

AN ABSTRACT OF THE DISSERTATION OF

Georgianne W. Moore for the degree of Doctor of Philosophy in Environmental Sciences presented on September 10, 2003.

Title: Drivers of Variability in Transpiration and Implications for Stream Flow in Forests of Western Oregon

Abstract approved:

Barbara J. Bond

Julia A. Jones

I compared transpiration among different types of forest stands in the western Cascades of Oregon. The three major questions were: 1) How does transpiration compare between a young and old stand and why? 2) Does diversity of overstory trees affect transpiration? and 3) How is transpiration related to stream flow? Transpiration was quantified using thermal dissipation sap flow measurements scaled to a ground-area basis using sapwood surveys for periods during the summer months of 2000, 2001, and 2002, and in a subset of plots, for a full year. I found that a young, rapidly growing stand (~40 years since disturbance) used 3.3 times more water during the growing season than an old-growth stand (~450 years since disturbance) because the young stand had 2.3 times higher sap flow rates per unit sapwood in Douglas-fir, had a 21% greater

total sapwood basal area, and had a larger component of hardwoods that use 1.41 times more water than conifers per unit sapwood. In two-species mixtures of Douglas-fir and red alder, I found evidence that mixtures are less productive and have lower annual transpiration than monocultures of these two species. The observed differences were probably due to altered biomass rather than diversity itself, but diversity likely played a role in altering biomass.

Such stand age- and diversity-related differences in transpiration potentially impact stream flow. In a small watershed with a 450-yr-old forest, I examined the role of vegetation in stream flow patterns at hourly, daily, and storm scales. Transpiration apparently controlled stream flow during the summer at hourly scales with lags of at least five hours. In contrast, at daily and storm scales, soil water apparently controlled both stream flow and transpiration during the dry season, but there was no relationship during the wet season. These results indicate that forest management practices that reduce stand age and decrease diversity may lead to increased transpiration and consequently may reduce summer stream flow.

©Copyright by Georgianne W. Moore
September 10, 2003
All Rights Reserved

Drivers of Variability in Transpiration and Implications for Stream Flow in
Forests of Western Oregon

by
Georgianne W. Moore

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented September 10, 2003
Commencement June 2004

Doctorate of Philosophy dissertation of Georgianne W. Moore presented on September 10, 2003.

APPROVED:

Co-Major Professor, representing Environmental Sciences

Co-Major Professor, representing Environmental Sciences

Head of the Environmental Sciences Program

Dean of the Graduate School

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

Georgianne W. Moore, Author

ACKNOWLEDGEMENTS

I would like to thank my major professors, Julia Jones and Barbara Bond, for their guidance and valuable feedback throughout this process. This project was meant to bridge the gap between their two disciplines: hydrology and tree physiology. I believe that we've accomplished just that, and that the two of them combined have helped to make this project (and my journey) a whole. Thanks are also due to the members of my committee, especially Renee Brooks who provided for the isotopic analyses and made possible fellowship funds from NASA, and James Irvine who agreed to step in at the eleventh hour to serve as a sixth committee member.

The extensive fieldwork would not have been possible without the help of John Moreau. His help with equipment and data maintenance was truly beyond my wildest expectations. Thanks to John, the stream of data was unending through the dark and snowy winter of 2001. Many undergraduate students provided valuable aid in the field and lab, and I learned a lot working closely with them. They were (in order of appearance): H. McCarthy, M. Van Horne, C. Hurst, K. Stein, P. Valko, N. Czarnomski, M. Becklund, R. Geesman, J. T. Sayre, T. Fielder, and G. Onsgaard. Thanks to Andy Gray and David Hibbs for lending me field equipment. Manuela Huso and Lisa Ganio provided help with the statistical analysis. Don Henshaw and the Forest Science Database provided climatological

and hydrological datasets. Hazel Hammond wrote the program that extracted storm information from the stream flow record.

Funding for this project was provided by grants from NASA, NSF Long Term Ecological Research Program, and NSF Research Experience for Undergraduates.

I am grateful for the support of the members of my extended lab family for their support and advice: J. Campbell, S. Van Tuyl, T. Pypker, T. Ocheltree, J. Licata, M. Pruyn, J. Swenson, K. George, O. Sun, and P. Schwarz.

I am grateful to my loving family, who molded me into the person I am today, and who always were there when I needed them. My mother gave me strength and self-confidence. My father gave me curiosity and drive.

Last but certainly not least, I am grateful to my husband, Darrin Moore, for his inspiration, patience, support, and love during the last four years, as always.

CONTRIBUTION OF AUTHORS

Drs. Nathan Phillips and Frederick C. Meinzer assisted with the conception, analysis, interpretation, and editing of Chapter 2.

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
STRUCTURAL AND COMPOSITIONAL CONTROLS ON TRANSPIRATION IN A 40- AND A 450-YR-OLD RIPARIAN FOREST IN WESTERN OREGON, USA	8
Abstract	9
Introduction	11
Methods	15
Study area	15
Climate	16
Xylem sap flow	17
Vegetation survey	21
Leaf area index	22
Scaling up to the riparian area	23
Statistical analyses	24
Results	25
Variations in water use per unit sapwood area based on tree age and species	25
Variations in basal area and sapwood area	30
Leaf area index	33
Scaling up tree water use to the riparian area	34
Discussion	36
Implications for land use	40
Conclusions	41
Acknowledgements	42

TABLE OF CONTENTS (CONTINUED)

	<u>Page</u>
DO THERMAL DISSIPATION SAP FLOW SENSORS YIELD CONSISTENT ESTIMATES OF SAP FLOW FOR MULTIPLE YEARS?.....	44
Abstract.....	44
Introduction.....	45
Methods	51
Results.....	56
Discussion.....	64
Acknowledgements.....	68
DOES DIVERSITY OF OVERSTORY TREES AFFECT TRANSPIRATION?.....	69
Abstract.....	69
Introduction.....	70
Diversity, productivity, and resource use	71
Using replacement series plots to study forest transpiration.....	72
Resource Use Efficiency.....	75
Study Objectives	78
Methods	81
Study Area	81
Replacement Series	81
Stand Characteristics.....	83
Sap flow	84

TABLE OF CONTENTS (CONTINUED)

	<u>Page</u>
Atmospheric evaporative demand.....	86
Soil water availability	86
Nutrient status	87
Results.....	88
Discussion.....	99
Acknowledgements.....	102
HOW IS VEGETATION WATER USE RELATED TO STREAM FLOW AT THE SMALL WATERSHED SCALE?	103
Abstract.....	103
Introduction.....	104
Methods	108
Study Area	108
Data collection	109
Data pretreatment.....	113
Statistical analyses	115
Results.....	116
Discussion.....	128
Acknowledgements.....	133

TABLE OF CONTENTS (CONTINUED)

	<u>Page</u>
CONCLUSIONS.....	134
Stand age comparison.....	134
Sensor degradation.....	136
Species diversity comparison	136
Stream-vegetation coupling.....	138
Future directions	139
BIBLIOGRAPHY.....	143
APPENDICES	155

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Map of study site locations.....	17
2. (a) Total solar radiation ($\text{MJ m}^{-2} \text{d}^{-1}$), (b) daily average vapor pressure deficit (kPa) and daily total precipitation (mm) for the study period of 1999 (gray bars, dotted line) and 2000 (black bars, solid line).....	27
3. (a) Effects of age on sap flux density ($\text{kg m}^{-2} \text{day}^{-1}$) in the young (thin black line, mean of 7 trees) and old (-thick black line, mean of 3 trees) <i>P. menziesii</i> from early June until late October 2000. (b) Effects of species on sap flux density in <i>A. rubra</i> (gray line, mean of 7 trees) and <i>P. menziesii</i> (thin black line, mean of 7 trees) in the young stand from early July until early September 1999. (c) Effects of species on sap flux density in <i>P. menziesii</i> (thick black line, mean of 3 trees) and <i>T. heterophylla</i> (thick gray line, mean of 3 trees) in the old-growth stand from early June until late November 2000. (d) Magnification of late-season fluxes for <i>P. menziesii</i> and <i>T. heterophylla</i> in (c) from mid-September until late November 2000.....	28
4. The relationship between seasonal average sap flux density ($\text{kg m}^{-2} \text{d}^{-1}$) for the individual trees equipped with sap flow sensors and the sapwood basal area (m^2) of those individual trees.....	30
5. The relative amount of total basal area (%) in the young stand (solid bars) and old stand (hatched bars) by size.....	31
6. (a) Differences in total basal area ($\text{m}^2 \text{ha}^{-1}$) among the young stand (solid bars) and old stand (hatched bars) by species and (b) summarized by grouping. (c) Differences in total sapwood basal area ($\text{m}^2 \text{ha}^{-1}$) among the young stand (solid bars) and old stand (hatched bars) by species and (d) summarized by grouping. (e) Ratio of total sapwood basal area and basal area among the young stand (solid bars) and old stand (hatched bars) by species and (f) summarized by grouping.....	32
7. Estimated water use per unit ground area (mm day^{-1}) in the young stand (thin line) and the old-growth stand (thick line) from late June until late October 2000.....	35

LIST OF FIGURES (CONTINUED)

<u>Figure</u>	<u>Page</u>
8. The relationship between daily transpiration (mm d^{-1}) in the young stand (solid circles) and old stand (open circles) and daily average vapor pressure deficit (kPa), as measured at a nearby weather station.....	35
9. Example demonstrating potential mechanisms that can cause changes in long-term sensor performance..	48
10. Daily sap flux density (S) for 11 sensors in Douglas-fir in a) 2001 and b) 2002 and for 12 sensors in red alder in c) 2001 and d) 2002.....	57
11. Volumetric soil water content (Θ) to a depth of 45 cm at 32 locations throughout the study area during the year 2001 (solid circles) and 2002 (open squares).....	58
12. The relationship between sap flux density (S) and vapor pressure deficit (δ) for Douglas-fir (solid symbols; $n = 11$ sensors) and red alder (open symbols; $n = 12$ sensors) during the period between April 27 th and July 1 st of 2001 (circles) and 2002 (squares), before (panels a, b, e, and f) and after (panels c, d, g, and h) natural log transformation of the x-axis.	59
13. The relationship between measured and modeled sap flux density (S) for the period between April 27 th and July 1 st 2002 for all 23 sensors.....	63
14. A comparison of the measured relationship between sap flux density (S) and log transformed vapor pressure deficit (δ) in 2001 and the modeled relationship for 2002 in a random sampling of four of the 23 trees: a) Douglas-fir #3, b) Douglas-fir #4, c) red alder #17, and d) red alder #22.....	64
15. Hypothesis a: sensor degradation occurs gradually (incrementally) over time. Hypothesis b: sensor degradation occurs mostly over a short time period (threshold). Hypothesis c: a combination of incremental and threshold changes are occurring.....	66
17. The combined effect of diversity on water use efficiency (WUE) when either facilitation or competition alters productivity and resources are either more readily utilized or conserved.....	80
18. Plot layout at both sites showing the location of the sap flow trees (numbered 1-8), mortality (open squares), distribution of Douglas-fir (dots) and red alder (diagonal lines) in the four plot types.	82

LIST OF FIGURES (CONTINUED)

<u>Figure</u>	<u>Page</u>
19. Mean daily total sap flux density of Douglas-fir (solid dark line, n=32) and red alder (dotted line, n=32) through an annual cycle; data were smoothed (7-day running means) to remove day-to-day variation and to show overall trends.....	89
20. The seasonal course of surface soil moisture (volumetric water content, Θ) between 0 to 45 cm (a, b) and 45 to 90 cm (c, d) depth the upper and lower replacement series sites, respectively..	91
21. The proportion of water lost (%) from deep soil layers (45-90 cm) relative to the upper soil (0-45 cm) during the time period between June 28 and September 19, 2001 and a) total sapwood basal area per plot (m^2) or b) the proportion of total sapwood that is red alder relative to Douglas-fir (%).	92
22. The relationship between sap flux density ($kg\ m^{-2}\ d^{-1}$) and vapor pressure deficit (mbar) of a) Douglas-fir and b) red alder in monoculture (triangles, solid line), mixed (circles, dotted line), and mixed-delayed (squares, dashed line) plots at the upper replacement series site.	93
23. Average predawn water potential (bar) at the upper (closed symbols) and lower (open symbols) replacement series sites in each plot [DF monoculture (squares); RA monoculture (circles); mixed (triangles); and mixed-delayed (inverted triangles).	94
24. Annual total transpiration and proportion of alder biomass (%) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites.	95
25. Average annual net primary productivity between 1998 and 2002 and proportion of alder biomass (%) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites.	96
26. Annual total transpiration and total woody biomass (kg) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites.	96
27. The amount of carbon gained per unit water lost (WUE or transpiration efficiency) and proportion of alder biomass (%) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites.	97

LIST OF FIGURES (CONTINUED)

<u>Figure</u>	<u>Page</u>
28. The a) nitrogen concentration (%) and b) isotopic composition ($\delta^{15}\text{N}$, ppt) in the soil (open bars), Douglas-fir needles (diagonal hatched), and red alder leaves (cross hatched) in each plot in at the lower (LR) and upper (UR) replacement series sites.....	98
29. Conceptual diagram illustrating the linkages between stream flow (Q), soil moisture (S), transpiration (T), vapor pressure deficit (V), and precipitation (P).	107
30. Frequency distributions of (a, b, c) stream flow (Q); (d, e, f) soil moisture (S); (g, h, i) transpiration (T); and (j, k, l) vapor pressure deficit (V) at the hourly (I), daily (II) and storm (III) scales.....	114
31. a) Coefficient of variation by time interval for precipitation (closed circles, solid lines), vapor pressure deficit (open circles, dotted lines), soil moisture (closed inverted triangles, dashed lines), transpiration (open inverted triangles, dash/dot lines), and stream flow (closed squares, long dashed lines) at hourly, daily, weekly, monthly, and seasonal time scales between 8/1/00 and 9/30/02 (hourly transpiration only between June and November 2000). b) Coefficient of variation by season for variables at the daily time scale during the spring (April-May), summer (June-August), fall (September-November), and winter (December-February) based on daily mean values between 4/13/01 and 6/1/02.	117
32. Temporal variation in water fluxes through a small, forested watershed for water years 2000, 2001, and 2002.	119
33. Temporal variation in water fluxes through a small, forested watershed by month of year for the period 4/13/01 – 9/30/02.....	120
34. Lag correlation coefficients (Pearson's R) for the six possible pairs: Q v. S, Q v. T, Q v. V, S v. T, S v. V, and T v. V during the summer of 2000, 2001, and 2002.....	121
35. Relative stream flow recession during the first day after the peak for two time periods, wet season (black solid lines, December-March) and dry season (gray dotted lines, June-October).....	123

LIST OF FIGURES (CONTINUED)

<u>Figure</u>	<u>Page</u>
36. Cumulative variation in stream flow explained (multiple r^2 values) in a) all seasons, b) wet season only (December through April), and c) dry season only (June through September) with sequential addition of explanatory variables in multiple regression: S, S+T, S+T+VPD, S+T+VPD+P at the daily (circles) and storm (squares) scale (models are given in Table 5).....	127

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Specific information about trees in which sap flow measurements were taken.....	19
2. Description of potential variables and their symbols for use in the forward selection of a suitable multiple linear regression model.....	54
3. Estimates for intercept (β_0) and slope (β_1) for each sensor corresponding to Equation 2.....	61
4. Specific information about individual sap flow measurement trees, including plot location and type, the coordinates within the plot (treeID), species, number of live neighbors by species, diameter at breast height (DBH, cm), height (m), total basal area (BA, cm ²), and sapwood basal area (SBA, cm ²).....	85
5. A list of attributes of each of the study plots including the number of live trees remaining from the 25 initially planted, the relative proportion of red alder (RA) sapwood basal area (SBA) and biomass, measured and estimated leaf area index (LAI), annual net primary productivity, soil water loss from the upper (0-45 cm) and lower (45-90) soil layers, and total annual transpiration.....	89
6. Description of model parameters, their symbols in the tables of results, and units.....	111
7. Hourly lag correlations (simple regression) between all possible pairs of variables (dependent – Y ; independent – X) for periods during June, July, August, and September, including the amount of lag in hours at the maximum correlation (Pearson's r) and the corresponding p -values.....	122
8. Slope estimates for the relationship between stream flow (Q) and patterns in soil moisture (S), transpiration (V), vapor pressure deficit (V), and precipitation (P) at the hourly, daily, and storm scale.....	124
9. Results from sequential multiple regression at the hourly (h 1-4), daily (d 1-4), and storm scale (s 1-4) for periods spanning all seasons, dry season only, wet season only, and fall and spring only.....	125

LIST OF TABLES (CONTINUED)

<u>Table</u>	<u>Page</u>
10. Multiple regression models selected based on a sequential F-test.....	126

LIST OF APPENDIX TABLES

<u>Appendix</u>	<u>Page</u>
A. One-way regression model results at the hourly time scale.....	156
B. One-way regression model results at the daily time scale.	157
C. One-way regression model results at the storm time scale.	158
D. One-way regression model results at the storm time scale that have been log transformed.	159
E. Descriptors and units for variables used in regression analyses.	160

DRIVERS OF VARIABILITY IN TRANSPIRATION AND IMPLICATIONS FOR STREAM FLOW IN FORESTS OF WESTERN OREGON

INTRODUCTION

Changes in the land cover by human activities such as forest harvest or conversion to agriculture can lead to large impacts on water resources (Jackson et al. 2001). Therefore, improved understanding of the role of vegetation water use in the water cycle can contribute to predicting how land cover change will affect our increasingly strained water resources.

Of increasing priority to forest managers is the protection and preservation (and in some cases, enhancement) of water resources. For example, 30% of watersheds in the northeastern US are owned and controlled for the purpose of water management (Black and Fisher 2001), and 80% of US freshwater sources originate on national forest land (Houston et al. 2002). Because humans depend on ecosystem goods and services such as ample, clean water and renewable forest resources, and because there is a critical threshold for the use of water resources, policy is written to protect and preserve these vital commodities (Black and Fisher 2001). Yet forest managers are challenged to optimize goods and services while simultaneously sustaining ecosystem health and stability (Fujimori 2001).

For example, recent water shortages in Colorado during drought prompted debate over a policy initiative to thin forests on a massive scale in order to

increase snow packs and spring runoff (Stein 2002). Such water harvesting techniques (Brooks et al. 1997) have been popular in dry regions for decades. In 1948 in western Australia, catchments were cleared and compacted in order to supply water for livestock and small towns (Burdass 1975). In extreme cases, entire catchments have been paved or otherwise made impervious in order to capture water for human use. Such elaborate engineering feats can be fiscally worthwhile, but the potential for environmental and water quality degradation as well as increased risk of flooding breeds controversy. Certainly the value of water will only increase in the future, when water and timber will more often generate comparable revenue on an acre-by-acre basis. This is especially likely to occur in highly urbanized, developed countries where it is cheaper to import forest products and in regions where forests are important recreational resources.

Forests provide many beneficial timber products, but it has long been known that traditional forestry practices have the ability to dramatically alter water yields (Bosch and Hewlett 1982). In the first controlled watershed experiment, initiated in 1909 at Wagon Wheel Gap, Colorado, Bates and Henry (1928) articulated “It is not enough to know whether forests influence streamflow; it is necessary to know how much, at what seasons, and under what conditions of climate, soil, and topography, and the variations between different kinds of forests, as well.” Today, scientists are still seeking answers to these questions.

The interdisciplinary science called “Ecohydrology” has emerged as a new concept in environmental problem solving. According to Zalewski (2002),

ecohydrology is based on the suggestion that sustainable water use depends on the ability to maintain (or manage for) evolutionarily established processes of water circulation and energy flows at the watershed scale.

Ecohydrology addresses key questions in hydrology and ecophysiology. A key theoretical question of hydrology is: How can we model water storage and fluxes in a heterogeneous vegetated landscape? Although much has been learned from spatially explicit modeling (Band et al. 1991) and direct tracers (Hooper et al. 1990; Uhlenbrook et al. 2002), it is also possible to deduce water fluxes through hydrologic systems by examining statistical relationships among water storages and fluxes in various portions of the system, such as precipitation, evapotranspiration, and stream flow (e.g. Post and Jones 2001).

A key theoretical question of ecophysiology is: How do leaf-scale processes scale to the ecosystem? Wherein past measurements were made on individual leaves at isolated points in time (Running 1976), we now have better capabilities than ever to measure continuous water fluxes from vegetation at the stand scale (Baldocchi et al. 1988; Baldocchi et al. 1996). Sap flow sensors (Granier 1987; Smith and Allen 1996) measure water flux continuously through stems and can be scaled to the stand with stem surveys (Kostner 2001). A major advantage of sap flow techniques is that they allow for the measurement of transpiration excluding other evaporating components (e.g. soil evaporation, interception).

Combining questions and approaches of hydrology and ecophysiology has promise for revealing mechanisms by which vegetation influences water availability; such knowledge has theoretical value, but may also contribute to land use policy and management. The impact of land management on water resources is controversial. The effects of forest harvest on water are debated; forest harvest increases peak runoff (Jones 2000), but can lead to decreased summer low flows as vigorously growing young conifer stands repopulate an area (Hicks et al. 1991). Changes in age structure (Roberts et al. 2001; Vertessy et al. 2001), conversions from deciduous to coniferous forest (Swank and Douglass 1974), and afforestation projects (Bosch and Hewlett 1982) are associated with changing water yield. However, in some cases these resulted in only temporary, small changes in water yield (Federer et al. 1990; Swank and Crossley 1988). For example, paired watershed studies in deciduous forests of the eastern US (Coweeta WS 37) have resulted in less than a 260 mm change in annual water yield after 100% forest removal followed by full recovery in less than 15 years (Swank and Crossley 1988). In other cases there were large changes in water yield that lasted for many decades. For example, paired watershed studies in coniferous forests of the western US (Andrews WS 1) have resulted in a 500 mm change in annual water yield after 100% forest removal (Hicks et al. 1991) followed by a slow recovery period that has not returned to pre-harvest conditions after 35 years (HJ Andrews Experimental Forest, unpublished data).

The reasons why harvest leads to large changes in yield in some cases as opposed to small changes in other cases is not clear, but is likely associated with interactions among vegetation type, abundance, and climate. Coniferous forests generally have the largest influence on water yield (40 mm change in annual water yield per 10% change in forest cover) compared to deciduous forests (25 mm) or scrubland (~10 mm), but the resultant increases in water yields after harvest are highly variable (Bosch and Hewlett 1982).

Nonetheless, the majority of studies concerned with the effect of forest harvest on stream flow have simply implied that altered evapotranspiration leads to the observed change rather than measuring water uptake explicitly (but see Vertessy et al. 2001). Alterations of aboveground components that control transpiration (such as vegetation age, species composition, and species diversity) will likely impact belowground processes and subsequently runoff (Post and Jones 2001; Zhang et al. 2001), but unless transpiration is measured explicitly, it is difficult to differentiate among the many other key controls such as soil evaporation, canopy interception, and snow distribution/melt (Bren 1997; Jones 2000). A better integration of aboveground and belowground processes relating to water resources at various temporal scales is essential to understanding how changes in vegetation impact water resources.

This study contributes to the field of ecohydrology and forest management by addressing how changes in vegetation age, structure, species composition, and species diversity affect transpiration in forests of western Oregon, USA, and

furthermore by investigating the role of transpiration in controlling temporal patterns in stream flow in a small basin vegetated with an old-growth forest. Singling transpiration out among all the evaporative components of the water balance enables a better understanding of the active role vegetation plays in water resource dynamics.

In the Pacific Northwest and around the world, forest management practices and natural disturbance have created a patchwork mosaic of stands of varying age, density, and species composition. Chapter Two presents a comparison of transpiration in a young-mature and old-growth riparian stand, in which the relative contributions of three factors: Douglas-fir age, species composition, and stand sapwood basal area, are examined.

Sap flow sensors are increasingly popular tools for the measurement of transpiration. More and more these instruments are relied upon for transpiration studies that span multiple growing seasons. In Chapter Three, I develop a method for detecting and correcting for changes in sap flow sensor performance after long periods of continuous use.

In addition to reducing stand age across a landscape, forest management often reduces overstory tree diversity. Chapter Four explores how overstory diversity affects annual transpiration with a comparison of mixed-species and monoculture stands of Douglas-fir and red alder. Because of the difficulty of studying physiological processes in large, slow-growing trees, few studies have dealt with the effects of tree species diversity on ecosystem processes. In this

chapter a pre-existing study designed to examine growth responses of Douglas-fir and red alder in mixtures vs. monocultures is employed to compare transpiration, productivity, and water use efficiency of these species combinations.

The primary goal of Chapters Two and Four is to examine the controlling factors that lead to transpiration (i.e. vertical fluxes) differences among forest stands. Implications for stream flow (i.e. horizontal fluxes) are inferred.

Finally, in Chapter Five, I explore the linkages between horizontal and vertical fluxes within the confines of a small, forested watershed in the Pacific Northwest. There is a need to clarify at which scales and during what periods vegetation is most strongly coupled to stream flow, and at what scales/periods stream flow is largely independent of vegetation. Chapter Five provides an assessment of vegetation-stream coupling at three hydrologic time scales. The strength of coupling is compared between the wet and dry season, and a conceptual framework is developed to provide a means to quantify vegetation-stream flow interactions.

**STRUCTURAL AND COMPOSITIONAL CONTROLS ON
TRANSPIRATION IN A 40- AND A 450-YR-OLD RIPARIAN FOREST IN
WESTERN OREGON, USA**

Georgianne W. Moore, Barbara J. Bond, Julia A. Jones, Nathan Phillips and
Frederick C. Meinzer⁵

Tree Physiology
Heron Publishing
202, 3994 Shelbourne St.
Victoria, B. C.
V8N 3E2
Canada
In Press

Abstract

Large areas of forests in the Pacific Northwest are being transformed to younger forests, yet little is known about the impact this may have on hydrological cycles. Previous work suggests that old trees use less water per unit leaf area or sapwood area than young, mature trees of the same species in similar environments. Do old forests, therefore, use less water than young, mature forests in similar environments, or are there other structural or compositional components in the forests that compensate for tree-level differences? We investigated the impacts of tree age, species composition and sapwood basal area on stand level transpiration in adjacent watersheds at the HJ Andrews Forest in the western Cascades of Oregon, one containing a young-mature (about 40 years since disturbance) conifer forest and the other an old-growth (about 450 years since disturbance) forest. Sap flow measurements were used to evaluate the degree to which differences in age and species composition affect water-use. Stand sapwood basal area was evaluated based on a vegetation survey for species, basal area, and sapwood basal area in the “riparian” area of two watersheds. A simple scaling exercise derived from estimated differences in water-use as a result of differences in age, species composition, and stand sapwood area was used to estimate transpiration from late June through October within the entire riparian area of these watersheds. Transpiration was higher in the young stand due to greater sap flux density (sap flow per unit sapwood area) by age class and species, and greater total stand sapwood area. During the measurement period, daily sap

flux density averaged 2.30 times higher in young compared with old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees. Sap flux density was 1.41 times higher in young red alder (*Alnus rubra* Bong.) compared to young *P. menziesii* trees, and was 1.45 times higher in old *P. menziesii* compared to old western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees. Overall, sapwood basal area was 21% higher in the young stand. In the old forest, *T. heterophylla* is an important co-dominant, accounting for 58% of total sapwood basal area, whereas in the young stand, *P. menziesii* is the only dominant conifer. Angiosperms accounted for 36% of total sapwood basal area in the young stand, but only 7% in the old stand. All factors combined, we estimated 3.27 times more water use by vegetation in the riparian area of the young stand over the measurement period. Tree age had the greatest effect on stand differences in water use, followed by differences in sapwood basal area, and finally species composition. The large differences in transpiration found in this study provide further evidence that forest management alters site water balance via elevated transpiration in vigorous young stands.

Introduction

Forest management in the Pacific Northwest has led to large shifts in stand ages. In western Oregon forests, for example, almost 20% of the total 4.6 million hectares of forest was clear-cut between 1972 and 1995 (Cohen et al. 2002).

Fundamental differences in structure and composition that alter ecosystem function occur as a consequence of these changes in the age class of forest cover.

This study aims to test whether such changes can alter stand-level transpiration.

Because evapotranspiration is such a large component of the water budget in forestlands (Hewlett 1982), it is critical to understand how changes in transpiration, combined with other elements of the water cycle, affect site water balance.

There are multiple reasons why young-mature trees can potentially transport water more efficiently (i.e. more flow per unit leaf area or cross-sectional sapwood area) than old trees of the same species in similar environments. For example, changes in stem and branch hydraulics with age (Domec and Gartner 2001; McDowell et al. 2002b) may decrease the maximum rate at which old trees can transport water and increase stomatal sensitivity to vapor pressure deficit (Hubbard et al. 1999). Evidence suggests that older Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and *Pinus* sp. have lower whole-tree leaf-specific hydraulic conductances than young trees of the same species (Hubbard et al. 1999; Phillips et al. 2002; Yoder et al. 1994), and are more vulnerable to cavitation (Domec and Gartner 2002). However, decreased leaf

area: sapwood area ratio with age (al:as, McDowell et al. 2002a) tends to offset the differences in whole-tree leaf-specific hydraulic conductance. Some age or size related changes in water use can be attributed to factors directly associated with height, such as the pressure gradient due to gravity and increased hydraulic resistance (Ryan et al. 2000; Ryan and Yoder 1997). Also, as trees progress from juvenile to young-mature stages, roots may access increasingly deeper water reserves (Irvine et al. 2002). But this process may only be important during early developmental stages.

If young-mature trees use more water per unit sapwood area than old trees, do young-mature forests use more water than old-growth forests on a ground area basis? Or, instead, do changes in species composition or stand density tend to compensate for the age-related changes? Changes in species composition with stand age may affect stand-level transpiration independently from changes in stand-level sapwood area or leaf area. There is abundant evidence for physiological differences between species at the leaf scale (e.g. Bond and Kavanagh 1999; Running 1976). At a whole plant scale, sap flow measurements have revealed that co-occurring species respond differently to drought (Cienciala et al. 1998), with varying sensitivities to soil moisture and vapor pressure deficit (Pataki et al. 1998; Pataki et al. 2000). Different species may also access different soil water reserves (Cermak et al. 1995; Cienciala et al. 1998; Stratton et al. 2000). But do differences between species at the leaf and whole-tree levels result in differences at the stand scale?

The magnitude and seasonal timing of water use in Pacific Northwest forests may change as species composition changes through succession (Bredensteiner 1998; Franklin and Hemstrom 1981). In the Pacific Northwest and many temperate ecosystems, young mesic or riparian forests typically have greater angiosperm abundance compared with older late successional forests. Mesic angiosperms typically have the ability to transport more water per unit of sapwood area than conifers because their xylem contains vessels while that of conifers does not (Jarvis 1975). Since deciduous angiosperms are leafless during the winter, potential transpiration varies more widely in deciduous than coniferous forests as a function of seasonal dynamics in leaf area, although large changes in leaf area may also occur from spring through fall in coniferous forests as new cohorts of needles are formed and the oldest cohorts lost. In contrast with young forests, late successional forests are increasingly dominated by slow-growing, shade tolerant species. Slow-growing species probably use less water – at least while they are in the understory – although it is not known what happens when they become components of the overstory.

Total basal area is typically much higher in old compared with young forests, but sapwood basal area may be less. At the stand scale, forest succession leads to differences in tree spacing and crown diameters that can either increase or decrease transpiration. As forests age, self-thinning reduces stem density after canopy closure occurs, which alters stand-level $a_l:a_s$ while tree diameters gradually increase (Callaway et al. 2000). Thinning experiments have

demonstrated that trees compensate for reduced stem density by expanding crowns and increasing $a_l:a_s$ (Morikawa et al. 1986; Whitehead et al. 1984).

Other structural differences between young and old forests may also be important to transpiration. For example, the profound changes in both the amount and vertical distribution of leaf area that can occur as stands age can alter canopy conductance. Leaf area index (LAI) typically increases with stand age, but in some late-successional forests, LAI declines (Ryan et al. 1997). LAI is often considered the most important determinant of differences in transpiration among different forest stands (Hewlett 1982). Generally, young forests (e.g. *P. menziesii* forests of the Pacific Northwest) have most of their leaf area in a single canopy layer, whereas old-growth forests are characterized by more evenly distributed vertical leaf area profiles (Parker et al. 2002). These changes in stem and leaf distribution may have marked effects on transpiration from canopies. In this study, we considered changes in LAI but not distribution of leaf area within canopies.

The objectives of this study were to evaluate the effect of *P. menziesii* age, species composition, and sapwood area on transpiration in the riparian areas of two forests, an old-growth coniferous stand (about 450 years since disturbance) compared with a vigorously growing young coniferous stand (about 40 years since disturbance). We used a simple scaling exercise to estimate potential differences in water use at the stand level, using the general approach:

$$(1) \quad E = f * A$$

Where E is transpiration, or sap flow per unit ground area, f is sap flux density, and A is sapwood area per unit ground area.

We expected that the younger *P. menziesii* trees would exhibit higher sap flux density during the growing season, based on previous evidence in similar forests (Phillips et al. 2002). There is evidence, as cited above, to suggest that angiosperms (more abundant in young forests) may use more water per unit sapwood than conifers. Shade tolerant species (more abundant in old forests) use less water per unit sapwood while in the understory than shade intolerant species, but it is unknown whether these differences persist when the shade tolerant species emerge into the overstory. Total basal area is greater in older stands than younger stands, but sapwood basal area and LAI could be either greater or less. This case study was designed to examine these structural and compositional alternatives in a 40- and a 450-yr-old riparian forest.

Methods

Study area

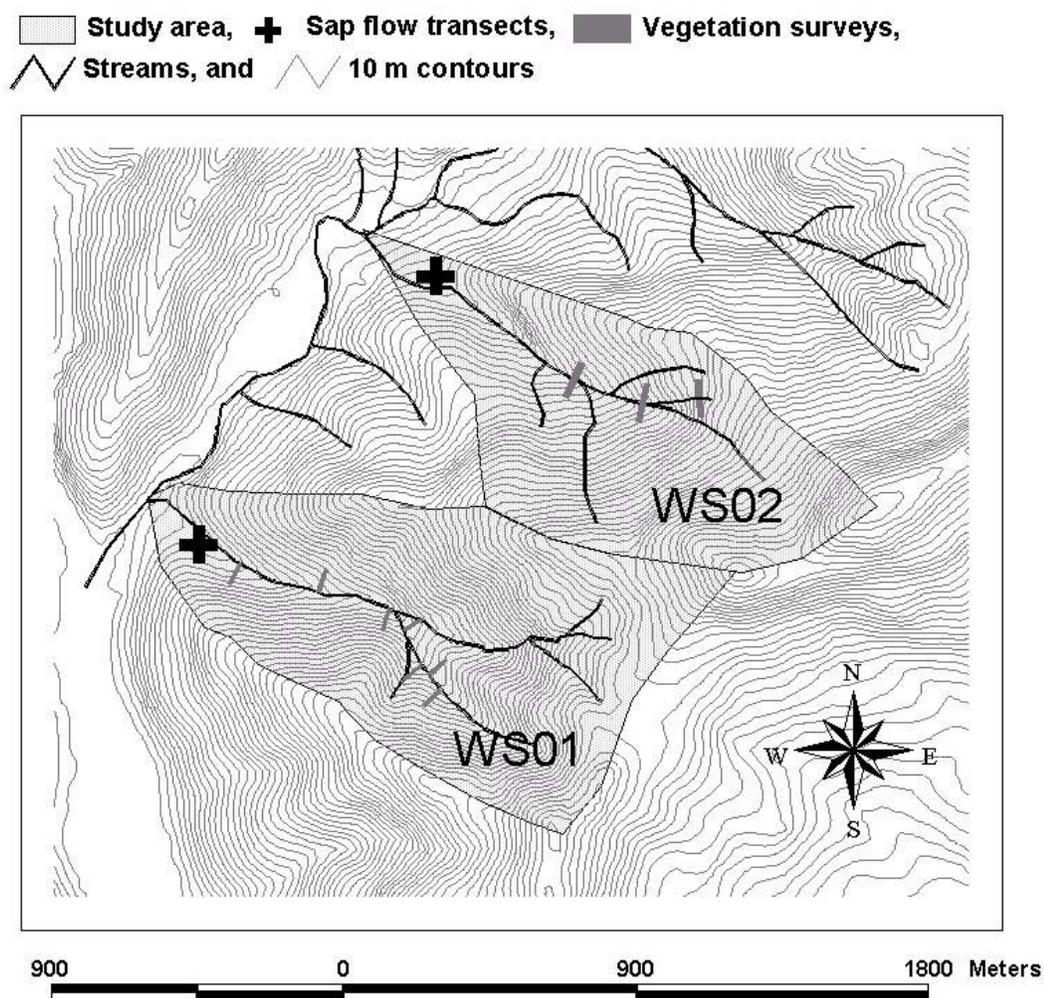
Our study was conducted at the HJ Andrews Experimental forest, located in the western Cascades of central Oregon, U.S.A. (44.2 °N, 122.2 °W). Two main study sites were established in the “riparian areas” (defined in this study as within a 100-m swath centered on the stream within which the vegetation survey was conducted) of adjacent watersheds (Figure 1). The vegetation of Watershed

One (WS01) was harvested in the mid 1960's; the regenerating young forest consists primarily of *P. menziesii*, but also has a significant angiosperm component. Watershed Two (WS02), whose last major disturbance occurred around 450 years ago, has a mix of primarily old-growth *P. menziesii* and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Swanson and James (Swanson and James 1975) described the local geology and geomorphology, where the predominant soil type is classified as gravelly clay loam. The western Cascades have a maritime climate, with wet, mild winters and dry, cool summers (mean annual rainfall is 2300 mm). Mean monthly temperature ranges from about 1 °C in January to 18 °C in July. The growing season extends from late April until late September.

Climate

Climatic conditions were monitored at a nearby weather station (HJ Andrews Primary Meteorological Station) within 0.75 km of the study area. Meteorological data sets were provided by the Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon.

Figure 1 – Map of study site locations. WS01 is the young stand (~40 years since disturbance) and WS02 is the old stand (~450 years since disturbance). Topographic and stream coverages provided by the Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon.



