3.5
M-3	39	14.6	5602	8.5 ± 0.2	0.38	31.9	9.9 ± 0.7	3.8
M-4	37	14.5	7198	6.5 ± 0.2	0.40	28.1	8.4 ± 0.4	3.7
M-5	63	12.5	5857	8.0 ± 0.2	0.61	28.0	12.1 ± 0.4	3.0
M-6	39	14.4	3803	9.3 ± 0.3	-0.55	29.5	15.1 ± 0.5	3.7
L-1	46	11.5	10197	5.4 ± 0.2	0.39	35.5	7.5 ± 0.3	2.8
L-2	41	7.4	22282	3.2 ± 0.1	0.31	26.4	5.2 ± 0.1	3.1
L-3	46	8.7	27502	3.8 ± 0.1	1.11	51.4	6.4 ± 1.1	3.5
L-4	41	8.5	27852	3.3 ± 0.1	1.03	21.6	5.1 ± 0.5	3.8
L-5	41	9.6	22282	3.5 ± 0.1	1.02	30.1	5.3 ± 0.3	2.3
L-6	40	11.5	30239	3.3 ± 0.1	1.54	28.8	5.0 ± 0.2	3.2

Note: Means ± one standard error.

[1] Site Index (height in m at age 50)

[2] mean diameter at breast height (1.3 m)

[3] stand Basal Area

[4] Leaf Area Index

Table 4-2 Mean diameter at breast height (dbh), height (ht), leaf area (AL), crown projection area (CPA), crown volume (CVOL), and leaf area density (LAD) of dominant (D), co-dominant (CD), and suppressed (SP) sample trees from medium and low sites.

	Medium Sites					
Crown Class	dbh (cm)	ht (m)	A_L (m^2)	CPA (m^2)	CVOL (m^3)	LAD ($m^2\ m^{-3}$)
D[a]	13.3 ± 0.6	11.2 ± 0.2	10.2 ± 1.3	2.6 ± 0.7	8.7 ± 2.0	1.4 ± 0.4
CD	8.9 ± 0.5	10.8 ± 0.8	3.2 ± 0.4	1.3 ± 0.2	3.6 ± 0.5	1.0 ± 0.1
SP	4.5 ± 0.5	6.1 ± 0.5	0.4 ± 0.1	0.5 ± 0.1	0.9 ± 0.3	0.5 ± 0.1
	Low Sites					
D	8.7 ± 0.7	8.1 ± 0.7	4.9 ± 0.7	1.3 ± 0.3	4.0 ± 1.1	1.6 ± 0.3
CD	5.4 ± 0.4	6.3 ± 0.4	1.2 ± 0.2	0.6 ± 0.1	1.3 ± 0.2	1.1 ± 0.2
SP[a]	2.4 ± 0.4	3.0 ± 0.2	0.1 ± 0.02	0.3 ± 0.08	0.3 ± 0.1	0.6 ± 0.2

Note: Means ± one standard error.

[a] n=5, n=6 for all other groups

Table 4-3 Mean nitrogen and phosphorus concentration (g kg-1) for needles from all sites combined.

	D	CD	SP
N	10.2 a	9.7 a	11.5 b
P	1.1 a	1.0 a	1.3 b

Note. Means within rows (by variable) followed by the same letter are not significantly different at the 0.05 level according to the Student-Newman-Keuls test.

Figure 4-1 Means across crown dominance classes and site qualities in terms of (a) annual volume growth from 1994-1999, (b) annual volume growth per unit projected leaf area (*GE*), (c) annual volume growth per unit crown projection area (*CE*), and (d) hydraulic capacity under a unit hydraulic gradient (Q_h). Error bars represent one and standard error.

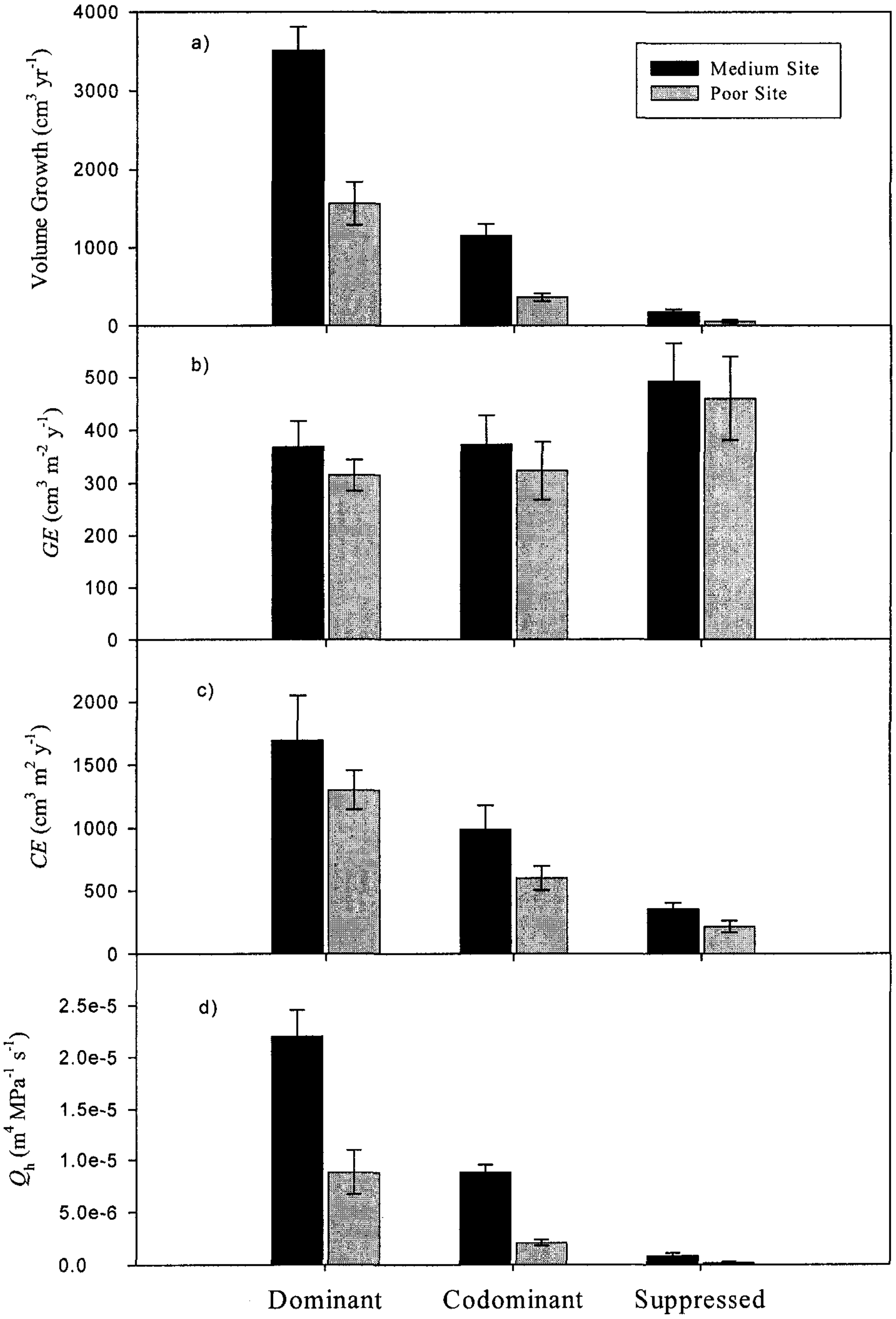


Figure 4-2 Volume growth from 1994-1999 versus: (a) hydraulic capacity under a unit hydraulic gradient (Q_h), and (b) leaf area. Regression lines are for all data combined. Data symbols represent dominant (circles) codominant (squares) and suppressed (triangles) trees from medium (filled) and low (open) sites.

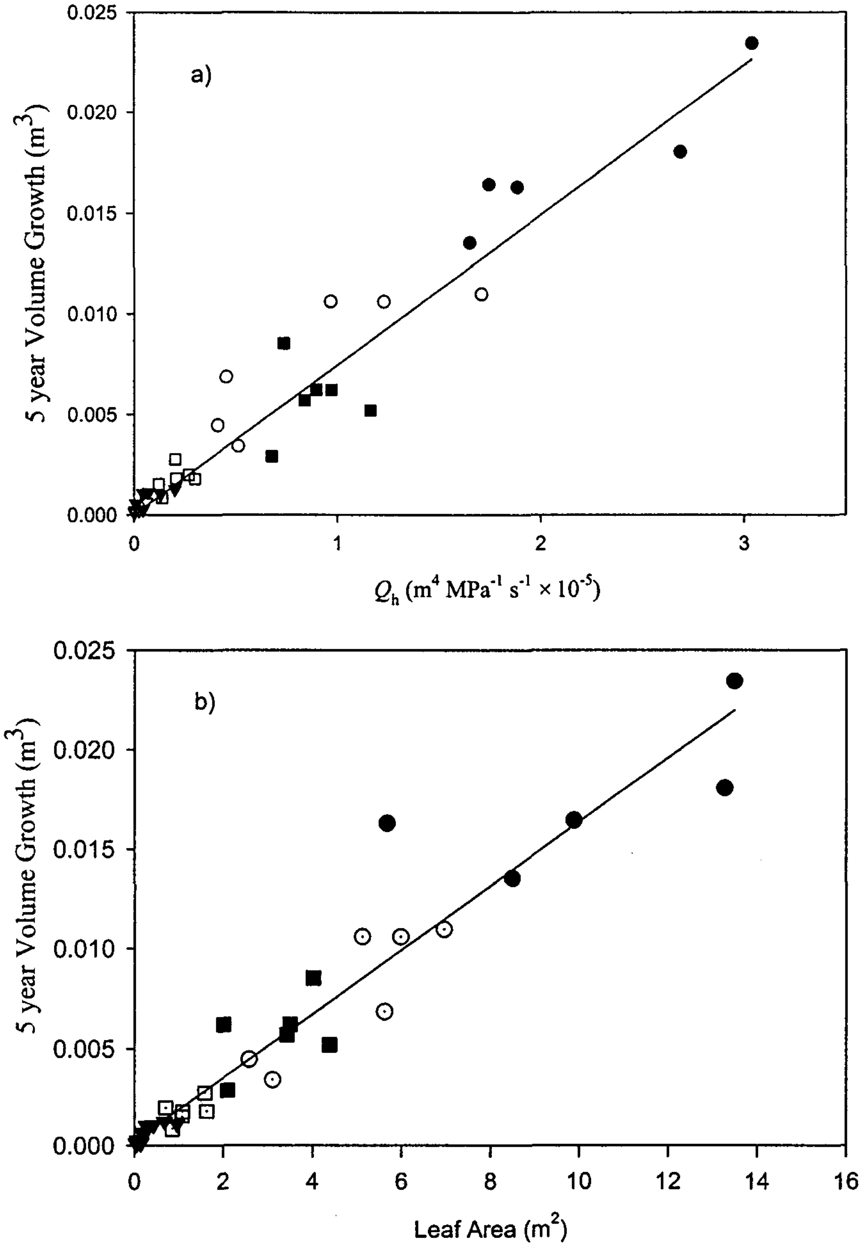


Figure 4-3 (a) Volume growth from 1994-1999 per unit leaf area (*GE*) versus leaf specific hydraulic capacity (Q_L) by dominance class. (b) Permeability (k) versus radial growth from 1994-1999 for all trees combined. Data symbols represent dominant (circles), codominant (squares) and suppressed (triangles) trees from medium (filled) and low (open) sites.

