

## Whole-plant water flux in understory red maple exposed to altered precipitation regimes

STAN D. WULLSCHLEGER, PAUL J. HANSON and TIM J. TSCHAPLINSKI

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

Received January 29, 1997

**Summary** Sap flow gauges were used to estimate whole-plant water flux for five stem-diameter classes of red maple (*Acer rubrum* L.) growing in the understory of an upland oak forest and exposed to one of three large-scale (0.64 ha) manipulations of soil water content. This Throughfall Displacement Experiment (TDE) used subcanopy troughs to intercept roughly 30% of the throughfall on a “dry” plot and a series of pipes to move this collected precipitation across an “ambient” plot and onto a “wet” plot. Saplings with a stem diameter larger than 10 cm lost water at rates 50-fold greater than saplings with a stem diameter of 1 to 2 cm (326 versus 6.4 mol H<sub>2</sub>O tree<sup>-1</sup> day<sup>-1</sup>). These size-class differences were driven largely by differences in leaf area and cross-sectional sapwood area, because rates of water flux expressed per unit leaf area (6.90 mol H<sub>2</sub>O m<sup>-2</sup> day<sup>-1</sup>) or sapwood area (288 mol H<sub>2</sub>O dm<sup>-2</sup> day<sup>-1</sup>) were similar among saplings of the five size classes. Daily and hourly rates of transpiration expressed per unit leaf area varied throughout much of the season, as did soil matrix potentials, and treatment differences due to the TDE were observed during two of the seven sampling periods. On July 6, midday rates of transpiration averaged 1.88 mol H<sub>2</sub>O m<sup>-2</sup> h<sup>-1</sup> for saplings in the “wet” plot, 1.22 mol H<sub>2</sub>O m<sup>-2</sup> h<sup>-1</sup> for saplings in the “ambient” plot, and 0.76 mol H<sub>2</sub>O m<sup>-2</sup> h<sup>-1</sup> for saplings in the “dry” plot. During the early afternoon of August 28, transpiration rates were sevenfold lower for saplings in the “dry” plot compared to saplings in the “wet” plot and 2.5-fold lower compared to saplings in the “ambient” plot. Treatment differences in crown conductance followed a pattern similar to that of transpiration, with values that averaged 60% lower for saplings in the “dry” plot compared to saplings in the “wet” plot and 35% lower compared to saplings in the “ambient” plot. Stomatal and boundary layer conductances were roughly equal in magnitude. Estimates of the decoupling coefficient ( $\Omega$ ) ranged between 0.64 and 0.72 for saplings in the three TDE treatment plots. We conclude that red maple saplings growing in the understory of an upland oak forest are responsive to their edaphic and climatic surroundings, and because of either their small stature or their shallow root distribution, or both, are likely to be impacted by precipitation changes similar to those predicted by global climate models.

**Keywords:** *Acer rubrum*, boundary layer conductance, decoupling coefficient, global change, sap flow, stomatal conductance, transpiration, water stress.

### Introduction

Anthropogenic emissions of carbon dioxide, methane, chlorofluorocarbons, nitrous oxides, and other so-called greenhouse gases are expected to increase global mean temperatures by 2 to 5 °C within the next century (Mitchell et al. 1990). Forest trees and ecosystems will respond directly to these changes in temperature (Melillo et al. 1990, Kirschbaum and Fischlin 1995). Temperature, however, is only one of many climatic perturbations that will potentially affect the productivity of native vegetation. It is expected, for example, that the hydrologic cycle will also become more intense in a warmer climate (Mitchell et al. 1990, Loaiciga et al. 1996). Some regions of the globe will experience an increased frequency of precipitation, whereas other regions will face a greater likelihood of drought as a result of decreased precipitation or increased evaporative demand, or both (Rind et al. 1990). Forests are particularly vulnerable to extremes in soil water content as evidenced by manipulative studies on large trees (Ěermák and Kuèera 1993, Ěermák et al. 1993), field investigations on seedlings and saplings (Abrams et al. 1990, Kubiske and Abrams 1994), and as shown in computer simulations (Pastor and Post 1988, Running and Nemani 1991, Lüdeke et al. 1995, Martin 1996).

Current general circulation models cannot spatially resolve the probability of an area receiving increased or decreased precipitation in a warmer climate. Yet shifts in regional precipitation may lead to important changes in forest productivity, species recruitment and mortality, and water resource availability (Loaiciga et al. 1996). Given these uncertainties, there is a need to study the response of forested ecosystems to both above- and below-normal precipitation. Therefore, we established a large-scale (1.92 ha) Throughfall Displacement Experiment (TDE) for modifying the distribution of precipitation across an upland oak forest (Hanson et al. 1995). The facility was designed to transfer precipitation from one experimental plot to another, thereby allowing hypotheses regarding the potential response of trees and ecosystems to regional shifts in

precipitation to be addressed. Our overall goal was to develop an improved understanding of how forest organisms respond to changes in precipitation or soil water content, or both, with a particular emphasis on plant, pest, pathogen, and microbial processes that control carbon, water, and nutrient cycling in terrestrial systems.

Here we report on the seasonal pattern of whole-plant water flux for five size classes of understory red maple (*Acer rubrum* L.) exposed to altered precipitation regimes. Previous studies have indicated that red maple saplings are sensitive to seasonal drought conditions despite low irradiances, moderate vapor pressure deficits, and low wind speeds that often characterize the understory environment of closed-canopy forests (Kloppel et al. 1993, Abrams and Mostoller 1995). Our objectives were to: (1) use sap flow gauges to estimate seasonal and daily patterns of whole-plant water flux in understory red maple saplings that varied in stem diameter from 0.5 to 13 cm; (2) relate size-dependent differences in water flux to leaf area and cross-sectional sapwood area; (3) examine seasonal and daily patterns of transpiration in relation to the “wet,” “ambient” and “dry” treatments of the TDE; and (4) assess the dependency of hourly rates of transpiration and crown conductance on vapor pressure deficit. We conclude by discussing the sensitivity of understory saplings and overstory trees to precipitation changes similar in magnitude to those predicted by global climate models.

