

A review of whole-plant water use studies in trees

STAN D. WULLSCHLEGER,¹ F. C. MEINZER² and R. A. VERTESSY³

¹ Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6422, USA

² Hawaii Agriculture Research Center, 99-193 Aiea Heights Drive, Suite 300, Aiea, HI 96701-3911, USA

³ CSIRO Division of Water Resources, GPO Box 1666, Canberra, ACT 2601, Australia

Received July 24, 1997

Summary Weighing lysimeters, large-tree potometers, ventilated chambers, radioisotopes, stable isotopes and an array of heat balance/heat dissipation methods have been used to provide quantitative estimates of whole-tree water use. A survey of 52 studies conducted since 1970 indicated that rates of water use ranged from 10 kg day⁻¹ for trees in a 32-year-old plantation of *Quercus petraea* L. ex Liebl. in eastern France to 1,180 kg day⁻¹ for an overstory *Euphorbia purpurea* Bth. tree growing in the Amazonian rainforest. The studies included in this survey reported whole-tree estimates of water use for 67 species in over 35 genera. Almost 90% of the observations indicated maximum rates of daily water use between 10 and 200 kg day⁻¹ for trees that averaged 21 m in height. The thermal techniques that made many of these estimates possible have gained widespread acceptance, and energy-balance, heat dissipation and heat-pulse systems are now routinely used with leaf-level measurements to investigate the relative importance of stomatal and boundary layer conductances in controlling canopy transpiration, whole-tree hydraulic conductance, coordinated control of whole-plant water transport, movement of water to and from sapwood storage, and whole-plant vulnerability of water transport to xylem cavitation. Techniques for estimating whole-tree water use complement existing approaches to calculating catchment water balance and provide the forest hydrologist with another tool for managing water resources. Energy-balance, heat dissipation and heat-pulse methods can be used to compare transpiration in different parts of a watershed or between adjacent trees, or to assess the contribution of transpiration from overstory and understory trees. Such studies often require that rates of water use be extrapolated from individual trees to that of stands and plantations. The ultimate success of this extrapolation depends in part on whether data covering short time sequences can be applied to longer periods of time. We conclude that techniques for estimating whole-tree water use have provided valuable tools for conducting basic and applied research. Future studies that emphasize the use of these techniques by both tree physiologists and forest hydrologists should be encouraged.

Keywords: cavitation, decoupling coefficient, forest hydrology, hydraulic conductance, sap flow, scaling, stomatal conductance, transpiration, water storage.

Introduction

Forest scientists have long sought to develop reliable techniques for estimating whole-plant water use in trees. Early attempts to infer rates of canopy water use from data collected on excised leaves and branches were largely unsuccessful (Parker 1957, Rutter 1966), as were efforts to provide quantitative estimates of water use for large trees based on data obtained with potted seedlings. These failures are not surprising because the vast majority of early studies were conducted under conditions that failed to reproduce both the climate and, more importantly, the structure of forest stands. Whole-plant water use by subcanopy trees, for example, has been shown to differ from that of canopy and emergent individuals (Arneeth et al. 1996). Recent attempts to obtain *in situ* estimates of leaf transpiration using porometers and cuvettes, and the extrapolation of such results to the canopy have met with mixed success (Schulze et al. 1985, Roberts et al. 1993, Ansley et al. 1994) because of the poorly quantified influence of boundary layers in limiting whole-plant transpiration (Jarvis and McNaughton 1986) and because of inadequate characterization of variation in water use along canopy gradients of leaf age, radiation and humidity.

Whole-tree estimates of water use are becoming increasingly important in forest science. Tree physiologists utilize estimates of water use to partition the control of canopy transpiration between stomatal and boundary layer conductances (Hinckley et al. 1994, Meinzer et al. 1995) and to assess the radial pattern of xylem water flux in non-, diffuse- and ring-porous tree species (Phillips et al. 1996). Forest hydrologists rely on such information to help resolve issues of water resource management (Schiller and Cohen 1995, Loustau et al. 1996), to evaluate the role of transpiration in forest and woodland hydrology (Barrett et al. 1996) and to quantify the water requirements of short-rotation forests (Cienciala and Lindroth 1995, Lindroth et al. 1995). Sixty years ago, Raber (1937) recognized that future foresters would benefit from whole-plant techniques for measuring water use when he concluded a review of water utilization by forest trees with the statement:

The fact that trees are large and not easy to handle... increases the difficulties (of measuring the water requirements of trees), but they should not be insurmountable; for

no really satisfactory results can be expected until more data are obtained on forest trees and stands under natural conditions, supplemented by laboratory work on a scale comparable with the size of the problem involved.

Since the mid-1930s, weighing lysimeters, large-tree potometers, ventilated chambers, radioisotopes, stable isotopes and several thermal-based methods have been used to obtain quantitative estimates of whole-plant water use. This review examines how these techniques have contributed to our understanding of water transport, storage and use in trees. Techniques for measuring whole-plant water use have enabled quantitative estimates of water utilization to be derived. These techniques also provide valuable insights into whole-tree physiology when estimates of xylem water flux are supplemented with measurements of stomatal conductance and leaf water potential, and when estimates of water flux are made at multiple heights in a tree. Several research areas are highlighted to illustrate how these concepts are being used to broaden our understanding of whole-plant water relations. We conclude with an examination of how information on water flux can be extrapolated to tree, stand and watershed scales, and briefly comment on the insights gained through these extrapolations.

Techniques for estimating whole-tree water use

A complete description of the techniques available for estimating the water use of large trees is beyond the scope of this paper. The reader should consult some of the many papers and reviews that provide detailed information on each technique: e.g., lysimeters (Fritschen et al. 1973, Edwards 1986), large-tree potometers (Roberts 1977, Knight et al. 1981), tent enclosures or ventilated chambers (Greenwood and Beresford 1979, Dunin and Greenwood 1986), chemical tracers (Greenidge 1955), radioisotopes like tritium (Kline et al. 1970, Waring and Roberts 1979), stable isotopes like deuterium (Calder et al. 1986, Dye et al. 1992) and energy-balance, heat dissipation and heat-pulse techniques (Swanson 1994, Smith and Allen 1996).

Each of these techniques has merits and drawbacks. Weighing lysimeters are sensitive to small changes in water lost from the soil-plant system, but roots occupy a limited soil volume and lysimeters are expensive to construct and maintain. The use of large-tree potometers in so-called "cut tree" experiments are intrusive and often induce changes in leaf water potential and stomatal conductance that may otherwise preclude physiological interpretation of data (Roberts 1978). Ventilating chambers offer a method to measure both water vapor and CO₂ exchange in trees (Denmead et al. 1993), although it is argued that estimates of water-use efficiency derived with this technique are confounded by the effects of vapor pressure deficit (Lindroth and Cienciala 1995). The use of radio-tracers like tritium and ³²P are increasingly subject to regulatory constraints and seasonal patterns of water use are difficult to obtain with these methods. The use of deuterium overcomes many of these limitations and stable isotopes have largely replaced tritium as a tracer-based technique for quantifying

rates of water use. Estimates of water use derived from energy-balance, heat dissipation and heat-pulse techniques suffer from uncertainties as a result of empirical calibrations, thermal gradients and variation in water flux with sapwood depth (Granier et al. 1996b), but these systems are inexpensive, easy to use and readily interfaced with data loggers for remote operation.

Quantitative estimates of whole-tree water use

Table 1 presents data from 52 studies published between 1970 and 1998 in which weighing lysimeters, large-tree potometers, ventilated chambers, radioisotopes, stable isotopes, or thermal techniques were used to provide quantitative estimates of whole-plant water use for trees growing in stands or plantations. Data included in this table are restricted to studies that report rates of daily water use of 10 kg day⁻¹ or greater. The studies included in this survey report whole-tree estimates of water use for 67 species in over 35 genera. Most of the tree species were examined in only one study, although three or more reports of water use are available for *Eucalyptus grandis* W. Hill ex Maiden, *Picea abies* (L.) Karst., *Pinus radiata* D. Don, *Pseudotsuga menziesii* (Mirb.) Franco and *Quercus petraea* L. ex Liebl. More than half of the observations were made with thermal-based techniques (51/92), followed by radioactive or stable isotopes (16/92), ventilated chambers (16/92), and lysimeters/large-tree potometers (9/92). Thirty-two of these studies were published during the past decade; 30 of them used energy-balance, heat dissipation or heat-pulse methods, two used lysimeters (Steinberg et al. 1990, Olbrich 1991) and one used the stable isotope deuterium (Dye et al. 1992). Estimates of water use for trees enclosed in ventilated chambers were last reported by Greenwood et al. (1985).

The studies compiled in Table 1 indicate that quantitative rates of water use range from 10 kg day⁻¹ for trees in a 32-year-old stand of *Quercus petraea* in eastern France (Bréda et al. 1993b) to 1,180 kg day⁻¹ for a large overstory *Euphorbia purpurea* Bth. tree in the Amazonian rainforest (Jordan and Kline 1977). Three of the 52 studies reported whole-tree rates of water use greater than 400 kg day⁻¹ (Kline et al. 1976, Jordan and Kline 1977, Ěermák et al. 1982). Trees in these three studies ranged in height from 33 to 76 m and in the case of *Pseudotsuga menziesii*, had a diameter that approached 1.4 m (Kline et al. 1976). Large trees and high water-use rates were the exception in this survey—90% of the observations (83/92) indicated rates of water use between 10 and 200 kg day⁻¹ for trees that averaged 21 m in height (Table 1).

