

Hydrologic balance in an intact temperate forest ecosystem under ambient and elevated atmospheric CO₂ concentration

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Abstract

Increasing atmospheric CO₂ concentration decreases stomatal conductance in many species, but the savings of water from reduced transpiration may permit the forest to retain greater leaf area index (*L*). Therefore, the net effect on water use in forest ecosystems under a higher CO₂ atmosphere is difficult to predict. The free air CO₂ enrichment (FACE) facility ($n = 3$) in a 14-m tall (in 1996) *Pinus taeda* L. stand was designed to reduce uncertainties in predicting such responses. Continuous measurements of precipitation, throughfall precipitation, sap flux, and soil moisture were made over 3.5 years under ambient (CO₂^a) and elevated (CO₂^e) ambient + 200 μmol mol⁻¹). Annual stand transpiration under ambient CO₂ conditions accounted for 84–96% of latent heat flux measured with the eddy-covariance technique above the canopy. Under CO₂^e, *P. taeda* transpired less per unit of leaf area only when soil drought was severe. *Liquidambar styraciflua*, the other major species in the forest, used progressively less water, settling at 25% reduction in sap flux density after 3.5 years under CO₂^e. Because *P. taeda* dominated the stand, and severe drought periods were of relatively short duration, the direct impact of CO₂^e on water savings in the stand was undetectable. Moreover, the forest used progressively more water under CO₂^e, probably because soil moisture availability progressively increased, probably owing to a reduction in soil evaporation caused by more litter buildup in the CO₂^e plots. The results suggest that, in this forest, the effect of CO₂^e on transpiration was greater indirectly through enhanced litter production than directly through reduced stomatal conductance. In forests composed of species more similar to *L. styraciflua*, water savings from stomatal closure may dominate the response to CO₂^e.

Keywords: canopy transpiration, elevated CO₂, *Liquidambar styraciflua*, *Pinus taeda*, *Ulmus alata*, water balance

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Introduction

Forest evapotranspiration returns to the atmosphere c. 60% of the water entering the system by precipitation (Otto, 1994; Peck & Meyer, 1996). Physiological and ecological responses of forests to future increases in atmospheric CO₂ have the potential to modify the biosphere–atmosphere exchanges of mass and energy (Henderson-Sellers *et al.*, 1995), and thus influence global water and carbon cycles (Lockwood, 1999; Kirschbaum,

2000). Elevated CO₂ (CO₂^e) can reduce stomatal conductance (Bazzaz, 1990; Lockwood, 1999), potentially reducing canopy transpiration (E_C , Henderson-Sellers *et al.* 1995). At a given precipitation input, lower E_C should keep soil moisture availability higher, and combined with the greater availability of carbohydrates from enhanced photosynthetic rates (Ellsworth, 1999) would result in higher equilibrium leaf area index (L ; Woodward, 1990). Higher L would increase evaporation of intercepted rainfall (I), and cause a partial recovery of E_C (Woodward, 1990; Overdieck & Forstreuter, 1994; Field *et al.*, 1995; Lockwood, 1999). Thus, at equilibrium, forests in higher atmospheric CO₂ will probably have higher canopy

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photosynthesis, yet use the same amount of water, although, based on a model proposed by Woodward (1990), the partitioning of water used in I will increase relative to E_C . Verifying such theoretical predictions of stomatal and canopy response to is critical for correct simulation of regional and global water and carbon cycles (Levis *et al.*, 2000). However, until recently technical limitations have prevented canopy-scale quantification of the potential responses of intact forest ecosystems to higher atmospheric CO_2 (Norby *et al.*, 1999; Wullschleger & Norby, 2001).

Responses to above-current atmospheric CO_2 are available mostly from leaf-level measurements in forests (Ellsworth *et al.*, 1995; Ellsworth, 1999; DeLucia & Thomas, 2000), and system-level measurements in artificial environments (Pataki *et al.*, 1998), or environments in which CO_2 concentration is highly variable (e.g. CO_2 springs, Tognetti *et al.*, 1999). Transpiration and conductance rate in tree seedlings grown in pots showed a range of responses to CO_2^e , from being unaffected in some species (Tolley & Strain, 1985; Guehl *et al.*, 1994; Tschaplinski *et al.*, 1995; Groninger *et al.*, 1996; Heath & Kerstiens, 1997), reduced in others (Tschaplinski *et al.*, 1995), in showing inconsistent responses (Overdieck & Forstreuter, 1994 vs. Heath & Kerstiens, 1997). It is difficult to extrapolate results from many studies to forests because studies on seedlings do not reproduce the variation in climate, ontogeny, acclimation of plants, rooting volume, and interspecies competition (Körner, 1995, 1996; Norby *et al.*, 1999). Even experiments in open top chambers with unrestricted rooting volume and with near-natural variation in climate, suffer shortcomings because light and horizontal air movement are attenuated (e.g. Körner & Arnone, 1992; see review in Norby *et al.*, 1999), and because responses of canopy leaf area cannot be readily extrapolated from discrete to continuous canopies. Furthermore, the response may depend on the duration of the exposure (Gunderson & Wullschleger, 1994; Lee & Jarvis, 1995; Hättenschwiler & Körner, 1996; Medlyn *et al.*, 1999; Medlyn *et al.*, 2001). Although a meta-analysis of a large number of data sets showed that stomatal conductance generally does not respond to increased atmospheric CO_2 (Curtis, 1996; Curtis & Wang, 1998), another such analysis showed that responses can be significant for long-term studies (Medlyn *et al.*, 2001).

Although certain important physiological responses from studies on seedlings and saplings in confined settings can be quantified and used in modeling of forest behaviour in higher CO_2 atmosphere, results cannot be directly extrapolated to forest ecosystems. Indeed, a recent study on *Liquidambar styraciflua* L. performed in the free air CO_2 enrichment (FACE) facility showed that results from less natural settings may not be representative of the behaviour at the stand level

(Wullschleger & Norby, 2001). The FACE system provides a setting in which the effects of higher atmospheric CO_2 can be evaluated in otherwise intact forest ecosystem (Körner, 1995; Norby *et al.*, 1999). Here we report on the effect of atmospheric CO_2 on the major components of forest hydrologic balance in a maturing *Pinus taeda* L. forest over 3.5 years.

The objective of this study was to test whether a reduction in stand transpiration ensued as atmospheric CO_2 enrichment began. If reduction in transpiration were found, we would assess its consequences to predictions for a final steady state condition according to Woodward (1990). Leaf area index under CO_2^e may increase directly with higher availability of carbohydrates if other resources are not greatly limiting. We will therefore examine this potential response of L to CO_2 enrichment. Ultimately, we will assess whether the major components of the hydrologic balance, e.g. interception, transpiration, drainage, were altered in response to CO_2^e .

Materials and methods

Study site

The site was located in the blackwood division of the Duke forest, North Carolina, USA (35°58'-N, 79°05'-W), in a *Pinus taeda* L. (loblolly pine) plantation established in 1983. A hardwood component has developed and is dominated by *Liquidambar styraciflua* L. (sweetgum) in mid- to upper-canopy, and *Acer rubrum* L. (red maple), *Ulmus alata* Michx. (winged elm) and *Cornus florida* L. (flowering dogwood) in low- to mid-canopy. The local climate was characterised by an average annual temperature of 15.5 °C and precipitation of 1140 mm. The moderate fertility soil was an acidic Hapludalf of the Enon series with a clay pan at c. 30 cm depth.

Part of this stand was designated as a forest atmosphere carbon transfer and storage, FACTS-1, site. Six circular experimental plots (30 m in diameter) were delineated for the FACE experiment in 1996 (for plot characteristics see Table 1). Since August 1996 three plots were exposed to ambient CO_2 concentration ($\text{CO}_2^a \sim 370 \mu\text{mol mol}^{-1}$) and three to (ambient + 200 $\mu\text{mol mol}^{-1}$) delivered by 32 vertical pipes surrounding each plot (further details see Hendrey *et al.*, 1999). The enrichment with CO_2 continues the entire year at times in which the ambient temperature was above 5 °C and wind speed was below 5.0 m s⁻¹. Each plot had radial boardwalks orientated north-south and east-west, and a central tower.