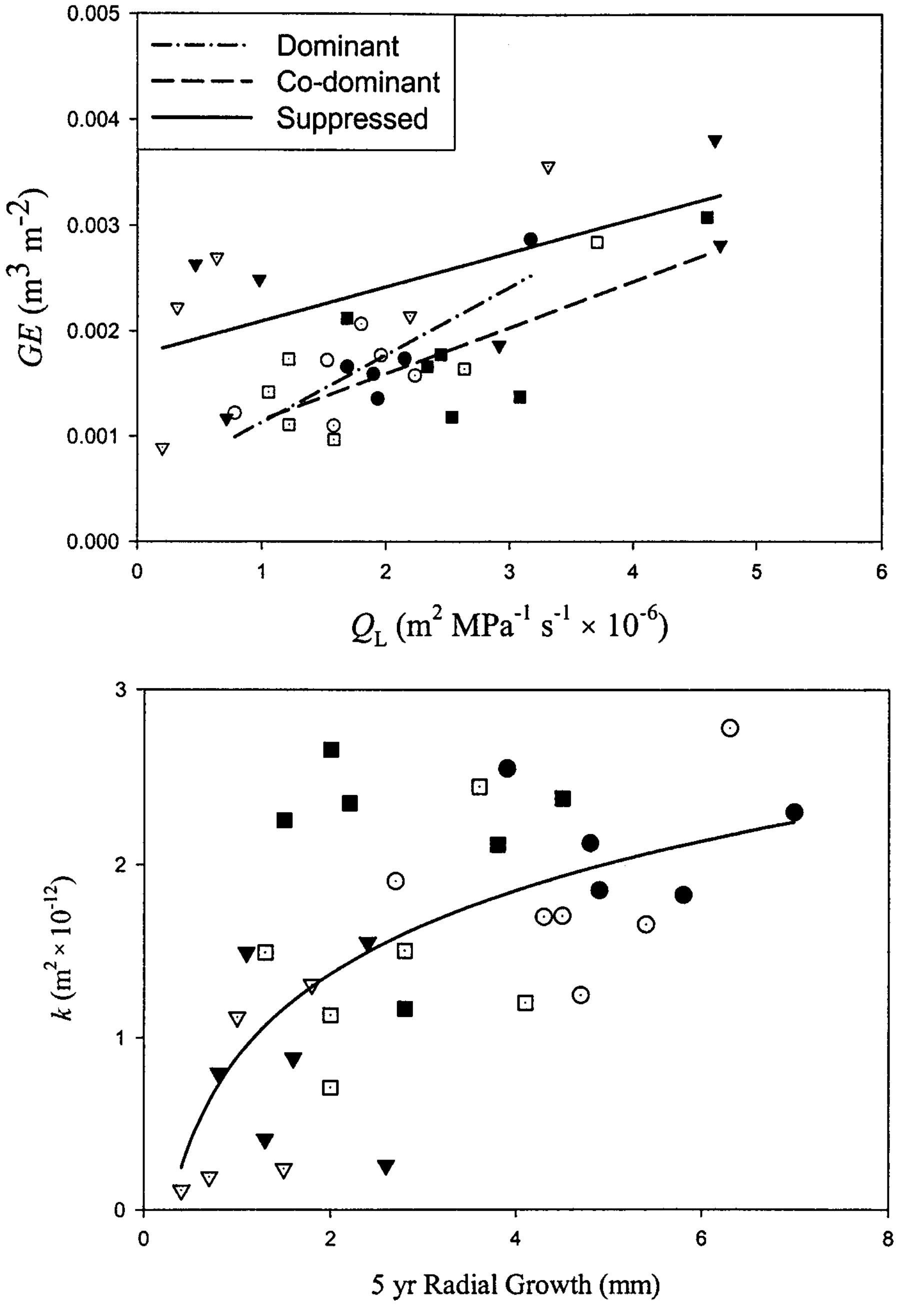


Figure 4-4 Means across crown dominance classes and site qualities for (a) leaf area density and (b) stem sapwood volume per unit leaf area. Error bars represent one standard error.

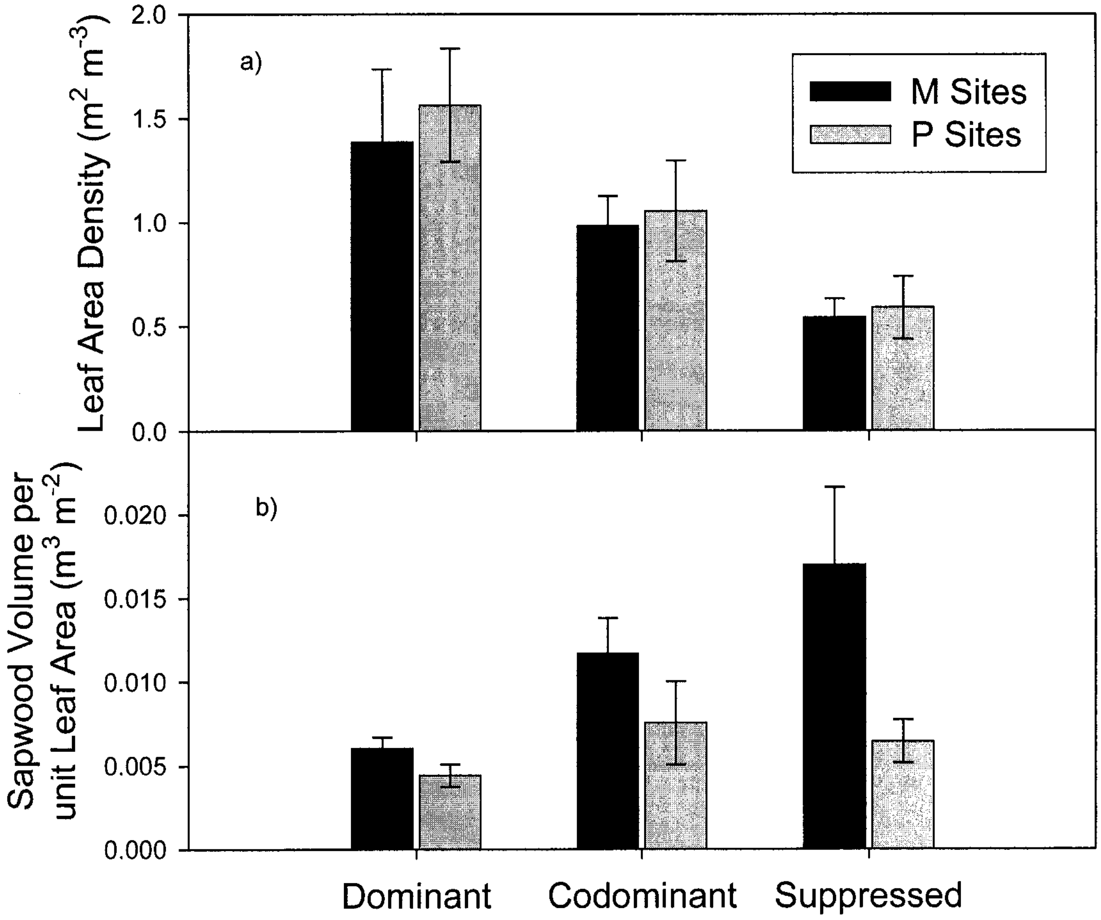
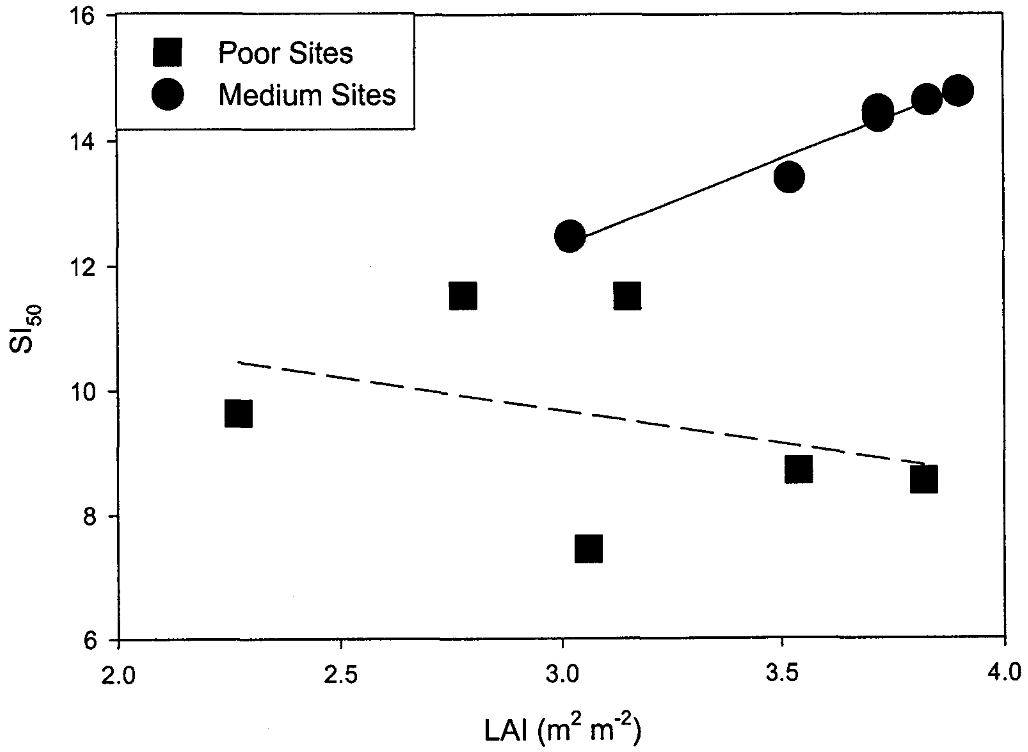


Figure 4-5 Site index (SI_{50}; height in m at reference age 50) versus leaf area index (LAI) for medium and low sites.



References

Assmann, E. 1970. The principles of forest yield study. Pergamon Press, Oxford, UK.

Beckingham, J.D., Corns, I.G.W., and Archibald, J.H. 1996. Field guide to ecosites of west-central Alberta. Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent., Edmonton. Spec. Rep. 9, 630 p.

Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H.R., and Fownes, J. 2002 Age-Related decline in forest ecosystem growth: an individual tree, stand structure hypothesis. Ecosystems 5: 58-67.

Cannell, M.G.R., and Dewar, R.C. 1994. Carbon allocation in trees: a review of concepts for modelling. Adv. Ecol. Res. 25: 59-104.

Comeau, P.G., Macdonald, R., and Bryce, R. 2002. SLIM Version 2.1i (Spot Light Interception Model). B.C. Ministry of Forests.

Coyea, M.R., and Margolis, H.A. 1994. The historical reconstruction of growth efficiency and its relationship to tree mortality in balsam fir ecosystems affected by spruce budworm. Can. J. For. Res. 24(11): 2208-2221.

Day, R.J. 1997. The ancient and orderly European discipline of thinning is now a reality in North America. In Stand Density Management:Planning and Implementation. Proceedings of a conference held November 6–7 in Edmonton, Alberta. Ed. C. Bamsey. Clear Lake Ltd., Edmonton, AB, pp. 24–33.

Farnden, C., and Herring, L. 2002. Severely repressed lodgepole pine responds to thinning and fertilization: 19-year results. For. Chron. 78 (3): 404-414.

Gilmore, D.W., and Seymour, R.S. 1996. Alternative measures of stem growth efficiency applied to *Abies balsamea* from four canopy positions in central Maine, USA. For. Ecol. Manag. 84(1-3): 209-218.

Gower, S.T., McMurtrie, R.E., and Murty, D. 1996. Aboveground net primary production decline with stand age: Potential causes. Trends Ecol. Evol. 11(9): 378-382.

Huang, S. 1994. Ecologically based individual tree volume tables for lodgepole pine (*Pinus contorta* var. *latifolia Engelm.*). Edmonton: Alberta Environmental Protection, Land and Forest Services, Forest Management Division, 1994. 121 p.

Huang, S., Monserud, R.A., Braun, T., Lougheed, H., and Bakowsky, O. 2004. Comparing site productivity of mature fire-origin and post-harvest juvenile lodgepole pine stands in Alberta. Canadian Journal of Forest Research 34, 1181-1191.

Huang, S., Titus, S.J., and Klappstein, G. 1997. Development of a sub-region based compatible height–site index–age model for young and mature lodgepole pine in Alberta. Land and Forest Service, For. Manage. Res. Note No. 6, Pub. No. T/353, Edmonton, AB, pp 1–51.

Hubbard, R.M., Ryan, M.G., Stiller, V., and Sperry, J.S. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine Plant Cell Environ 24(1): 113-121.

Jack, S.B., and Long, J.N. 1992. Forest production and the organization of foliage within crowns and canopies. For. Ecol. Manag. 49(3-4): 233-245.

Kaufmann, M.R., and Ryan, M.G. 1986. Environmental, physiographic, and stand effects on individual tree growth in sub-alpine forests. Tree Physiology. 2: 47-59.

Keane, M.G., and Weetman, G.F. 1987. Leaf area–sapwood cross-sectional area relationships in repressed stands of lodgepole pine. Can. J. For. Res. 17: 205–209.