## Materials and methods

### Site description

Studies of whole-plant water flux were conducted on the Walker Branch Watershed, a part of the U.S. Department of Energy's Oak Ridge Reservation, Anderson County, TN (35°58' N and 84°17' W). The study area occupies 1.92 ha and extends 240 m along the edge of a ridge and 80 m down a 20-m elevation gradient. Trees in this unevenly aged upland oak-hickory (*Quercus-Carya* spp.) forest range in age from 40 to 75 years, with a few individuals older than 150 years. The overstory is dominated by chestnut oak (*Q. prinus* L.), white oak (*Q. alba* L.), black gum (*Nyssa sylvatica* Marsh.), and red maple (*Acer rubrum*), with scattered yellow poplar (*Liriodendron tulipifera* L.), Northern red oak (*Q. rubra* L.), and sugar maple (*A. saccharum* Marsh.). The understory consists of flowering dogwood (*Cornus florida* L.) and sapling red maple (Hanson et al. 1995).

Mean annual rainfall (30-year average) at the study site is 134 cm and mean temperature is 14.4 °C. Soils are acidic (pH 3.5 to 4.6) and mostly typic paleudults formed in the residuum and colluvial deposits. A full description of the climate, vegetation, soils, and land use history of the Walker Branch Watershed can be found in Johnson (1989).

### Design of the Throughfall Displacement Experiment

The TDE was designed to supply a large forested area with above- and below-normal precipitation throughout the year. Throughfall is intercepted in 2000 subcanopy troughs (0.3 × 5 m) suspended above the forest floor of the “dry” plot. These

troughs cover 33% of the ground area and hence intercept approximately one-third of the incoming precipitation. Throughfall is moved by gravity flow across an “ambient” plot and is distributed onto a “wet” plot through paired drip holes located at 1-m spacing along a 5-cm diameter distribution pipe. Boardwalks have been constructed along each transfer pipe to reduce soil compaction and site disturbance caused by foot traffic. Each treatment plot is 80 × 80 m (0.64 ha) in size.

During 1995, soil water contents (0–35 cm) were measured at least once a month with a time-domain reflectometer (Soil Moisture Equipment Corp., Santa Barbara, CA). Values were corrected for coarse fragment content (Drungil et al. 1987). A total of 310 sampling locations were installed across the site for monitoring the effectiveness of the throughfall displacement system. At each location a pair of stainless steel wave guides was installed in a vertical orientation. Soil water contents were converted to matrix potential (MPa) based on soil water release curves for the AE horizon (R. Augé, Institute of Agriculture, University of Tennessee, Knoxville, TN, unpublished data).

Instruments for measuring air and soil temperature, relative humidity, and irradiance (PPFD) were located at upper, middle, and lower slope positions within each of the three treatment plots. Soil temperatures were measured at a depth of 10 cm. All climatic data were measured automatically once a minute, averaged hourly, and recorded by a data logger (LI-1000, Li-Cor, Inc., Lincoln, NE). Rainfall was measured in a clearing close to the TDE site and with tipping bucket rain gauges located in the understory.

### Plant material and allometric equations

A total of 53 red maple saplings were selected from the understory for measurements of whole-plant water flux. Eighteen of the saplings were located in the “wet” plot, 15 in the “ambient” plot, and 20 in the “dry” plot. All trees occupied upper to mid-slope positions on the site. Stem diameters at 10 cm above the ground were measured in two directions with a digital caliper (Brown and Sharpe Mfg. Co., North Kingstown, RI) and the mean of the readings was calculated. Based on these data, saplings were subdivided into one of five arbitrary size classes (< 1, 1 to 2, 2 to 5, 5 to 10, and > 10 cm). Sapling heights were measured with a telescopic measuring rod (Hastings Fiberglass Products, Inc., Hastings, MI).

Allometric relationships were established between stem diameter (cm) and total leaf area (m<sup>2</sup>), cross-sectional sapwood area (cm<sup>2</sup>), and approximate age (years). Twenty-eight saplings ranging in diameter from 0.34 to 13.6 cm were harvested from an area adjacent to the TDE site. Leaves were removed from each sapling, placed in plastic bags, stored on ice, and taken to the laboratory where projected leaf areas were determined (LI-3100, Li-Cor, Inc.). Total leaf area ranged from 0.02 to 38.5 m<sup>2</sup> tree<sup>-1</sup>. Stems were cut within 10 cm of ground level, cross-sectional surfaces polished with sandpaper, and sapwood areas calculated. Most saplings displayed little or no heartwood, although some heartwood formation (visible discoloration) was observed on stems greater than 4 cm in diameter. The number of growth rings was counted and approximate tree age

related to stem diameter. Three allometric equations were thus derived for understory red maple. One describing the relationship of leaf area ( $\text{m}^2$ ) to stem diameter (cm):

$$\text{Leaf area} = 0.297 \times \text{Diameter}^{1.892}; r^2 = 0.98; \quad (1)$$

another describing the relationship of sapwood area ( $\text{cm}^2$ ) to stem diameter (cm):

$$\text{Sapwood area} = 0.638 \times \text{Diameter}^{1.986}; r^2 = 0.94; \quad (2)$$

and one describing the relationship of age (years) to stem diameter (cm):

$$\text{Age} = 8.3 + 2.6 \times \text{Diameter}; r^2 = 0.97. \quad (3)$$

#### *Estimates of whole-plant water flux and crown conductance*

Whole-plant estimates of water flux were obtained during seven 2 to 3-day intensive measurement sessions in 1995. Session dates were May 26–28, June 9–11, July 6–7, July 22–23, August 27–28, October 7–9, and October 25. Not all of the five size classes were measured at each session. Saplings < 1 cm were measured once, saplings 5 to 10 cm were measured three times, saplings > 10 cm were measured six times, and saplings 1 to 2 cm and 2 to 5 cm were measured at all seven sessions.