For this study, a subplot extending 1.5 m to each side of the boardwalks, hereafter referred to as the measurement plot, was used for measurement and scaling in each experimental plot. In November of each year diameter

Table 1 Stand characteristics of the six experimental (exp.) and measurement (meas.) plots in 1998. The measurement plots were a subsample of the entire experimental plot. CO₂^a indicates ambient plots, and CO₂^e indicates elevated treatment plots. The L is leaf area index, and ΔL change in L during the study period (1998–2000)

	Treatment	Basal area (m ² ha ⁻¹)		Hardwood basal area (m ² ha ⁻¹)		Hardwood (% of BA)	Stems (ha ⁻¹)	max.L (m ² m ⁻²)	ΔL
		exp.	meas.	exp.	meas.				
Plot 1	CO ₂ ^a	32.6	36.4	5.1	3.3	15.6	5253	3.6	1.0
Plot 2	CO ₂ ^e	32.5	35.7	6.2	5.6	19.1	4375	3.6	1.1
Plot 3	CO ₂ ^e	46.5	53.5	2.6	3.5	5.5	3663	3.8	1.4
Plot 4	CO ₂ ^e	41.0	46.2	2.6	2.4	6.3	4239	3.8	1.0
Plot 5	CO ₂ ^a	48.7	51.5	2.9	3.6	5.9	4133	3.9	1.6
Plot 6	CO ₂ ^a	44.1	44.3	2.1	1.9	4.7	4239	3.7	0.8

of all trees in the measurement plot (≥ 25 mm at 1.4 m above-ground) was measured. Diameter measurements were corrected for bark thickness and used to estimate sapwood area per unit ground area ($A_S:A_G$) for each species. Based on stem cores taken outside of the experimental plots concurrently with diameter measurements, *P. taeda* trees of the same diameter range as in the measurement plots have not yet formed heartwood. Destructive harvest of individuals from the major hardwood species yielded similar results. Maximum leaf area (i.e. in mid-growing season for the broadleaf species and end of growing season for the conifers) was estimated based on allometric relationships with diameter derived from biomass harvests in 1998 for *Liriodendron tulipifera* L. (tulip poplar) and *A. rubrum* (Naumburg E, unpublished), and *L. styraciflua* and *C. florida* (Naumburg E & Schäfer K, unpublished) and in 1999 for *U. alata* (Schäfer K., unpublished), as well as published relationships for *P. taeda* (Pataki *et al.*, 1998). For *P. taeda*, the diameter at 1.4 m was used to estimate sapwood area at the base of the crown, which was then used to estimate leaf area based on Pataki *et al.* (1998). For the hardwood species the diameter was used directly to estimate leaf area. The aforementioned species comprise c. 90% or more of total basal area in any measurement plot (Table 1). For species for which allometric functions were not available, the relationship of the most closely resembling species was used. Leaf area index was then calculated by summing the leaf area of all the individuals in each measurement plots and dividing them by the ground area. Based on the previous studies, it was assumed that the allometric relationships were not affected by CO₂^e (Pataki *et al.*, 1998; Gielen *et al.*, 2001; Norby *et al.*, 2001).

Environmental measurements

Air temperature (T_{air} , in °C) and relative humidity, used for calculating vapour pressure deficit (D), was measured

in the upper third of the canopy (Vaisala HMP35C and HMP45C, Helsinki, Finland). Soil temperature (T_{soil} in °C) was measured at ~12 cm depth in each plot, and stem temperature below the bark (T_{stem} in °C) was measured at 1.4 m above-ground in four cardinal direction on one tree and towards north on two additional trees, all in plot #1. In each plot, average soil moisture θ (m³ m⁻³) of the upper 30 cm soil layer was measured with four sensors (CS615 Campbell Scientific, Logan, Utah, USA), and soil water potential Ψ_s (kPa) within the 15–20 cm layer was measured with one sensor (EQ2, Delta-T-Devices, Cambridge, UK). On the central tower above the canopy of plot #4, sensors for measurements of photosynthetic photon flux density PPF (Q190, LiCor, Lincoln, Nebraska, USA), net radiation R_n (REBS Q*7, Radiation and Energy Balance System Inc., Seattle, Washington, USA), and precipitation P_0 (tipping bucket TI, Texas Instruments, Austin, Texas, USA) were mounted. All sensors were sampled every 30 s, and 30 min averages were stored in a data logger (21X or CR23X, Campbell Scientific, Logan, Utah, USA). In addition, in each measurement plot precipitation through fall P_T (mm) was measured with four 0.1 m diameter rain gauges (Productive Alternatives Inc., Fergus Falls, MN, USA) randomly distributed in the plot and manually recorded (at 0.2 mm accuracy) at least once a week.

Sap flux measurements

In each measurement plot, eight *P. taeda* and four *L. styraciflua* trees were selected in May 1997 for sap flux measurements with the Granier-type sensor (cf 1987, 1996). In April 1998 *C. florida* and *U. alata* trees in and plots were equipped for sap-flux measurement. Only five trees of each species were available for these measurements in each treatment, and these were not distributed in all plots. For *C. florida* the distribution of the trees would not allow a species specific analysis,

and data were used only for scaling to stand level water use in assessing the effect of on the hydraulic balance.

The Granier-type sensor consists of a heated (200 mW) and a reference probe, 20 mm long and 2 mm in diameter. The heated probe was placed 10 cm above the reference probe to prevent thermal interference; the distance is sufficiently small to avoid large natural thermal gradients in the tree trunk (Goulden & Field, 1994). Sensors were installed in the outer 20 mm of the xylem towards north and covered with a radiation shield to protect from direct radiation. Two of the eight *P. taeda* trees were additionally equipped with an inner xylem sap flux sensors, extending 20–40 mm from the cambium, and two trees were equipped with outer sensors (0–20 mm from the cambium) installed at the south side of the tree to quantify radial and azimuthal patterns, respectively. Heat flux densities were measured every 30 s, and 30 min averages were stored on the logger used for storage of environmental data. The signal was converted to sap flux density (J_S in $\text{g}_{\text{H}_2\text{O}} \text{m}^{-2} \text{sapwood s}^{-1}$) according to Granier (1987).

Sap flux density in the outer 20 mm of the xylem was scaled in *P. taeda* to a mean sap flux density of the entire xylem. Sap flux density was similar in the north and south side of *P. taeda* trees ($P > 0.1$), and thus the sap flux density of the northern side of trees, available for a larger number of trees in each plot, was used in all subsequent analyses. There was no difference in the ratio of inner to outer sap-flux density in *P. taeda* between treatments ($P = 0.69$), nor was there a relationship between tree size and outer J_S ($P = 0.42$), and thus inner-to-outer sap flux densities ratios of individuals from both the treatments were averaged for further analyses. The mean ratio of inner-to-outer sap flux density in *P. taeda* had a seasonal pattern ($r^2 = 0.40$, $P < 0.0001$, Fig. 1a) and the residuals of this relationship for the individual trees depended on tree size ($r^2 = 0.66$, $P = 0.008$, Fig. 1b).

To scale sap flux in the outer xylem of each tree to its entire hydroactive xylem, a relationship between the inner and outer sap flux density was generated using the 12 trees with both the measurement depths. Then, for each *P. taeda* tree in all plots measured, sap flow in each band of xylem depth (E_{ti} , $\text{g}_{\text{H}_2\text{O}} \text{s}^{-1}$, where i represents the two aforementioned bands, and a third region inner to 40 mm from the cambium) was calculated, and summed for the tree. Sap flow for each xylem band was calculated using (i) mean sap flux density from 0 to 20 mm of all measured *P. taeda* trees within each plot, (ii) a reduction factor (m_1) from outer to inner flux depending on day of year (DoY) and tree size for the xylem band from 20 to 40 mm, and (iii) a reduction factor (m_2) for xylem depth exceeding 40 mm. Sap flux density of each xylem band was multiplied by their respective sapwood area and summed to total tree transpiration, E_t , as:

$$E_t = \bar{J}_s^* A_{S0-20} + \bar{J}_s^* m_1^* A_{S20-40} + \bar{J}_s^* m_2^* A_{S>40}, \quad (1)$$

Where, m_1 is a function of the DoY (Fig. 1a) and size of the tree (see Fig. 1b) and $m_2 = 0.41$ (Phillips *et al.*, 1996) or $m_2 = m_1$ if $m_1 < 0.41$, \bar{J}_s is mean sap flux density of all measured individuals in each measurement plot in the outermost xylem (0–20 mm), A_{S0-20} is sapwood area in 0–20 mm xylem depth, A_{S20-40} sapwood area in 20–40 mm xylem depth, $A_{S>40}$ is innermost sapwood area exceeding 40 mm sapwood depth (in m^2). The functions used to calculate m_1 are regression fits on the seasonal pattern of the means (Fig. 1a) and the residuals of the individuals (Fig. 1b):

$$m_1 = 0.7429 + 0.2078^* \sin\left(\frac{2\pi^* DoY}{446.8424} + 2.0820\right) + (-0.2872 + 0.0032^* e^{0.0202^* dia}), \quad (2)$$

where, dia is diameter at breast height (1.4 m above ground) in mm. Dividing E_t (i.e. $\sum E_{ti}$) of each tree by the tree's total sapwood area provides an estimate of mean tree J_S .