Kollenberg, C.L., and O'Hara, K.L. 1996. Leaf area and tree increment dynamics of even-aged and multiaged lodgepole pine stands in Montana. Can. J. For. Res. 29(6): 687-695.

Liu, X., Silins, U., Lieffers, V.J., and Man, R. 2003. Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. Can. J. For. Res. 33(7): 1295–1303.

Long, J.N. 1985. A practical approach to density management. For. Chron. 61:23–27.

Long, J.N., and Smith, F.W. 1988. Leaf-area sapwood area relations of lodgepole pine as influenced by stand density and site index. Can. J. For. Res. 18(2): 247-250.

Long, J.N., and Smith, F.W. 1990. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests – The influence of site quality and stand structure. J. Appl. Ecol. 27(3): 847-856.

Long, J.N., and Smith, F.W. 1992. Volume increment in *Pinus contorta* var. *latifolia* – The influence of stand development and crown dynamics. For. Ecol. Manag. 53(1-4): 53-64.

Magnani, F., Mencuccini, M., and Grace, J. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant Cell Environ. 23:251-263

Mencuccini, M. and Grace, J. 1996. Hydraulic conductance, light interception and needle nutrient concentration in scots pine stands and their relations with net primary productivity. Tree Physiology 16: 459-468.

Naidu, S.L., DeLucia, E.H., and Thomas, R.B. 1998. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. Can. J. For. Res. 28(8): 1116-1124.

O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can J For Res. 18: 859-866.

Oliver, C.D., and Larson, B.D. 1990. Forest Stand Dynamics. McGraw-Hill Inc., New York.

Reid, D.E.B., Silins, U., and Lieffers, V.J. 2003. Stem sapwood permeability in relation to crown dominance and site quality in self-thinning fire-origin lodgepole pine stands. Tree Physiology 23:833–840.

Ryan, M.G., and Waring, R.H. 1992. Maintenance respiration and stand development in a sub-alpine lodgepole pine forest. Ecology 73(6): 2100-2108.

Stadt, K.J., and Lieffers, V.J. 2000. MIXLIGHT: a flexible light transmission model for mixed-species forest stands. Ag. For. Meteorol. 102(4): 235-252.

Sterba, H., and Amateis, R.L. 1998. Crown efficiency in a loblolly pine (*Pinus taeda*) spacing experiment. Can. J. For. Res. 28: 1344-1351.

Tyree, M.T. 2003. Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. Trees 17(2): 95-100.

Walcroft, A.S., Silvester, W.B., Grace, J.C., Carson, S.D., and Waring, R.H. 1996. Effects of branch length on carbon isotope discrimination in *Pinus radiata*. Tree Physiology 16:281-286.

Waring, R.H., Theis, W.G., and Muscato, D. 1980. Stem growth per unit of leaf area – a measure of tree vigor. For. Sci. 26(1): 112-117.

Waring, R.H., Schroeder, P.E., and Oren, R 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. 12(3): 556-560.

Waring, R.H., and Pitman, G.B. 1983. Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. J. Appl. Entomol. 96(3): 265-270.

Waring, R.H., and Schlesinger, W.H. 1985. Forest Ecosystems: Concepts and Management. Academic Press, Orlando.

Waring, R.H., and Silvester, W.B. 1994. Variation in foliar $\delta^{13}C$ values within the crowns of Pinus radiata trees. Tree Physiology 14:1203-1213.

Weiner, J., and Thomas, S.C. 1986. Size variability and competition in plant monocultures Oikos 47:211-222.

Whitehead, D., Edwards, W.R.N., and Jarvis P.G. 1984. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. Can. J. For. Res. 14:940–947.

Worall, J. 1995. Height growth stagnation in lodgepole pine: all (well almost all) is revealed. Branchlines 6(3): 5.

Worall, J., Draper, D.A., and Anderson, S.A. 1985. Shoot characteristics of stagnant and vigorous lodgepole pines, and their growth after reciprocal grafting. Can. J. For. Res. 15: 365-370.

Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., and Kaufmann, M.R. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40(3): 513-527.

Zar, J.H. 1996. Biostatistical Analysis, 3rd ed. Prentice Hall, Upper Saddle River New Jersey.

Chapter 5

Water use in response to atmospheric demand in thinned and un-thinned lodgepole pine from sap flow measurements

Introduction

Following wildfire, lodgepole pine is known to establish at very high densities that can result in intense intra-specific competition and reduced growth rates for individual trees and stands (Huang et al. 2004). Thinning is a management strategy that increases the available growing space for retained trees, and is widely employed as a strategy to improve growth rates in managed temperate and boreal forests (Day 1997). Trees left behind after thinning may experience improved water relations because of reduced competition for water (Donner and Running 1986). Conversely, trees may experience water stress following thinning due to increases in stem sap flow rates and associated declines in leaf water potential (Jarvis 1975). Other factors increasing post-thinning water stress may include increased illumination of crowns stimulating stomatal opening (Lopushinsky 1975) and greater wind loading (Rudnicki et al. 2002), which increases atmospheric moisture demand. Greater wind loading may also negatively affect sapwood hydraulic conductivity due to bending stress (Silins et al. unpublished). Physiological limitations on water movement within the tree, and changes in environmental conditions for retained trees may limit their ability to take advantage of reduced competition after thinning. In many cases improved growth rates are not observed for several years following thinning (Yang 1988, Youngblood 1991), particularly in fire origin lodgepole pine stands (Worall 1995). Density management combined with appropriate fertilization, nevertheless, has the potential to dramatically increase height growth and yield, even from severely repressed lodgepole pine stands (Farnden and Herring 2002).

In a recent study of the effects of thinning on stem hydraulic properties of fire origin lodgepole pine trees, Liu et al. (2003), observed a decline in height growth and sapwood permeability (*k*) four growing seasons after thinning. Increased allocation to early-wood in thinned trees was not sufficient to counter apparent damage to conducting sapwood xylem, resulting in lower sapwood permeability (Liu et al. 2003). Paradoxically, retained trees in thinned stands had significantly greater leaf area, sapwood area, hydraulic capacity (Q_h), and radial growth rates relative to unthinned controls. It is unclear how these physiological changes associated with thinning affect transpiration and stomatal conductance in response to the change in environmental conditions for the crowns of retained trees.

Thermal dissipation sap flow techniques (Granier 1987) can be effectively used to measure water use of individual trees in the field on a continuous basis, and have been used to study changes in tree water use following thinning. When appropriate climatic data are collected concurrently with sap flow data, these techniques can provide powerful insights into atmospheric-biological controls of whole tree water use (Whitehead and Jarvis 1981). Increased individual tree sap flow has been observed in *Chamaecyparis obtusa* (Morikawa et al. 1986), *Eucalyptus nitens* (Medhurst et al. 2002), and *Quercus petraea* (Bréda et al. 1995) following thinning. Others have reported that variability between individual trees in response to environmental variables increases following thinning (Lagergren and Lindroth 2002), and that strip rows used for vehicle traffic when thinning mixed stands of Scots pine and Norway spruce are associated with lower sap flow in the spruce (Lagergren and Lindroth 2004). However, differences in tree water use between thinned and unthinned lodgepole pine trees in relation to the environmental variables driving water movement have not been explored.

The objective of this study was to explore initial and longer term (5 yr.) biological adjustment of whole-tree water use regulated by stomatal behavior combined with alteration in xylem hydraulic properties in thinned vs. unthinned trees in one of the stands used in the study of Liu et al. (2003). We sought to determine whether damage to sapwood resulting in lower sapwood permeability was experienced during the growing season immediately following thinning. We anticipated that thinned trees would experience greater transpiration, consistent with the model proposed by Jarvis (1975). Furthermore, since stem sapwood in trees from thinned stands might be initially less permeable (Liu et. al. 2003), and their canopies experience greater exposure to light and wind, we anticipated they would be more likely to experience water stress and thus reduce stomatal conductance during hot dry weather.

Materials and Methods

The experiment was conducted in a juvenile Lodgepole pine stand 6 km south of Swan Hills, Alberta (54°45'N, 115°45'W, 1260 m elevation). This stand established naturally following wildfire in 1978. The site was classified as a bilberry/arnica – lodgepole pine ecosite, characteristic of the Upper Foothills natural region (Strong and Leggat 1992). Based upon 15-year weather records from the two closest weather stations (Flesch and Wilson 1993), mean annual precipitation is 440 mm, and mean annual temperature is 3°C.

Thinned (JT) and control (C) plots were established in May 2002 adjacent to plots (30 × 30m) thinned in 1998 (5T) by Liu et. al (2003). Thinning removed the smaller trees in the stand and thinning slash was left on site. The JT and C plots were both 15 × 30 m in size, and immediately east of the 5T plot. The C plot (28,383 tpha of 4 m+ pine and 18,038 tpha of < 2m black spruce) was established north of the JT plot. The density of the JT plot was reduced from 24,271 to 2,733 tpha, very similar to the 5T plot at 2,800 tpha of pine. There was also a significant understory of spruce in the 5T (42,654 tpha) and JT (20,292 tpha) plots. Measurements were made on 5T trees (n = 11), JT trees (n = 11), and C trees (n = 10) located throughout the central portion of the established plots. Trees were also selected based on proximity to a central location to accommodate connection of sap flow probes to data loggers.

Whole-tree water use

Whole-tree water use was determined using thermal dissipation sap flow probes to measure sap flow velocity. Thermal dissipation sap flow techniques utilize the rate of heat dissipation by convection (water movement in sapwood) as the basic measurement principle for estimating sap flow velocity. The two probe design of Granier (1987) in which the upper probe contains a thermocouple and heater, and the lower probe contains only a thermocouple allows for measurement of the temperature difference between probes and isolation of convective heat transport (from conductive heat transport within the solid matrix of the sapwood) to enable sap flow velocity determination.

Sap flow probe construction and installation

A pair of fine-wire copper-constantan thermocouples (CT) were connected at the constantan leads, allowing the measurement of temperature difference (ΔT), from the voltage difference between the two copper leads. The two thermocouples were installed at the midpoint of 1.5 mm-diameter steel needles, and then inserted into aluminum tubes as described by Phillips et al (1997). Each probe was 2.5 mm in diameter and 250 mm long. Fine wire constantan heater coils and durable connecting wires were constructed and tested in the laboratory. Power to the CT pairs was regulated from a 12V DC source to supply 200 mW of power to the upper probe in each pair. The power dissipates as heat into the sapwood and the vertical sap flux surrounding the probe. The temperature difference between the heated upper probe and unheated lower probe can be used to measure changes in vertical sap flow (Granier 1987, Kostner et al. 1996). When vertical sap flow is minimal, heat dissipation is governed by conduction. When vertical sap flow is high, the applied heat is dissipated more rapidly due to convection and the ΔT between the CT pair will decline. The amount of heat produced by the upper probe is a function of the regulated electric current, and the electronic resistance of the heater coil. Electronic resistance (Ω ohms) of the heater coils and thermocouple pairs was monitored throughout the experiment to ensure stability of all connections. Any change in electronic resistance of CT pair components was interpreted as damage to the instrument, and they were promptly repaired or replaced.

During periods of zero sap flux, typically after several hours of darkness, a stable maximum temperature difference (ΔT_{max}) is observed which can be used to evaluate subsequent changes in velocity (Granier 1987). Mean sap flux density (velocity) (v_s, m s^{-1}) along a radius can be estimated after Granier (1987) as:

Equation 5-1 $$v_s = 119 \times 10^{-6} (\Delta T_{\mathrm{max}} - \Delta T/\Delta T)^{1.231}$$

I use the symbol 'v_s' as suggested by Edwards et al. (1996) to facilitate easy comparison with other studies reporting sap flow. This sap flow probe design generally performed well. Subsequent sap flow measurements made on stem samples transported from the field and installed into a hanging water column permeameter in the lab produced very good agreement (± 2%) with the outflow recorded using an electronic balance (unpublished).

CT pairs were installed in the outer 2 cm of sapwood at 1.0 m height, separated 10 cm vertically. CT pairs were inserted radially into the sapwood on the north azimuth and protected from solar heating with reflective thermal insulation. Further correction for vertical temperature gradients resulting from solar heating of the instrumented tree stems was made using two non-heated CT pairs similarly installed into one tree in the 5T plot and one tree in the C plot. Between June 22 and August 30, 2002, v_s was measured in treated and control trees every 30 seconds to calculate and store 10-min averages using a CR10X (Campbell Scientific). The daily maximum ΔT was used as $\Delta T_{\max}$ for each 24-hour period.

