Oecologia (1998) 117:47–52

Diane E. Pataki, Ram Oren, David T. Tissue

Elevated carbon dioxide does not affect average canopy stomatal conductance of *Pinus taeda* L.

Received: 13 March 1998 / Accepted: 8 July 1998

Abstract While photosynthetic responses of C_3 plants to elevated CO_2 are fairly well documented, whole-plant water use under such conditions has been less intensively studied. Woody species, in particular, have exhibited highly variable stomatal responses to high CO_2 as determined by leaf-level measurements. In this study, sap flux of *Pinus taeda* L. saplings was periodically monitored during the 4th year of an open-top chamber CO_2 fumigation experiment. Water use per unit sapwood area did not differ between treatments. Furthermore, the ratio of leaf area to sapwood area did not change under high CO_2, so that average canopy stomatal conductance (on a unit leaf area basis) remained unaffected by the CO_2 treatment. Thus, the only effect of high CO_2 was to increase whole-plant water use by increasing sapling leaf area and associated conducting sapwood area. Such an effect may not directly translate to forest-level responses as the feedback effects of higher leaf area at the canopy scale cannot be incorporated in a chamber study. These feedbacks include the potential effect of higher leaf area index on rainfall and light interception, both of which may reduce average stomatal conductance in intact forest canopies.

Key words *Pinus taeda* · Stomatal conductance · Elevated CO_2 · Whole-plant water use

Introduction

As atmospheric partial pressures of CO_2 increase, the effects of elevated CO_2 on terrestrial vegetation have become of interest. While a majority of studies have found increases in photosynthetic rates in C_3 plants under elevated CO_2, particularly when resources are abundant (Eamus and Jarvis 1989; Mousseau and Saugier 1992; Ceulemans and Mousseau 1994), responses of stomatal conductance (g_s), and therefore water use, have been considerably more variable (Eamus and Jarvis 1989; Field et al. 1995).

As stomatal aperture is moderated in part by substomatal partial pressures of CO_2 (Mott 1988), reductions in g_s that increase water use efficiency (WUE) under high CO_2 have been hypothesized, and this effect has been observed in many studies (Morison and Gifford 1984). However, recent reviews suggest that the magnitude of the response of woody species may be far less than that of herbaceous crops (Curtis 1996). Among tree species, responses are highly variable. In a review of the responses of g_s to high CO_2 in 23 tree species, Field et al. (1995) found a mean 23% decrease across all studies. However, individual responses ranged from a 36% increase in g_s in *Liriodendron tulipfera* seedlings (Norby and O'Neill 1991) to an 87% decrease in *Cecropia obtusifolia* seedlings (Reekie and Bazzaz 1989).

As photosynthetic responses to CO_2 are generally greater in deciduous than conifer species (Ceulemans and Mousseau 1994; Guehl et al. 1994), a similar trend may be expected for responses of g_s. In fact, there is preliminary evidence that this is the case (Tolley and Strain 1985; Picon et al. 1996; Saxe et al. 1998). However, for all functional groups, existing data have been primarily collected at the leaf level, so that water-use responses of whole crowns to elevated CO_2 are generally not known (Ceulemans and Mousseau 1994). Sap flow studies of crop species crowns have heretofore found small or no CO_2 effects on a whole plant or ground area basis (Dugas et al. 1994; Senock et al. 1996). As increases in leaf area and reductions in g_s have been reported for the same species (Akita and Moss 1972; Morison and Gifford 1984; Bhattacharya et al. 1994), sap flow presumably incorporated compensatory changes in both parameters. However, in the absence of

D.E. Pataki (✉)[1] · R. Oren
Nicholas School of the Environment, Duke University,
Durham, NC 27708, USA

Present address:
[1]Desert Research Institute, P.O. Box 19040,
Las Vegas, NV 89132, USA
Fax: +1-702-8950427, Tel.: +1-702-8950481, e-mail: dep@dri.edu

D.T. Tissue
Department of Biological Sciences, Texas Tech University,
Lubbock, TX 79409, USA

concurrent measurements of leaf area, sap flow measurements alone may provide information on the effects of CO_2 on whole-canopy fluxes, but not on associated physiological mechanisms.