Scaling from individual tree sap-flux density to canopy transpiration E_C for each species is commonly done by multiplying mean sap flux density of all measured trees (\bar{J}_s , $\text{g m}^{-2} \text{sapwood s}^{-1}$) with sapwood area per unit ground area (Oren *et al.* 1998b). This was done for all the hardwood species, where the mean \bar{J}_s of the three hardwood species was used for species in which sap flux was not measured. However, given the earlier findings (Fig. 1), a different scaling approach was taken with *P. taeda*. In *P. taeda* J_S was scaled to E_C by first estimating E_t of each individual tree in the measurement plots based on \bar{J}_s , sapwood area, and scaling factors that are dependent on time-of-year and tree-size (Eqn 1), and then summing the transpiration of all trees and dividing by the plot area.

Hydrological balance

By performing a local water balance, we expect closure of the water budget with drainage and overland flow directly estimated based on physical parameters.

The accuracy of estimates of the main components of the hydrologic balance was evaluated by measuring latent heat flux (LE^*) with eddy-covariance instruments (Lai *et al.*, 2000). It is expected that LE^* will fall between E_C and total stand water use. Eddy covariance measurements account for total evapotranspiration between rain events, and are thus expected to result in higher values than E_C , but the instruments do not perform well during and soon after rain events, thus underestimating the evaporation from leaves and forest floor. Naturally, this leads to a systematic underestimation of evapotranspiration for long intervals. Conventional eddy covariance

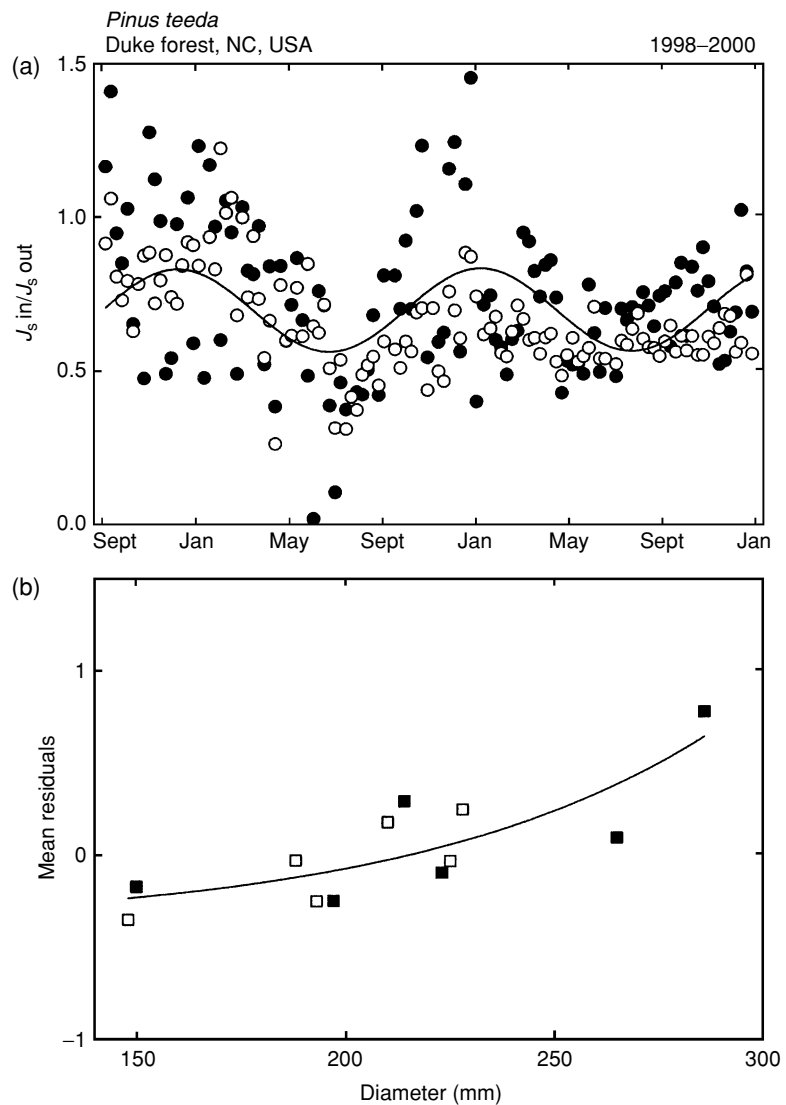


Fig. 1 (a) Seasonal cycle of the ratio of inner to outer sap-flux density for *P. taeda* from September 1998 to December 2000; (b) averaged residuals as a function of tree size obtained by removing the seasonal cycle (shown in a) from the ratio of inner-to-outer sap flux density of each individual tree. Open symbols denote ambient and solid symbols elevated atmospheric CO₂ conditions.

measurements were made at the central tower of plot #1, an CO₂^a plot, 1 m above the canopy with a 3-D sonic anemometer (CSAT3, Campbell Scientific, Logan, Utah, USA) and an infrared gas analyser (LiCor 6262, LICOR, Lincoln, Nebraska, USA). For details on measurement frequency, gap-filling methodology, and data analysis see Lai *et al.* (2000) and Falge *et al.* (2001). Latent heat flux was compared to estimates of transpiration and stand water use averaged for the three plots.

On an annual basis, the local water balance can be used to estimate the residual component R that is not directly measured. In closed systems, water input, output and storage must balance. Thus, :

$$P_0 = I + LE^* + F_O + Q + \Delta S + R^*, \quad (3)$$

Where, P_0 is precipitation, I is evaporation from intercepted precipitation, LE^* is LE measured between rain

events such that I is not entirely included, F_O is overland flow, Q is drainage, and ΔS is the change in soil moisture content (i.e. change in water storage) measured within the soil column between 0 and 30 cm; all expressed in mm. In this balance, R^* represents the sum of lateral flow within the soil and errors (e.g. in estimating I as the difference between P_0 and P_T , not accounting for stem flow). Such a balance can apply only for ambient conditions for which eddy covariance estimate of LE^* was available (plot #1 and surrounding forest), and cannot be used to assess the effect of atmospheric CO₂ on the relative contribution of transpiration to the hydrologic balance. However, Eqn (3) can be rewritten as:

$$P_0 = I + E_C + F_O + Q + DS + R, \quad (4)$$

in which, R includes also litter, soil, and early morning plant surface evaporation and transpiration of species

other than trees, and trees <25 mm in diameter (all captured in LE^* in Eqn 3).

Drainage Q from a plane positioned at the bottom of the 30 cm root zone can be modeled based on the soil moisture at the bottom of the layer and the physical properties of the soil. A two-layer model was constructed to account for differences in soil properties between the upper 35 cm layer and the layer below (Oren *et al.*, 1998a). The model was parameterised from a relationship between Ψ_S and θ after Clapp & Hornberger (1978). Soil physical properties used in the model are given in Table 2. Saturated soil moisture content θ_S is higher in CO_2^e plots reflecting higher organic matter under CO_2^e (Schlesinger & Lichter, 2001). Because θ was measured only as an average for the upper layer, θ at the bottom of the layer was estimated by predicting a vertical profile of θ –50 cm at discrete 1.5 cm intervals. The θ profile was predicted by setting initial conditions of the mean measured θ through the profile on January 1, allowing E_C to remove water from the soil in proportion to the root distribution (Matamala & Schlesinger, 2000) and soil water potential Ψ_S according to Katul *et al.* (1997). This creates a Ψ_S gradient that causes redistribution of moisture within the soil, and may result in water flow into the root zone from below. Throughfall precipitation, excluding overland flow (F_O was set to conditions of $P_T > 3 * K_S$), was also distributed according to Ψ_S gradient. With F_O and Q , thus modeled R can be estimated. If R is small, as has been estimated previously in this stand (Oren *et al.*, 1998a), then the sum of all the measured and calculated

components should not be significantly different from P_0 (Oren *et al.*, 1998b).