Sap flow gauges (Dynamax, Inc., Houston, TX), which operate on the theory of heat balance, were used to estimate rates of whole-plant water flux (Baker and van Bavel 1987). These gauges apply a constant input of heat to the stem and the resulting heat fluxes in the radial and vertical direction (above and below the gauge) are measured with a thermopile and a series of thermocouples. Convective heat flux, and therefore the rate of water flux along the stem, can be calculated by subtraction. Various gauge sizes were used (Models SGA-5, SGA-10, SGA-13, SGB-25, SGB-50, and SGA-100) depending on sapling diameter. Closed-cell foam (AP Armaflex, Armstrong World Industries, Inc., Lancaster, PA) was used to insulate the gauge and stem, and the entire assembly was wrapped in aluminum foil. A data logger (CR10, Campbell Scientific Corp., Logan, UT) was located in each treatment plot and recorded data every minute and stored estimates of mean water flux every half hour. Minimum sheath conductance was determined as the mean value between 0100 and 0600 h, when whole-plant sap flow was assumed to be zero. Estimates of whole-plant water flux were divided by total leaf area to derive rates of transpiration. Leaf water potentials were measured on fully expanded leaves with a pressure chamber (PMS Instruments Co., Corvallis, OR).

Crown conductance was calculated as described by Meinzer et al. (1995):

$$g_c = EP/VPD, \quad (4)$$

where  $g_c$  is crown conductance expressed on a leaf area basis ( $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ ),  $E$  is transpiration,  $P$  is atmospheric pressure, and VPD is vapor pressure deficit. Vapor pressure

deficit (kPa) was calculated from values of relative humidity recorded in the understory, air temperature, and the assumption that leaf temperatures in the understory were similar to air temperatures. As the term is used here, crown conductance includes both a stomatal and a boundary layer component. Stomatal conductance ( $g_s$ ) was measured on several occasions with both a steady-state porometer (LI-1600) and a closed-loop photosynthesis system (LI-6200; Li-Cor, Inc.). Boundary layer conductance ( $g_b$ ) was calculated according to Meinzer et al. (1995). Mean values of  $g_c$  and  $g_b$  were used to estimate a dimensionless decoupling coefficient ( $\Omega$ ) as outlined by Jarvis and McNaughton (1986) and modified by Martin (1989) to include radiative coupling between vegetation and the atmosphere.

#### *Statistical analyses*

Although rates of whole-plant water flux were estimated for 53 understory saplings, a lack of sufficient replication made testing for a significant “size class” effect at any of the seven sampling dates difficult. Therefore, data gathered throughout the season and across treatments were pooled and subjected to a one-way analysis of variance. If a significant size class effect was indicated ( $P = 0.05$ ), means were separated with a Duncan’s multiple range test. Significant differences in rates of transpiration due to the various treatments (“wet,” “ambient,” and “dry”) were then identified by analysis of variance applied to each of the seven sampling dates.

## **Results**

#### *Soil water availability and understory microclimate*

Precipitation at the Walker Branch Watershed study site was 114 cm in 1995 compared to a 30-year mean of 134 cm. Much of this deficit occurred during June, July, and August when less than 12 cm of precipitation was received (Figure 1A). Measurements of soil water content indicated that the upper 35 cm of soil dried considerably during this period with matrix potentials declining below  $-1.2$  MPa on July 16 and below  $-1.7$  MPa on September 10 (Figure 1B). Soil water availability also differed throughout much of the season for the three TDE treatment plots. On July 6, mean matrix potentials were  $-0.4$  MPa for the “wet” plot,  $-0.7$  MPa for the “ambient” plot, and  $-0.9$  MPa for the “dry” plot. Later in August, mean matrix potentials were  $-0.4$  MPa for the “wet” plot,  $-0.5$  MPa for the “ambient” plot, and  $-0.8$  MPa for the “dry” plot (Figure 1B).

Midday vapor pressure deficits in the understory varied across the seven sampling dates from a low of 0.33 kPa (June 11) to a high of 2.72 kPa (August 28). These values were typically reached between 1200 and 1500 h, coinciding with air temperatures that ranged from 18 to 33 °C and relative humidities that varied from 45 to 85% (data not shown). Overstory trees intercepted the majority of PPFD. Midday PPFD was between 48 and 285  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 2 m above the forest floor. No differences in VPD, soil or air temperature, or relative humidity were observed among the TDE treatments, indicating that subcanopy troughs were not appreciably altering the microclimate of the “dry” plots (Hanson et al. 1995).

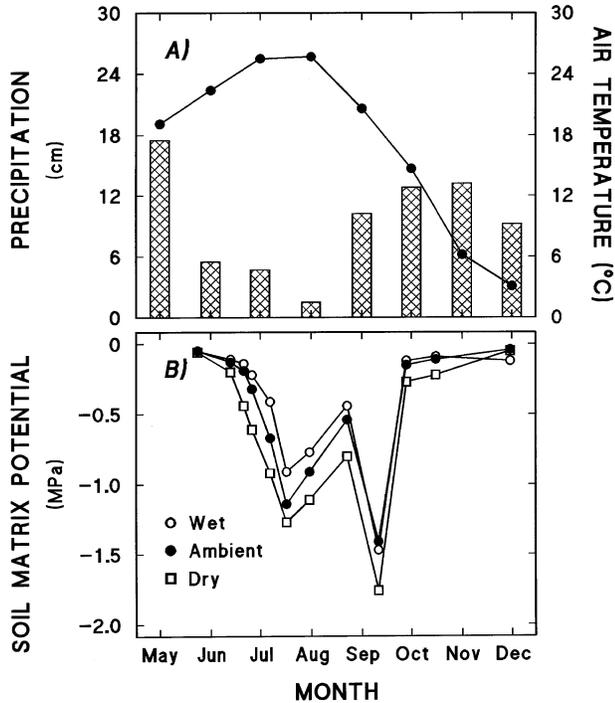


Figure 1. Seasonal patterns of (A) monthly precipitation (bar graph) and mean air temperature during 1995, and (B) soil matrix potential for the three TDE treatment plots. Soil water contents were measured with a time-domain reflectometer and matrix potentials calculated from soil water release curves.

Wind speeds in the understory were low and typically ranged from 0.25 to 0.60  $\text{m s}^{-1}$  (D.D. Baldocchi, NOAA, Oak Ridge, TN, personal communication).

#### Size-dependent differences in water flux

Given that sap flow gauges were installed on red maple saplings that ranged in diameter from 0.51 to 13.0 cm and in height from 0.59 to 13.7 m (Table 1), it is not surprising that daily rates of water flux varied between the five size classes (Figure 2). Saplings with a stem diameter larger than 10 cm lost water during June 9–11 at rates 50-fold greater than saplings with a stem diameter of 1 to 2 cm (326 versus 6.4 mol

Table 1. Characteristics of red maple saplings of different diameter classes growing in the understory of an upland oak–hickory forest. Stem diameter and height were measured directly for each sapling, whereas age, leaf area, and sapwood area were derived from allometric relationships.