Xylem sap flow

Sap flow was measured during the growing season using constant-heat sap flow sensors (Granier 1987) in seven *P. menziesii* and seven red alder (*Alnus*

rubra Bong.) trees in the young stand, and in three *P. menziesii* and three *T. heterophylla* individuals in the old stand. We used solar panels to supply power. The need for close access to a canopy gap for maximum solar exposure inevitably restricted our sampling design. Trees were selected along a 60-m transect normal to the stream near the base of each watershed (Figure 1). Sensors were installed at two to five positions around the circumference of each tree at radial depths of 0 to 20 (outer sapwood) or 20 to 40 mm (inner sapwood) at a height of ~0.5 m in the young trees and ~5 m in the old-growth trees in order to minimize potential influences of buttressing. More extensive radial and circumferential sampling in individual trees offset the lower sample size of trees in the older stand. Specific information about individual measurement trees can be found in Table 1. Instantaneous measurements taken at 30-second intervals were averaged every 20 minutes and recorded on a data logger (CR10X, Campbell Scientific, Logan, UT).

We scaled measurements from individual sensors to whole-tree average flux per unit sapwood per day. First, sapwood depths were measured at the height of the sap flow sensors on each tree by visual examination of a 5 mm diameter core (Table 1). For *A. rubra*, a 0.2% safranin dye injection was used to aid in the visual assessment of sapwood depth. To account for radial patterns in sap flux, in *T. heterophylla*, a linear decline to zero was used to estimate fluxes in sapwood between 20 mm and the heartwood boundary based on our own observations from these trees plus an additional six trees with radial profiles of flow measured at 20, 50, 100, and 150 mm (F. Meinzer, unpublished data) with variable length constant

Table 1 – Specific information about trees in which sap flow measurements were taken. These include tree height, diameter at breast height, sapwood depth (SD), sapwood basal area (SBA), and the number of sensors at each depth in the sapwood (N-Outer and N-Inner). Outer sensors are in the outer 0 to 20 mm of xylem; inner sensors are in the inner 20 to 40 cm of xylem - except in four *A. rubra* trees where an additional sensor was placed from 40 to 60 mm. Numbers in parentheses are standard errors based on three cores in the old-growth trees and two cores in the young *P. menziesii*.

Age Class	Species	Ht. (m)	Diam. (m)	SD (mm)	SBA (m ²)	N-Outer	N-Inner
old-growth	<i>Pseudotsuga menziesii</i>	59.4	1.41	56 (9)	0.212	3	2
old-growth	<i>Pseudotsuga menziesii</i>	79.3	1.56	54 (5)	0.218	3	2
old-growth	<i>Pseudotsuga menziesii</i>	63.1	1.27	42 (4)	0.146	3	0
old-growth	<i>Tsuga heterophylla</i>	46.8	0.60	97 (16)	0.144	3	2
old-growth	<i>Tsuga heterophylla</i>	41.0	0.59	93 (10)	0.134	3	2
old-growth	<i>Tsuga heterophylla</i>	44.5	0.75	102 (18)	0.193	3	1
young	<i>Pseudotsuga menziesii</i>	27.9	0.27	35 (4)	0.022	2	1
young	<i>Pseudotsuga menziesii</i>	24.3	0.22	37 (11)	0.018	2	1
young	<i>Pseudotsuga menziesii</i>	24.8	0.30	35 (19)	0.026	2	1
young	<i>Pseudotsuga menziesii</i>	21.7	0.22	36 (0.7)	0.018	2	1
young	<i>Pseudotsuga menziesii</i>	18.0	0.17	28 (13)	0.010	2	1
young	<i>Pseudotsuga menziesii</i>	25.7	0.28	36 (13)	0.025	2	1
young	<i>Pseudotsuga menziesii</i>	27.2	0.27	40 (8)	0.025	2	1
young	<i>Alnus rubra</i>	27.7	0.35	85	0.066	2	0
young	<i>Alnus rubra</i>	27.3	0.32	80	0.056	2	0
young	<i>Alnus rubra</i>	16.9	0.24	66	0.032	2	2*
young	<i>Alnus rubra</i>	25.5	0.29	135	0.059	2	2*
young	<i>Alnus rubra</i>	17.8	0.26	111	0.045	2	2*
young	<i>Alnus rubra</i>	18.6	0.32	140	0.071	2	2*
young	<i>Alnus rubra</i>	24.0	0.28	142	0.053	2	0

*20-40 and 40-60 mm

heat sensors (James et al. 2002). In *P. menziesii*, the relationship between inner ring sap flux (15 – 35 mm beneath cambium) to outer ring sap flux (0 – 20 mm beneath cambium) and diameter at breast height (DBH) from Phillips et al. (2002) was used to account for radial patterns in sap flux. Our own observations of radial patterns of sap flux in *P. menziesii* fell within the range cited in Phillips et al. (2002). We assumed that there was no change in flux between the depth of the “inner” sensor and the heartwood boundary. Since sapwood depth is rarely much

greater than 40 mm in *P. menziesii* (the range in the trees we measured was 28 to 56 mm), any errors introduced will be small. In *A. rubra*, the average relationship between inner ring sap flux (20 - 40 and 40 - 60 mm beneath cambium) and outer ring sap flux (0 - 20 mm beneath cambium) in the four trees with inner sensors (Table 1) was used to account for radial patterns in sap flux in the remaining three trees. The flux within each “ring” of sapwood was calculated as the product of the area of that ring and the measured or predicted flux; then we summed the fluxes for each sapwood depth to estimate the total flux per tree. Finally, for all species, the total flux per tree was divided by the total sapwood area to estimate average flux per unit sapwood area for each tree. These calculations were performed for each 20-minute time step. Total daily fluxes are the summation of the 20-minute observations. This paper focused on daily totals because of our primary interest in differences in seasonal, stand-level water use. Details of water flux dynamics at the sub-daily level will be addressed in a future paper.

In some cases, especially in the late season when the number of sensors was restricted by power limitations, individual sensors were not functional over periods of several days. We interpolated to fill “missing” data (around 10%) based on relationships among the sensors when all functioned properly.

Estimates of sap flow using the constant heat measurement approach are sensitive to natural temperature gradients between sensors in the absence of applied heat (Do and Rocheteau 2002). The maximum potential effect on sap flow estimates due to background temperature gradients was evaluated and found to be

detectable yet small. Based on measurements taken of background temperature gradients during six warm, sunny days in July, we found that sap flow may be underestimated by a maximum of $3.7\% \pm 0.5\%$ and $0.2\% \pm 0.5\%$ per day in young and old *P. menziesii* respectively, and overestimated by a maximum of $6.0\% \pm 1.1\%$ in *T. heterophylla* during the month of July. Therefore we did not correct estimated sap flow for errors due to temperature gradients.

Vegetation survey

To estimate species composition and sapwood basal area in the two study areas, we sampled vegetation along transects that ran normal to the stream at the same distance from the stream as the sap flow transects (Figure 1, rectangular bars). In WS01, 50-m transects containing five contiguous 10 x 10 m plots were established approximately every 200 meters alternating north and south sides of stream, beginning at a random location near the mouth of the watershed for a total of seven transects. In WS02, 60-m transects containing three contiguous 20 x 20 m plots were established approximately every 200 meters on north and south sides of stream, beginning at a random location near the mouth of the watershed for a total of six transects. We used a larger plot size in the old growth stand because the trees were so much larger. All of the above spatial dimensions are given in horizontal distances (i.e. corrected for slope angle). In each plot, species and diameter at breast height (DBH, 1.37 m) were recorded for each woody plant greater than 0.01 m in diameter. For up to 5 individuals of each species in each

plot larger than about 0.08 m DBH, height and sapwood depth (based on visual inspection of a 5 mm diameter tree core) was recorded. Sapwood basal area was calculated or estimated based on measured trees for each tree in each plot. The estimated sapwood basal area was categorized into functional groups representing the classes we used for sapflow measurements: in the young stand, these were gymnosperms and angiosperms, in the old stand these were *P. menziesii*, *T. heterophylla*, and angiosperms.

Leaf area index

To determine the approximate leaf area index (LAI) within the vicinity of the sap flow measurements, LAI was estimated at four random locations dispersed within each sap flow transect using a LAI 2000 (Licor Inc., Lincoln, NE). Runyon et al. (1994) found that this instrument compared well with two other common methods for measuring LAI in forests. The same four locations at both sites were visited on May 25th, July 30th, and August 30th 2001. The May and August measurements were taken in the evening at dusk under uniform clear sky conditions and the July measurement was taken during the late morning under uniform overcast sky conditions. Of the five zenith angles recorded, we removed the lowest angle to avoid interference with obstructions. A correction factor (1.89 for the young stand, based on clumping in young *P. menziesii*; 1.94 for the old stand, based on average clumping in old *P. menziesii* and *T. heterophylla*) was used to compensate for within-shoot leaf clumping (Frazer et al. 2000). Stem interference was accounted for by subtracting the wood area index (W), which

was estimated from the vegetation survey in the young stand ($W = 0.525$) and old stand ($W = 0.746$) using the methods from Law et al. (2001).

Scaling up to the riparian area

Results of sap flow measurements and the vegetation survey were combined to estimate vegetation water use in the entire riparian area of each study watershed using species-specific versions of equation (1):

$$(2) \quad E_y = f_{PSMEy} * A_{GYMy} + f_{ALRUy} * A_{ANGy}$$

And

$$(3) \quad E_o = f_{PSMEo} * A_{PSMEo} + f_{TSHEo} * A_{TSHEo} + f_{PSMEandTSHEo} * A_{OTHER GYM_o} + f_{ALRUy} * A_{ANG_o}$$

The area used for sap flux density (f , $\text{kg m}^{-2} \text{d}^{-1}$) measurement is different from the area used for estimating sapwood basal area (A , $\text{m}^{-2} \text{ha}^{-1}$) and only represents a small fraction of the sapwood basal area in the stand. This was a consequence of limited power supply for sapflow measurements, and admittedly may produce errors in extrapolating the sap flow data, but at least the approach was similar for the two watersheds. Sap flow of young (y) *P. menziesii* (PSME) was used to estimate water use by all gymnosperms (GYM) in the young stand (*P. menziesii* constitutes 90% or more of gymnosperm basal area). Sap flow of *A. rubra* (ALRU) in the young stand was used to estimate water use by all angiosperms (ANG) in both the young and old (o) stand. We acknowledge that using *A. rubra* to represent all angiosperms is not ideal, but our experimental capability precluded including more species. The only other prevalent angiosperms in the

young stand are vine maple (*Acer circinatum* Pursh) and bigleaf maple (*Acer macrophyllum* Pursh) (< 20% of total basal area combined). Sap flux of *A. rubra* was only measured in 1999, so a relationship was established to predict *A. rubra* in the year 2000 (days 175 to 301) based on the ratio between *A. rubra* and *P. menziesii* in 1999:

$$(4) \quad f_{yALRU} / f_{yPSME} = -163.3 + 165.1 * (1 - e^{-0.0293 * t})$$

Where t is day of year between days 182 and 251 ($n = 62$, $r^2 = 0.78$, $p < 0.0001$). It was necessary to include t in this equation to allow for seasonal differences.

Average sap flow of old *P. menziesii* and old *T. heterophylla* (TSHE) was used to estimate water use by the remaining gymnosperms in the old stand (*P. menziesii* and *T. heterophylla* combined constituted 90% or more of gymnosperm basal area).

Statistical analyses

Least squares regression models were used to predict sapwood area (A) for individual trees of each species from either diameter or total cross sectional area of wood (basal area, BA). The choice of a linear vs. non-linear model, and the choice of independent variables, differed for each species to obtain the model with the best predictive power for each species. We defaulted to a linear model except when there was justification to use a power function. The small-diameter species, particularly angiosperms such as *A. circinatum*, rhododendron (*Rhododendron macrophyllum* L.), and California hazel (*Corylus cornuta* (A. DC.) Sharp) were assumed to be entirely sapwood, minus the estimated bark

depth. The same was also assumed for small individuals of other species (*P. menziesii* and *A. macrophyllum* in the young stand) for diameters smaller than 6 cm. Linear equations ($A = a + b \cdot BA$) were used for bitter cherry (*Prunus emarginata* Dougl.) and *A. macrophyllum* in the young stand and *P. menziesii* in the old stand ($r^2 = 0.80, 0.71, \text{ and } 0.48$ respectively), which were only used to predict sapwood areas in small individuals (all large trees were measured explicitly). Power function equations ($A = a + b \cdot BA^c$) were used for all other species (for *P. menziesii* and *T. heterophylla* combined for the young stand and *T. heterophylla*, pacific yew (*Taxus brevifolia* Nutt.), *A. macrophyllum*, and western redcedar (*Thuja plicata* Donn.) in the old stand, $r^2 = 0.94, 0.91, 0.79, 0.68, \text{ and } 0.91$, respectively). The model for *P. menziesii* in the old stand was only used to predict eight trees out of the 32 total for that species; sapwood area of the rest was measured explicitly.

A T-test was used to test for significant differences in LAI among sites. T-tests were also used to compare mean sap flow among each individual measurement tree of each species or age class for each day.

Results

Variations in water use per unit sapwood area based on tree age and species

Over the measurement period, we noted a seasonal decline in sap flux density for all species and both ages of *P. menziesii* (Figure 3). Simultaneously, light (Figure 2a) and vapor pressure deficit (Figure 2b) decreased. Young *P.*

menziesii averaged 2.30 times greater sap flux density than old *P. menziesii* on a daily basis (Figure 3a) from late June until late October 2000 (day 175-301, $SE = 0.017 \text{ kg m}^{-2} \text{ d}^{-1}$). Significant differences were observed during the majority of the measurement period except for rainy or cloudy days when sap flow was low (Figures 2 and 3). The rate of change of sapflow over the measurement period was much greater for young than for old *P. menziesii* (Figure 3a); thus, it may be inferred that young trees were more responsive to climatic variability than were old trees. Tree-to-tree variation was quite large, especially in old growth ($CV = 0.42$ and 0.63 in young and old trees, respectively).

Young *A. rubra* averaged 1.41 times more sap flux density than young *P. menziesii* (Figure 3b) from early July until early September 1999 (day 182-251, $SE = 0.017 \text{ kg m}^{-2} \text{ d}^{-1}$). Water use by *A. rubra* declined only slightly through the season compared to *P. menziesii*, and thus water use by *A. rubra* (and, we infer, angiosperms in general) comprised an increasingly greater proportion of vegetation water use in the young stand throughout the growing season. The difference was statistically different ($p < 0.05$) starting in late July (day 207) and continuing thereafter. Sap flux density in *A. rubra* reached a maximum almost a month later than *P. menziesii*. Tree-to-tree variation was slightly higher in *P. menziesii* throughout the measurement period ($CV = 0.37$ and 0.36 in *P. menziesii* and *A. rubra*, respectively).

Figure 2 – (a) Total solar radiation ($\text{MJ m}^{-2} \text{d}^{-1}$), (b) daily average vapor pressure deficit (kPa) and daily total precipitation (mm) for the study period of 1999 (gray bars, dotted line) and 2000 (black bars, solid line).

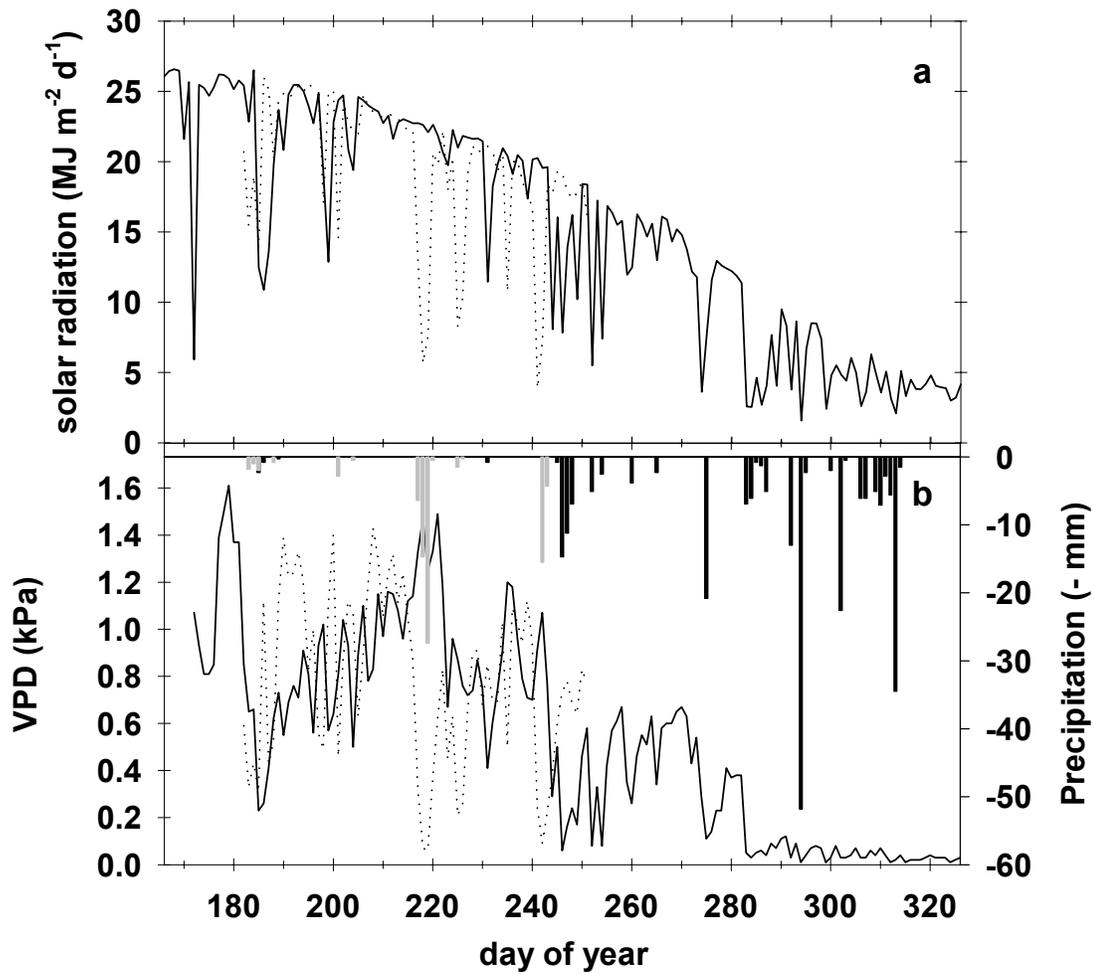
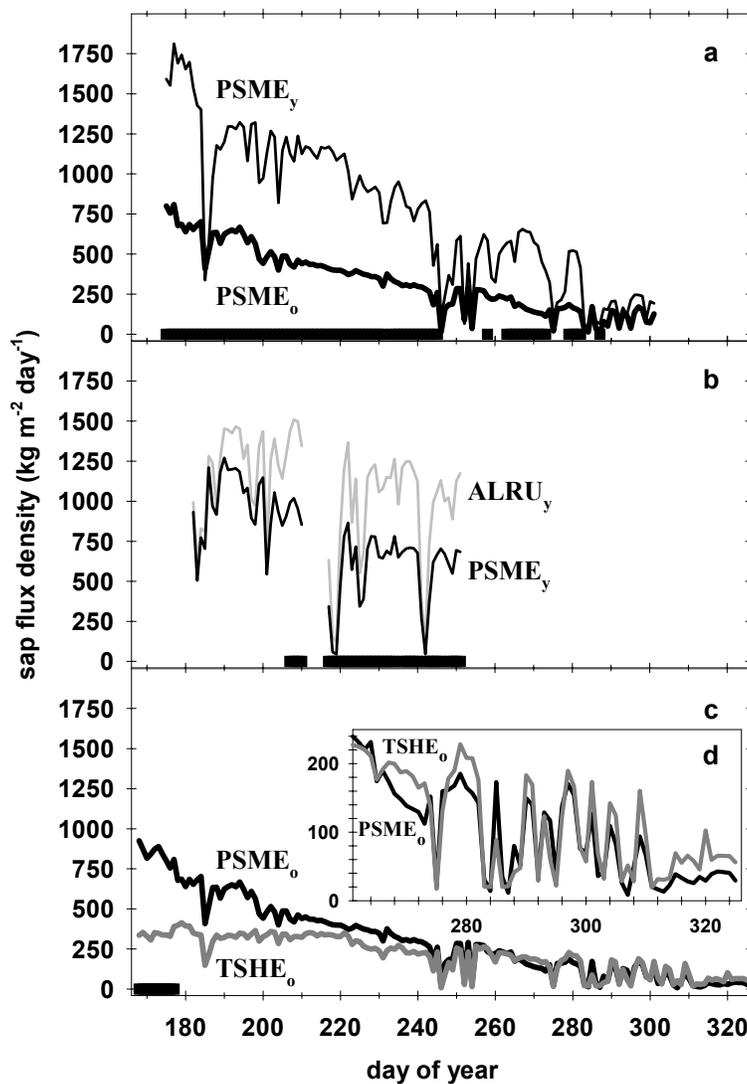


Figure 3 – (a) Effects of age on sap flux density ($\text{kg m}^{-2} \text{ day}^{-1}$) in the young (thin black line, mean of 7 trees) and old (-thick black line, mean of 3 trees) *P. menziesii* from early June until late October 2000. (b) Effects of species on sap flux density in *A. rubra* (gray line, mean of 7 trees) and *P. menziesii* (thin black line, mean of 7 trees) in the young stand from early July until early September 1999. (c) Effects of species on sap flux density in *P. menziesii* (thick black line, mean of 3 trees) and *T. heterophylla* (thick gray line, mean of 3 trees) in the old-growth stand from early June until late November 2000. (d) Magnification of late-season fluxes for *P. menziesii* and *T. heterophylla* in (c) from mid-September until late November 2000. The black bar at the bottom of graphs a, b, and c represents days when the mean sap flux density among trees in the two groups was significantly different ($p < 0.05$ from a Studentized t-test).

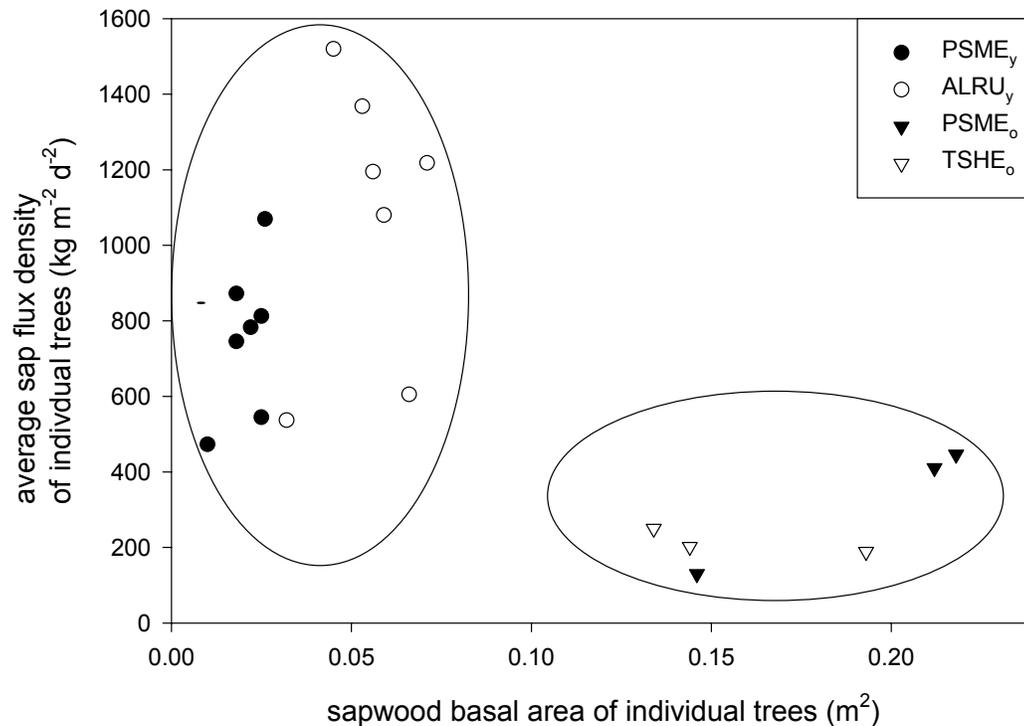


Sap flux density in old *P. menziesii* averaged 1.45 times greater than in old *T. heterophylla* (Figure 3c) from late June until late November 2000 (day 168-325, $SE = 0.010 \text{ kg m}^{-2} \text{ d}^{-1}$). *P. menziesii* consistently used more water throughout most of the growing season on a daily basis, but water use declined more steeply in *P. menziesii* than *T. heterophylla*. As a result, *T. heterophylla* used slightly more water than *P. menziesii* at the end of the season (Figure 3d). Due to low sample size and high tree-to-tree variation this difference was statistically significant only during early summer (day 168-177). Tree-to-tree variation was especially large in *P. menziesii* ($CV = 0.62$ and 0.34 in *P. menziesii* and *T. heterophylla*, respectively).

We found no trend in seasonal average sap flux density and sapwood basal area of individual sap flow trees within species (Figure 4). Rather points tend to group within age categories (Figure 4).

Overall, differences in sap flux density between tree ages (measured in *P. menziesii* only) were greater than those between different species of a similar age. Surprisingly, there was a slightly greater difference between the two old-growth conifer species than between the young *A. rubra* and young *P. menziesii*.

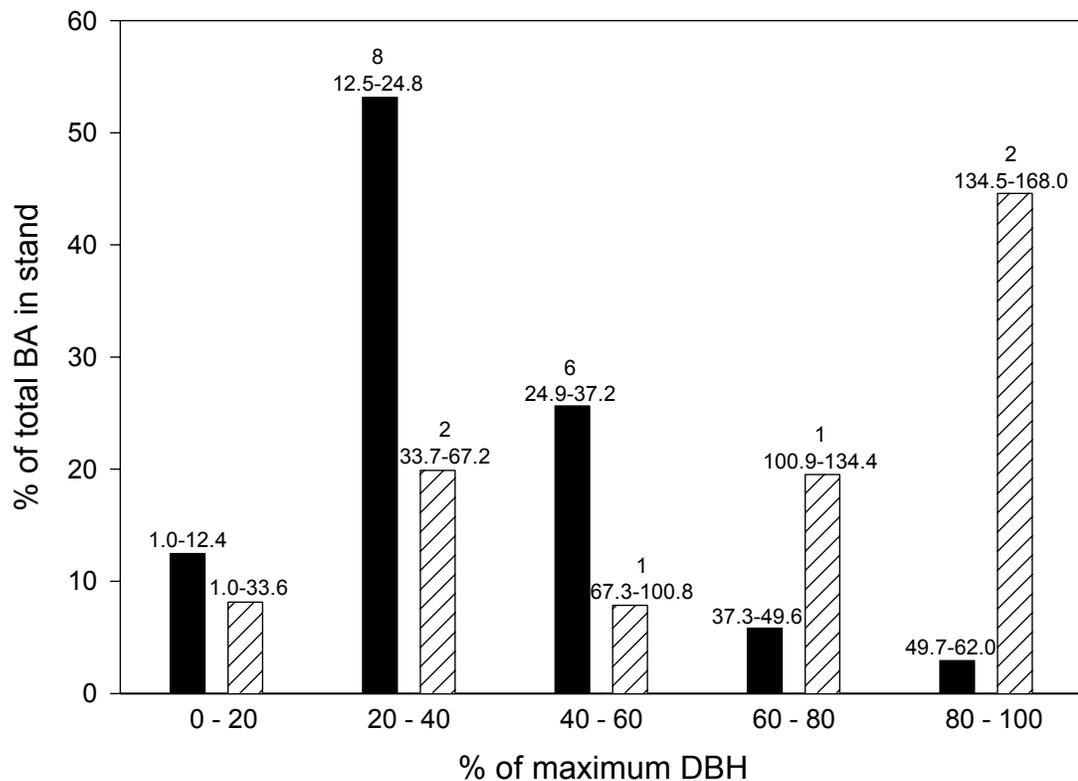
Figure 4 – The relationship between seasonal average sap flux density ($\text{kg m}^{-2} \text{d}^{-1}$) for the individual trees equipped with sap flow sensors and the sapwood basal area (m^2) of those individual trees. Note that trees in the young stand (circled at left) seem to group together, as do trees in the old stand (circled at right), but there is no clear trend within species.



Variations in basal area and sapwood area

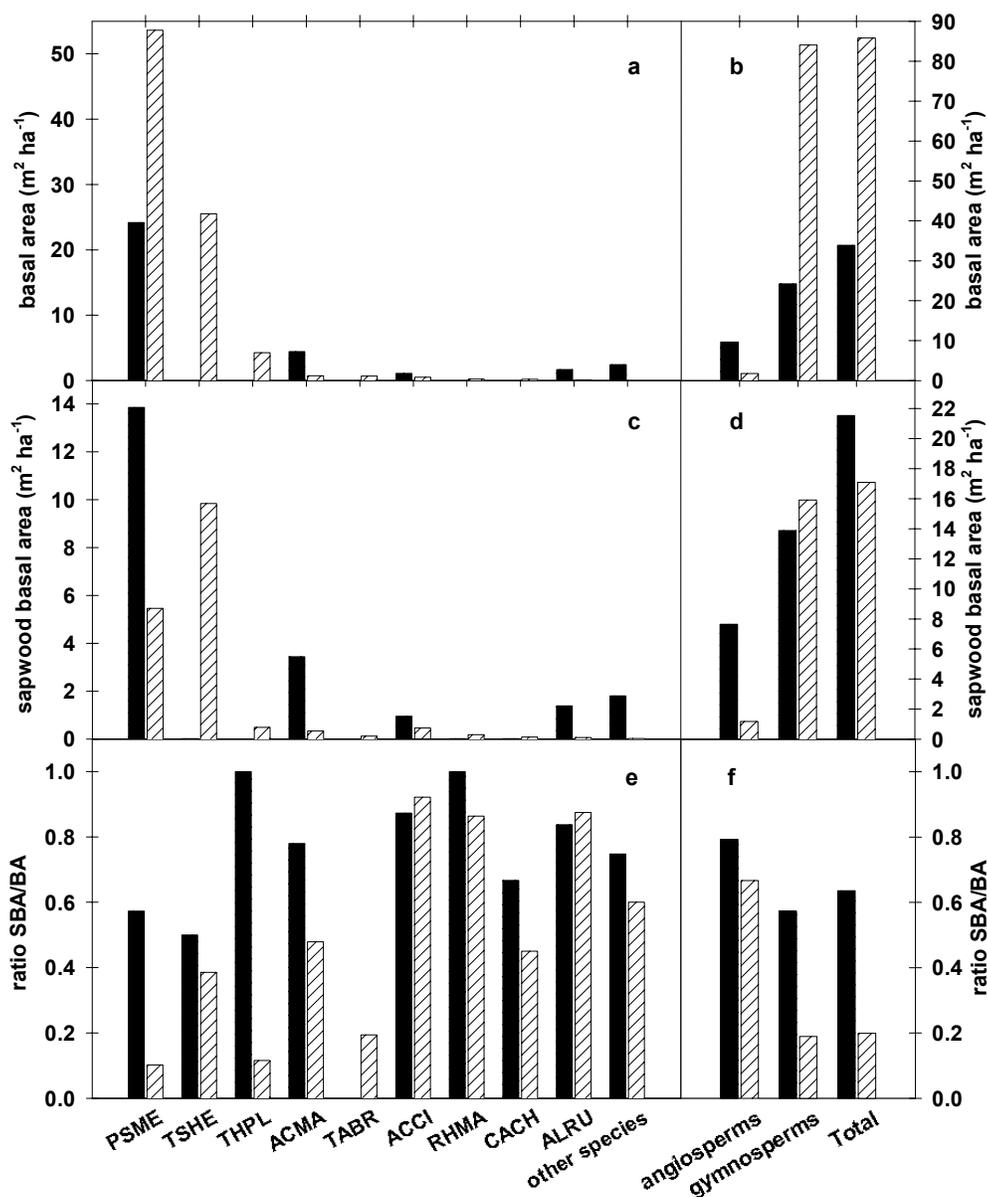
Tree size was normally distributed in the young stand but bimodally distributed in the old stand, indicative of a more pronounced understory component; however, more than 40% of the basal area was in the largest 20% of the trees in that stand (Figure 5).

Figure 5 – The relative amount of total basal area (%) in the young stand (solid bars) and old stand (hatched bars) by size. Size is broken down into five groups relative to the maximum diameter at breast height in the stand. Actual diameter ranges in centimeters and the number of sap flow measurement trees in each group are noted above each bar.



There was more than twice as much total basal area in the riparian area in the old stand than in the young stand (Figure 6a), $85.8 \text{ m}^2 \text{ ha}^{-1}$ and $33.3 \text{ m}^2 \text{ ha}^{-1}$, for the old and young stands, respectively. In contrast, sapwood basal area in the riparian area in the young stand was estimated 21% greater than in the riparian area of the old stand (Figure 6b), due to the large amount of heartwood in old-growth trees. Old gymnosperms had much less sapwood per unit basal area than young gymnosperms or angiosperms (Figure 6e and 6f).

Figure 6 – (a) Differences in total basal area ($\text{m}^2 \text{ha}^{-1}$) among the young stand (solid bars) and old stand (hatched bars) by species and (b) summarized by grouping. (c) Differences in total sapwood basal area ($\text{m}^2 \text{ha}^{-1}$) among the young stand (solid bars) and old stand (hatched bars) by species and (d) summarized by grouping. (e) Ratio of total sapwood basal area and basal area among the young stand (solid bars) and old stand (hatched bars) by species and (f) summarized by grouping. PSME = *Pseudotsuga menziesii*, TSHE = *Tsuga heterophylla*, THPL = *Thuja plicata*, ACMA = *Acer macrophyllum*, TABR = *Taxus brevifolia*, ACCI = *Acer circinatum*, RHMA = *Rhododendron macrophyllum*, CACH = *Castanopsis chrysophylla*, ALRU = *Alnus rubra*. Other species includes *Cornus nuttallii*, *Vaccinium parvifolium*, *Prunus emarginata*, *Amelanchier alnifolia*, *Populus tremuloides*, *Holodiscus discolor*, *Rhamnus purshiana*, and *Corylus cornuta* var. *californica*.



The riparian area of the young stand had over six times greater sapwood basal area of angiosperms than that of the old stand (Figure 6d). In the young stand, *P. menziesii* comprised almost 100% of the coniferous sapwood basal area and 64% of the total sapwood basal area, whereas in the old-growth stand, *T. heterophylla* comprised 62% of the coniferous sapwood basal area and 58% of the total sapwood basal area. This is in contrast to the total basal area (sapwood plus heartwood) of *T. heterophylla* and *P. menziesii* in the old stand, where *P. menziesii* makes up 64% of the coniferous basal area. This is because sapwood depth of *P. menziesii* is small (average of 7% of bole radius), whereas *T. heterophylla* has very thick sapwood (average of 50% of bole radius) (Figure 6e). Since *T. heterophylla* dominance is associated with late-successional forests in the Pacific Northwest (Franklin and Hemstrom 1981), the large *T. heterophylla* component in the old stand indicates that this stand is in the stages of late succession. *A. rubra*, *Acer macrophyllum*, and *Acer circinatum* make up the majority of angiosperms in both stands, but are a much smaller component of the old stand. Additionally, *Rhododendron*, almost non-existent in the young stand, is a significant component of the old stand angiosperms, albeit a small component of sapwood basal area.

Leaf area index

LAI was approximately 14% higher ($p = 0.04$) in the old stand (LAI = $12.1 \pm 0.3 \text{ m}^2 \text{ m}^{-2}$) than in the young stand (LAI = $10.6 \pm 0.5 \text{ m}^2 \text{ m}^{-2}$) on July 30th.

Similar values were obtained on May 25th and August 30th, although on these dates the measurements were not statistically different between the two stands ($p > 0.05$; 9.5 ± 0.4 and $10.5 \pm 0.5 \text{ m}^2 \text{ m}^{-2}$ for the young and 11.0 ± 0.5 and $11.5 \pm 0.4 \text{ m}^2 \text{ m}^{-2}$ for the old stand, respectively). No phenological trend in LAI was detected over the measurement period. Our estimates for LAI in both stands average about 1 to 3 $\text{m}^2 \text{ m}^{-2}$ larger than those determined by others for similar stands (Michael Lefksky and Osbert Sun, unpublished data, Thomas and Winner 2000; Turner et al. 2002). This may be a measurement error rather than a real difference, due to problems with stem interference and branch clumping. The LAI 2000 instrument is known to have errors of 15 to 20% associated with it under typical forest conditions (Jon Welles, Licor Inc., pers com).

Scaling up tree water use to the riparian area

Estimated tree water use in the young stand was 3.27 times greater than that of the old stand during the period from late June until late October 2000 (day 175-301, Figure 7). All three of the factors considered in this study, *P. menziesii* age, species composition, and sapwood area, contributed to this large difference. The seasonal trends for the two stands were similar, declining steadily through the measurement period. At low levels of vapor pressure deficit, the difference in transpiration between the two stands was much smaller than at high levels of vapor pressure deficit (Figure 8).

Figure 7 – Estimated water use per unit ground area (mm day^{-1}) in the young stand (thin line) and the old-growth stand (thick line) from late June until late October 2000.

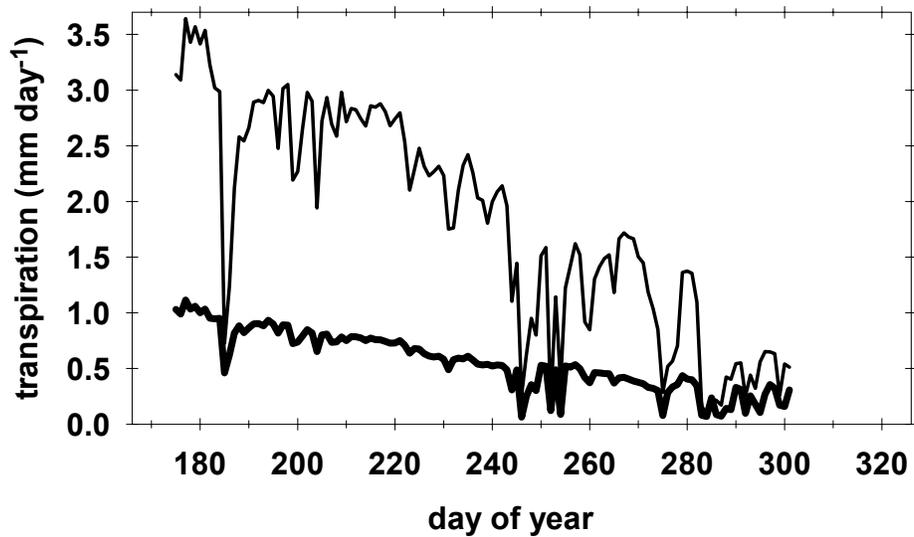
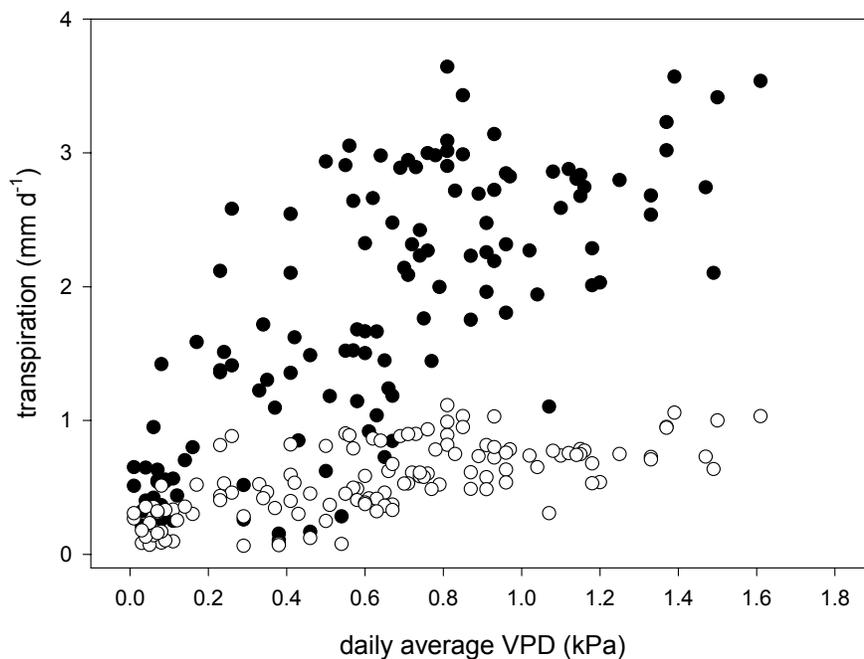


Figure 8 – The relationship between daily transpiration (mm d^{-1}) in the young stand (solid circles) and old stand (open circles) and daily average vapor pressure deficit (kPa), as measured at a nearby weather station.