Statistical analysis

For calculating budgets, missing data were estimated via regression analysis of a given variable among plots, e.g. air temperature from plot 1 to plot 2, etc., to ensure a continuous data set from June 1997 for the calculations of water balance components. However, statistical analyses of the responses to CO_2 enrichment were made on the original data sets. Analysis was done on daily sums (Q , F_O , E_C , ΔS , J_S) or means (T_{soil} , T_{air} , D , Ψ_S , θ) as a repeated measures ANOVA for $n=3$ treatment pairs. For the purpose of statistical tests, treatment plots were paired by total sapwood area per unit ground area ($A_S:A_G$), composed mostly of *P. taeda*. This resulted in all the three sapwood bands (Eqn 1) being similar in both treatments until 1999 ($P > 0.05$, Table 3), time at which faster diameter growth rate under CO_2^e (DeLucia *et al.*, 1999) produced greater inner $A_S:A_G$ than under CO_2^a (in 1999 $P = 0.054$ and $P = 0.008$ in 2000). Although pairing plots by total sapwood area resulted in a similar *P. taeda* sapwood area in the two treatments, there was 12% greater hardwood $A_S:A_G$ under CO_2^e ($P > 0.35$, Table 3), but this represented only 10% of the total sapwood area $A_S:A_G$ summarised in Table 3. After plot-pairing, the coefficient of variation of $A_S:A_G$ for *P. taeda* within each treatment was smaller (20–25%), than that for the hardwood species, but none showed significant treatment effect ($P > 0.30$). The

Table 2 Soil physical properties for ambient (CO_2^a) and elevated atmospheric CO_2 (CO_2^e) plots used for modeling according to Clapp & Hornberger (1978), where b is an empirical parameter, K_S saturated hydraulic conductivity, Ψ_{Sat} saturated soil water potential and θ_S saturated soil moisture (Oren *et al.* 1998a)

Layer	b	K_S (mm d ⁻¹)	Ψ_{Sat} (cmH ₂ O)	θ_S CO_2^a (m ³ m ⁻³)	θ_S CO_2^e (m ³ m ⁻³)
0–35 cm	2.49	80.0	79	0.54	0.60
35–50 cm	13.70	6.3	79	0.54	0.54

Table 3 Sapwood area per unit ground area ($A_S:A_G$) for ambient (CO_2^a) and elevated atmospheric CO_2 (CO_2^e) measurement plots used for scaling. Values given are means of $n=3$ with SE in parenthesis

	$A_S:A_G$ m ² ha ⁻¹	<i>P. taeda</i>	<i>L. styraciflua</i>	<i>U. alata</i>	<i>C. florida</i>	Other hard-woods	Other conifers	total
1997	CO_2^a	31.5 (3.91)	1.03 (0.40)	0.43 (0.12)	0.22 (0.13)	1.03 (0.50)	0.12 (0.10)	34.4 (3.90)
	CO_2^e	32.0 (5.06)	1.83 (0.63)	0.39 (0.30)	0.11 (0.04)	1.20 (0.33)	0.01 (0.01)	35.5 (4.40)
1998	CO_2^a	32.5 (4.00)	1.12 (0.44)	0.47 (0.13)	0.24 (0.14)	1.12 (0.54)	0.13 (0.11)	35.5 (4.00)
	CO_2^e	33.0 (5.21)	1.99 (0.68)	0.43 (0.32)	0.12 (0.04)	1.29 (0.35)	0.01 (0.01)	36.8 (4.50)
1999	CO_2^a	34.4 (3.99)	1.22 (0.49)	0.50 (0.15)	0.22 (0.15)	1.12 (0.55)	0.14 (0.12)	37.6 (3.90)
	CO_2^e	36.0 (5.35)	2.13 (0.74)	0.47 (0.35)	0.13 (0.05)	1.34 (0.38)	0.01 (0.01)	40.1 (4.60)
2000	CO_2^a	38.0 (4.00)	1.34 (0.52)	0.56 (0.17)	0.24 (0.17)	1.28 (0.62)	0.14 (0.13)	41.6 (3.88)
	CO_2^e	40.0 (6.10)	2.28 (0.79)	0.55 (0.41)	0.14 (0.05)	1.42 (0.47)	0.01 (0.01)	44.4 (5.25)

variation reflected pretreatment conditions (Naidu & DeLucia, 1999). In all, 21% of LE^* measurements, 14% of the measurements of environmental variables, and an average of 19% (10% for the pine during the entire year and 35% for the hardwood data during the growing season) of sap flux data were missing. Statistical analyses were performed using SAS (Version 8.0, Cary, NC, USA) or Sigmaplot (Version 5.0, SPSS Inc. San Rafael, CA, USA).

Results

Environmental conditions

Soil and air temperatures were not significantly different among treatments in any year (Fig. 2a). The same was true for relative humidity (not shown), and thus for the calculated D (Fig. 2b). Soil moisture was significantly higher under CO₂^a in 1997, 1999 and 2000 (repeated measures ANOVA on daily means, $P = 0.0001$), but not in 1998 ($P > 0.05$; Fig. 2c). The difference increased during the course of this experiment from 0.03 m³ m⁻³ in 1997 to 0.08 m³ m⁻³ in 1999 and 0.10 m³ m⁻³ in 2000 relative to. However, the difference in θ between treatments was not reflected in Ψ_s at 15–20 cm depth in 1999 and 2000 ($P > 0.55$, Fig. 2c). This apparent discrepancy is related to the fact that θ was an integrated measure over 30 cm layer that includes the organic horizon, while Ψ_s was measured in the mineral soil, below the zone where most of the fine roots are found (Matamala & Schlesinger, 2000). The impact of the different amounts of organic matter influencing the two measurements will be discussed later.

Large interannual variation was measured in all environmental variables. For example, PPFd increased by 7% from 1998 to 1999 and 2000 being similar to 1999 (Fig. 2d). The corresponding values for P_0 were decreased by 14% followed by a further decrease by 17%. Mean temperatures for the 3 years were 15.4 °C, 14.8 °C, and 13.9 °C.

Sap flux density of individual species

Sap flux density in the outer 0–20 mm xylem of *P. taeda* was similar in both treatments throughout the study, but J_s in the middle xylem band was ~8% higher under CO₂^e in 2000, owing to larger trees in this treatment at that time, and the impact of tree size on sap flux (Fig. 1b). Thus, mean tree J_s was similar in both the treatments during 1997–99, but in 2000 mean tree J_s was greater in CO₂^e than in CO₂^a by 7% ($P = 0.002$; Fig. 3a). Sap-flux density in *L. styraciflua* under CO₂^e progressively decreased relative to the CO₂^a plots, it was 8% lower in 1997 ($P > 0.05$), 18% in 1998, and stabilised at c. 25% in 1999 and 2000 ($P < 0.0001$ in the latter years; Fig. 3b). Sap flux density of *U. alata* was similar in both the treatments in all the years ($P > 0.05$; Fig. 3c).

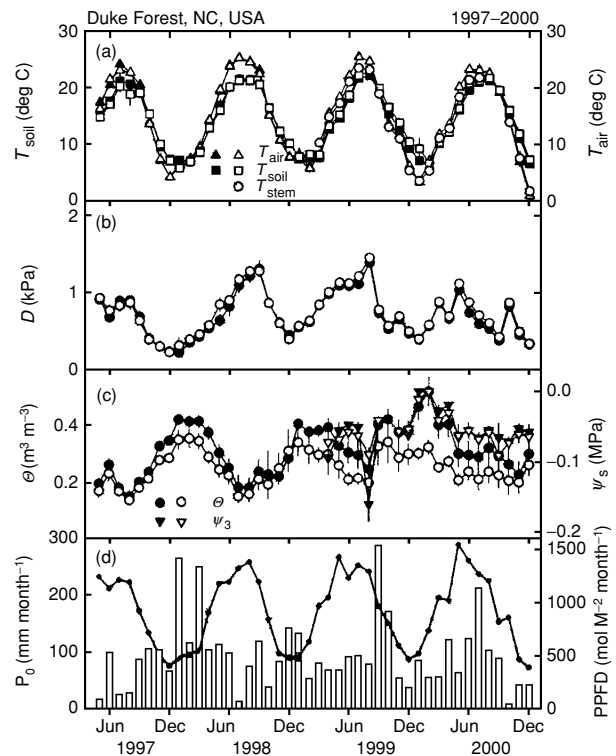


Fig. 2 (a) Monthly average soil temperature (T_{soil} , ■), air temperature (T_{air} , ▲) and stem temperature (T_{stem} , ●) for ambient and elevated CO₂ plots; (b) monthly daytime averaged vapour pressure deficit (D); (c) monthly averaged volumetric soil moisture content (θ , ●) and soil water potential (Ψ_s , ▲); (d) monthly summed precipitation (P_0 , open bars) and monthly sum of photosynthetic photon flux density PPFd (dots). Open symbols denote ambient and solid symbols elevated atmospheric CO₂ conditions (when solid symbols are not seen they are hidden behind open symbols). Vertical bars represent one SE. ($n = 3$).