A "roving sensor" method was used (Simpson 2000, Vertessey et al. 1995) wherein one reference tree was monitored continuously within each treatment with two CT pairs (the second on the south side of the stem). Six other trees in each treatment were simultaneously monitored for portions of the study period with a single CT pair. There were no significant differences between north and south v_s in any of the reference trees. Over 2-3 day periods highly significant (r^2 0.87-0.98) linear correlations between reference tree v_s and roving tree v_s were used to estimate roving tree v_s during periods where the tree was not instrumented.

Whole tree sap flow (Q, $m^3\ s^{-1}$; Edwards et al. 1996) was estimated from v_s by multiplying by sapwood area (m^2), measured digitally at the probe locations from stem cross-sectional images collected using a desktop scanner. For each 10 minute period, whole tree water use was determined from Q, and daily water use (Q_d, $m^3\ day^{-1}$) calculated from the sum of all periods within each calendar day. Transpiration per unit leaf area, or leaf related sap flow (Q_l) was determined by dividing Q by tree leaf area (A_l, m^2) during each measurement interval. To facilitate comparison with other published transpiration data, all Q_l data were converted to molar units (mmol $m^{-2}\ s^{-1}$) based on the molar mass of water (18.02 g mol^{-1}) and assuming water has a density of 1g cm^{-3}. I calculated mean mid-day Q_l from data collected between 11:00-14:00 MST during each day of the measurement period.

Tree measurements

All instrumented trees were harvested at the end of August 2002. Tree height, diameter at breast height (1.3 m), live crown length, and the length of the terminal leader were recorded. The total leaf area (A_L, m^2) of each tree was estimated by sampling the entire crown as follows. Differences in branch morphology and specific weight of needles between crown positions were accounted for by dividing crowns into upper, mid and lower sections. All needles from each crown were transported to the lab in moistened plastic bags in a cooler and stored overnight in the dark at 5°C. Sub-samples of fresh needles from each section of each crown were scanned, and one-sided projected leaf area (A_L; m^2) was measured using Sigma Scan-Pro® image analysis software. All needles were dried at 78°C until weight stabilized. Needle specific area (A_n, $m^2\ g^{-1}$) was determined from the dry weight of the scanned sub-sample. The leaf area of each crown section (A_L; m^2) was calculated from:

Equation 5-2 $$A_L = A_n * w_n$$

where w_n is the dry weight (g) of needles from the section. Crown section leaf areas were summed to determine total tree leaf area.

Xylem hydraulic measurements

Stem sections (~1 m long) from each instrumented tree were collected during sampling and stored in sealed plastic bags that were placed in a cold, moist insulated cooler for transport to the laboratory. In the laboratory, saturated sapwood permeability (k, m^2), of a ~15 cm stem section sub-sampled from near the base of the live crown (above the location where probes were installed) was measured using a permeameter as described by Reid et al. (2003). Hydraulic conductivity (K_Ψ) was also determined from these same flow measurements, and used to calculate the hydraulic capacity ($Q_h = K_\Psi \times A_s$, m^4 Pa^{-1} s^{-1}), and the leaf specific hydraulic capacity (Q_L; m^2 Pa^{-1} s^{-1}). See Chapter 2 for a detailed discussion of the terms used to describe hydraulic properties of xylem.

Meteorological measurements

Concurrent with sap flow measurements, meteorological measurements were made every 30 seconds, and 10-min averages recorded. Relative humidity (W_a) and air temperature (T_a, K), were measured on site using an HMP-45 relative humidity probe (Viasala, Finland) shielded against direct radiation, and used to calculate saturation vapor pressure (e_s, kPa) and ambient vapor pressure (e_a, kPa). Incident shortwave radiation above the canopy was measured using a pyranometer, and net radiation (Q*, W m^{-2}) estimated according to Linacre (1969) assuming an albedo of 0.1, typical for pine forest (Stewart 1971). Wind speed (u; m s^{-1}) was measured at 3.1 m using a 3-cup anemometer (RM Young, USA). Atmospheric moisture demand, or potential evaporation (E_o, mm day^{-1}), was estimated using the original Penman-combination equation (Giambelluca and Nillet 1992):

Equation 5-3 $$E_o = \frac{(\Gamma\,\Pi) + \gamma\left((0.263 + 0.138u)D\right)}{(\Gamma + \gamma)}$$

where Γ is the slope of the saturation vapor pressure vs. temperature curve (kPa K^{-1}), Π is net radiation (Q^*) expressed as an equivalent water depth [Π (mm day^{-1}) = 0.0353 Q^* (W m^{-2}); Giambelluca and Nillet 1992)], γ is the psychrometric constant (0.067 kPa K^{-1}), and D is the vapor pressure deficit of the air (e_s - e_a; kPa). This approach combines the atmospheric effects of wind, radiation, and momentum to predict the rate of evaporation of water from a surface with unlimited supply (Dingman 2002). We augmented our site meteorological data with cumulative precipitation data collected twice daily (morning and afternoon) at a nearby fire tower. When we were on-site for consecutive days, we also measured overnight precipitation using a non-recording rain gauge.

Evaporation from a vegetated surface will not be at the same rate as open pan evaporation because stomatal behavior can reduce canopy conductance in response to water stress. Monteith (1965) showed that by including the relationship between canopy conductance and atmospheric conductance in a Penman type equation, evaporation from a vegetated surface can be more reasonably quantified. For aerodynamically rough pine forests or plantations, atmospheric conductance is generally very large in relation to canopy conductance, typically resulting in values associated with wind and vapor pressure deficit (i.e. $\gamma((0.263 + 0.138u)\,D\;)$ in Equation 5-3) up to 20 times larger than those associated with incident radiation (i.e.($\Gamma\,\Pi$) in Equation 5-3), allowing simplification of the Penman-Monteith equation (Whitehead and Jarvis 1981). Whole tree canopy stomatal conductance (G_c mm s^{-1}) was estimated from leaf-related sap flow and an inversion of the simplified Penman-Monteith equation (Whitehead and Jarvis 1981, Martinez-Vilalta et al. 2003):

Equation 5-4

$$G_c = \gamma\,\lambda\,Q_l\,/\,\rho_a\,c_a\,D$$

where λ is the latent heat of vaporization of water (MJ kg^{-1}, estimated from T_a), Q_l is whole tree transpiring sap flow per unit leaf area (m^3 s^{-1} m^{-2}) ρ_a is the density of air (kg m^{-3}), and c_a is the heat capacity of air (1.0×10^{-3} MJ kg^{-1} K^{-1}). Periods where D was less than 0.1 kPa were not considered since there is a tendency to overestimate values of G_c determined using Equation 5-4 at low vapor pressure deficits (Phillips and Oren, 1998).

Analysis

In light of my inability to quantitatively test treatment effects because site is not replicated, I limit myself to a qualitative analysis of the temporal changes in Q_d , Q_l and G_c. I plotted E versus the mean Q_l for each treatment during five three-day periods of high irradiance and D. The data presented were taken from 1 hour before sunrise, till one hour after solar noon. The remaining data were not included to avoid the natural hysteresis typically observed for sap flow in trees. I used these scatter plots to qualitatively analyze the relationship between atmospheric demand and transpiration within each treatment. Differences in tree characteristics between treatments were compared using one-way ANOVA. Post hoc comparisons made using the LSD test in SAS (v. 8.0), and are reported as significant at the 0.05 level.

Results

Thinning treatment in 1998 resulted in greater diameter growth (dbh) and less leader growth (Table 5-1) on this site. Leader growth may very well be responsible for the weak effect of thinning on height (Table 5-1), after only five growing seasons.

Despite similar live crown length (Table 5-1), 5T trees had almost twice as much leaf area and approximately 30% more sapwood area than the C trees and JT trees. There were no significant differences in leaf area or sapwood area between JT and C trees at the time of sampling. The leaf area to sapwood area ratio (S) of 5T trees was 36% higher than that of C trees and 26% higher than JT trees; JT and C trees were not significantly different. Saturated sapwood permeability (k) determined in the lab at the end of the measurement period was 22% higher in C trees compared to JT and 5T trees combined, which did not differ at the 0.05 level (Table 5-1). There was significant variation in hydraulic capacity (Q_h) between treatments (p=0.04, Table 5-1), but only JT (lowest) and 5T trees (highest) were significantly different according to the post hoc comparison. Despite apparent damage and loss of permeability, Q_h of 5T and C trees was not significantly different due to the larger sapwood conducting area of the 5T trees. JT trees had the lowest Q_h , though not significantly different from C trees. More importantly, due to the large leaf area maintained by 5T trees, leaf specific hydraulic capacity (Q_L) was 43% lower than that of C trees. Similarly, significantly lower sapwood k, combined with non-significant differences in leaf area and sapwood area, resulted in C trees having a Q_L that was 30% greater than that of JT trees.

Mean apparent sap flux density (v_s) (Granier 1987) typically increased quickly in the morning hours to a maximum in the late morning, followed by a relatively stable period during mid-day, and then a steep decline to very low flows at night (Figure 5-1). This pattern was closely linked to diurnal patterns of net radiation (Q^*) and vapor pressure deficit (D). Drastic mid-day depressions in v_s (e.g. July 14, Figure 5-1) were sometimes observed associated with dramatic changes in Q^* and D presumably due to variable cloud cover (Figure 5-2). Less dramatic declines were typically observed on hot dry days during mid-day periods where v_s remained stable (e.g. July 15, Figure 5-1). Zero flows (ΔT_{max}) were generally observed during predawn hours when D was at a minimum, and stomatal opening was not yet stimulated by incident solar radiation. Measurement of low flows is difficult using this probe design, and zero flows may not always occur every night. Use of a daily ΔT_{max} accounts for changes in ambient temperature of the sapwood in which the CT pairs are installed, but can reduce the accuracy of low flow measurements at night.

Maximum daily v_s (v_{MAX}) was typically observed in late morning or early afternoon (see Figure 5-1) and generally consistent from day to day between and within groups on all trees measured. Over the entire course of the measurement period (data not shown) v_{MAX} also occurred at other times of the day both within and between treatments; it was observed as late as 18:20 on August 25th in one JT tree. Within each treatment the maximum v_s that I observed typically occurred on the same day for most trees, but the day on which v_s peaked differed between treatments. Amongst 5T trees, the maximum v_s was observed in 9 of 11 trees on June 29 during a cool moist period. Maximum v_s in the C plot was observed in 7 of 10 trees on July 13th following thunder storms during the two previous nights that deposited 24 mm and 12 mm of rain respectively on the study site. In the JT plot, there was not one single day on which maximum v_s was observed in most of the trees.

Meteorological data collected during the measurement period varied considerably, typical of subalpine environments in Alberta during the summer. Mean mid-day (11:00-14:50) values for collected variables are presented (Figure 5-2) to provide an indication of atmospheric conditions during peak daily v_s. The summer of 2002 was generally very warm with mean mid-day air temperature (T_a) of 17.8 °C; a maximum of 28 °C was observed on June 26th and a minimum of 5.4 °C on August 2nd (Figure 5-2a). There were many sunny days with high Q^* (max. 718 W m^{-2} on June 30th), which averaged 485.8 W m^{-2}, but infrequent cloudy days (min. 135 W m^{-2} on

August 2nd) also occurred (Figure 5-2b). Variation in D from day to day generally mirrored that of Q^* (Figure 5-2b), and averaged 1.7 kPa; maximum mid-day D of 2.9 kPa was observed on June 26th, and the minimum mid-day D of 0.07 kPa was observed on July 31st. These variables, along with wind data contributed to the variation in E_o observed (Figure 5- 2a). Mid-day potential evaporation (E_o) averaged 0.71 mm hr^{-1}, but was as low as 0.20 mm hr^{-1} on August 2nd and as high as 1.06 mm hr^{-1} on June 30th.