Discussion

As shown previously (Phillips et al. 2002), sap flux density was greater in young-mature *P. menziesii* than in old-growth *P. menziesii* trees. In fact the age/size-related differences were much greater in this study than reported previously (Phillips et al. 2002). We speculated that other structural and compositional characteristics of the stands would tend to compensate for the change in tree-level water use. However, on the contrary, we found that greater sapwood basal area and a larger component of angiosperms in the young stand only increased the total water use of that ecosystem compared with the old-growth ecosystem. *A. rubra* had greater sap flux density than *P. menziesii* in the young stand, consistent with previous comparisons of mesic angiosperms vs. gymnosperms (Jarvis 1975). Shade tolerant species (overstory *T. heterophylla*), in addition to growing slower, had less sap flux density than *P. menziesii* in the old stand, But *T. heterophylla* had much greater sapwood area per unit basal area. And total sapwood basal area was significantly greater in the young stand than the old.

The lower early-season sap flux density in *T. heterophylla*, compared to that of *P. menziesii* (Figure 3c), could be partially attributed to its slightly lower average height and thus partial shading by adjacent trees. However, if this were entirely the case, we would expect the differences to intensify in the late summer as the solar zenith increases. Instead, sap flux density in *T. heterophylla* became more similar to *P. menziesii* as the season progressed, eventually surpassing it

(Figure 3d). A possible explanation for seasonal differences is that *T. heterophylla* is less sensitive to vapor pressure deficit than *P. menziesii*, but at very high levels of vapor pressure deficit, stomatal conductance is higher in *T. heterophylla* than in *P. menziesii* (Waring and Franklin 1979). However, it is also possible that rooting or hydraulic differences may explain the same trend. It is reasonable to expect that *T. heterophylla*, as a shade tolerator, uses less water when it is in the understory compared with overstory *P. menziesii*, but our results indicate that the differences between species may persist when *T. heterophylla* emerged into the overstory and received full sunlight, suggesting that the physiological adaptations associated with being shade tolerant are not erased upon reaching overstory status.

Our estimates of stand transpiration are sensitive to the scaling techniques utilized. Much attention has been paid to the topic of scaling sap flow measurements to estimate stand transpiration (Cermak et al. 1995; Granier et al. 1996; Granier et al. 1990; Hogg et al. 1997; Oliveras and Llorens 2001; Oren et al. 1998; Saugier et al. 1997). Others who have used species-specific estimates have determined that they are useful in multi-species stands (Kostner 2001; Wullschleger et al. 2001). In this study, at least nine sap flow sensor per species were utilized, whereas other studies have determined that 6-12 (Cermak et al. 1995) or 5-10 (Granier et al. 1996) sensors are necessary to represent the stand, although more may be needed in older, heterogeneous stands (Kostner et al. 1998). As in similar studies (Cermak et al. 1995; Granier et al. 1996; Hogg et al. 1997; Martin et al. 1997; Oliveras and Llorens 2001; Saugier et al. 1997)

selection of trees for sap flow measurement encompassed a range of representative size classes (Figure 5).

Our estimates of basal area in these stands (34 and 86 m² ha⁻¹ in the young and old stand, respectively) compare well with those made in similar aged stands in other studies carried out in the Pacific Northwest. Within this old-growth plot, slightly higher estimates of *P. menziesii* basal area (66 and 67 m² ha⁻¹) and slightly lower estimates of *T. heterophylla* basal area were found (21 and 8 m² ha⁻¹, Dyrness and Acker 1999) compared to this study. These survey areas contained proportionately less riparian area, consistent with lower density of *T. heterophylla*. Franklin and Hemstrom (1981) reported a basal area of 27 m² ha⁻¹ for *P. menziesii* and a total basal area of 98 m² ha⁻¹ for forests of ages 350 to 600 years throughout the Oregon and Washington Cascades. In other studies, estimated basal areas of *P. menziesii* - *T. heterophylla* forests ranged from 25 to 44 m² ha⁻¹ for young stands (age 30-50) and from 69 to 92 m² ha⁻¹ for old-growth stands (Cohen et al. 1995; Means et al. 1999; Spies and Franklin 1991).

A. rubra constituted 18% of the angiosperm sapwood basal area in the young stand and 6% of the angiosperm sapwood basal area in the old stand. Using *A. rubra* from the young stand to represent angiosperms in the old stand introduced very little error, since hardwoods are such a small component (7%) of the sapwood basal area in the old stand -- especially for overstory trees, where it is essentially zero. Power limitations also inhibited adequate sampling of the magnitude and variation in sap flow among understory species in the old stand.

Since these trees receive low or patchy amounts of light, we expect that they may use significantly less water than their overstory counterparts. In future studies we plan to address understory water use.

It is often assumed that LAI is the most important determinant of differences in transpiration among different forest stands (Hewlett 1982). In models of forest transpiration, LAI often plays a theoretical role in determining differences among forest stands (Running and Coughlan 1988; Williams et al. 1996). This was not the case in our study. We did note a small increase in LAI in the older stand, but in fact estimated transpiration was actually lower in that stand. Several chronosequence studies have found a decline in leaf area in older forests (Ryan et al. 1997). In forests of similar type and age, others have found LAI to be about $2 \text{ m}^2 \text{ m}^{-2}$ less in old compared to young *P. menziesii* – *T. heterophylla* forests (Michael Lefsky and Osbert Sun, unpublished data). However, despite the small increases or decreases in LAI with forest age, there appears to be a general trend toward reduced transpiration in old-growth stands. Maximum transpiration rates reported in the literature for 20- to 60-yr-old conifer stands ranged between 1.8 and 3.9 mm d^{-1} (mean = 3.0 mm d^{-1} , Alsheimer et al. 1998; Granier et al. 1990; Irvine et al. 1998; Martin et al. 1997; Morikawa et al. 1986; Roberts et al. 2001). Whereas, in conifer forests over 240 years of age, maximum transpiration ranged between 0.4 and 1.5 mm d^{-1} (mean = 0.9 mm d^{-1} , Irvine et al. 2002; Unsworth et al. In Press; Zimmermann et al. 2000). There must be some

explanation other than LAI for transpiration differences between young and old stands.

In a meta-analysis of 13 whole-tree studies, McDowell et al. (2002a) found that the ratio between leaf area and sapwood area ($a_l:a_s$) is typically reduced as trees grow taller and older. They proposed that the change in $a_l:a_s$ could at least partially compensate for the impact of increased height on leaf-specific hydraulic conductance. Interestingly, McDowell et al. (2002a) noted two exceptions to the general trend of decreasing $a_l:a_s$ with increasing tree height. In both of these studies, $a_l:a_s$ was calculated from stand-level surveys in stands that included an abundance of shade tolerant species, such as Norway spruce (*Picea abies* (Linnaeus)) or balsam fir (*Abies balsamea* (L.) Mill.). Our study appears consistent with these exceptions. Given that sapwood basal area in our study was substantially lower in the old growth stand than in the young stand, the slightly higher LAI in the older stand means that $a_l:a_s$ was greater in the old stand than the young (0.67 and 0.47 m² cm⁻², respectively). It is possible that during late succession, the emergence of shade tolerant species with very high $a_l:a_s$ caused stand level $a_l:a_s$ to change in the direction opposite from tree-level trends that occur as early successional species reach maturity (McDowell et al. 2002a).

Implications for land use

Evapotranspiration by forest canopies influences seasonal hydrologic trends in the Pacific Northwest (Jones 2000; Post and Jones 2001). Our study indicates that the many changes in the structure and composition of forests as they

age may significantly increase evapotranspiration in younger forests, potentially depleting summer low flows in streams. Our previous findings and those of others suggest that streamflow in watersheds covered by young stands is dynamically influenced by rapidly transpiring young vegetation (Bond et al. 2002; Bren 1997). However, water use by dominant tree species alone presents an incomplete picture of how streamflow volumes during summer low flow can be impacted by forest management practices (Hicks et al. 1991).

We found that the largest differences in water use between young and old stands occurred during late spring, but that differences persisted throughout the measurement period (Figure 7), corresponding with the period of low streamflow. Trends in streamflow after harvest in managed forests have demonstrated that streamflow can be reduced to below pre-harvest levels in young regenerating stands during low flows (Hicks et al. 1991; Lane and Mackay 2001; Perry et al. 2001). Few studies have directly evaluated the role of transpiration, independent of evaporation, by forests on water yield (Vertessy et al. 2001). We intend to explore relationships between transpiration and water yield in further analyses using existing streamflow data from these sites.

Conclusions

We posed the question: If young, mature trees use more water per unit sapwood area than old trees, do young-mature forests use more water than old-growth forests on a ground area basis? Or, instead, do changes in species composition or stand density tend to compensate for the age-related changes? We

found evidence that all factors investigated (age- and species-related differences in water use, and structurally-related changes in sapwood area distribution within stands) contribute to decreased stand-level water use with age from that of a closed canopy younger stand. Each of the three factors alone led to increases in young-stand transpiration compared with the old-growth forest, but when combined, they accrue very large differences between old and young stands. Holding all else constant and substituting into Equations 2 and 3 we were able to rank these three factors according to their relative impact on stand transpiration. For example, if the sap flux density of *P. menziesii* in the young stand was the same as *P. menziesii* in the old stand ($f_{PSMEy} = f_{PSMEo}$), young stand transpiration would be reduced by 32%. We found that *P. menziesii* age had the greatest effect on stand-level differences in water use, followed by differences in sapwood basal area, and finally species composition.

Acknowledgements

Funding for this research was provided by the Long-Term Ecological Research (LTER) program small watersheds funds, National Science Foundation (NSF) Research Experience for Undergraduates Program, and NSF start-up funds. Further support was provided by Oregon State University and the U.S. Forest Service Pacific Northwest Research Station (NSF grants: DEB-7611978, BSR-9011663). Significant funding for climate and spatial data was provided by the NSF LTER program (NSF grants: BSR-90-11663 and DEB-96-32921). Many

thanks to J. Moreau, C. Hurst, M. Van Horne, H. McCarthy, S. McNulty, K. Stein, P. Valko, and A. Schauer for help with field data collection. This manuscript has benefited from the suggestions by the journal editor and two anonymous reviewers.

DO THERMAL DISSIPATION SAP FLOW SENSORS YIELD CONSISTENT ESTIMATES OF SAP FLOW FOR MULTIPLE YEARS?

Abstract

The thermal dissipation sap flow measurement technique has become increasingly popular in recent years. The technique involves an empirically-derived relationship between sap flux and the temperature differential between a heated thermocouple and a nearby reference thermocouple inserted into the sapwood. This relationship has been tested in laboratory and field studies with a variety of species; however, these tests have been conducted almost exclusively with “newly installed” sensors. Increasingly, sensors are used for many months if not years. After a period of several months, although a sensor may still be functioning electronically, its ability to accurately represent flow rates in a tree may be impaired due to growth, wounding, or other changes in the flow path of water in the xylem. This study sought to determine whether the relationship between sensor output and sap flux density (S , sap flux per unit cross-sectional area of sapwood) was consistent over periods of more than one year. We installed 23 sensors in 15-year-old Douglas-fir and red alder (one sensor per tree) in the western Cascades of Oregon and measured daily average “apparent” S from late April through early July of both 2001 and 2002. We assumed that the measurements from the first year represented “truth”, and that the response of S to vapor pressure deficit (δ) should be consistent from one year to the next given the

same soil moisture conditions. We attributed differences from this assumption to “sensor decline”. During the study period, soil moisture, as measured to 90 cm using time-domain reflectometry, did not differ on similar calendar dates from 2001 to 2002, yet the slope of S vs. δ decreased significantly ($p < 0.01$) in the second year. Apparent S averaged $540 \text{ kg m}^{-2} \text{ d}^{-1}$ less in 2002 than 2001 in Douglas-fir and $455 \text{ kg m}^{-2} \text{ d}^{-1}$ less in red alder, which amounts to a 45% and 30% reduction in flow, respectively. These differences could not be explained by variations in δ . We developed a correction for long-term sensor performance to improve estimates of S from sensors that had been in trees for more than one year. The species differences in sensor degradation over time provide insight into underlying causal mechanisms.

Introduction

The thermal dissipation method developed by Granier (1987) is perhaps the most common method used for measuring sap flow in large woody plants. Between 1996 and 2003, 210 published papers involving sap flow measurements cited Granier (Web of Science search May 2003). Most of these studies lasted for less than a single growing season (e.g. Cienciala et al. 1999; Vertessy et al. 2001) or sensors were reinstalled for additional growing seasons (e.g. Cienciala et al. 1998; Moren et al. 2000). However, many other studies maintained sensors for two or more growing seasons (Hogg et al. 1997; Irvine et al. 2002; Lundblad and

Lindroth 2002; Phillips and Oren 2001). Certainly, longer-term experiments are useful in understanding how extrinsic factors influence sap flux density (S , sap flux per unit cross-sectional area of sapwood) (Lamb and Muller 2002), and by using the same set of sensors over multiple seasons, the integrity of the experimental design is enhanced and time and money are saved. But especially given that these sensors rely on an empirically-derived relationship, it is important to determine whether these sap flow sensors can be considered dependable over more than one growing season.

In this paper, we use the term “long-term sensor performance” or “sensor degradation” to represent possible changes in the relationship between the true velocity of water flow and the apparent velocity as measured by sensors over long time periods. We note, however, that this definition does not imply that something has gone awry with the sensor itself. Instead, impairment of long-term sensor performance is most likely associated with changes in the wood that immediately surrounds the sensors such that the robustness of the *interpretation* of measurements degrades. The purpose of this study was to determine whether there is evidence for sensor degradation in sensors installed over a 17-month period in young red alder and Douglas-fir.

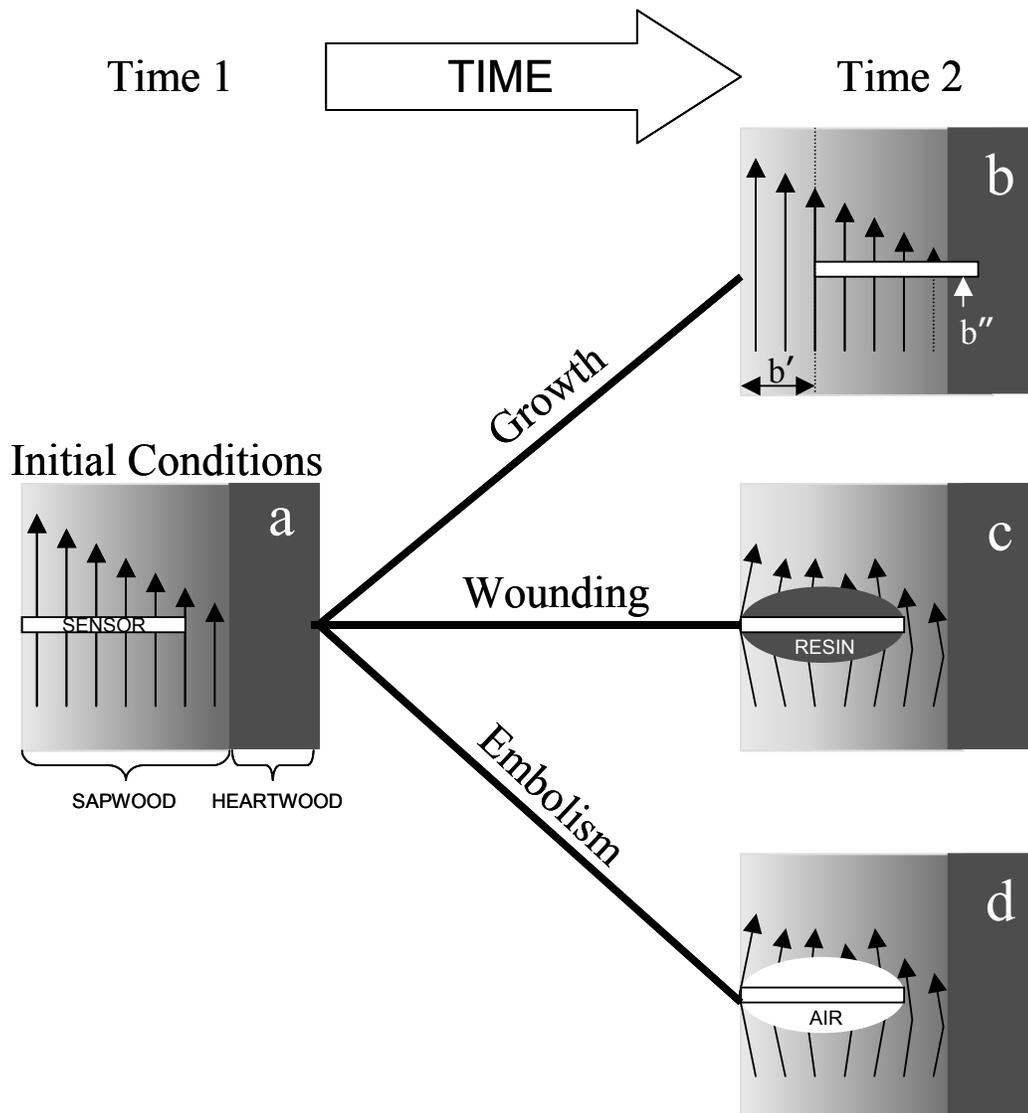
The long-term performance of sapflow sensors is probably related to the type of sensor {e.g. thermal dissipation (Granier 1987), heat pulse (Cohen et al. 1984), or heat balance (Cermak et al. 1973; Kucera et al. 1977)} and specifications (length, diameter, wattage, etc.) of the sensor. In this study we used

20 mm thermal dissipation probes, as designed by Granier (1987) and replicated by Phillips et al. (1997).

Thermal dissipation sap flow sensors detect a temperature differential between two thermocouples, which are placed about 10 cm apart in the active xylem of wood. The upper sensor is supplied a constant current of 0.1 amps, and the lower sensor measures the “background” temperature of the wood. The temperature difference between the two sensors is at a maximum when water is not moving and decreases as sap flow increases, carrying heat away from the sensor. Operationally, sap flux velocity is inferred from an empirically-derived relationship between the temperature differential and the velocity of water flow through the wood (Granier 1985). Sap flux density (S) is the sap flux velocity divided by the cross-sectional sapwood area.

The thermal dissipation method for measuring sapflow has been extensively tested, and the empirical relationship of sensor signal output to actual velocity has been found robust (Clearwater et al. 1999; Granier 1987; Granier et al. 1994; Granier et al. 1996; Granier et al. 1990; Saugier et al. 1997; Smith and Allen 1996; Swanson 1994; Vertessy et al. 1997). However, all of these examinations have involved newly-installed sensors. It is possible that wood growth, wound response, or refilling of embolized tissue could alter the relationship between sap velocity and the temperature differential (Figure 9).

Figure 9 - Example demonstrating potential mechanisms that can cause changes in long-term sensor performance. Under initial conditions (a), a sensor is installed in the outermost layer of sapwood that has a pronounced radial decline in flow with depth (black arrows). After a period of time, growth (b), tissue wounding (c), and/or embolism (d) may lead to sensor degradation. Growth can lead to a sensor becoming deeper in the sapwood (b'), shifted in position relative to the radial flow profile, and/or can lead to a sensor becoming partially in heartwood (b'').



In fast-growing trees, the position of the sensor relative to the cambium (Figure 9b') changes as the tree produces new xylem tissue. Unless the user is aware of and compensates for this change, data are subject to misinterpretation. This is especially likely when there is a pronounced radial pattern in sap flux (Cermak et al. 1992; Granier et al. 1994; Phillips et al. 1996). Small changes in the radial range over which sensors are positioned results in dramatically different measured flows. In an extreme case, sensors that are initially installed near the sapwood-heartwood boundary may end up partially imbedded in heartwood as sapwood is converted to heartwood (Figure 9b''), altering the relationship between the signal from the sensor and true S (Clearwater et al. 1999).

A wound response may lead to filling of xylem elements with air, resin, or other exudates (Kramer and Boyer 1995) or tumor formation (Taiz and Zeiger 1991). Although the wounding effects caused by heat pulse velocity sensors has been well documented (Barrett et al. 1995; Swanson and Whitfield 1981), the extent to which thermal dissipation sensors, a relatively less invasive technique, cause wounding or are affected by wounding is unknown, especially over long periods. Because the installation of sap flow sensors inevitably severs tracheids and/or vessels, xylem anatomy may be altered in the immediate area surrounding the sensor to the extent that water flow is increasingly diverted or restricted over time (Figure 9c). For example, Granier et al. (1994) attributed a reduction in S to the mechanical damage of vessels when the bark was removed. Wood density is

related to S (Barbour and Whitehead 2003), which may change as a result of tissue injury. This wound response could be species-specific depending on properties of wood anatomy.

During the winter, freeze-thaw events cause embolism of xylem that is typically refilled in the trunk of most softwood and diffuse-porous species (Cochard et al. 2001; Wang et al. 1992). In ring-porous species, winter embolism is not repaired and results in severe reductions in flow rates in older tissues (Cochard and Tyree 1990; Granier et al. 1994; Wang et al. 1992). Additionally, drought promotes cavitation (Grace 1993). It is possible that xylem in close proximity to sap flow sensors has an impaired ability to repair cavitated or embolized tissue due to the disruption of cell structure (Taiz and Zeiger 1991; Figure 9d). It follows that this would reduce the exchange of heat between water in the xylem stream and the thermocouples of the sap flow sensor, leading to an apparent decline in measured flow rates in sensors left in trees after freezing or drought. Because the sensitivity to cavitation and the ability to recover varies greatly among species and climates (Grace 1993), the relative impact on the sap flow measurement over time should be species- and climate-dependent.

As part of a larger study, we measured S of young Douglas-fir and red alder over a 17 month period. We used measurements from late April through early July of both 2001 and 2002 to determine whether there was evidence for a change in the relationship between the sensor signal and sapflow, and if so, to contrast long-term sensor performance in a moderately fast-growing softwood

with a faster-growing hardwood species. The xylem anatomy of these species is quite different (ex. no vessels in Douglas-fir). Red alder is more vulnerable to drought cavitation (Bond and Kavanagh 1999) and also more likely to have winter frost embolism (Sperry et al. 1994). Sap flow rates in alder are significantly faster than in Douglas-fir (Chapter 2), and the optimum soil and atmospheric water conditions for maximum transpiration differ in the two species (Bond and Kavanagh 1999; Minore 1979).

The specific objectives of this study were to a) examine the integrity of sensor performance in the two species over a 17-month period, b) compare and contrast the magnitude and pattern of long-term sensor performance between Douglas-fir and red alder, and c) develop a method to correct for the observed change in the relationship between sensor signal and sapflow, if any. We also attempted to infer potential mechanisms from the observed trends.

Methods

We used 20-mm constant-heat sap flow sensors (Granier 1987) that were produced in our laboratory according to the method of Phillips et al. (1997). Sensors were installed in the outer 20 mm of sapwood in eleven Douglas-fir and twelve red alder trees (one sensor per tree), and measurements were made continuously for 17 months beginning in late April 2001 and ending in early July 2002. This study focused on the 65-day overlapping time period between late April until early July (days 117-182) of both 2001 and 2002. We assumed that

the measurements from the first year represented “truth”, and that response of S to vapor pressure deficit (δ) should be consistent from one year to the next given the same soil moisture conditions.

Soil moisture (as volumetric water content) was monitored periodically (two to four week intervals) in June through August of each year at 32 locations using time domain reflectometry (Model 1502C, Tektronix, Inc., Beaverton, OR, Gray and Spies 1995). The sampling positions for soil moisture were located within 20 meters of the sap flow trees; 45 and 90 cm rods were installed vertically at each location. Vapor pressure deficit (δ) was monitored hourly at a climatic station located 2.6 – 4.3 km away using a HMP 35C temperature/humidity sensor (Vaisala, Helsinki, Finland) and averaged over daily time intervals. Although the true δ around experimental trees may have differed from that of the climate station, we assumed that the relationship between δ measured at the climate station and local δ in the two measurement years was constant.

To compare S in the two years, a multiple linear regression approach was used to estimate long-term sensor performance after accounting for the effect of environmental conditions and tree size. To determine whether apparent S differed in year two compared with year one, after accounting for environmental differences, we used a first order change model to quantify “difference in S ”. The environmental drivers were also expressed as differences (Table 2) such that:

If: $S_{x,1}$ = sap flow on day x in year 2001
 $S_{x,2}$ = sap flow on day x in year 2002

$E_{x,1}$ = environmental driver(s) on day x in year 2001
 $E_{x,2}$ = environmental driver(s) on day x in year 2002

$$\text{Then: } \Delta S = S_{x,2} - S_{x,1} = B_0 + B_1 (E_{x,2} - E_{x,1}) \quad (\text{Equation 1})$$

Potential multiple regression model parameters are described in Table 2. The best model was found using a forward selection process from the following models.

1. $\Delta S \sim f \{ \Delta \ln(\delta) \}$
2. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor} \}$
3. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor} \}$
4. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age} \}$
5. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta \}$
6. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta, \Delta \theta \times \text{sensor} \}$
7. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta, \Delta \theta \times \text{sensor}, \text{height} \}$
8. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta, \Delta \theta \times \text{sensor}, \text{SBA} \}$

*See table 2 for a description of variables

Because additional variables will always improve the model performance, and in efforts to keep the final model relatively simple, additional parameters were only added if they improved the model by more than 5%, as measured by the coefficient of determination (Rawlings et al. 1989).

Table 2 - Description of potential variables and their symbols for use in the forward selection of a suitable multiple linear regression model.

Symbol	Description
ΔT	**The difference between sap flux density ($\text{kg m}^{-2} \text{ day}^{-1}$) on day x of 2002 and day x of 2001
sensor	Categorical variable to allow for unique estimates by sensor
species	Categorical variable to allow for unique estimates by species
$\Delta \ln(\delta)$	(mbar) that has been natural log transformed for linearity on day x of 2002 and day x of 2001
$\Delta \theta$	Continuous variable of the difference between volumetric soil moisture (%) on day x of 2002 and day x of 2001
height	Continuous variable of tree heights (m) for each sensor/tree
SBA	sensor/tree
sensor age	Continuous variable of accumulated time (days) since installation

**Dependent/response variable

Sensor degradation could either be punctuated in time (e.g. a step function or threshold effect) or change incrementally with time (e.g. an additive or growth function). To test for an incremental temporal pattern of degradation, a term “sensor age”, which could vary between 0 and 65 days, was included in the multiple regression models. If this term proved to be significant in the model, long-term sensor performance “degraded” linearly on a day-by-day basis as a function of the number of days that had elapsed since the sensor was first installed.

A multiple linear regression model that included a species term was utilized to compare and contrast long-term sensor performance between Douglas-fir and red alder. If this term proved to be significant in the model, sensor degradation differs in the two species, and separate models for each species would

be necessary due to a violation of statistical assumptions (i.e. homoscedasticity, Berry and Feldman 1985). A potential benefit of this approach is that individual models for each species, if different, could provide insights into the mechanisms causing sensor degradation (Figure 9) and evidence of species-specificity. For example, if one species has grown more in diameter, all else being equal, sensor degradation should be more pronounced in that species.

To estimate the *average* magnitude of sensor degradation for all the sensors combined, we used a random slopes linear mixed effects model (Rawlings et al. 1989 p. 579). Mixed effects models are useful in analyzing grouped data that include both random and fixed components. Our model was:

$$\Delta S_{ij} = B_0 + B_{1j} * \Delta \ln(\delta) + \varepsilon_{ij} \quad (\text{Equation 2})$$

where: $B_{1j} \sim N(\gamma_0, \sigma^2_1)$; $\varepsilon_{ij} \sim N(0, \sigma^2_\varepsilon)$; $COV(B_1, \varepsilon) = 0$;
 ΔS_{ij} = change in S between day i of 2002 to day i of 2001 ($i = 117, 118, 119 \dots 182$) of sensor j ($j = 1, 2, 3 \dots 11$ if Douglas-fir; $j = 1, 2, 3 \dots 12$ if red alder);
 B_0 = average change in S when $\Delta \ln(\delta)$ is zero, and so represents sensor degradation between 2001 and 2002;
 B_{1j} = additional discrepancy between S on the same day of 2001 and 2002 due to the difference in vapor pressure ($\Delta \ln(\delta)$) on those days; B_{1j} is assumed to be normally distributed with a mean γ_0 and variance σ^2_1 ;
 ε_{ij} is assumed to be normally distributed with a mean of zero and a variance σ^2_ε ; and
The covariance (COV) of B_{1j} and ε_{ij} is assumed to be zero.

As in the multiple regression models (above), the response variable was the “difference in S ”. As a result, the intercept term in the mixed effects model represents the average sensor degradation after one year (i.e. the average difference in S for all measurement dates between 2001 and 2002 when all other variables are held constant).

The final models were used to predict a corrected S during the period between April 27 and July 1 of the second year, 2002 after accounting for differences in long-term sensor performance. In order to do this, the intercept term (representing individual sensor degradation, Equation 1) was subtracted from the second-year estimate of S .

Results

Visually, for both species, daily total apparent S was higher in 2001 than 2002 during the same period, 1187 and 612 kg m⁻² d⁻¹, respectively, for Douglas-fir (Figure 10a and b) and 1517 and 1007 kg m⁻² d⁻¹, respectively, for red alder (Figure 10c and d). As expected (Chapter 2), S was generally higher in red alder than Douglas-fir. Average S was relatively constant over time throughout the study period for both years (see running mean, Figure 10a, b, and c), except in red alder in the year 2002 where it increased slightly (see running mean, Figure 10d).

Comparing soil moisture over days 140 - 250 in 2001 and 2002, average soil moisture to a depth of 45 cm (Figure 11) and 90 cm (data not shown) did not differ significantly (Figure 11). Thus, the reduced apparent S during the second year is not likely due to less soil water availability.

Figure 10 - Daily sap flux density (S) for 11 sensors in Douglas-fir in a) 2001 and b) 2002 and for 12 sensors in red alder in c) 2001 and d) 2002. Seven-day running means are represented by grey lines.

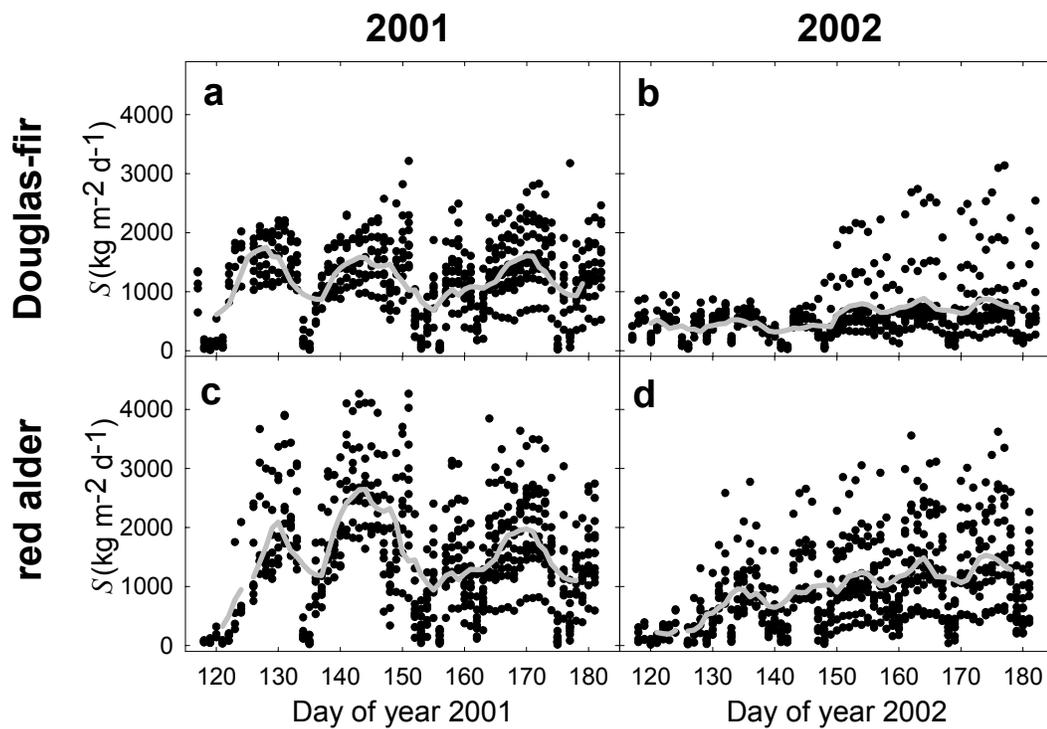
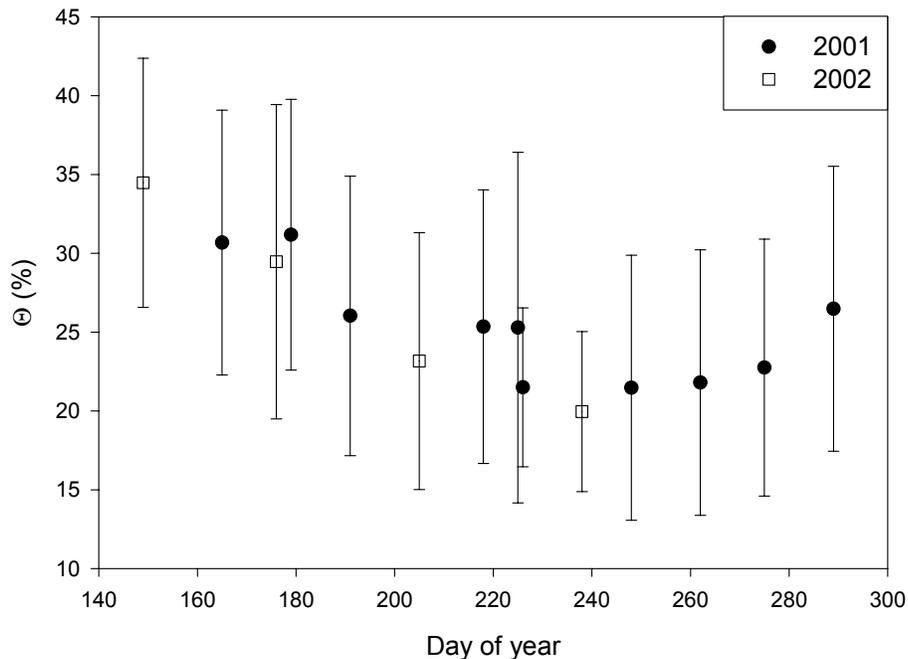


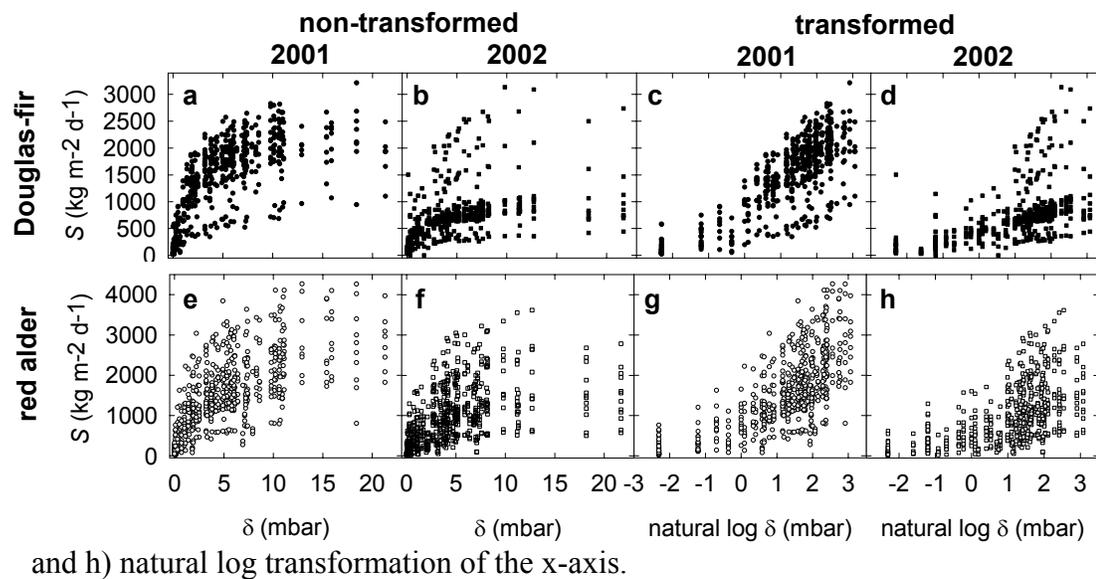
Figure 11 - Volumetric soil water content (Θ) to a depth of 45 cm at 32 locations throughout the study area during the year 2001 (solid circles) and 2002 (open squares). Error bars denote one standard deviation.



The slope of the relationship between apparent S and δ was significantly less in the second year (Figure 12). Maximum S was much lower the second year than the first year in 10 out of 11 Douglas-fir (Figure 12a and b) and 11 out of 12 red alder (Figure 12e and f) sensors. We log-transformed δ to normalize and linearize the relationship with S for our statistical analyses. There was substantial variation in slopes among individual sensors in 2001 (Figure 12c and g; Coefficient of variation (cv , %), $cv_{2001} = 33\%$), and even greater variation in 2002 (Figure 12d and h; $cv_{2002} = 60\%$). However, slopes for individual sensors were

generally lower in the second year for Douglas-fir (Figure 12c and d) and red alder (Figure 12g and h).