Diameter class (cm)	<i>n</i>	Age (years)	Height (m)	Leaf area ( $\text{m}^2$ )	Sapwood area ( $\text{cm}^2$ )
< 1	12	10	0.9	0.13	0.3
1–2	17	12	2.5	0.7	1.6
2–5	13	18	5.1	3.8	9.4
5–10	7	26	8.7	11.4	29.3
> 10	4	40	12.3	32.8	88.9

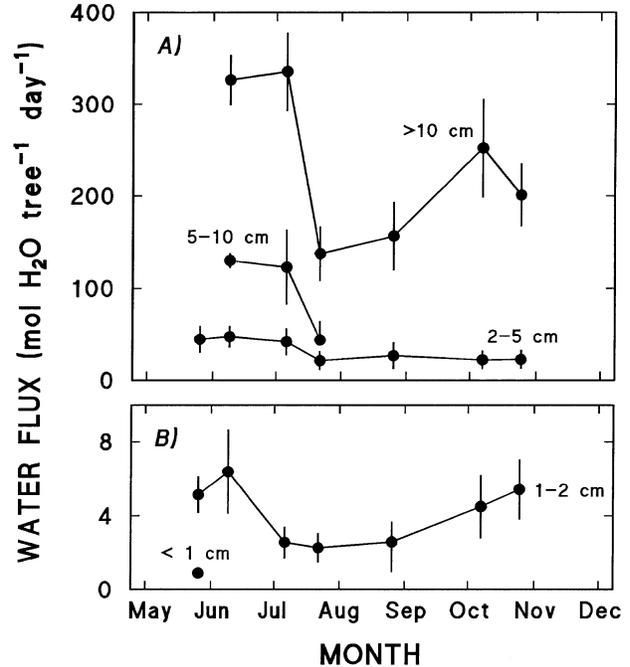


Figure 2. Whole-plant rates of water flux for red maple saplings in (A) the three larger size classes (2 to 5, 5 to 10, and > 10 cm diameter) and (B) in the two smaller size classes (< 1 and 1 to 2 cm diameter). Note differences in the y-axis scale.

$\text{H}_2\text{O tree}^{-1} \text{ day}^{-1}$ ). These diameter-dependent differences varied somewhat during the season, although on October 25, water flux rates for red maple saplings larger than 10-cm in diameter were still 35-fold greater than for saplings of 1 to 2 cm in diameter (201 versus 5.4  $\text{mol H}_2\text{O tree}^{-1} \text{ day}^{-1}$ ).

Averaged over the seven sampling dates, estimates of whole-plant water flux increased as stem diameters increased. These differences were driven by diameter class differences in leaf area and sapwood area (Table 1), as water flux rates expressed per unit leaf area or sapwood area were similar between saplings of the five diameter classes (Table 2). Mean water flux rates across all diameter classes and dates were 6.90 mol  $\text{H}_2\text{O}$

Table 2. Water flux rates for understory red maple saplings of different diameter classes expressed per unit tree, per unit leaf area, and per unit cross-sectional sapwood area. Values (mean  $\pm$  SE) are means of all sampling dates. Data within a column followed by the same letter are not significantly different at  $P = 0.05$ .

Diameter (cm)	Water flux rates		
	$\text{mol tree}^{-1} \text{ day}^{-1}$	$\text{mol m}^{-2} \text{ day}^{-1}$	$\text{mol dm}^{-2} \text{ day}^{-1}$
< 1	0.89 $\pm$ 0.13 c	6.70 $\pm$ 0.84 a	322 $\pm$ 39 a
1–2	4.31 $\pm$ 0.87 c	5.82 $\pm$ 1.14 a	259 $\pm$ 51 a
2–5	33.1 $\pm$ 8.6 c	7.46 $\pm$ 1.51 a	304 $\pm$ 61 a
5–10	98.4 $\pm$ 26.9 b	8.98 $\pm$ 2.19 a	349 $\pm$ 86 a
> 10	217.9 $\pm$ 58.0 a	6.89 $\pm$ 1.89 a	254 $\pm$ 69 a

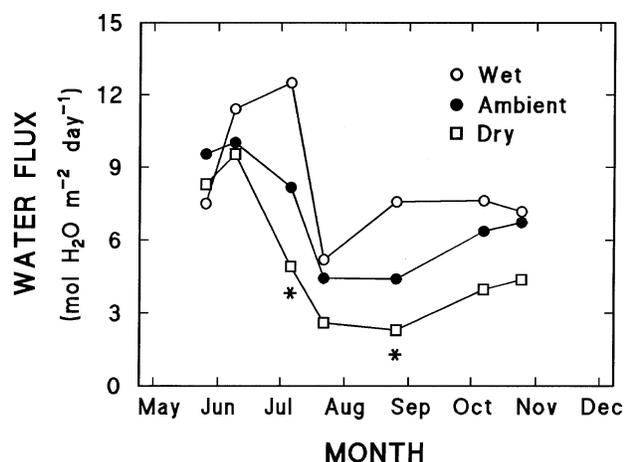


Figure 3. Daily rates of transpiration (expressed per unit leaf area) for red maple saplings growing on the three treatment plots of the TDE site. The two asterisks indicate that significant differences in transpiration between the “wet,” “ambient,” and “dry” plots were observed during the July 6 and August 27 sampling sessions.

$\text{m}^{-2}$  leaf area  $\text{day}^{-1}$  and  $288 \text{ mol H}_2\text{O dm}^{-2}$  sapwood area  $\text{day}^{-1}$  ( $n = 126$ ).