Insights gained from studies of whole-tree water use—a physiologist's perspective

Although each of the techniques for estimating whole-plant water use has improved our quantitative appreciation of water utilization in trees, the challenge remains to use these techniques so that meaningful physiological insights are derived. Five areas of research are used to illustrate that estimates of water use contribute most to our understanding of tree water

Table 1. Maximum daily rates of whole-plant water use as reported by studies using weighing lysimeters or large-tree potometers (L/P), ventilated chambers (VC), radioactive or stable isotopes (R/SI), and thermal balance or heat dissipation methods (TM). Height (m), diameter (cm), leaf area (m²), cross-sectional sapwood area (cm²), and water use (kg day⁻¹) for measured trees are given.

Species	Method	Height	Diameter	Leaf area	Sapwood area	Water use	Reference
<i>Abies amabilis</i>	TM	18	40	151	—	98	Martin et al. 1997
<i>Acacia dealbata</i>	TM	—	25	—	279	59	Vertessy et al. 1995
<i>Anacardium excelsum</i>	TM	35	102	—	5,100	379	Goldstein et al. 1998
<i>Aspidosperma album</i>	R/SI	—	—	—	150	40	Jordan and Kline 1977
<i>Aspidosperma cruentum</i>	R/SI	—	—	—	448	179	Jordan and Kline 1977
<i>Banksia grandis</i>	VC	—	—	22	—	101	Greenwood et al. 1985
	VC	—	—	10	—	36	Greenwood et al. 1985
<i>Betula alba</i>	TM	—	—	—	—	70	Ěermák and Kučera 1993
	TM	—	—	—	—	42	Kučera et al. 1977
<i>Carapa procera</i>	TM	37	38	—	355	52	Granier et al. 1996a
<i>Carya illinoensis</i>	L/P	4	8	43	—	150	Steinberg et al. 1990
	TM	4	8	43	—	123	Steinberg et al. 1990
<i>Caryocar glabrum</i>	TM	27	26	—	282	48	Granier et al. 1996a
<i>Cassipourea guianensis</i>	TM	18	17	—	186	24	Granier et al. 1996a
<i>Cecropia longipes</i>	TM	18	20	—	200	47	Goldstein et al. 1998
<i>Dacryodes excelsa</i>	R/SI	20	55	—	—	372	Kline et al. 1970
<i>Dicorynia guianensis</i>	TM	44	57	—	707	212	Granier et al. 1996a
<i>Dryobalanops aromatica</i>	TM	40–60	75	—	—	310	Becker 1996
<i>Eperua falcata</i>	TM	35	45	—	535	166	Granier et al. 1996a
<i>Eperua grandifolia</i>	TM	33	55	—	796	151	Granier et al. 1996a
<i>Eperua leucantha</i>	R/SI	—	—	—	131	91	Jordan and Kline 1977
<i>Eperua purpurea</i>	R/SI	—	—	—	1,521	1,180	Jordan and Kline 1977
<i>Eucalyptus camaldulensis</i>	VC	—	—	5	—	29	Greenwood and Beresford 1979
<i>Eucalyptus cladocalyx</i>	VC	—	—	7	—	30	Greenwood and Beresford 1979
<i>Eucalyptus kondininensis</i>	VC	—	—	2	—	17	Greenwood and Beresford 1979
<i>Eucalyptus fastigata</i>	L/P	3	—	59	—	154	Edwards 1986
<i>Eucalyptus globulus</i>	VC	—	—	17	—	37	Greenwood and Beresford 1979
<i>Eucalyptus grandis</i>	L/P	56	41	219	371	174	Olbrich 1991
	R/SI	23	18	73	216	94	Dye et al. 1992
	TM	34	30	71	—	141	Dye 1996
<i>Eucalyptus leucoxylon</i>	VC	—	—	2	—	23	Greenwood and Beresford 1979
<i>Eucalyptus loxophleba</i>	VC	—	—	2	—	20	Greenwood and Beresford 1979
	TM	—	—	—	—	125	Barrett et al. 1996
<i>Eucalyptus occidentalis</i>	VC	—	—	4	—	20	Greenwood and Beresford 1979
<i>Eucalyptus platypus</i>	VC	—	—	3	—	28	Greenwood and Beresford 1979
<i>Eucalyptus regnans</i>	TM	—	37	147	452	151	Vertessy et al. 1995
	TM	58	89	330	618	285	Vertessy et al. 1997
<i>Eucalyptus robusta</i>	VC	—	—	3	—	19	Greenwood and Beresford 1979
<i>Eucalyptus saligna</i>	VC	—	—	4	—	23	Greenwood and Beresford 1979
<i>Eucalyptus sargentii</i>	VC	—	—	4	—	28	Greenwood and Beresford 1979
<i>Eucalyptus wandoo</i>	VC	—	—	4	—	27	Greenwood and Beresford 1979
	VC	—	—	62	—	150	Greenwood et al. 1982
<i>Fagus sylvatica</i>	TM	35	54	—	—	137	Ěermák et al. 1993
<i>Ficus insipida</i>	TM	30	54	—	2,100	164	Goldstein et al. 1998
<i>Grevillea robusta</i>	TM	—	—	—	—	12	Lott et al. 1996
<i>Hirtella glandulosa</i>	TM	31	32	—	395	62	Granier et al. 1996a
<i>Larix gmelinii</i>	TM	20	25	—	76	67	Arneith et al. 1996
<i>Larix</i> sp.	TM	20	—	—	—	74	Schulze et al. 1985
<i>Lecythis idatimon</i>	TM	34	39	—	515	94	Granier et al. 1996a
<i>Licania</i> sp.	R/SI	—	—	—	103	34	Jordan and Kline 1977
<i>Luehea seemannii</i>	TM	29	37	—	1,000	129	Goldstein et al. 1998
<i>Micranda spruceana</i>	R/SI	—	—	—	421	140	Jordan and Kline 1977
<i>Nothofagus fusca</i>	TM	34	60	—	—	110	Kelliher et al. 1992
<i>Nothofagus</i> spp.	TM	36	—	—	—	84	Köstner et al. 1992
<i>Ocotea</i> sp.	R/SI	—	—	—	547	396	Jordan and Kline 1977
<i>Picea abies</i>	TM	25	—	—	—	63	Schulze et al. 1985
	TM	11	10	—	—	10	Granier and Claustres 1989
	TM	15	19	—	—	49	Cienciala et al. 1992
	TM	—	—	—	—	23	Ěermák et al. 1995
	TM	25	36	447	—	175	Herzog et al. 1995
	TM	17	15	—	—	66	Köstner et al. 1998
<i>Pinus caribaea</i>	R/SI	7	13	—	—	100	Sansigolo and Ferraz 1982
<i>Pinus contorta</i>	R/SI	20	25	—	—	25	Owston et al. 1972
	L/P	—	20–26	—	—	44	Knight et al. 1981
<i>Pinus halepensis</i>	TM	9	—	—	134	49	Schiller and Cohen 1995

Table 1, continued next page...

Table 1. Continued...

Species	Method	Height	Diameter	Leaf area	Sapwood area	Water use	Reference
<i>Pinus pinaster</i>	TM	20	34	—	523	161	Granier et al. 1990
	TM	26	35	—	642	125	Loustau et al. 1996
<i>Pinus radiata</i>	VC	16	22	—	—	179	Greenwood et al. 1981
	L/P	6	—	265	412	150	Edwards 1986
	TM	25	42	300	1,089	349	Teskey and Sheriff 1996
<i>Pinus sylvestris</i>	L/P	—	—	—	—	13	Roberts 1977
	R/SI	15	—	—	—	29	Waring and Roberts 1979
	TM	—	—	—	—	13	Ěermák et al. 1995
<i>Pinus taeda</i>	R/SI	5	8	—	—	40	Luvall and Murphy 1982
<i>Populus × euramericana</i>	L/P	5	—	26	133	109	Edwards 1986
<i>Populus trichocarpa × P. deltoides</i>	TM	15	15	—	—	51	Hinckley et al. 1994
	TM	4	—	—	—	108	Ansley et al. 1994
<i>Protium</i> sp.	R/SI	—	—	—	62	41	Jordan and Kline 1977
<i>Pseudotsuga menziesii</i>	L/P	28	38	—	—	64	Fritschen et al. 1973
	R/SI	76	134	—	4,020	530	Kline et al. 1976
	TM	18	20	—	—	22	Granier 1987
<i>Quercus petraea</i>	TM	—	—	—	—	12	Bréda et al. 1993a
	TM	15	9	—	—	10	Bréda et al. 1993b
	TM	—	10	—	—	11	Bréda et al. 1995
<i>Quercus robur</i>	TM	—	—	—	—	10	Bréda et al. 1993a
	TM	33	—	—	—	400	Ěermák et al. 1982
<i>Quercus sessilis</i>	TM	—	—	—	—	129	Kuèera et al. 1977
<i>Salix fragilis</i>	TM	—	—	38–47	—	103	Ěermák et al. 1984
<i>Salix matsudana</i>	L/P	5	—	28	86	106	Edwards 1986
<i>Sloanea berteriana</i>	R/SI	18	27	—	—	140	Kline et al. 1970
<i>Spodias mombin</i>	TM	23	44	—	600	80	Goldstein et al. 1998
<i>Vouacapoua americana</i>	TM	28	49	—	288	29	Granier et al. 1996a

relations when they are combined with additional leaf, branch and whole-plant measurements. These supplemental observations provide data from which several properties of trees can be derived, including: (1) the role of stomatal and boundary layer conductance in controlling rates of canopy transpiration, (2) whole-tree hydraulic conductance, (3) the coordinated control of vapor and liquid phase water transport, (4) movement of water to and from sapwood storage, and (5) whole-plant vulnerability of water transport to cavitation.

