1

OF/DE

1

PM-1 3 1/2 x 4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

PRECISIONSM RESOLUTION TARGETS

Regulation of Transpiration in Naturally-Occurring
Picea mariana (Mill.) B.S.P.

David S. Kubien, B.Sc. (For.)

A Thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of the requirements
for the degree of
Master of Science
Department of Biology

Carleton University
Ottawa, Ontario
Canada

© David S. Kubien, 1996.

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395, Wellington Street
Ottawa (Ontario)
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file *Notre référence*

Your file *Notre référence*

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

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

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

ISBN 0-612-19539-2

Canada

Name _____

Dissertation Abstracts International and Masters Abstracts International are arranged by broad, general subject categories. Please select the one subject which most nearly describes the content of your dissertation or thesis. Enter the corresponding four-digit code in the spaces provided.

SUBJECT TERM

UMI

SUBJECT CODE:

Subject Categories

THE HUMANITIES AND SOCIAL SCIENCES

COMMUNICATIONS AND THE ARTS

Architecture 0729
Art History 0337
Cinema 0900
Dance 0378
Fine Arts 0357
Information Science 0723
Journalism 0391
Library Science 0399
Mass Communications 0708
Music 0413
Speech Communication 0459
Theater 0465

EDUCATION

General 0515
Administration 0514
Adult and Continuing 0516
Agricultural 0517
Art 0273
Bilingual and Multicultural 0282
Business 0488
Community College 0275
Curriculum and Instruction 0272
Early Childhood 0518
Elementary 0524
Finance 0277
Guidance and Counseling 0519
Health 0480
Higher 0745
History of 0520
Home Economics 0278
Industrial 0521
Language and Literature 0279
Mathematics 0280
Music 0522
Philosophy of 0998
Physical 0523

Psychology 0525
Reading 0535
Religious 0527
Sciences 0714
Secondary 0533
Social Sciences 0534
Sociology of 0340
Special 0529
Teacher Training 0530
Technology 0710
Tests and Measurements 0288
Vocational 0747

LANGUAGE, LITERATURE AND LINGUISTICS

Language 0679
Ancient 0289
Linguistics 0290
Modern 0291
Literature 0401
Classical 0294
Comparative 0295
Medieval 0297
Modern 0298
African 0316
American 0591
Asian 0305
Canadian (English) 0352
Canadian (French) 0355
English 0593
Germanic 0311
Latin American 0312
Middle Eastern 0315
Romance 0313
Slavic and East European 0314

PHILOSOPHY, RELIGION AND THEOLOGY

Philosophy 0422
Religion 0318
General 0321
Biblical Studies 0319
Clergy 0320
History of 0322
Philosophy of 0469
Theology 0323

SOCIAL SCIENCES

American Studies 0323
Anthropology 0324
Archaeology 0326
Cultural 0327
Physical 0310
Business Administration 0272
General 0270
Accounting 0454
Banking 0338
Marketing 0385
Canadian Studies 0501
Economics 0503
General 0505
Agricultural 0508
Commerce-Business 0509
Finance 0510
History 0511
Labor 0358
Theory 0366
Folklore 0351
Geography 0578
Gerontology 0578
History 0578
General 0578

Ancient 0579
Medieval 0581
Modern 0582
Black 0328
African 0331
Asia, Australia and Oceania 0332
Canadian 0334
European 0335
Latin American 0336
Middle Eastern 0333
United States 0337
History of Science 0585
Law 0398
Political Science 0615
General 0616
International Law and Relations 0617
Public Administration 0614
Recreation 0814
Social Work 0452
Sociology 0626
General 0627
Criminology and Penology 0938
Demography 0631
Ethnic and Racial Studies 0628
Individual and Family 0629
Studies 0630
Industrial and Labor 0700
Relations 0344
Public and Social Welfare 0709
Social Structure and Development 0999
Theory and Methods 0453
Transportation 0453
Urban and Regional Planning 0453
Women's Studies 0453

THE SCIENCES AND ENGINEERING

BIOLOGICAL SCIENCES

Agriculture 0473
General 0285
Agronomy 0475
Animal Culture and Nutrition 0476
Animal Pathology 0359
Food Science and Technology 0478
Forestry and Wildlife 0479
Plant Culture 0480
Plant Pathology 0817
Plant Physiology 0777
Range Management 0746
Wood Technology 0306
Biology 0287
General 0308
Anatomy 0309
Biochemistry 0329
Botany 0353
Cell 0369
Ecology 0793
Entomology 0410
Genetics 0307
Limnology 0317
Microbiology 0416
Molecular 0403
Neuroscience 0821
Oceanography 0778
Physiology 0472
Radiation 0786
Veterinary Science 0760
Zoology 0760
Biophysics 0760
General 0760
Medical 0760

Geology 0370
Geography 0372
Geophysics 0373
Hydrology 0388
Mineralogy 0411
Palaeontology 0345
Paleoecology 0426
Paleogeography 0418
Paleontology 0985
Palynology 0427
Physical Geography 0368
Physical Oceanography 0415

HEALTH AND ENVIRONMENTAL SCIENCES

Environmental Sciences 0768
Health Sciences 0566
General 0300
Audiology 0992
Chemotherapy 0567
Dentistry 0350
Education 0769
Hospital Management 0758
Human Development 0982
Immunology 0564
Medicine and Surgery 0347
Mental Health 0569
Nursing 0570
Nutrition 0380
Obstetrics and Gynecology 0354
Occupational Health and Safety 0381
Ophthalmology 0571
Pathology 0519
Pharmacology 0572
Pharmacy 0382
Physical Therapy 0573
Public Health 0574
Radiology 0575
Recreation 0575

Speech Pathology 0460
Toxicology 0383
Home Economics 0386

PHYSICAL SCIENCES

Pure Sciences 0465
Chemistry 0749
General 0486
Agricultural 0487
Analytical 0488
Biochemistry 0738
Inorganic 0490
Nuclear 0491
Organic 0494
Physical 0495
Pharmaceutical 0754
Polymer 0405
Radiation 0405
Mathematics 0405
Physics 0405
General 0986
Acoustics 0406
Astronomy and Astrophysics 0408
Atmospheric Science 0748
Atomic 0407
Electronics and Electricity 0798
Elementary Particles and High Energy 0799
Fluid and Plasmas 0409
Molecular 0410
Nuclear 0782
Optics 0754
Radiation 0411
Solid State 0463
Statistics 0346
Applied Sciences 0984
Applied Mechanics 0984
Computer Science 0984

Engineering 0537
General 0538
Aerospace 0539
Agricultural 0540
Automotive 0541
Biomedical 0542
Chemical 0543
Civil 0544
Electronics and Electrical 0348
Heat and Thermodynamics 0545
Hydraulic 0546
Industrial 0547
Marine 0794
Materials Science 0548
Mechanical 0743
Metallurgy 0551
Mining 0552
Nuclear 0549
Packaging 0745
Petroleum 0554
Sanitary and Municipal 0790
System Science 0428
Geotechnology 0796
Operations Research 0795
Plasma Technology 0994
Textile Technology 0994

PSYCHOLOGY

General 0421
Behavioral 0384
Clinical 0422
Developmental 0423
Experimental 0424
Industrial 0425
Personality 0989
Physiological 0349
Psychiatry 0432
Psychometrics 0451
Social 0451

EARTH SCIENCES

Biogeochemistry 0425
Geochemistry 0996

The undersigned recommend to the Faculty of Graduate Studies and Research
acceptance of the Thesis

"Regulation of Transpiration in Naturally-Occurring *Picea mariana* (Mill.)
B.S.P."

submitted by David. S. Kubien in partial fulfillment of the requirements for the
degree of Master of Science.

Thesis Supervisor

Departmental Chair

Carleton University, 1996

Abstract

Concurrent measurements of sap-flow, leaf gas-exchange and meteorological parameters were made in a mature *Picea mariana* (Mill.) B.S.P. stand during June and July of 1995. Whole-tree transpiration was about 2.0 mm day⁻¹ early in the study, and had declined to about 0.75 mm day⁻¹ by early July. The study period was warmer and drier than normal, but the trees made extensive use of readily available groundwater. Low transpiration rates and high vapour pressure deficits resulted in very low total conductances to water vapour, typically less than 25 mmol m⁻² s⁻¹. Although stomatal conductances were low, the arrangement of the foliage was such that the boundary layer provided an important resistance to diffusion. Transpiration was found to be poorly coupled to the atmosphere, with average Ω values of 0.59 and 0.82 in the upper and lower canopy, respectively. This surprising result has important implications for scaling porometric transpiration data to the stand level.

Acknowledgements

I would like to take the opportunity to thank my supervisor, Dr. Larry Flanagan, for being so enthusiastic about science in general and the boreal forest in particular. This enthusiasm has rubbed off. Along the same line, thanks to Dr. Rob Guy (UBC) for helping me find my way to Carleton and Larry's lab.

Dr. Tim Williams has provided steady contact with reality, and many helpful conversations about what exactly it is that plants do. Dr. Martin Canny has helped me learn to question things that I might previously have taken for granted. Other researchers have been willing and able to share insights and information: Dr. Tom Hatton (CSIRO, Australia), Dr. Renee Brooks (U. of Utah), Jason Vogel and Mary Williams (U. of Wisconsin), and Tim Martin (U. of Washington).

Carleton has been a treat of a place in which to work, thanks in large part to Greg, Rob, Mikalu, Steve, Claudia, Joan, and Mother Angela. Giles and Natalie at the U. of Ottawa Stable Isotope Facility are extremely patient and helpful.

Thanks as always to my family, especially to Karyn for not freaking out while I did.

In Saskatchewan, the sh*tter folk have left fond memories. Thanks also to the fire folk, especially Eric (49) and Jack (202), for not letting the study site go up in smoke. Those people and Juan Valdez let the field season happen.

Thanks to Carleton University, the Natural Science and Engineering Research Council of Canada, and the Atmospheric Environment Service of Environment Canada for financial support.

Lastly, I wish to thank Paul Sargent, who provided this rather green grad student with a good foil and a stellar field assistant. No sir, this would not have been as much fun without his help, insight and ability to deal with any *situation*.

'...and the trees were all kept equal by hatchet, axe, and saw.'

Peart, 1978.

Table of Contents

Acceptance Form	ii
Abstract	iii
Acknowledgements	iv
Table of Contents	v
List of Tables, Figures and Appendices	vi
List of Symbols and Abbreviations	viii
Introduction	1
Review of the Literature	
Omega Theory	4
Sap-Flow Measurement	8
Stable Isotopes and Water Sources	12
Methods and Materials	
Site Description	17
Sap-Flow in Branches	17
Whole Tree Sap-Flow	19
Sampling for Isotope Analysis	20
Gas-Exchange Measurements	21
Micrometeorological Measurements	22
Leaf Area Determination	23
Calculation of the Omega Coefficient	24
The Ω Data Set	25
Results	27
Discussion	
Validity of the Heat-Balance Measurements	43
Error Analysis	43
Transpiration and Stomatal Conductance in <i>Picea mariana</i>	46
The Source of Water for <i>Picea mariana</i>	48
The Role of the Boundary Layer	49
The Decoupling Coefficient	51
The Effect of Decoupling on Scaling Transpiration	54
Conclusions	56
References	65
Appendices	73

List of Tables

	Page
1. Characteristics of black spruce branches used in this study.	26
2. Observed and expected weather conditions for the study site.	32
3. Uptake of recent precipitation by <i>Picea mariana</i> .	33

List of Figures

1. Schematic diagram of the heat-balance sap-flow gauge.	15
2. Stable hydrogen isotopic composition of precipitation collected at Prince Albert SK (53°13'N 105°41'W).	16
3. Comparison of heat-balance and lysimetric measurements of water-use by <i>Picea mariana</i> seedling.	34
4. Average branch-level transpiration in a <i>Picea mariana</i> forest.	35
5. Average course of PAR at the branch-level and in the canopy of a <i>Picea mariana</i> forest.	36
6. Average branch-level transpiration and PAR in the lower canopy branch.	37
7. Whole-tree transpiration expressed on a ground-area basis.	38
8. Stable hydrogen isotopic composition of stem and soil water.	39
9. Average stomatal, boundary layer, and total conductances to water vapour in <i>Picea mariana</i> .	40
10. Vapour-pressure deficit between the branch and the canopy air, and calculated at the leaf surface in <i>Picea mariana</i> .	41
11. Average Ω values in the upper and lower canopy of a <i>Picea mariana</i> forest.	42
12. The effect of direct light on the accuracy of the thermocouples	57

	Page
13. Transpiration as a function of VPD and VPDs.	58
14. A theoretical normalized wind profile for the study site.	59
15. Transpiration as a function of stomatal conductance and isothermal net radiation.	60
16. Measured transpiration against the imposed and equilibrium component rates.	61
17. Actual transpiration against the Ω -weighted prediction.	62
18. A comparison of Ω calculated with and without consideration of radiative coupling.	63
19. Scaling of branch-level isothermal net radiation to compare with ground-area based measurements.	64

List of Appendices

	Page
A. Analysis of variance summary tables describing the differences between branches and time periods.	73
B. Error calculations for the data set.	75
C. Calculation of the theoretical wind profile.	76
D. Calculation of the effective lengths of black spruce needles, from the wind profile and the boundary layer conductance observations.	77
E. Calculation of the isothermal net radiation.	79