Figure 12 - The relationship between sap flux density (S) and vapor pressure deficit (δ) for Douglas-fir (solid symbols; $n = 11$ sensors) and red alder (open symbols; $n = 12$ sensors) during the period between April 27th and July 1st of 2001 (circles) and 2002 (squares), before (panels a, b, e, and f) and after (panels c, d, g,



and h) natural log transformation of the x-axis.

Based on these preliminary observations, the forward selection process proceeded with the following models:

1. $\Delta S \sim f \{ \Delta \ln(\delta) \}$ r^2 : DF = 0.57; RA = 0.57
2. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor} \}$ r^2 : DF = 0.77; RA = 0.79
3. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor} \}$ r^2 : **DF = 0.85; RA = 0.84**
4. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age} \}$ r^2 : DF = 0.85; RA = 0.86
5. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta \}$ r^2 : DF = 0.85; RA = 0.86
6. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta, \Delta \theta \times \text{sensor} \}$ r^2 : DF = 0.86; RA = 0.86
7. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta, \Delta \theta \times \text{sensor}, \text{height} \}$ r^2 : DF = 0.86; RA = 0.86
8. $\Delta S \sim f \{ \Delta \ln(\delta), \text{sensor}, \Delta \ln(\delta) \times \text{sensor}, \text{sensor age}, \Delta \theta, \Delta \theta \times \text{sensor}, \text{SBA} \}$ r^2 : DF = 0.87; RA = 0.87

*See table 2 for a description of variables

The third model was selected to be the final (i.e. “best”) model because additional parameters minimally improved the model performance, as measured by the multiple r^2 values. Our criterion was to discard models with additional terms if multiple r^2 increased by less than 5%. The final model took the general form:

$$\Delta S_j = B_{0j} + B_{1j} \times \Delta \ln(\delta) \quad (\text{Equation 3})$$

Unique coefficients were estimated for each of the eleven Douglas-fir and twelve red alder sensors ($j = 1,2,3 \dots 11$ if Douglas-fir; $j = 1,2,3 \dots 12$ if red alder; see Table 3 for coefficient estimates). Apparent S in most sensors declined substantially the second year (negative intercept estimates) at the same level of δ . Only 2 out of the 23 trees, one Douglas-fir and one red alder, had positive intercept estimates, which indicates a slight increase in apparent S from one year to the next at the same level of δ (Table 3), but this increase was marginally or not statistically significant for those trees ($p = 0.06$ and 0.14 , respectively). Because the variance around apparent S was much greater in red alder than Douglas-fir (violates the constant variance assumption for regression, Ramsey and Schafer 1997), separate regressions were run for each species.

The average decline in sensor performance in Douglas-fir was 540 ± 100 $\text{kg m}^{-2} \text{d}^{-1}$ ($p < 0.01$, linear mixed effects). That amounts to a 45% decline in measured S after one year that cannot be accounted for by changes in the primary environmental drivers of transpiration, δ , and θ . The change in apparent S for sensors installed in red alder was somewhat less, declining by 455 ± 152 $\text{kg m}^{-2} \text{d}^{-1}$.

¹ ($p < 0.01$, linear mixed effects), which amounts to a 30% decline in average S after about one year of operation, compared to the expected flow based on the previous year's performance. The variability in long-term sensor performance among individual sensors was large, and this variability was greater in red alder than in Douglas-fir.

Table 3 - Estimates for intercept (β_0) and slope (β_1) for each sensor corresponding to Equation 2.

Species	Sensor	β_0	β_1
fir	1	-916	270
fir	2	-665	257
fir	3	-804	152
fir	4	-954	344
fir	5	-736	395
fir	6	-348	219
fir	7	-322	162
fir	8	-116	593
fir	9	77	363
fir	10	-510	203
fir	11	-646	245
alder	12	-314	262
alder	13	-156	502
alder	14	-451	354
alder	15	-92	465
alder	16	-164	164
alder	17	-157	295
alder	18	-239	363
alder	19	106	651
alder	20	-1613	561
alder	21	-754	281
alder	22	-250	505
alder	23	-1352	438

There was a significant difference between species in average long-term sensor performance ($p < 0.01$, multiple regression). Also the pattern of decline (either a threshold or incremental response) appears to be different for the two species. To test for the pattern of decline, the fourth model included a term “sensor age” that allowed the long-term sensor performance to change

incrementally by day depending on the number of days that had elapsed since installation. The model suggested an incremental pattern in red alder ($p < 0.01$, from multiple regression). For every additional day after the sensors were in place a full year (sensor age = 1 year + 1 day), apparent S declined by an additional $9 \text{ kg m}^{-2} \text{ d}^{-1}$ in red alder. For example, when a sensor in red alder had been installed for a year, S declined by about $450 \text{ kg m}^{-2} \text{ d}^{-1}$. After a year and a week, the estimated difference between S measured in 2001 and S measured in 2002 was $450 + 9 \times 7$ or $513 \text{ kg m}^{-2} \text{ d}^{-1}$. In contrast, we found no evidence of an incremental change by day in Douglas-fir ($p = 0.12$), suggesting a threshold pattern of sensor degradation. All of the change in sensor performance in Douglas-fir occurred prior to April 27th of the second year.

After modeling the change in S between the two years, we developed correction factors for sensor degradation in the second year of measurements. First, the estimates of intercept and slope for simple regression models applied to individual sensors (Table 3) were used to predict S for the period between April 27 and July 1 of 2002 for each tree based on δ (Equation 3). There was good agreement between measured and modeled data in 2002 (Figure 13, $r^2 = 0.74$). Again, our underlying assumption was that the response of S to environmental variables (θ and δ) should be the same in 2002 as it was in 2001, in which case the intercept estimate becomes an estimate of sensor degradation. Secondly, the modeled data in 2002 was corrected for sensor degradation by subtracting the

intercept. Upon overlaying the corrected data for 2002 with the measured data during the same time period in 2001, there was also good agreement in terms of their response to δ (Figure 14).

Figure 13 - The relationship between measured and modeled sap flux density (S) for the period between April 27th and July 1st 2002 for all 23 sensors. Heavy solid line denotes 1:1 relationship. Thin line denotes linear regression.

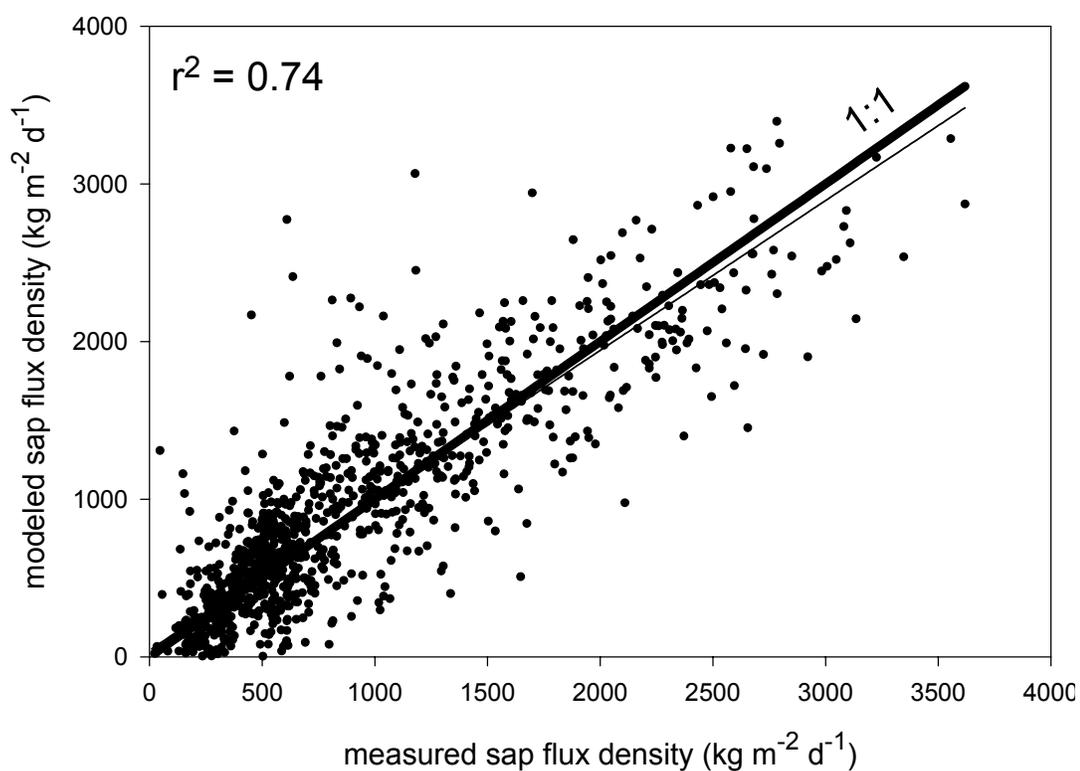
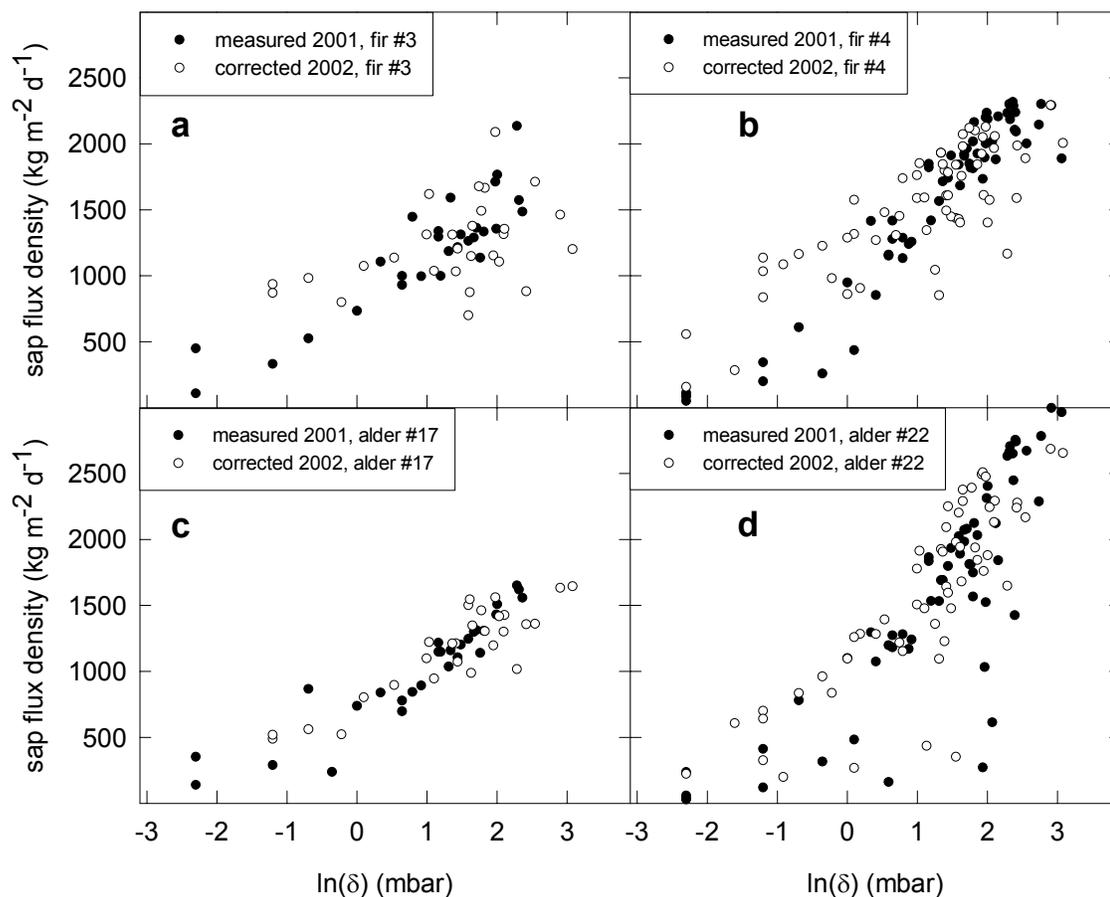


Figure 14 - A comparison of the measured relationship between sap flux density (S) and log transformed vapor pressure deficit (δ) in 2001 and the modeled relationship for 2002 in a random sampling of four of the 23 trees: a) Douglas-fir #3, b) Douglas-fir #4, c) red alder #17, and d) red alder #22.



Discussion

Thermal dissipation sap flow sensors are increasingly popular and utilized for a wide assortment of research applications that potentially go beyond the capabilities of the technique. It is important to understand and quantify the temporal limitations of sensor installations. Here we present a framework for testing for and correcting for sensor degradation based on two environmental

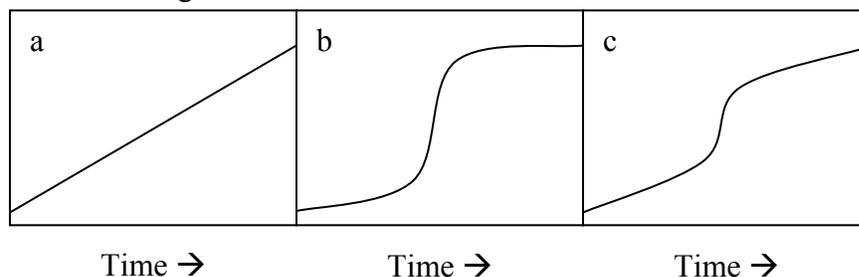
drivers for transpiration: the soil water supply (θ) and atmospheric vapor pressure deficit (δ).

Because soil water supply was comparable on the same dates in 2001 and 2002, the difference in S during the same period of successive years was related most strongly to the difference in δ , and was unique for each sensor. After accounting for differences due to environmental conditions, the apparent S had declined by 45% in 15-yr-old Douglas-fir and 30% in 15-yr-old red alder after one year of use, compared to the expected flow based on the previous year's measurements. We found that the magnitude and pattern of the decline was different in Douglas-fir than red alder.

Insights about potential causes of sensor degradation (i.e. growth, tissue injury, or xylem embolism) can be gained from this study. Incremental change (Figure 15a) in sensor performance supports either a growth- or wounding-related hypothesis; threshold change (Figure 15b) supports an embolism-related hypothesis; or, there could be a combination of gradual and threshold change (Figure 15c) from which multiple causes in sensor degradation could be inferred. Because all of the change in sensor performance for Douglas-fir occurred prior to April of 2002, we infer a threshold pattern (Figure 15b). It is possible that growth during the study period was too slow and/or radial patterns were not steep enough to produce a significant change in sensor performance during the study period, but that late summer drought-induced cavitation and/or winter embolism may explain

the observed pattern. Because most of the change in sensor performance for red alder occurred prior to April of 2002 and a small incremental change was detected between April and July 2002, we infer a combination incrementing/threshold pattern (Figure 15c). It is possible that late summer drought-induced cavitation and/or winter embolism may explain the threshold portion of the pattern and radial growth and/or a gradual wound response may explain the incremental portion of the pattern.

Figure 15 - Hypothesis a: sensor degradation occurs gradually (incrementally) over time. Hypothesis b: sensor degradation occurs mostly over a short time period (threshold). Hypothesis c: a combination of incremental and threshold changes are occurring.



It is possible that red alder grew much faster than Douglas-fir during this period and that gradual changes in ΔS in Douglas-fir were too small to detect. However, our field observations indicate that growth should be a factor in both species. Many trees of both species had grown substantially over the seventeen-month period such that the sensors were often difficult or impossible to remove from the tree.

Radial variation in flow occurs in both of these species (Chapter 2) and thus the relative flow rate changes substantially with depth, but red alder has a steeper radial decline in sap flux with depth wherein small amounts of new growth could lead to erroneous interpretations of the measurements. This may explain why we found a measurable “sensor age” effect in red alder.

It is unlikely that many (if any) of the sensors were in heartwood during the second year (Figure 9b’). Average sapwood depth at sensor height was 127 mm in red alder and 35 mm in Douglas-fir, compared to the 20 mm depth of the sap flow sensors at initial installation (Figure 9a). However, five of the Douglas-fir sensors were in trees with sapwood depths less than 25 mm (measured at the same height on the tree as the sensor).

The more pronounced sensor degradation in Douglas-fir compared to red alder might be indicative of species-specific wound responses. However, previous studies do not support this. Oliveras and Llorens (2001) placed new sensors next to sensors that had been in place for three years and concluded that azimuthal variation is likely greater than any potential tissue injury-induced variation.

This paper calls to attention the need for caution when using constant heat sap flow sensors for more than one growing season; however, we demonstrated a means for testing for and correcting for potential sensor degradation. Although further investigation is needed to determine the precise mechanism(s) that lead to

long-term sensor degradation, our results provide guidance when considering time-consuming and expensive reinstallations after one year of operation.

Acknowledgements

Meteorological data sets were provided by the Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon. Significant funding for these data was provided by the National Science Foundation Long-Term Ecological Research program (NSF Grant numbers BSR-90-11663 and DEB-96-32921). Substantial statistical advice was provided by Manuela Huso.

DOES DIVERSITY OF OVERSTORY TREES AFFECT TRANSPIRATION?

Abstract

One of the greatest differences between natural and managed forests lies in overstory species diversity. Accumulating evidence points to the fact that diversity enhances ecosystem resilience and animal habitat, and recently the goals of forest management have been shifting to encourage greater plant species diversity. However, much remains to be learned about relationships between species diversity and ecosystem functions, especially in woody perennials. Do these relationships change depending on site conditions and with varying species proportions? What are the impacts of species composition on resource utilization and the efficiency of resource use relative to growth? Emerging hypotheses such as “complementary resource use” predict that combinations of species should be able to access more resources from a site, in part due to different occupation of niches through space and time, and thus the total site productivity should increase. If this is generally true, utilization of light, water and nutrient resources should increase with increasing diversity. The primary question in this study was: Do mixed-species forests transpire more or less water than the average of similar-density monocultures of the same species? Of interest were two species expected to utilize water differently – a conifer (Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco) that is known to be relatively tolerant of dry soils and to transpire throughout the year, and a deciduous broadleaf (red alder, *Alnus rubra* Bong.) that

is known to use more water per unit sapwood, and have deeper roots at the sapling stage, than Douglas-fir. This study took place at the H.J. Andrews Forest in the Western Cascades of Oregon. Transpiration was measured using constant heat sap flow sensors in 15-year-old red alder and Douglas-fir planted at 1100 trees per hectare as either monocultures or mixed 50:50 plantings in 20 x 20 meter plots. I found no evidence to support the complementary resource use hypothesis; transpiration and productivity in mixed plots was either less than or not different from the average of the monocultures, depending on plot biomass and site-level nutrient status. Plot-level transpiration efficiency of carbon gain (i.e. seasonal water use efficiency) did not vary with diversity. Also tested was if nitrogen-fixing alder supplied nutrients to co-occurring Douglas-fir and no evidence was found that leaf nitrogen concentration or N-isotopic ratio increased in Douglas-fir needles when trees were grown in mixtures with red alder compared to Douglas-fir monocultures. These findings provide forest managers in the Pacific Northwest with new evidence that competition between these two species, when co-occurring, can potentially lead to decreased yields, although the amount of water in streams draining these systems may increase.

Introduction

Biological diversity is a fundamental descriptor of ecosystems. Yet much remains to be learned about the relationship between species diversity and ecosystem function. The bulk of recent work, primarily in small plots with

herbaceous plants, is focused on how diversity affects productivity. The focus of this study is how diversity affects resources and resource utilization, both intimately tied to productivity. The species of interest were trees rather than herbaceous plants, which presents challenges for controlled experiments. Although diversity can be defined in multiple ways, in this study, diversity is referred to as a measure of overstory species richness (the number of overstory species present) and species evenness (the relative proportions of individual species).

Diversity, productivity, and resource use

As early as 1858, Darwin and Wallace (1858) suggested that diversity could affect ecosystem function, and that a diverse mixture of plants should be more productive on an ecosystem scale than monoculture of the individual species. In recent studies, increased diversity was associated with increases in productivity (Johnson et al. 1996), although in some cases productivity decreased (Berntsen 1961; Rothe and Binkley 2001; Shainsky and Radosevich 1992) or no effect was found (Hooper 1998; Wardle et al. 2000) (Figure 16a).

Darwin and Wallace's hypothesis predicts that intact, diverse communities function more efficiently (in terms of resource capture) and are more stable than communities that have lost species, due to a greater variety of positive, complementary interactions (Purvis and Hector 2000). A growing consensus among researchers is mounting that more diverse systems are more stable (Johnson et al. 1996; McCann 2000) in terms of resisting invasion (Tilman 1997),

withstanding drought (Tilman and Downing 1994), and tempering biomass fluctuations in varying environmental conditions (Tilman 1996). Stability is likely due to increased functional group representation (ex. nitrogen-fixing vs. non-nitrogen-fixing) rather than species richness itself (Wardle et al. 2000). In this study, ecosystem stability is assessed by evaluating the response of dominant plant species, each belonging to a different functional group, to drought stress.

Wet winters and dry summers characterize the climate of the Pacific Northwest such that the growing season coincides with a period of low soil moisture and high atmospheric demand for water vapor (i.e. vapor pressure deficit or VPD). Although the response of individual tree species to drought stress is well documented (Kozlowski et al. 1991), little is known about how diversity in forest ecosystems may ameliorate or exacerbate drought stress. In one example, Köstner (2001) observed that mixed species stands of Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) transpired more than monoculture stands of spruce per unit leaf area index at the same level of VPD, providing evidence of drought stress amelioration.

Using replacement series plots to study forest transpiration

In the Pacific Northwest, impacts of forest management on water resources are becoming increasingly important. Under current management practices, managed stands in the Pacific Northwest are typically grown as monocultures. Hardwoods are removed. This study seeks to understand the impact

of monoculture stands on water resources (and by inference, stream flow) compared to mixed hardwood/conifer overstory.

Much attention has been given to the topic of tree species diversity (especially in tropical forests), but there are limitations to studying its affect on ecosystem processes, simply because trees are slow growing, and difficult to study under controlled conditions. However, progress has been made by weed scientists, who have been working for a long time to determine how mixtures of weedy plants with crop plants affect productivity (Radosevich et al. 1997). Weed ecologists have developed several experimental approaches to overcome some of these study design challenges. In this study, one of these approaches was utilized, a replacement plot study design (Radosevich 1987). Such substitutive experiments abate criticisms of field plot competition studies that use an additive approach, by holding plant density constant while varying species proportions (Radosevich 1987).

Following the paradigm developed by Radosevich (Radosevich 1987), there are three alternative hypotheses for the effect of diversity on annual total productivity (Figure 16a). First, if facilitation dominates, then productivity of mixtures may be greater than the average of monocultures. If competition dominates, then productivity of mixtures may be less than the average of monocultures. Finally, if there is no interaction between these two species, productivity of mixtures is simply equal to the average of monocultures.

In this study, this same paradigm is expanded upon to investigate the effects of diversity on water resources, namely transpiration. Again, there are three alternative hypotheses (Figure 16b). Theory predicts that the niche interactions drive differences in resource use in species mixtures relative to monocultures. Examples of plant niches are the occupancy of three-dimensional space, either intercepting more light aboveground (Naeem et al. 1994), or accessing more water and nutrients belowground. There are also temporal niches such as length of the growing season or timing of flowering. First, if more resources are used, as predicted by niche theory, then transpiration of mixtures may be greater than the average of monocultures. If more resources are conserved, then transpiration of mixtures may be less than the average of monocultures. Finally, if niches do not overlap, there may be no interaction between these two species that causes transpiration in mixtures to be a simple average of transpiration in the individual monocultures.

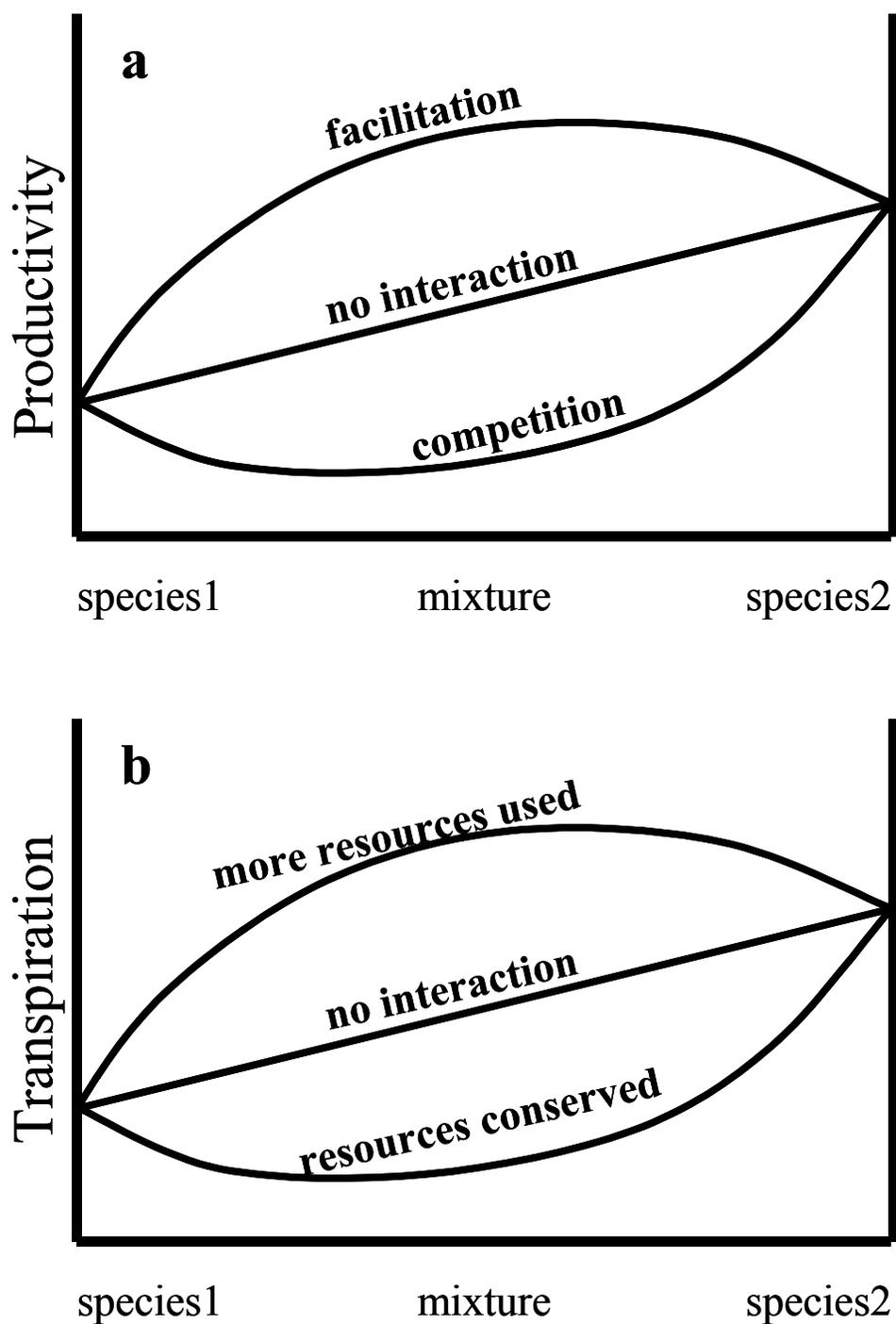
I took advantage of an existing experiment that was designed to investigate how differing proportions of two species affect productivity. My study complements the overall study by investigating how mixtures of two species affect transpiration relative to monocultures. The two species were Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red alder (*Alnus rubra* Bong.), each belonging to a different functional group, a conifer and a nitrogen-fixing (N-fixing) deciduous broadleaf. There are multiple reasons to expect that these species would utilize water differently. Douglas-fir is more tolerant of dry soils

(Minore 1979) and this, plus its evergreen habit, means it has the potential to transpire through a much greater portion of the year than red alder. Red alder is known to use more water per unit sapwood (see Chapter 1) and has deeper roots than Douglas-fir at the sapling stage (Hibbs et al. 1994). Red alder is also more productive than Douglas-fir during early stages of stand development, often out-competing Douglas-fir for light (Chan et al. 2003). If red alder is more productive than Douglas-fir, at least during early stand development (Hibbs et al. 1994), then does it follow that red alder is more competitive for water than Douglas-fir? If so, mixed plots of both species may be expected to have greater summer transpiration or a steeper decline in soil moisture during the summer drought than Douglas-fir monocultures, but would differences persist on an annual scale?

Resource Use Efficiency

Also of interest is whether species combinations affected resource use efficiency. The amount of water transpired per unit carbon produced is referred to as water use efficiency (WUE). As a type of resource efficiency (Binkley et al. Draft), WUE is an important measure of the resources needed to grow. Different combinations of species may alter WUE in tree stands.

Figure 16 – Three alternative outcomes for a) productivity and b) transpiration in two-species mixtures relative to monocultures.



Emerging hypotheses such as “complementary resource use” (Ewel 1986) predict that combinations of species should be able to access more resources from a site, in part due to different occupation of niches through space and time, and thus the total site productivity should increase. If the complementary resource use hypothesis holds true (notable exceptions: Grime 1997; Hooper and Vitousek 1997; Tilman et al. 1997; Wardle et al. 1997), with increasing loss of global biodiversity, the services that ecosystems provide will likely be altered or impaired (Ehrlich and Wilson 1991; Naeem et al. 1994). Despite the increasing interest in whether complementary resource use is driving differences in productivity (Hooper 1998; Naeem et al. 1994; Shainsky and Radosевич 1992; Tilman 1999), many studies focus on light (Chan et al. 2003; Naeem et al. 1994), nutrient (Hooper 1998), and soil water (Chan et al. 2003) *availability* rather than light, nutrient or water *utilization* (notable exceptions: Binkley et al. Draft; Stratton et al. 2000; Tilman et al. 1996), (Stape et al. 2003).

In this study the complementary resource use hypothesis is tested, along with three alternative hypotheses, for the effects of diversity on water use efficiency (Figure 17). By definition, the complementary resource use hypothesis predicts that if productivity increases with diversity, so should transpiration (Figure 17a). To account for the possibility of reduced resource use with diversity, I introduce the term “compensatory resource use” (Figure 17d). In either scenario, WUE should be the same in species mixtures as in monocultures, if the change in productivity and transpiration are proportionate. If changes in productivity and

transpiration are opposing or disproportionate, then WUE in mixtures could be either greater (Figure 17b) or less (Figure 17c) than in monocultures.

Water use and WUE by red alder and Douglas-fir in mixtures may also be impacted by the fact that red alder is a nitrogen fixer. In this study I investigate nutrient status as a potential covariant with diversity that may explain differences in productivity and transpiration.

Study Objectives

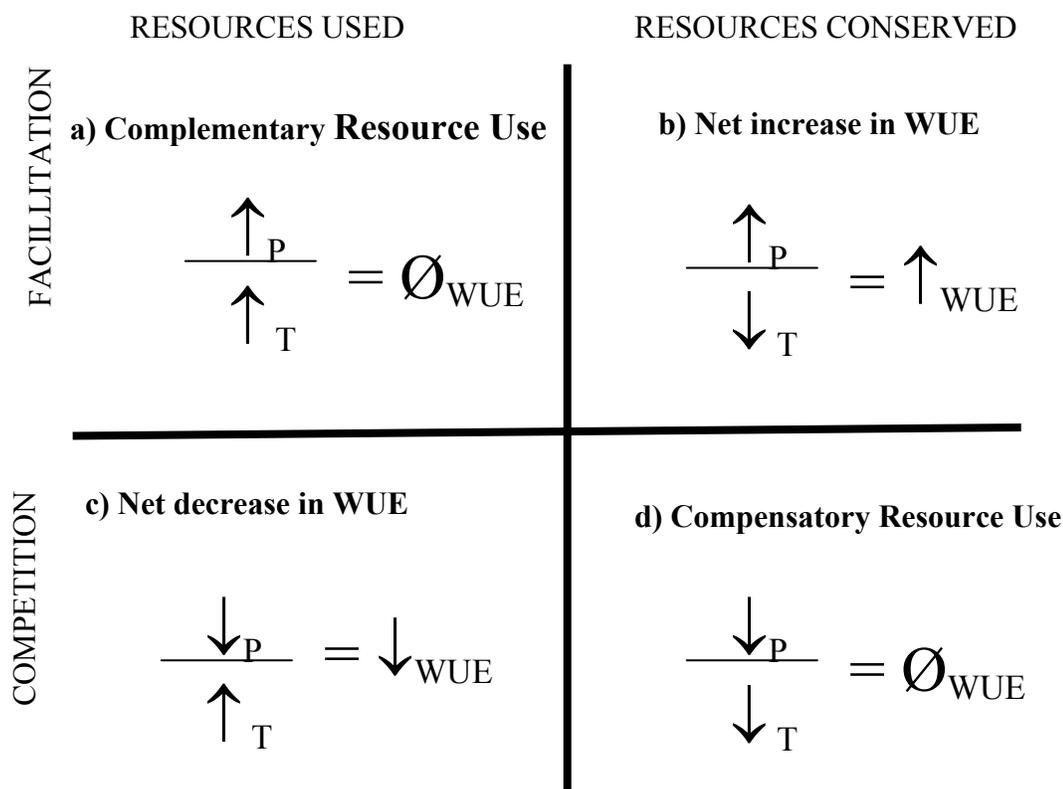
The objectives of this study were (1) to compare water use by Douglas-fir and red alder in mixtures and monocultures in terms of a) temporal and spatial partitioning of resource niches and b) their response to drought stress; (2) to investigate the role of diversity in a two-species mixture on a) biomass and net primary productivity, b) transpiration, and c) water use efficiency; and (3) to determine whether the nutrient status of Douglas-fir is enhanced by the co-occurrence of nitrogen-fixing red alder.

As in prior studies (Chapter 2), average water use per unit sapwood is expected to be greater in red alder than Douglas-fir during the summer, but greater in Douglas-fir than red alder during the winter when red alder is leafless. Further, I expected to find additional evidence of temporal niches by contrasting timing of peak water use of these two species. In terms of spatial partitioning of niches, I expected to find evidence that either more water is taken up from the soil profile in mixed plots, or evidence that trees in red alder monocultures uptake water from deeper in the soil profile than trees in Douglas-fir monocultures.

The greatest differences in resource use are expected to occur in conditions of drought stress (i.e. high VPD and/or low soil moisture), or to put it another way, mixed plots transpire more than monoculture plots under extreme conditions. Some evidence suggests that drought stress may be ameliorated in species mixtures relative to monocultures (Kostner 2001).

Based on expectations of niche differentiation and drought stress amelioration, I expected to find evidence of complementary resource use such that both productivity and transpiration are enhanced in mixed species plots on an annual basis.

Figure 17 – The combined effect of diversity on water use efficiency (WUE) when either facilitation or competition alters productivity and resources are either more readily utilized or conserved. Four alternative outcomes are possible: a) complementary resource use, where productivity and transpiration increase with diversity thus lead to no net change in WUE; b) net increase in efficiency, where productivity increases and transpiration decreases; c) net decrease in efficiency, where productivity decreases and transpiration increases; and d) compensatory resource use, where productivity and transpiration decrease with diversity thus lead to no net change in WUE. Complementary and compensatory resource use produces the same outcome in WUE, but demonstrate opposing consequences of diversity.



Methods

Study Area

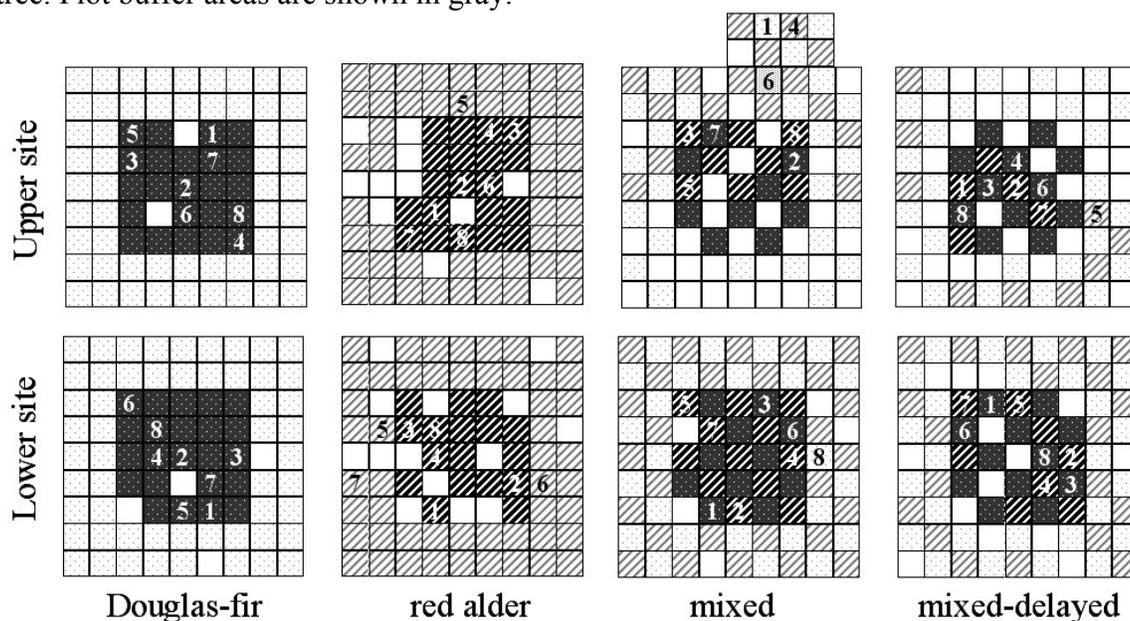
This study took place at the H.J. Andrews Forest in the Western Cascades of Oregon. Managed early seral forests of this region are dominated by Douglas-fir. In the western Cascades, red alder typically regenerates in riparian areas following disturbance. In the coast range, red alder is more common throughout the landscape. Douglas-fir and red alder commonly co-occur, especially in younger stands, having generally similar autecology (Minore 1979). The climate is characterized as maritime with wet winters and dry summers (mean annual rainfall 2300 mm). Mean monthly temperature ranges from about 1 degree C in January to 18 degrees C in July. Soils are classified predominantly as gravelly clay loam.