#### Whole-plant transpiration and crown conductance

Transpiration rates varied both throughout the season and between the three treatment plots of the TDE (Figure 3). Rates of transpiration were generally greatest for understory saplings in the early summer (June 9–11), decreasing to minimum rates in late July, with rates recovering somewhat by the August 27–28 and October 7–9 sampling dates. Leaf water potentials decreased from a midday mean of  $-0.88 \text{ MPa}$  on June 8 to

$-1.80 \text{ MPa}$  on July 27. Treatment effects were also observed for saplings across the three TDE plots, with significant differences in transpiration occurring between the “wet,” “ambient,” and “dry” plots on the July 6–7 ( $P = 0.01$ ) and August 27–28 ( $P = 0.04$ ) sampling dates. Rates of transpiration for these dates were 61 to 70% lower for saplings in the “dry” compared to saplings in the “wet” plot and 40 to 48% lower compared to saplings in the “ambient” plot. Midday leaf water potentials on July 7 were  $-1.59 \text{ MPa}$  in the “wet” plot,  $-1.68 \text{ MPa}$  in the “ambient” plot, and  $-2.13 \text{ MPa}$  in the “dry” plot, whereas on August 30 values were  $-1.94 \text{ MPa}$  in the “wet” plot,  $-2.08 \text{ MPa}$  in the “ambient” plot, and  $-2.44 \text{ MPa}$  in the “dry” plot. No TDE-imposed effects on transpiration or leaf water potential were observed at or near the time of maximum water stress (July 22–23). Sapling water loss per unit leaf area integrated across all sampling dates (May 26 to October 25) was  $1273 \text{ mol H}_2\text{O m}^{-2}$  in the “wet” plot,  $982 \text{ mol H}_2\text{O m}^{-2}$  in the “ambient” plot, and  $672 \text{ mol H}_2\text{O m}^{-2}$  in the “dry” plot.

Treatment differences for saplings measured on the “wet,” “ambient” and “dry” plots during the July 6–7 and August 27–28 sampling dates were clearly evident in the diurnal pattern of transpiration (Figure 4). On July 6, midday (1500 h) transpiration rates were  $1.88 \text{ mol H}_2\text{O m}^{-2} \text{ h}^{-1}$  for saplings in the “wet” plot,  $1.22 \text{ mol H}_2\text{O m}^{-2} \text{ h}^{-1}$  for saplings in the “ambient” plot, and  $0.76 \text{ mol H}_2\text{O m}^{-2} \text{ h}^{-1}$  for saplings in the “dry” plot. Transpiration rates had decreased by the August 27–28 sampling date, although treatment differences were still observed (Figure 4). During the early afternoon (1300 h) of August 28, transpiration rates were almost sevenfold lower for saplings in the “dry” plot compared to those in the “wet” plot and over 2.5-fold lower compared to saplings in the “ambient” plot.

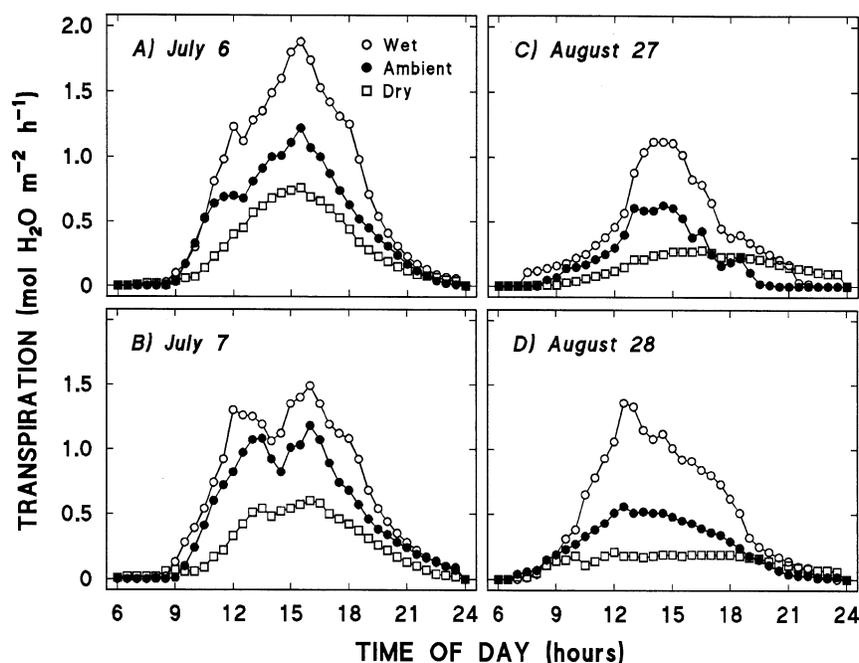


Figure 4. Diurnal rates of transpiration for saplings measured on the three TDE treatment plots during the (A, B) July 6–7 and (C, D) August 27–28 sampling sessions. It was on these dates that significant differences in transpiration were observed between the “wet,” “ambient,” and “dry” treatments.

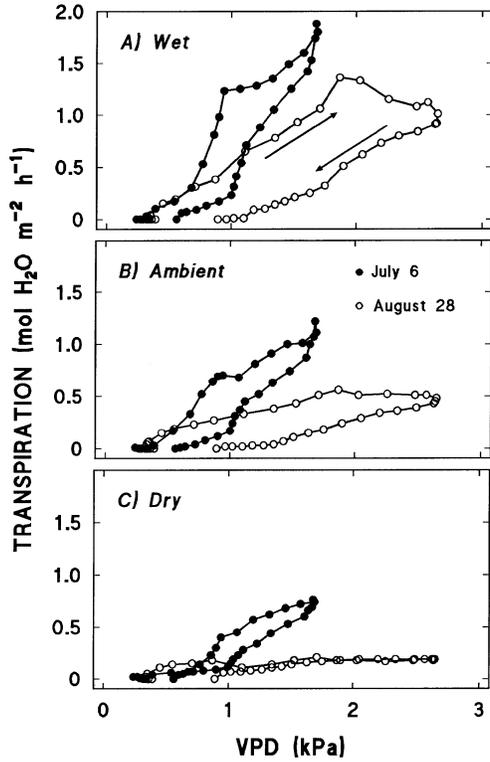


Figure 5. Observed relationship between transpiration and vapor pressure deficit (VPD) for saplings of the (A) "wet," (B) "ambient," and (C) "dry" treatment plots. Note the degree of hysteresis that exists between these two parameters for the two sampling dates.

There was a strong dependency of transpiration on vapor pressure deficit (VPD) on July 6 and August 28 (Figure 5). Overall, as VPD increased so too did rates of transpiration. For

a given VPD, however, transpiration was higher in the morning as VPD increased compared to the afternoon when VPD decreased. Notwithstanding this diurnal behavior, the dependency of transpiration on VPD (i.e., the slope) was less for values taken on August 28 compared with those taken on July 6. This occurred despite VPD being greater during the later sampling date. The slope also apparently differed between saplings of the "wet," "ambient," and "dry" treatments (Figure 5).