List of Symbols and Abbreviations

C_p	Heat capacity of air ($\text{J g}^{-1} \text{ } ^\circ\text{C}^{-1}$)
C_{pw}	Heat capacity of water ($\text{J g}^{-1} \text{ } ^\circ\text{C}^{-1}$)
C_s	Heat capacity of sap ($\text{J g}^{-1} \text{ } ^\circ\text{C}^{-1}$)
C_w	Heat capacity of wood ($\text{J g}^{-1} \text{ } ^\circ\text{C}^{-1}$)
dbh	Diameter at breast height (cm)
E	Transpiration rate ($\text{mmol m}^{-2} \text{ s}^{-1}$, or mm day^{-1})
e_a	Atmospheric vapour pressure (mbar)
e_i	Intercellular vapour pressure (mbar)
E_{eq}	Equilibrium transpiration rate ($\text{mmol m}^{-2} \text{ s}^{-1}$)
E_{imp}	Imposed transpiration rate ($\text{mmol m}^{-2} \text{ s}^{-1}$)
E_{pred}	Transpiration predicted from Ω ($\text{mmol m}^{-2} \text{ s}^{-1}$)
g_r	Radiative transfer conductance ($\text{mmol m}^{-2} \text{ s}^{-1}$)
g_{wb}	Boundary layer conductance to water vapour ($\text{mmol m}^{-2} \text{ s}^{-1}$)
g_{ws}	Stomatal conductance to water vapour ($\text{mmol m}^{-2} \text{ s}^{-1}$)
g_{wt}	Total conductance to water vapour ($\text{mmol m}^{-2} \text{ s}^{-1}$)
HASL	Leaf surface area (cm^2 , or m^2)
h_c	Convection coefficient ($\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$)
LAI	Leaf area index
P	Atmospheric pressure (mbar)
PAR	Photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
P_{in}	Power applied to heat-balance gauge (W)
PR_{ni}	Predicted isothermal net radiation (W m^{-2})
Q_d	Downstream conductive heat flux (W)
Q_f	Convective heat flux (W)
Q_r	Radial heat flux (W)
Q_u	Upstream conductive heat flux (W)
RH	Relative humidity (%)
R_n	Net radiation (W m^{-2})
R_{ni}	Isothermal net radiation (W m^{-2})
SMOW	Standard mean ocean water
T_a	Air temperature ($^\circ\text{C}$)

T_l	Leaf temperature ($^{\circ}\text{C}$)
V_h	Heat pulse velocity (m s^{-1})
V_h'	Wound corrected heat pulse velocity (m s^{-1})
VPD	Vapour pressure deficit (mbar)
VPD _s	Vapour pressure deficit at the leaf surface (mbar)
V_s	Sap velocity (m s^{-1})
β	Bowen ratio
ϵ	Ratio of increase of latent to sensible heat content
λ	Heat of vapourisation of water (J mol^{-1})
ρ	Density of air (g m^{-3})
ρ_s	Density of sap (g m^{-3})
ρ_w	Density of wood (g m^{-3})
σ	Stefan-Boltzman constant ($\text{W m}^{-2} \text{ }^{\circ}\text{K}^{-4}$)
Ω	Decoupling coefficient

Introduction

The past several decades have brought increased concern over the effects that the human population may be having on the terrestrial biosphere. Public pressure to determine the impact of land-use practices and increasing concentrations of the so-called 'greenhouse gases' has risen steadily during this period. It is now widely supposed that forests play important roles in regulating many processes in the biosphere, such as landscape water balances (Dawson 1993a, Sellers et al. 1996). Understanding the function of such systems is a crucial step toward predicting the results of increased deforestation and climate changes.

Predicting the future structure and behaviour of forested ecosystems requires the construction of detailed, rigorous models. Modelling is essential since we cannot, in many cases, conduct experiments to determine the impacts of global changes (for example, increasing concentrations of CO_2) at very large scales (Jarvis 1995). 'Bottom-up' models represent the classic approach of using observations made at a certain scale to make predictions at a larger scale (Jarvis 1993). Models produced by physiologists tend to be valid on small spatial (such as the leaf or the individual plant) and temporal scales (such as one diurnal cycle). It is important that these models be linked to larger spatial and temporal scales if they are to be used to predict wider environmental processes (Whitehead and Hinckley 1991).

Increasing the useful scale of physiological models can be done in a general sense by summing (integrating) the predicted fluxes. Integration assumes that the controlling factors at one scale have the same impact at a larger scale (Whitehead and Hinckley 1991). Such assumptions are not always met. Jarvis and McNaughton (1986) showed that at very small spatial scales (such as an individual stomate) a proportional change in stomatal conductance to water vapour results in an equal change

in transpiration. At the landscape level the same change in stomatal conductance has a much smaller effect; transpiration from a vegetated landscape is controlled largely by the net flux of radiation and the ambient temperature (Jarvis and McNaughton 1986). By changing the scale of reference, the same process (transpiration) is subject to contradictory interpretation of the controlling force: each interpretation is correct at its own scale. This demonstrates a common problem associated with shifting between scales: controlling variables can vary in time and space (Baldochi 1993).

Integrating physiological processes directly fails to recognize that counteractive processes may come into effect. Accounting for any negative feedback mechanisms (encountered upon changing spatial or temporal reference) requires the use of scaling factors (McNaughton and Jarvis 1991). A severe constraint in scaling transpiration from the leaf to the community is the influence of the boundary layer (Meinzer 1993). The omega (Ω) factor permits effective scaling of the forces that drive transpiration from individual leaves to the forest community (Whitehead and Hinckley 1991). In essence, Ω describes the extent to which transpiration is coupled to the atmosphere: low values of Ω indicate close coupling, or strong physiological control of transpiration. Conversely, high values of Ω indicate that transpiration is poorly coupled to ambient atmospheric conditions, and that physiological control of transpiration is relatively poor.

The Boreal-Ecosystem Atmosphere Study (BOREAS) was established to examine the interaction between the boreal forest biome and the atmosphere. Boreal forests comprise one of earth's largest ecosystems, and are expected to have a significant role in the global cycles of CO_2 and water (D'Arrigo et al. 1987). During the BOREAS field season in 1994 surprisingly low evaporation rates, corresponding to high Bowen ratios (β), were observed throughout the study area, indicating a strong control on

transpiration (Sellers et al. 1995). This study was undertaken to describe this control, and to examine the role of groundwater and precipitation on transpiration, in a mature *Picea mariana* (Mill.) B.S.P. forest. Recent technical and conceptual advances have simplified the process of determining Ω (Hinckley et al. 1994). Simultaneous measurements of transpiration, gas-exchange, and micrometeorological parameters have been used to assess the control of transpiration in a variety of tropical and temperate species (e.g. Meinzer et al. 1993, Hinckley et al. 1994, Meinzer et al. 1995). A similar strategy was employed here to determine the coupling between branch-level transpiration and the canopy atmosphere in black spruce. An analysis of the stable hydrogen isotopes of water was added to the approach, in order to identify the role of precipitation inputs to the system.

Review of the Literature

Omega Theory

Equations using a combination of aerodynamic and energy balance theory have been successfully used to analyse the relationships between transpiration, meteorological factors, and the properties of the vegetation. Considering for the moment an individual leaf, the Penman-Monteith equation can be written (Jarvis 1985):

$$E = \Omega E_{eq} + (1 - \Omega) E_{imp} \quad (1)$$

so that transpiration (E) is expressed as a combination of an equilibrium term (E_{eq}) and an imposed term (E_{imp}). The equilibrium transpiration is:

$$E_{eq} = \frac{\epsilon R_n}{\lambda(\epsilon + 1)} \quad (2)$$

where ϵ is the rate of change of latent heat content to sensible heat content of saturated air, R_n is net radiation, and λ is the latent heat of vaporisation of water. The imposed term is:

$$E_{imp} = \frac{g_{ws} VPD}{P} \quad (3)$$

where g_{ws} is the stomatal conductance to water vapour, VPD is the ambient vapour pressure deficit, and P is atmospheric pressure. The VPD is determined at a reference point chosen such that it is unaffected by changes in stomatal conductance (e.g. outside of the leaf boundary layer) (Jarvis and McNaughton 1986). The relative importance of

each term is described by the dimensionless decoupling coefficient Ω , which ranges between zero and one. For an amphistomatous leaf (e.g. stomata on both sides), Ω has a value of:

$$\Omega = \frac{\epsilon + 1}{(\epsilon + 1 + g_{wb} / g_{ws})} \quad (4)$$

where g_{wb} is the boundary layer conductance to water vapour. Low values of Ω arise when $g_{wb} \gg g_{ws}$; in this case the ambient vapour pressure deficit is imposed at the surface of the leaf, and transpiration is well-coupled to the atmosphere. A proportional change in stomatal conductance will result in a equal change in transpiration when $\Omega=0$, and will not affect the VPD experienced by the plant. In the opposite case (e.g. Ω tending toward one) transpired water vapour accumulates in the boundary layer, and the VPD experienced by the plant attains an equilibrium value. When g_{wb} is relatively low, transpiration is effectively decoupled from the atmosphere, and proceeds at the equilibrium rate.

This derivation implicitly assumes that net radiation is independent of surface temperature (McNaughton and Jarvis 1991) although net radiation is dependent on this variable to some extent (Monteith and Unsworth 1990). This dependence can be treated by using the isothermal net radiation, defined as: 'the net radiation that would be received in the same environment by an identical surface at air temperature' (Monteith 1973, p. 163). Martin (1989) used this concept to derive new expressions for Ω ,

$$\Omega = \frac{\epsilon + 1 + g_r / g_{wb}}{\epsilon + 1 + (g_r + g_{wb}) / g_{ws} + g_r / g_{wb}} \quad (5)$$

and for the equilibrium transpiration rate:

$$E_{eq} = \frac{\epsilon R_{ni}}{\lambda(\epsilon + 1 + g_r / g_{wb})} \quad (6)$$

where R_{ni} is the isothermal net radiation, and g_r is the radiative transfer conductance.

The imposed transpiration rate is unchanged. The radiative conductance has a value of:

$$g_r = \frac{4\sigma T_a^3}{\rho c_p} \quad (7)$$

where σ is the Stefan-Boltzmann constant, T_a is air temperature, ρ and C_p are the density and the specific heat of air, respectively (Monteith and Unsworth 1990). When the leaf is in radiative equilibrium with the surrounding air (i.e. the temperature difference between the leaf and the air is zero) Ω will have the same value with either formulation. In the case where radiative coupling is poor, the original formulation of Ω (equation 4) overestimates the extent of the decoupling of transpiration to the atmosphere (Martin 1989).

Transpiration becomes less sensitive to changes in stomatal conductance as Ω tends toward one. It is possible to define a reference point for the measurement of VPD such

that it is unaffected by changes in stomatal conductance. Indeed, in order to examine the effect of changing stomatal conductance on transpiration solely, such a reference must be defined. This was done explicitly in the analysis of Jarvis and McNaughton (1986). Clearly then, an Ω coefficient can be defined at different scales, although the essential meaning remains the same. The calculation of a leaf-level decoupling coefficient (Ω_l) was shown in equations 4 and 5, although in practice clusters of leaves are usually considered. When leaves form part of an extended canopy, VPD within the canopy will no longer be independent of changes in stomatal conductance (Jarvis 1985). In this case, the reference location must be located outside of the boundary layer of the canopy, and a canopy conductance (g_{wc}) must be determined in order to calculate a canopy-level decoupling coefficient (Ω_c).

Omega Values for Various Species

Relatively few values of Ω appear in the literature, and most studies have dealt with broad-leafed species. Kostner et al. (1992) measured whole-tree transpiration rates, calculated g_{wh} from wind-profile theory, and determined a maximum Ω_c value of 0.35 in *Nothofagus* spp. Jarvis and McNaughton (1986) report that Ω_l varies between 0.5 and 0.1 for both beech and apple, as wind speed increases. An average Ω_l value of 0.2 was found for *Fagus sylvatica* L., using a calculated boundary layer conductance (Herbst 1995). Using the approach upon which the current study was modelled, Meinzer and his co-workers (1993, 1995) determined an Ω_c of 0.75 and an Ω_l of 0.54 in the tropical tree species *Miconia argentea* (SW.) DC. and *Anadcardium excelsium* (Bertero and

Balb.) Skeels, respectively. The same approach was used to determine Ω_l of 0.66 in a *Populus* hybrid (Hinckley et al. 1994).

Coniferous species are expected to be well-coupled to the atmosphere, although few values have been reported (Whitehead and Hinckley 1991). Using a boundary layer conductance calculated from wind profiles, Lafleur (1992) calculated an Ω_l value of 0.1 for *Picea mariana*. In *Pinus sylvestris* L., Ω_c was as high as 0.4 (Whitehead et al. 1984). Jarvis and McNaughton (1986) report that Ω_l in *Picea sitchensis* (Bong.) Carr. can be as high as 0.46 when wind speeds are very low, although most of the values reported were less than 0.2.

Sap-Flow Measurement

Sap-flow measurements provide direct methods for obtaining estimates of transpiration (Dugas 1990). Two thermal methods for measuring sap flow in plants have been utilized. With the heat-balance approach, either a constant or compensating supply of heat is applied to the stem, and the mass flow of water is calculated by balancing the fluxes of heat into and out of the stem (Baker and Van Bavel 1987). The heat-pulse method uses heat as a tracer to determine the sap velocity, which can be multiplied by the conducting area to obtain an estimate of flux (Swanson and Whitfield 1981).