In terms of precipitation, 2002 was generally a dry year in northern Alberta. Total rainfall recorded at the nearby Swan Hills fire look-out tower from May 1st to June 21st was 44.4 mm, and during the measurement period was only 159.1 mm; Normal (1971-2000) precipitation for this region is 163 mm in May and June, and 191 mm in July and August (Environment Canada). Total potential evaporation from Equation 4 over the course of the measurement period was 452 mm. A series of thunderstorms produced 24mm on July 11-12th and 12mm on July 12-13th. These values are considerably larger than the values recorded at the fire tower on those days (Figure 5-2a), reflective of the spatial variability typical of deposition from summer thunderstorms. The low temperatures and precipitation recorded between July 31st and August 5th were due to a major low pressure system which covered most of the province of Alberta. During this time T_a dropped as low as -0.6 °C (Aug 3 @ 6:20) and precipitation recorded at the fire tower included 0.4 cm of snow between August 1st and 2nd.

There appeared to be large differences in daily water use of trees (Q_d) between treatments over the course of the study (Figure 5-3a). On average Q_d was 2.7 litres for 5T trees, 1.9 litres for JT trees and 1.3 litres for C trees from June 22nd to August 30th 2002. Individual trees transpired as much as 10.8 litres (5T tree on July 10th), and as little as 0.04 litres (C tree on August 2nd) in a single day. At the beginning of the measurement period, Q_d of 5T trees was nearly double that of both the JT and C trees (Figure 5-3a). From July 10th until the cold wet period from July 29 to August 5, Q_d of JT trees was generally less than that of the 5T trees, but greater than the C trees. During the remainder of August, Q_d of JT trees was similar to that of the 5T trees, and about twice that of the C trees.

Differences in Q_l were also apparent between treatments during the measurement period (Figure 5-3b). From June 22nd until July 5th, mid-day Q_l of the 5T trees was higher than either the JT or C trees. Through the remainder of July, mid-day Q_l did not differ between treatments. Following the cool wet period in early August, mean mid-day Q_l of JT trees seemed to be consistently higher than that of C trees and 5T trees. From August 20th to 30th, mid-day Q_l of JT trees was 52% greater than that of 5T trees and 85% greater than that of C trees.

Though canopy stomatal conductance (G_c) also periodically appeared to differ between treatments, G_c was generally not as variable among treatments as Q_d or Q_l (Figure 5-3c). From June 22nd to July 1st, G_c appeared to be higher for the 5T trees than the JT and C trees. For the remainder of the month of July, despite sometimes dramatic variability in G_c between days, there were no apparent differences between treatments. On August 1st and 3rd G_c appeared to be higher for the JT and 5T compared to the C trees, and on August 2nd they ranked JT > 5T > C. For the remainder of August, G_c was consistently highest in the JT trees. During this month G_c of 5T trees were either greater than or equal to that of C trees.

During all of the clear sky periods examined, Q_l increased with increasing E_o in the morning, and tended to flatten out as E_o continued to increase in the early afternoon (Figure 5-4). In all cases, the data are presented without any time lag between E_o and observed Q_l. Figure 5-4 illustrates the dynamic responses of Q_l in JT, C and 5T trees to increasing E_o. The asymptotic nature of this relationship suggests a Q_l threshold above which stomatal control limits transpiration. For June 23-25 (DOY 174-176), the plot for the C trees appears almost linear, but these data represent the mean Q_l for all trees in the C treatment, obscuring the declining non-linear trends of the individual trees. In the early part of the growing season 5T and C trees experienced their highest Q_l of all five three-day periods, while the apparent Q_l threshold of the JT was the lowest observed (Figure 5-4, top row). In July (rows 2 & 3), the Q_l threshold appeared to increase for the JT trees, and at the same time either decline (5T trees) or remain stable (C trees) in the other groups. In early August, following several days of cool wet weather (row 4) all three groups appear to be transpiring at similar rates. During this period, there was an apparent lag between increasing E_o and Q_l in instrumented trees from all treatments. After several days of relatively stable Q_d, however (bottom row), the apparent Q_l threshold for JT trees was significantly higher than 5T and C trees, which seemed to also have their lowest Q_l threshold of the summer.

Discussion

My observations of daily water use over the period measured indicate that dramatic increases in water use by lodgepole pine trees in thinned stands can occur in the growing season immediately following thinning. As expected, total daily water use (Q_d, m^3 day^{-1}) was generally higher for trees in the thinned areas. Though Q_d of 5T trees was consistently higher (~×2) than that of C trees in the unthinned stand, there seemed to be a general trend of declining Q_d with time for both the 5T and C trees (Figure 5-3a), perhaps as a result of buildup of drought conditions. The most striking observation, however, was the dramatic change in Q_d of JT trees over the measurement period. Water use by JT trees was initially similar to C trees, but increased over the measurement period, and by the end of the measurement period appeared to be equivalent to 5T trees. Available soil moisture from spring snowmelt, large tree leaf area (Table 5-2), and full exposure to sunlight likely contributed to the fact that the highest Q_d values were observed in 5T trees in June (22nd to 30th, DOY 173-181). Lower soil water availability in the fully occupied stand due to higher interception (Aussenac and Granier 1988) and sustained dry conditions likely contributed to the lower Q_d in C trees. The dramatic change in Q_d for JT trees over the measurement period suggests that following an initial period of water stress, their access to soil water improved. Increased allocation to root growth in the year following pre-commercial thinning has been observed in other conifer species (Ruel et al. 2003), and has been proposed as a mechanism by which Douglas fir and lodgepole pine trees meet increases in evaporative demand after release from the understory (Kneeshaw et al. 2002). In the latter case, increases in root growth occurred immediately following thinning (Kneeshaw et al. 2002), which could explain how the JT trees I measured were able to increase Q_d in such a short period.

Differences in leaf related sap flow (Q_l) were considered to be equivalent to the midday transpiration rate, by assuming minimal carry-over of stored water (Phillips et al. 2003) in the relatively small stems we examined. Generally, Q_l responded quickly to increasing E_o in the morning (Figure 5- 4), though there did sometimes appear to be a lag, particularly in August. On these days, the canopy was likely to have been at le heat capacity of air (1.0×10^{-3} MJ kg^{-1} K^{-1})ast partially de-coupled from the atmosphere during the early morning, because of the accumulation of dew on the foliage. For 5 hours during the pre-dawn morning of July 24 (DOY 205), for several hours each night on August 7-9 (DOY 219-221), and for a couple of hours each night on August 21-23 (DOY 235-237) D was at the dew point indicating probable dew formation. Assuming that my midday observations of Q_l (Figure 5-3) were unaffected affected by dew, Q_l can generally be considered equivalent to the transpiration rate during the most photosynthetically important hours of the day. There was a consistent decline in Q_l with increasing E_o, as would be expected in trees that close stomata to limit water loss to the atmosphere, suggesting stomatal behavior had a strong influence on transpiration during clear days throughout the experiment.

Differences in leaf related sap flow (Q_l) between the three groups, particularly in June (DOY 173-181) and August (DOY 213-241) (Figure 5- 3b), suggest that transpiration rates were affected by the thinning treatment. As expected, 5T trees had higher Q_l compared to C trees in early and late summer. During these times, transpiration rates in 5T trees were higher, so the additional leaf area they maintained did not account for their higher Q_d, as has been observed between large and small *Pinus radiata* trees (Teskey and Sheriff 1996). During the hot and dry parts of the day in late June (DOY 174-176), JT trees appeared to be experiencing water stress with lower Q_l (Figure 5-3b), and greater stomatal closure in response to E_o (Figure 5-4, top row). Because thinning occurred only one month prior, these trees may not have acclimated to increased exposure to full sunlight, known to stimulate rapid opening of stomata (Lopushinsky 1975), and an increase in evaporative demand due to higher wind speeds experienced in thinned lodgepole pine stands (Rudnicki 2002). This change in environment is likely to have resulted in increased crown water stress (Jarvis 1975), known to cause stomatal closure in lodgepole pine (Bassman and Koch 1996). The generally dry soil conditions during this period may also have contributed to the low transpiration rates I observed in JT trees at this time.

Canopy stomatal conductance (G_c), showed remarkable consistency between the three treatments in response to atmospheric demand for water (Figure 5-3c), despite the limited resolution of a single point measurement. All treatments appear to co-vary, likely in response to similar soil water availability between treatments (Misson et al. 2004). All trees restricted water loss on clear days, but there did appear to be differences between thinned and control trees in June and August (Figure 5-3c). These observations are consistent with an increase in water availability to thinned trees (Donner and Running 1986). On August 14 (DOY 226), the day of a large rain event, G_c increased dramatically for 5T and JT trees relative to C trees, suggesting they were able to immediately take advantage of increased water availability in the rooting zone.

Water movement in thinned trees does not appear to be limited by declines in sapwood permeability (k) associated with thinning. The lower Q_l threshold of JT trees in June (Figure 5-4, top row) suggests that cavitation and/or bending stress might have occurred immediately in the JT trees. Damage would have most likely occurred in June, since winds were generally light throughout the measurement period (Only 3 of 81 days where mean wind speed > 2.5 m/s; June

29-July1), and rainfall was well below normal in May and June. Declines in k are thus likely due to cavitation during the hot dry period in June. It is unclear if the increase of Q_l in JT trees I observed from June to August were associated with repair of embolism (Holbrook and Zwieniecki 1999), or simply due to the combination of increased soil water availability and greater exposure to radiation and atmospheric demand for water. Never-the-less is appears that there was excess capacity of the stem to move water to the crowns.

Declines in k associated with thinning (Liu et al. 2003) do not appear to limit the supply of water to crowns of lodgepole pine. Increases in radial growth of 5T trees compensated for declines in k, producing the highest Q_h among the trees studied. Allocation to radial growth over height growth may be a strategy to ensure hydraulic supply since the genus *Pinus*, appears to be particularly vulnerable to development of embolism among the Pinaceae (Martinez-Vilalta et al. 2004). Extra hydraulic capacity may enable lodgepole pine trees to survive during periodic drought, in contrast to the suggestion that there is a close balance between leaf area and stem hydraulic capacity (Tyree and Sperry 1988). Thinning was, however, associated with a decline in Q_L for both JT and 5T trees. This apparent loss of hydraulic sufficiency to deliver water to leaves did not, however, appear to limit flow during the measurement period since transpiration rates of thinned trees were consistently higher than the controls.

Table 5-1 Mean height (H), diameter at breast height (dbh), crown length (CL), leader length (LL), leaf area (A_L), sapwood basal area (A_s), sapwood permeability (k), hydraulic capacity (Q_h), and leaf specific hydraulic capacity (Q_L) recorded at the conclusion of the measurement period (± standard error) and test statistics from ANOVA for trees thinned in 1998 (5T), trees thinned in 2002 (JT), and un-thinned controls (C).

	5T (n = 11)	**JT (n = 11)**	**C (n = 10)**	**F**	**p**
H (m)	4.8 ± 0.21	5.2 ± 0.15	5.3 ± 0.15	2.9	0.07
dbh (cm)	6.6 ± 0.3	5.7 ± 1.3	5.4 ± 0.2	6.5	0.004
CL (m)	3.7 ± 0.2	3.6 ± 0.2	3.7 ± 0.1	n/s 0.17	n/s 0.84
LL (cm)	25.9 ± 3.2	38.1 ± 1.9	43.8 ± 1.7	15.5	<0.001
A_L **(m^2)**	5.9 ± 0.7	3.7 ± 0.3	3.2 ± 0.4	12.2	0.0001
A_s **(cm^2)**	28.3 ± 2.7	21.3 ± 1.1	19.4 ± 1.5	6.2	0.006
S **($m^2\ cm^{-2}$)**	0.22 ± 0.02	0.17 ± 0.01	0.16 ± 0.01	4.4	0.02
k **($\times 10^{-12}\ m^2$)**	1.97 ± 0.10	2.10 ± 0.10	2.47 ± 0.11	6.2	0.006
Q_h **($\times 10^{-12}\ m^4\ Pa^{-1}\ s^{-1}$)**	5.44 ± 0.72	3.72 ± 0.26	4.07 ± 0.35	3.48	0.04
Q_L **($\times 10^{-12}\ m^2\ Pa^{-1}\ s^{-1}$)**	0.93 ± 0.10	1.02 ± 0.06	1.33 ± 0.07	6.16	0.006

Figure 5-1 Diurnal changes in mean sap velocity on a sapwood area basis (v_s) for trees thinned in 1998 (5T), trees thinned in 2002 (JT) and un-thinned controls (C), observed during 5 clear days from July 13th (DOY 194) to July 17th (DOY 198), 2002.