Stomatal and boundary layer control of whole-plant water use

Traditionally, the role of stomata in controlling transpiration has been inferred from leaf-level measurements of stomatal conductance obtained with porometers. Measurements of stomatal conductance obtained in the crowns of large trees indicate a considerable degree of responsiveness to environmental and plant physiological variables. This is consistent with observations reported for other plants. Nevertheless, extrapolation from these leaf measurements to rates of whole-tree water use is not straightforward because the impact of stomatal movements on transpiration is diminished by the diffusive resistance of boundary layers surrounding each leaf and the entire canopy. These boundary layers allow transpired water vapor to humidify the air near the leaves, uncoupling the vapor pressure at the leaf surface from that in the bulk air (Jarvis and McNaughton 1986). This micrometeorological feedback alters the driving force for transpiration and therefore ultimately the rate of leaf and whole-plant transpiration. The magnitude of this decoupling effect depends largely on the ratio of stomatal

to boundary layer conductance rather than the absolute magnitude of boundary layer conductance. The sensitivity of leaf or canopy transpiration to a marginal change in stomatal conductance has been described quantitatively by Jarvis and McNaughton (1986) in terms of a dimensionless decoupling coefficient (Ω) which ranges between zero and one. Stomatal control of transpiration grows progressively weaker as Ω approaches 1.0 because the vapor pressure at the leaf surface becomes increasingly decoupled from that in the bulk air. In general, Ω increases with increasing stomatal conductance in a manner determined by prevailing boundary layer conductance. The stomatal decoupling coefficient for a given species will thus be characterized by a range of values rather than a specific value.

Examination of Ω estimated for trees in both natural stands and plantations reveals a large range of values (Table 2). As expected, Ω is lowest (0.05 to 0.08) in coniferous species because of their small leaves, large boundary layer conductance and relatively low values of stomatal conductance. Decoupling of transpiration from stomatal control increases sharply with increasing leaf size, partly because of the inevitable reduction in boundary layer conductance, but also because stomatal conductance tends to be greater in large-leaved species than in small-leaved species. Thus, in a species such as *Tectona grandis* L.f., where leaf size is 700 cm² and stomatal conductance is more than an order of magnitude greater than in a typical conifer, Ω may approach 1.0 (Table 2). Inspection of Table 2 reveals that it is difficult to generalize about expected values of Ω for a given species or vegetation type. For example, Roberts et al. (1990) reported a mean Ω value of 0.28

Table 2. Values of Ω estimated for temperate and tropical trees and shrubs growing in a variety of sites. Prevailing stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$), leaf area (cm^2) and wind speed (m s^{-1}) are also given. Concurrent measurement of whole-plant water use is indicated by a + sign.

Species	Site	Location	Stomatal conductance	Leaf area	Wind speed	Ω	Water use	Reference
<i>Acer rubrum</i>	Understory	Tennessee	55	80	< 0.5	0.72	+	Wullschleger et al. 1998
<i>Anacardium excelsum</i>	Tropical forest (upper canopy)	Panama	90	250	–	0.54	+	Meinzer et al. 1993
<i>Cecropia longipes</i>	Tropical forest (upper canopy)	Panama	340	830	0.6	0.84	+	Meinzer et al. 1997
<i>Fagus sylvatica</i>	100-yr-old plantation	Germany	100	–	–	0.20	+	Herbst 1995
<i>Ficus insipida</i>	Tropical forest (upper canopy)	Panama	430	90	0.4	0.82	+	Meinzer et al. 1997
<i>Gmelina arborea</i>	Plantation	Nigeria	750	300	1.0	0.87		Jarvis and McNaughton 1986
<i>Luehea seemannii</i>	Tropical forest (upper canopy)	Panama	370	32	0.5	0.80	+	Meinzer et al. 1997
<i>Miconia argentea</i>	Tropical forest (treefall gap)	Panama	200	300	< 0.25	0.75	+	Meinzer et al. 1995
<i>Nothofagus fusca</i>	Pristine forest	New Zealand	200	4	2	0.26	+	Köstner et al. 1992
<i>Pinus pinaster</i>	64-yr-old stand	Portugal	50	–	3 to 4	0.08	+	Loustau et al. 1996
<i>Populus trichocarpa</i> × <i>P. deltoides</i>	3-yr-old plantation	Washington	310	210	–	0.66	+	Hinckley et al. 1994
<i>Spondias mombin</i>	Tropical forest (upper canopy)	Panama	340	31	0.4	0.79	+	Meinzer et al. 1997
<i>Tectona grandis</i>	Plantation	Nigeria	1,250	700	1.0	0.94		Jarvis and McNaughton 1986
Various upper canopy trees	Amazonian terra firme forest	Brazil	140	–	2.0	0.28		Roberts et al. 1990
Various understory shrubs	Amazonian terra firme forest	Brazil	80	–	0.2	0.78		Roberts et al. 1990

for the upper canopy of an Amazonian forest, whereas Meinzer et al. (1997) obtained a mean value of about 0.81 for four species in the upper canopy of a Panamanian forest. The difference in Ω values between the two sites can largely be reconciled when differences in prevailing stomatal conductance and wind speed are taken into account (Table 2).

Estimates of Ω provide insights into whether leaf-level observations truly reflect stomatal control of transpiration in canopies. Porometric measurements of transpiration in coniferous species that have low values of Ω may be interpreted as actual canopy-scale fluxes (e.g., Schulze et al. 1985). However, for most of the species listed in Table 2, reliance on porometric data alone could lead to misinterpretation of the significance of stomatal movements to whole-plant transpiration, regardless of leaf size or tree exposure and *a priori* assumptions about boundary layer conductance. Wullschleger et al. (1998) estimated an Ω value of 0.64 to 0.72 for *Acer rubrum* L. saplings growing in the understory of an upland oak forest and calculated that a 10% change in stomatal conductance would result in a modest 2.6% change in transpiration. The pitfalls associated with the relatively common practice of

implicitly or explicitly scaling from porometric measurements of stomatal conductance to transpirational fluxes without taking Ω into account are further illustrated in Figure 1. Here transpiration estimated as the product of stomatal conductance and the leaf-to-air vapor pressure difference is compared with simultaneous determinations of transpiration from branch water flux measurements in a large upper canopy tree (Figure 1A) and in a 2-m tall sapling growing in a small treefall gap (Figure 1B). In both examples, the magnitude of the error associated with porometry-based estimates of transpiration increased sharply with increasing actual transpiration and therefore with increasing stomatal conductance. This behavior is consistent with Ω theory stating that boundary layer resistance becomes increasingly limiting as stomatal conductance increases. The influence of the boundary layer is not considered in the measurement of stomatal conductance with most porometers (the exception is the Delta-T Devices, Model AP4 porometer which has an unstirred leaf cuvette; Delta-T Devices, Cambridge, U.K.) because the boundary layer is essentially disrupted by the fan in the ventilated chamber. The smaller degree of scatter evident in the relationship shown in

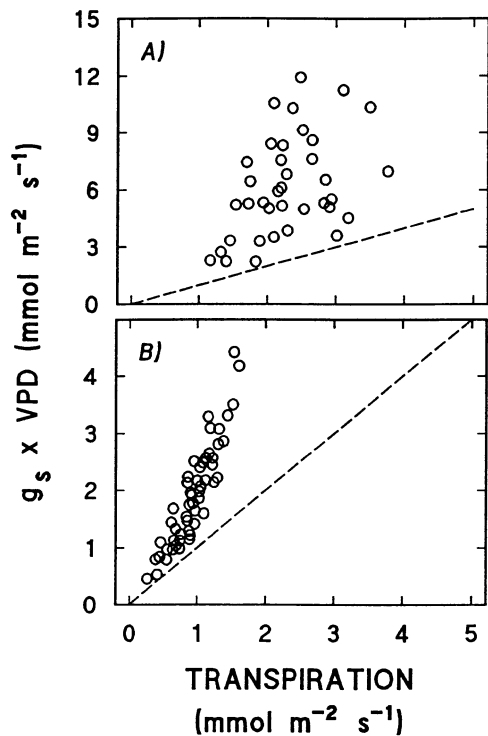


Figure 1. Relationship between transpiration estimated as the product of stomatal conductance (g_s) and the leaf-to-bulk air VPD, and actual transpiration determined from sap flow through branches for (A) the upper crown of a 30-m tall *Ficus insipida* tree growing in a forest in Panama, and (B) entire crowns of 1.5 to 2-m-tall *Miconia argentea* saplings growing in treefall gaps in a Panamanian forest. The dashed lines represent the 1:1 relationships between estimated and measured transpiration. Data in (B) adapted with permission from Meinzer et al. (1995).

Figure 1B compared with data in Figure 1A is probably attributable to the lower wind speed and the more stable boundary layer conditions in the treefall gap than in the upper canopy.

Whole-tree estimates of hydraulic conductance

Estimates of whole-plant water use expressed either per unit sapwood area or leaf area can be related to leaf water potential, and this relationship can be used to describe the total hydraulic conductance (G_t) of the soil-root-leaf pathway to water (Landsberg et al. 1976). Such information is critical to understanding how the hydraulic design of trees influences the movement of water from roots to leaves (Tyree and Ewers 1991). Spatial variation in G_t has important implications for patterns of transpiration and leaf water potential observed within forest canopies, for assessing the trade-offs between G_t and vulnerability of woody stems to xylem cavitation, and for evaluating the significance of stored water supplies to the survival of trees during severe drought.