Crown conductances followed a pattern similar to that of transpiration, especially with respect to TDE treatments (Figure 6). On July 6, midday (1200–1500 h) estimates of  $g_c$  averaged  $29 \text{ mmol m}^{-2} \text{ s}^{-1}$  for saplings in the "wet" plot,  $19 \text{ mmol m}^{-2} \text{ s}^{-1}$  for saplings in the "ambient" plot, and  $12 \text{ mmol m}^{-2} \text{ s}^{-1}$  for saplings in the "dry" plot. Averaged across treatments, stomatal conductance ( $40 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) was similar in magnitude to boundary layer conductance ( $34 \text{ mmol m}^{-2} \text{ s}^{-1}$ ), with the stomatal component being the larger of the two conductances (Table 3). Calculated values of the decoupling coefficient ( $\Omega$ ) ranged between 0.64 and 0.72 for saplings in the three TDE treatment plots.

## Discussion

Red maple saplings growing in the understory of an upland oak forest displayed distinct patterns of response to seasonal and TDE-imposed periods of water stress. Rates of daily transpiration decreased throughout June and July, coinciding with periods of low to moderate VPD, low precipitation and soil matrix potentials, and leaf water potentials that for saplings in the "dry" plot approached  $-2.5 \text{ MPa}$ . Midseason reductions in leaf water potential of this magnitude have been shown to affect whole-plant water flux in 30-year-old trees of *Quercus petraea* L. ex Liebl. and *Q. robur* L. (Bréda et al. 1993), in

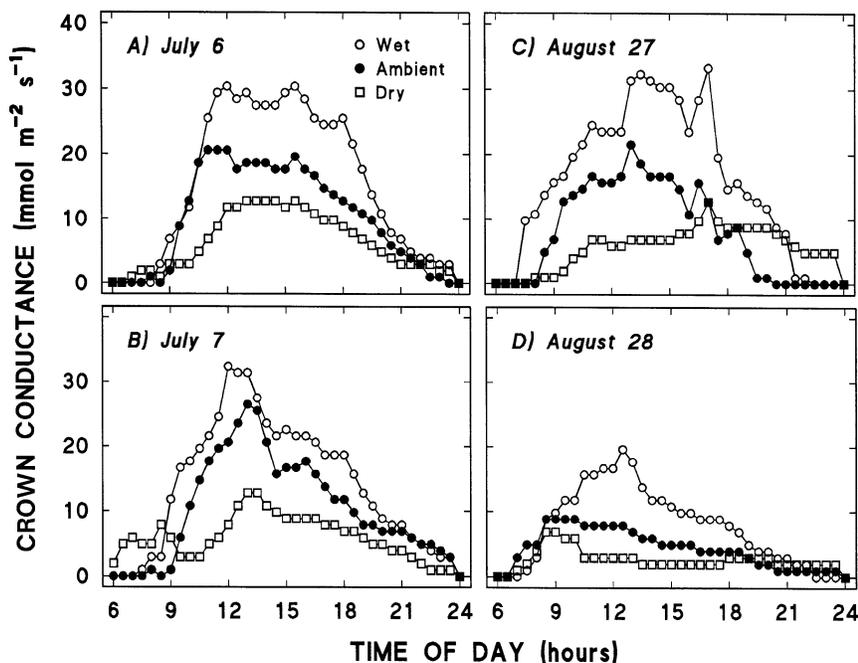


Figure 6. Diurnal patterns of crown conductance,  $g_c$ , for red maple saplings measured on the three treatment plots during the (A, B) July 6–7 and (C, D) August 27–28 sampling sessions. It was on these dates that significant differences in transpiration were observed between the "wet," "ambient," and "dry" treatments.

Table 3. Vapor phase conductances for understory red maple saplings growing in the three TDE treatment plots. A decoupling coefficient ( $\Omega$ ) describing stomatal control of transpiration was derived as outlined by Jarvis and McNaughton (1986) and as modified by Martin (1989).

Treatments	Conductance ( $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ )			$\Omega$
	Crown	Stomatal	Boundary	
Wet	29	61	55	0.64
Ambient	19	55	29	0.72
Dry	12	33	19	0.68
Mean	20	40	34	

plantation-grown trees of *Eucalyptus grandis* W. Hill ex Maiden. (Dye 1996), in saplings of *Pinus sylvestris* L. (Jackson et al. 1995), in 14-year-old *Pinus halepensis* Mill. trees (Schiller and Cohen 1995), and in open-grown trees of *Acer saccharum* (Dawson 1996). Water flux per unit sapwood area (sap flux density) was reduced 70% in both *Q. petraea* and *Q. robur* as leaf water potential dropped to  $-3.0$  MPa (Bréda et al. 1993), and canopy transpiration decreased by 55 to 70% in both large and small *A. saccharum* trees as leaf water potential dropped from  $-0.5$  to  $-2.5$  MPa (Dawson 1996). Our observations that whole-plant water flux decreased by 40 to 45% for red maple saplings with leaf water potentials that ranged from  $-1.68$  to  $-2.08$  MPa are consistent with these findings.

Despite recent efforts to assess the water relations of trees, few studies have examined whole-plant rates of water flux for vegetation in the forest understory. Greenwood et al. (1985) used a ventilated-chamber approach to estimate transpiration from middle-story trees within a dense stand of eucalypts. They concluded that water loss from such trees was a sizeable component of the annual water budget for these stands. We suspect that red maple saplings and other hardwood species (i.e., *Cornus florida*) growing in the understory of an upland oak forest in East Tennessee make only a modest contribution to daily and seasonal evapotranspiration. Sap flux density for saplings measured in our study varied from 250 to 350  $\text{mol H}_2\text{O dm}^{-2} \text{day}^{-1}$  (Table 2) compared to 855  $\text{mol H}_2\text{O dm}^{-2} \text{day}^{-1}$  for a 27-m-tall red maple tree growing at the same location (data not shown). Comparatively low rates of sap flux density for understory saplings combined with estimated sapwood areas of 3  $\text{m}^2 \text{ha}^{-1}$  for saplings and 10  $\text{m}^2 \text{ha}^{-1}$  for overstory trees suggests that understory species contribute less than 20% of seasonal evapotranspiration at this site. D.D. Baldocchi (personal communication) used eddy-covariance methods to estimate rates of evapotranspiration for a forest stand located less than 2 km from our study site and concluded that water lost from understory vegetation accounted for less than 15% of daily evapotranspiration.