Replacement Series

The study plots were part of a replacement series experiment initiated in 1986 at three locations in Oregon and Washington, the purpose of which was to study the effects of species mixtures on productivity (Radosevich et al. 1997). A randomized block design was employed with an assortment of treatments at a fixed density with varying proportions of Douglas-fir and red alder. There are two types of mixed-species plots, “mixed” and “mixed-delayed”. In the “mixed” plots, both species were planted in 1986; in the “mixed-delayed” plots, red alder was planted five years later. This study utilized a subset of plots within the replacement series located at the HJ Andrews Forest in the western Cascades of

Oregon. I used Douglas-fir and red alder monoculture plots and 50/50 mixture plots of the two species (Figure 18). There were two replicate sites, separated by 2.3 km, with elevations of 660 and 760 meters, at the “lower” and “upper” site, respectively. The upper site faces west, while the lower site faces north. Therefore I had a total of eight plots, two of each type (Douglas-fir monoculture, red alder monoculture, mixed, and mixed-delayed). In all plots, trees were planted in 3x3 m spacing (1100 tree/ha) in 20x20 m plots. Hence, there was a 5x5 tree interior grid of trees surrounded by a two additional rows of trees as a buffer (Figure 18).

Figure 18 – Plot layout at both sites showing the location of the sap flow trees (numbered 1-8), mortality (open squares), distribution of Douglas-fir (dots) and red alder (diagonal lines) in the four plot types. Each square represents a single tree. Plot buffer areas are shown in gray.



Stand Characteristics

After 15 years, mortality and differential growth has changed the initial proportion of DF and RA in the 50/50 mixture plots. Thus the conditions of the initial experimental design no longer represent the true relative “impact” of the two species. I measured tree height, basal diameter, sapwood depth, and leaf area. Diameters of all trees in the plot interiors were measured at breast height and also at the height of sap flow sensors. In order to scale sapflow measurements from individual sensors to whole trees, I needed to determine sapwood basal area. Sapwood depth in Douglas-fir was measured with visual assessment of a 5-mm increment core. The difference in color is clearly discernable; sapwood appears darker and wetter than heartwood. Because sapwood in red alder cannot be distinguished from heartwood visually, I used a safrinin dye injection method to aid in the determination of sapwood depth (Bamber and Fukazawa 1985; Booker 1984; Kutscha and Sachs 1962). After injecting dye in 7 trees (dominant and subdominant, two replicates each), I found no evidence of heartwood, and thus concluded that the wood of these young alders consisted entirely of sapwood. Leaf area (LAI) was estimated at four random locations dispersed within each plot using a LAI 2000 (Licor Inc., Logan, UT). To avoid the influence of adjacent plots, I used a 90-degree mask on the optic sensor of the LiCor, leaving an open quartile facing the plot centers.

Measurements were repeated monthly for six months on April 5, May 4, June 20, July 23, August 29, and September 10, 2001. Prior to alder leaf

emergence in early spring of 2002 (March 22), LAI measurements were made to compare LAI with and without alder leaves. The March, April, and May measurements were taken during the day under uniform overcast sky conditions and the June, July, August, and September measurement were taken in the evening at dusk under uniform clear sky conditions. Of the five zenith angles recorded, I removed the lowest angle to avoid interference with obstructions. I detected no discernable phenological pattern in LAI, so the six replicate measurements in 2001 (excluding March 2002) were averaged. A variety of other stand characteristics are described in Grotta (2002) and D'Amato (2002).

Sap flow

I selected eight trees per plot for sap flow measurement, four of each species in mixed plots, for a total of 64 trees for the entire experiment (Figure 18, Table 4). Trees were selected based on having a high proportion of live neighbors (up to eight total, see Table 4). I used the thermal dissipation sap flow technique (Granier 1987). Sensors were constructed in our laboratory as described by Phillips et al. (1997). Sap flow sensors (one-per-tree) were installed at a height of 0.5 – 1.0 m, below the height of the lowest live branches. Instantaneous measurements taken at 30-second intervals were averaged every 20 minutes and recorded on a data logger (CR10X, Campbell Scientific, Logan, UT).

Table 4 – Specific information about individual sap flow measurement trees, including plot location and type, the coordinates within the plot (treeID), species, number of live neighbors by species, diameter at breast height (DBH, cm), height (m), total basal area (BA, cm²), and sapwood basal area (SBA, cm²).

site	plot	treeID	sapflowID	species	DF nbors	RA nbors	DBH	height	BA	SBA
upper	mixed	-3,4	1	DF	3	4	13.8	10.6	134.8	114.4
upper	mixed	2,5	2	DF	2	3	22.5	11.5	426.4	274.6
upper	mixed	-1,4	6	DF	2	4	17.5	10.5	283.5	219.9
upper	mixed	1,2	7	DF	1	4	17.1	11.4	283.5	225.4
upper	mixed	1,1	3	RA	5	2	10.4	9.5	83.3	51.9
upper	mixed	-3,5	4	RA	4	3	10.5	10.6	78.5	49.0
upper	mixed	3,1	5	RA	4	2	9.7	10.1	73.9	46.1
upper	mixed	1,5	8	RA	4	2	11.0	9.9	84.9	52.9
upper	mix-delay	3,2	3	DF	4	3	9.3	6.3	91.6	82.5
upper	mix-delay	2,3	4	DF	4	2	12.9	8.9	172.0	141.8
upper	mix-delay	3,4	6	DF	4	2	18.2	11.4	286.5	235.0
upper	mix-delay	4,1	8	DF	5	2	19.1	11.0	301.7	261.0
upper	mix-delay	3,1	1	RA	5	1	4.0	5.5	109.4	68.2
upper	mix-delay	3,3	2	RA	4	2	6.2	4.6	29.2	18.2
upper	mix-delay	4,6	5	RA	3	2	11.2	10.3	95.0	59.2
upper	mix-delay	4,4	7	RA	4	1	6.3	6.7	111.2	69.3
upper	DF	1,4	1	DF	7	0	14.1	9.4	138.9	73.9
upper	DF	3,3	2	DF	7	0	7.6	6.8	55.4	40.2
upper	DF	2,1	3	DF	8	0	17.9	10.9	339.8	264.4
upper	DF	5,5	4	DF	8	0	12.3	8.6	147.4	125.3
upper	DF	1,1	5	DF	8	0	9.9	7.0	81.7	70.4
upper	DF	4,3	6	DF	7	0	12.4	9.3	122.7	100.7
upper	DF	2,4	7	DF	7	0	14.7	10.9	188.7	155.5
upper	DF	4,5	8	DF	8	0	12.4	9.5	126.7	102.9
upper	RA	4,2	1	RA	0	6	18.1	13.2	229.7	143.1
upper	RA	3,3	2	RA	0	7	14.7	12.9	213.8	133.3
upper	RA	1,5	3	RA	0	8	12.2	11.7	98.5	61.4
upper	RA	1,4	4	RA	0	8	16.2	11.9	216.4	134.9
upper	RA	0,3	5	RA	0	8	11.1	10.8	116.9	72.9
upper	RA	3,4	6	RA	0	6	13.5	12.5	122.7	76.5
upper	RA	5,1	7	RA	0	6	9.2	11.3	60.8	37.9
upper	RA	5,3	8	RA	0	6	10.5	11.3	83.3	51.9
lower	mixed	5,2	1	DF	4	3	7.5	3.2	38.5	30.4
lower	mixed	1,4	3	DF	4	4	9.1	7.4	73.9	59.4
lower	mixed	2,5	6	DF	3	4	3.1	2.9	15.2	10.7
lower	mixed	3,6	8	DF	3	4	9.5	5.9	73.9	55.0
lower	mixed	5,3	2	RA	4	4	19.1	15.7	346.4	215.9
lower	mixed	3,5	4	RA	4	4	18.3	15.2	283.5	176.7
lower	mixed	1,1	5	RA	3	4	24.9	14.4	522.8	325.9
lower	mixed	2,2	7	RA	3	4	14.8	13.9	248.8	155.1
lower	mix-delay	1,2	1	DF	3	2	19.0	10.8	366.4	294.1
lower	mix-delay	4,5	3	DF	4	4	13.6	8.2	158.4	140.3
lower	mix-delay	2,1	6	DF	4	3	15.0	8.7	274.6	225.6
lower	mix-delay	3,4	8	DF	4	3	10.8	7.2	88.2	87.5
lower	mix-delay	3,5	2	RA	4	4	12.6	10.7	128.7	80.2
lower	mix-delay	4,4	4	RA	4	3	7.1	7.3	44.2	27.5
lower	mix-delay	1,3	5	RA	4	2	6.1	6.0	41.9	26.1
lower	mix-delay	1,1	7	RA	3	1	8.3	6.6	52.8	32.9
lower	DF	5,4	1	DF	7	0	13.5	8.7	162.9	119.9
lower	DF	3,3	2	DF	7	0	12.5	10.1	143.1	121.1
lower	DF	3,5	3	DF	7	0	16.1	9.5	237.8	209.5
lower	DF	3,2	4	DF	7	0	12.1	9.2	113.1	101.8
lower	DF	5,3	5	DF	7	0	14.5	11.3	196.1	159.7
lower	DF	1,1	6	DF	8	0	15.2	8.9	206.1	173.9
lower	DF	4,4	7	DF	7	0	15.7	10.3	196.1	165.9
lower	DF	2,2	8	DF	8	0	12.5	9.3	147.4	120.1
lower	RA	5,2	1	RA	0	5	20.8	17.7	376.7	234.8
lower	RA	4,5	2	RA	0	5	11.7	14.2	268.8	167.5
lower	RA	2,1	3	RA	0	4	21.5	18.6	373.3	232.6
lower	RA	3,2	4	RA	0	7	10.5	14.4	80.1	49.9
lower	RA	2,0	5	RA	0	4	15.5	15.5	213.8	133.3
lower	RA	4,6	6	RA	0	6	15.6	18.7	260.2	162.2
lower	RA	4,-1	7	RA	0	4	6.3	8.3	29.2	18.2
lower	RA	2,2	8	RA	0	6	6.6	9.5	29.2	18.2

Measurements were scaled from individual sensors to whole-tree average flux per unit sapwood per day using the methods described in Chapter 1. The total flux per tree was divided by the total sapwood area to estimate average flux per unit sapwood area for each tree. These calculations were performed for each 20-minute time step. Total daily fluxes are the summation of the 20-minute observations. Instrumentation began on April 4, 2001 and was completed on June 20, 2001. Measurements continued until July 1, 2002. A correction was made for sap flow after April 27th 2002 due to sensor degradation (Chapter 3).

Atmospheric evaporative demand

Vapor pressure deficit was monitored hourly at a climatic station located 2.6 and 4.3 km away from the upper and lower site, respectively, using a HMP 35C temperature/humidity sensor (Vaisala, Helsinki, Finland) and averaged over daily time intervals. The Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon, provided climate data sets (<http://www.fsl.orst.edu/lter/>).

Soil water availability

Soil moisture was monitored as volumetric water content periodically (two to four week intervals) in June through August of each year at 32 locations (four locations per plot, randomly located within the plot interiors) using time domain reflectometry (Model 1502C, Tektronix, Inc., Beaverton, OR, Gray and Spies 1995); 45 and 90 cm rods were installed vertically at each location.

Predawn leaf water potential (Ψ_p) was measured bimonthly (on 6/13, 6/28, 7/12, 7/26, 8/7, 8/31, 9/6, and 9/21 of 2001) using a pressure chamber (PMS Instruments, Corvallis, OR), with four replicate twig samples per plot (two from each species in mixed plots).

Nutrient status

Sunlit leaves were sampled from the tops of trees (four trees per plot of each species, with three replicates each, pooled for a single sample per tree) in September 2001. They were subsequently oven dried, ground to a fine powder, and analyzed for bulk nitrogen concentration ([N]) and isotopic composition ($\delta^{15}\text{N}$). Soil cores (5 cm diameter) were collected at a depth from 10 to 15 cm at four locations per plot in late July 2002. They were subsequently oven dried, sieved through a 2 mm mesh, ground to a fine powder, and analyzed for bulk nitrogen concentration ([N]) and isotopic composition ($\delta^{15}\text{N}$). Both leaf and soil $\delta^{15}\text{N}$ was analyzed using an elemental analyzer (ESC 4010, Costech Analytical Technologies, Valencia, CA, USA) in line with isotope ratio mass spectrometer (Delta Plus, Finnigan, Bremen, Germany) at the Integrated Stable Isotope Research Facility (ISIRF) at the Environmental Protection Agency in Corvallis, OR. Precision for $\delta^{15}\text{N}$ was assessed using a NIST certified standard, with an average standard deviation of 0.08.

Results

Of the 25 trees planted per plot, between 1 and 7 trees had been lost due to mortality (Table 5). The greatest mortality occurred in the mixed and mixed-delayed plots at the upper replacement series site. Because of mortality and differential growth since 1986, the proportion of the two species as of 2002 was no longer 50/50, and varied substantially. At the upper site, 18 years after the study was initiated, only 19 and 18 out of the 25 trees planted were alive in the mixed and mixed-delayed plots, respectively. Mortality was less severe at the lower site, with 24 and 20 trees alive, respectively. Either on a sapwood area or biomass basis, three of the four mixed plots had shifted towards Douglas-fir dominance, whereas the mixed plot at the lower replacement series was red alder dominated. Leaf area index (LAI) was generally higher at the lower replacement series site and tended to be lower in plots with higher mortality.

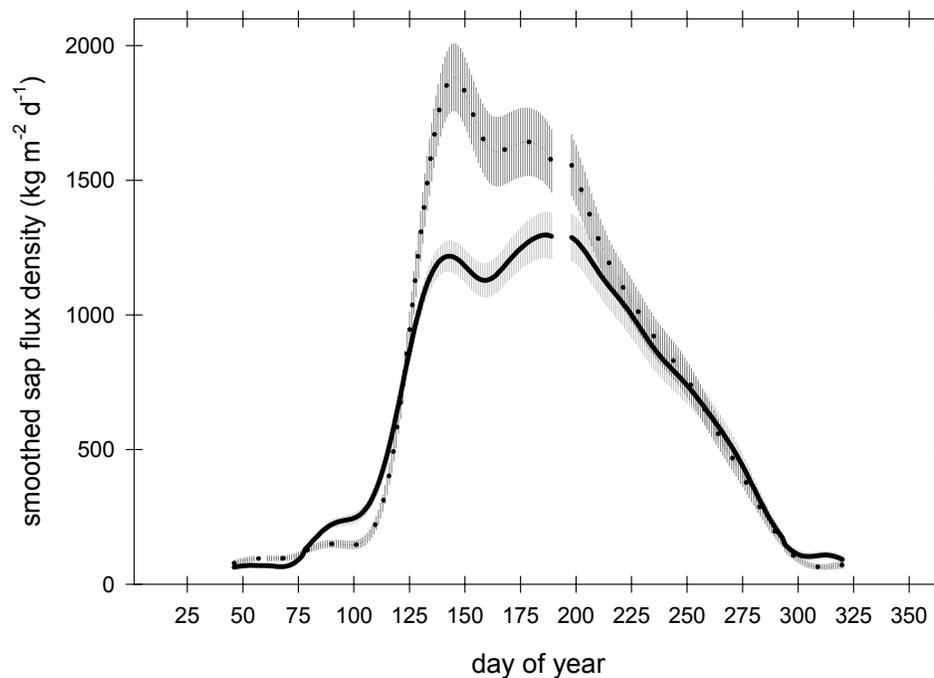
The timing of peak sap flow was different in the two species (Figure 19). Peak sap flow was higher and occurred about 40 days earlier in red alder (on May 25) compared to peak sap flow in Douglas-fir (on July 5). The magnitude and pattern of sap flow was surprisingly similar in both species during the fall, winter, and spring, with the notable exception of the earlier rise in sap flow of Douglas-fir preceding red alder leaf out in the spring around mid-March. During the mid-summer, sap flow increased in Douglas-fir at the same time it decreased in red alder.

Table 5 – A list of attributes of each of the study plots including the number of live trees remaining from the 25 initially planted, the relative proportion of red alder (RA) sapwood basal area (SBA) and biomass, measured and estimated leaf area index (LAI), annual net primary productivity, soil water loss from the upper (0-45 cm) and lower (45-90) soil layers, and total annual transpiration.

attribute	units	Upper Replacement Series Site				Lower Replacement Series Site			
		mixed	mixed-delayed	DF monoculture	RA monoculture	mixed	mixed-delayed	DF monoculture	RA monoculture
# live trees	count	19	18	23	22	24	20	23	20
relative RA SBA	%	36	10	0	100	87	21	0	100
relative RA biomass	%	35	5	0	100	91	18	0	100
LAI	m ² m ⁻²	1.75	0.88	2.39	2.46	4.74	3.02	5.51	3.65
estimated LAI	m ² m ⁻²	2.62	2.24	2.88	2.73	2.99	2.48	3.07	4.08
total SBA	m ² plot ⁻¹	0.21	0.17	0.22	0.26	0.26	0.19	0.23	0.28
RA SBA	m ² plot ⁻¹	0.08	0.02	0.00	0.26	0.23	0.04	0.00	0.28
DF SBA	m ² plot ⁻¹	0.13	0.15	0.22	0.00	0.03	0.15	0.23	0.00
LA:SA ratio	plot ⁻¹	8.41	5.17	11.05	9.63	17.93	15.99	23.84	13.00
biomass	kg in 2002	1126	1019	1354	1692	2002	1213	1413	2396
biomass RA	kg in 2002	397	55	0	1692	1830	221	0	2396
biomass DF	kg in 2002	729	964	1354	0	172	991	1413	0
NPP	g m ⁻² yr ⁻¹	384	461	557	538	717	637	673	717
loss from 0-45	mm*	37.54	49.27	32.27	39.57	30.52	36.40	42.41	21.69
loss from 0-90	mm*	37.63	49.71	55.54	75.27	84.43	51.60	NA	36.05
loss from 45-90	mm*	0.09	0.44	23.27	35.70	53.91	15.20	NA	14.37
relative loss from 45-90	%*	0.24	0.88	41.89	47.42	63.85	29.45	NA	39.85
total transpiration	mm year ⁻¹	96.12	84.75	108.41	144.30	107.40	88.15	95.03	104.49

* for the time period of June 28 through Sept 19, 2001.

Figure 19 – Mean daily total sap flux density of Douglas-fir (solid dark line, n=32) and red alder (dotted line, n=32) through an annual cycle; data were smoothed (7-day running means) to remove day-to-day variation and to show overall trends. Standard error bars are shown in gray. Data between days 189 and 198 are missing.



The seasonal pattern in surface soil moisture was generally similar among all plots at both sites during the period in which soil moisture was monitored (Figure 20a and 20b). Generally, the lower site was moister than the upper site and had greater within-plot variation. There was much greater variability among measurements of soil moisture to a depth of 90 cm. There was no discernable difference between soil moisture in mixed and monoculture plots at either site in the upper 45 cm (Figure 20a and b), but there may be some plot-level differences in the 45 – 90 cm soil layer (Figure 20c and d). The red alder monoculture plot at the lower site had noticeably higher soil moisture due to the small stream that ran through the plot center (Figure 20b and d).

I found some evidence that the spatial partitioning of roots differed among species. The total water lost throughout the period in which soil moisture was measured varied among plots and soil layers. Plots with greater total sapwood area had proportionally more water lost from deeper soil layers (Figure 21a, $r^2 = 0.68$, $p = 0.04$). This also correlated with plots with more alder sapwood, but not significantly (Figure 21b, $r^2 = 0.35$, $p = 0.22$).

At the upper replacement series site, sap flow of both species at high atmospheric evaporative demand was generally lower in mixed and mixed-delayed plots than monoculture plots, but it did not differ between mixed and mixed-delayed plots (Figure 22, DF vs. mixed, $p = 0.02$; DF vs. mixed-delayed, $p = 0.0001$ (Figure 22a); RA vs. mixed, $p = 0.98$; RA vs. mixed-delayed, $p = 0.03$

(Figure 22b)). The exception was red alder in the mixed plot, but that plot had a higher proportion of red alder biomass (Table 5). At the lower replacement series site, sap flow responses to increasing evaporative demand did not differ between mixed and monoculture plots (data not shown).

Predawn water potential decreased through the summer in all plots (Figure 23). It does not appear that the pattern is any different in mixed plots than monocultures or between sites.

Figure 20 – The seasonal course of surface soil moisture (volumetric water content, Θ) between 0 to 45 cm (a, b) and 45 to 90 cm (c, d) depth the upper and lower replacement series sites, respectively. Standard error bars are included for the mixed (circles), mixed-delayed (squares), DF monoculture (triangles), and RA monoculture (inverted triangles) plots.

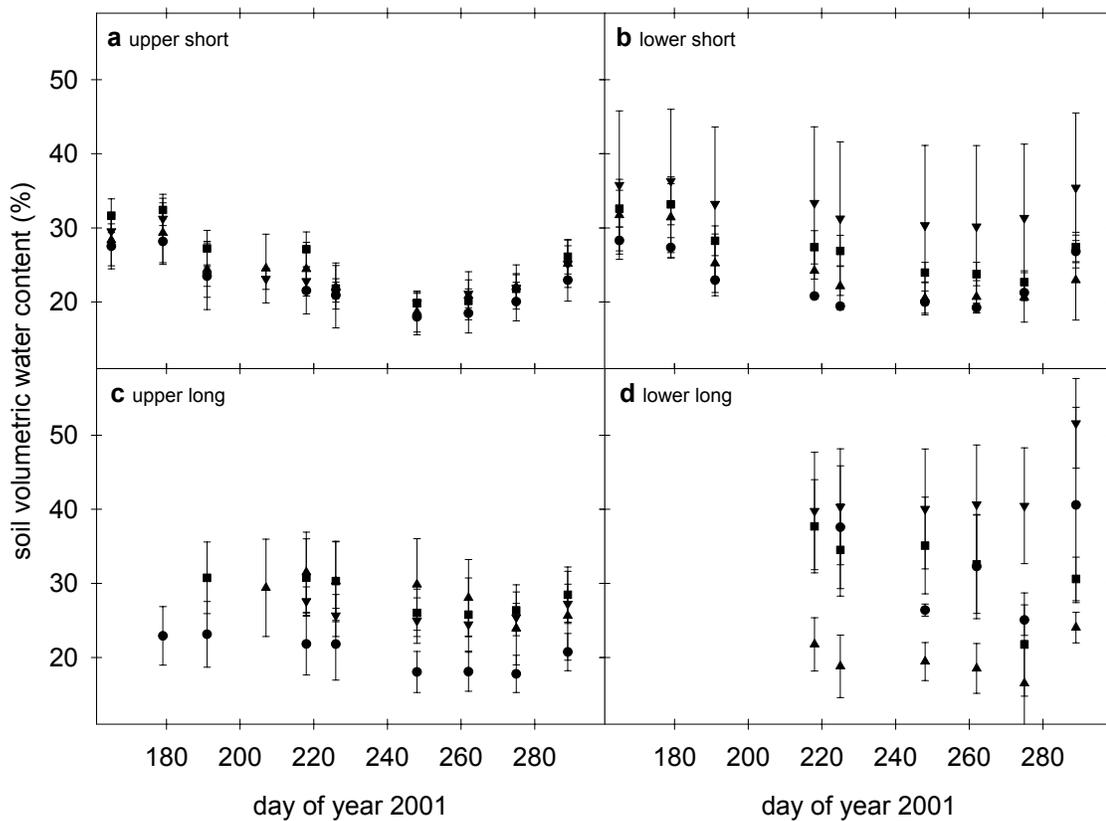


Figure 21 – The proportion of water lost (%) from deep soil layers (45-90 cm) relative to the upper soil (0-45 cm) during the time period between June 28 and September 19, 2001 and a) total sapwood basal area per plot (m^2) or b) the proportion of total sapwood that is red alder relative to Douglas-fir (%). The DF and RA monoculture plots at the lower site were excluded because of anomalies such as saturated soils in the RA plot and substantial buried wood in the DF plot.

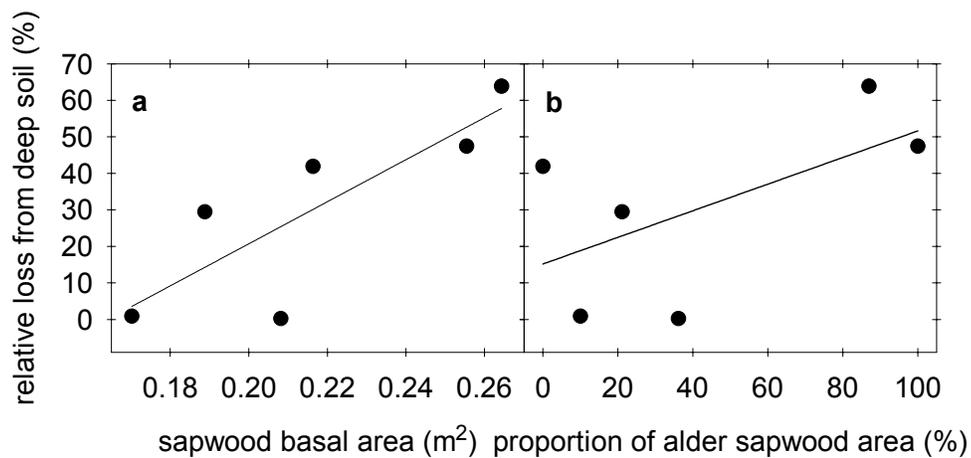


Figure 22 – The relationship between sap flux density ($\text{kg m}^{-2} \text{d}^{-1}$) and vapor pressure deficit (mbar) of a) Douglas-fir and b) red alder in monoculture (triangles, solid line), mixed (circles, dotted line), and mixed-delayed (squares, dashed line) plots at the upper replacement series site.

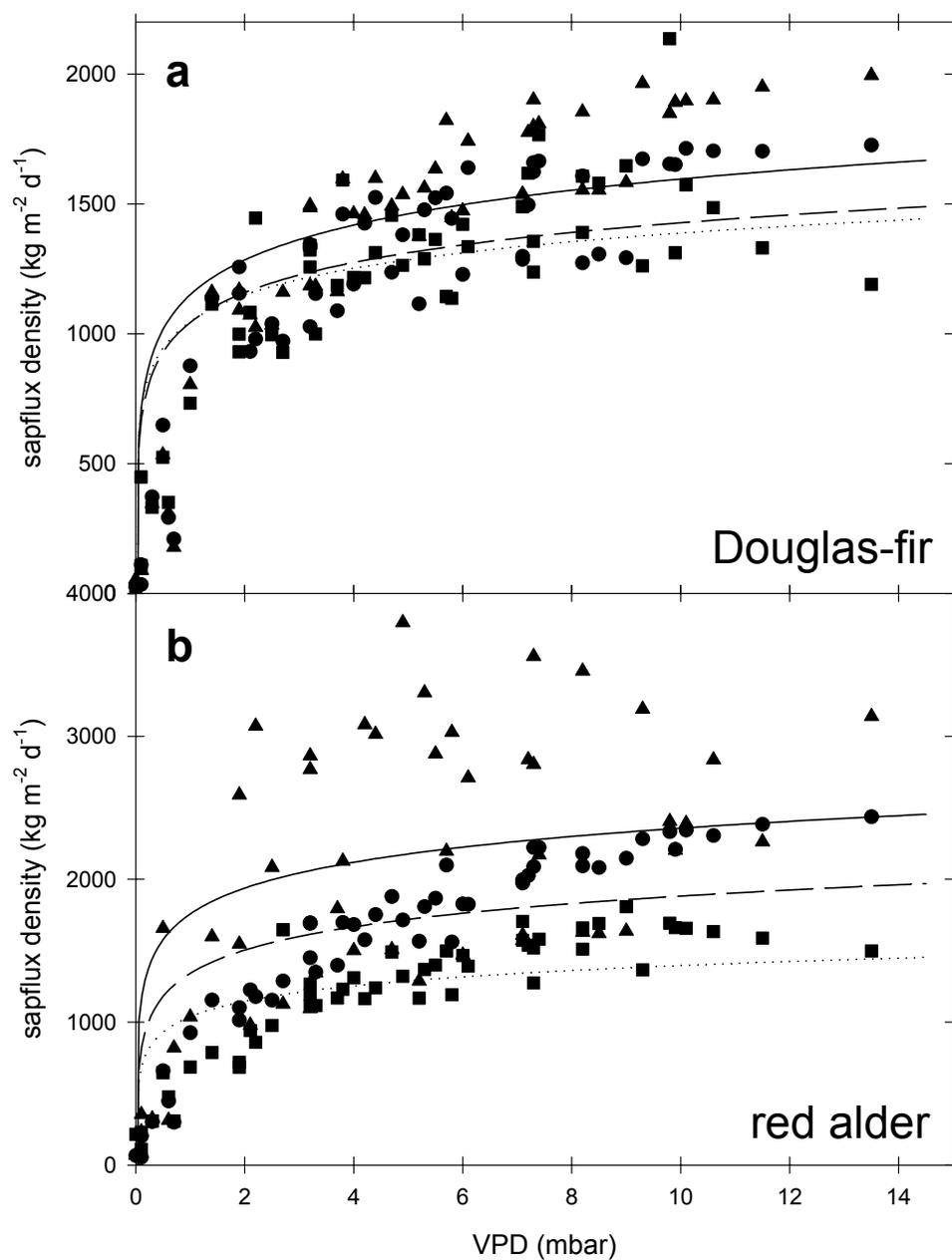
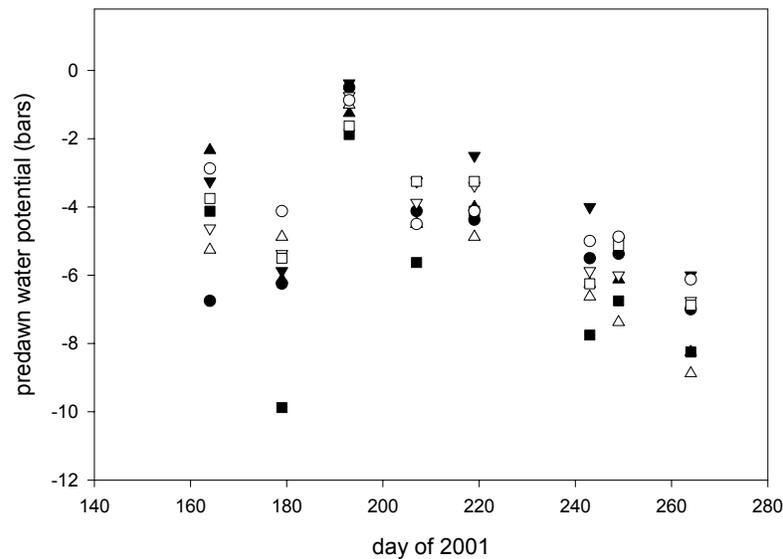


Figure 23 – Average predawn water potential (bar) at the upper (closed symbols) and lower (open symbols) replacement series sites in each plot [DF monoculture (squares); RA monoculture (circles); mixed (triangles); and mixed-delayed (inverted triangles)].



As expected, on an annual basis as well as a daily basis in the early season, transpiration was greater for red alder than for Douglas-fir monocultures at both sites, but the differences between sites (upper and lower) were greater than the differences between species (Figure 24). At the upper site, the Douglas-fir monoculture plot transpired 108 mm annually, compared to 144 mm in the red alder monoculture. At the lower site, the Douglas-fir monoculture transpired 95 mm annually, compared to 104 mm in the red alder monoculture. Annually, mixed-species plots at the upper site transpired much less than the average of monocultures (Figure 24). This difference did not occur at the lower site.

Between 1998 and 2002, annual net primary productivity did not vary greatly between Douglas-fir and red alder monocultures (Figure 25). Mixed plots at the upper site were less productive than the average of monocultures. This difference did not occur at the lower site.

Biomass tended to be lower in mixed plots than monoculture plots (Figure 26, Table 5). There was a strong linear relationship between biomass and transpiration ($r^2 = 0.98$ and 0.99 at the upper and lower sites, respectively).

Figure 24 – Annual total transpiration and proportion of alder biomass (%) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites. Plots with 0% alder biomass are DF monocultures; plots with 100% alder biomass are RA monocultures.

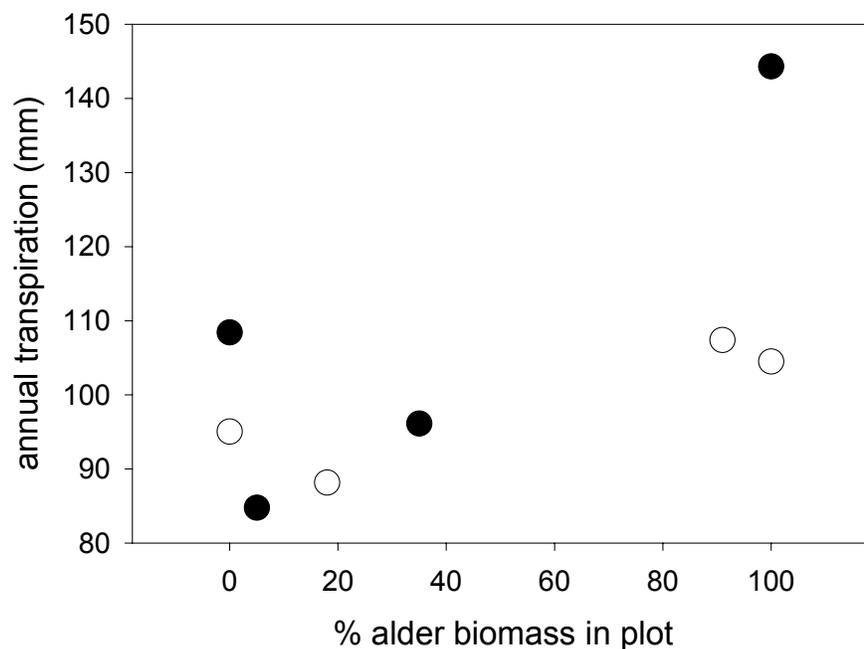


Figure 25 – Average annual net primary productivity between 1998 and 2002 and proportion of alder biomass (%) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites. Plots with 0% alder biomass are DF monocultures; plots with 100% alder biomass are RA monocultures.

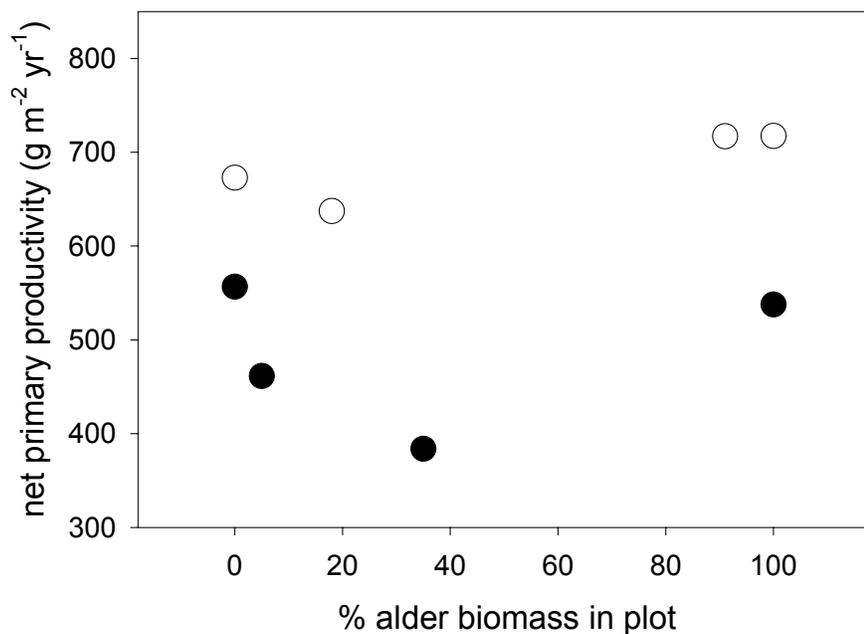
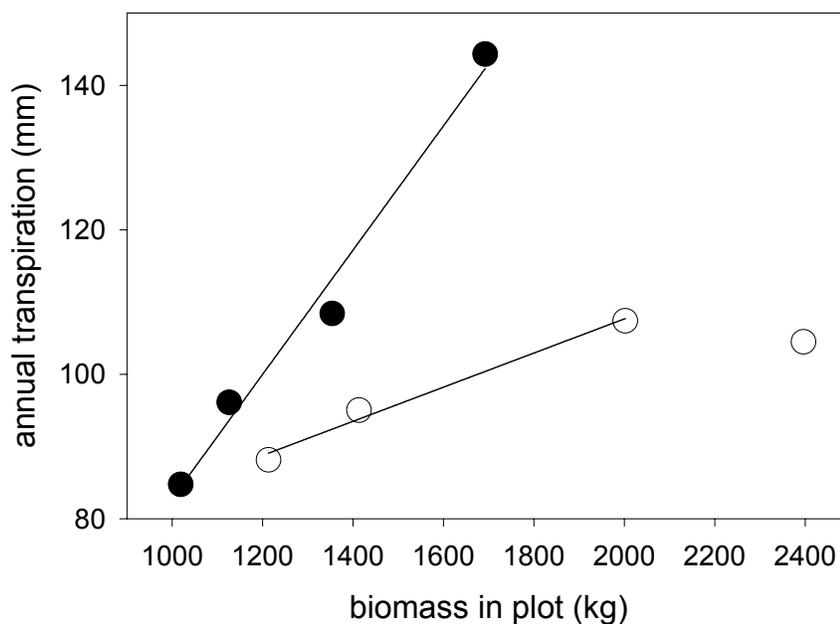
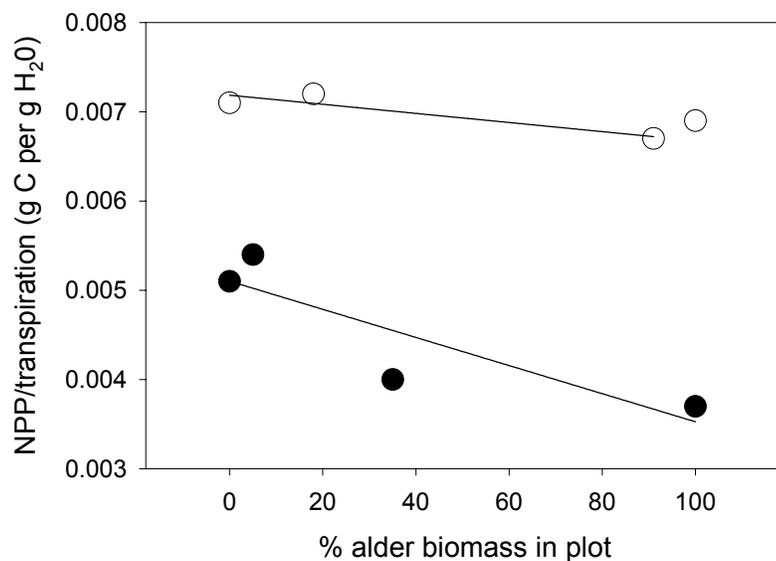


Figure 26 – Annual total transpiration and total woody biomass (kg) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites. Lines represent least squares regression (excludes RA monoculture at lower replacement series site).