In this study, rates of water flux per unit active sapwood area (J_s, g H_2O cm^{-2} sapwood day^{-1}) were periodically monitored in loblolly pine (*Pinus taeda* L.) saplings with constant heat sap flow gauges (Granier 1987). Saplings were grown under ambient or elevated CO_2 (+30 Pa) during a 4-year experiment to determine the long-term effects of elevated CO_2 on carbon assimilation and water use in this common southeastern species. Based on previous work on leaf-level stomatal conductance (g_s) in *P. taeda*, (Tolley and Strain 1985; Ellsworth et al. 1995) we hypothesized that reductions in whole-canopy stomatal conductance (G_s) would be minimal under elevated CO_2. Therefore, changes in J_s would not be detected unless elevated CO_2 altered the ratio of leaf area (A_l) to cross sectional-sapwood area (A_s). However, as saplings grown under high CO_2 were significantly larger (Tissue et al. 1997), we hypothesized that whole-tree water use, estimated as the product of $J_s$and A_s, would be greater in the elevated CO_2 treatment.

Materials and methods

Experimental design

The study was conducted in open-top chambers in the Durham Division of the Duke Forest, North Carolina. The chambers were planted with 1-month-old seedlings of *P. taeda* in May 1992, as described previously by Tissue et al. (1997). Briefly, seedlings were germinated and grown in the Duke University phytotron at ambient or +30 Pa CO_2 concentrations before transplant into six 3 m × 3 m tall cylindrical open-top chambers supplied with standardized soil mixtures of native clay: topsoil: sand at 1:1:1 v/v to 1 m depth. Three chambers were supplied with ambient air, and three received ambient +30 Pa CO_2. Each plot initially contained 24 seedlings, growing at ambient light, temperature, and soil moisture conditions. During the 4-year study, two seedlings from each treatment were harvested during nine harvest periods for biomass measurements. As seedlings grew, chambers were increased in height.

Sap flow measurements

In the last year of the study, two saplings from each chamber treatment were chosen for sap flux monitoring. Granier-type sap flow gauges were installed after Granier (1987) and Oren et al. (1998). Gauges were 2 cm in length and placed at approximately 0.5 m. Each gauge was carefully insulated to prevent radial heat loss due to small stem diameters (5–9 cm in November 1994). Sap flux measurements were logged on a datalogger (DL2, Delta-T Devices Ltd., Cambridge, UK) at 30-s intervals, averaging every 30 min. In November 1994, trees used in sap flux measurements were harvested, and biomass, including leaf area, were determined. Leaf area values used to calculate canopy stomatal conductance per unit leaf (G_s) after Pataki et al. (1998) are on an all-sided needle area basis as described in Tissue et al. (1997). Sap flux was used to calculate G_s with an inverted form of the Penman-Monteith equation, assuming large aerodynamic conductance as a result of chamber wind speed (>1 m s^{-1}):

$$G_s = \frac{\gamma \lambda J_s A_s}{\rho c_p D A_l}$$

where A_l is leaf area (m^2), γ is the psychrometric constant (kPa K^{-1}), λ is the latent heat of vaporization (J kg^{-1}), ρ is the density of moist air (kg m^{-3}), c_p is the volumetric heat capacity of moist air (J kg^{-1} K^{-1}), D is the vapor pressure deficit (kPa), and A_s is sapwood area (m^2), which for the diameter range in this study is equal to the cross-sectional stem area inside bark (Monteith and Unsworth 1990). Values for ambient daily D were calculated from a temperature and relative humidity sensor (Vaisala HMP 35C, Campbell Scientific Inc., Logan, Utah, USA) located in the canopy of a nearby pine plantation in Duke Forest. Maximum differences between ambient and chamber temperatures were found to be less than 1.5°C during autumn and winter (Tissue et al. 1997).