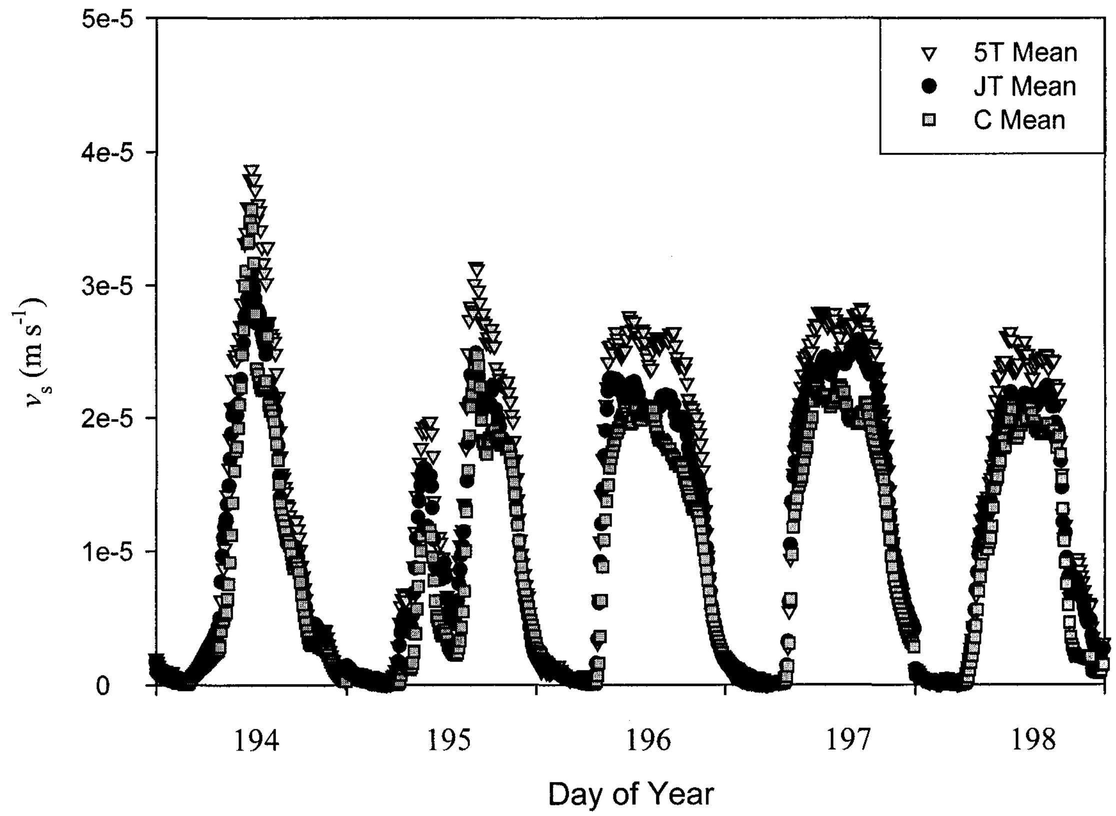


Figure 5-2 Mean midday potential evapotranspiration (E_o), air temperature (T_a), net radiation (Q^*) and air vapour pressure deficit (D) recorded at the study site. Shaded bars denote cumulative precipitation for each day recorded at the Swan Hills fire-lookout tower approximately 10 km from the site.

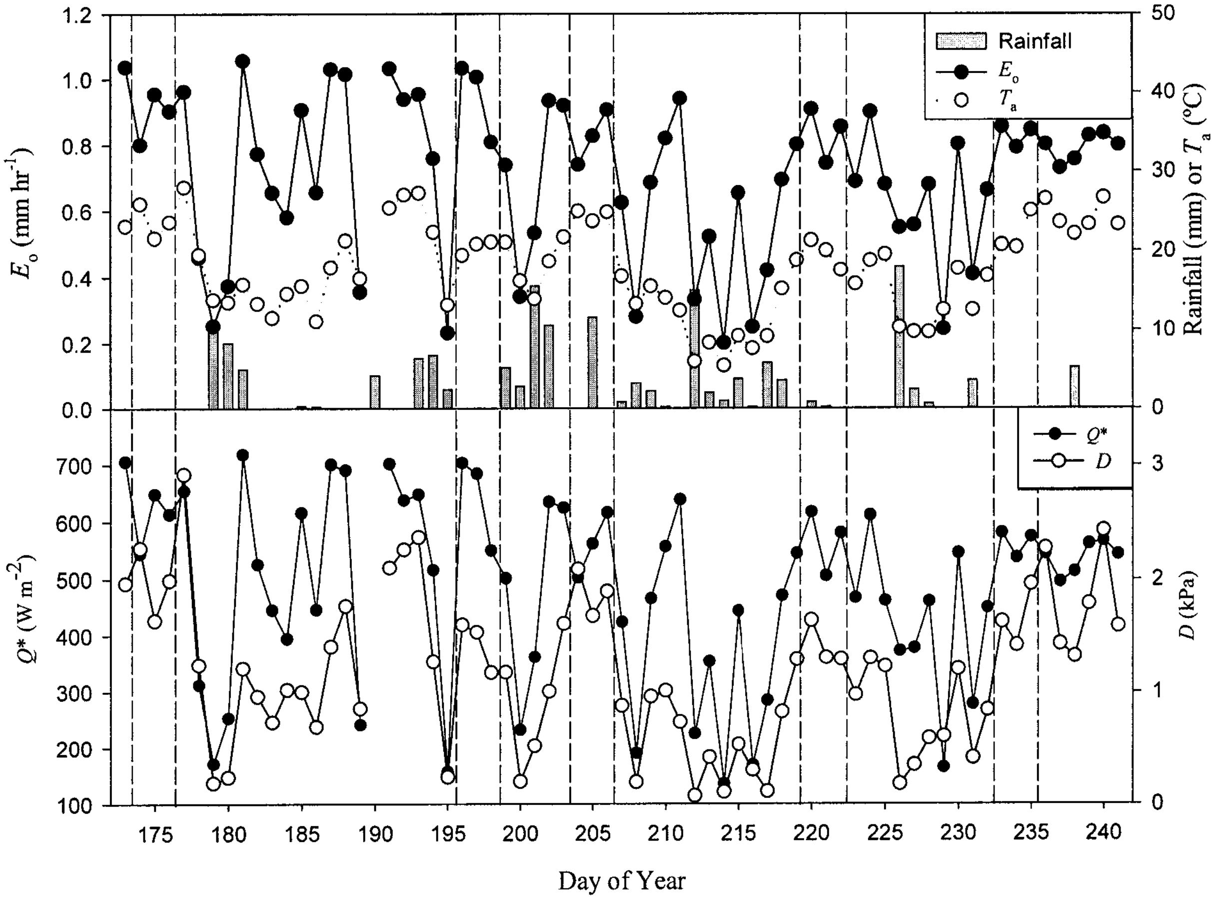


Figure 5-3 Daily means for a) total sap flow (Q_d), b) mid-day leaf-related sap flow (Q_l), and c) mid-day whole canopy average stomatal conductance (G_c). Error bars represent one standard error, and are only presented where at least one does not overlap either of the other two. Dashed vertical lines illustrate the boundaries of three-day periods used to examine the relationship between E_o and Q_l.

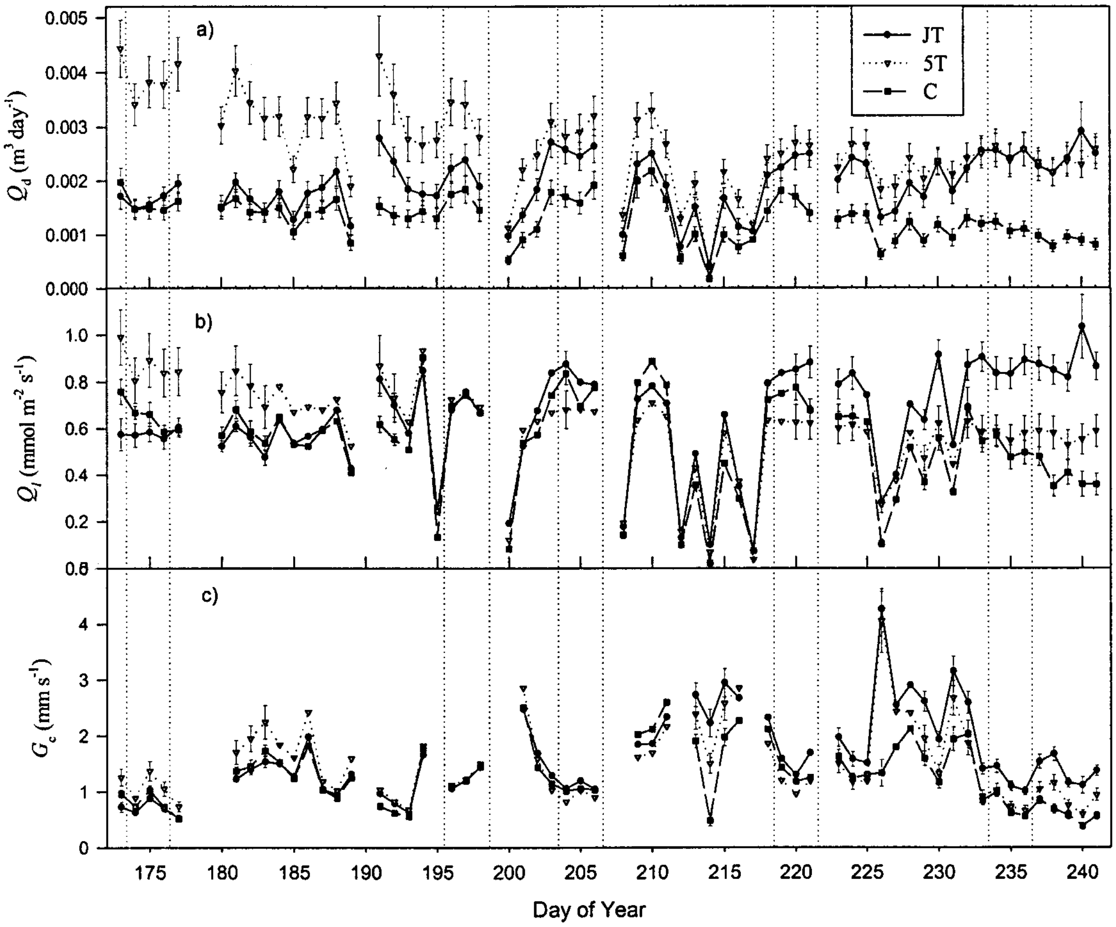
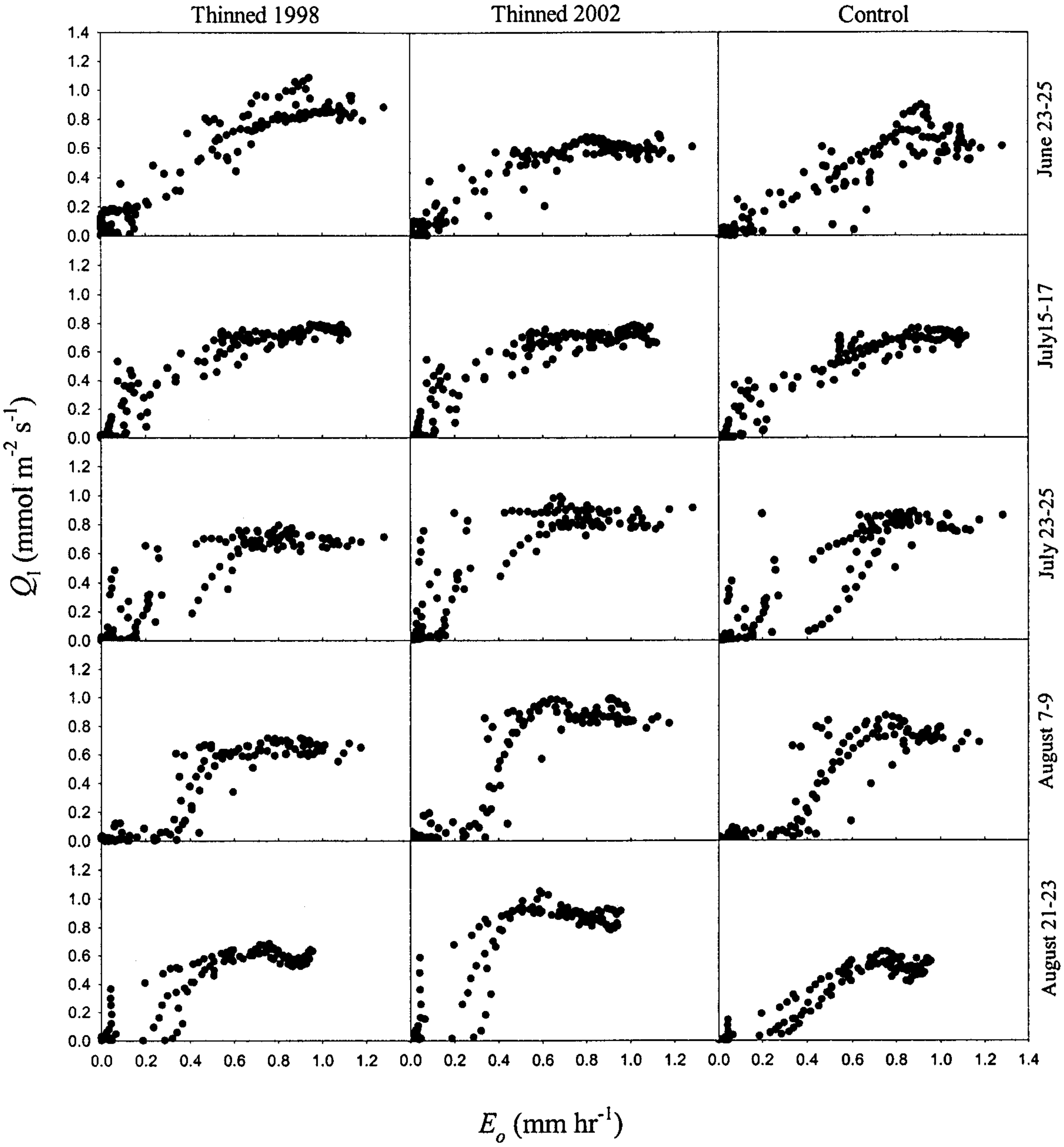