Water use efficiency was slightly greater in Douglas-fir than red alder (Figure 27). WUE in mixed stands did not differ from that of monocultures, rather was a linear mixture of the monoculture conditions ($r^2 = 0.77$ and 0.86 at the upper and lower sites, respectively).

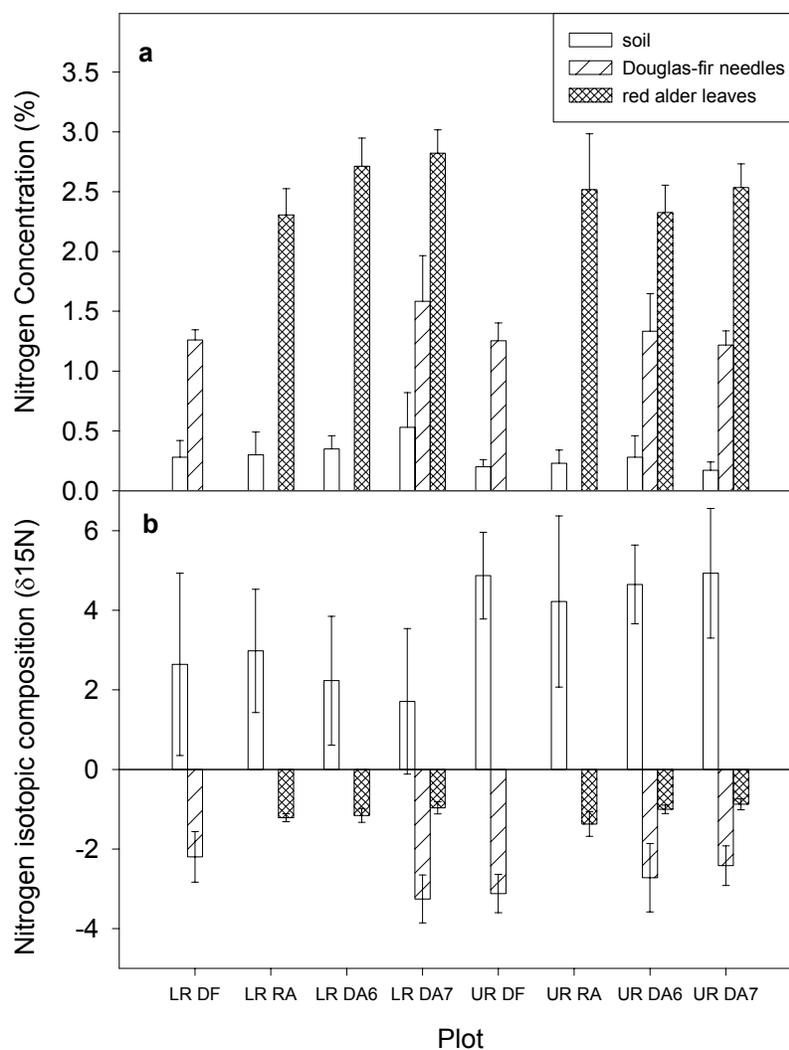
Figure 27 – The amount of carbon gained per unit water lost (WUE or transpiration efficiency) and proportion of alder biomass (%) by plot at the upper (closed symbols) and lower (open symbols) replacement series sites. Plots with 0% alder biomass are DF monocultures; plots with 100% alder biomass are RA monocultures.



The lower site had significantly greater soil N availability than the upper site ($p = 0.02$, Figure 28a), and the alder leaves had a higher concentration of nitrogen than the Douglas-fir needles. There was no difference in leaf [N] between mixed and monoculture plots in either species. The lower site had a lighter nitrogen isotopic ratio than the upper site ($p = 0.003$, Figure 28b). In all

plots, the soil nitrogen was isotopically heavier than the alder leaves, which was heavier than the Douglas-fir needles. Red alder was likely fixing nitrogen because the leaf $\delta^{15}\text{N}$ was significantly higher in the alder leaves than in Douglas-fir needles ($p < 0.0001$), yet there was no difference in Douglas-fir needle $\delta^{15}\text{N}$ between mixed and monoculture plots ($p = 0.67$).

Figure 28 – The a) nitrogen concentration (%) and b) isotopic composition ($\delta^{15}\text{N}$, ppt) in the soil (open bars), Douglas-fir needles (diagonal hatched), and red alder leaves (cross hatched) in each plot in at the lower (LR) and upper (UR) replacement series sites. Error bars are one standard deviation from the mean.



Discussion

Surprisingly, transpiration was more closely related to plot biomass than to any measure of species diversity. First I'll discuss how water use is partitioned between these two species in space and time, and how these species respond to drought stress when grown in mixtures compared to monocultures. Then I'll discuss how diversity affected plot-level productivity, transpiration, and water use efficiency at the two sites.

Temporal partitioning of resource utilization was found between Douglas-fir and red alder. The timing of peak sap flow was earlier in red alder than Douglas-fir, probably indicative of greater sensitivity of soil moisture by red alder (Minore 1979; Shainsky et al. 1994), and initial spring increases in sap flow were earlier in Douglas-fir than red alder, probably because alder had not yet obtained full leaf elongation. However, temporal soil moisture patterns (at least to the measured depths) were the same in mixed-species and monoculture plots. The differences in water uptake from the upper 0-45 cm and 45-90 cm depths suggest that water utilization by Douglas-fir and red alder may have been spatially different as well. There was some evidence of differential vertical organization of roots among species. But did the expanded access to resources lead to greater stability in the mixed plots under drought conditions?

Lower sap flow in mixed-species plots at high VPD suggests drought amelioration may play a role in more diverse plots. However, there was no evidence of increased soil drought in more diverse plots; and predawn water

potential decreased through the summer in all plots, but it was no different in mixed than monoculture plots.

The true proportion of species in the 50/50 mixed species plots after 18 years of differential growth and mortality is no longer 50/50 proportions in terms of biomass. As a result, species proportions in mixed plots were expressed on a biomass basis. Total biomass tended to be lower in mixed plots than monoculture plots. This was probably due to the much higher mortality in the mixed plots, which is the most likely explanation for the observed patterns in productivity and transpiration. Surprisingly, there was a strong linear relationship between biomass and transpiration. It is possible that the effects of diversity on resource use are conserved and instead are an indirect consequence of altered plot biomass – future studies are needed to better shed light on this notion.

In addition to productivity, relative yield total (RYT) is a useful measure in comparing mixed and monoculture plots (Radosevich et al. 1997) because it relates to how species use resources in relation to each other. RYT values near 1 indicate a sharing of resources (no limitation), less than 1 indicates a competitive or antagonistic relationship, and greater than 1 indicates a symbiotic or facilitative relationship. The RYT was generally low at the upper site, 0.61 and 0.89, but much higher at the lower site, 1.08 and 0.96 in the mixed and mixed-delayed plots, respectively. This complements my findings of reduced productivity and transpiration at the upper site and no discernable interaction in mixed plots at the lower site. It is important to note, however, that the red alder monoculture plot at

the lower site has a small stream running through it. As a result, potential differences in canopy microclimate may explain its lower transpiration.

Annually, mixed plots at the upper site transpired much less than the average of monocultures (Figure 24), indicating a possible antagonistic relationship between the two species (Figure 16a). This pattern was not as clear at the lower site. I found no evidence of a reduction in transpiration. As suggested by the greater soil nitrogen concentration at the lower site, it is possible that resources are not limiting at this site and thus competition is negligible. However, neither trend supports the complementary resource use hypothesis (Figure 17a).

Water use efficiency was slightly greater in Douglas-fir than red alder (Figure 27). This is expected because deciduous species are typically less water use efficient than conifers under the same conditions. WUE in mixed stands did not differ from that of monocultures. This supports the compensatory resource use hypothesis (Figure 17d) that if productivity is reduced by competition, water use should also decrease due to less leaf area and total biomass.

Nutrients probably played a big role in explaining the greater productivity and WUE at the lower site, which had almost twice the soil nitrogen concentration than the upper site (Figure 28). It is also possible that nutrient limitations caused greater competition in mixed plots at the upper site (Figure 16b).

However, even though evidence from this study suggests that red alder was fixing nitrogen, I found no evidence that Douglas-fir benefited from red alder (Figure 28b). The differences in water use and WUE between mixed and

monoculture plots is not likely due to differences in nutrient availability caused by alder as a N-fixer, but rather are likely due to interactions among the species themselves.

In conclusion, the old adage “size does matter” applies. Transpiration was more closely related to biomass than species diversity. But therein lies the elegant organization of these two species in space and time after 18 years of co-occurrence. In this snapshot of succession, differences in diversity probably brought about the observed differences in biomass that was the driving force behind differences in transpiration.

Acknowledgements

I am endlessly grateful for the field support from John Moreau, who helped to supply power and provided support for maintaining data integrity. In addition, several students provided critical field support: Kirstin Stein, Phil Valko, Nicole Czarnomski, and Greta Onsgaard. The National Science Foundation Long-Term Ecological Research program provided significant funding for this study (NSF Grant numbers BSR-90-11663 and DEB-96-32921). Thanks to Anthony D’Amato for 2001 height data and Claudio Ghersa and Steve Radosevich for 1998 height and DBH data.

HOW IS VEGETATION WATER USE RELATED TO STREAM FLOW AT THE SMALL WATERSHED SCALE?

Abstract

Forest managers are faced with the challenge of understanding how management practices affect water resources. In this case study, I explore the linkages between horizontal fluxes (typically studied by hydrologists) and vertical fluxes (typically studied by ecophysiologicalists) within the confines of a 64 hectare forested watershed in the western Cascades of Oregon. The direction and strength of relationships among precipitation, vapor pressure deficit, transpiration, soil moisture, and stream flow were examined at three temporal scales: hourly, daily, and storm. I expected strong coupling between the soil and stream and between the vegetation and atmosphere, but the focus of this study was on the potential coupling between the vegetation and soil and between the vegetation and the stream. Such coupling was found at all three temporal scales during the dry season and was absent in the wet season. In the dry season, I found that within-day variation in stream flow is *negatively* correlated with transpiration, driven by diel patterns in vapor pressure deficit. In contrast, variation in daily stream flow and storm recession time is *positively* correlated with transpiration because transpiration is highest at the beginning of the dry season when stream flow is high and storm recession times are long and declines through the dry season as soil water is depleted.

Introduction

A major focus for hydrologists is “where does water go when it rains?” (McDonnell 2003). Hydrologic models for watersheds track precipitation inputs and outflows in a more or less “black box” approach (Labat et al. 2000), with a major focus on soil conductivity (Hewlett and Hibbert 1963; McDonnell 1990) and topography (Beven and Kirkby 1979; Quinn et al. 1995). Although there are some new modeling approaches that are much better at looking inside the “black box” and more accurately taking vegetation into account (Band et al. 1991; Zhu and Mackay 2001), it is not clear at which scales and during what periods vegetation is most strongly coupled to stream flow, and at what scales/periods stream flow is largely independent of vegetation.

Certainly much work in the field of ecophysiology has advanced our understanding of the coupling between the soil, vegetation, and atmosphere via the soil-plant-atmosphere continuum concept (SPAC, (Nobel 1991)). But this understanding has not been extrapolated to explore coupling between the SPAC (i.e. vertical fluxes) and water reservoirs (i.e. horizontal fluxes) such as lakes, streams, or aquifers. In this case study, I explore the linkages between horizontal and vertical fluxes within the confines of a small, forested watershed in the Pacific Northwest. Horizontal fluxes through soils might be expected to dominate stream flow during periods when water is abundant (in the soil, and usually as a consequence, abundant in the atmosphere) because percolation is the dominant process. In contrast, vertical fluxes of water might be important during periods

when less water is available in the system (again, both in the soil and atmosphere) because evapotranspiration is the dominant process.

The Pacific Northwest is an ideal location to compare wet and dry periods because of its maritime climate. The vast majority of precipitation occurs during the winter months; soils are very wet, and evaporative demand is very low. During summer months, water becomes limiting, surface soils dry out, evaporative demand is high, and stream flow volumes decline to levels that threaten aquatic wildlife (Hicks et al. 1991).

If ecophysiologicalists and hydrologists are to join forces to better understand the role of vegetation in the water cycle, then the first step is to develop a language of temporal scales at which various processes are operating (Jones and Swanson 2001). At sub-daily scales, responses may be lagged with respect to one another (Bond et al. 2002). In a young, rapidly growing Douglas-fir forest in the Pacific Northwest, Bond et al. (Bond et al. 2002) observed a strong coupling between diel patterns in vegetation and stream flow at lags of 4 to 8 hours during the summer dry period. Diel patterns observed in soil moisture have also been attributed to vegetation water use (Brooks et al. 2002). In this study, I expand upon the work by Bond et al. (2002) by asking if the same coupling exists in an adjacent old-growth forest. I was also interested in the intermediate coupling between the stream and soil and between the soil and vegetation, and how time lags change over the course of the summer.

Processes that dominate at short time scales may not be important at long time scales. The stream may be responding to vegetation at diel scales, but the vegetation may be responding to soil moisture at larger time scales. Further, do streams respond to rain events during the wet season differently than during the dry season because of a vegetation influence?

The goal of this study is to better understand the coupling among fluxes of water via precipitation, vapor pressure deficit, transpiration, soil moisture, and stream flow in a small forested watershed in the western Cascades of Oregon at three hydrologically relevant time scales: hourly, daily, and storm.

Conceptual model

The water balance can be expressed as:

$$\{1\} \quad Q = P - ET + \Delta S + \Delta G$$

where Q = stream flow, P = precipitation, ET = evapotranspiration, and ΔS and ΔG are changes in soil moisture and groundwater storage. Assuming no net changes in evaporative fluxes or groundwater recharge, this can be rewritten for a given time period t as:

$$\{2\} \quad Q_t = P_t - T_t - \Delta S_t$$

Transpiration depends upon vapor pressure deficit V in time period t (Figure 29):

$$\{3\} \quad T_t = f(V_t)$$

During periods when soil moisture is near saturation, i.e. during the wet season, or just after (winter) precipitation events, soil moisture drainage (i.e.

gravitational potential exceeds matric potential). Also, vapor pressure deficits are small, so transpiration may be relatively small. Therefore in wet periods, soil moisture changes may be very large relative to transpiration losses, and the water balance simplifies to (Figure 29):

$$\{4\} \quad Q_t = P_t - \Delta S_t$$

Figure 29 – Conceptual diagram illustrating the linkages between stream flow (Q), soil moisture (S), transpiration (T), vapor pressure deficit (V), and precipitation (P).

On the other hand, during periods when soil moisture is very low, i.e. during the dry season, or just after small summer precipitation events, soil moisture drainage is slow (i.e. water is bound to the matrix and gravitational potential is relatively low). Also, vapor pressure deficits are large, so transpiration may be relatively large. Therefore in dry periods, soil moisture changes may be very small relative to transpiration losses, and the water balance simplifies to:

$$\{5\} \quad Q_t = P_t - T_t$$

During dry periods with no precipitation (between storms in summer in the climate of the Pacific Northwest), the water balance simplifies to (Figure 29):

$$\text{(Abdul and Gillham)} \quad Q_t = - T_t$$

or, given {3},

$$\{7\} \quad Q_t = - V_t$$

These relationships can be tested using observed data on Q, P, S, T and V for various time periods t: daily, hourly, and storms. Equations 2 and 3 can be

tested using multiple regression models with average hourly and daily data. Two approaches can be used to account for delayed storage and release of water in the soil. At the daily time scale, P can be expressed as an antecedent precipitation index (API, Fedora and Beschta 1989):

$$\{8\} \quad \text{API}_t = P_t + k * P_{t-1}$$

where k is some coefficient. At the hourly time scale, during periods when P = 0, Equation 2 becomes:

$$\{9\} \quad Q_t = - T_{t-n} - \Delta S_{t-n}$$

or,

$$\{10\} \quad Q_t = - V_{t-n} - \Delta S_{t-n}$$

where T_{t-n} and S_{t-n} are transpiration and soil moisture some n number of hours previous to t. Equations 9 and 10 can be tested using lag correlation models.

Methods

Study Area

This study took place in a 60-hectare small watershed (WS2) in the HJ Andrews forest in the western Cascades of Oregon (see Chapter 2, Figure 1). The climate, vegetation, and geology of WS2 were described in Chapter 2. Briefly, the vegetation of WS2 consists of old-growth Douglas-fir/western hemlock forests (450 years since last disturbance). There is a long history of small watershed studies at the HJ Andrews Experimental Forest of which WS2 has been an integral part. Stream flow has been continuously monitored at a gauging station

located at the outflow of WS2 since November 1952. Beginning in late June 1999, a v-notch weir was installed during low flow periods to better capture low flow stream flow variation.

Beginning in June 2000, a study area at the base of WS2 was established for monitoring transpiration, soil moisture, and climatic variables within the forest canopy (“sap flow study area”). It is located just below the weir in an area approximately 20x70 meters in size (See Chapter 2 for a detailed description).

Data collection

Continuous stream flow discharge (Q) records at 15-minute resolution were obtained from WS2 for three water years (October 1, 1999 until September 30, 2002) (<http://www.fsl.orst.edu/lter/>) and aggregated to mean hourly, daily cfs, and storm recession time scales. Hourly and daily data were averages of the original 15-minute data.

Storm recession times (R) were identified for a set of individual storm events between October 1, 1999 and September 30, 2002 using a program developed by H. Hammond of the US Forest Service PNW Research Station (see Jones 2000; Jones and Grant 1996 for descriptions). Storms were selected based on a 0.1 cfsm increase in unit area flow. Beginning, peak, and ending times were identified to the nearest minute. Ending times for storms were determined as the time at which gage height dropped to within 20% of the initial gage height. In addition, alternate ending times for storms were determined as the time before which the hydrograph began to rise again for a new storm event (identified by

sight from the hydrograph). Six measures of R were calculated for each storm (Table 6).

Soil moisture (S, integrated volumetric water content of the top 0.30 m of the soil in $\text{m}^3 \text{m}^{-2}$) was measured hourly using four water content reflectometers (Model CS615, Campbell Scientific, Logan, UT) distributed within the sap flow study area for the time periods between August 2000 - November 2000, and April 2001 – September 2002. Instantaneous measurements taken every ten seconds were recorded on an hourly basis for each sensor and then averaged over the four sensors (Table 6). The initial S averaged on the day prior to the beginning of a storm event was used for storm scale analyses.

Table 6 - Description of model parameters, their symbols in the tables of results, and units

name	log	symbol	reg	units	description
total hours by sight	V1		r1	hours	the duration of the recession as determined by sight looking at the hourly hydrograph
total hours by gage ht	V2		r2	hours	the duration of the recession time as determined by the peak and end times in Hazeli's storm program output
hours to 37% peak	V3		r3	hours	the time it takes for the recession to drop below 37% of the peak
hours to 50% peak	V4		r4	hours	the time it takes for the recession to drop below 50% of the peak
hours to 80% peak	V5		r5	hours	the time it takes for the recession to drop below 80% of the peak
hours to 1/e of peak	V6		r6	hours	the time it takes for the recession to drop below 1/e ² peak of the peak
total precip	V7		p1	mm	the total amount of rainfall between the beginning of hydrograph rise (as determined by Hazeli's storm program (BHSP) and the peak (as determined by sight looking at the hourly hydrograph (PST))
max precip	V8		p2	mm	the max amount of rain fall between BHSP and PST
hours precip	V9		p3	hours	the numbers of hours between BHSP and PST
average intensity	V10		p4	mm /15min	the average precip intensity between BHSP and PST (=total precip/hours precip)
total precip -3	V11		p5	mm	the total amount of rain fall between three hours before BHSP and PST
max precip -3	V12		p6	mm	the max amount of rain fall between three hours before BHSP and PST
hours precip -3	V13		p7	hours	the numbers of hours between three hours before BHSP and PST
average intensity -3	V14		p8	mm /15min	the average precip intensity between three hours before BHSP and PST (=total precip/hours precip)
rising hydro slope	V15		p9	cts/hr	the difference between begin and peak cts divided by the difference between begin and peak time
initial soil moisture			WCR	m2/m2	volumetric water content (4WCR's) at time the storm begins
potential transpiration	log pot. T		pot. T	mm	potential daily transpiration at time of peak, given time of year (based on smoothed DF at 404 and 405)
avg log(VP D) recession				m bar	the average vapor pressure deficit that occurred during the storm recession
log(avg AP10.1)	avg logAP11		avg AP11	mm	the average antecedent precipitation index during the rising limb of the storm (based on 15-min precip at PRIMET)
log(precip during recession)	log p.d.r.		precip.during.recession	mm	the total amount of precipitation that occurred during the storm recession (based on hourly precip at PRIMET)

Transpiration (T) was determined from constant heat sap flow (Granier 1987) monitored in the two dominant species, Douglas-fir and western hemlock (three overstory individuals each), within the sap flow study area between June 2000 and July 20, 2002. The data were scaled up to represent total transpiration (T, mm) of woody species within the riparian area of WS2 (see Chapter 2 for full description of scaling) at hourly and daily intervals. To represent T during storm recessions only, an index of potential T (ranging from 0 to 100) on the day of the storm peak was generated based on smoothed transpiration of 18-year-old Douglas-fir trees at a nearby site (Table 6; see Chapter 4 for methods).

Vapor pressure deficit (V, mbar) was calculated hourly from temperature and humidity measurements taken above the canopy (67 meters) within the sap flow study area (Vaisala HMP35C, Campbell Scientific, Logan, UT) between September 2000 and September 2002. Hourly and daily average V was used for those scales. To represent V during storm recessions, measurements were averaged between the peak and ending time of the storms (Table 6).

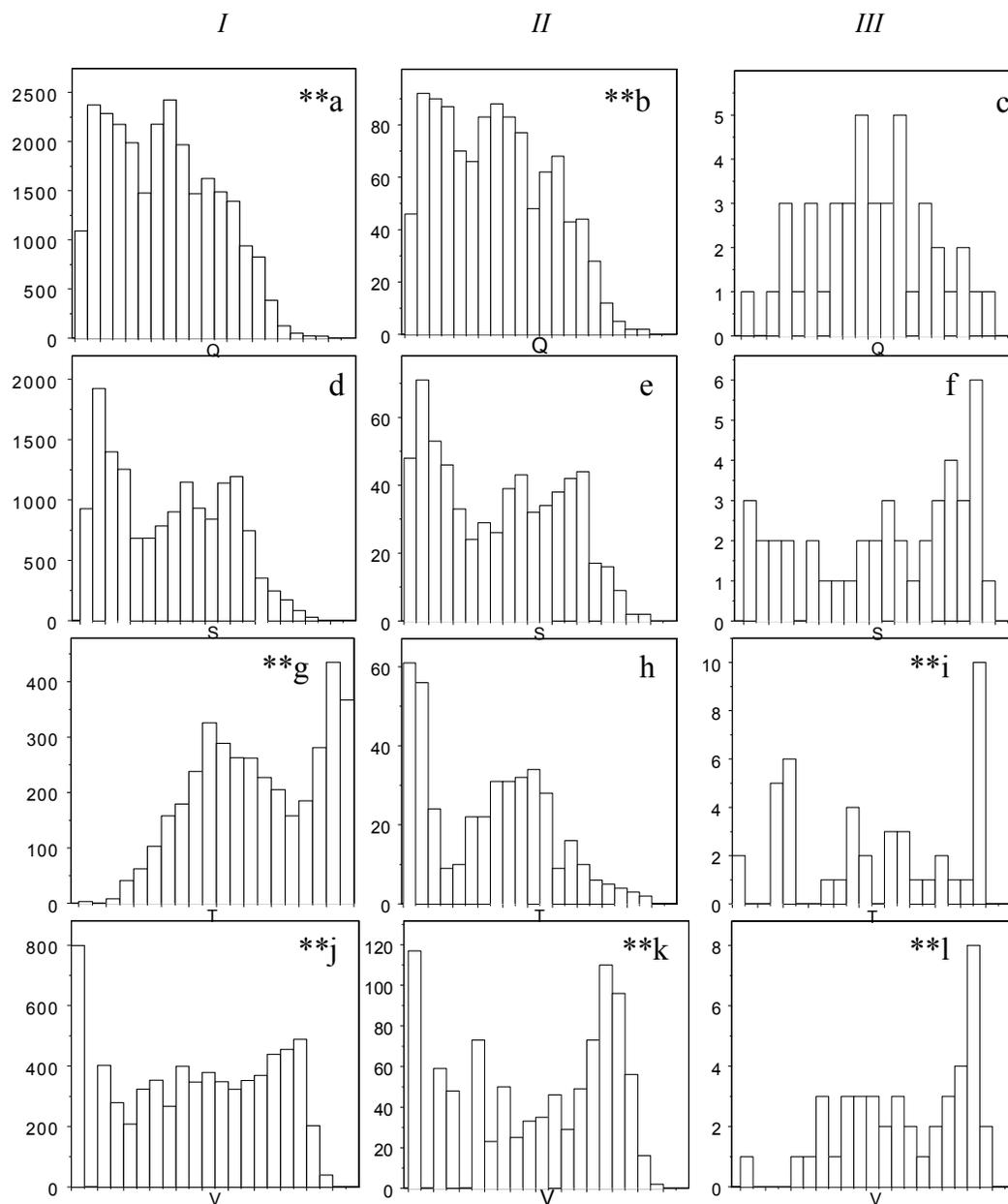
Precipitation (P, mm) was recorded from the WS2 climate station located within the sap flow study area using a U.S. weather bureau standard 8" gage at 15-minute intervals (totaled from 5-minute resolution data) between October 1999 and September 2002. Hourly and daily totals were used the analyses at those scales. The 15-minute data were used to generate ten metrics to represent P for each storm. These were the slope of the rising limb of the hydrograph, the duration, total, maximum, and average precipitation intensity during the time

period between the beginning and peak of the storm and starting three hours before the beginning of the storm, and finally the amount of precipitation during the storm recession (Table 6). Antecedent precipitation indices were calculated from hourly precipitation according to the methods in Fedora and Beschta (1989).

Data pretreatment

Data were tested for normality and independence. Q required log transformation at the hourly and daily scales (Figure 30a and b), but not for storms (Figure 30c). After the necessary transformations, Q was normally distributed at all three scales. S did not require transformation at any scale (Figure 30d, e, f). S was normally distributed at the hourly scale, but was bimodally distributed at the daily scale, with a sharp peak at low values, corresponding to summer, and a broad peak at higher values, corresponding to winter. T required log transformation at the hourly and storm scales (Figure 30g and i), but not the daily scale (Figure 30h). T was bimodally distributed at the daily scale, with a sharp peak at very low values, corresponding to the wet season and moist summer days, and a broad peak at higher values, corresponding to typically dry summer days. V required log transformation at all three scales (Figure 30j, k, l). After log transformation, the frequency of low V was higher at the hourly scale because dew point is reached each night during the vast majority of days of the year, regardless of how high V reached during the mid-day. Transformed V was

Figure 30 – Frequency distributions of (a, b, c) stream flow (Q); (d, e, f) soil moisture (S); (g, h, i) transpiration (T); and (j, k, l) vapor pressure deficit (V) at the hourly (I), daily (II) and storm (III) scales. Parameters marked with a (**) have been log transformed.



bimodally distributed at the daily scale such that on an annual basis the air was generally very dry or very moist, but rarely in between (Figure 30j). This was only the case after log transformation; non-transformed V was highly skewed towards low values (data not shown). The storms selected for this study represented a wide range of values for each variable examined (Figure 30-III). Some measures of storm recession length were transformed (Table 6).

Hourly and daily data were corrected for autocorrelation (lack of independence). To account for autocorrelation at the daily scale, the dataset was reduced to one in seven days by selecting every seventh day starting at day 1. Analyses at the hourly scale were restricted to lag correlations because of strong autocorrelation. Storm data were assumed to be independent because of the storm selection procedure.

Statistical analyses

Generalized least squares (simple and multiple regression) models were fitted to daily and storm scale data. At the hourly and daily scales, the response variable for simple regression was Q and the independent variables were P, S, T and V. At the storm scale, the response variables for simple regression was R and the independent variables were P before and during recessions, P intensity, antecedent S, potential T, and average V during recessions (some were log transformed, see Table 6). Multiple regression models involved sequential (forwards) addition of independent variables in the order S, T, V, and P using a manual procedure following the conceptual model (Figure 29). Final multiple

regression models were selected for each time period using a sequential F-test procedure (Ramsey and Schafer 1997). In this test, for each variable not already included in the model, a F-statistic was calculated to test whether it significantly improved the model.

For hourly data lag cross-correlations were calculated for multi-day periods in early and late August of 2000, June, July, August, and September of 2001, and June 2002. Periods were determined by the existence of overlapping records of Q, S, T, and V. Periods interrupted by precipitation were excluded. Lag correlations (Pearson's R) were tested between all six possible pairs: Q v. S, Q v. T, Q v. V, S v. T, S v. V, and T v. V. P-values denote the significance of slope estimates for the relationships.

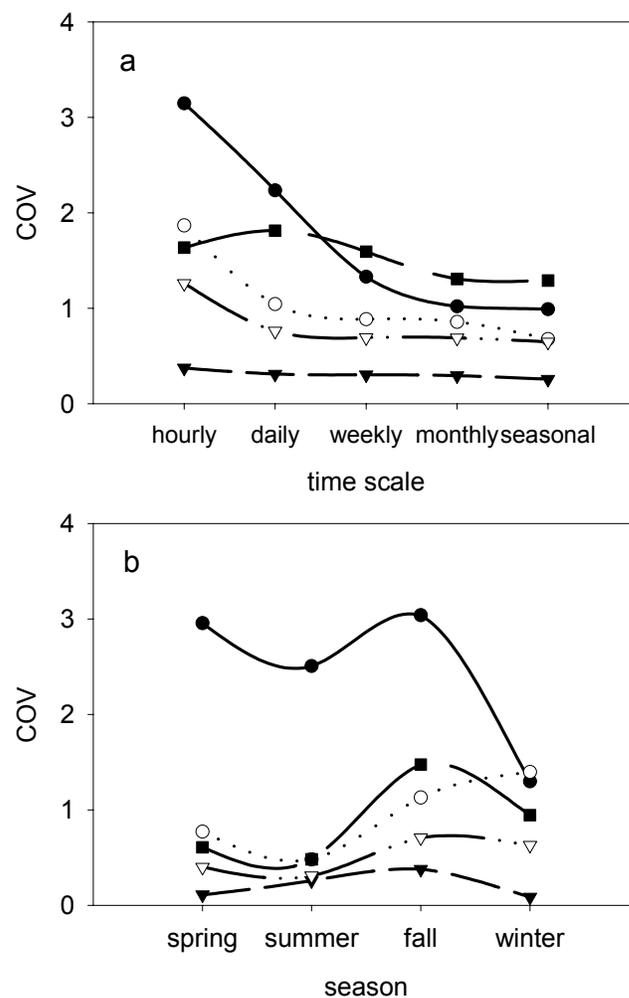
Models were evaluated based on goodness of fit determined from the highest significant r^2 -values for simple regressions, and the highest Pearson's r -values for lag correlations. For multiple regressions, the final models included only the variables whose coefficients were significant ($p < 0.05$).

Results

The change in variance with time scale was similar for P, V, T, and S, with the greatest variation at the shortest time scale; and at all scales, variance of $P > V > T > S$ (although this depends in part on the form in which data are expressed, Figure 31a). In contrast, patterns in Q were most variable at the daily scale.

Year around, variance in P was generally greater than in other hydrologic fluxes (Figure 31b). Variance in P was greatest in the spring and fall,

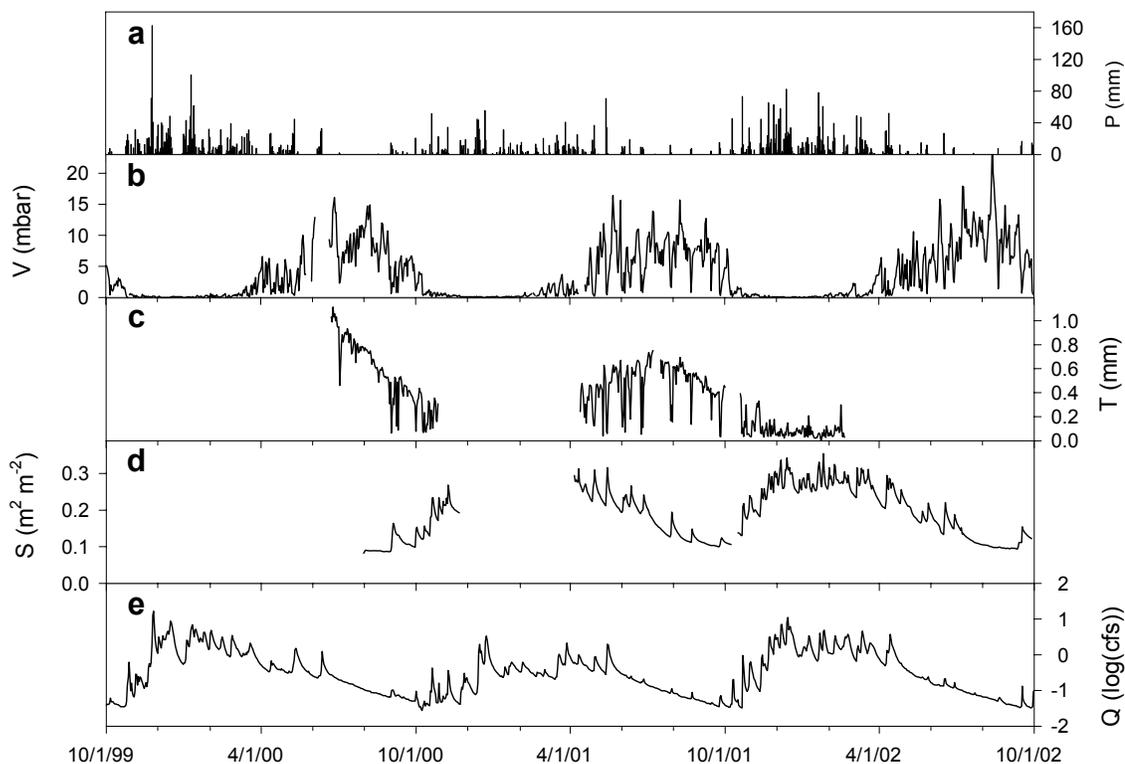
Figure 31 – a) Coefficient of variation by time interval for precipitation (closed circles, solid lines), vapor pressure deficit (open circles, dotted lines), soil moisture (closed inverted triangles, dashed lines), transpiration (open inverted triangles, dash/dot lines), and stream flow (closed squares, long dashed lines) at hourly, daily, weekly, monthly, and seasonal time scales between 8/1/00 and 9/30/02 (hourly transpiration only between June and November 2000). b) Coefficient of variation by season for variables at the daily time scale during the spring (April-May), summer (June-August), fall (September-November), and winter (December-February) based on daily mean values between 4/13/01 and 6/1/02.



corresponding to transition periods between the wet and dry season, and lowest in the winter, corresponding to many days of steady wet-season rainfall. The lowest variability in Q, T, and V occurred in the dry summer months; in contrast, the lowest variability in S occurred in the wet winter and spring. The seasonal pattern of variance in Q was particularly dynamic, with a sharp increase in the fall when storms produced a “flashy” response in the stream, followed by a sharp, progressive decrease in the winter and summer as saturated soils or lack of precipitation delivered a more steady supply of water to the stream.

Visually, S was closely related to Q, and V was closely related to T, at the daily time scale during the three water years (Figures 32 and 33). Average Q declined steadily from January and reached a minimum in October (Figure 33a). Monthly Q did not vary much during the summer, but was highly variable during the fall. Minimum S occurred one month earlier than minimum Q (Figure 33b). Annual patterns in T (Figure 33c) resembled annual patterns in temperature and solar radiation. The highest variability in T occurred in the spring (April) and early fall (September). Sporadic cool, moist days in the summer greatly reduced T, producing low outliers. V was closely related to T, but although maximum T occurred in July, maximum V was not until August (Figure 33d). T declined between July and September while V was fairly constant, corresponding to the sharp reduction in soil moisture during these months. Therefore, at the daily time scale, daily Q appears to be positively related to P and S and negatively related to T and V.

Figure 32 – Temporal variation in water fluxes through a small, forested watershed for water years 2000, 2001, and 2002. a) Daily total precipitation (P, mm); b) Daily average vapor pressure deficit (V, mbar) measured at the nearby Primary climate station; c) Daily total transpiration (T, mm); c) Daily average soil moisture (S, $\text{m}^2 \text{m}^{-2}$); d); and e) Log transformed daily average stream flow (Q, $\log(\text{cfs})$).



The duration of lags at the hourly time scale and how they change through the dry season revealed the strength of coupling between hydrologic fluxes in the system. At hourly time scales in June, July, August, and September, Q responded to S, and T responded to V, but other variables were only weakly related except in August of 2000 when S responded to T (Figure 34). Q was strongly positively related to S at lags of 1 to 7 hours, and T was strongly positively related to V at

lags of less than 1 hour in all periods (June, July, August, September) (Figure 34, Table 7). Q was weakly negatively related to T and V at lags of 4 to 12 hours, if at all. S was weakly negatively correlated with T and V at lags of 2 to 4 hours in June, July, and September, and strongly negatively correlated with T at lags of 3 to 4 hours in August of 2000. For the only year with continuous data (2001), the lag between S and Q, and the lag between T and S, increased by several hours from June to September, while the lag between V and T remained constant at less than one hour (Table 7).

Figure 33 – Temporal variation in water fluxes through a small, forested watershed by month of year for the period 4/13/01 – 9/30/02. Box plots indicate monthly mean values, box areas include one standard deviation from the mean, whiskers include two standard deviations from the mean, and outliers are indicated when present for a) log transformed stream flow (Q); b) soil moisture (S); c) transpiration (T); and d) natural log transformed vapor pressure deficit (V).