Our results indicate that relative plant stature made little difference in determining the seasonal and TDE-imposed response of understory saplings to water stress. Although a rigorous test of this hypothesis was limited by the availability

of replicates at any one sample date, it was clear that although whole-plant water flux increased with stem diameter, these size-class differences were not observed when rates were expressed on either a leaf area or a sapwood area basis. In a study of *Pinus radiata* D. Don, Teskey and Sheriff (1996) observed that daily water flux was greater for large trees than for small trees in a 16-year-old plantation, but transpiration per unit leaf area was nearly identical between size classes. Others have shown a similar dependency of transpiration on leaf area and sapwood area (Vertessy et al. 1995) and recently Armeth et al. (1996) observed that large differences in whole-plant water flux between emergent, canopy, and subcanopy trees in a 130-year-old *Larix gmelinii* (Rupr.) Rupr. ex Kuzen. forest could be explained solely on the basis of projected crown area. This dependency of daily transpiration on leaf area, sapwood area, and crown area does not preclude, however, a possible differential sensitivity of seedlings, saplings and trees to drought. Dawson (1996) reported that rates of canopy transpiration for large (9–14 m) *A. saccharum* trees were higher than those measured for small (3–5 m) trees. Hydrogen isotope analyses of xylem sap indicated that large trees with their deeper roots could access groundwater, whereas small trees with limited root development were restricted to shallow soil water resources. Dawson (1996) concluded from this study that small trees will probably show a greater variation in water flux during the season and will exhibit a greater sensitivity to environmental factors that influence plant transpiration, such as soil water deficits and increased evaporative demand.

Although understory saplings are not often used in whole-plant studies of water flux, we expected that the environmental regulation of canopy transpiration would be similar to that observed in large trees. Field studies have shown previously that hourly rates of transpiration follow closely the diurnal patterns of global radiation (Lopushinsky 1986) and VPD (Granier et al. 1996). Within the shaded environment of the forest understory, we observed that VPD was the primary factor regulating transpiration. Almost 80% of the variability measured in midday transpiration could be explained by VPD. However, such an analysis is complicated by the fact that radiation, VPD, wind, and humidity are not independent variables, but rather covary throughout the day. Gutiérrez et al. (1994) showed that covariance can obscure stomatal responses to single climatic variables and, as a result, can introduce hysteresis into the relationship between transpiration (or crown conductance) and VPD. Gutiérrez et al. (1994) and Meinzer et al. (1995) have both used several normalization procedures to study environmental regulation of transpiration and conclude that hysteresis is seldom observed when transpiration or crown conductance is plotted against VPD normalized to the stimulus for stomatal opening (i.e., PPF/D). In apparent agreement with these findings, we note that a plot of canopy transpiration versus VPD/PPFD for the saplings of the three TDE treatments (a reanalysis of Figure 5) yielded a family of curves in which transpiration decreased as VPD/PPFD increased and there was no evidence of hysteresis.

Estimates of canopy transpiration and crown conductance for red maple saplings were low compared to rates reported for

trees of the forest overstory. On July 6, transpiration rates reached  $0.55 \text{ mmol m}^{-2} \text{ s}^{-1}$  for saplings in the “wet” plot and  $0.21 \text{ mmol m}^{-2} \text{ s}^{-1}$  for saplings in the “dry” plot (recalculated from Figure 4). These values are much lower than the rates of 1.50 to  $1.70 \text{ mmol m}^{-2} \text{ s}^{-1}$  reported for *Coffea arabica* L. (Gutiérrez et al. 1994), for *Anacardium excelsum* (Bertero & Balb.) Skeels (Meinzer et al. 1993), and for *Miconia argentea* (SW.) DC. (Meinzer et al. 1995). Crown, stomatal, and boundary layer conductances in understory red maple were also low compared to these studies. A low stomatal conductance combined with a slightly lower boundary layer conductance yielded a decoupling coefficient of 0.64 to 0.72 (Table 3). Similar values have been reported for trees of a lowland tropical forest (0.54; Meinzer et al. 1993), gap-colonizing shrub and tree species (0.75; Meinzer et al. 1995), and short-rotation hardwoods (0.66; Hinckley et al. 1994). A decoupling coefficient of this magnitude suggests poor stomatal control of transpiration and indicates that large changes in stomatal conductance can occur with little or no consequence to transpiration. Given the conductance values in Table 3 for saplings of the “ambient” plot, it can be shown that a 10% change in  $g_s$  results in only a modest 2.6% change in transpiration. Failure to estimate or take into account the importance of both  $g_s$  and  $g_b$  in calculations of transpiration may add uncertainty to intersite and interspecies comparisons made with conventional leaf gas-exchange methods (Kloppel et al. 1993, Kubiske and Abrams 1994).

Sap flow gauges were used in this study to assess mechanisms by which whole-plant water flux responds to seasonal and TDE-imposed changes in soil water content. Our findings indicate that red maple saplings will be influenced by quantitative changes in precipitation. Above-normal precipitation will favor increased transpiration, whereas below-normal precipitation will lead to decreased soil water resources and if severe enough will contribute to reductions in sapling growth (P.J. Hanson, Oak Ridge National Laboratory, Oak Ridge, TN, personal communication). How these responses impact the carbon and water balance of forest ecosystems and how forest composition will be affected must be considered as we seek to understand more about how forests respond to global climate change.

#### Acknowledgments

We thank N.T. Edwards and R.J. Norby for their helpful reviews of an earlier draft manuscript. Special thanks to F.C. Meinzer who provided assistance in calculations of the stomatal decoupling factor. 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. 4708, Environmental Sciences Division, Oak Ridge National Laboratory.