Figure 5-4 Potential evaporation (E_o) vs. mean leaf-related sap flow (Q_l) during 5 three-day periods of high evaporative demand.



References

Bassman, J.H. and Koch, P. 1996. Physiology *In* Lodgepole Pine in North America. Ed. P. Koch, Forest Products Society, Madison Wisconsin. pp. 77-137.

Breda, N., Granier, A., and Aussenac, G. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt) Liebl). Tree Physiology 15: 295-306.

Day, R.J. 1998. The ancient and orderly European discipline of thinning is now a reality in North America. *In* Stand Density Management: Planning and Implementation. Proceedings of a conference held November 6 & 7 in Edmonton, Alberta, Canada. Ed. C. Bamsey, Clear Lake Ltd., Edmonton, AB, pp 24-33.

Donner, B.L. and Running, S.W. 1986. Water stress response after thinning *Pinus contorta* stands in Montana. Forest Science 32(2): 614-625.

Dingman, S.L. 2002. Physical hydrology, 2nd Ed. Prentice Hall, Englewood Cliffs, N.J.

Edwards, W.R.N., Becker, P., and Čermák, J. 1997. A unified nomenclature for sap flow measurements. Tree Physiology 17: 65-67.

Farnden, C. and Herring, L. 2002. Severely repressed lodgepole pine responds to thinning and fertilization: 19-year results. Forestry Chronicle 78: 404-414.

Flesch, T.K., and Wilson, J.D. 1993. Extreme value analysis of wind gusts in Alberta. Forestry Canada and Alberta Land and Forestry Services, University of Alberta, Edmonton, Alta. Can.–Alta. Partnership Agree. For. Proj. A-8033-107.

Giambelluca, T.W., and Nullet, D. 1992. Evaporation at high elevations in Hawaii. Journal of Hydrology 136: 219-235

Granier, A. 1987. Evaluation of transpiration in a douglas-fir stand by means of sap flow measurements. Tree Physiology 3: 309-319.

Holbrook, N.M. and Zwieniecki, M.A. 1999. Embolism repair and xylem tension: Do we need a miracle? Plant Physiology 120: 7-10.

Huang, S., Monserud, R.A., Braun, T., Lougheed, H., and Bakowsky, O. Comparing site productivity of mature fire-origin and post-harvest juvenile lodgepole pine stands in Alberta. Canadian Journal of Forest Research 34, 1181-1191. 2004.

Kneeshaw, D., Williams, H., Nikinmaa, E., and Messier, C. 2002. Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. Canadian Journal of Forest Research 32: 255-265.

Köstner, B., Biron, P., Siegwolf, R. and Granier, A. 1996. Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. Theoretical and Applied Climatology 53: 105-113.

Lagergren, F. and Lindroth, A. 2002. Transpiration response to soil moisture in pine and spruce trees in Sweden. Agricultural and Forest Meteorology 112: 67-85.

Lagergren, F. and Lindroth, A. 2004. Variation in sapflow and stem growth in relation to tree size, competition and thinning in a mixed forest of pine and spruce in Sweden. Forest Ecology and Management 188: 51-63.

Liu, X.D., Silins, U., Lieffers, V.J., and Man, R.Z. 2003. Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. Canadian Journal of Forest Research 33: 1295-1303.

Lopushinsky, W. 1975. Water relations and photosynthesis in Lodgepole pine. *In* Management of Lodgepole Pine Ecosystems, symposium proceedings. Pullman, Washington October 9-11, 1973. Ed. D.M. Baumgartner, Washington State University Cooperative Extension Service. pp. 135-153.

Monteith, J.L., 1965. Evaporation and environment. *In* The State and Movement of Water in Living Organisms, 8-12 September 1964, Swansea. Symp. Soc. Exp. Biol., 19: 205-234.

Martínez-Vilalta, J. Sala, A. and Piñol, J. 2004. The hydraulic architecture of Pinaceae – a review. Plant Ecology 171: 3–13.

Martinez-Vilalta, J., Mangiron, M., Ogaya, R., Sauret, M., Serrano, L., Penuelas, J., and Pinol, J. 2003. Sap flow of three co-occurring mediterranean woody species under varying atmospheric and soil water conditions. Tree Physiology 23: 747-758.

Medhurst, J.L., Battaglia, M., and Beadle, C.L. 2002. Measured and predicted changes in tree and stand water use following high-intensity thinning of an 8-year-old *Eucalyptus nitens* plantation. Tree Physiology 22: 775-784.

Misson, L., Panek, J.A., and Goldstein, A.H. 2004. A comparison of three approaches to modeling leaf gas exchange in annually drought-stressed ponderosa pine forests. Tree Physiology 24: 529-541.

Morikawa, Y., Hattori, S., and Kiyono, Y. 1986. Transpiration of a 31-year-old *Chamaecyparis obtusa* Endl. stand before and after thinning. Tree Physiology 2: 105-114.

Phillips, N.G., Ryan, M. G., Bond, B. J., Mcdowell, N. G., Hinckley, T. M., and Čermák, J. 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest. Tree Physiology 23: 237–245.

Phillips, N. and Oren, R. 1998. A comparison of daily representations of canopy conductance based on two conditional time-averaging methods and the dependence of daily conductance on environmental factors. Annales Des Sciences Forestieres 55: 217-235.

Phillips, N., Nagchaudhuri, A., Oren, R., and Katul, G. 1997. Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. Trees-Structure and Function 11: 412-419.

Reid, D.E.B., Silins, U., and Lieffers, V.J. 2003. Stem Sapwood Permeability in Relation to Crown Dominance and Site Quality in Self-Thinning Fire-Origin Lodgepole Pine Stands. Tree Physiology 23: 833-840.

Rudnicki, M. 2002. Group tree sway of lodgepole pine, associated crown interactions and their potential role in mediating crown shyness. Ph.D. thesis, University of Alberta, Edmonton, Alta.

Rudnicki, M., Lieffers, V.J., and Silins, U. 2003. Stand structure governs the crown collisions of lodgepole pine. Canadian Journal of Forest Research 33: 1238-1244.

Ruel, J.C., Larouche, C., and Achim, A. 2003. Changes in root morphology after precommercial thinning in balsam fir stands. Canadian Journal of Forest Research 33: 2452-2459.

Simpson, D.G. 2000. Water use of interior Douglas-fir. Canadian Journal of Forest Research 30: 534-547.

Sperry, J.S., Adler, F.R., Campbell, G.S., and Comstock, J.P. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. Plant Cell and Environment 21: 347-359.

Stewart, J.B. 1971. The albedo of a pine forest. Quarterly Journal of the Royal Meteorology Society. 99: 561-564.

Strong, W.L., and Leggat, K.R. 1992. Ecoregions of Alberta. Alberta Forestry, Land and Wildlife, Land Information Services Division, Resource Information Branch, Edmonton, Alta.

Teskey, R.O. and Sheriff, D.W. 1996. Water use by pinus radiata trees in a plantation. Tree Physiology 16: 273-279.

Vertessy, R.A., Benyon, R.G., Osullivan, S.K., and Gribben, P.R. 1995. Relationships between stem diameter, sapwood area, leaf-area and transpiration in a young mountain ash forest. Tree Physiology 15: 559-567.

Whitehead, D. and Jarvis, P.G. 1981. Coniferous forests and plantations: water uptake and movement. Water Deficits and Plant Growth 6, 50-152.

Worall, J. 1995. Height growth stagnation in lodgepole pine: all (well almost all) is revealed. Branchlines 6: 5.

Yang, R.C. 1998. Foliage and stand growth responses of semi-mature lodgepole pine to thinning and fertilization. Canadian Journal of Forest Research 28: 1794–1804.

Youngblood, A.P. 1991. Radial growth after a shelterwood cut in a mature stand of white spruce. Canadian Journal of Forest Research 21: 410–413.

Chapter 6

Synthesis

Towards a Unified Theory of Water Movement in Trees

My proposal for the adoption of a single set of consistent terminology and symbols to describe the hydraulic properties of sapwood xylem (Table 2-1) clarifies the meaning of terms used to describe the hydraulic architecture of trees. The theoretical framework provided by Darcy's law can be used to quantify hydraulic conductivity (K_Ψ) independent of the length and conducting surface area of sapwood xylem in a branch, stem or root. Permeability (k) is independent of changes in fluid viscosity, but otherwise equivalent to K_Ψ. Movement of water is driven by a water potential gradient in the direction of flow, and more importantly, the amount of water that can be delivered through a branch or stem under a unit hydraulic gradient, i.e. hydraulic capacity (Q_h), can be determined. From my research I have come to the same conclusion as others before me (Tyree and Zimmerman 2002), that the balance between hydraulic capacity and leaf area, or leaf specific hydraulic capacity (Q_L), is the most useful measure of the hydraulic sufficiency of a stem or branch to deliver water to leaves. Darcy's law and Ohm's law are mathematically equivalent, allowing the continued use of accepted electrical terminology (e.g. conductance, G) in relation to water flow through trees. Consistent use of the symbols and units I have proposed will make the important findings of tree and plant physiologists more accessible to those in related hydrological fields, and provide a useful tool for students and future researchers.

Darcy's law provides a means by which the resistance to water flow imposed by the hydraulic properties of xylem can be easily understood, but cannot be used to model the flow of water in living trees without further refinement. This is principally because the assumption that the porous medium, the sapwood, is completely saturated with liquid water across it's entire length and cross section is likely to be violated at least part of the time in portions of the sapwood. Because water in trees is under tension, it is in a metastable state (Tyree 1999) and spontaneous cavitation can result in vessels or tracheids becoming embolised or air filled (Sperry Donnelly and Tyree 1988). Under drought stress, this can result in the sacrifice of large portions of the crown (Rood et al. 2000) or even tree death (Tyree et al. 2002). Separation of the stem from its roots and leaves for the measurement of hydraulic properties relaxes the tension on the water column, and likely allows small cavitated bubbles to be dissolved. The removal of embolism by flushing (Sperry Donnelly and Tyree 1988) is necessary to accurately measure hydraulic properties, since embolized tracheids or vessels will result in loss of conducting surface area, but can be very difficult to achieve in conifers (Reid unpublished, Stout and Sala 2003). The torus-margo structure of bordered pits in gymnosperms appears to be a compromise to the conflict between allowing water flow between functional tracheids, and preventing air flow from an embolized tracheid (Hacke et al. 2003), and likely contributes to the difficulties encountered in attempting to remove embolisms from conifer sapwood. Where bordered pits isolate embolized tracheids, water flow through the remaining tracheids is likely to be saturated in stem sections which have been kept submerged for several hours. Thus, flow measurements of excised stem segments can provide a meaningful measure of the hydraulic properties of the stem at the time of sampling provided the limitations of the theory are recognized. Given the close relationship between Q_h and leaf area in a variety of conifer species and the apparent influence of Q_L on *GE* reported here and elsewhere, measurement of the hydraulic properties of excised stem and branch segments is likely to continue to provide insights into the link between productivity and sapwood hydraulic properties.