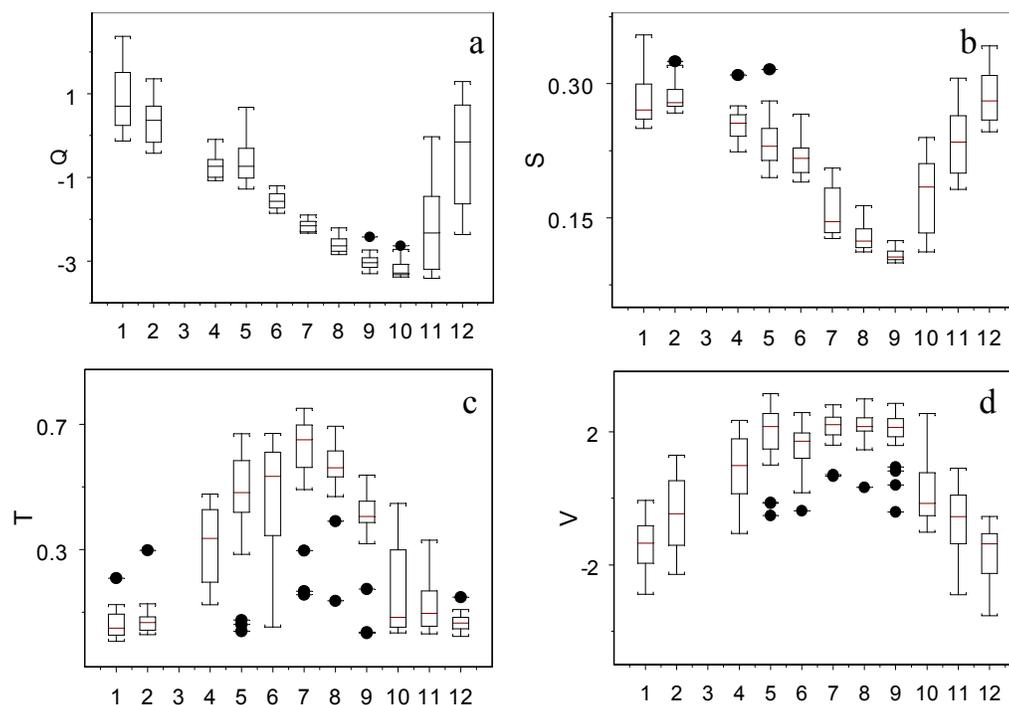


Figure 34 – Lag correlation coefficients (Pearson's R) for the six possible pairs: Q v. S, Q v. T, Q v. V, S v. T, S v. V, and T v. V during the summer of 2000, 2001, and 2002. In each case the y-axis is different to magnify the patterns. The seven different line types represent the seven periods of time: August 1-6 (gray solid) and 19-31 (gray dotted) of the year 2000; June 14-21 (black solid), July 2-8 (black dashed), August 1-21 (gray dashed), and September 1-23 (black dash-dotted) of the year 2001; and June 1-11 (black dotted) of the year 2002.

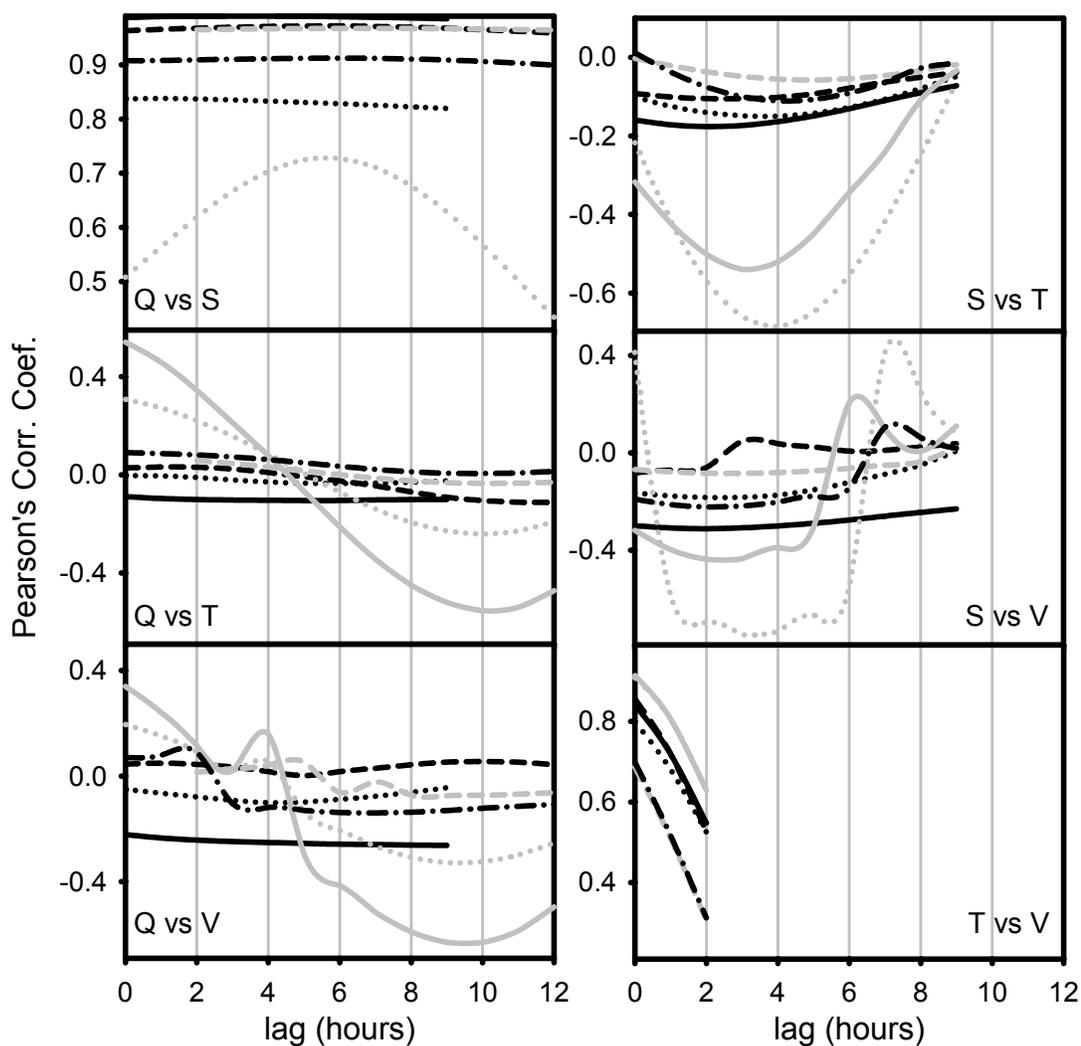
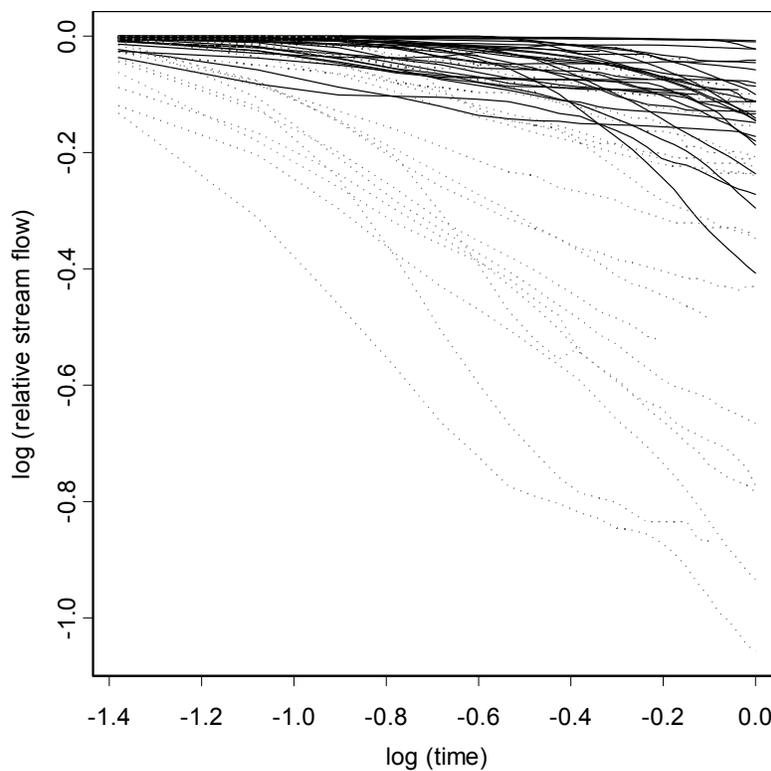


Table 7 – Hourly lag correlations (simple regression) between all possible pairs of variables (dependent – Y ; independent – X) for periods during June, July, August, and September, including the amount of lag in hours at the maximum correlation (Pearson's r) and the corresponding p -values.

Y	X	month	days	year	lag (hours)	Pearson's r	p -value
Q	S	June	14-21	2001	3 to 4	0.99	<0.0001
Q	S	June	1-11	2002	1	0.84	<0.0001
Q	S	July	2-8	2001	6	0.97	<0.0001
Q	S	Aug	1-6	2000	0	-0.54	<0.0001
Q	S	Aug	19-31	2000	6	0.73	<0.0001
Q	S	Aug	1-21	2001	6 to 7	0.97	<0.0001
Q	S	Sept	1-23	2001	6	0.91	<0.0001
Q	T	June	14-21	2001	-	-	ns
Q	T	June	1-11	2002	-	-	ns
Q	T	July	2-8	2001	-	-	ns
Q	T	Aug	1-6	2000	10	-0.55	<0.0001
Q	T	Aug	19-31	2000	10	-0.24	<0.0001
Q	T	Aug	1-21	2001	-	-	ns
Q	T	Sept	1-23	2001	0	0.09	0.0338
Q	V	June	14-21	2001	9+	-0.26	<0.0001
Q	V	June	1-11	2002	-	-	ns
Q	V	July	2-8	2001	-	-	ns
Q	V	Aug	1-6	2000	9	-0.63	<0.0001
Q	V	Aug	19-31	2000	9	-0.33	<0.0001
Q	V	Aug	1-21	2001	9	-0.07	0.0984
Q	V	Sept	1-23	2001	7	-0.14	0.0011
S	T	June	14-21	2001	2	-0.18	0.0074
S	T	June	1-11	2002	4	-0.15	0.0157
S	T	July	2-8	2001	-	-	ns
S	T	Aug	1-6	2000	3	-0.54	<0.0001
S	T	Aug	19-31	2000	4	-0.69	<0.0001
S	T	Aug	1-21	2001	-	-	ns
S	T	Sept	1-23	2001	4	-0.11	0.0095
S	V	June	14-21	2001	2	-0.31	<0.0001
S	V	June	1-11	2002	2	-0.18	0.0029
S	V	July	2-8	2001	-	-	ns
S	V	Aug	1-6	2000	2	-0.44	<0.0001
S	V	Aug	19-31	2000	3	-0.75	<0.0001
S	V	Aug	1-21	2001	3	-0.08	0.0599
S	V	Sept	1-23	2001	2	-0.22	<0.0001
T	V	June	14-21	2001	0	0.84	<0.0001
T	V	June	1-11	2002	0	0.80	<0.0001
T	V	July	2-8	2001	0	0.86	<0.0001
T	V	Aug	1-6	2000	0	0.91	<0.0001
T	V	Aug	19-31	2000	0	0.91	<0.0001
T	V	Aug	1-21	2001	0	0.69	<0.0001
T	V	Sept	1-23	2001	0	0.70	<0.0001

At the storm scale, trends also differed between the dry and wet seasons. Storms receded significantly faster in the dry season than in the wet season ($p < 0.05$, Figure 35). There was considerable variation in slopes of these recessions.

Figure 35 - Relative stream flow recession during the first day after the peak for two time periods, wet season (black solid lines, December-March) and dry season (gray dotted lines, June-October).



Q was closely positively related to S at the daily and hourly time scales, but less so at the storm scale (Table 8). Q was weakly related to T, V, and P at daily, hourly, and storm time scales (Table 8). Most of the variation in daily and hourly Q was explained by S. The antecedent precipitation index greatly improved the model fits at the daily scale, with the best fit at a k-value of 0.9.

Multivariate models do not show much improvement in predicting Q by adding T, V, and P to unlagged models at daily and storm scales (see Table 9 for results from all models). The final models from sequential multiple regression reflect the importance of soil moisture compared to T and V for explaining Q (Table 10, Figure 36). When considering all seasons (Figure 36a), S explained much of the variation at daily and storm scales, but was most closely related to Q at the daily scale. All four variables combined still did not explain more than half the variation in Q at hourly or storm scales.

Table 8 – Slope estimates for the relationship between stream flow (Q) and patterns in soil moisture (S), transpiration (V), vapor pressure deficit (V), and precipitation (P) at the hourly, daily, and storm scale. All relationships were significant ($p < 0.05$). The coefficients of determination (r^2 values) for all the relationships are given in parentheses. Hourly models are described in Appendix A (model 2,11; 2,12; 2,14; and 2,1, respectively). Daily models are described in Appendix B (model 2,7; 2,8; 2,9; and 2,1, respectively). Storm-based models are described in Appendix D (model 2,10; 2,12; 2,13; and 2,1, respectively). Note that the slope estimates are given, but they are primarily in log-transformed units that will not make much sense to most readers. The useful information here is whether the slopes are positive or negative and the strengths of the individual relationships (r^2 's in parentheses).

	hourly	daily	storm
Q v. S	+7.96 (0.81)	+8.05 (0.82)	+2.37 (0.29)
Q v. T	+3.96 (0.10)	-1.17 (0.27)	-0.23 (0.12)
Q v. V	ns	-0.40 (0.29)	ns
Q v. P	+0.23 (0.07)	+0.32 (0.12)	+0.31 (0.09)

Table 9 - Results from sequential multiple regression at the hourly (h 1-4), daily (d 1-4), and storm scale (s 1-4) for periods spanning all seasons, dry season only, wet season only, and fall and spring only. Reported results include p -values (p_0 , p_1 , p_2 , etc.) for coefficient estimates (B0, B1, B2, etc.), coefficient of determination (r^2), residual degrees of freedom (d.f.), sequential F-statistic (F-value), the corresponding p -value that relates to adding an additional variable to the model (p-value), and an indicator for the selected (BEST) model in each set of models.

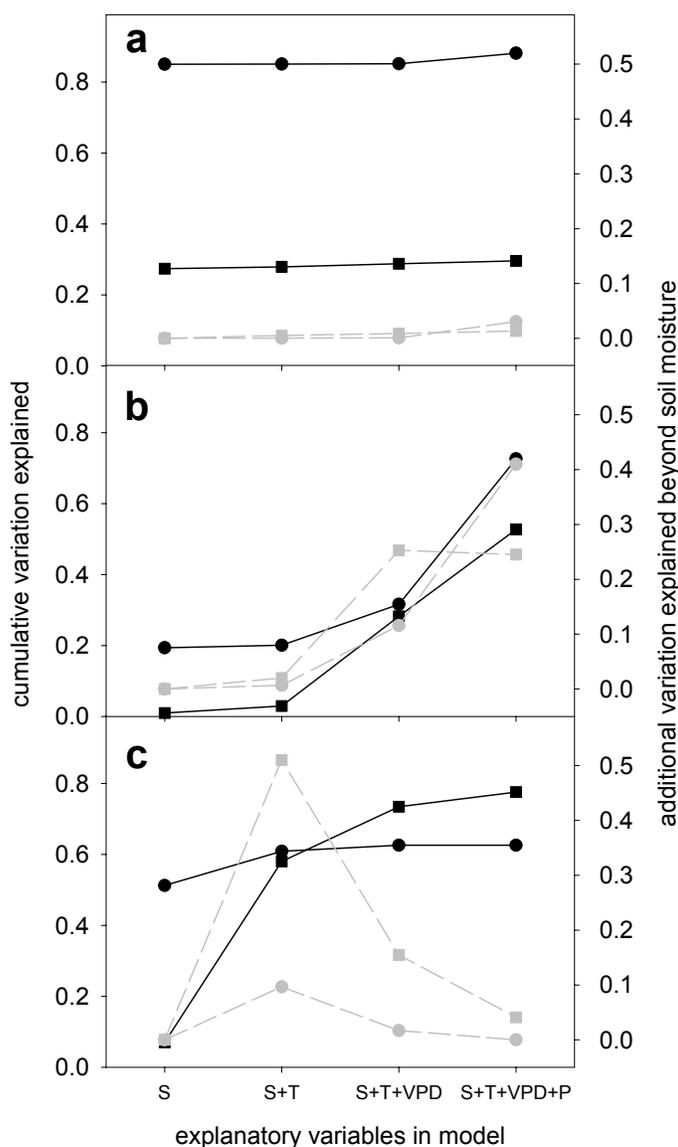
MODEL PERIOD	p0	p1	p2	p3	p4	B0	B1	B2	B3	B4	r^2	d.f.	F-value	P-value	BEST	
h-1	all	<0.001	<0.001			-2.17	7.76				0.76	8952		-		
h-2	all	<0.001	<0.001	<0.001		-2.20	7.83	1.10			0.76	8951	55.71	<0.05		
h-3	all	<0.001	<0.001	<0.001	<0.05	-2.21	7.86	0.83	0.01		0.76	8950	4.44	<0.05		
h-4	all	<0.001	<0.001	<0.001	n.s.	<0.001	-2.31	8.20	0.90	-0.01	0.00	0.77	8949	238.37	<0.05	*****
h-1	dry	<0.001	<0.001			-1.71	4.59				0.76	4000		-		
h-2	dry	<0.001	<0.001	<0.001		-1.72	4.58	0.48			0.76	3999	31.13	<0.05		
h-3	dry	<0.001	<0.001	<0.001	<0.001	-1.72	4.52	1.17	-0.03		0.77	3998	50.69	<0.05		
h-4	dry	<0.001	<0.001	<0.001	<0.001	<0.001	-1.78	4.76	1.37	-0.04	0.00	0.78	3997	228.10	<0.05	*****
h-1	wet	<0.001	<0.001			-1.90	7.95				0.52	765		-	*****	
h-2	wet	<0.001	<0.001	n.s.		-1.91	7.97	1.15			0.52	764	0.90	n.s.		
h-3	wet	<0.001	<0.001	n.s.	n.s.	-1.90	7.93	1.44	-0.01		0.52	763	0.57	n.s.		
h-4	wet	<0.001	<0.001	n.s.	n.s.	<0.001	-1.68	7.23	1.82	0.00	0.00	0.54	762	21.18	<0.05	
d-1	all	<0.001	<0.001			-2.10	7.54				0.85	45		-		
d-2	all	<0.001	<0.001	n.s.		-2.15	7.67	0.07			0.85	44	0.12	n.s.		
d-3	all	<0.001	<0.001	n.s.	n.s.	-2.16	7.54	0.22	-0.07		0.85	43	0.23	n.s.		
d-4	all	<0.001	<0.001	n.s.	n.s.	<0.05	-2.07	6.04	0.08	0.12	0.00	0.88	42	10.60	<0.05	*****
d-1	dry	<0.001	<0.001			-1.62	3.75				0.51	29		-		
d-2	dry	<0.001	<0.001	<0.05		-1.87	4.27	0.39			0.61	28	6.90	<0.05	*****	
d-3	dry	<0.001	n.s.	n.s.		-1.87	4.54	0.11	0.15		0.63	27	1.22	n.s.		
d-4	dry	<0.001	n.s.	n.s.	n.s.	n.s.	-1.87	4.55	0.12	0.14	0.00	0.63	26	0.00	n.s.	
d-1	wet	n.s.	n.s.			-0.99	4.73				0.19	5		-	none	
d-2	wet	n.s.	n.s.	n.s.		-1.07	4.92	0.35			0.20	4	0.03	n.s.		
d-3	wet	n.s.	n.s.	n.s.	n.s.	-1.73	6.63	1.24	-0.18		0.32	3	0.51	n.s.		
d-4	wet	n.s.	n.s.	n.s.	n.s.	n.s.	-0.08	-1.42	4.34	0.28	0.01	0.73	2	2.99	n.s.	
s-1	all	<0.001	<0.05			0.77	2.37				0.27	41		-	*****	
s-2	all	<0.05	<0.05	n.s.		0.65	2.66	0.05			0.28	40	0.29	n.s.		
s-3	all	<0.05	<0.05	n.s.	n.s.	0.78	2.61	-0.05	0.08		0.29	39	0.48	n.s.		
s-4	all	n.s.	<0.05	n.s.	n.s.	n.s.	0.69	2.61	-0.04	0.08	0.07	0.30	38	0.44	n.s.	
s-1	dry	<0.05	n.s.			1.06	1.00				0.07	7		-		
s-2	dry	n.s.	n.s.	<0.05		-0.64	-0.39	1.00			0.58	6	7.29	<0.05	*****	
s-3	dry	n.s.	n.s.	n.s.	n.s.	-0.96	1.38	0.80	0.54		0.74	5	2.92	n.s.		
s-4	dry	n.s.	n.s.	n.s.	n.s.	n.s.	-1.12	1.40	0.79	0.61	0.12	0.78	4	0.74	n.s.	
s-1	wet	n.s.	n.s.			1.86	-1.16				0.01	11		-	none	
s-2	wet	n.s.	n.s.	n.s.		2.28	-2.31	-0.21			0.03	10	0.21	n.s.		
s-3	wet	n.s.	n.s.	n.s.	n.s.	2.57	-2.22	-0.53	0.20		0.28	9	11.27	<0.05		
s-4	wet	<0.05	n.s.	n.s.	<0.05	n.s.	2.87	-4.14	-0.50	0.23	0.22	0.53	8	-6.79	n.s.	
s-1	fall & spr	<0.05	<0.001			0.58	3.02				0.29	32		-		

Table 10 - Multiple regression models selected based on a sequential F-test. See Appendix E for variable descriptors and units. When considering all seasons combined, a 50 mm increase in API 0.9 was associated with a 60% increase in daily Q, holding all else constant. For all seasons, a 5 % increase in daily S was associated with a doubling of daily Q, holding all else constant. A 5% increase in initial S was associated with a 30% increase in median recession time during the entire year. A 0.2 mm increase in summer daily T was associated with a 20% increase in daily Q, holding all else constant A 5% increase in summer daily S was associated with a 60% increase in daily Q, holding all else constant. During the summer, a doubling of T was associated with doubling of recession time. None of the models were adequate to explain variation in winter daily Q or winter storm recession time, thus winter Q was a function of something other than these four factors.

scale	period	final model
daily	all	$Q = -2.07 + 6.04 * S + 0.004 * P$
daily	summer	$Q = -1.86 + 4.27 * S + 0.39 * T$
daily	winter	Q is a function of something other than these four variables
storm	all	$R = 0.77 + 2.37 * S$
storm	summer	$R = 1.00 * T$
storm	winter	R is a function of something other than these four variables

However, by subdividing the data at each scale into the wet (December-April) and dry (June-September) seasons, different patterns emerged that reflect the relative importance of each of the four factors (Figure 36b and c). Models for the wet season improved with the addition of V and P, but not T, whereas models for the dry season improved with the addition of T, but not V or P, especially for hourly data (Figure 36b and c).

Figure 36 – Cumulative variation in stream flow explained (multiple r^2 values) in a) all seasons, b) wet season only (December through April), and c) dry season only (June through September) with sequential addition of explanatory variables in multiple regression: S, S+T, S+T+VPD, S+T+VPD+P at the daily (circles) and storm (squares) scale (models are given in Table 5). Also shown is the variation explained by the addition of each individual parameter after soil moisture (gray, dashed lines). Chosen order follows logical expectations rather than order of explanatory power. S = average or initial soil moisture; T = transpiration or potential transpiration; VPD = log(vapor pressure deficit); and P = log(precipitation) or total precipitation preceding storm peak. The number of data points in (a) are 46 and 43, in (b) are 30 and 13, and in (c) are 6 and 9, at the daily and storm scales, respectively.



Discussion

Stream flow was related to vegetation water use at hourly, daily, and storm scales during the dry season, but not the wet season. At the daily and storm scale, stream flow was positively correlated with vegetation water use because transpiration was highest at the beginning of the dry season when stream flow was high and storm recession times were long and declined progressively as soil water was depleted. In contrast, at the hourly scale, stream flow was negatively correlated with vegetation water use, driven by daily water withdrawals from the soil by vegetation that is translated to the stream at lags of about 10 hours.

It is reasonable to expect that the general trends found here would hold true for other forested watersheds, but the strength of coupling between fluxes probably depend both on forest age and type (deciduous vs. evergreen). Water fluxes from vegetation covering this small watershed (i.e. old-growth, ~450 years since disturbance) with a mixed overstory of Douglas-fir and western hemlock) may be lower than that of a vigorously growing young stand (Chapter 2), which means that transpiration may play an even greater role in stream flow patterns in younger stands (Bond et al. 2002). Further, it appears that the maritime climate led to contrasting patterns between the wet and dry season that are likely unique to regions with dry summers, which tend to have evergreen vegetation.

The climate during the time period investigated may have been somewhat drier than normal. The years 2000 and 2001 represented periods of particularly dry weather. The year 2000 had normal amounts of winter precipitation, but less

than normal amounts of summer precipitation. The winter of 2001 was much drier than normal. 2002 was a more normal year. Drier years may have higher summer transpiration, but there may be more of a decoupling between surface soils on the hill slope and patterns in stream flow if surface soils are extremely dry.

Stream flow measured at the base of the watershed is an integrated measure of both horizontal and vertical fluxes over the watershed. Whereas precipitation, vapor pressure deficit, transpiration, and soil moisture were all measured at one discrete location near the base of the watershed (in fact, the location is slightly outside the watershed boundary). Hence this analysis was structured to examine how the strength of coupling between vertical and horizontal + vertical Q fluxes change over time and at various temporal scales.

It is not known how representative the measurements of P, S, T, and V are of vertical fluxes over the entire watershed. The driving force for evaporation (i.e. vapor pressure deficit) should be fairly conserved across the entire watershed, yet problems arise with low sun angles in mountainous terrain whereby some parts of the landscape may be in shade while others are in full sun. The unexplained error in some statistical models relating Q to P, S, T, and V may be attributable to having only a single point, rather than an integrated area measurement of these vertical fluxes.

An important issue when working with data at different temporal scales is that variability changes with scale (Figure 31a). In general, more variability occurs at shorter time scales. The more highly varying properties at a given time

scale are likely to appear in fitted statistical models (assuming the correct lag is built in). The zero-lag multiple regression models (Table 9) indicate a decrease in explanatory power from daily to hourly time scales as variability increases. On the other hand, the best overall fits were obtained using the hourly lag corrections, which used the most variable data.

This study demonstrates that, as expected, the coupling between vegetation and the atmosphere, and the coupling between soil moisture and stream flow, persist in a conifer forest watershed throughout a water year (Figure 29, Equations 3 and 4). For most of the water year, soil moisture tension is so low compared to vapor pressure and sap flow gradients that streamflow responds only to soil moisture (Table 10). However, this study demonstrates a novel finding that during the dry season when soil moisture tension is high, the entire system becomes connected, so that stream flow is (albeit weakly) coupled directly to the atmosphere, through the soil and vegetation (Equations 6 and 7).

At the hourly scale, stream flow was very strongly coupled to soil moisture (Figure 34 Q v. S) from June until September at all lags up to 12 hours (except August 2000). Even though the coupling between stream flow and transpiration was only strongly apparent during August of a very dry year 2000 (Figure 35 Q v. T), seasonal trends in the year 2001 indicated that time lags among all possible pairs were extended as the season progressed. This is in agreement with the seasonal trends found in an adjacent watershed with younger vegetation during the year 2000 (Bond et al. 2002). In addition, lags between the

stream and soil, and between the soil and vegetation, also extended as the season progressed.

During the dry season, daily and storm-scale stream flow was associated with patterns in transpiration, but during the wet season stream flow was more closely associated with precipitation (Table 10). This makes sense because during the wet season, streams respond to large rain events that input water to the system. During the dry season, vegetation removes water from the system (and slow soil drainage) while there are minimal precipitation inputs.

Conclusions

Vegetation is the critical link in a chain of hydrologic pathways that connect the land to the atmosphere. This study affirms that diel patterns in transpiration drive diel patterns in stream flow during dry summer periods in old-growth conifer forests of western Oregon. Further, diel patterns in soil moisture are connected both to diel patterns in vegetation and stream flow. On any given day in the summer, stream flow is most closely related to soil moisture and transpiration. Surprisingly, daily patterns in stream flow during the winter could not be predicted. Winter daily stream flow is a function of something other than the four variables tested in this study. I also found that the factors controlling storm recessions differ seasonally. Antecedent soil moisture was an important predictor of storm recession time when considering storms throughout the year, but potential transpiration was most important in the summer. As with daily

patterns, winter storm recession time is a function of something other than the four variables tested in this study.

At the daily scale, stream flow is *positively* correlated with transpiration because more water is available for vegetation during periods when stream flow is higher. During times of year when precipitation is scarce, vegetation relies on available water left over from the wet season. As that becomes less available, transpiration declines. During the wet season, the limiting factor for transpiration is vapor pressure deficit rather than soil water, and any impact transpiration may have on stream flow is miniscule in comparison to the large influxes of water from precipitation.

However at the hourly scale, stream flow is *negatively* correlated with transpiration, particularly in the dry season. During periods when the soil water in the rooting zone is connected to the stream and there are no new inputs of water from precipitation, the mechanism responsible for within-day variations in the delivery of water to the stream is the removal of water from the surface soil by evapotranspiration.

We are only beginning to scratch the surface in our understanding of the linkages between streams and vegetation water use. Much more work is needed to solidify the patterns observed here and to evaluate how they may change in landscapes with different land cover types, vegetation age/structure (Chapter 2), and climates. Given the rising interest in protecting our water resources, forest

managers will benefit from an improved understanding of vegetation-stream coupling.

Acknowledgements

This research was supported by National Science Foundation grant DEB-96-32921 (HJ Andrews LTER) and by the USDA Forest Service support of long-term stream flow monitoring at the HJ Andrews forest. Stream flow and climate data were provided by the HJ Andrews LTER Database under the leadership of Don Henshaw. John Moreau contributed valuable support in the field. Additional field support was provided by Nathan Phillips, Andy Schauer, Christine Hurst, Phil Valko, Kirstin Strom, Nicole Czarnomski, and Richard Geesman. I would like to thank H. Hammond for the storm program, D. A. Post for advice about analyzing storm recession data, and I. Tromp Van Meerveld, K. McGuire, T. Vitvar, and W. Van Verseveld for motivating discussions.

CONCLUSIONS

The results from this study demonstrate that changes in vegetation age, structure, species composition, and species diversity can have dramatic effects on transpiration in forests of western Oregon, USA. Because forest management practices alter vegetation attributes such as stand age and species diversity, it is necessary to consider the consequences of such alterations on water resources. In the western Cascades, groundwater storage is minimal, thus stream flow is a vital water resource for both humans and wildlife. This study demonstrates the close coupling between water use by vegetation and patterns in stream flow at the small watershed scale.

Stand age comparison

Despite similar leaf area index (LAI), a 40-yr-old stand used an estimated 3.3 times more water than a 450-yr-old stand during the period from late June to October 2000. These large differences are attributed to structural and compositional changes that occur during succession. The old stand used less water because 1) young sapwood in dominant Douglas-fir conducts water more efficiently than in old trees (2.3 times more total sap flux density), 2) the old stand had more total basal area, but 21% less sapwood basal area than the young stand, 3) the young stand had more water-loving hardwoods (35% vs. 7% of sapwood area), and 4) the old stand had water-conserving shade-tolerant hemlocks (58% of sapwood area).

If LAI had been used to estimate transpiration in these stands, as is common practice, old-growth water use would have been grossly overestimated. Hydrologic models that rely exclusively on LAI to predict transpiration (i.e. Penman-Monteith based models) may not always be appropriate to compare stands with contrasting age and species composition. For example, in a chronosequence of *Pinus sylvestris* stands, canopy transpiration more closely followed trends in sapwood area rather than LAI (Zimmermann et al. 2000).

Despite the greater dry season water use observed in the young riparian stand, annual stream flow was greater in the young watershed (Hicks et al. 1991). This may be explained by spatial variation in transpiration within the entire watershed, temporal variation in transpiration on an annual basis, or perhaps more likely, changes in other components of the water cycle (e.g. interception, soil evaporation, or snow distribution/melt). Nevertheless, the surplus of water in the young watershed has declined over the 40 years since harvest in the early 1960's, and a stream flow deficit relative to the old stand has been apparent in the young watershed during the later part of the dry season since 1969 (Hicks et al. 1991). Following the methods of Hicks et al. (1991), August stream flow deficits since 1988 have become more dramatic, with the years 1999-2002 having August deficits of 3 to 4 mm.

Stream flow recovered to pre-harvest conditions more rapidly in another paired watershed study where Douglas-fir was the dominant species; however, in that case the vegetation in the control watershed was less than 80 years old

(Keppeler and Ziemer 1990). It is possible that age is an important determinant of evapotranspiration throughout the mature stage of stand development.

Results from this study suggest that if logging initiatives are implemented to enhance water yields, as is under consideration in Colorado (Stein 2002), cutting forests may initially increase yields, but could be followed by periods of low yields during stages of rapid growth in young stands.

Sensor degradation

Heat dissipation sap flow sensors, commonly used to measure transpiration over long periods, are subject to deterioration when used for more than a year. In this study, apparent sap flow in Douglas-fir and red alder declined by 45% and 30%, respectively, after 17 months of continuous sensor use. Such degradation may be due to unknown changes in the sapwood surrounding the sensor such as tissue injury, new growth, or air embolism, rather than problems with the sensor itself, or changes in environmental conditions (i.e. soil moisture and vapor pressure deficit).

Use of sap flow sensors for long periods may pose problems, but can potentially be accounted for using a modeling approach similar to that demonstrated here. Future sap flow studies should carefully consider reinstallation of sap flow sensors each year.

Species diversity comparison

Although species mixtures are sometimes advocated on the grounds that they can more efficiently utilize resources, this study revealed a compensatory

rather than a complementary interaction between 18-yr-old Douglas-fir and red alder in mixed-species plots. There was evidence of decreased productivity and transpiration at the upper site (760 m elevation, west-facing) in mixed species plots compared to monoculture plots, but no evidence of an interaction between species at the lower site (660 m elevation, north-facing). The differences in transpiration observed were strongly associated with biomass ($r^2 > 0.98$), which was extremely variable among plots and tended to be lower in mixed-species plots than in monoculture plots, especially at the upper site. Thus, the lower water use by mixed-species plots at the upper site was probably due more to reduced tree size and number resulting from previous competition between the species than to physiological differences caused by species interactions during the measurement period. It is not clear why this competition was more intense at the upper site or why it resulted in such large reductions in total biomass in mixed-species plots. The upper site had lower soil nitrogen, and this may have led to increased competition. Interestingly, productivity and transpiration varied proportionately irrespective of species composition or density so that the water use efficiency remained relatively constant among plots at each site.

This study represented the first attempt at measuring sap flow in Douglas-fir and red alder during the winter months. Much higher winter transpiration rates in Douglas-fir were expected than observed because of its evergreen foliage. However it may not be surprising to find low winter transpiration rates given the cool, wet climatic conditions. The low winter sap flow rates are related to the very

low vapor pressure deficits (VPD) and cloudy weather during the winter months. A modest increase in daily sap flow rates of Douglas-fir was observed on relatively warm, dry winter days.

A similar comparison of annual transpiration of a conifer and deciduous species in a milder climate with sunny winters may lead to a greater contrast in species-specific annual patterns in transpiration. For example, in the Southeastern US, loblolly pine plantations use more water annually than diverse natural deciduous stands, as inferred from stream flow comparisons (Swank and Douglass 1974). It is likely that winter transpiration of pines contributed to the observed differences.

Stream-vegetation coupling

Vegetation-atmosphere coupling and its effects on stream flow vary seasonally, such that, in a 60-ha basin dominated by 450-yr-old Douglas-fir/western hemlock forests, the atmosphere-vegetation-soil-stream continuum is connected in dry periods, but disconnected in wet periods. Stream flow was strongly coupled to soil moisture and transpiration was strongly coupled to VPD at three hydrologically relevant scales: hourly, daily, and storm scales. Connections existed between these two “systems” during the summer dry season, but the direction of “causality” was scale-dependent.

During dry summer periods, moisture fluxes are predominantly upward, through the vegetation, driven by the atmosphere, although some deep soil drainage effects also are discernible. Hence, soil moisture and streamflow patterns

lag VPD and transpiration by a few hours. In contrast, during storms and the wet season, moisture fluxes are predominantly horizontal, driven by precipitation inputs, infiltration, and percolation along hillslopes, and are consistent with these processes as included in typical hydrological models.

However, during dry summer periods, transpiration is high when soils are moist and vegetation is not limited by temperature or VPD. Hence, transpiration "follows" soil moisture (i.e. is correlated with it) and streamflow is predominantly controlled by soil moisture at daily and storm scales.

Results from this study suggest that it may be necessary to create separate models of stream flow for wet and dry conditions, or at least better incorporate vegetation water use into models of stream flow dynamics (e.g. Band et al. 1991, Farmer et al. 2003). For example, a sensitivity analysis of hydrologic models at various time scales revealed that required model complexity increases with decreasing timescale (annual, monthly, daily, and hourly), and increasing dryness index, mostly attributed to difficulty in predicting soil water storage (Atkinson et al. 2002).

Future directions

This study provides some intriguing indications of how transpiration changes throughout succession. The stand-age comparison (Chapter 2) represented a case study that compared two discrete points in succession, at only two sites. Replicated studies spanning a wider range of age classes of both deciduous and conifer forests are needed to better understand how changes

throughout succession impact transpiration. If young-mature forests indeed use more water than old forests, for how long are such differences maintained? Will the difference become even more dramatic before the young forest approaches old forest conditions?

Although not directly addressed in this study, the findings reported here indicate that transpiration changes with position on the landscape. The old and young stands investigated in this study were located within a 70-meter swath in the riparian area of adjacent watersheds. More spatially extensive transpiration measurements are needed in order to determine basin-wide transpiration that is necessary to compare with stream flow and other components of the water budget on a volume per volume basis. With the aid of new models, we may soon be able to close the water balance in small watersheds at this site, separating evaporation, transpiration, and interception components.

In the future, by understanding the specific mechanisms that cause sensor degradation, we may soon be able to predict its onset, thus improving the long-term accuracy of sap flow measurements. The technique will likely continue to be used in an expanding array of applications that require the use of sensors for prolonged periods.

The lessons learned from the Douglas-fir/red alder replacement series experiment provoke new questions relating to how diversity affects resource use such as transpiration. Are other early successional native tree species as highly

competitive with Douglas-fir as red alder? How does canopy closure and stem exclusion influence water use in mixed-species stands?

Future studies using similar statistical approaches in regions outside the Northwestern U.S. can provide further insight into how the strength and direction of coupling between stream flow, precipitation, soil moisture, vegetation, and the atmosphere is related to climate, geology, and ecotype. Is coupling stronger in drier climates? Is coupling detectable in compact soils with slower drainage at longer time lags? What happens in ecosystems with more shallow rooted vegetation?

In conclusion, this work goes inside the process of transpiration to reveal how factors associated with stand structure and composition can lead to variability that is not otherwise apparent using traditional approaches. This work further reveals how such variability is translated to hydrologic patterns at the small watershed scale. The thermal dissipation sap flow method is showcased as a useful tool to discern variability among individual stand components, provided that care is taken not to exceed the temporal limits of the sensors.