The origin of the steady-state heat-balance method can be traced back to G.H. Vieweg and H. Ziegler (1960, cited by Baker and Van Bavel 1987). This approach uses a flexible heater encircling the stem (providing a steady amount of heat), which is enclosed by a layer of insulation. Strategically placed temperature sensors monitor the temperature gradients which are used to resolve the heat-balance. The method is non-

invasive, and does not require empirical calibration (Dugas 1990). A schematic diagram of a typical heat-balance sap-flow gauge is shown in Figure 1. The continuous heat input must be balanced by the flow of heat out of the stem, which can be either radiated outward, conducted up or down the stem, or carried convectively by the sap (Baker and Van Bavel 1987). The upward conductive heat flux (Q_u , in Watts), is calculated as:

$$Q_u = k_{st} A dT_{up} \quad (8)$$

where k_{st} is the thermal conductivity of the stem, A is the cross sectional area, and dT_{up} is the output of two differentially wired thermocouples (see Figure 1). The downward conductive heat flux is calculated in a similar manner, but using dT_{down} . Determination of the radial heat flux (Q_r , in Watts) is simplified as:

$$Q_r = K_{sh} TH \quad (9)$$

where K_{sh} is the 'sheath conductance', and TH is the output of the thermopile that measures the radial temperature gradient. The sheath conductance is a function of various parameters which are constant for a given gauge configuration. In practice, it is determined during periods of zero flow. The residual heat flux is carried by the sap:

$$Q_f = P_{in} - Q_u - Q_d - Q_r \quad (10)$$

where the constant heat is P_{in} (W). Calculating the mass flow of water requires that the temperature increase of the sap be known. Thermocouples immediately adjacent to the heater are wired differentially to measure this increase ($T_{out} - T_{in}$, in Figure 1). The sap-flow is then:

$$F = \frac{Q_f}{C_{pw}(T_{out} - T_{in})} \quad (11)$$

where C_{pw} is the heat capacity of water. Throughout the calculations, it is assumed that

temperature gradients are uniform over the cross-section of the stem (Baker and Van Bavel 1987). A detailed mathematical analysis indicates that this assumption is not strictly valid, particularly at high flow rates, leading to errors in the conductive heat fluxes (Baker and Nieber 1989). However, the errors tend to cancel out, so that the actual convective heat flux is still predicted with reasonable accuracy.

Numerous studies have reported on the accuracy of the transpiration measurements made with heat-balance approach. Steinberg et al. (1990) found that heat-balance and lysimetric measurements of transpiration were within 8% over a 24 hour period in pecan. In *Eucalyptus gunnii* (Hook) F. and *Prunus serrulata* Lindl., heat-balance estimates were more closely related to actual transpiration (measured gravimetrically) than estimates made using porometry or a deuterium tracer (Dugas et al. 1993). The method gave good agreement with gravimetric measurements in soybean and corn, although at high flow rates errors of as much as 20% were noted in the monocot (Cohen et al. 1993). Groot and King (1992) applied the method to coniferous seedlings, and found good agreement with gravimetric measurements at flow rates greater than about 5 g h^{-1} .

The earliest use of the heat as a tracer to measure sap flow has be credited to Huber (1932, cited by Marshall 1958). The general heat-pulse approach is to insert a heater probe and a temperature probe(s) into a stem, and to monitor the output of the temperature probe(s). Movement of the heat-pulse is governed by conduction through wood, and by convectional transport through the sap stream (Barrett et al. 1995). Early attempts featured a single temperature probe inserted above the heater (e.g. Marshall 1958), but such a system does not allow conductive heat transport to be discerned from convection. The compensating heat-pulse technique uses temperature probes above and below the heater. The velocity of the heat pulse (V_h) is inversely proportional to the

time taken for the temperature difference between the two sensors to return to zero:

$$V_h = \frac{x_1 + x_2}{2t_0} \quad (12)$$

where x_1 and x_2 are the distances to the upstream and downstream temperature probes (from the heater) respectively, and t_0 is the time required for the temperature difference to return to zero. When the heat-pulse is applied, the downstream sensor warms by convection and conduction, the upstream sensor warms by conduction only, and the temperature differential will initially be positive. Convection of the heat pulse is affected by the presence of the probes, and by the injury to the xylem associated with their installation (Swanson and Whitfield 1981). A correction for this interruption has been determined:

$$V'_h = a + bV_h + cV_h^2 \quad (13)$$

where V'_h is the wound-corrected heat-pulse velocity and the coefficients a, b, and c were determined numerically for a given wound width and probe spacing (Swanson and Whitfield 1981). The velocity of the heat-pulse is not, however, directly indicative of the sap velocity (Marshall 1958). The sap velocity (V_s) is calculated as:

$$V_s = \frac{V'_h \rho_w (C_w + mC_s)}{\rho_s C_s} \quad (14)$$

where ρ is density, C is specific heat, the subscripts w and s refer to wood and sap, respectively, and m is the moisture content of the sapwood (Barrett et al. 1995). The

sap velocity is then multiplied by the conducting wood area, to obtain a measurement of sap flux (Closs 1958).

As with the heat-balance approach, the accuracy of the heat-pulse method has been tested in several studies. Closs (1958) applied external pressure to a poplar stem segment, and found excellent agreement between the amount of water exuded and the estimates made from heat-pulse measurements. Decker and Skau (1964) monitored the vapour pressure within a plastic tent that enclosed a whole tree (*Pinus halepensis* Mill., *Juniperus osteosperma* (Torr.) Little, or *J. deppeana* Steudl.) and found good agreement with the heat-pulse measurements. Heat-pulse and lysimetric measurements of transpiration agree very well in soybean, but the heat-pulse technique consistently underestimated the actual sap flux in corn (Cohen et al. 1993). A cut-tree experiment with *Eucalyptus populnea* F.J. Muell. found that the method underestimated actual water use by 15% (Hatton et al. 1995). Tesky and Sheriff (1996) found very close agreement between heat-pulse estimates and the amount of water used by a juvenile *Pinus radiata* D. Don tree.

Stable Isotopes and Water Sources

The analysis of stable isotopes (particularly those of carbon, oxygen and hydrogen) is gaining increased use in the plant sciences (see Ehleringer et al. 1993). Analysis of the abundance of deuterium (^2H , or D) relative to hydrogen (H) has been used extensively in research into plant-water relations (Dawson 1993b). Isotopic compositions are conventionally expressed in 'delta' notation, so that for the ratio of D/H:

$$\delta\text{D} = \left[\frac{(\text{D}/\text{H})_{\text{sample}}}{(\text{D}/\text{H})_{\text{standard}}} - 1 \right] \times 1000 \quad (15)$$

where δD is in parts per thousand (per mil, ‰). The accepted standard for hydrogen (and oxygen) is SMOW (standard mean ocean water) (Ehleringer and Rundel 1988).

The natural variation in isotopic composition depends on thermodynamic (equilibrium) and kinetic fractionation processes (Ehleringer and Rundel 1988). The isotopic composition of precipitation varies because of the fractionation associated with phase changes, and the slower diffusion of the heavier species (Gedzelman and Arnold 1994). For example, heavy water (eg HDO) has a lower vapour pressure than H₂O (and therefore condenses more readily) and is subsequently depleted in the vapour phase, but enriched in the liquid or solid phase. As a result, the δD of precipitation varies spatially and temporally. The isotopic composition of groundwater will reflect a weighted average of the annual precipitation input (Ehleringer and Dawson 1992), which enables this pool of water to be discerned from individual events. Figure 2 shows the seasonal variation in δD of precipitation collected over the course of one year at Prince Albert, Saskatchewan.

The usefulness of δD values in identifying plant water sources arises from the observation that there is no fractionation associated with the uptake of water by roots (White et al. 1985, Ehleringer and Dawson 1992, Flanagan et al. 1992). An exception may be some mangrove species, which seem to discriminate against deuterium during water uptake in association with the exclusion of salts (Lin and Sternberg 1993). Consequently, provided that the water in the plant has not been subject to isotopic enrichment (e.g. in the leaves) the δD of xylem water will be the same as the δD of the source water. It is also possible to determine the relative contribution of different water sources to the transpiration stream, by using two-end mixing models (White et al.

1985):

$$P_{ew2} = \frac{\beta(ew1 - xw)}{\beta(ew1 - ew2)} \quad (16)$$

where P_{ew2} is the proportion of one of the end-members in the transpiration stream, β is the difference between the δD values, where xw is the xylem water.

The analysis of hydrogen isotopes has been used in a number of studies to identify the source water used by various plants. White et al. (1985) identified the importance of summer rains on the water uptake of *Pinus strobus* L. growing on dry, wet and intermediate sites. Dawson and Ehleringer (1991) were able to demonstrate that large, mature *Quercus* and *Acer* trees growing in a riparian zone did not utilize stream water, whereas younger trees used this water source extensively. The δD of stem water from co-occurring trees and shrubs in a pinyon-juniper woodland indicated different use of recent precipitation, which was consistent with differences in the rooting pattern of the plants and apparent water stress measured with the pressure chamber (Flanagan et al. 1992). Lin and Sternberg (1992) found that scrub mangroves use different sources of water during different seasons.

Figure 1. Schematic diagram of the heat-balance sap-flow gauge (not to scale). The principle heat fluxes are indicated by the bold arrows. A detailed explanation of the diagram can be found in the text. Redrawn with permission from Baker and Van Bavel (1987).

Figure 2. Hydrogen isotopic composition of precipitation collected at Prince Albert SK (53°13'N 105°41'W). The straight line indicates the volume-weighted average δD (-140.6 ‰).

Methods and Materials

Site Description

All field studies were carried out in central Saskatchewan, at the BOREAS southern old-black spruce site (OBSS) (53°99'N, 105°12'W, elev. 617 m) from 14 June to 9 July, 1995. The site is approximately 100 km northeast of Prince Albert, SK (53°13'N, 105°41'W, elev. 428 m). Black spruce (*Picea mariana*) is the principle tree species present, and the forest is interspersed with tamarack (*Larix laricina* (Du Roi) Koch) and Jack pine (*Pinus banksiana* Lamb.). The site features almost continuous moss coverage, with *Pleurozium schreberi* and *Sphagnum* spp. being the most abundant. Vascular plants in the understory include *Ledum groenlandicum* Oeder, *Cornus canadensis* L., and *Vaccinium* spp. Average canopy height and stand-density were 12 m and 4300 stems/ha, respectively, and leaf area index (LAI) was 6.2 (S.T. Gower, Univ. of Wisc., unpublished data).

Sap-Flow in Branches

Commercially available stem heat-balance gauges (SGA-13 and SGB-16, Dynamax Inc., Houston, Texas, USA) were used to measure sap-flow in four black spruce branches in the upper reaches of the canopy (about 7.0 m), and one branch closer to the ground (2.4 m). Table 1 shows a brief description of each branch, including the size of the heat-balance gauge employed. A scaffold-tower was used to attain access to the upper canopy. Each gauge consisted of a flexible heater, a thermopile, and three pairs of thermocouples, all mounted in a foam-rubber sleeve. Differentially wired pairs of thermocouples were located above, below, and across the heater. Each branch was prepared for installation of the sap-flow gauge by removing loose bark, and smoothing the stem with a flexible sanding block. Care was taken to avoid any damage to the sapwood. A generous amount of dielectric silicone (G4, Dow Corning Corp., Midland,

MI, USA) was applied to each branch, to ensure good electrical contact with the gauge. Each gauge was tightly secured to the branch, and an aluminum shield supplied by the manufacturer was fastened over the gauge with clear tape. Additional silicone was applied to the ends of the gauges, to prevent the entry of water.

A pre-assembled system (Flow 32, Dynamax) consisting of a data-logger, power regulator, and multiplexer was used to control and monitor the sap-flow gauges. Constant power was supplied to the heater, and radial and longitudinal temperature gradients were recorded by the thermopile and thermocouples, respectively. The sensors were read once per-minute, and average values were stored every 30 minutes for later analysis. The thermal conductance constant for each gauge (K_{sh}) was determined from values measured between 0200 and 0400 hours (CST), when transpiration was assumed to be zero. Flow calculations were done automatically by the data-logger, and follow those discussed above (equations 8-11). For consistency with the gas-exchange data, transpiration was expressed on a leaf-area basis. For comparison with the whole-tree data (see below) branch-level transpiration rates were also scaled to stand-level values, using leaf-area index as a scalar, and expressed on a ground-area basis.

Tests of the stem heat-balance technique were conducted in the lab, to verify the accuracy of the gauges at low flow rates. A four year-old, greenhouse-grown black spruce seedling in a 6 l pot was fitted with a sap-flow gauge (SGA-13, Dynamax). The gauge was installed as described above, and the output was stored every 15 minutes by the data-logger. The seedling was placed in a growth chamber, and exposed to a 12-hour photoperiod with day/night temperatures set at 25/20 °C. Photosynthetically active radiation (PAR) at the top of the seedling was about $250 \mu\text{mol m}^{-2} \text{s}^{-1}$. The pot was placed in a plastic bag, which was sealed just below the sap-flow gauge, to eliminate

evaporation from the soil. Sap-flow was monitored for 5 days; the seedling was periodically weighed on an electronic balance to provide a lysimetric measurement of transpiration.

To examine the minimum flow-rate detectable by the heat-balance technique, a branch from a mature white spruce (*Picea glauca* (Moench) Voss) was excised, re-cut under water in the lab, and allowed to rehydrate for 3 days in the dark. The branch was fitted with a gauge (SGA-13, Dynamax) as described above. The cut-end was inserted in a rubber sleeve under water, and attached to a potometer tube such that the exposed xylem was never in contact with air. The potometer was filled with tap-water, and a few drops of mineral oil were added to the tube to prevent evaporation. The system was closely monitored for leaks. The branch/gauge/potometer assembly was placed in the growth chamber, and PAR at the branch height was about $150 \mu\text{mol m}^{-2} \text{s}^{-1}$. The gauge and potometer were monitored for 3 days, with output being stored every 15 minutes. Very low flow rates ($<2 \text{ g h}^{-1}$) were achieved with this system.

Whole Tree Sap-Flow

A commercial compensating heat-pulse system (SF300, Greenspan Technologies Ltd., Warwick, Queensland, Australia) was used to measure sap-flow in four dominant or co-dominant black spruce individuals. Each gauge consists of a heater probe (90 mm long) and two sensor probes (80 mm long), which are inserted into holes drilled horizontally in the stem. The sensor probes contain thermistors placed 5 mm from their tips, and are located 10 mm above (i.e. downstream) and 5 mm below (i.e. upstream) the heater. Each gauge is connected to a datalogger/control unit, which supplies the heat-pulse and monitors the thermistor readings.