Several methods have been devised to estimate G_t in trees. Schulze et al. (1985) used measurements of xylem water flux and water potential to quantify G_t for 72-year-old *Picea abies* trees and for 33-year-old trees of mixed *Larix* species. They showed that a regression approach could be used to calculate

G_t from the inverse relationship between canopy water use (transpiration) and leaf water potential. This approach has been used to estimate G_t in saplings and smaller trees where a generally close relationship is observed between transpiration and leaf water potential (Figure 2A). The movement of water to and from storage compartments within the stem or crown of larger trees during the day may, however, introduce lags or hysteresis into the relationship between transpiration and water potential (Figure 2B). If these lags are pronounced, they can make calculations of G_t by the regression method difficult. This problem can be avoided by using branch-level measurements of water flux to approximate canopy transpiration more closely. Others have used a simpler single-point method to estimate G_t according to the expression:

$$G_t = E / \Delta\Psi, \quad (1)$$

where E is an estimate of current transpiration rate and $\Delta\Psi$ (MPa) is the difference between predawn (maximum) and the current leaf water potential. Meinzer et al. (1995) applied this approach to branch measurements of water flux and derived estimates of G_t for several tropical tree and shrub species. Cochard et al. (1996) showed that both the regression technique and the single-point method yield similar results in 35-year-old *Quercus petraea* trees, but suggested that the latter method may be preferable because of its simplicity.

Various studies have estimated G_t based on water flux data

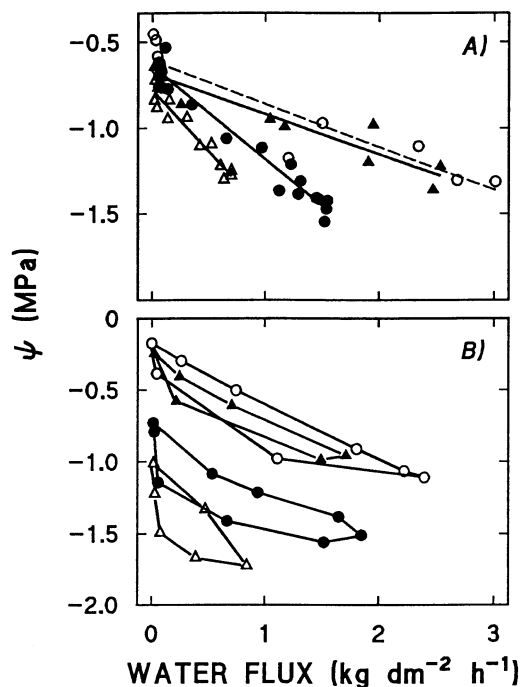


Figure 2. Hourly estimates of sap flux density related to corresponding leaf water potential for (A) trees of *Pinus pinaster* exposed to a range of soil water content and (B) for trees of *Abies bornmulleriana* subjected to imposed drought. Data in (A) and (B) are from Loustau and Granier (1993) and Granier et al. (1989), respectively. Both datasets were adapted with permission.

obtained for branches and entire trees (Schulze et al. 1985, Granier et al. 1989, Bréda et al. 1993b, Meinzer et al. 1995). Whole-tree estimates of G_t expressed per unit sapwood area vary between 3.4 and 5.5 mol m⁻² s⁻¹ MPa⁻¹, whereas G_t expressed per unit leaf area ranges from 0.30 to 9.9 mmol m⁻² s⁻¹ MPa⁻¹ (Table 3). It is not known why the leaf area-specific estimates of G_t vary by more than 30-fold. One explanation (among many) for this variation involves species-related differences in leaf area per unit cross-sectional sapwood area (LA/SA). Trees or branches with low LA/SA may possess a hydraulic advantage to transport and deliver water to leaves for a given water potential gradient. Few studies have addressed this topic, but such a hypothesis suggests that a homeostatic balance exists between leaf area, sapwood area, and the hydraulic sufficiency of the stem to supply water to leaves distal to that stem (Tyree and Ewers 1991). The long-term implications of this balance would be that adjustments in leaf area and sapwood area could serve to maintain similar water potential gradients in trees despite, for example, climatic differences between sites (Mencuccini and Grace 1995).

There is little seasonal variation in G_t of trees growing under favorable soil water conditions except for an early season decline associated with canopy leaf expansion (Bréda et al. 1993b). Granier et al. (1989) observed that G_t was rather constant for dominant, co-dominant, intermediate and isolated trees. However, in *Picea abies*, G_t was lowest in rain-deprived trees and in *Abies bornmulleriana*, it decreased as predawn leaf water potentials dropped from -0.18 to -1.14 MPa. Sup-

plemental measurements of xylem water flux at a mid-canopy location indicated that G_t of the mid-crown to twig pathway did not decrease as water stress increased and it was concluded that stress-induced effects on G_t were located primarily across the soil-root interface (Granier et al. 1989). Multiple estimates of water flux in *Picea abies* were similarly used to infer G_t along the soil-leaf pathway and Granier and Claustres (1989) concluded that almost half of G_t was located between the soil and the base of the crown. These studies illustrate that estimates of water flux at locations along the soil-root-leaf pathway can be coupled with measurements of leaf or stem water potential to partition G_t among the individual segments of the total pathway. Such estimates provide insights into whole-tree hydraulic architecture and the techniques can be easily applied to trees growing in plantations or forest stands. Bréda et al. (1993a) observed a large loss of G_t in petioles and twigs of *Quercus petraea*, presumably because of stress-induced xylem cavitation, and noted that the loss did not strongly affect total whole-tree water use. They suggested that the main resistance to water flow through the soil-root-leaf pathway was located between the soil-root interface and in large branches, and that major changes in a minor component of G_t , like petioles and twigs, had few consequences for total water use.

Coordinated control of stomatal and hydraulic conductance

Transpiration is physically limited by the vapor phase conductances of stomata and boundary layers. Restriction of G_t within the plant without concurrent restriction of stomatal conductance would lead to leaf desiccation because the driving force for water movement through the soil-plant-atmosphere continuum is greatest at the liquid-vapor interface between leaves and the air. Ideally, stomatal conductance should remain in balance with variations in soil-leaf hydraulic conductance. This coordination would contribute to maintenance of leaf water potential above minimum values associated with leaf desiccation, nonstomatal inhibition of photosynthetic carbon acquisition, and xylem cavitation. Cochard et al. (1996) studied this balance between leaf water potential, stomatal conductance and whole-tree water transport capacity in *Quercus petraea* and concluded that stomatal conductance and G_t play a major role in the control of xylem embolism by maintaining minimum water potentials above a threshold (-2.5 to -2.8 MPa) for xylem dysfunction.

There is substantial evidence that stomatal conductance and transpiration are positively correlated with the hydraulic conductance of the soil-root-leaf pathway (Aston and Lawlor 1979, Küppers 1984, Meinzer et al. 1988, Reich and Hinckley 1989, Meinzer and Grantz 1990, Sperry and Pockman 1993, Meinzer et al. 1995). Stomatal conductance and leaf transpiration often increase sharply with increasing G_t and then become asymptotic as G_t continues to increase (Meinzer et al. 1988, Sperry and Pockman 1993). Meinzer et al. (1995) estimated leaf area-specific G_t for five tropical tree and shrub species, and supplemented these with porometer-based measurements of stomatal conductance and leaf transpiration. An asymptotic relationship was observed across all species for G_t and both stomatal conductance and transpiration. Such a pattern sug-

Table 3. Whole-tree estimates of hydraulic conductance (G_t) as reported by studies that relate rates of water flux to leaf water potential. Values of hydraulic conductance are expressed either per unit sapwood area (mol m⁻² s⁻¹ MPa⁻¹) or per unit leaf area (mmol m⁻² s⁻¹ MPa⁻¹).

Species	G_t		Reference
	Sapwood area	Leaf area	
<i>Abies bornmulleriana</i>	3.7	—	Granier et al. 1989
<i>Cecropia insignis</i>	—	9.4	Meinzer et al. 1995
<i>Cecropia obtusifolia</i>	—	2.7	Meinzer et al. 1995
<i>Coccoloba manzanillensis</i>	—	3.3	Meinzer et al. 1995
<i>Larix</i> sp.	—	0.45	Schulze et al. 1985
<i>Miconia argentea</i>	—	1.8–9.9	Meinzer et al. 1995
<i>Palicourea guianensis</i>	—	1.3	Meinzer et al. 1995
<i>Picea abies</i>	3.4	—	Granier et al. 1989
	—	0.30	Granier and Claustres 1989
	—	0.36	Schulze et al. 1985
<i>Pinus pinaster</i>	4.0	—	Granier et al. 1989
	5.5	—	Loustau and Granier 1993
<i>Quercus marilandica</i>	—	2.1	Reich and Hinckley 1989
<i>Quercus petraea</i>	3.4	—	Bréda et al. 1993a
	3.5	—	Bréda et al. 1995
	4.5	—	Cochard et al. 1996
<i>Quercus rubra</i>	—	1.7	Reich and Hinckley 1989

gests that the stomata of these five species (and perhaps all species) responded similarly to changes in water transport efficiency on a leaf area basis and that stomatal adjustments to changing G_t coordinated transpiration with water transport efficiency rather than with bulk leaf water status.