As a whole, this work is an exploration of how transpiration changes under different vegetation conditions in time (i.e. seasonally and through succession) and space (i.e. within stands), and how the influence of transpiration on stream flow in a small watershed with old-growth vegetation changes under different environmental conditions and temporal scales (i.e. hourly, daily, storm, and seasonal scales).

In forests of the Pacific Northwest, and likely beyond, forest transpiration is not only dependent on the amount of vegetation, but also what type and even probably how it is arranged. Similarly, the degree to which transpiration exerts an influence on stream flow patterns is not only dependent on the amount of transpiration, but also soil moisture conditions tend to dictate when transpiration is more or less linked to the stream.

This study provides a better understanding of the role of western Oregon forests in the water cycle. It is to be hoped that this work will also be useful in predicting how land cover change will affect our valuable water resources.

BIBLIOGRAPHY

- Abdul, A.S. and R.W. Gillham 1984. Laboratory studies of the effect of the capillary fringe on streamflow generation. *Water Resources Research*. 20:691-698.
- Alsheimer, M., B. Kostner, E. Falge and J.D. Tenhunen 1998. Temporal and spatial variation in transpiration of Norway spruce stands within a forested catchment of the Fichtelgebirge, Germany. *Annales Des Sciences Forestières*. 55:103-123.
- Atkinson, S.E., R.A. Woods and M. Sivapalan 2002. Climate and landscape controls on water balance model complexity over changing timescales. *Water Resources Research*. 38:1-17.
- Baldocchi, D.D., B.B. Hicks and T.P. Meyers 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*. 69:1331-1340.
- Baldocchi, D.D., R. Valentini, S.W. Running, W. Oechel and R. Dahlman 1996. Strategies for measuring and modelling carbon dioxide and water vapor fluxes over terrestrial ecosystems. *Global Change Biology*. 2:159-168.
- Bamber, R.K. and K. Fukazawa 1985. Sapwood and heartwood: a review. *Forestry Abstracts*. 46:567-580.
- Band, L., D.L. Peterson, S.W. Running, J.C. Coughlan, R.B. Lammers and R. Nemani 1991. Forest ecosystem processes at the watershed scale: basis for distributed simulation. *Ecological Modeling*. 56:171-196.
- Barbour, M.G. and D. Whitehead 2003. A demonstration of the theoretical prediction that sap velocity is related to wood density in the conifer *Dacrydium cupressinum*. *New Phytologist*. 158:477-488.
- Barrett, D.J., T.J. Hatton, J.E. Ash and M.C. Ball 1995. Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south-eastern Australia. *Plant, Cell, and Environment*. 18:463-469.
- Bates, C.G. and A.J. Henry 1928. Forest and stream-flow experiment at Wagon Wheel Gap, Colo. *Monthly Weather Review*. Suppl. No. 30:79.
- Berntsen, C.M. 1961. Growth and development of red alder compared with conifers in 30-year-old stands. USDA Forest Service PNW Forest and Range Experiment Station, Portland, OR, p. 20.
- Berry, W.D. and S. Feldman 1985. *Multiple Regression in Practice*. Sage University, Newbury Park, CA.
- Beven, K.J. and M.J. Kirkby 1979. A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences*. 24:45-?
- Binkley, D., J.L. Stape and M.G. Ryan Draft. Thinking about efficiency of resource use in forests

- Black, P.E. and B.L. Fisher 2001. Conservation of Water and Related Land Resources. Lewis Publishers, Boca Raton, FL. 493 p.
- Bond, B.J., J.A. Jones, G. Moore, N. Phillips, D.A. Post and J.J. McDonnell 2002. The zone of vegetation influence on baseflow revealed by diel patterns of streamflow and vegetation water use in a headwater basin. *Hydrological Processes*. 16:1671-1677.
- Bond, B.J. and K.L. Kavanagh 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. *Tree Physiology*. 19:503-510.
- Booker, R.E. 1984. Dye-flow apparatus to measure the variation in axial xylem permeability over a stem cross-section. *Plant, Cell, and Environment*. 7:623-628.
- Bosch, J.M. and J.D. Hewlett 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology*. 55:3-23.
- Bredensteiner, K. 1998. An investigation of vegetation : hydrology interactions in watershed 1 at the H.J. Andrews Experimental Forest. *In Botany and Plant Pathology*. Oregon State University, Corvallis, OR, p. 168.
- Bren, L.J. 1997. Effects of slope vegetation removal on the diurnal variations of a small mountain stream. *Water Resources Research*. 33:321-331.
- Brooks, J.R., F.C. Meinzer, R. Coulombe and J. Gregg 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology*. 22:1107-1117.
- Brooks, K.N., P.F. Ffolliott, H.M. Gregersen and L.F. DeBano 1997. *Hydrology and the Management of Watersheds*. Iowa State University Press, Ames, IA. 502 p.
- Burdass, W.J. 1975. Water harvesting for livestock in western Australia. *In The Water Harvesting Symposium* Ed. G.W. Frasier. USDA Agricultural Resources Service.
- Callaway, R.M., A. Sala and R.E. Keane 2000. Succession may maintain high leaf area: sapwood ratios and productivity in old subalpine forests. *Ecosystems*. 3:254-268.
- Cermak, J., E. Cienciala, J. Kucera and J.-E. Hallgren 1992. Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing. *Tree Physiology*. 10:367-380.
- Cermak, J., E. Cienciala, J. Kucera, A. Lindroth and E. Bednarova 1995. Individual variation of sap-flow rate in large pine and spruce trees and stand transpiration: a pilot study at the central NOPEX site. *Journal of Hydrology*. 168:17-27.
- Cermak, J., M. Deml and M. Penka 1973. A new method of sap flow rate determination in trees. *Biologia Plantarum*. 15:171-178.
- Chan, S.S.N., S.R. Radosevich and A.T. Grotta 2003. Effects of contrasting light and soil moisture availability on the growth and biomass allocation of

- Douglas-fir and red alder. *Canadian Journal of Forest Research*. 33:106-117.
- Cienciala, E., J. Kucera and A. Lindroth 1999. Long-term measurements of stand water uptake in Swedish boreal forest. *Agricultural and Forest Meteorology*. 98-99:547-554.
- Cienciala, E., J. Kucera, M.G. Ryan and A. Lindroth 1998. Water flux in boreal forest during two hydrologically contrasting years; species specific regulation of canopy conductance and transpiration. *Annales Des Sciences Forestières*. 55:47-61.
- Clearwater, M.J., F.C. Meinzer, J.L. Andrade, G. Goldstein and N.M. Holbrook 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiology*. 19:681-687.
- Cochard, H., D. Lemoine, T. Ameglio and A. Granier 2001. Mechanisms of xylem recovery from winter embolism in *Fagus Sylvatica*. *Tree Physiology*. 21:27-33.
- Cochard, H. and M.T. Tyree 1990. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology*. 6:393-407.
- Cohen, W.B., T.A. Spies, R.J. Alig, D.R. Oetter, T.K. Maiersperger and M. Fiorella 2002. Characterizing 23 years (1972-95) of stand replacement disturbance in western Oregon forests with Landsat imagery. *Ecosystems*. 5:122-137.
- Cohen, W.B., T.A. Spies and M. Fiorella 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. *International Journal of Remote Sensing*. 16:721-746.
- Cohen, Y., F.M. Kelliher and T.A. Black 1984. Determination of sap flow in Douglas-fir trees using the heat pulse technique. *Canadian Journal of Forest Research*. 15:422-428.
- D'Amato, A.W. 2002. Interference dynamics in mixed red alder/Douglas-fir forests. *In Forest Science*. Oregon State University, Corvallis, OR, p. 104.
- Darwin, C. and A. Wallace 1858. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *Zoological Journal of the Linnean Society*. 3:45-62.
- Do, F. and A. Rocheteau 2002. Influence of natural temperature gradients on measurements of xylem sap flow with thermal dissipation probes. 1. Field observations and possible remedies. *Tree Physiology*. 22:641-648.
- Domec, J.C. and B.L. Gartner 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees*. 15:204-214.
- Domec, J.C. and B.L. Gartner 2002. Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. *Tree Physiology*. 22:91-104.

- Dyrness, C.T. and S.A. Acker 1999. Reference Stands in or near the H.J. Andrews Experimental Forest. Permanent Plots of the Pacific Northwest. Report Number 2, (<http://www.fsl.orst.edu/lter/pubs/webdocs/permplot.cfm>).
- Ehrlich, P.R. and E.O. Wilson 1991. Biodiversity studies: science and policy. *Science*. 253:758-762.
- Ewel, J.J. 1986. Designing agricultural ecosystems for the humid tropics. *Annual Review of Ecology and Systematics*. 17:245-271.
- Farmer, D., M. Sivapalan and C. Jothityangkoon 2003. Climate, soil, and vegetation controls upon the variability of water balance in temperate and semiarid landscapes: downward approach to water balance analysis. *Water Resources Research*. 39:1-21.
- Federer, C.A., L.D. Flynn, C.W. Martin, J.W. Hornbeck and R.S. Pierce 1990. Thirty years of hydrometeorologic data at the Hubbard Brook Experimental Forest, New Hampshire. USDA Forest Service Northeastern Forest Experiment Station, Radnor, PA.
- Fedora, M.A. and R.L. Beschta 1989. Storm runoff simulation using an antecedent precipitation index (*API*) model. *Journal of Hydrology*. 112:121-133.
- Franklin, J.F. and M.A. Hemstrom 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. *In Forest Succession: Concepts and Application* Eds. D.C. West, H.H. Shugart and D.B. Botkin. Springer-Verlag, New York, NY, pp. 212-229.
- Frazer, G.W., J.A. Trofymow and K.P. Lertzman 2000. Canopy openness and leaf area in chronosequences of coastal temperate rainforests. *Canadian Journal of Forest Research*. 30:239-256.
- Fujimori, T. 2001. *Ecological and Silvicultural Strategies for Sustainable Forest Management*. Elsevier, Amsterdam. 398 p.
- Grace, J. 1993. Consequences of xylem cavitation for plant water deficits. *In Water Deficits: Plant Responses From Cell To Community* Eds. J.A.C. Smith and H. Griffiths. BIOS Scientific, Oxford, UK, pp. 109-128.
- Granier, A. 1985. Une nouvelle methode pour la mesure du flux de seve brute dan the tronc des arbres. *Annales Des Sciences Forestières*. 42:193-200.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*. 3:309-320.
- Granier, A., T. Anfodillo, M. Sabatti, H. Cochard, E. Dreyer, M. Tomasi, R. Valentini and N. Breda 1994. Axial and radial water flow in the trunks of oak trees: a quantitative and qualitative analysis. *Tree Physiology*. 14:1383-1396.
- Granier, A., P. Biron, N. Breda, J.Y. Pontailler and B. Saugier 1996. Transpiration of trees and forest stands: short and long-term monitoring using sapflow methods. *Global Change Biology*. 2:265-274.
- Granier, A., V. Bobay, J.H.C. Gash, J. Gelpe, B. Saugier and W.J. Shuttleworth 1990. Vapor flux density and transpiration rate comparisons in a stand of

- Maritime pine (*pinus pinaster* Ait.) in Les Landes forest. *Agricultural and Forest Meteorology*. 51:309-319.
- Gray, A.N. and T.A. Spies 1995. Water content measurement in forest soils and decayed wood using time domain reflectometry. *Canadian Journal of Forest Research*. 25:376-385.
- Grime, J.P. 1997. Biodiversity and ecosystem function: the debate deepens. *Science*. 277:1260-1262.
- Grotta, A.T. 2002. Competitive interactions in young, coastal Douglas-fir/red alder mixtures: implications for wood quality. *In Wood Science and Forest Science*. Oregon State University, Corvallis, OR, p. 109.
- Hewlett, J.D. 1982. *Principles of Forest Hydrology*. University of Georgia Press, Athens, GA. 183 p.
- Hewlett, J.D. and A.R. Hibbert 1963. Moisture and energy conditions within a sloping soil mass during drainage. *Journal of Geophysical Research*. 68:1081-1087.
- Hibbs, D.E., D.S. DeBell and R.F. Tarrant 1994. *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, OR. 256 p.
- Hicks, B.J., R.L. Beschta and R.D. Harr 1991. Long-term changes in streamflow following logging in Western Oregon and associated fisheries implications. *Water Resources Bulletin*. 27:217-226.
- Hogg, E.H., T.A. Black, G.d. Hartog, H.H. Neumann, R. Zimmermann, P.A. Hurdle, P.D. Blanken, Z. Nestic, P.C. Yang, R.M. Staebler, K.C. McDonald and R. Oren 1997. A comparison of sap flow and eddy fluxes of water vapor from a boreal deciduous forest. *Journal of Geophysical Research*. 102:28,929 - 28,937.
- Hooper, D.U. 1998. The role of complementary and competition in ecosystem responses to variation in plant diversity. *Ecology*. 79:704-719.
- Hooper, D.U. and P.M. Vitousek 1997. The effects of plant composition and diversity on ecosystem processes. *Science*. 277:1302-1305.
- Hooper, R.P., N. Christophersen and N.E. Peters 1990. Modelling streamwater chemistry as a mixture of soilwater end members - an application to the Panola Mountain Catchment, Georgia, USA. *Journal of Hydrology*. 116:321-343.
- Houston, L.L., J.D. Kline and R.J. Alig 2002. Economic research supporting water resource stewardship in the Pacific Northwest. USDA Forest Service PNW Research Station, Portland, OR, p. 72.
- Hubbard, R.M., B.J. Bond and M.G. Ryan 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology*. 19:165-172.
- Irvine, J., B.E. Law, P.M. Anthoni and F.C. Meinzer 2002. Water limitations to carbon exchange in old-growth and young ponderosa pine stands. *Tree Physiology*. 22:189-196.

- Irvine, J., M.P. Perks, F. Magnani and J. Grace 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiology*. 18:393-402.
- Jackson, R.B., S.R. Carpenter, C.N. Dahm, D.M. McKnight, R.J. Naiman, S.L. Postel and S.W. Running 2001. Water in a changing world. *Ecological Applications*. 11:1027-1045.
- James, S.A., M.J. Clearwater, F.C. Meinzer and G. Goldstein 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiology*. 22:277-283.
- Jarvis, P.G. 1975. Water transfer in plants. *In* Heat and Mass Transfer in the Environment of Vegetation Ed. Dubrovnik, Washington, D. C., pp. 369-394.
- Johnson, K.H., K.A. Vogt, H.J. Clark, O.J. Schmitz and D.J. Vogt 1996. Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology and Evolution*. 11:372-377.
- Jones, J.A. 2000. Hydrologic processes and peak discharge response to forest removal, regrowth, and roads in 10 small experimental basins, western Cascades, Oregon. *Water Resources Research*. 36:2621-2642.
- Jones, J.A. and G.E. Grant 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. *Water Resources Research*. 32:959-974.
- Jones, J.A. and F.J. Swanson 2001. Hydraulic inferences from comparisons among small basin experiments. *Hydrological Processes*. 15:2363-2366.
- Keppeler, E.T. and R.R. Ziemer 1990. Logging effects on streamflow: water yield and summer low flows at Casper Creek in northwestern California. *Water Resources Research*. 26:1669-1679.
- Kostner, B. 2001. Evaporation and transpiration from forests in Central Europe - relevance of patch-level studies for spatial scaling. *Meteorology and Atmospheric Physics*. 76:69-82.
- Kostner, B., E. Falge, M. Alsheimer, R. Geyer and J.D. Tenhunen 1998. Estimating tree canopy water use via xylem sapflow in an old Norway spruce forest and a comparison with simulation-based canopy transpiration estimates. *Annales Des Sciences Forestières*. 55:125-139.
- Kozlowski, T.T., P.J. Kramer and S.G. Pallardy 1991. The Physiological Ecology of Woody Plants. *In* Physiological Ecology Ed. H.A. Mooney. Academic Press, Inc, San Diego, CA. 657 p.
- Kramer, P.J. and J.S. Boyer 1995. *Water Relations of Plants and Soils*. Academic Press, San Diego, California.
- Kucera, J., J. Cermak and M. Penka 1977. Improved thermal method for continual recording of transpiration flow rate dynamics. *Biologia Plantarum*. 19:413-420.

- Kutscha, N.P. and I.B. Sachs 1962. Color tests for differentiating heartwood and sapwood in certain softwood tree species. USDA Forest Service, Madison, WI, p. 17.
- Labat, D., R. Ababou and A. Mangin 2000. Rainfall-runoff relations for karstic springs. Part I: convolution and spectral and spectral analysis. *Journal of Hydrology*. 238:123-148.
- Lambs, L. and E. Muller 2002. Sap flow and water transfer in the Garonne River riparian woodland, France: first results on poplar and willow. *Annales Des Sciences Forestières*. 59:301-315.
- Lane, P.N.J. and S.M. Mackay 2001. Streamflow response of mixed-species eucalypt forests to patch cutting and thinning treatments. *Forest Ecology and Management*. 143:131-142.
- Law, B.E., S. Van Tuyl, A. Cescatti and D.D. Baldocchi 2001. Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. *Agricultural and Forest Meteorology*. 108:1-14.
- Lundblad, M. and A. Lindroth 2002. Stand transpiration and sapflow density in relation to weather, soil moisture and stand characteristics. *Basic and Applied Ecology*. 3:229-243.
- Martin, T.A., K.J. Brown, J. Cermak, R. Ceulemans, J. Kucera, F.C. Meinzer, J.S. Rombold, D.G. Sprugel and T.M. Hinckley 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. *Canadian Journal of Forest Research*. 27:797-808.
- McCann, K.S. 2000. The diversity-stability debate. *Nature*. 405:228-233.
- McDonnell, J.J. 1990. A rationale for old water discharge through macropores in a steep, humid catchment. *Water Resources Research*. 26:2821-2832.
- McDonnell, J.J. 2003. Where does water go when it rains? Moving beyond the variable source area concept of rainfall-runoff response. *Hydrological Processes*. 17:1869-1875.
- McDowell, N., H. Barnard, B.J. Bond, T. Hinckley, R.M. Hubbard, F.C. Meinzer, N. Phillips, M.G. Ryan and D. Whitehead 2002a. The relationship between tree height and leaf area: sapwood area ratio. *Oecologia*. 132:12-20.
- McDowell, N.G., N. Phillips, C. Lurch, B.J. Bond and M.G. Ryan 2002b. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology*. 22:763-774.
- Means, J.E., S.A. Acker, D.J. Harding, J.B. Blair, M.A. Lefsky, W.B. Cohen, M.E. Harmon and W.A. McKee 1999. Use of large-footprint scanning airborne Lidar to estimate forest stand characteristics in the western Cascades of Oregon. *Remote Sensing of the Environment*. 67:298-308.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species - a literature review. Pacific Northwest Forest and Range Experiment Station, Portland, OR, p. 72.

- Moren, A.-S., A. Lindroth, J. Flower-Ellis, E. Cienciala and M. Molder 2000. Branch transpiration of pine and spruce scaled to tree and canopy using needle biomass distributions. *Trees*. 14:384-397.
- Morikawa, Y., S. Hattori and Y. Kiyono 1986. Transpiration of a 31-year-old *Chamaecyparis obtusa* Endl. stand before and after thinning. *Tree Physiology*. 2:105-114.
- Naeem, S., L.J. Thompson, S.P. Lawler, J.H. Lawton and R.M. Woodfin 1994. Declining biodiversity can alter the performance of ecosystems. *Nature*. 368:734-6.
- Nobel, P.S. 1991. *Physiochemical and environmental plant physiology*. Academic Press, San Diego, CA. 635 p.
- Oliveras, I. and P. Llorens 2001. Medium-term sap flux monitoring in a Scots pine stand: analysis of the operability of the heat dissipation method for hydrological purposes. *Tree Physiology*. 21:473-480.
- Oren, R., N. Phillips, G. Katul, B.E. Ewers and D.E. Pataki 1998. Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. *Annales Des Sciences Forestières*. 55:191-216.
- Parker, G.G., M.M. Davis and S.M. Chapotin 2002. Canopy light transmittance in Douglas-fir - western hemlock stands. *Tree Physiology*. 22:147-157.
- Pataki, D.E., R. Oren, G. Katul and J. Sigmon 1998. Canopy conductance of *Pinus taeda*, *Liquidambar styraciflua* and *Quercus phellos* under varying atmospheric and soil water conditions. *Tree Physiology*. 18:307-315.
- Pataki, D.E., R. Oren and W.K. Smith 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology*. 81:2557-2566.
- Perry, C.H., R.C. Miller and K.N. Brooks 2001. Impacts of short-rotation hybrid poplar plantations on regional water yields. *Forest Ecology and Management*. 143:143-151.
- Phillips, N., B. Bond, N. McDowell and M.G. Ryan 2002. Canopy and hydraulic conductance in young, mature, and old Douglas-fir trees. *Tree Physiology*. 22:205-211.
- Phillips, N., A. Nagchaudhuri, R. Oren and G. Katul 1997. Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees*. 11:412-419.
- Phillips, N. and R. Oren 2001. Intra- and Inter-annual variation in transpiration of a pine forest. *Ecological Applications*. 11:385-396.
- Phillips, N., R. Oren and R. Zimmermann 1996. Radial patterns of xylem sap flow in non-, diffuse-, and ring-porous tree species. *Plant, Cell, and Environment*. 19:983-990.
- Post, D.A. and J.A. Jones 2001. Hydrologic regimes of forested, mountainous, headwater basins in New Hampshire, North Carolina, Oregon, and Puerto Rico. *Advances In Water Resources*. 24:1195-1210.

- Purvis, A. and A. Hector 2000. Getting the measure of biodiversity. *Nature*. 405:212-219.
- Quinn, P.F., K.J. Beven and R. Lamb 1995. The $\ln(\alpha/\tan\beta)$ index: how to calculate it and how to use it within the TOPMODEL framework. *Hydrological Processes*. 9:161-182.
- Radosevich, S.R. 1987. Methods to study interactions among crops and weeds. *Weed Technology*. 1:190 - 198.
- Radosevich, S.R., J. Holt and C. Ghersa 1997. *Weed Ecology: Implications for Management*. John Wiley & Sons, Inc., New York.
- Ramsey, F.L. and D.W. Schafer 1997. *The Statistical Sleuth: A Course in Methods of Data Analysis* Ed. C. Mazow. Duxbury Press, Belmont, CA. 742 p.
- Rawlings, J.O., S.G. Pantula and D.A. Dickey 1989. *Applied Regression Analysis: A Research Tool* Eds. G. Casella, S. Fienberg and I. Olkin. Springer-Verlag, New York. 657 p.
- Roberts, S., R.A. Vertessy and R. Grayson 2001. Transpiration from *Eucalyptus sieberi* (L. Johnson) forests of different age. *Forest Ecology and Management*. 143:153-161.
- Rothe, A. and D. Binkley 2001. Nutritional interactions in mixed species forests: a synthesis. *Canadian Journal of Forest Research*. 31:1885-1870.
- Running, S.W. 1976. Environmental control of leaf water conductance in conifers. *Journal of Forest Resources*. 6:104-112.
- Running, S.W. and J.C. Coughlan 1988. A general model of forest ecosystem processes for regional applications I. hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling*. 42:125-154.
- Runyon, J., R.H. Waring, S.N. Goward and J.M. Welles 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Ecological Applications*. 42:226-237.
- Ryan, M.G., D. Binkley and J.H. Fownes 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research*. 27:213-262.
- Ryan, M.G., B. Bond, B.E. Law, R.M. Hubbard, D. Woodruff, E. Cienciala and J. Kucera 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia*. 124:553-560.
- Ryan, M.G. and B.J. Yoder 1997. Hydraulic limits to tree height and tree growth. *BioScience*. 47:235-242.
- Saugier, B., A. Granier, J.Y. Pontailier, E. Defrene and D.D. Baldocchi 1997. Transpiration of a boreal pine forest measured by branch bag, sap flow and micrometeorological methods. *Tree Physiology*. 17:511-519.
- Shainsky, L.J. and S.R. Radosevich 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. *Ecology*. 73:30-45.

- Shainsky, L.J., B.J. Yoder, T.B. Harrington and S.S.N. Chan 1994. Physiological Characteristics of Red Alder: Water Relations and Photosynthesis. *In* The Biology and Management of Red Alder Eds. D.E. Hibbs, D.S. DeBell and R.F. Tarrant. OSU Press, Corvallis, OR, pp. 73-91.
- Smith, D.M. and S.J. Allen 1996. Measurement of sap flow in plant stems. *Journal of Experimental Botany*. 47:1833-1844.
- Sperry, J.S., K.L. Nichols, J.E.M. Sullivan and S.E. Eastlack 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of Northern Utah and interior Alaska. *Ecology*. 75:1736-1752.
- Spies, T.A. and J.F. Franklin 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. *In* Wildlife and Vegetation of Unmanaged Douglas-fir Forests Eds. K.B. Aubry and M.H. Brookes. USDA Forest Service PNW Research Station, Portland, OR, pp. 91-110.
- Stape, J.L., D. Binkley, M.G. Ryan and A.N. Gomes 2003. Water, light and nitrogen use efficiency in clonal *Eucalyptus grandis* x *urophylla* plantations along a climatic gradient in northeastern Brazil. *Forest Ecology and Management*. In Press
- Stein, T. 2002. A clear-cut drought solution? Logging urged to boost runoff, but eco-groups object. *In* Denver Post, Denver, CO.
- Stratton, L.C., G. Goldstein and F.C. Meinzer 2000. Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia*. 124:309-317.
- Swank, W.T. and D.A. Crossley 1988. *Forest Hydrology and Ecology at Coweeta*. Springer-Verlag, New York. 459 p.
- Swank, W.T. and J.E. Douglass 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science*. 185:857-859.
- Swanson, F.J. and M.E. James 1975. Geology and geomorphology of the H. J. Andrews Experimental Forest, western Cascades, Oregon. PNW Forest Range Experiment Station, Portland, OR, p. 14.
- Swanson, R.H. 1994. Significant historical developments in thermal methods for measuring sap flow in trees. *Agricultural and Forest Meteorology*. 72:113-132.
- Swanson, R.H. and W.A. Whitfield 1981. A numerical analysis of heat pulse velocity theory and practice. *Journal of Experimental Botany*. 32:221-239.
- Taiz, L. and E. Zeiger 1991. *Plant Physiology* Ed. E.B. Brady. The Benjamin/Cummings Publishing Company, Inc., Redwood City, CA. 565 p.
- Thomas, S.C. and W.E. Winner 2000. Leaf area index of an old-growth Douglas-fir forest estimated from direct structural measurements in the canopy. *Canadian Journal of Forest Research*. 30:1922-1930.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology*. 77:350-363.

- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*. 78:81-92.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*. 80:1455-1474.
- Tilman, D. and J.A. Downing 1994. Biodiversity and stability in grasslands. *Nature*. 367:363-365.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie and E. Siemann 1997. The influence of functional diversity and composition on ecosystem processes. *Science*. 277:1300-1302.
- Tilman, D., D. Wedin and J. Knops 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*. 379:718-720.
- Turner, D.P., M. Guzy, M.A. Lefsky, S. Van Tuyl, O. Sun, C. Daly and B.E. Law 2002. Effects of land use and fine scale environmental heterogeneity on net ecosystem production over a temperate coniferous forest landscape. *Tellus*. In Press
- Uhlenbrook, S., M. Frey, C. Leibundgut and P. Maloszewski 2002. Hydrograph separations in a mesoscale mountainous basin at event and seasonal timescales. *Water Resources Research*. 38
- Unsworth, M.H., N. Phillips, T. Link, B. Bond, M. Falk, M. Harmon, T. Hinckley, D. Marks and K.-T. Paw U In Press. Components and controls of water flux in an old-growth Douglas-fir / western hemlock ecosystem. *Ecosystems*
- Vertessy, R.A., T.J. Hatton, P. Reece, S.K. O'Sullivan and R.G. Benyon 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiology*. 17:747-756.
- Vertessy, R.A., F.G.R. Watson and S.K. O'Sullivan 2001. Factors determining relations between stand age and catchment water balance in mountain ash forests. *Forest Ecology and Management*. 143:13-26.
- Wang, J., N.E. Ives and M.J. Lechowicz 1992. The relation of foliar phenology to xylem embolism in trees. *Functional Ecology*. 6:469-475.
- Wardle, D.A., K.I. Bonner and G.M. Barker 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. *OIKOS*. 89:11-23.
- Wardle, D.A., O. Zackrisson, G. Hornberg and C. Gallet 1997. The influence of island area on ecosystem properties. *Science*. 277:1296-1299.
- Waring, R.H. and J.F. Franklin 1979. Evergreen coniferous forests of the Pacific Northwest. *Science*. 204:1380-1386.
- Whitehead, D., P.G. Jarvis and R.H. Waring 1984. Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment. *Canadian Journal of Forest Research*. 14:692-700.
- Williams, M., E.B. Rastetter, D.N. Fernandes, M.L. Goulden, S.C. Wofsy, G.R. Shaver, J.M. Melillo, J.W. Munger, S.-M. Fan and K.J. Nadelhoffer 1996. Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand

- at Harvard Forest: the regulation of stomatal conductance by light, nitrogen, and soil/plant hydraulic properties. *Plant, Cell, and Environment*. 19:911-927.
- Wullschlegel, S.D., P.J. Hanson and D.E. Todd 2001. Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. *Forest Ecology and Management*. 143:205-213.
- Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann 1994. Evidence of reduced photosynthetic rates in old trees. *Forest Science*. 40:513-527.
- Zalewski, M. 2002. Guidelines for the Integrated Management of the Watershed - Phytotechnology and Ecohydrology. *In* Freshwater Management Series No. 5. United Nations Environment Programme, Osaka, Japan. 188 p.
- Zhang, L., W.R. Dawes and G.R. Walker 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research*. 37:701-708.
- Zhu, A.X. and D.S. Mackay 2001. Effects of spatial detail of soil information on watershed modeling. *Journal of Hydrology*. 248:54-77.
- Zimmermann, R., E.-D. Schulze, C. Wirth, E.-E. Schulze, K.C. McDonald, N.N. Vygodskaya and W. Ziegler 2000. Canopy transpiration in a chronosequence of Central Siberian pine forests. *Global Change Biology*. 6:25-37.

APPENDICES

Appendix A - One-way regression model results at the hourly time scale.

	1			2		
	hourly streamflow			hourly log(streamflow)		
	<i>n</i>	<i>r</i> ²	<i>p</i>	<i>n</i>	<i>r</i> ²	<i>p</i>
1 log(total hourly precip)	-	-	-	6794	0.07	<0.001
2 hourly log(API 0.1)	-	-	-	16303	0.08	<0.001
3 hourly log(API 0.2)	-	-	-	18060	0.11	<0.001
4 hourly log(API 0.3)	-	-	-	19552	0.13	<0.001
5 hourly log(API 0.4)	-	-	-	21016	0.15	<0.001
6 hourly log(API 0.5)	-	-	-	22517	0.17	<0.001
7 hourly log(API 0.6)	-	-	-	23913	0.20	<0.001
8 hourly log(API 0.7)	-	-	-	25101	0.22	<0.001
9 hourly log(API 0.8)	-	-	-	25899	0.23	<0.001
10 hourly log(API 0.9)	-	-	-	26185	0.21	<0.001
11 avg hourly soil moisture	15461	0.41	<0.001	15461	0.81	<0.001
12 total hourly transpiration	3791	0.06	<0.001	3791	0.10	<0.001
13 log(transpiration)	3791	0.03	<0.001	3791	0.04	<0.001
14 log(avg hourly VPD)	-	-	-	6773	0.0004	0.09
15 hourly ASMI 0.1	-	-	-	15461	0.81	<0.001
16 hourly ASMI 0.2	-	-	-	15461	0.82	<0.001
17 hourly ASMI 0.3	-	-	-	15461	0.82	<0.001
18 hourly ASMI 0.4	-	-	-	15461	0.82	<0.001
19 hourly ASMI 0.5	-	-	-	15461	0.82	<0.001
20 hourly ASMI 0.6	-	-	-	15461	0.82	<0.001
21 hourly ASMI 0.7	-	-	-	15461	0.82	<0.001
22 hourly ASMI 0.8	-	-	-	15461	0.82	<0.001
23 hourly ASMI 0.9	-	-	-	15461	0.82	<0.001

Appendix B - One-way regression model results at the daily time scale.

DAILY		1			2		
		daily streamflow			daily log(streamflow)		
		<i>n</i>	<i>r</i> ²	<i>p</i>	<i>n</i>	<i>r</i> ²	<i>p</i>
1	log(total daily precip)	-	-	-	467	0.12	<0.001
2	daily API 0.5	1096	0.54	<0.001	-	-	-
3	daily API 0.6	1096	0.60	<0.001	-	-	-
4	daily API 0.7	1096	0.65	<0.001	-	-	-
5	daily API 0.8	1096	0.68	<0.001	-	-	-
6	daily API 0.9	1096	0.68	<0.001	-	-	-
7	avg daily soil moisture	648	0.43	<0.001	648	0.82	<0.001
8	total daily transpiration	415	0.21	<0.001	415	0.27	<0.001
9	log(avg daily VPD)	-	-	-	940	0.29	<0.001
10	daily ASMI 0.1	648	0.44	<0.001	-	-	-
11	daily ASMI 0.2	648	0.44	<0.001	-	-	-
12	daily ASMI 0.3	648	0.44	<0.001	-	-	-
13	daily ASMI 0.4	648	0.44	<0.001	-	-	-
14	daily ASMI 0.5	648	0.44	<0.001	-	-	-
15	daily ASMI 0.6	648	0.44	<0.001	-	-	-
16	daily ASMI 0.7	648	0.43	<0.001	-	-	-
17	daily ASMI 0.8	648	0.41	<0.001	-	-	-
18	daily ASMI 0.9	648	0.37	<0.001	-	-	-

Appendix C - One-way regression model results at the storm time scale. Significance levels for precipitation variables (1-9) was adjusted using a Bonferroni interval of 0.013.

STORM	r1			r2			r3			r4			r5			r6		
	total hours by sight n	r ²	p	total hours by gage ht n	r ²	p	hours to 37% peak n	r ²	p	hours to 50% peak n	r ²	p	hours to 80% peak n	r ²	p	hours to 1/e of peak n	r ²	p
total precip	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
max precip	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
hours precip	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
average intensity	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
total precip -3	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
max precip -3	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
hours precip -3	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
average intensity -3	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
rising hydro slope	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
initial soil moisture	~	~	ns	44	0.25	0.001	19	0.18	0.07	~	~	ns	40	0.08	0.07	~	~	ns
potential transpiration	~	~	ns	88	0.05	0.03	30	0.13	0.05	~	~	ns	~	~	ns	~	~	ns
log(pot. transpiration)	~	~	ns	88	0.11	0.002	~	~	ns	~	~	ns	~	~	ns	34	0.12	0.04
avg log(VPD) recession	56	0.18	0.001	~	~	ns	22	0.17	0.06	~	~	ns	~	~	ns	~	~	ns
log(precip during recession)	45	0.16	0.01	45	0.19	0.002	~	~	ns	~	~	ns	~	~	ns	17	0.21	0.06

Appendix D - One-way regression model results at the storm time scale that have been log transformed. Significance levels for precipitation variables (1-9) was adjusted using a Bonferroni interval of 0.013. The best metric to represent storm recession appeared to be the total hours for Q to reach 20% of initial gage height (Appendix D column "log r²"). S was again closely coupled to Q at the storm scale (29% variation explained), but not nearly as close as it was at the hourly or daily scales (Table 2). Potential T explained 12% of the variation. V was not significantly related. Several metrics were explored to represent P at the storm scale (Appendix C, D). Those that were significantly related to storm recession (hours to reach 20% gage ht) include the total P between the beginning and peak hydrograph raise (similarly when you include three hours prior to storm beginning), and the slope of the rising limb of the hydrograph. I found that the amount of P occurring during the recession itself was also important (Appendix D; 24% variation explained). Storms receded faster in the wet season (95% CI = -0.0959+/-0.012 log(cfs)/log(hour)) than the dry season (95% CI = -0.2924+/-0.056 log(cfs)/log(hour)).

STORM	log(t1)			log(t2)			log(t3)			log(t4)			log(t5)			log(t6)		
	n	r ²	p	n	r ²	p	n	r ²	p	n	r ²	p	n	r ²	p	n	r ²	p
total precip	~	~	ns	88	0.09	0.004	~	~	ns	~	~	ns	70	0.14	0.002	~	~	ns
max precip	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
hours precip	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
average intensity	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
total precip -3	~	~	ns	88	0.10	0.003	~	~	ns	~	~	ns	70	0.12	0.004	~	~	ns
max precip -3	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
hours precip -3	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
average intensity -3	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
rising hydro slope	~	~	ns	88	0.08	0.009	~	~	ns	~	~	ns	~	~	ns	~	~	ns
initial soil moisture	~	~	ns	44	0.29	<0.001	19	0.30	0.02	24	0.19	0.03	40	0.22	0.002	19	0.31	0.01
potential transpiration	~	~	ns	88	0.03	0.09	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(pot. transpiration)	~	~	ns	88	0.12	0.001	~	~	ns	~	~	ns	~	~	ns	34	0.10	0.07
log (avg V/PD) recession	56	0.18	0.001	~	~	ns	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.1)	~	~	ns	88	0.04	0.06	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.2)	~	~	ns	88	0.04	0.05	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.3)	~	~	ns	88	0.04	0.05	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.4)	~	~	ns	88	0.04	0.05	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.5)	~	~	ns	88	0.04	0.05	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.6)	~	~	ns	88	0.05	0.05	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.7)	~	~	ns	88	0.05	0.04	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.8)	88	0.03	0.07	88	0.05	0.03	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(avg API0.9)	88	0.04	0.07	88	0.04	0.05	~	~	ns	~	~	ns	~	~	ns	~	~	ns
log(precip during recession)	45	0.13	0.02	45	0.24	0.001	~	~	ns	~	~	ns	~	~	ns	17	0.27	0.03

Appendix E - Descriptors and units for variables used in regression analyses.

VARIABLE	hourly	daily	storm
streamflow	Q, log(cfs) log(streamflow)	Q, log(cfs) log(streamflow)	R, log(hours) log(recession time by gage ht.)
soil moisture	S, m ² m ⁻² soil moisture	S, m ² m ⁻² soil moisture	S, m ² m ⁻² initial soil moisture
transpiration	T, mm transpiration	T, mm transpiration	T, log(mm) log(potential transpiration)
VPD	V, log(mbar) log(VPD)	V, log(mbar) log(VPD)	V, log(mbar) log(avg. VPD during recession)
precipitation	P, mm API 0.8	P, mm API 0.9	P, log(mm) log(total precip. prior to storm peak)