#### References

- Abrams, M.D. and S.A. Mostoller. 1995. Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. *Tree Physiol.* 15:361–370.
- Abrams, M.D., J.C. Schultz and K.W. Kleiner. 1990. Ecophysiological responses in mesic versus xeric hardwood species to an early-season drought in Central Pennsylvania. *For. Sci.* 36:970–981.
- Arneith, 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.
- Baker, J.M. and C.H.M. van Bavel. 1987. Measurement of the mass flow of water in stems of herbaceous plants. *Plant Cell Environ.* 10:777–782.
- Bréda, N., H. Cochard, E. Dreyer and A. Granier. 1993. 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.
- Dawson, T.E. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the role of tree size and hydraulic lift. *Tree Physiol.* 16:263–272.
- Drungil, C.E.C., T.J. Gish and K. Abt. 1987. Soil moisture determinations in gravelly soils with time domain reflectometry. *Am. Soc. Agric. Engineers Paper No.* 87–2568, 10 p.
- Dye, P.J. 1996. Response of *Eucalyptus grandis* trees to soil water deficits. *Tree Physiol.* 16:233–238.
- Ěermák, J. and J. Kuěera. 1993. Extremely fast changes in xylem 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, Cambridge, pp 181–190.
- Ěermák, J., R. Matyssek and J. Kuěera. 1993. Rapid response of large, drought-stressed beech trees to irrigation. *Tree Physiol.* 12:281–290.
- Granier, A., R. Huc and S.T. Barigah. 1996. Transpiration of natural rain forest and its dependence on climatic factors. *Agric. For. Meteorol.* 78:19–29.
- 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.
- Gutiérrez, M.V., F.C. Meinzer and D.A. Grantz. 1994. Regulation of transpiration in coffee hedgerows: covariation of environmental variables and apparent responses of stomata to wind and humidity. *Plant Cell Environ.* 17:1305–1313.
- Hanson, P.J., D.E. Todd, N.T. Edwards and M.A. Huston. 1995. Field performance of the Walker Branch Throughfall Displacement Experiment. *In* Ecosystem Manipulation Experiments: Scientific Approaches, Experimental Design and Relevant Results. Eds. A. Jenkins, R.C. Ferrier and C. Kirby. Commission of the European Communities, Ecosystems Res. Rep. No. 20, pp 307–313.
- Hinckley, T.M., J.R. Brooks, J. Ěermák, R. Ceulemans, J. Kuěera, F.C. Meinzer and D.A. Roberts. 1994. Water flux in a hybrid poplar stand. *Tree Physiol.* 14:1005–1018.
- Jackson, G.E., J. Irvine and J. Grace. 1995. Xylem cavitation in Scots pine and Sitka spruce saplings during water stress. *Tree Physiol.* 15:783–790.
- Jarvis, P.G. and K.G. McNaughton. 1986. Stomatal control of transpiration: Scaling up from leaf to region. *Adv. Ecol. Res.* 15:1–49.

- Johnson, D.W. 1989. Site description. *In* Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed. Eds. D.W. Johnson and R.I. Van Hook. Springer-Verlag, New York, pp 6–20.
- Kirschbaum, M.U.F. and A. Fischlin. 1995. Climatic change impacts on forests. *In* Climate Change 1995—Impacts, Adaptations and Mitigation of Climate Change: Scientific–Technical Analyses. Eds. R.T. Watson, M.C. Zinyowera, R.H. Moss and D.J. Dokken. Cambridge University Press, Cambridge, pp 95–129.
- Kloppel, B.D., M.D. Abrams and M.E. Kubiske. 1993. Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. *Can. J. For. Res.* 23:181–189.
- Kubiske, M.E. and M.D. Abrams. 1994. Ecophysiological analysis of woody species in contrasting temperate communities during wet and dry years. *Oecologia* 303–312.
- Loaiciga, H.A., J.B. Valdes, R. Vogel, J. Garvey and H. Schwarz. 1996. Global warming and the hydrologic cycle. *J. Hydrol.* 174:83–127.
- Lopushinsky, W. 1986. Seasonal and diurnal trends of heat pulse velocity in Douglas-fir and ponderosa pine. *Can. J. For. Res.* 16:814–821.
- Lüdeke, M.K.B., S. Dönges, R.D. Otto, J. Kindermann, F.W. Badeck, P. Ramage, U. Jäkel and G.H. Kohlmaier. 1995. Responses in NPP and carbon stores of the northern biomes to a CO<sub>2</sub>-induced climatic change, as evidence by the Frankfurt Biosphere Model (FBM). *Tellus* 47B:191–205.
- Martin, P. 1989. The significance of radiative coupling between vegetation and the atmosphere. *Agric. For. Meteorol.* 49:45–53.
- Martin, P. 1996. Climate change, water stress, and fast forest response: A sensitivity study. *Clim. Change* 34:223–230.
- 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. Gutiérrez 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.
- Melillo, J.M., T.V. Callaghan, F.I. Woodward, E. Salati and S.K. Sinha. 1990. Effects on ecosystems. *In* Climate Change, The IPCC Scientific Assessment. Eds. J.T. Houghton, G.T. Jenkins and J.J. Ephraums. Cambridge University Press, Cambridge, pp 283–310.
- Mitchell, J.F.B., S. Manabe, V. Meleshko and T. Tokioka. 1990. Equilibrium climate change—and its implications for the future. *In* Climate Change, The IPCC Scientific Assessment. Eds. J.T. Houghton, G.T. Jenkins and J.J. Ephraums. Cambridge University Press, Cambridge, pp 131–172.
- Pastor, J. and W.M. Post. 1988. Response of northern forests to CO<sub>2</sub>-induced climate change. *Nature* 334:55–58.
- Rind, D., R. Goldberg, J. Hansen, C. Rosenzweig and R. Ruedy. 1990. Potential evaporation and the likelihood of future drought. *J. Geophys. Res.* 95:9983–10004.
- Running, S.W. and R.R. Nemani. 1991. Regional hydrologic and carbon balance responses of forests resulting from potential climatic change. *Clim. Change* 19:342–368.
- Schiller, G. and Y. Cohen. 1995. Water regime of a pine forest under a Mediterranean climate. *Agric. For. Meteorol.* 74:181–193.
- Teskey, R.O. and D.W. Sheriff. 1996. Water use by *Pinus radiata* trees in a plantation. *Tree Physiol.* 16:273–279.
- 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.