The selected trees were evenly spaced along a transect that ran from northwest to southeast, approximately 30 m north of the scaffold-tower. Mosses covered the forest

floor at the northwest (wet) end of the transect, while the southeast (dry) end was a small clearing in which lichens dominated the forest floor. The gauges were installed at a bearing of 180° on each stem, with the drill-guide supplied by the manufacturer being used to ensure precise alignment of the holes. The installation depth of each gauge was chosen such that the thermistors were located in the middle of the sap-wood. Sapwood area and water content were determined from cores taken from each tree, at the beginning and at the end of the sampling period. The system was set up to apply a 1.4 s heat-pulse every ten minutes. The gauge/stem assemblies were insulated from direct sunlight by enclosing them in aluminum foil. Calculations were done using an analytical program (SAPCAL, Greenspan Technologies), and follow equations 12-14. Whole tree transpiration was then expressed on a ground area basis.

Sampling for Isotope Analysis

To examine the effect of rainfall on transpiration, precipitation, stem water and organic-soil water samples were collected during the study period. Rain was collected throughout the study in a brass-collector located near the scaffold-tower; samples of each event were transferred to 7 ml glass vials, and stored frozen until analysis. Stem and soil samples were collected weekly throughout the study, and for five-consecutive days following the rain-event of 17-18 June. Three stem-samples were collected from each of 8 trees on each date, along the transect of the whole-tree transpiration measurements. Stems were from branches with live-foliage, and the segment used was upstream (i.e. towards the bole) of all needles. Segments were sealed in glass-tubes, and stored frozen until being analysed. Black spruce is typically rooted in the organic material (Lamhamedi and Bernier 1994), and so soil was sampled from this area. Soil samples were collected at each end of the transect, sealed in glass tubes, and stored frozen. An additional sample was collected at each point, and used to determine

gravimetric water content.

Stem and soil water was extracted by cryogenic vacuum-distillation (see Ehleringer and Osmond 1989). The three samples from each tree were pooled (equal volumes of each sample were combined). Water samples were prepared for hydrogen isotope analysis by reacting 3 μ l of water with zinc in an evacuated tube at 500 °C (Coleman et al. 1982). The hydrogen gas was then analysed on an isotope ratio mass spectrometer (602E, Micromass, Middlewich, Cheshire, UK). Isotope composition was expressed in delta notation (see above, equation 15). Standards of a known isotopic composition were run on the mass-spectrometer to continuously verify the accuracy of the instrument. The precision of the standard measurements was $\pm 2.6\text{‰}$ ($\pm$ sd).

Gas-Exchange Measurements

An extensive series of gas-exchange measurements was made to determine the stomatal conductance to water vapour. Measurements were made using a closed-loop portable photosynthesis system (LI-6200, LI-COR Inc., Lincoln NB, USA) with a 0.25 l leaf-chamber (LI-6000-13, LI-COR Inc.). The gas-analyser was calibrated in the field each day, using a gas-bottle of known CO₂ concentration. The system was allowed to equilibrate with ambient conditions for a minimum of 30 minutes prior to use. Leaf chamber gaskets were changed daily, and soda-lime and dessicant were changed as required.

For each branch on which transpiration was monitored, three twigs were chosen and prepared for gas-exchange measurements. Terminal buds (or the newly flushed needles) and the previous years' foliage (i.e. 1994) were removed; all gas-exchange measurements were made on foliage that had flushed in 1993. A further short length of the twig, toward the main stem, was cleared of needles so that the leaf chamber could maintain a good seal. The same three twigs on each branch were used for gas-exchange

measurements throughout the study. Two-year old needles were chosen deliberately, because it was felt that this foliage would be representative of the average conductance across the whole branch. Net assimilation decreases with increasing needle age in black spruce, and this is related to a decline in stomatal conductance (Lamhamedi and Bernier 1994). Positive assimilation has been noted in 13 year-old needles, however (Greenway et al. 1992). Taking leaf area into account as well (e.g. the leaf area of a given age class should be greater than that of the previous year) it was felt that two year-old needles would be representative of the stomatal conductance across all of the needle age-classes on a branch.

On a given day, all branches in either the upper or lower canopy were measured several times. The three individual measurements on each branch (i.e. on each of the prepared twigs) were averaged (after correcting for leaf area, see below) to obtain a single estimate of stomatal conductance at a point in time. These averaged values were used in further calculations. In total, over 650 individual measurements of leaf gas-exchange were made.

Micrometeorological Measurements

Environmental sensors, fixed to one-metre aluminum booms, were mounted on the scaffold-tower at heights of 7.6 m and 2.4 m. Each boom faced toward the south-east. Air temperature (T_a) at 7.6 m was monitored with an aspirated chromel-constantan (type-E) thermocouple (model ASPTC, Campbell Scientific, Logan, Utah, USA). At 2.4 m, T_a was measured with a copper-constantan (type-T) thermocouple. Relative humidity (RH) was measured at both heights with a shielded probe (207RH, Campbell Scientific). Photosynthetically active radiation (PAR) was measured with vertically orientated quantum sensors (LI-190SA, LI-COR Inc., Lincoln, Neb., USA). Precipitation was recorded with a tipping-bucket rain-gauge (TE525, Campbell

Scientific), which was positioned beneath a canopy opening 5 m north of the scaffold-tower. The rain gauge was mounted on a short post, approximately one metre above the ground.

On each branch fitted with a sap-flow gauge, leaf temperature (T_l) was measured with three fine-wire type-T thermocouples. Each thermocouple was constructed with a small loop of wire remaining between the junction and the insulated wire. This loop was carefully placed over a needle, so that the junction was in contact with the lower surface. A wire-tie was used to secure each thermocouple to the twig. The thermocouples were positioned toward the distal end of the branch (i.e. away from the bole) and were separated by about 10 cm. The three thermocouples were connected in parallel, an arrangement that estimates the average temperature (Ehleringer 1989). The thermocouples were checked daily throughout the study, and adjusted as necessary to ensure that the junctions remained in the closest possible contact with the needles.

Branch-level PAR measurements were made using gallium-arsenide-phosphide (GaAsP) photodiodes (G1118, Hamamatsu Corp, Bridgewater, NJ, USA). Each photodiode was calibrated against a quantum sensor prior to the field session. Photodiodes were mounted to the distal end of a branch with an alligator clip, and orientated as close as possible to the vertical.

An electronic datalogger (CR-10, Campbell Scientific) with a 32-channel multiplexer (AM 416, Campbell Scientific) was used to monitor the environmental sensors. Readings were made once a minute, and 30 minute averages were stored by the datalogger.

Leaf Area Determination

At the conclusion of the field measurements (8 and 9 July) each branch was cut from the main trunk, sealed in a plastic bag, and transported to the lab for leaf area

measurement. In keeping with the conventions of BOREAS, leaf area is reported as one-half of the total surface area (HASL). The volume displacement method was used to measure the leaf area of the gas-exchange twigs and sap-flow branches (Sellers et al. 1994):

$$\text{HASL} = (X(VnL)^{1/2})/2 \quad (17)$$

where HASL half of the total surface area of the needles (cm^2), X is a correction factor that allows for the shape of the needles ($X=4$, assuming the needles to be square in cross-section), V is the volume of the needles (cm^3), n is the number of needles, and L is the average needle length (cm).

To obtain an estimate of the effective ground-area occupied by the crowns of the trees used for whole-tree transpiration measurements, leaf area was divided by LAI. The leaf area of each tree was determined by a relationship between leaf area and stem diameter developed for *Picea mariana* at the study site ($R^2=0.861$) (J. Vogel, Univ. of Wisc., pers. comm.):

$$\text{HASL} = 10^{(-0.645 + 1.806 \log(\text{dbh}))} + 1.148 \quad (18)$$

where 'dbh' is the diameter of the stem.

Calculation of the Omega Coefficient

The total conductance to water vapour (g_{wt}) was calculated from transpiration and the vapour pressure deficit (VPD). The VPD was determined from the leaf temperature, and from the air temperature and relative humidity measurements at the appropriate canopy level. Stomatal conductance (g_{ws}) and g_{wt} were used to calculate boundary layer conductance to water vapour by the subtraction of resistances in series (Hinckley et al 1994):

$$g_{wb} = \left[\frac{1}{g_{wt}} - \frac{1}{g_{ws}} \right]^{-1} \quad (19)$$

Stomatal and boundary layer conductances were then used to calculate Ω , based on the formulation of Martin (1989) that accounts for radiative coupling between the branch and the atmosphere (see equation 5).

The Ω Data Set

Calculation of boundary layer conductance, and hence of Ω , could only be carried out when a complete set of leaf gas-exchange, transpiration, and meteorological data was obtained at a given time. Because the heat-balance system cannot resolve extremely low flow rates (see below) it was possible to measure stomatal conductance at times when transpiration was *determined to be zero*. When this occurred, negative boundary layer conductance values were calculated. This occurred most often in branch 2 in the upper canopy, and in the lower canopy branch. Those points were removed from the Ω analysis, although the leaf gas exchange data were still used to compute mean stomatal conductances. The complete set of Ω data consists of 101 individual estimates, with 10 of those being in the lower canopy. Except for daily trends and leaf gas-exchange, all of the data discussed here is concerned with this discreet data set.

Table 1. Characteristics of the black spruce branches fitted with Dynamax sap-flow gauges. Leaf areas were determined by the volume displacement method, as described in the text.

Branch	Height (m)	Leaf Area (m ²)	Gauge diameter (cm)
1	7.4	0.425	1.3
2	7.0	0.332	1.3
3	6.6	0.615	1.6
4	6.0	0.519	1.6
5	2.4	0.450	1.6

Results

The measurements of transpiration by the stem heat-balance technique were within 7% of the lysimetric data over a 5-day period (Figure 3). There were no statistically significant differences between the lysimetric and heat-balance rates on any of the first three days, when more regular lysimetric measurements were made ($p > 0.4$, t-test). The sap-flow rates measured here (about 20 g h^{-1}) were reasonably similar to the values observed in the field. During the cut-branch experiment, the flow rates measured by the potometer were slightly less than 2 g h^{-1} . The heat-balance method could not detect such low flows, and returned a default value of zero. Once the system was set up, no leaks were observed, and so the loss of water from the potometer is confidently attributed to sap-flow through the branch.

The site was considerably drier than expected during the study period (Table 2). At the beginning of the field session, the moss hollows contained no standing water, and the understory plants showed signs of water stress. Only about two-thirds of the normal precipitation was observed, most of which fell in two days early in the study (June 17-18). After this initial rainfall, rapid green-up and flowering was observed in the understory. Mean daily temperatures were similar to those observed during the same period of 1994, and to the expected values for June or July (Table 2). The average temperature during daylight hours (approx. 0400 to 2200 CST) was approximately 20.6°C , which was about 5°C higher than was observed during 1994. It should be noted, however, that the 1994 average was taken from a sensor located 24 m above the ground (i.e. at about twice the height of the canopy). The warm conditions during the day lead to high leaf-air vapour pressure deficits: mid-day VPD's generally exceeded 20 mbar, although values exceeding 30 mbar were frequently observed early in the study period.

Very low transpiration rates (E) were measured in individual black spruce branches. Strong diurnal patterns of transpiration are apparent in the upper canopy branches (Figure 4) but the data was quite variable (standard errors as high as 30% of the average). The two smallest diameter branches (branch 1 and 2) show the highest peak and average flows in the upper canopy: mid-day transpiration rates exceeded $0.3 \text{ mmol m}^{-2} \text{ s}^{-1}$. Transpiration in branch 3 began after, and ended before, transpiration in the other branches, even though the daily pattern of PAR on branches 1 and 3 was very similar (Figure 5). However branch 3 occupied the largest amount of space, and so the branch level PAR measurement was not completely representative of the light received by all of the foliage on that branch. It is important to note that the quantum sensors and the branch-mounted GaAsP sensors used to characterize PAR levels in this study were mounted vertically. As a result, they are not completely representative of the PAR received by black spruce foliage, which is orientated to capture light from several directions. The problem was particularly apparent for the lower canopy branch, which received an early morning sunfleck that was not detected by the branch-mounted GaAsP sensor. The average daily pattern of transpiration in the lower canopy shows at least three distinct peaks, with early morning values of $0.4 \text{ mmol m}^{-2} \text{ s}^{-1}$ being observed (Figure 6a). The second and third peaks of transpiration were correlated to sun-flecks detected by the GaAsP sensor (Figure 6b).

Figure 7 shows the total daily transpiration from the canopy trees in the stand, on a ground-area basis. Technical problems with the data-logger led to incomplete whole-tree transpiration data at the outset of the study. To fill in these gaps, data were extrapolated linearly to determine daily values. Stand-level transpiration was about 2.0 mm day^{-1} at the beginning of the study period, and had fallen to less than 0.75 mm day^{-1} by 20 June. It should be emphasized that these values indicate the

transpiration from the principle canopy species only, and that no account for the understory is made. General agreement exists between the whole-tree values and the scaled branch-values, which were obtained by multiplying the daily transpiration (average of the 5 branches) by the leaf-area index. Transpiration was also calculated from the average stomatal conductance (see below) and the maximum VPD for a particular day (Figure 7). This value represents the transpiration that would occur in the absence of boundary layer resistance. It is worth noting that the porometric measurements of transpiration consistently overestimated the actual transpiration rate, except for the first few days of the study.