A close coordination between vapor and liquid phase conductance can restrict variation in daily minimum leaf water potential under a wide range of conditions (Whitehead et al. 1984, Meinzer et al. 1992) and thereby limit the utility of leaf water potential *per se* as a predictor of stomatal conductance and transpiration. Plots of stomatal conductance and transpiration versus predawn leaf water potential, a presumed surrogate for soil water potential, often show an initial precipitous decline over a negligible range of water potential during the early stages of soil drying that is probably attributable to an initial rapid decline in soil-leaf G_t rather than in water potential *per se* (Reich and Hinckley 1989, Saliendra and Meinzer 1989). Thus, leaf-level measurements of water potential alone may yield weak or variable associations with stomatal conductance and transpiration both within and among species (Figure 3A). On the other hand, when stomatal conductance or transpiration are plotted against the total leaf area-specific G_t of the soil-leaf pathway, a common relationship may be observed both within and among diverse species growing under similar conditions at the same site (Figure 3B).

Sapwood water storage

Whole-tree measurements of water flux can be used to estimate sapwood water storage and its contribution to daily water use. In saplings and small trees, the mass flow rate of water through the main stem is essentially equivalent to canopy transpiration. In larger trees, however, a considerable lag may be observed between fluctuations in transpiration and fluctuations in water flux measured near the base of the stem (Schulze et al. 1985, Loustau et al. 1996, Phillips et al. 1997, F.C. Meinzer et al. unpublished observations). This lag can range from several minutes to several hours and is presumably caused by the exchange of water between the transpiration stream and stem storage compartments above the point at which water flux is being measured.

Concurrent measurements of water flux in upper branches, near the base of the stem, and intermediate points within the

canopy, can be exploited to characterize both the quantity of water withdrawn daily from internal storage and the dynamics of water exchange between the transpiration stream and stem storage compartments. If water flux in the upper crown is assumed to be a surrogate for transpiration, then the magnitude and sign of the difference between crown and basal water flux can be used to estimate the magnitude and direction of water flux between the transpiration stream and internal storage compartments. For example, in the morning, crown water flux may be greater than basal water flux, indicating a net removal of water from internal storage (Schulze et al. 1985). Conversely, in the afternoon, basal water flux may exceed crown water flux, indicating recharge of internal water reserves. Estimates of stem water storage obtained in this manner range from about 10 to 25% of total daily transpiration (Schulze et al. 1985, Loustau et al. 1996, F.C. Meinzer et al. unpublished observations). The extent to which these values are typical is uncertain given the lack of studies in which multiple measurements of water flux at various heights within the same tree have been used to estimate diurnal water storage capacity. Schulze et al. (1985) measured water flux at two locations along the stem of *Larix* spp. and *Picea abies*, and estimated that the crown served as a major compartment for whole-plant water storage compared to the stem. An estimated 18.3 kg of stored water was used over a 24-h period in 20 to 25-m tall *Larix* spp. with 16.7 kg coming from the crown and only 1.6 kg from the trunk. More observations like those of Schulze et al. (1985) are clearly needed. These measurements will come as improvements are made in access to tree crowns via towers and canopy cranes (Parker et al. 1992) and by increased availability of relatively inexpensive techniques for making multiple measurements of water flux (Granier 1985).

Insights gained from studies of whole-tree water use—a hydrologist's perspective

Techniques for estimating water use have provided the tree physiologist with increasingly sophisticated tools to study whole-plant water transport and storage. These tools can be used to better understand both the rates and control of leaf and crown transpiration within the context of an individual tree. The forest hydrologist can also apply these techniques to

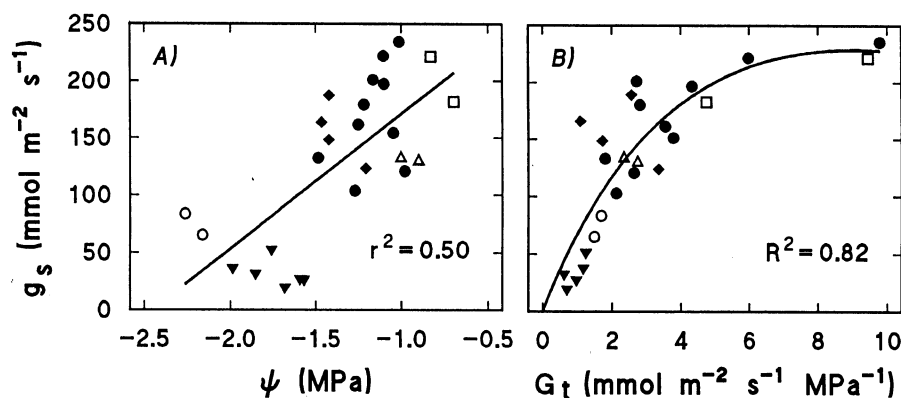


Figure 3. Stomatal conductance (g_s) in relation to (A) midday leaf water potential (Ψ_L) and (B) leaf area-specific total hydraulic conductance of the soil-root-leaf pathway (G_t) for five tropical forest gap colonizing species in Panama. Tree and shrub species include *Miconia argentea* in two sites (\circ , \bullet), *Pali-courea guianensis* (\blacktriangledown), *Cecropia obtusifolia* (\triangle), *Cecropia insignis* (\square) and *Cocoloba manzanillensis* (\blacklozenge). Adapted with permission from Meinzer et al. (1995).

extrapolate water-use rates of single trees to transpiration from forests, woodlands and plantations. Such extrapolations have proved useful for evaluating the potential impact of thinning or clear-cutting on site water balance (Greenwood et al. 1985), investigating the hydrologic impact of *Eucalyptus* plantations in India (Calder et al. 1993) and comparing rates of stand transpiration in different parts of catchments or between trees adjacent to one another (Barrett et al. 1996). Here we address how modern techniques of estimating whole-plant water use complement existing descriptions of forest water balance and how these techniques have improved our ability to assess forest water utilization. We also discuss some of the technical problems that confront the hydrologist in scaling up individual tree water use to the stand level.

Transpiration in estimates of stand water balance

Before 1990, most forest water balance studies treated plant transpiration as a residual term, deduced by subtracting rainfall interception, soil water storage changes, and surface runoff from rainfall (Bosch and Hewlett 1982, Moran and O'Shaughnessy 1984). This catchment water balance approach to estimating plant transpiration resulted in considerable uncertainty because such estimates were affected by errors in all of the other measurements. Deep drainage losses were also often ignored in these calculations and further contributed to estimate uncertainty. Other studies adopted a soil water balance approach to infer plant water uptake (Cooper 1979, Eastham et al. 1988), but this approach also proved problematic because techniques for measuring soil water such as neutron probes, tensiometers, and even the latest time-domain reflectometry methods are prone to significant error. Problems related to high spatial variability in soil water content and the difficulty of defining the soil zero-flux plane beneath which drainage occurs (Cooper 1979) also contributed to uncertainty.

Not all forest hydrology studies, however, have inferred rates of canopy transpiration indirectly. Several studies have measured transpiration directly using micrometeorological techniques such as the Bowen ratio and eddy correlation methods (Denmead 1984, Hatton and Vertessy 1990, Baldocchi and Vogel 1996). These approaches yield important insights into forest hydrological processes, but their application has been limited by a variety of constraints. They cannot be applied in rough terrain and can only be used in areas where the surface cover is homogeneous. This is because of the implicit requirement for smooth, even fetch conditions, uncomplicated by water vapor flux from surfaces atypical of the point of interest, and air flow separation over and around obstacles. Bowen ratio and eddy correlation methods must also be made above the forest canopy and are thus both expensive and logistically difficult to implement.

Attempts to overcome some of these limitations by extrapolating single-tree estimates of water use to that of stands or plantations have met with reasonable success. Studies report estimates of stand transpiration that range from 3.8 mm day⁻¹ for *Quercus petraea* plantations in eastern France (Bréda et al. 1993b), 4.8 mm day⁻¹ for hybrid poplar stands in Washington, USA (Hinckley et al. 1994), 2.3 mm day⁻¹ for *Larix gmelinii*

(Rupr.) Rupr. *ex* Kuzen. trees in eastern Siberia (Arneth et al. 1996), 4.3 mm day⁻¹ for a tropical rainforest in French Guiana (Granier et al. 1996a) and 6.8 mm day⁻¹ for a *Pinus radiata* plantation in southern Australia (Teskey and Sheriff 1996). These rates are well within the range of values given by Rutter (1968) and relatively good agreement has been found in studies that compare extrapolated results of stand transpiration with those obtained by the Bowen ratio (Dunin and Greenwood 1986) and eddy correlation methods (Köstner et al. 1992, Berbigier et al. 1996). These studies are encouraging; however, such agreement is not universally observed (Hatton and Vertessy 1990, Arneth et al. 1996), suggesting that there is still much to be learned about the extrapolation process.