Scaling sap flux density to canopy transpiration

In only a part of the year 1997 sap flux density was measured (May–Dec), thus, most of our analyses will concentrate on the 1998–2000 period. Seasonally, differences in canopy transpiration between treatments were apparent only during the growing season (April–October; Fig. 4b). In 1997, average daily canopy transpiration was 2.0 (1SE = 0.3; SE = standard error) mm d⁻¹ in the growing season (data not available for April) and 0.6 (1SE = 0.1) mm d⁻¹ in the nongrowing season (data not available for Jan–March). During the following years, repeated measures ANOVA showed that mean daily E_C during the nongrowing season (Nov–Mar) was changed from being higher under CO₂^e in 1998 to being similar in both treatments (Table 4), but that E_C during the growing season changed from being lower under CO₂^e in 1998 to being higher in 2000 (Fig. 4b, Table 4). Evaluating

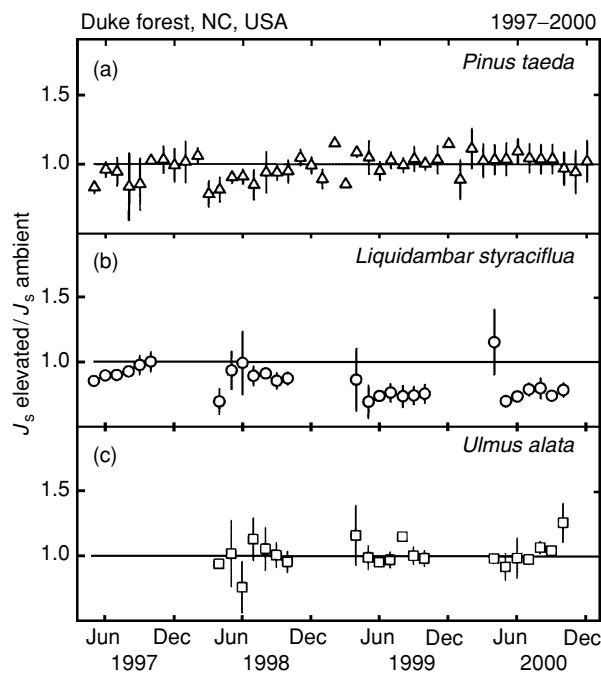


Fig. 3 Ratios of elevated to ambient monthly sap-flux densities and standard errors for $n = 3$ for (a) *Pinus taeda*; (b) *Liquidambar styraciflua*; and (c) *Ulmus alata*. Vertical bars represent one SE ($n = 3$).

separately the contribution of *P. taeda* and the hardwood species to E_C revealed that the pattern described above for the growing season was attributed to the responses of *P. taeda*, which increased in transpiration over the 3 years under CO_2^e more than under CO_2^a . Specifically, E_C of *P. taeda* under CO_2^e was 96% of that under CO_2^a in summer 1998, decreasing further during the dry months of July and August to 88% in compared to CO_2^a ($P = 0.09$), whereas E_C of the hardwoods under CO_2^e was 123% of that under CO_2^a ($P = 0.0001$; data not shown). In 1999, E_C of *P. taeda* was not different among treatments ($P = 0.97$), but hardwood E_C was reduced under CO_2^e to c. 93% of that under CO_2^a causing overall transpiration to be slightly higher under CO_2^e ($P = 0.08$, Table 4). In 2000, growing season E_C of *P. taeda* under CO_2^e was 112% that of CO_2^a ($P < 0.0001$), but hardwood component of E_C was not different between treatments ($P = 0.90$) despite higher $A_S:A_G$ under CO_2^e (Table 3). Although the pattern of flux in the hardwood species opposed that of *P. taeda*, L was dominated by *P. taeda* and the flux pattern of this species dominated E_C .

Hydrologic balance

Leaf area index influences both rainfall interception and canopy transpiration. In order to interpret annual quantities of these hydrologic balance components, we

Table 4 Mean daily canopy transpiration (E_C) for growing and nongrowing season for ambient (CO_2^a) and elevated atmospheric CO_2 (CO_2^e) plots. All units are in mm d^{-1}

Year		CO_2^a	CO_2^e	P -values*
1998	Growing season	1.88 (0.17)	1.88 (0.19)	0.0854
	Nongrowing season	0.86 (0.11)	0.92 (0.09)	0.0053
1999	Growing season	1.91 (0.15)	1.96 (0.15)	0.0848
	Nongrowing season	0.81 (0.10)	0.80 (0.09)	0.0910
2000	Growing season	1.96 (0.16)	2.16 (0.19)	0.0001
	Nongrowing season	0.65 (0.18)	0.69 (0.21)	0.9270

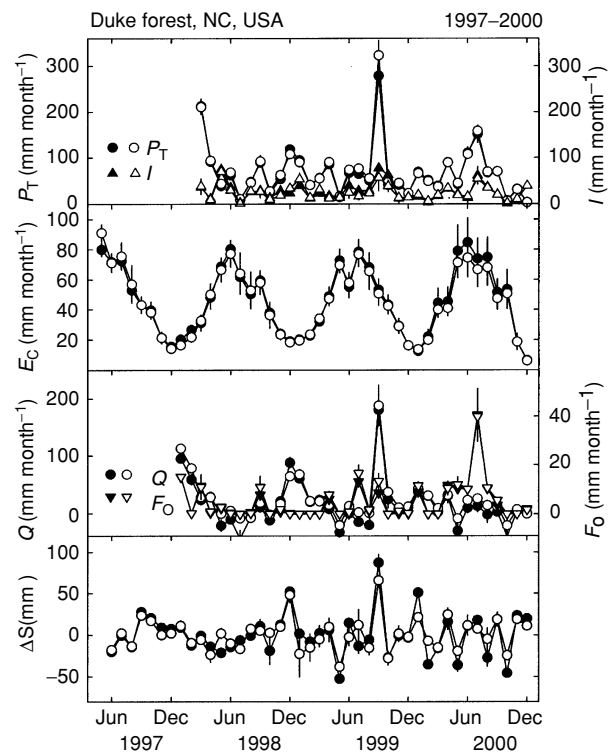


Fig. 4 (a) Monthly sum of precipitation throughfall (P_T , circles) and interception (L , triangles); (b) monthly sum of canopy transpiration (E_C); (c) monthly sum of drainage (Q , circles) and overland flow (F_O); and (d) monthly change in soil water storage in the upper 30 cm of the soil (ΔS). Open symbols denote ambient and solid symbols elevated atmospheric CO_2 conditions. Vertical bars represent one SE ($n = 3$).

proceed by first evaluating the effect of CO_2^e on the annual dynamics of L . From 1998 to 1999 the maximum L (early September in each year) increased significantly under CO_2^e (paired t -test, $P = 0.007$) but not under CO_2^a ($P = 0.179$). Leaf area index increased significantly from 1999 to 2000 in both the treatments ($P < 0.05$). However, L was not different within each year between treatments ($P > 0.4$). Data on L in 1998, and the change in L between 1998 and 2000 are shown in Table 1. The allometrically based

Table 5 Annual hydrological budget for ambient (CO₂^a) and elevated atmospheric CO₂ (CO₂^e) plots. The P_0 is precipitation, I is interception losses, P_T is throughfall precipitation, LE^* is latent heat flux, E_C is canopy transpiration, F_O is overland flow, Q is drainage, ΔS is change in soil water storage, and R is the residual component (see text). The mean ($n=3$ plots) and standard error where available (in parenthesis) and are provided. None of the components in the budget within each year are different between the CO₂ treatments across years ($P > 0.05$) except Q in (1999) ($P = 0.02$)

Year Treatment	1998		1999		2000	
	CO ₂ ^a	CO ₂ ^e	CO ₂ ^a	CO ₂ ^e	CO ₂ ^a	CO ₂ ^e
P_0	1407.2		1213.6		1005.8	
I	376.8	392.7	310.7	368.6	272.3	271.2
P_T	1030.5 (37.3)	1014.5 (6.5)	938.5 (73.4)	859.5 (34.3)	733.5 (41.2)	734.6 (47.4)
LE^*	537.1	–	575.0	–	614.3	–
E_C	518.5 (80.0)	529.0 (23.9)	532.9 (56.4)	541.1 (64.3)	518.5 (75.8)	568.0 (112.8)
F_O	44.0 (7.8)	22.1 (1.5)	42.0 (9.7)	29.4 (3.1)	101.7 (11.7)	97.4 (16.9)
ΔS	22.8 (23.6)	–1.6 (7.1)	37.4 (21.1)	3.0 (8.5)	5.3 (6.2)	–20.5 (1.6)
$Q_{>30\text{ cm}}$	337.6 (36.9)	235.9 (37.4)	369.1 (41.0)	269.2 (55.0)	167.6 (31.2)	58.4 (96.9)
R	107.0 (23.5)	211.0 (34.8)	31.9 (88.8)	16.8 (17.5)	–59.6 (68.8)	31.3 (20.9)

estimate of L showed a 7% lower ($P = 0.48$) value than those from canopy gap fraction (LAI2000, LiCor, Lincoln Nebraska; Ellsworth unpublished) without a CO₂ effect in either 1997 or 2000 ($P > 0.1$). The slightly higher values based on the gap fraction method can be attributed to stems and branches, as has been shown in similar forests (Smolander & Stenberg, 1996; Pataki *et al.*, 1998).