Analysis of the stable hydrogen-isotopes of water showed that at the outset of the study, the trees in this stand were using almost exclusively groundwater. After the rain events of 17-18 June ($\delta D_{\text{rain}} = -51.1 \text{ ‰}$), δD_{stem} values increased, indicating the uptake of the isotopically heavier water (Figure 8a). Using a two-end mixing model, as much as 39% of the transpiration stream consisted of the rain event by the end of the study (Table 3). This uptake of recent water input was not accompanied by an increase in transpiration (Figure 7). Groundwater remained an important source for the canopy species, however, as the stem-water was considerably lighter than the soil-organic matter (o.m.). The $\delta D_{\text{o.m.}}$ rose sharply after the rain event at the southeast (dry) end of the transect, but at the wet-end of the transect, $\delta D_{\text{o.m.}}$ was consistently more depleted in heavy isotopes (Figure 8b). The gravimetric water content of the organic-soil rose sharply following the rain-event. The interception of the rainfall by the moss layer at the 'wet' end of the transect was evident by the lower water content during the first few days following the precipitation.

Analysis of the gas-exchange data by ANOVA indicated that there were no

significant differences in the stomatal conductance to water vapour (g_{ws}) among any of the upper canopy branches ($p>0.5$) (Appendix A). The standard deviation between the individual measurements on a given branch was typically less than $0.02 \text{ mmol m}^{-2} \text{ s}^{-1}$. The average gas-exchange characteristics of an upper and a lower canopy branch are shown in Figure 9. Stomatal conductance early in the day was quite variable in the upper canopy ($73 \pm 25 \text{ mmol m}^{-2} \text{ s}^{-1}$), and there was a large reduction in g_{ws} by late morning. In contrast, g_{ws} in the lower canopy remained consistently low throughout the day, averaging about $30 \text{ mmol m}^{-2} \text{ s}^{-1}$; the difference between the upper and lower canopy was not statistically significant ($p>0.4$, t-test) (Appendix A). The overall mean stomatal conductance, including both the upper and lower canopy, was $40.0 \pm 4.6 \text{ mmol m}^{-2} \text{ s}^{-1}$. The total conductance to water vapour (g_{wt}) was very low ($<25 \text{ mmol m}^{-2} \text{ s}^{-1}$) throughout the day in both the upper and lower canopy (Figure 9), a result of the high VPD and low transpiration rates. As a consequence of the low g_{wt} and g_{ws} , there was a very low boundary layer conductance (g_{wb}) throughout the canopy, throughout the day. The boundary layer surrounding these branches promoted local humidification: the VPD measured between the branch and the canopy atmosphere was considerably greater than the VPD calculated at the leaf surface (Figure 10).

The consistent difference between VPD and VPD_s indicated that transpiration in *Picea mariana* was poorly coupled to the canopy atmosphere. During the day, Ω in the upper canopy declined from 0.74 ± 0.04 in the early morning, to 0.55 ± 0.04 in the late afternoon (Figure 11). Branch 2 was the most closely coupled to the atmosphere, with an average Ω of 0.46 ± 0.04 . This branch was statistically different from the others, for

reasons that are unclear (Appendix A). The overall average decoupling in the upper canopy was 0.59 ± 0.02 . The branch closer to the ground was even more decoupled from the atmosphere, with an average Ω of 0.82 ± 0.03 ; this was statistically different from the upper canopy ($p < 0.01$, t-test) (Appendix A).

Table 2. Observed and expected weather conditions at the study site. The expected values are taken from the Environment Canada normals for the station at Waskesiu Lake, Saskatchewan (53°55'N, 106°05'W, elev. 532m), about 70km west of the study site. The observed data for 1994 were collected at the OBSS from 14 June to 07 July, inclusive (P.G. Jarvis, U. of Edinburgh, pers. comm.). The observed data for 1995 were collected from 14 June to 07 July, inclusive. Instrumentation is described in the text.

	Expected- June	Expected- July	Observed- 1994	Observed- 1995
Daily Mean	13.9	16.3	13.3	16.5
Temperature (°C)				
Average	67.2	79.7	71.0	49.1
Precipitation (mm)				
Days with Rain	12	14	12	9

Table 3. Uptake of recent precipitation by *Picea mariana*. A two-end mixing model was used to determine the proportion of rain-water in the xylem water (P_{rain}), using groundwater (-140.6 ‰) and the precipitation event of 17-18 June (-51.1 ‰) as the end-members. The δD of the xylem water is the mean of 8 stems.

Date	δD Xylem Water (‰) ($\pm se$)	P_{rain} (%)
14-June	-140.4 (± 2.97)	NA
19-June	-136.6 (± 2.23)	4.4
21-June	-120.6 (± 17.52)	22.3
29-June	-105.7 (± 4.46)	39.0

Figure 3. Comparison of heat-balance (line) and lysimetric (symbols) measurements of water-use by a *Picea mariana* seedling in a growth chamber.

Figure 4. Average branch-level transpiration (E) in a *Picea mariana* forest. The maximum standard error of each mean is shown. Each branch was in the upper canopy of the stand, ranging in height from 7.4 to 6.0 m.

Figure 5. Average course of PAR at the branch-level (closed symbols) and in the canopy (open symbols) in a *Picea mariana* forest. The maximum standard error of each branch-level mean is shown. Each branch was in the upper canopy of the stand, ranging in height from 7.4 to 6.0 m. Branch-level measurements were made with GaAsP photodiodes, and canopy values were obtained with a quantum sensor.

Figure 6. (a) Average transpiration (E) in the lower canopy branch, with the maximum standard error of the mean indicated. (b) Average course of PAR at the branch-level (closed symbols) and in the lower canopy (open symbols).

Figure 7. Whole-tree transpiration expressed on a ground-area basis during the study period. Open squares indicate measurements made with the heat-pulse technique (mean $\pm$ se, $n=4$). Closed squares indicate heat-pulse measurements that were extrapolated to whole-day values. Diamonds indicate branch-level measurements that were scaled to whole-tree values (mean $\pm$ se, $n=5$). Triangles indicate transpiration as calculated from the average stomatal conductance and the maximum VPD measured for that particular day.

Figure 8. Stable hydrogen isotope composition of (a) stem water (mean $\pm$ se, $n=8$), and (b) organic-soil water, where open and closed symbols represent the dry and wet ends of the transect, respectively. The hatched area in (b) represents the expected composition of groundwater (-140 ± 2 ‰). Numbers in parenthesis indicate the gravimetric water content, on a percent basis.

Figure 9. Average ($\pm$ se, $3 < n < 10$) stomatal (g_{ws}), boundary layer (g_{wb}) and total (g_{wt}) conductances to water vapour in an upper and lower canopy branch. The first g_{wb} and g_{wt} values for the lower canopy represent single points.

Figure 10. Vapour pressure deficit measured between the branch and the canopy air (VPD) and calculated at the leaf surface (VPDs) in *Picea mariana*. VPDs was calculated as: EP/g_{ws} , where P is atmospheric pressure (Meinzer et al. 1995).

Figure 11. Average values ($\pm$ se, $1 < n < 25$) of the decoupling coefficient in the upper (open symbols) and lower (closed symbols) canopy of a *Picea mariana* forest. Error bars for the lower canopy are obscured by the symbol; the first point is a single value.

Discussion

Validity of the Heat-Balance Measurements

Sap-flow rates determined by heat-balance in other species have generally been greater than observed here. Transpiration rates ranging between 0.5 and 6 mmol m⁻² s⁻¹ have been reported in tropical species (Meinzer et al. 1993, 1995). Transpiration varied between 1 and 4 mmol m⁻² s⁻¹ among lower and upper canopy branches of *Populus* hybrids (Hinckley et al. 1994). The accuracy of the heat-balance approach at low flow rates has been verified here (Figure 3) and in other studies (Groot and King 1992). A minimum detectable flow rate of at least 2 g h⁻¹ was discerned through the cut-branch experiment, although Groot and King (1992) were able to resolve such flows in both black spruce and Jack pine seedlings. They constructed their own gauge, however, which may not have characteristics identical to the commercial gauge used here. The existence of actual sap-flow below the resolution of the gauge would explain the occasional occurrence of negative boundary layer conductances, and provides a justification for excluding such points.

Error Analysis

Because of the large number of measurements involved in the calculation of Ω , the potential error is substantial. For example, three measurements (T_a , T_l , and RH) are required to determine the vapour pressure deficit. Errors in the estimates of VPD and transpiration will consequently affect the calculation of g_{wt} , g_{wb} and Ω . I have attempted to determine the effect that these equipment errors may have on the Ω values. The general approach was to calculate an upper and a lower estimate for each parameter, for each point in the Ω data-set. These estimates were based upon random errors, either

suggested by the manufacturer, or determined in the lab. After accounting for measurement error, the uncertainty in calculated values was determined by calculating the worst case. For example, the upper estimate of VPD was made with the upper value for leaf temperature, and the lower values for RH and air temperature. The lower estimate of the Ω value was made using the lower estimate of g_{ws} and the upper estimate of g_{wb} . A detailed description of the error calculations is shown in Appendix B.

The humidity sensor employed here was accurate to within 5% over a range of relative humidities from 12 to 100%, and this value was used to determine the error associated with VPD. The principle error associated with thermocouple measurements is the solar radiation load (Ehleringer 1989). As described in the Methods, leaf-thermocouples were mounted on the underside of the needles in the field, and were checked regularly to ensure that the correct contact and orientation was maintained. The air-temperature sensors, particularly the aspirated thermocouple used in the upper canopy, were shielded from direct sunlight. Although direct radiation should not have been a severe problem on these temperature measurements, a test of the effect of direct light on the accuracy of the thermocouples was conducted. A leaf-thermocouple assembly (e.g. three junctions wired in parallel) was placed in a leaf chamber and exposed to various levels of direct light. This 'leaf' temperature was compared to the temperature of the chamber, after allowing the system to equilibrate for 10 minutes following changes in the light levels. Overall, the agreement between the two sensors is quite good; the difference is less than 1 °C at light levels less than about 1650 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 12). Although the thermocouples in the field were shielded from direct sunlight, to be cautious I have assigned an error of ± 1 °C to the temperature measurements. The estimate of the ambient vapour pressure (e_a) depends upon air

temperature and relative humidity: the error associated with this parameter was determined to be about 9%. Similarly, the estimate of the vapour pressure within the intercellular air-spaces of a leaf (e_i) depends on leaf temperature: the error in the estimate of e_i was calculated to be about 6%. The error associated with the VPD measurement was about 16%.

The error associated with the Dynagauge heat-balance sap-flow system is typically less than 10%, according to the manufacturer. As described above, the test of the system at low flow rates was within 7% of the lysimetric estimate of water use. A further error in the transpiration data lies in the determination of leaf area; a small error in the balance is involved, but the largest error here would certainly be human. In the interest of caution, I assigned a value of 15% to the error in the transpiration data. With this value, and the calculated uncertainty in VPD, the error in the total conductance to water vapour may be as high as 45%.

There are several sources of potential error associated with measurements of leaf gas-exchange parameters (McDermitt 1990). Temperature changes or debris in the chamber can lead to the absorption or desorption of water within the system (Pearcy et al. 1989). Such problems can be largely overcome by taking rapid measurements, as in this study. Errors in flow-meter calibration or zero-set, in humidity sensors, and in the accuracy of the temperature measurements may occur, leading to uncertainty in the calculated values. For the system used here, the accuracy of the flow meter and RH sensor are 1% and 3% respectively. Leaf and air temperature uncertainties are 4% and 2%, respectively. Multiplying these errors results in an uncertainty of 10.4% in the accuracy of the gas-exchange equipment. This treatment does not account for errors in leaf-area measurement; an uncertainty in the stomatal conductance measurements of 15% is used in further analysis..

Using the potential range of g_{wt} and g_{ws} values, the error associated with the estimates of boundary layer conductance is about 63%. Although substantial, the errors in g_{wb} and g_{ws} seem to cancel, with the result that the error associated with the Ω measurements is less than 21%. Again, it is worth emphasising that these error estimates are considered to be very cautious, and are believed to represent the worst-case scenario. The error in the measurement of boundary layer conductance is particularly large: calculation of this variable requires the use of no less than six parameters, each with an associated uncertainty. Given the difficulties involved with this type of field work, an uncertainty of 21% in the Ω values is encouraging. Further, the standard error's associated with the means are less than 10%, indicating that the actual spread of the data is less than the potential measurement error.

Transpiration and Stomatal Conductance in Picea mariana

Mid-day branch-level transpiration rates were as high as $0.3 \text{ mmol m}^{-2} \text{ s}^{-1}$ during this study. No previous reports of branch-level transpiration using the heat-balance method in naturally-occurring black spruce are available. Most previous studies have employed either porometer or energy-balance techniques. Lamhamedi and Bernier (1994) cite various porometric measurements of transpiration in black spruce seedlings, under controlled conditions, of between 2 and $90 \mu\text{mol g}^{-1} \text{ s}^{-1}$ (e.g. between 0.2 and $9.0 \text{ mmol m}^{-2} \text{ s}^{-1}$, following their assumption of 100 g cm^{-2}). Rates of as high as $80 \mu\text{mol g}^{-1} \text{ s}^{-1}$ ($8 \text{ mmol m}^{-2} \text{ s}^{-1}$) have been reported for seedlings planted in a well-drained garden plot (Zine el Abidine et al. 1995). Porometric measurements of transpiration have been reported in other conifers. In mature, naturally occurring *Larix* hybrids and *Picea abies* (L.) Karst. transpiration was as high as $0.4 \text{ mmol m}^{-2} \text{ s}^{-1}$ and $14 \text{ mmol m}^{-2} \text{ s}^{-1}$,

respectively (Schulze et al. 1985).