Following the harvest period, sap flow gauges were moved to two other saplings in each chamber treatment. In January 1995 these saplings were harvested for biomass determination, and sap flow gauges were moved to the two remaining saplings in each treatment. These saplings were harvested at the conclusion of the study in November 1995, after four growing seasons of continuous CO_2 enrichment.

Statistical analyses

We chose sap flux measurement intervals between each harvest period when signals were free of electrical interference, thermal stem gradients, or other sensor malfunctions. These dates were 5–6 November 1994, 1 January 1995, and 3–20 September 1995. Treatment effects on water use during these intervals were evaluated with several statistical methods. A multivariate ANOVA (Proc MANOVA, SAS software, SAS Institute Inc., Carey, N.C., USA) was used to detect effects across intervals, with daily sap flux averaged for each chamber within each interval. During the last interval, sap flux measurements were available from three ambient chambers and two CO_2 chambers. Therefore, treatment effects during this period were tested with a three-way nested ANOVA (Proc GLM, SAS software) with CO_2 level, chamber replicate nested within CO_2 level, and day as a repeated measure as effects. Sap flux values were daily chamber means. To ensure that small sample size was not obscuring treatment effects, the analysis was repeated with pseudo-replication, maintaining individual tree values as replicates rather than chamber averages.

Results

No treatment effect of elevated CO_2 on water use was found with any statistical method, including the analysis with pseudo-replication ($P > 0.05$). Figure 1 shows mean daily J_s in each measurement period for ambient and elevated CO_2. Although J_s was not different for each period, or for all periods combined, percentage differences from ambient are shown. No consistent trend in J_s differences was found, nor did time of day affect J_s differences, as shown in a representative diurnal pattern given in Fig. 2. It should be noted that some variability across measurement periods may be attributed to the use of different individual trees in each period. In the second period, the flux was actually greater under elevated CO_2 (Fig. 1), although this effect was not statistically significant ($P > 0.05$). This harvest period was the only one in which A_l and A_s of the sample trees were not affected by CO_2 (Table 1).

To calculate A_l/A_s, all-sided leaf area was regressed against basal area for each measurement period to obtain the A_l/A_s values given in Table 1. The intercepts of these models were not different from zero ($P > 0.05$), so that regression models were driven through the origin. The residual sum of squares (RSS) of these models, which combined both treatments, was then tested against the RSS of models which included treatment level as a categorical variable (Weisberg 1985). No treatment differences in the relationships were found for any measurement period ($P > 0.05$), although differences in absolute values between measurement periods were evident (Table 1). This reflected seasonal changes in leaf area, with low winter leaf area occurring during the second measurement period in January 1995.

Daily canopy stomatal conductance was calculated with Eq. 1 to illustrate treatment effects on stomatal behavior. During the last measurement period 12 days without precipitation were chosen to evaluate the potential interacting effects of increasing soil drought and elevated CO_2 concentration. The pattern of G_s for ambient- and elevated-CO_2 treatments during this period is

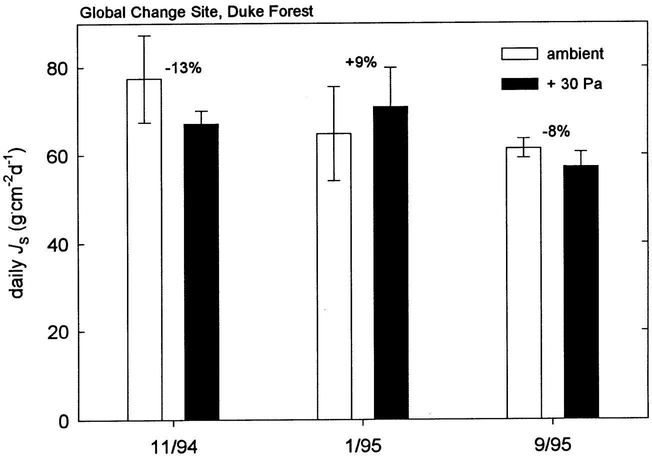

Fig. 1 Daily sap flux (J_s, g cm^{-2} sapwood s^{-1}) for ambient and elevated CO_2 (+30 Pa) treatments is shown during three measurement periods. Percent changes from ambient are given, although treatment means for each period are not different ($P > 0.05$). *Error bars* represent the standard error of the mean. The sample size is three chambers for each treatment, with the exception of the last measurement period, when two elevated-CO_2 chambers were available