Precipitation throughfall (P_T) was similar in both the treatments in each year both seasonally (Fig. 4a) and annually (Table 5), resulting in similar interception losses (I) (Fig. 4a, Table 5). The modeled F_O , Q from the bottom of the root zone (set to 30 cm depth; Fig. 4c), and the calculated ΔS in the root zone (Fig. 4d) were also similar (except for Q in 1999), reflecting the similarity between treatments in P_T and E_C on an annual basis ($P > 0.05$; Table 5).

Total canopy transpiration of the CO₂^a plots was similar to the latent heat flux measured with eddy covariance in months of $LE^* \leq 60$ mm, but departed from a linear relationship such that during months with highest LE^* , $E_C/LE^* = 0.75$ (Fig. 5; $P < 0.0001$, for a second degree polynomial least square regression). Combining E_C with interception losses increased the variability in the relationship with LE^* (a linear fit, $r^2 = 0.36$; $P < 0.0001$), but resulted in that during the growing season $LE^* \approx E_C + I$, indicating that eddy covariance estimates of LE^* accounted for most of the interception losses during the summer. In winter, when I dominates evapotranspiration, LE^* is approximately half of $E_C + I$.

Discussion

We evaluated the responses of maturing *P. taeda* stand, including its minor hardwood component, to the first

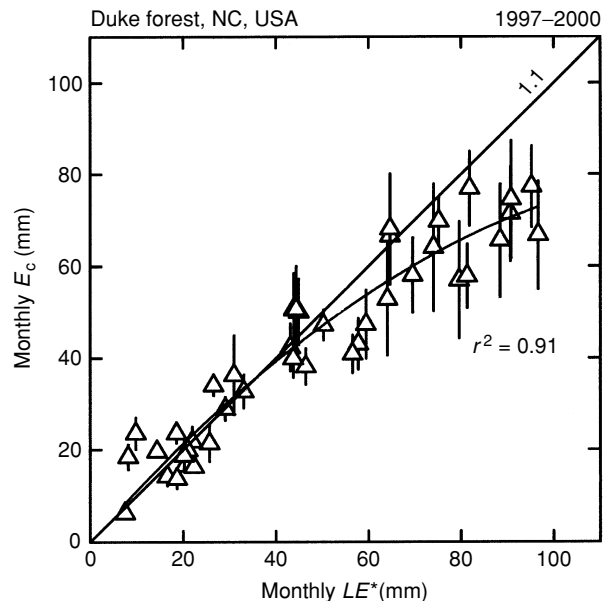


Fig. 5 Comparison of canopy transpiration (E_C) under ambient conditions with latent heat flux (LE^*) above the canopy. The one-to-one line is also shown. Vertical bars represent one SE ($n = 3$).

3.5 years of CO₂ enrichment both in terms of a reduction in transpiration owing to stomatal closure, and increase in transpiration owing to increasing leaf area index with increasing carbohydrate availability. We found some evidence of stomatal closure in *L. styraciflua*, but not in *P. taeda* or *U. alata*. In fact, by the end of the study, *P. taeda* transpired more per unit of leaf area under CO₂^e, probably as a result of increasing soil moisture availability. We have found no evidence of increasing L . The increase in leaf level transpiration of the dominant *P.*

taeda exerted the main effect of CO₂^e on the hydrology of this forest.

Evaluation of the hypothetical responses

Conceptually, stomatal closure under CO₂^e in canopies with high boundary layer conductance would save water (i.e. reduce transpiration per unit of leaf area, E_L , and thus E_C), and where water availability limits maximum canopy leaf area, leaf area index may increase to a new steady-state value (Woodward, 1990; Fig. 6a). In canopies that are less well-coupled to the atmosphere (i.e. with high aerodynamic resistance) a number of feedback processes may compensate for reductions in stomatal conductance, maintaining evapotranspiration relatively unaltered (Jarvis & McNaughton, 1986; Jacobs & DeBruin, 1997). In several experiments in agricultural crops based on models and measurements, large reductions in stomatal conductance under CO₂^e translated to small or insignificant decreases in evapotranspiration (Cure & Acock, 1986; Dugas *et al.*, 1994; Carlson & Bunce, 1996; Bunce *et al.*, 1997; Wilson *et al.*, 1999). In contrast, in well-coupled canopies, stomatal closure in response to CO₂^e translates to a reduction in E_C , as was found in a beech model ecosystem despite an increase in L (Overdieck & Forstreuther, 1994), and in a *L. styraciflua* stand (by 12%, Wullschlegel & Norby, 2001). We note that aerodynamic resistance is low in *P. taeda* forests (Ewers & Oren, 2000). This was evident in the similarity of D in all plots during the study despite the range in L (from 4.7 to 6.1 among plots), and of particular relevance to evaluating the conceptual model, in the similarity of D between the CO₂ treatments (Fig. 2b). In addition, *P. taeda* maintains leaf temperature similar to air temperature over a wide range of environmental conditions and stand leaf area index (Ewers & Oren, 2000). As a result, in *P. taeda*, stomatal closure should translate to savings of water. Given that leaf to sapwood area ratio is not changing under CO₂^e (Pataki *et al.*, 1998; Gielen *et al.*, 2001; Norby *et al.*, 2001), a reduction in stomatal conductance would be reflected in a lower sap flux density. Ultimately, it is expected that the forest would reach a new steady state when the increment in L under CO₂^e uses the saved water in a somewhat recovered transpiration and higher rainfall interception.

We evaluated stomatal response in terms of sap flux density under CO₂^e relative to the sap flux density under CO₂^a (Fig. 3). Although 1998 was the wettest year in the study period, precipitation during the growing season was about half of that in the following 2 years. In *P. taeda*, the only continuous period in which the flux in trees under CO₂^e was lower relative to CO₂^a was during the drought period of 1998 (Figs 2c and 3a). Thus, it appears that *P. taeda* growing under CO₂^e becomes

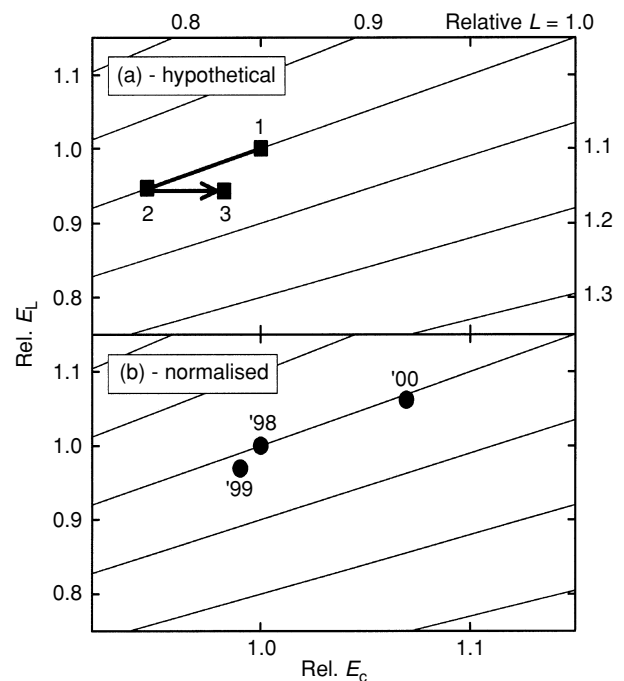


Fig. 6 (a) Hypothetical and (b) Normalised response of relative canopy transpiration (E_C) to elevated atmospheric CO₂ concentration in relation to canopy transpiration per unit leaf area (E_L). Diagonal lines show relative leaf area index (L) for elevated vs. ambient. In (a), 1 represents steady-state conditions before atmospheric CO₂ is increased, 2 represents the outcome of immediate decrease in stomatal conductance to elevated CO₂, and 3 represents the new steady-state conditions under elevated CO₂ based on the assumption that rainfall interception increased with L .

more sensitive to decreasing soil moisture. However, because such conditions do not prevail, lower sap flux under CO₂^e was rarely apparent (Fig. 3a), and sap flux for the entire year was not different between treatments, consistent with the findings from porometric measurements of stomatal conductance at this site (Ellsworth, 1999). Furthermore, progressively during the study, sap flux of *P. taeda* under CO₂^e became greater relative to that under CO₂^a; this behaviour will be discussed later. *U. alata* behaved similarly to *P. taeda*, but a inter annual pattern in the ratio is apparent for *L. styraciflua*. Small changes in bud break and bud set phenology of *U. alata* under CO₂^e could produce similar patterns as seen at the beginning and end of the growing season (Fig. 3).