The abundance of research effort focused on the hydraulic architecture of trees in recent decades has inspired a number of models that aim to more accurately describe water flow in living trees. The analogy to Ohm's law has proven very useful, but is not associated with a theoretical framework to describe the three dimensional dynamics of water storage in the sapwood of large trees (Phillips et al. 2003). Time lags in water flow between the top and base of trees (Martin et al. 1997), and declines in K_Ψ with decreases in saturation of the sapwood (Tyree et al. 1999, Magnani and Borghetti 1995, Sellin 1991) cannot be explained by basic saturated flow models. Observations of embolism repair (Holbrook et al. 2001) suggest that the flow of water through xylem of living trees is much more complex than has been previously suggested (Tyree and Ewers 1991). Emerging ideas about the internal organization of sapwood xylem (West et al 1999, McCulloch et al. 2003) as well as experimental evidence (Koch et al. 2004) continue to support the validity of the cohesion tension theory. Application of the theories of unsaturated flow to water movement in trees (Aumann and Ford 2002) may provide an opportunity to move beyond the use of an analogy, to more forthright approach to dealing with unsaturated flow in xylem as is probably the case in trees experiencing cavitation and seasonal changes in sapwood water content. I believe that collaboration between tree physiologists and researchers in related hydrological fields who have the mathematical sophistication needed to understand these more complex models (Früh and Kurth 1999, Aumann and Ford 2002) will be necessary to achieve a unified theory of water flow in trees.

Sapwood Permeability and Height Repression

I have demonstrated that faster growing lodgepole pine (*Pinus contorta* var. *latifolia*) trees have sapwood xylem that is more permeable (k) (Figure 3-1), and provides greater hydraulic capacity under a hydraulic gradient (Q_h) (Figure 4-1) thanks to a higher proportion of early-wood in their sapwood (Figure 3-3). Trees of dramatically different sizes and growth rates in naturally established stands nevertheless maintain similar leaf specific capacity (Q_L), by either maintaining less leaf area or retaining greater sapwood area in slower growing trees with lower k. All trees thus achieve a homeostatic balance between the amount of photosynthetic tissue and their water supply capability, as was originally suggested by the unit pipe theory (Shinozaki et al. 1964). In all stands, because growth and k are linked by the physiological development of early- and late-wood tracheids, there is a close relationship between k and competitive rank. In the height repressed stands I studied however, excessive competition and slow growth result in significantly lower k in all trees. By maintaining less leaf area, and retaining sufficient sapwood cross sectional area, however, the availability of water to leaves in height repressed trees does not appear to be limited by declines in k.

My work shows that height repression in lodgepole pine is not due to a hydraulic limitation imposed by sapwood on existing leaf area, but due to the combined effects of competition and physiological limitations (light, nutrients and water) on growth and survival of trees within high density stands. Trees in high density stands are not significantly less efficient in their utilization of leaf area for stem growth (Figure 4-1b), and all trees are more efficient at higher Q_L (Figure 4-3a). Surprisingly, suppressed trees have the highest *GE* (Figure 4-1b) due to superior nutrient status and sufficient available water to small crowns. Suppressed trees in height repressed stands with low LAI are likely to have sufficient light, and have greater sapwood volume in relation to leaf area (Figure 4-4b) providing a buffer against water stress. Physiologically, these trees are thus able to meet requirements of survival, slowing the rate of self-thinning, and limiting the space available for crown expansion by neighboring trees. The small crowns typical of trees in height repressed stands are simply too small to achieve the potential growth rate for a given site, resulting in height repression.

I am (to my knowledge) the first to show an opposite trend of *GE* and crown efficiency (*CE*) between crown classes (Figure 4-1). This finding suggests that *GE* is not a good measure of tree vigor for lodgepole pine in naturally established stands, and that *CE* is a more useful measure of stem growth potential. Some degree of height repression appears to result following natural establishment across a range of densities (Huang et al. 2004), so gains in productivity may be possible through density management. Managers hoping to reduce competition and realize gains in productivity through thinning should target retention of dominant lodgepole pine trees with high *CE*.

Thinning, Conductivity, and Water Use

Declines in *k* observed following thinning (Liu et al. 2003), are likely due to cavitation in sapwood xylem under increased atmospheric demand and bending stress (Rudnicki 2002) in retained trees. I have shown that despite a decline in *k*, transpiration rates (m^3 s^{-1} m^{-2} leaf area) are greater than in retained trees under water stress relative to un-thinned controls. Daily water use by lodgepole pine trees under drought appears to be determined primarily by the behavior of stomata in response to soil water availability. My hypothesis, that lodgepole pine trees maintain extra hydraulic capacity to tolerate cavitation under periodic soil moisture deficits, requires further testing.

Lodgepole Pine Stem Hydraulics and Stand Dynamics

In naturally established stands, differences in growth rates between individual trees over time result in differentiation into crown dominance classes (Oliver and Larson 1990), and eventually self-thinning (Peet and Christensen 1987). In light of my observations of increased transpiration rates in trees with lower *k* (Chapter 5, JT trees), the relationship between stem hydraulic properties and crown dominance is likely to be simply a reflection of the effect of fast growth on the dimensions of tracheid lumens. I found no evidence to suggest that water availability to existing leaf area is limited by sapwood hydraulic properties between trees of dramatically different growth rates. Over the course of the entire growing season, water availability to transpiring leaves is more likely to be a function of soil water availability and the foraging capacity of the tree's roots than the hydraulic properties of sapwood xylem. The only time the hydraulic properties of stem xylem will impart a competitive advantage in delivering water to leaves will be when soil water availability is not limited and there is no loss of conductivity due to cavitation. This situation is likely to be infrequent in the interior range of *Pinus contorta* var. *latifolia*. Thus, crown class differentiation in even-aged, fire-origin lodgepole pine forests is more likely to be due to competition for light, as has been suggested for plant monocultures in general (Weiner and Thomas 1986).

My research suggests that though sapwood hydraulic properties may not limit water availability to crowns, they can improve survival in height repressed and suppressed lodgepole pine trees with small crowns. Water storage in the sapwood of large trees (Phillips et al. 2000) which have survived the self-thinning phase of stand development is an important buffer against drought and likely contributes to the long lifespan of many conifer trees. By contributing to survival, particularly in high density and old-growth forests, I believe sapwood hydraulic properties have a profound impact on stand dynamics in lodgepole pine forests.

Unanswered Questions

- Independent testing is required to assess the validity of recently proposed theoretical models of water movement in trees, and whether or not they provide an improvement over the simple and useful linear transport model of Darcy's law. The novel theory proposed by Aumann and Ford (2002), which suggests unsaturated flow is the norm has not been tested experimentally. The assumption that capacitance and axial conductivity are homogeneous across a stem or branch segment within a refinement of the Ohm's law analogy (Fruh and Kurth 1999) also requires testing.
- How do suppressed lodgepole pine trees maintain higher needle nutrient status? Possible mechanisms include internal crown dynamics (leaf growth and retention) or intraspecific commensalism via intact root grafts in high density stands (Fraser unpublished). This issue needs to be researched further.
- Dramatic differences in K have been observed between samples collected in spring and summer compared to fall (Reid unpublished). These differences may be due to buildup and repair of embolism over the growing season, and/or changes in sapwood water content. Seasonal changes in sapwood water content have been reported for lodgepole pine. Seasonal

dynamics of cavitation, embolism and repair in lodgepole pine have not been reported. Technical difficulties in the measurement of embolism in lodgepole pine stems need to be overcome so that this issue can be researched further.

References

Aumann, C.A. and Ford, E.D. 2002. Modeling tree water flow as an unsaturated flow through a porous medium. Journal of Theoretical Biology 219: 415-429.

Fruh T., and Kurth, W. 1999. The hydraulic system of trees: theoretical framework and numerical simulation. Journal of Theoretical Biology 201: 251-270.

Hacke, U.G., Sperry, J.S., and Pittermann, J. 2004. Analysis of circular bordered pit function - II. gymnosperm tracheids with torus-margo pit membranes. American Journal of Botany 91: 386-400.

Holbrook, N.M., Ahrens, E.T., Burns, M.J., and Zwieniecki, M.A. 2001. In vivo observation of cavitation and embolism repair using magnetic resonance imaging. Plant Physiology 126: 27-31.

Koch, G.W., Sillett, S.C., Jennings, G.M., and Davis, S.D. 2004. The limits to tree height. Nature 428: 851-854.

Liu, X.D., Silins, U., Lieffers, V.J., and Man, R.Z. 2003. Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. Canadian Journal of Forest Research 33: 1295-1303.

Magnani, F. and Borghetti, M. 1995. Interpretation of seasonal-changes of xylem embolism and plant hydraulic resistance in *Fagus sylvatica*. Plant Cell and Environment 18: 689-696.

Martin, T.A., Brown, K.J., Cermak, J., Ceulemans, R., Kucera, J., Meinzer, F.C., Rombold, J.S., Sprugel, D.G., and Hinckley, T.M. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. Canadian Journal of Forest Research 27: 797-808.

Mcculloh, K.A., Sperry, J.S., and Adler, F.R. 2003. Water transport in plants obeys Murray's law. Nature 421: 939-942.

Oliver, C.D. and Larson, B.C. 1990. Forest stand dynamics. McGraw-Hill Pub. Co, New York.

Peet, R.K. and Christensen, N.L. 1987. Competition and tree death. Bioscience 37: 586-595.

Phillips, N.G., Ryan, M.G., Bond, B.J., Mcdowell, N.G., Hinckley, T.M., and Cermak, J. 2003. Reliance on stored water increases with tree size in three species in the pacific northwest. Tree Physiology 23: 237-245.

Rood, S.B., Patino, S., Coombs, K., and Tyree, M.T. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. Trees-Structure and Function 14: 248-257.

Rudnicki, M. 2002. Group tree sway of lodgepole pine, associated crown interactions and their potential role in mediating crown shyness. PhD Thesis, University of Alberta, and Dept. of Renewable Resources.

Sellin, A. 1991. Hydraulic conductivity of xylem depending on water saturation level in Norway spruce (*Picea abies* L. Karst). Journal of Plant Physiology 138: 466-469.

Shinozaki, K., Yoda, K., Hozumi, K., and KIra, T. 1964. A quantitative analysis of plant form - the unit pipe model theory. I. basic analyses. Japanese Journal of Ecology 14: 97-105.

Sperry, J.S., Donnelly, J.R., and Tyree, M.T. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell and Environment 11: 35-40.

Tyree, M.T. and Ewers, F.W. 1991. The hydraulic architecture of trees and other woody-plants. New Phytologist 119: 345-360.

Tyree, M.T., Salleo, S., Nardini, A., Lo Gullo, M.A., and Mosca, R. 1999. Refilling of embolized vessels in young stems of laurel. Do we need a new paradigm? Plant Physiology 120: 11-21.

Tyree, M.T. and Zimmermann, M.H. Xylem structure and the ascent of sap. 2nd ed. 283. 2002. Berlin ; New York , Springer.

Tyree, M.T, Vargas, G., Engelbrecht, B. M. J., and Kursar, T. A. 2002. Drought until death do us part: a case study of the desiccation-tolerance of a tropical moist forest seedling-tree, *Licania platypus* (Hemsl.) Fritsch. Journal of Experimental Botany 53: 2239-2247.

Weiner, J. and Thomas, S.C. 1986. Size variability and competition in plant monocultures. Oikos 47: 211-222.

West, G.B., Brown, J.H., and Enquist, B.J. 1999. A general model for the structure and allometry of plant vascular systems. Nature 400: 664-667.