Scalars in the extrapolation of whole-tree water use

Hydrologists need to estimate transpiration on a ground area basis. The best way to determine the transpiration rate of a stand is to measure the water use of every tree in a plot large enough to be unaffected by edge effects. This ideal is rarely achieved because of cost and logistic considerations, and so forest hydrologists must rely on scaling up estimates of water use obtained on a limited number of representative trees. This scaling process is facilitated by selecting a scalar that is easy to survey at the stand level and water use is then determined in a sample of trees that span the range of values for that scalar. The relationship between tree water use and the scalar (normally a regression equation) is then used to determine water use for the entire stand. Scalars that have been used include tree domain, defined either by distance between stems (Hatton and Vertessy 1990) or the area covered by the crown (Hatton et al. 1995), basal area (Teskey and Sheriff 1996), stem diameter at breast height (Vertessy et al. 1995, 1997), leaf area (Hatton et al. 1995) and sapwood area (Dunn and Connor 1993). The suitability of any scalar depends largely on the site. Stem diameter worked well in the study by Vertessy et al. (1995) because the stands they studied were of a single species (*Eucalyptus regnans* F.J. Muell.), even aged and young enough for their basal area to be dominated by sapwood. Hatton et al. (1995) compared the relative performance of five scalars in estimating transpiration of a poplar box (*Eucalyptus populnea* F.J. Muell.) woodland and showed that all, except tree domain estimated by distance between stems, performed well. This was particularly true if the sample trees were selected by stratified, rather than random sampling. It was concluded that the main source of error in estimating transpiration in the stand was in the estimate of water use for individual trees and not in the scaling up process.

Although much research has been directed toward spatial scaling, there have been few reports on the problem of temporal scaling. It is common in water balance studies for observations of transpiration to be made over relatively short periods of time. This is usually less than one year and the question arises as to whether these results are typical of what happens over longer periods of time or under conditions not representative of the measurement period. Similarly, it is of interest to know whether spatial scaling rules developed from data covering short time sequences can be applied confidently to

other periods of time.

Hatton and Wu (1995) investigated the problems associated with temporal scaling in a study of water use estimates of various eucalypt woodlands. They found that water use of individual trees was linearly related to leaf area during periods of abundant soil water, as has been observed in previous studies. However, Hatton and Wu (1995) demonstrated that this relationship was not temporally stable and became non-linear during periods of water-deficit stress, with large trees transpiring proportionately less per unit leaf area than small trees. Furthermore, the shape of the relationship varied considerably and appeared to depend on soil water status and time of year (Figure 4), indicating that some scalars have short-term temporal dependence. The leaf area example given above is a scalar likely to have a strong short-term temporal dependence, particularly in settings where trees are prone to water stress. Because leaf turnover is slow, but transpiration varies rapidly in response to changing environmental conditions, it is not surprising that temporal mismatches in these two variables should arise.

Problems attributable to long-term temporal dependence of whole-tree water use scalars may also arise in areas where water stress is uncommon. For instance, Vertessy et al. (1995) reported a strong relationship between daily water use and stem diameter for a 15-year-old mountain ash (*Eucalyptus regnans*) forest (Figure 5). However, when similar measurements were performed for a 57-year-old stand, Vertessy et al. (1997) found that a different relationship existed. Although the measurements for the two age classes were made at different times, they were nonetheless made under similar climatic conditions and over a long enough period so that temporal variability was minimal. The comparison shown in Figure 5 indicates that whole-tree water use increases less steeply with respect to stem diameter in the older forest than in the younger forest. Similar trends have been observed in stem diameter-leaf area relationships across a mountain ash chronosequence (Watson and Vertessy 1996) and this partially explains the pattern of water use shown in Figure 5. Because of this long-term temporal dependence, it is particularly complicated to

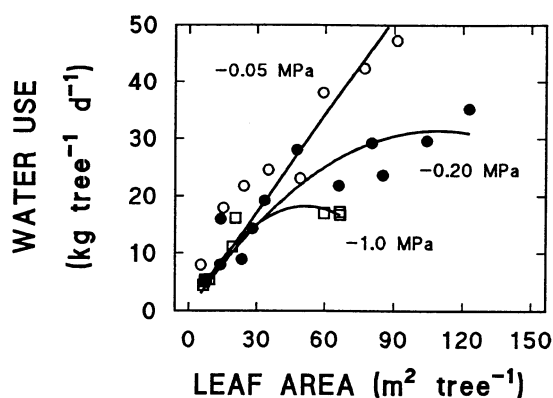


Figure 4. Dependency of whole-tree water use on leaf area per tree for individuals in a eucalypt woodland during periods of water-deficit stress. Adapted with permission from Hatton and Wu (1995).

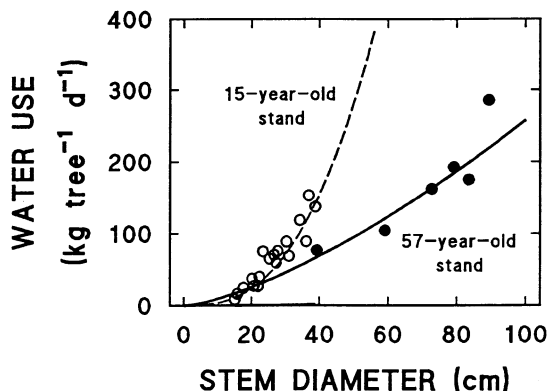


Figure 5. Relationship between whole-tree water use and stem diameter for trees from two *Eucalyptus regnans* stands of different ages. Adapted with permission from Vertessy et al. (1995) and Vertessy et al. (1997).

estimate how water use varies with age for mountain ash stands, an issue of great practical importance to catchment managers (Vertessy et al. 1994).

Haydon et al. (1996) approached this problem of water use differences among stands of various ages without relying on spatial scalars. They measured sapwood area of the overstory in mountain ash stands of different ages and observed that it reached a peak of $10.5 \text{ m}^2 \text{ ha}^{-1}$ in 15-year-old stands and then declined gradually to $2.4 \text{ m}^2 \text{ ha}^{-1}$ in 200-year-old stands. Dunn and Connor (1993) reported earlier that mean sap velocities in the stems of 37 mountain ash trees did not vary significantly between stands aged 50, 90, 150 and 230 years old. Haydon et al. (1996) used these data to develop a stand age-transpiration relationship for mountain ash by simply multiplying measured sapwood area by an annual transpiration rate of $72 \text{ mm year}^{-1} \text{ m}^{-2}$ sapwood area (Dunn and Connor 1993). Calculated rates of stand transpiration and estimates of net interception losses were subtracted from total precipitation to derive expected annual streamflow. Haydon et al. (1996) showed that annual streamflow in the catchments surrounding Melbourne, Australia could increase by 600 mm as forests destroyed by fire in 1939 make the gradual transition from regrowth (30 years old) to old-growth (200 years old) stands. Much of this increase in simulated annual water yield was the result of reductions in transpiration for old-growth stands of mountain ash (related to sapwood area) and to some degree by changes in interception losses. Findings such as these have helped the forest hydrologist explain the large water yield differences observed between old-growth and re-growth mountain ash catchments (Kuczera 1987) and provided useful information to catchment managers as they plan for the future water needs of a growing metropolitan population.

Conclusions

Throughout the last 60 years there has been a steady increase in the availability and use of techniques for estimating whole-tree water utilization. Weighing lysimeters, large-tree po-

tometers, ventilated chambers, radioisotopes, stable isotopes and an array of thermal methods have been used to address the seemingly simple question posed by R.H. Swanson (1972): "How do we determine the amount of water used by a tree?" The techniques developed in search of an answer to this question are today providing the tree physiologist with unique insights into the control of water transport and storage, and are being applied in novel ways to explore interrelationships among stomatal conductance, leaf water potential, leaf area, sapwood area and hydraulic conductance in trees. These techniques are also allowing the forest hydrologist to address, in more detail than previously possible, the fundamental biology that underlies much of water resource management.

There is little doubt that the use of energy-balance, heat dissipation and heat-pulse systems will continue to yield meaningful information in the forest sciences. Studies that combine these techniques with instruments for detecting acoustic emissions (Jackson and Grace 1996), *in situ* estimates of root hydraulic conductance (Tyree 1995) and approaches based on natural isotope abundance to identify water resource partitioning (Jackson et al. 1995) should be encouraged. So too should the use of the Bowen ratio and eddy correlation methods in conjunction with studies that focus on the extrapolation of individual tree water use to forest stands and plantations. This latter effort, although partly a comparative exercise, should attempt to extract stand-level information on the soil and plant-based controls of site water balance. The merits of this approach are clearly seen in the studies of Kelliher et al. (1992) and Köstner et al. (1992). These two studies serve to illustrate how the tree physiologist and forest hydrologist can both contribute to and benefit from collaborative investigations.

Acknowledgments

This paper is dedicated to the memory of Dr. John P. Decker whose early creativity in the design and application of tent enclosures or ventilated chambers for measuring the water use of trees growing in his backyard reflects a professional curiosity that is worth noting in the forest sciences. Special thanks to Roxie Decker who took time to reminisce about her late-husband's accomplishments and to Pete Decker who provided articles highlighting his father's early work. The authors also thank N.T. Edwards, P.J. Hanson and R.J. Norby for manuscript reviews. This research was sponsored by the Program for Ecosystem Research, Environmental Sciences Division, Office of Health and Environmental Research, U.S. Department of Energy under Contract No. DE-AC05-96OR22464 with Lockheed Martin Energy Research Corp. Publication No. 4790, Environmental Sciences Division, Oak Ridge National Laboratory.

References

Ansley, R.J., W.A. Dugas, M.L. Heuer and B.A. Trevino. 1994. Stem flow and porometer measurements of transpiration from honey mesquite (*Prosopis glandulosa*). *J. Exp. Bot.* 45:847–856.