In contrast to *P. taeda*, which showed an inter annually increasing sap flux density under CO₂^e relative to CO₂^a, *L. styraciflua* showed a progressive decline in the ratio, stabilising at *c.* 25% lower flux under CO₂^e (Fig. 3b). In the nearby companion study conducted at an earlier stage of canopy development, two other subcanopy species showed a progressive decline in sap flux as understory

light decreased from 65% to 41% of full sunlight (Phillips & Oren, 2001). However, at the same time, flux in the fast growing *L. styraciflua* increased over time, as it became dominant along with *P. taeda*. Faster canopy closure by *P. taeda* under CO₂^e in this study could have caused the observed pattern. However, such a process should have affected *U. alata*, a smaller stature subcanopy species, even more. Leaf area index at the beginning of this study allowed ~22% of sunlight to reach the understory, and the increase in *L* over the duration of the study reduced it to 14%, a change that is probably too small to impel a discernible effect on *U. alata*'s sap flux. Furthermore, observations in the canopy of the study plots detected no apparent discrepancy in the canopy position of *L. styraciflua* in the two treatments. Thus, the interannual pattern in flux seen for *L. styraciflua* (Fig. 3b) may have its origin not associated with canopy development.

The pattern in flux seen for *L. styraciflua* might have been caused by several linked physiological responses to CO₂^e: a progressively increasing vulnerability to cavitation in the branch xylem of *L. styraciflua* (Schäfer, unpublished data) could have reduced leaf-specific hydraulic conductivity, resulting in a reduction in stomatal conductance. A reduction in stomatal conductance of *L. styraciflua* has been shown to vary in FACE experiments from 7% (Herrick *et al.*, 2001) to 24% (Gunderson & Sholtis, 2001). A 13% reduction in sap velocity of *L. styraciflua* during the second year of enrichment in a FACE study was recently reported (Wullschleger & Norby, 2001) similar to the 18% found here for the second year. Assuming that leaf-to-sapwood area ratio was unaffected by CO₂^e, the reduced flux ratio in this study would translate to 25% lower mean canopy stomatal conductance (Granier & Bréda, 1996; Granier *et al.*, 1996) reducing the potential benefit from growing under CO₂^e. Indeed, *L. styraciflua* in our stand did not show a CO₂-induced growth enhancement, while the growth of *U. alata* and *P. taeda*, for both of which stomata did not respond to CO₂^e, was stimulated (DeLucia *et al.*, 1999; Naidu & DeLucia, 1999). The lower transpiration under CO₂^e in *L. styraciflua* dominated forests may lead to water savings and ultimate increase in *L*. Thus, expected effects of CO₂^e on the hydrologic balance in forests under enriched atmosphere in the future (Henderson-Sellers *et al.*, 1995) appears highly dependent on species composition.

Responses of leaf area index

Leaf area index was unaffected by CO₂^e although it increased over the duration of the experiment (Table 1). This finding appears contradictory to another in this experiment, showing a greater increase in interception losses under CO₂^e over 2.5 years of enrichment,

presumably owing to the increase in *L* (Lichter *et al.* 2000). We failed to detect such a pattern over 3.5 years of enrichment (Fig. 4a; Table 5). To reconcile the contradictory results, we used the relatively large seasonal variations in *L* and the increase in *L* from the start of the study to assess how much signature of changing *L* is noticeable in the interception losses. We searched for the signature of *L* in the pattern of interception by:

- 1 analysing, in each year, the proportion of precipitation intercepted at the beginning of the growing season and in September when *L* increases by a factor of 2.3, using the amount of precipitation in each event as a covariant,
- 2 as in (1) but accounting for air temperature as well, as an index of energy available for evaporation during rain events, and
- 3 analysing the long-term change in the proportion of precipitation intercepted with long-term increase in *L* (30% from 1998 to 2000).

None of the analyses supported a significant effect of the changes in *L* on interception. These findings are consistent with those from recent studies in *Pseudotsuga menziesii* (Mirb.) stands, in which *L* was reduced by a third through thinning with no effect on interception (Van Wijk *et al.*, 2001), and in *P. taeda* stands in which a 50% decrease in *L* reduced *I* by only 10% (Stogsdill *et al.*, 1989). Thus, measurements of throughfall can reveal only large differences among treatments, differences beyond any expected in response to CO₂^e in this stand.

Because photosynthetic rate and biomass production was higher under CO₂^e (DeLucia *et al.*, 1999; Ellsworth, 1999), the absence of response in *L* indicates that carbohydrates were not limiting the development of *L*. Could the fact that *L* was not higher under CO₂^e despite having more soil water (Fig. 2c) mean that water too was not limiting the development of *L* at this site? Evidence for water limitation to growth was apparent in a nearby study in the same stand. In that study, wood production in both CO₂ treatments increased slightly from 1998 to 1999, and appreciably from 1999 to 2000 (Oren *et al.*, 2001), mimicking the pattern found in increment of *L* in this study (data not shown), even though *P_T* decreased from year-to-year during the same period. In this site, limited rooting depth (<30 cm) permits little water storage within the reach of roots, and results in a rapid decline of stomatal conductance as soil moisture decreases below *c.* 0.20 m³ m⁻³ (Oren *et al.*, 1998a). The greater growth in 2000 despite lower *P_T* was owing to a better distribution of rainfall during the growing season, which is reflected in higher soil moisture during that year (Fig. 2c), and a continuous wood increment, as opposed to mid-season pause in increment during a long dry spell in 1999 (Oren

et al. 2001). Thus, it appears that the annual increase in leaf area at this stand was at least partially limited by water availability.

That CO₂^e plots did not display higher *L* (Fig. 6b), despite having consistently higher soil moisture (Fig. 2b) may reflect the quality of the site, the species involved, and the stage of development of this stand when enrichment commenced. In other studies using the FACE approach, *L. styraciflua* and three *Populus* genotypes showed no difference in *L* among treatments after canopy closure (Gielen *et al.*, 2001; Norby *et al.*, 2001). A number of studies in areas with both high and low precipitation show that site nutrient availability may limit *L* more than water (Bergh *et al.*, 1999; Ewers *et al.*, 2000). On high quality sites, or fertilised sites with ample water, *P. taeda* stands can support *L* reaching ~7 (Vose & Allen, 1988), owing the relatively low potential *L* under such favourable conditions to the shade intolerant nature of this species. On moderately poor fertility sites, such as the site in this study, *L* in *P. taeda* stands may only reach ~5 (Vose, 1988). The effect of CO₂ on *L* in our stand might have been curtailed because the stand was nearing its maximum *L* when the experiment begun, allowing relatively small increases since that time (on average from ~3.7 in 1998 to 4.9 in 2000). Thus, in addition to forests that do not suffer from moisture limitations, forests on sites with limited fertility (Norby *et al.*, 1999), and forests composed of species with low shade tolerance are not likely to follow the hypothetical response to CO₂^e (Fig. 6a).

Evidence for indirect effect of CO₂ on transpiration

The overall response of the forest to CO₂^e reflected the responses of *P. taeda* that dominated the stand. The measured responses of the stand *E_L* to CO₂ were quite different from the hypothetical responses (Fig. 6a). However, the measured responses reflect not only the effect of CO₂ enrichment but also the variation in weather. On an annual basis, 1999 was somewhat cooler (lower mean annual *D*, Fig. 2b) and drier than 1998, yet both *L* and mean annual *E_L* increased slightly from 1998 to 1999. Thus, although annual *P_T* decreased, *E_C* increased in both the treatments (Table 5). In 2000, further decline in *P_T* was associated with a large increase in *L* that was similar in both the treatments, but both showed large reductions in *E_L*. The combined effect of these changes was an *E_C* in 2000 similar to that in 1998 under CO₂^a, but 7% higher under CO₂^e.