Comparison of this whole-tree and canopy-level transpiration data to previously reported values is also difficult. Stand-level transpiration, measured by the heat-pulse technique, was generally less than 1.0 mm day^{-1} during the present study. Canopy-level measurements using energy-balance techniques at this BOREAS site during 1994 indicated average evapotranspiration rates of 2.0 mm day^{-1} throughout the growing season (Sellers et al. 1995). However, these values represent water loss from the whole forest, including the understory vegetation and evaporation from the soil. This point, and the fact that 1995 was considerably drier than 1994, suggest that the current values are reasonable. Values of 4 mm day^{-1} have been reported for black spruce stands (Lafleur 1992), although this study indicated that as much as 80% of the total evapotranspiration originated from the forest floor. Rates as high as 2.5 mm day^{-1} have been reported for a mixed black spruce/tamarack canopy (Fitzjarrald and Moore 1994), although the proportion from the forest floor is unclear. Arneth et al. (1996) found whole-tree rates of between 1.5 and 2.8 mm day^{-1} in *Larix gmelinii* (Rupr.) Rupr., a larch native to the boreal forests of Siberia. Cermak et al. (1995) used the heat-balance approach in *Picea abies* and found whole-tree values of 0.2 mm day^{-1} during dry conditions.

The values of g_{ws} shown here (e.g. mid-day values of about $40 \text{ mmol m}^{-2} \text{ s}^{-1}$) correspond well to measurements made at the same site during the 1994 field season. Brooks et al. (1996) measured an average g_{ws} of $30 \pm 10 \text{ mmol m}^{-2} \text{ s}^{-1}$. These measurements of g_{ws} also agree well with other published values for naturally occurring black spruce. Macdonald and Lieffers (1990) found that g_{ws} varied between 20.8 and $55.1 \text{ mmol m}^{-2} \text{ s}^{-1}$ over the course of a growing season. Dang and his co-workers

(1991) found that stomatal conductance to CO_2 varied between 12 and 30 $\text{mmol m}^{-2} \text{s}^{-1}$, corresponding to g_{ws} values of between 20 and 48 $\text{mmol m}^{-2} \text{s}^{-1}$ over the course of a hot, dry day. Decreasing stomatal conductance with increasing foliage age, linked to a reduction in photosynthetic capacity, has been reported (Greenway et al. 1992). However, the values observed during the current study are consistent with published accounts, despite the fact that stomatal conductance was measured on two-year old needles.

The Source of Water for Picea mariana.

The low transpiration rates observed during the study do not appear to reflect a limited water supply. Precipitation inputs were utilized by these trees, but groundwater was a large component of the xylem sap throughout the study period (Figure 8, Table 3). Moreover, the rain-event of 17-18 June did not result in increased transpiration from the principle canopy species (Figure 7). If these trees were water-stressed, then it is probable that substantial rainfall should have resulted in a greater transpiration rate. Evaporative enrichment of the soil water at the dry end of the transect was substantial, but the hydrogen isotope composition of the xylem water in the principle canopy species was generally more depleted than the soil water at that end. The change in $\delta\text{D}_{\text{o.m.}}$ following rain at the wet end of the transect was substantially less than at the dry end, suggesting that the moss layer intercepted much of the input, preventing it from entering the soil. Black spruce is typically shallow-rooted (Lamhamedi and Bernier 1994) but the water table in such forests is normally high (Macdonald and Lieffers 1990). It seems reasonable to expect the water table to have receded from it's maximum during this study. While a receding water table could potentially account for the observed decline in transpiration, the water in the organic layers was consistently depleted in heavy isotopes,

relative to the major rain-event. This indicates that the water table did not recede below the level of the rooting zone, and so it appears unlikely that water availability *per se* is responsible for the low transpiration rates observed during this study.

The Role of the Boundary Layer.

Although low stomatal conductance places a limitation on transpiration, the surprisingly low boundary layer conductances that were observed here are important. Consistent with this notion, transpiration was more closely related to VPD at the leaf surface (VPD_s) than to VPD between the branch and the canopy air (Figure 13). That the measured VPD should nonetheless account for some of the variation in transpiration is inevitable, since water vapour must still diffuse from the boundary layer of air surrounding the branch. The VPD at the leaf surface is the more appropriate variable to describe transpiration; stomata are believed to respond to changes in the transpiration rate (Mott and Parkhurst 1991) and the driving force for water vapour through the stomatal pore must be the VPD_s . In this instance the argument is admittedly circular, since the transpiration rate was used to determine VPD_s . However, alternative ways to measure VPD_s present technical and conceptual challenges (see below).

It is generally assumed that the boundary layer poses little resistance to the flux of water vapour through needle-leaved species (Jarvis et al. 1976). This is based on the small size of the needles, and on the irregular nature of the canopy. However, the arrangement of needles and branches on a tree must affect the movement of air through the canopy, and hence the boundary layer conductance. Needles in the upper canopy of this black spruce forest were very densely packed on the branch. This seems to result in a shelter effect, limiting the penetration of wind to the stem, and promoting the smooth flow of air over the branch. The clumped arrangement of foliage can reduce g_{wb} by as

much as 50% in some species (Jarvis and McNaughton 1986). The branches in the upper canopy were also clumped together, which would have the same sheltering effect, promoting smooth air flow around the crown of the tree. The arrangement of needles on the lower canopy branches was much more open, presumably to minimize mutual shading. However, since there is so little air movement close to the ground (see below, Figure 14) turbulence around a branch near the bottom of the crown should still be minimal.

Although no wind speed data was collected during this study, extensive wind measurements were made at the study site during the 1994 BOREAS campaigns. A theoretical wind speed profile was calculated for the study site (Figure 14a) based on observations made above the canopy during BOREAS 1994 (P.G. Jarvis, U. of Edinburgh, pers. comm.) and on wind profile equations reported for a similar forest (Amiro and Davis 1988, Amiro 1990). The details of the calculations are shown in Appendix C. Even using a conservative estimate of the wind-extinction coefficient (α), wind speed at the height of the upper canopy branches studied here is generally less than 1.0 m s^{-1} (Figure 14b). Wind speed at the level of the lower canopy branches is generally less than 0.25 m s^{-1} . These calculations are consistent with qualitative observations of wind speed at the top of the scaffold tower and on the ground below the tower. The decline in windspeed through the canopy resulted in lower g_{wb} closer to the ground, as indicated by Figure 9.

Using the constructed wind profile, I have calculated the effective dimensions of black spruce needles and branches that would be required to result in the observed boundary layer conductances, based on the equations of Nobel (1991). Details of the calculations are shown in Appendix D. It should be emphasised that these equations were derived from observations of flat leaves, and so this analysis serves an illustrative

purpose only. The effective needle length in the upper canopy branches is between 33 and 67 mm, and is about 183 mm in the lower canopy. The actual needle length was about 7 mm, so clearly these estimates exceed the actual length of black spruce needles by a considerable margin.

Using the boundary layer equations for a cylinder (Nobel 1991) the effective branch diameter varies between 16 and 32 mm in the upper canopy, and closer to the ground the effective diameter is about 87 mm (Appendix D). These values, at least in the upper canopy, seem to be reasonable in terms of the space occupied by the higher-order twigs on black spruce branches. The arrangement of the needles facilitates smooth air flow over the branch; air flows over the clusters of needles rather than through them, and the system seems to behave as a solid cylinder. In reality, it is likely that the boundary layers of the individual needles overlap (presumably adding as parallel resistances) but the point remains the same. This argument illustrates the conceptual difficulties involved in measuring VPD_s .

The Decoupling Coefficient.

The regulatory effect of the boundary layer on transpiration can be quantified by Ω . Although few in number, previous reports have indicated that conifers are more closely coupled to the atmosphere than the current result indicates. Leaf-level Ω values as high as 0.46 have been reported for *Picea sitchensis* (Bong.) Carr. when wind speeds are very low (Jarvis and McNaughton 1986), although most leaf-level values cited by the same authors are considerably lower. Lafleur (1992) measured an Ω_l of 0.1 in *Picea mariana*. Canopy-level Ω values ranging between 0 and 0.4 for *Pinus sylvestris* L. (Whitehead et al. 1984) have been reported. Most of the leaf and canopy-level reports have determined boundary layer conductances from empirical relationships of wind-speed

and leaf size (e.g. Whitehead et al. 1984, Lafleur 1992). The approach utilized here is a more direct measurement of the boundary layer conductance, and does not rely on theoretical predictions. As shown above, such relationships may not make adequate predictions about the boundary layer surrounding densely-clumped, needle-shaped foliage.

Several consequences arise as a result of the poor coupling between transpiration and the atmosphere. With a relatively high Ω value, transpiration should be fairly insensitive to stomatal conductance. Rather, it should be more closely related to radiation. Figure 15 shows that there is no clear relationship between transpiration and g_{ws} , but that variation in isothermal net radiation (R_{ni}) accounts for more than 60% of the variability in transpiration. The calculation of R_{ni} is described in Appendix E. It is worth noting that if the effect of surface temperature is ignored (e.g. net radiation (R_n) is used in place of R_{ni}) then the R-squared value is 0.49. Clearly, branch-level transpiration in this *Picea mariana* forest is controlled more by meteorological factors than by the physiological characteristics of the canopy vegetation. Consistent with this view, Figure 16 indicates that the imposed transpiration rate (i.e. the rate that would occur if the ambient VPD were imposed at the leaf surface, see equation 3) overestimates the actual transpiration from these black spruce branches. A similar conclusion is reached by examining the scaled-up porometer estimate of transpiration (Figure 7). The equilibrium term (using R_{ni} , see equation 6) slightly underestimates the actual rate. The result of using both estimates of transpiration, weighted by Ω , is shown in Figure 17; clearly this is in good agreement with the measured rates of transpiration. Of course, omega-theory has limited predictive value (since transpiration must be measured to determine the value

of Ω) but it does serve to explain the importance of the different potential controls.

A reduction in photosynthesis, linked to reduced stomatal conductance, has been observed in black spruce as needle age increases (Lamhamedi and Bernier 1994). In this study, g_{ws} was measured on two-year old needles, with the expectation that this would approximate the average stomatal conductance across all of the age classes. If older needles had been measured, then it is likely that g_{ws} would have been lower. Assuming that g_{wb} remains the same, a lower g_{ws} would have resulted in lower Ω values.

Conversely, measurements on newer foliage would have resulted in higher Ω values.

The magnitude of this expected age effect is uncertain, however, as even 13-year old needles can retain 40% of the maximum photosynthetic rate (Hom and Oechel 1983). With the methodology employed in this study it would be impossible to determine the extent of decoupling for a specific age class, because the transpiration rate was determined for all of the age-classes on each branch.

The difference between the two Ω formulations deserves some discussion. As shown in Figure 18, consideration of the radiative coupling indicates greater stomatal control of transpiration than if this effect is ignored. This was predicted by Martin (1989), and by McNaughton and Jarvis (1991) in a later treatment. Changes in transpiration affect changes in the net radiation of the branch; this feedback plays an important role in regulating transpiration. Martin (1989) refers to Jones (1976) for the incorporation of the isothermal net radiation, and radiative conductance. However, Jones (1976) uses a parallel resistance to radiative and sensible heat transfer, which he calls r_{hr} , rather than a term for radiative loss only (recall that Martin (1989) uses conductance, or $1/\text{resistance}$; see equations 5 and 6). Formulations of the Penman-Monteith equation

generally assume that the same value of the boundary layer conductance is valid for the diffusion of heat and water vapour (Monteith 1965), although this is not necessarily the case (Nobel 1991). A boundary layer resistance to sensible heat transfer would provide an additional feedback on the energy balance of the plant: the combined resistance should account for that effect. However, attempting to substitute such a term for g_l (i.e. g_{lr}) lead to solutions that were practically identical to the values predicted by the original formulation (i.e. equation 4) that does not include g_r ! Clearly, if this feedback is important, the appropriate equations must be derived anew, and my attempts to do so have met with little success.

The Effect of Decoupling on Scaling Transpiration

The poor coupling between black spruce branches and the canopy atmosphere has important implications for scaling. Bottom-up scaling of data obtained with a leaf-porometer results in large over-estimations of the actual transpiration rate in this black spruce forest (Figure 7). Early in the study period, the relationship between the scaled leaf gas-exchange data and the actual transpiration was reasonable. It should be noted that the measured transpiration rates were extrapolated to daily values in most of those instances, and the validity of this linear extrapolation is uncertain. It is clear, however, that scaling up measurements made with artificially high boundary layer conductances is inappropriate in this case. Scaling of the branch-level data results in good agreement with the whole-tree transpiration values. Both of these techniques measure transpiration with the boundary layer resistance intact.

An interesting scaling problem arises from consideration of the radiation data. As described in Appendix E, the isothermal net radiation for each branch was calculated from the sum of the sensible and latent heat fluxes. This calculation describes the radiation environment of the branch on a leaf-area basis, although it does assume that there is

energy-balance closure. It seems reasonable to expect that leaf area index would be an appropriate multiplier by which R_{ni} could be expressed on a ground area basis. However, the isothermal net radiation predicted from the relationship between solar radiation and PAR (PR_{ni} , Appendix E) is consistently greater than branch-level R_{ni} expressed on a ground-area basis (Figure 19a). The leaf-area index reported here is one-sided; multiplying the branch-level R_{ni} by twice the LAI appears to improve the relationship (Figure 19b), although no additional variability is explained. It is acknowledged that black spruce needles are not two-sided (at least in the sense that the foliage of a broad-leaved species can be considered two-sided), but because of the way in which it was determined, multiplying leaf-area by two does represent the total foliar surface area of these branches (see Equation 17). Scaling net radiation from branch-level to stand level is not entirely appropriate in this case, although the reasons for this are unclear. The influence of the boundary layer on the transfer of sensible heat is certainly important, but it appears likely that the measurements made here should include this effect. It is possible that energy balance closure is incomplete; this has been commonly observed by BOREAS investigators.