- Arneeth, 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.
- Aston, M.J. and D.W. Lawlor. 1979. The relationship between transpiration, root water uptake, and leaf water potential. *J. Exp. Bot.* 30:169–181.
- Baldocchi, D.D. and C.A. Vogel. 1996. Energy and CO₂ flux densities above and below a temperate broad-leaved forest and a boreal pine forest. *Tree Physiol.* 16:5–16.
- Barrett, D.J., T.J. Hatton, J.E. Ash and M.C. Ball. 1996. Transpiration by trees from contrasting forest types. *Aust. J. Bot.* 44:249–263.
- Becker, P. 1996. Sap flow in Bornean heath and dipterocarp forest trees during wet and dry periods. *Tree Physiol.* 16:295–299.
- Berbigier, P., J.M. Bonnefond, D. Loustau, M.I. Ferreira, J.S. David and J.S. Pereira. 1996. Transpiration of a 64-year-old maritime pine stand in Portugal. 2. Evapotranspiration and canopy stomatal conductance measured by an eddy covariance technique. *Oecologia* 107:43–52.
- Bosch, J.M. and J.D. Hewlett. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *J. Hydrol.* 55:3–23.
- Bréda, N., H. Cochard, E. Dreyer and A. Granier. 1993a. Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petraea* and *Quercus robur* under water stress. *Ann. Sci. For.* 50:571–582.
- Bréda, N., H. Cochard, E. Dreyer and A. Granier. 1993b. Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. *Can. J. For. Sci.* 23:1136–1143.
- Bréda, N., A. Granier and G. Aussenac. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiol.* 15:295–306.
- Calder, I.R., M.N. Narayanswamy, N.V. Srinivasalu, W.G. Darling and A.J. Lardner. 1986. Investigation into the use of deuterium as a tracer for measuring transpiration from eucalypts. *J. Hydrol.* 84:345–351.
- Calder, I.R., R.L. Hall and K.T. Prasanna. 1993. Hydrologic impact of *Eucalyptus* plantation in India. *J. Hydrol.* 150:635–648.
- Ďermák, J. and J. Kučera. 1993. Extremely fast changes of xylem water flow rate in tall trees caused by atmospheric, soil and mechanical factors. In *Water Transport in Plants Under Climatic Stress*. Eds. M. Borghetti, J. Grace and A. Raschi. Cambridge University Press, pp 181–190.
- Ďermák, J., J. Úlehla, J. Kučera and M. Penka. 1982. Sapflow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions. *Biol. Plant. (Praha)* 24:446–460.
- Ďermák, J., J. Jeník, J. Kučera and V. Zidek. 1984. Xylem water flow in a crack willow (*Salix fragilis* L.) in relation to diurnal changes of environment. *Oecologia* 64:145–151.
- Ďermák, J., R. Matyssek and J. Kučera. 1993. Rapid response of large, drought-stressed beech trees to irrigation. *Tree Physiol.* 12:281–290.
- Ďermák, J., E. Cienciala, J. Kučera, A. Lindroth and E. Bednářová. 1995. Individual variation in 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.

- Cienciala, E. and A. Lindroth. 1995. Gas-exchange and sap flow measurements of *Salix viminalis* trees in short-rotation forest. I. Transpiration and sap flow. *Trees* 9:289–294.
- Cienciala, E., A. Lindroth, J. Ěermák, J. Hällgren and J. Kuëra. 1992. Assessment of transpiration estimates for *Picea abies* trees during a growing season. *Trees* 6:121–127.
- Cochard, H., N. Bréda and A. Granier. 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? *Ann. Sci. For.* 53:197–206.
- Cooper, J.D. 1979. Water use of a tea estate from soil moisture measurements. *East Afr. Agric. For. J.* 43:102–121.
- Denmead, O.T. 1984. Plant physiological methods for studying evapotranspiration: problems of telling the forest from the trees. *Agric. Water Manag.* 8:167–189.
- Denmead, O.T., F.X. Dunin, S.C. Wong and E.A.N. Greenwood. 1993. Measuring water use efficiency of eucalypt trees with chambers and micrometeorological techniques. *J. Hydrol.* 150:649–664.
- Dunin, F.X. and E.A.N. Greenwood. 1986. Evaluation of the ventilated chamber for measuring evaporation from a forest. *Hydrol. Proc.* 1:47–62.
- Dunn, G.M. and D.J. Connor. 1993. Analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. *Tree Physiol.* 13:321–336.
- Dye, P.J. 1996. Response of *Eucalyptus grandis* trees to soil water deficits. *Tree Physiol.* 16:233–238.
- Dye, P.J., B.W. Olbrich and I.R. Calder. 1992. A comparison of the heat pulse method and deuterium tracing method for measuring transpiration from *Eucalyptus grandis* trees. *J. Exp. Bot.* 43:337–343.
- Eastham, J., C.W. Rose, D.M. Cameron, S.J. Rance and T. Talsma. 1988. The effect of tree spacing on evaporation from an agroforestry experiment. *Agric. For. Meteorol.* 42:355–368.
- Edwards, W.R.N. 1986. Precision weighing lysimetry for trees, using a simplified tared-balance design. *Tree Physiol.* 1:127–144.
- Fritschen, L.J., L. Cox and R. Kinerson. 1973. A 28-meter Douglas-fir in a weighing lysimeter. *For. Sci.* 19:256–261.
- Goldstein, G., J.L. Andrade, F.C. Meinzer, N.M. Holbrook, J. Cavelier, P. Jackson and A. Celis. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ.* In Press.
- Granier, A. 1985. Une nouvelle méthode pour la mesure de flux de sève brute dans le tronc des arbres. *Ann. Sci. For.* 42:193–200.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.* 3:309–320.
- Granier, A. and J.P. Claustres. 1989. Relations hydriques dans un épicéa (*Picea abies* L.) en conditions naturelles: variations spatiales. *Acta Oecol.* 10:295–310.
- Granier, A., N. Bréda, J.P. Claustres and F. Colin. 1989. Variation of hydraulic conductance of some adult conifers under natural conditions. *Ann. Sci. For.* 46(S):357–360.
- Granier, A., V. Bobay, J.H.C. Gash, J. Gelpe, B. Saugier and W.J. Shuttleworth. 1990. Vapour flux density and transpiration rate comparisons in a stand of Maritime pine (*Pinus pinaster* Ait.) in Les Landes forest. *Agric. For. Meteorol.* 51:309–319.
- Granier, A., R. Huc and S.T. Barigah. 1996a. Transpiration of natural rain forest and its dependence on climatic factors. *Agric. For. Meteorol.* 78:19–29.
- Granier, A., P. Biron, N. Bréda, J.-Y. Pontailler and B. Saugier. 1996b. Transpiration of trees and forest stands: short and long-term monitoring using sapflow methods. *Global Change Biol.* 2:265–274.
- Greenidge, K.N.H. 1955. Observations on the movement of moisture in large woody stems. *Can. J. Bot.* 33:202–221.
- Greenwood, E.A.N. and J.D. Beresford. 1979. Evaporation from vegetation in landscapes developing secondary salinity using the ventilated-chamber technique. I. Comparative transpiration from juvenile *Eucalyptus* above saline ground-water seeps. *J. Hydrol.* 42:369–382.
- Greenwood, E.A.N., J.D. Beresford and J.R. Bartle. 1981. Evaporation from vegetation in landscapes developing secondary salinity using the ventilated-chamber technique. III. Evaporation from a *Pinus radiata* tree and the surrounding pasture in an agroforestry plantation. *J. Hydrol.* 50:155–166.
- Greenwood, E.A.N., J.D. Beresford, J.R. Bartle and R.J.W. Barron. 1982. Evaporation from vegetation in landscapes developing secondary salinity using the ventilated-chamber technique. IV. Evaporation from a regenerating forest of *Eucalyptus wandoo* on land formerly cleared for agriculture. *J. Hydrol.* 58:357–366.
- Greenwood, E.A.N., L. Klein, J.D. Beresford, G.D. Watson and K.D. Wright. 1985. Evaporation from the understorey in the jarrah (*Eucalyptus marginata* Don ex Sm.) forest, southwestern Australia. *J. Hydrol.* 80:337–349.
- Hatton, T.J. and H.I. Wu. 1995. Scaling theory to extrapolate individual tree water use to stand water use. *Hydrol. Proc.* 9:527–540.
- Hatton, T.J. and R.A. Vertessy. 1990. Transpiration of plantation *Pinus radiata* estimated by the heat pulse method and the Bowen ratio. *Hydrol. Proc.* 4:289–298.
- 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.
- Haydon, S.R., R.G. Benyon and R. Lewis. 1996. Variation in sapwood area and throughfall with forest age in mountain ash (*Eucalyptus regnans* F. Muell.). *J. Hydrol.* 187:351–366.
- 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.
- Herzog, K.M., R. Häslér and R. Thum. 1995. Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. *Trees* 10:94–101.
- Hinckley, T.M., J.R. Brooks, J. Ěermák, R. Ceulmans, J. Kuëra, F.C. Meinzer and D.A. Roberts. 1994. Water flux in a hybrid poplar stand. *Tree Physiol.* 14:1005–1018.
- Jackson, G.E. and J. Grace. 1996. Field measurements of xylem cavitation: are acoustic emissions useful? *J. Exp. Bot.* 47:1643–1650.
- Jackson, P.C., J. Cavelier, G. Goldstein, F.C. Meinzer and N.M. Holbrook. 1995. Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* 101:197–203.
- Jarvis, P.G. and K.G. McNaughton. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15:1–49.
- Jordan, C.F. and J.R. Kline. 1977. Transpiration of trees in a tropical rainforest. *J. Appl. Ecol.* 14:853–860.
- Kelliher, F.M., B.M.M. Köstner, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, R. Meserth, P.L. Weir and E.-D. Schulze. 1992. Evaporation, xylem sap flow, and tree transpiration in a New Zealand broad-leaved forest. *Agric. For. Meteorol.* 62:53–73.
- Kline, J.R., J.R. Martin, C.F. Jordan and J.J. Koranda. 1970. Measurement of transpiration in tropical trees with tritiated water. *Ecology* 51:1068–1073.
- Kline, J.R., K.L. Reed, R.H. Waring and M.L. Stewart. 1976. Field measurement of transpiration in Douglas-fir. *J. Appl. Ecol.* 13:272–283.
- Knight, D.H., T.J. Fahey, S.W. Running, A.T. Harrison and L.L. Wallace. 1981. Transpiration from 100-year-old lodgepole pine forests estimated with whole-tree potometers. *Ecology* 62:717–726.