We attempted to account for the climatic variation, especially as reflected in precipitation, by removing the responses under CO₂^a from those under CO₂^e (i.e. normalising the responses under CO₂^e by those under CO₂^a), and normalising again by the value of 1998 (Fig. 6b). This allows evaluating the temporal responses

of the pine forest to increased atmospheric CO₂ alone. The adjusted response shows intriguing departures from the hypothetical. In the hypothetical response, immediate stomatal closure under CO₂^e would have brought the forest to position 2 (Fig. 6a). Our complete annual data begins in 1998, 1.5 years after the commencement of CO₂ enrichment so our stand should be well on the way from position 2–3. However, after removing environmental differences between years, *E_L* and *L*, and thus *E_C* are similar in 1998 and 1999. This may be taken as an indication that our stand has already reached position 3 by 1998. However, the hypothetical increase in *E_C* (change from position 2–3) is entirely dependent on a proportional increase in *L*, yet *L* increased 13% less in 1997 under CO₂^e than under CO₂^a, and it is unlikely that the forest completed its response to increasing atmospheric CO₂ in the few months of enrichment in 1996. Thus, it is more likely that, in terms of the three variables in Fig. 6, the forest did not respond to CO₂^e until 2000.

Several factors could affect *E_L* differently under CO₂^e vs. CO₂^a, including (i) an increase in mean stand height which reduces canopy conductance (Schäfer *et al.* 2000), and (ii) an increase in leaf area (Fig. 6b) that was not matched by the increase in fine root surface area (Matamala & Schlesinger, 2000), causing a reduction in root-to-leaf area ratio as was also previously observed elsewhere (Norby *et al.*, 1986; Idso & Kimball 1992; Norby *et al.*, 1992; Pregitzer *et al.*, 1995; Arnone, 1997), and thus leaf specific conductivity (Sperry *et al.*, 1998) and canopy conductance (Hacke *et al.*, 2000). However, both the explanations should cause a 'reduction' in *E_L*, and thus *E_C*, in CO₂^e relative to CO₂^a, in contrast to the findings shown in Fig. 6(b). Other factors that influence *E_L* include both *D* and water availability. The *D* was similar in both the treatments, but soil moisture progressively increased under CO₂^e vs. CO₂^a (Fig. 2c). In 2000, under CO₂^a soil moisture was below the level that limits stomatal conductance (0.20 m³ m⁻³; Oren *et al.*, 1998a) 18% of the time, but only 3% of the time under CO₂^e. Higher availability of soil moisture can support a greater stomatal conductance permitting higher *E_L* and *E_C*.

Following we assess the potential causes for increasing soil moisture under relative to using a local water balance (Oren *et al.*, 1998a).

Hydrologic balance and soil moisture

Comparison of monthly amounts of *LE** above the forest with *E_C* derived from sap-flux measurements in the three CO₂^a plots (Fig. 5) shows a great similarity between the two estimates up to c. 60 mm month⁻¹. Latent heat flux continues to increase linearly as radiation increases (not shown), but *E_C* increased progressively more slowly, reflecting the effect of stomatal closure under

high evaporative demand (Oren *et al.*, 1999). At the month with highest LE^* , E_C accounted for 75% of LE^* , similar to earlier values at this site several years earlier (c. 70%, Oren *et al.*, 1998a,b; Phillips & Oren, 2001). Over the 3 years, E_C accounted for 91% of LE^* with no discernible pattern among years. Annually, the sum of E_C and I exceeded LE^* from 29% to 66%, showing no indication of underestimation of scaled sap flux reported elsewhere (Wilson *et al.*, 2001). We did not measure stem flow and soil evaporation. An estimate of stem flow yielded c. 112, 97 and 81 mm y^{-1} for the 3 years (after Waring & Schlesinger, 1985), amounts similar to those expected from soil evaporation, ranging in forests from 10 to 14% of total evapotranspiration (Wedler *et al.*, 1996; Constantin *et al.*, 1999). Although we assume in our hydrologic budget that these two processes approximately balance each other and can be ignored, a likely decrease in soil evaporation owing to litter accumulation under CO₂^e will make this assumption somewhat incorrect for this treatment, and the decrease in evaporation should be reflected in increasing soil moisture in CO₂^e relative to CO₂^a plots, as seen in Fig. 2(c).

The hydrological budget was not balanced in 1998, in that the sum of all components was 14% less than precipitation ($P < 0.05$, Sokal & Rohlf, 1995); the budget was balanced for the following 2 years. Although annual precipitation decreased over the study period, E_C was maintained or increased, resulting in increasing proportion of P_T used for transpiration and decreasing proportion used for overland flow and drainage, without discernible differences between CO₂^a and CO₂^e treatments.

Drainage estimates were similar to those previously reported for piedmont *P. taeda* plantations (Amatya *et al.* 1996), and consistent with estimates in this forest stand (Oren *et al.*, 1998a). The poorly drained soil, with a relatively low permeability, resulted in a significant overland flow (Table 5). Furthermore, the very low saturated conductivity of the layer below the rooting zone (c. 35 cm) should cause lateral flow within the soil. The initial difference in soil moisture, averaging in 1998 0.29 m³ m⁻³ in the upper 30 cm under CO₂^e vs. 0.26 m³ m⁻³ under CO₂^a, could be explained by water flow pattern in the site. Soil moisture was higher in CO₂^e plots even before the treatment commenced in 1996, as has recently been verified in a comparison of soil cores taken adjacent to the plots (McLain *et al.*, in press). Despite the relative flatness of the site (~5% slope), topographic convergence index (Urban *et al.*, 2000) showed that because of their position in the terrain, water is likely to move out of two of the CO₂^a plots, and converge in two of the CO₂^e plots. This however, could not explain the 'increase' over the 3.5 years in soil moisture difference between CO₂^e and CO₂^a.

Increased soil moisture was also found in a calcareous grassland where, after 3 years of exposure to CO₂, increased litter production resulted in greater soil organic matter content and thus, higher soil water holding capacity (Niklaus *et al.*, 1998). However, the slight increase in soil organic matter, partially from higher root and leaf litter produced under CO₂^a (Finzi *et al.*, 2001; Matamala & Schlesinger, 2000; Schlesinger & Lichter 2001), was insufficient to have an effect on soil moisture holding capacity in the CO₂ enriched rings. A 1% increase in soil organic matter is needed to increase soil water holding capacity by ~5% (Kern, 1995), but the increase in soil carbon under CO₂^e was only 0.28% (Schlesinger & Lichter, 2001).

Soil moisture difference between the treatments increased over the study period, resulting in, that in 2000, average soil moisture was 0.34 m³ m⁻³ under CO₂^e vs. 0.24 m³ m⁻³ under CO₂^a. The increase in the difference may reflect a greater reduction in water loss through evaporation from the soil surface of the CO₂^e plots. Soil surface evaporation is reduced with increasing depth of the litter layer (Baldocchi *et al.*, 2000). In this study, only 21 mm reduction is annual soil surface evaporation would produce the observed differences in soil moisture. Over the course of the study, litter accumulated faster under CO₂^e, amassing 526 gm⁻² (29%) more litter under CO₂^e relative to CO₂^a by 1999 (Schlesinger & Lichter, 2001). The increase in litterfall under CO₂^e without an increase in L indicates a decrease in leaf longevity, as has been found in studies on both coniferous and broadleaf species (Ceulemans & Mousseau, 1994; Saxe *et al.*, 1998; Jach & Ceulemans, 1999; Gielen *et al.*, 2001). More litter accumulation coupled with a lateral water flow preferentially into CO₂^e plots and away from CO₂^a plots, are the likely cause for the observed progressive increase in θ in CO₂^e relative to CO₂^a plots (Fig. 2c).

Conclusion

The increase seen in transpiration from 1999 to 2000 is intriguing, and may reflect a secondary effect of CO₂^e. During this period, the relative change in L was barely detectable, so the large increase in E_C (7%) was mostly owing to a similar increase in E_L , again not according to the hypothetical response that is based on the direct effect of CO₂ on stomatal conductance. Although we have found no evidence of direct effect of CO₂^e on water savings by the canopy on an annual basis, soil moisture in the rooting zone was higher in plots subjected to CO₂^e conditions, and the difference between CO₂^a and CO₂^e plots increased over time (Fig. 2b). A supply of water through lateral flow to plots under CO₂^e, combined with a greater accumulation of litter on the forest floor (Finzi *et al.*, 2001; Schlesinger & Lichter, 2001), produced the most apparent and consistent response to CO₂^e – an

increase in soil moisture. Thus, it appears that future forests with similar characteristics to that investigated here will transpire more as a result of indirect effect of CO₂^e causing more litter accumulation and less evaporation, rather than transpire less owing to the direct effect causing stomatal closure. Furthermore, this increase in soil moisture has important implication to gas exchange between the soil and atmosphere, reducing CO₂ efflux from (Suwa *et al.* in press) and methane influx to (McLain *et al.*, in press) the forest floor.

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