Conclusions

Field studies were carried out in central Saskatchewan to examine the controls on transpiration in *Picea mariana*. An extensive series of sap-flow, gas-exchange, and meteorological measurements were made over a 5 week period during the middle of the growing season in 1995. Weather conditions were warmer and drier than normal, with only about two-thirds of the usual rainfall being observed. Whole-tree transpiration rates were quite low, with values less than 1.0 mm day^{-1} throughout most of the study. Hydrogen isotope analysis indicated that the trees were using mostly groundwater, although rainfall events were utilized to some extent. Stomatal conductance was also low, averaging about $40 \text{ mmol m}^{-2} \text{ s}^{-1}$, although it was quite variable early during the morning in the upper canopy. The leaf gas-exchange data were consistent with previously observed values for black spruce. Boundary layer and stomatal conductances were of a similar magnitude. This surprising result indicated that the boundary layer provided an important resistance to water loss, which is unexpected in needle-leaved coniferous species. Higher than expected Ω values (e.g. about 0.60 and 0.82 in the upper and lower canopy, respectively) indicated that transpiration was decoupled from the atmosphere; transpired water vapour accumulated in the boundary layer, reducing the diffusion gradient, and ultimately reducing the transpiration rate. The potential for measurement error was substantial, but the actual spread of the data was well within the likely range. Consistent with poor coupling, transpiration was poorly related to stomatal conductance, but isothermal net radiation was a reasonably strong predictor of water loss from black spruce. The strongly decoupled situation indicates that summation schemes are ineffective in scaling porometric transpiration estimates to whole-tree or stand-level values in black spruce. Such an effect must be taken into consideration before any detailed models of water vapour fluxes can be constructed.

Figure 12. The effect of direct light on the accuracy of the leaf-thermocouples. The difference between the temperature reported by the leaf-thermocouple and the chamber temperature is plotted on the y-axis (ΔT). The best fit line is $y = (1.835 \times 10^{-7})x^2 + (4.3031 \times 10^{-4})x - 0.17941$.

Figure 13. Transpiration as a function of the actual (VPD) and effective (VPD_e) vapour pressure deficits. The calculation of VPD_e is described in the caption accompanying Figure 10.

Figure 14. (a) A theoretical normalized wind profile for the study site, using three values of the wind extinction coefficient (α). (b) Actual windspeed above the canopy, and calculated for the top and two heights within the canopy, assuming conservatively that $\alpha=2.6$. Details of the calculations can be found in Appendix C.

Figure 15. Transpiration as a function of (a) stomatal conductance, and (b) isothermal net radiation (R_{ni}) in *Picea mariana*. The calculation of R_{ni} is described in Appendix E.

Figure 16. Measured transpiration rate (E) against the imposed (E_{imp}) and equilibrium (E_{eq}) rates. Open and closed symbols represent upper and lower canopy branches, respectively.

Figure 17. Measured transpiration rate (E) against the transpiration rate predicted from omega theory (E_{pred}). Open and closed symbols represent the upper and lower canopy branches, respectively.

Figure 18. A comparison of Ω calculated with and without consideration of radiative coupling. Open and closed symbols represent upper and lower canopy branches, respectively.

Figure 19. (a) Branch-level isothermal net radiation (R_{ni}) multiplied by leaf area index (LAI) and plotted against PR_{ni} , calculated from the relationship between solar radiation and PAR. (b) As above, but branch-level R_{ni} is multiplied by twice the LAI, to approximate the total foliar surface area. The necessary calculations are described in Appendix E.

References

- Amiro, B.D. 1990. Comparison of turbulence statistics within three boreal forest canopies. *Bound. Layer. Meteorol.* 51:99-121.
- Amiro, B.D. And P.A. Davis. 1988. Statistics of atmospheric turbulence within a natural black spruce forest canopy. *Bound. Layer. Meteorol.* 44:267-283.
- Arenth, A., F.M. Kelliher, G. Bauer, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, W. Ziegler, N.N. Vygodskaya, I. Milukova, A. Sogachov, A. Varlagin, and E.D. Schulze. 1996. Environmental regulation of xylem sap flow and total conductance of *Larix gmelinii* trees in eastern Siberia. *Tree Physiol.* 16:247-255.
- Arya, S.P. 1988. Introduction to Micrometeorology. Academic Press, New York, 307 p.
- Baker, J.M., and J.L. Nieber. 1989. An analysis of the steady-state heat balance method for measuring sap-flow in plants. *Agric. For. Meteorol.* 48:93-109.
- Baker, J.M. and C.H.M. Van Bavel. 1987. Measurement of mass flow of water in the stems of herbaceous plants. *Plant Cell Environ.* 10:777-782.
- Baldocchi, D.D. 1993. Scaling water vapour and carbon dioxide exchange from leaves to a canopy: rules and tools. In: *Scaling Physiological Processes. Leaf to Globe.* Eds. J.R. Ehleringer, and C.B. Field. Academic Press, New York, pp. 77-114.
- 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 Environ.* 18:463-469.
- Bernier, P.Y. 1993. Comparing natural and planted black spruce seedlings. I. Water relations and growth. *Can. J. For. Res.* 24:27-2434.
- Brooks, J.R., L.B. Flanagan, G.T. Varney, and J.R. Ehleringer. 1996. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO₂ within boreal forest canopies. *Tree Physiol.* In press.
- 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. *J. Hydrol.* 168:17-27.
- Closs R.L. 1958. The heat pulse method for measuring rate of sap flow in a plant stem. *N.Z.J. Sci.* 1:281-288.
- Cohen, Y., S. Takeuchi, J. Nozaka, and T. Yano. 1993. Accuracy of sap flow measurements using heat balance and heat pulse methods. *Agron. J.* 85:1080-1086.
- Coleman, M.L., T.J. Shepherd, J.J. Durham, J.E. Rouse, and G.R. Moore. 1982. Reduction of water with zinc for hydrogen isotope analysis. *Anal. Chem.* 54:993-995.
- Dang, Q.L., V.J. Lieffers, R.L. Rothwell, and S.E. Macdonald. 1991. Diurnal variation and interrelations of ecophysiological parameters in three peatland woody species under different weather conditions. *Oecologia.* 88:317-324.
- Dansgaard, W. 1964. Stable isotopes in precipitation. *Tellus.* 26:436-468.
- D'Arrigo, R., G.C. Jacoby, and I.Y. Fung. 1987. Boreal forests and atmosphere-biosphere exchange of carbon dioxide. *Nature.* 329:321-323.
- Dawson, T.E. 1993a. Woodland water balance. *TREE.* 8:120-121.
- Dawson, T.E. 1993b. Water sources of plants as determined from xylem-water isotopic composition: perspectives on plant competition, distribution, and water relations. In: *Stable Isotopes and Plant Carbon-Water Relations.* Eds. J.R. Ehleringer, A.E. Hall, and G.D. Farquhar. Academic Press, New York, pp. 465-496.
- Dawson, T.E. 1993c. Hydraulic lift and water use by plants: implications for water balance, performance, and plant-plant interactions. *Oecologia.* 95:565-574.
- Dawson, T.E. and J.R. Ehleringer. 1991. Streamside trees that do not use stream water. *Nature.* 350:335-337.
- Decker, J.P. and C.M. Skau. 1964. Simultaneous studies of transpiration rate and sap velocity in trees. *Plant Physiol.* 39:213-215.
- Dugas, W.A., J.S. Wallace, S.J. Allen, and J.M. Roberts. 1993. Heat balance

- porometer and deuterium estimates of transpiration from potted trees. *Agric. For. Meteorol.* 64:47-62.
- Dugas, W.A. 1990. Sap flow in stems. *Rem. Sens. Rev.* 5:225-235.
- Ehleringer, J.R. 1989. Temperature and Energy Budgets. In: *Plant Physiological Ecology: Field Methods and Instrumentation*. Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel. Chapman and Hall, London, pp 97-136.
- Ehleringer, J.R., A.E. Hall, and G.D. Farquhar, eds. 1993. *Stable Isotopes and Plant Carbon-Water Relations*. Academic Press, New York. 555 p.
- Ehleringer, J.R., and T.E. Dawson. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant Cell Environ.* 15:1073-1082.
- Ehleringer, J.R., and C.B. Osmond. 1989. Stable Isotopes. In: *Plant Physiological Ecology: Field Methods and Instrumentation*. Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel. Chapman and Hall, London, pp 281-300.
- Ehleringer, J.R. and P.W. Rundel. 1988. Stable isotopes: history, units and instrumentation. In: *Ecological Studies Vol. 68. Stable Isotopes in Ecological Research*. Eds. P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, Heidelberg, pp. 1-15.
- Environment Canada. 1990. *Canadian Climatic Normals: Waskesiu Lake*.
- Fitzjarrald, D.R. and K.E. Moore. 1994. Growing season boundary layer climate and surface exchanges in a subarctic lichen woodland. *J. Geophys. Res.* 99:1899-1917.
- Flanagan, L.B., J.R. Ehleringer, and J.D. Marshall. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant Cell Environ.* 15:831-836.
- Gedzelman, S.D., and R. Arnold. 1994. Modelling the isotopic composition of precipitation. *J. Geophys. Res.* 99:455-471.
- Greenway, K.J., S.E. MacDonald, and V.J. Lieffers. 1992. Is long-lived foliage in

- Picea mariana* an adaptation to nutrient poor-conditions? *Oecologia*. 91:184-191.
- Groot, A. and K.M. King. 1992. Measurement of sap flow by the heat balance method: numerical analysis and application to coniferous seedlings. *Agric. For. Meteorol.* 59:289-308.
- Gutierrez, M.V., R.A. Harrington, F.C. Meinzer, and J.H. Fownes. 1994. The effect of environmentally induced stem temperature gradients on transpiration estimates from the heat balance method in two tropical woody species. *Tree Physiol.* 14:179-190.
- Hatton, T.J., S.J. Moore, and P.H. Reece. 1995. Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiol.* 15:219-227.
- Herbst, M. 1995. Stomatal behaviour in a beech canopy: an analysis of Bowen ratio measurements compared with porometer data. *Plant Cell Environ.* 18:1010-1018.
- Hinckley, T.M., J.R. Brooks, J. Cernusak, R. Ceulemans, J. Kucera, F.C. Meinzer, and D.A. Roberts. 1994. Water flux in a hybrid poplar stand. *Tree Physiol.* 14:1005-1018.
- Hom, J.L. and W.C. Oechel. 1983. The photosynthetic capacity, nutrient content, and nutrient use efficiency of different needle age-classes of black spruce (*Picea mariana*) found in interior Alaska. *Can. J. For. Res.* 13:834-839.
- Jarvis, P.G. 1995. Scaling processes and problems. *Plant Cell Environ.* 18:1079-1089.
- Jarvis, P.G. 1993. Prospects for bottom-up models. In: *Scaling Physiological Processes. Leaf to Globe*. Eds. J.R. Ehleringer and C.B. Field. Academic Press, New York, pp. 115-126.
- Jarvis, P.G. 1985. Coupling of transpiration to the atmosphere in horticultural crops: the omega factor. *Acta. Hort.* 171:187-205.
- Jarvis, P.G. and K.M. McNaughton. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15:1-49.

- Jarvis, P.G., G.B. James, and J.J. Landsberg. 1976. Coniferous Forest. In: Vegetation and the Atmosphere, Vol. 2: Case Studies. J.L. Monteith, ed. Academic Press, London, pp. 171-240.
- Johnsen, K.H., J.R. Seiler, and J.E. Major. 1996. Growth, shoot phenology and physiology of diverse seed sources of black spruce: II. 23-year old field trees. *Tree Physiol.* 16:375-380.
- Kelliher, F.M., R. Leuning, and E.-D. Schulze. 1993. Evaporation and canopy characteristics of coniferous forests and grasslands. *Oecologia.* 95:153-163.
- Kostner, B.M.M., E.D. Schulze, F.M. Kelliher, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, R. Meserth, and P.L. Weir. 1992. Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia.* 91:350-359.
- Lafleur, P.M. 1992. Energy balance and evapotranspiration from a subarctic forest. *Agric. For. Meteorol.* 58:163-175.
- Lamhamedi, M.S. And P.Y. Bernier. 1994. Ecophysiology and field performance of black spruce (*Picea mariana*): a review. *Ann. Sci. For.* 51:529-551.
- Lin, G. and L. da S.L. Sternberg. 1993. Hydrogen isotopic fractionation by plant roots during water uptake in coastal wetland plants. In: Stable Isotopes and Plant Carbon-Water Relations. Eds. J.R. Ehleringer, A.E. Hall, and G.D. Farquhar. Academic Press, New York, pp. 497-510.
- Lin, G. and L. da S.L. Sternberg. 1992. Comparative study of water uptake and photosynthetic gas exchange between scrub and fringe red mangroves, *Rhizophora mangle* L. *Oecologia.* 90:399-403.
- Macdonald, S.E., and V.J. Lieffers. 1990. Photosynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix laricina* from drained and undrained peatlands. *Can. J. For. Res.* 20:995-1000.
- Marshall, D.C. 1958. Measurement of sap flow in conifers by heat transport. *Plant Physiol.* 33:385-396.
- Martin, P. 1989. The significance of radiative coupling between vegetation and the