- Köstner, B., R. Schupp, E.-D. Schulze and H. Rennenberg. 1998. Organic and inorganic sulfur transport in the xylem sap and the sulfur budget of *Picea abies* trees. *Tree Physiol.* 18:1–9.
- Köstner, 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.
- Kuèera, J., J. Èermák and M. Penka. 1977. Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol. Plant. (Praha)* 19:413–420.
- Kuczera, G.A. 1987. Prediction of water yield reductions following a bushfire in ash-mixed species eucalypt forest. *J. Hydrol.* 94:215–236.
- Küppers, M. 1984. Carbon relations and competition between woody species in a Central European hedgerow. II. Stomatal responses, water use, and hydraulic conductivity in the root/leaf pathway. *Oecologia* 64:344–54.
- Landsberg, J.J., T.W. Blanchard and B. Warrit. 1976. Studies on the movement of water through apple trees. *J. Exp. Bot.* 27:579–596.
- Lindroth, A. and E. Cienciala. 1995. Measuring water use efficiency of eucalypt trees with chambers and micrometeorological techniques—comment. *J. Hydrol.* 169:281–283.
- Lindroth, A., J. Èermák, J. Kuèera, E. Cienciala and H. Eckersten. 1995. Sap flow by the heat balance method applied to small size *Salix* trees in a short-rotation forest. *Biomass Bioenergy* 8:7–15.
- Lott, J.E., A.A.H. Khan, C.K. Ong and C.R. Black. 1996. Sap flow measurements of lateral tree roots in agroforestry systems. *Tree Physiol.* 16:995–1001.
- Loustau, D. and A. Granier. 1993. Environmental control of water flux through Maritime pine (*Pinus pinaster* Ait.). In *Water Transport in Plants Under Climatic Stress*. Eds. M. Borghetti, J. Grace and A. Raschi. Cambridge University Press, pp 205–218.
- Loustau, D., P. Berbigier, P. Roumagnac, C. Arruda-Pacheco, J.S. David, M.I. Ferreira, J.S. Pereira and R. Tavares. 1996. Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. *Oecologia* 107:33–42.
- Luvall, J.C. and C.E. Murphy, Jr. 1982. Evaluation of the tritiated water method for measurement of transpiration in young *Pinus taeda* L. *For. Sci.* 28:5–16.
- Martin, T.A., K.J. Brown, J. Èermák, R. Ceulmans, J. Kuèera, F.C. Meinzer, J.S. Rombold, D.G. Sprugel and T.M. Hinkley. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. *Can. J. For. Res.* 27:797–808.
- Meinzer, F.C. and D.A. Grantz. 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell Environ.* 13:383–88.
- Meinzer, F.C., M.R. Sharifi, E.T. Nilsen and P.W. Rundel. 1988. Effects of manipulation of water and nitrogen regime on the water relations of the desert shrub *Larrea tridentata*. *Oecologia* 77:480–486.
- Meinzer, F.C., G. Goldstein, H.S. Neufeld, D.A. Grantz and G.M. Crisosto. 1992. Hydraulic architecture of sugarcane in relation to patterns of water use during plant development. *Plant Cell Environ.* 15:471–477.
- 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.
- Meinzer, F.C., G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Gutierrez and J. Cavelier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. *Oecologia* 101:514–522.
- Meinzer, F.C., J.L. Andrade, G. Goldstein, N.M. Holbrook, J. Cavelier and P. Jackson. 1997. Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components. *Plant Cell Environ.* 20:1242–1252.
- Mencuccini, M. and J. Grace. 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiol.* 15:1–10.
- Moran, R.J. and P.J. O'Shaughnessy. 1984. Determination of the evapotranspiration of *E. regnans* forested catchments using hydrological measurements. *Agric. Water Manag.* 8:57–76.
- Olbrich, B.W. 1991. The verification of the heat pulse velocity technique for estimating sap flow in *Eucalyptus grandis*. *Can. J. For. Res.* 21:836–841.
- Owston, P.W., J.L. Smith and H.G. Halverson. 1972. Seasonal water movement in tree stems. *For. Sci.* 18:266–272.
- Parker, G.G., A.P. Smith and K.P. Hogan. 1992. Access to the upper forest canopy with a large tower crane. *Bioscience* 42:664–670.
- Parker, J. 1957. The cut-leaf method and estimations of diurnal trends in transpiration from different heights and sides of an oak and a pine. *Bot. Gaz.* 119:93–101.
- Phillips, N., R. Oren and R. Zimmermann. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant Cell Environ.* 19:983–990.
- Phillips, N., A. Nagchaudhuri, R. Oren and G. Katul. 1997. Time constants for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* 11:412–419.
- Raber, O. 1937. Water utilization by trees, with special reference to the economic forest species of the north temperate zone. United States Department of Agriculture, Misc. Pub. 257, 97 p.
- Reich, P.B. and T.M. Hinckley. 1989. Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance in two oak species. *Funct. Ecol.* 3:719–726.
- Roberts, J. 1977. The use of tree-cutting techniques in the study of the water relations of mature *Pinus sylvestris* L. *J. Exp. Bot.* 28:751–767.
- Roberts, J. 1978. The use of the “tree cutting” technique in the study of the water relations of Norway spruce, *Picea abies* (L.) Karst. *J. Exp. Bot.* 29:465–471.
- Roberts, J.R., O.M.R. Cabral and L.F. De Aguiar. 1990. Stomatal and boundary layer conductances in an Amazonian terra firme rain forest. *J. Appl. Ecol.* 27:336–353.
- Roberts, J., O.M.R. Cabral, G. Fisch, L.C.B. Molion, C.J. Moore and W.J. Shuttleworth. 1993. Transpiration from an Amazonian rainforest calculated from stomatal conductance measurements. *Agric. For. Meteorol.* 65:175–196.
- Rutter, A.J. 1966. Studies in the water relations of *Pinus sylvestris* in plantation conditions. 4. Direct observations on the rates of transpiration, evaporation of intercepted water, and evaporation from the soil surface. *J. Ecol.* 3:393–405.
- Rutter, A.J. 1968. Water consumption by forests. In *Water Deficits and Plant Growth*, Vol. II. Plant Water Consumption and Response. Ed. T.T. Koslowski. Academic Press, New York, pp 23–84.
- Saliendra, N.Z. and F.C. Meinzer. 1989. Relationship between root/soil hydraulic properties and stomatal behavior in sugarcane. *Aust. J. Plant Physiol.* 16:241–250.
- Sansigolo, C.A. and E.S.B. Ferraz. 1982. Measurement of transpiration and biomass in a tropical *Pinus caribaea* plantation with tritiated water. *Agric. Meteorol.* 26:25–33.
- Schiller, G. and Y. Cohen. 1995. Water regime of a pine forest under a Mediterranean climate. *Agric. For. Meteorol.* 74:181–193.

- Schulze, E.-D., J. Ěermák, R. Matyssek, M. Penka, R. Zimmermann, F. Vasíček, W. Gries and J. Kuèera. 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.
- Smith, D.M. and S.J. Allen. 1996. Measurement of sap flow in plant stems. *J. Exp. Bot.* 47:1833–1844.
- Sperry, J.S. and W.T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* 16:279–287.
- 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. 1972. Water transpired by trees is indicated by heat pulse velocity. *Agric. Meteorol.* 10:277–281.
- Swanson, R.H. 1994. Significant historical developments in thermal methods for measuring sap flow in trees. *Agric. For. Meteorol.* 72:113–132.
- Teskey, R.O. and D.W. Sheriff. 1996. Water use by *Pinus radiata* trees in a plantation. *Tree Physiol.* 16:273–279.
- Tyree, M.T. 1995. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. *J. Exp. Bot.* 46:83–94.
- Tyree, M.T. and F.W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119:345–360.
- Vertessy, R., R. Benyon and S. Haydon. 1994. Melbourne's forest catchments: effect of age on water yield. *Water* 21:17–20.
- Vertessy, R.A., R.G. Benyon, S.K. O'Sullivan and P.R. Gribben. 1995. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiol.* 15:559–567.
- Vertessy, R.A., T.J. Hatton, P. Reece, S.K. O'Sullivan and R.G. Benyon. 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiol.* 17:747–756.
- Waring, R.H. and J.M. Roberts. 1979. Estimating water flux through stems of Scots pine with tritiated water and phosphorus-32. *J. Exp. Bot.* 30:459–471.
- Watson, F.G.R. and R.A. Vertessy. 1996. Estimating leaf area index from stem diameter measurements in mountain ash forest. Cooperative Research Centre for Catchment Hydrology Report No. 96/7, Monash University, Victoria, Australia, 102 p.
- 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.
- Wullschleger, S.D., P.J. Hanson and T.J. Tschaplinski. 1998. Whole-plant water flux in understory red maple exposed to altered precipitation regimes. *Tree Physiol.* 18:71–79.