- atmosphere. *Agric. For. Meteorol.* 49:45-53.
- McDermitt, D.K. 1990. Sources of error in the estimation of stomatal conductance and transpiration from porometer data. *Hortscience.* 25:1538-1548.
- McNaughton, K.G., and P.G. Jarvis. 1991. Effects of spatial scale on stomatal control of transpiration. *Agric. For. Meteorol.* 54:279-301.
- McNaughton, K.G. and P.G. Jarvis. 1983. Predicting effects of vegetation changes on transpiration and evaporation. In: *Water Deficits and Plant Growth, Volume VII.* Ed. T.T. Kozlowski. Academic Press, New York, pp. 1-47.
- Meinzer, F.C. 1993. Stomatal control of transpiration. *TREE* 8:289-294.
- Meinzer, F.C., G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Gutierrez, and J. Cavelier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of the boundary layer and hydraulic properties. *Oecologia.* 101:514-522.
- Meinzer, F.C., G. Goldstein, N.M. Holbrook, P. Jackson, and J. Cavelier. 1993. Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant Cell Environ.* 16:429-436.
- Mott, K.A. And D.F. Parkhurst. 1991. Stomatal responses to humidity in air and helox. *Plant Cell Environ.* 14:509-515.
- Monteith, J.L. and M.H. Unsworth. 1990. *Principles of Environmental Physics.* Second Edition. Edward Arnold, London, 291 p.
- Monteith, J.L. 1973. *Principles of Environmental Physics.* Elsevier, New York, 241 p.
- Monteith, J.L. 1965. Evaporation and environment. In: *Symposia of the Society for Experimental Biology XIX. The State and Movement of Water in Living Organisms.* Cambridge University Press, Cambridge, pp. 205-234.
- Nobel, P.S. 1991. *Physiochemical and Environmental Plant Physiology.* Academic Press, New York, 635 p.
- Pearcy, R.W., E.D. Schulze, and R. Zimmermann. 1989. Measurement of transpiration and leaf conductance. In: *Plant Physiological Ecology: Field Methods and*

- Instrumentation. Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel. Chapman and Hall, London, pp 137-160.
- Schulze, E.D., J. Cermak, R. Matyssek, M. Penka, R. Zimmermann, F. Vasicek, W. Gries, and J. Kucera. 1985. Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees—a comparison of xylem flow, porometer and cuvette measurements. *Oecologia*. 66:475-483.
- Sellers, P.J., L. Bounoua, G.J. Collatz, D.A. Randall, D.A. Dazlich, S.O. Los, J.A. Berry, I. Fung, C.J. Tucker, C.B. Field, and T.G. Jensen. 1996. Comparison of radiative and physiological effects of doubled atmospheric CO₂ on climate. *Science*. 271:1402-1406.
- Sellers, P., F. Hall, H. Margolis, B. Kelly, D. Baldocchi, G. den Hartog, J. Cihlar, M.G. Ryan, B. Goodison, P. Crill, K.J. Ranson, D. Lettenmaier, and D.E. Wickland. 1995. The boreal ecosystem atmosphere study (BOREAS): an overview and early results from the 1994 field year. *Bull. Amer. Meteorol. Soc.* 76:1549-1577.
- Sellers, P.F., F.G. Hall, M. Apps, D. Baldocchi, J. Cihlar, G. den Hartog, B. Goodison, R.D. Kelly, D. Lettenmeier, H. Margolis, A. Nelson, J. Ranson, N. Roulet, M. Ryan, eds. 1994. Boreal Ecosystem-Atmosphere Study Experiment Plan. Version 3.0
- Steinberg, S.L., M.J. McFarland, and J.W. Worthington. 1990. Comparison of trunk and branch sap flow with canopy transpiration in pecan. *J. Exp. Bot.* 41:653-659.
- Swanson, R.H. and D.W.A. Whitfield. 1981. A numerical analysis of heat pulse velocity theory and practice. *J. Exp. Bot.* 32:221-239.
- Teskey, R.O. and D.W. Sheriff. 1996. Water use by *Pinus radiata* trees in a plantation. *Tree Physiol.* 16:273-279.
- United States Dept. of Agriculture. Forest Service. 1990. Silvics of North America. Volume 2: Conifers. Agriculture Handbook 654.
- White, J.W.C., E.R. Cook, J.R. Lawrence, and W.S. Broecker. 1985. The D/H ratios

of sap in trees: implications for water sources and tree ring D/H ratios. *Geochim. et Cosmo. Acta.* 49:237-246.

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

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

Zine el Abidine, A., J.D. Stewart, P.Y. Bernier, and A.P. Plamondon. 1995. Diurnal and seasonal variations in gas exchange and water relations of lowland and upland black spruce ecotypes. *Can. J. Bot.* 73:716-722.

Appendix A.

Table A1. Two-way ANOVA analysis of the stomatal conductance data for the upper canopy branches.

Source	df	ss	ms	F	p
Total	19	18016.0			
Time	4	10730.8	2682.7	5.18	0.006
Branch	3	1070.1	356.7	0.69	0.799
Error	12	6215.1	517.9		

Table A2. Two-way ANOVA analysis of the boundary layer conductance data for the upper canopy branches.

Source	df	ss	ms	F	p
Total	15	24741.6			
Time	3	12294.4	4098.1	3.40	0.036
Branch	3	1566.7	522.2	0.43	0.845
Error	9	10853.4	1205.9		

Table A3. Two-way ANOVA analysis of the Ω data for the upper canopy branches.

Source	df	ss	ms	F	p
Total	15	0.142			
Time	3	0.024	0.0079	2.16	0.512
Branch	3	0.085	0.0283	7.67	0.010
Error	9	0.033	0.0037		

Note: the first time interval (e.g. <1000 hrs) is not considered in the ANOVA for g_{wb} or Ω . The calculations of g_{wb} for branch 2 resulted in negative values during this

interval, and so the data set is essentially incomplete at this point. Indeed, if the ANOVA for Ω is done without branch 2, for all of the time intervals, the p-values are 0.045 and 0.621 for time and branch, respectively.

Table A4. Paired t-tests of the gas-exchange and Ω data for the upper and lower canopy branches. The average of the four upper canopy branches was used.

Variable	t-value	t-critical	p
g_{ws}	-0.897	2.776	0.420
g_{wh}	-2.45	2.776	0.071
Ω	4.95	2.776	0.008

Appendix B.

Table B1. Error calculations for the Ω data set. The Ω calculation includes the radiative coupling term (Equation 5). Units for vapour pressure (e_a and e_i) are millibars. Other units are not listed, but are the same as described throughout the text.

Parameter	High /Low	Calculated as:	Value	Parameter Mean	Percent Error
RH	High	RH+5%	47.97	45.68	5.0
	Low	RH-5%	43.40		
Ta	High	Ta+1°C	21.26	20.26	4.9
	Low	Ta-1°C	19.26		
Tl	High	Tl+1°C	23.35	22.35	4.5
	Low	Tl-1°C	21.35		
e_a	High	(Ta and RH)low	12.36	11.08	11.2
	Low	(Ta and RH)high	9.89		
e_i	High	Tl high	29.35	27.64	6.1
	Low	Tl low	26.01		
VPD	High	e_i high - e_a low	19.47	16.57	17.5
	Low	e_i low - e_a high	13.66		
E	High	E+15%	0.28	0.24	15.0
	Low	E-15%	0.21		
g_{wt}	High	Ehigh / VPDlow	19.02	12.26	42.4
	Low	Elow / VPDhigh	8.61		
g_{ws}	High	g_{ws} +15%	35.30	30.70	15.0
	Low	g_{ws} -15%	26.09		
g_{wb}	High	g_{wt} high and g_{ws} low	47.46	27.85	62.7
	Low	g_{wt} low and g_{ws} high	12.55		
Ω	High	g_{wb} low and g_{ws} high	0.78	0.64	20.3
	Low	g_{wb} high and g_{ws} low	0.52		

Appendix C.

The theoretical wind-profile (Figure 13) was calculated based on observations made during BOREAS 1994. Half-hourly wind speed and friction velocity measurements (made above the canopy, at 24m) from the period 14 June to 07 July (1994) were averaged to construct a diurnal pattern. Using this, wind speed at the top of the canopy was calculated using the equation given by Monteith and Unsworth (1990):

$$U(h) = \left[\frac{u^*}{k} \right] \ln \left[\frac{h - d_o}{z_o} \right] \quad (20)$$

where $U(h)$ is the wind speed at height h (in this case, the canopy height), u^* is the friction velocity, k is von Karman's constant, d_o is the zero-plane displacement, and z_o is the roughness length. Following Monteith and Unsworth (1990) d_o was estimated as $0.65z$ (where z is the height of the canopy), and z_o was estimated as $0.09z$. The windspeed at the top of the canopy was then used to calculate the profile within the canopy (Amiro 1990):

$$U(z) = U(h) \exp[\alpha(z/h - 1)] \quad (21)$$

where $U(z)$ is the windspeed at height z , and α is the wind extinction coefficient for the stand. Three values of α (4.8, 3.2, 2.6) are shown in Figure 13a; these correspond to the values determined by Amiro (1990) for black spruce, Jack pine, and aspen forests, respectively. The effect of increasing the value of α is to further reduce the wind speed closer to the forest floor.

Appendix D.

The effective length of black spruce needles, given the observed boundary layer conductance to water vapour, was calculated from the equations shown by Nobel (1991) for the boundary layer of flat leaves. The thickness of the boundary layer is related to g_{wb} (in units of m s^{-1}) by:

$$g_{wb} = \frac{D_{wv}}{\delta_{bl}} \quad (22)$$

where D_{wv} is the diffusion coefficient for water vapour in air ($2.42 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ at 20°C), and δ_{bl} is in metres. The thickness (mm) of the boundary layer of air surrounding a flat leaf of length l (m) and exposed to windspeed v (m s^{-1}) is:

$$\delta_{bl} = 4 \sqrt{\frac{l}{v}} \quad (23)$$

where the factor 4 has units of $\text{mm s}^{-1/2}$. By rearrangement, the length of the leaf can then be calculated. The thickness of the boundary layer surrounding a cylinder is related to windspeed and the diameter of the cylinder by a similar relationship, except that the constant has a value of $5.8 \text{ mm s}^{-1/2}$. For the purpose here, these calculations were carried out for the average boundary layer conductance for each branch, for the time intervals shown in Figure 9. The average windspeed for the appropriate time interval was used in the calculations (see Figure 14). The following tables summarize the results for the effective needle length and branch diameter.

Table D1. The effective length of black spruce needles based upon the observed boundary layer conductance to water vapour and the hypothetical wind speed profile within the canopy. The units are millimetres.

Branch	Alpha		
	2.6	3.2	4.8
1	33.6	27.8	16.7
2	32.7	27.0	16.3
3	47.5	39.3	23.7
4	67.1	55.4	33.4
5	183.4	124.3	57.1

Table D2. The effective diameter of black spruce twigs (assuming the twigs to be cylindrical). The units are millimetres.

Branch	Alpha		
	2.6	3.2	4.8
1	16.0	13.2	8.0
2	15.6	12.9	7.7
3	22.6	18.7	11.3
4	31.9	26.4	15.9
5	87.2	59.2	27.2

Appendix E.

The isothermal net radiation is, 'the net radiation that would be received in the same environment by an identical surface at air temperature' (Monteith 1973). It can be defined as:

$$R_{ni} = R_n + \sigma(T_s^4 - T_a^4) \quad (24)$$

where R_n is the net radiation, σ is the Stefan Boltzman constant, T is temperature ($^{\circ}\text{K}$), and the subscripts s and a refer to surface and air, respectively. In the ensuing discussion, the surface is considered to be the leaf. In this study, R_n was determined from the sum of the sensible and latent heat fluxes. The sensible heat flux was calculated based on the equation shown by Nobel (1991):

$$H = 2h_c(T_l - T_a) \quad (25)$$

where h_c is the convection coefficient. The convection coefficient is equal to the product of the heat capacity of air ($1212 \text{ J m}^{-3} \text{ }^{\circ}\text{C}^{-1}$) and the boundary layer conductance to heat (m s^{-1}) ($0.888g_{wb}$). The factor 2 arises because heat can be conducted across the boundary layers on either side of a leaf (Nobel 1991, p. 367). The latent heat flux is calculated as.

$$L = \lambda E \quad (26)$$

where λ is the heat of vaporisation of water (44 kJ mol^{-1}), and E is the transpiration rate. Because transpiration (and stomatal conductance) are measured for all leaf surfaces, there is no need to multiply equation 26 by two. Determined in this fashion, net radiation is expressed on a leaf area basis, and this calculation describes the radiation environment of

the individual branches.

Although direct measurements of net radiation were not made during this study, it is possible to calculate this parameter, based on previous information and a few assumptions. During BOREAS 1994, extensive micrometeorological measurements were made at this study site (P.G. Jarvis, pers. comm.). A strong linear relationship between PAR and solar radiation (SR) on a ground-area basis at the top of the canopy exists:

$$SR = 0.53162PAR - 13.7081 \quad (27)$$

which has an R^2 value of 0.99. This regression was based on half-hourly observations made from midnight on 14 June to midnight on 18 July, 1994. The radiation balance will depend on how much of this incident radiation is absorbed. Absorbed solar radiation is described by (Nobel 1991):

$$SR_{abs} = a(1 + R)SR \quad (28)$$

where a is the fraction of solar radiation that is absorbed by the leaf, and R is the fraction of solar radiation that is reflected onto the leaf by its surroundings. This reflectance is related to albedo (Nobel 1991). I have assigned a value of 0.5 for the absorbed fraction, based on what Nobel (1991) describes as 'typical'. The reflection coefficient for coniferous forests typically ranges between 0.05 and 0.15 (Arya 1988). During BOREAS 1994, typical albedos for spruce forests were about 0.075, with a slight variability over the course of a day (Sellers et al. 1995); this value was used here.

Infrared radiation is both absorbed and emitted by an object, in proportion to its temperature:

$$IR_{emitted} = 2\epsilon\sigma T^4 \quad (29)$$

where ϵ is the emissivity (0.96 for biological materials), and T is the temperature of the emitting surface. The infrared energy absorbed by a leaf was calculated using air temperature, being the nearest available approximation to the temperature of the surroundings. The predicted net radiation is then:

$$PR_n = SR_{abs} + IR_{abs} - IR_{emitted} \quad (30)$$

This can then be expressed as isothermal net radiation (PR_m), using leaf and air temperature as shown in Equation 24.

END

1 9 - 0 6 - 9 7

FIN