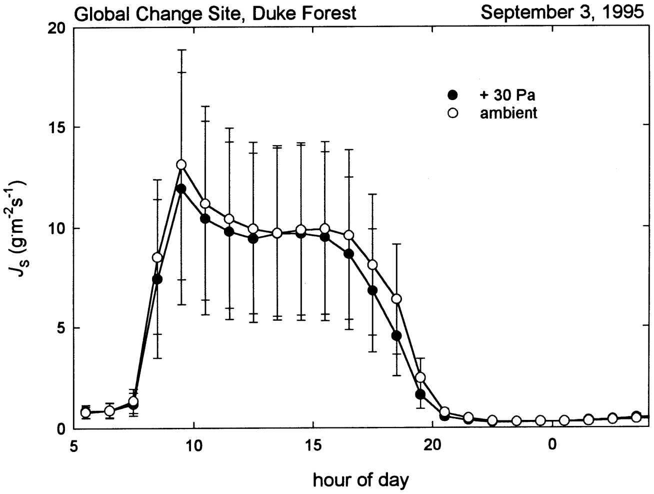

Fig. 2 Mean diurnal sap flux (J_s) is shown for saplings in ambient- and elevated-CO_2 chambers on 5 September 1995. *Error bars* represent the standard error of the mean. Sample size was three ambient-CO_2 and two elevated-CO_2 chambers

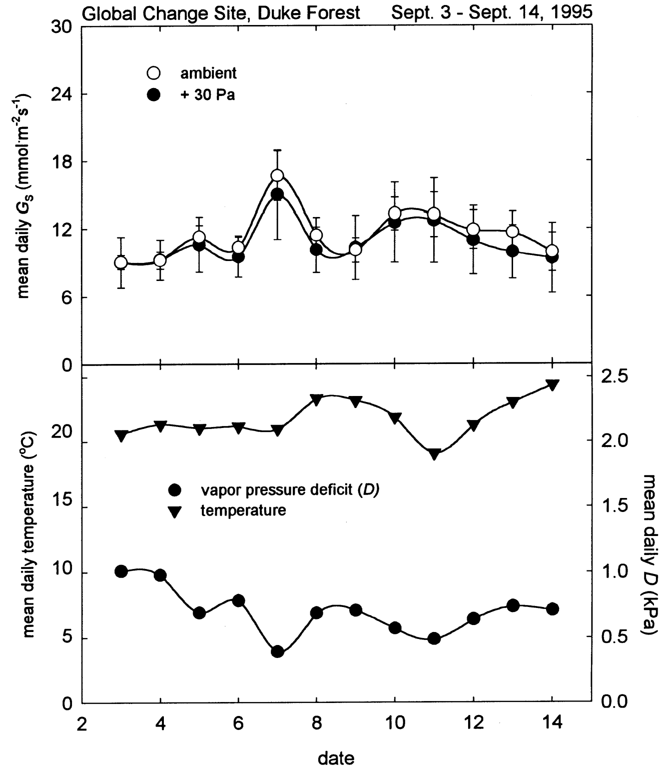

Fig. 3 Canopy stomatal conductance (G_s) calculated from sap flux is shown during a period without precipitation. *Error bars* represent the standard error of the mean. Sample size was three ambient CO_2 and two elevated CO_2 chambers. In the *lower panel*, mean daily temperature and vapor pressure deficit (*D*) are given for the same period

Table 1 All-sided leaf area (A_l, m^2), basal area (A_s, cm^2), and A_l/A_s (regression coefficient, m^2 cm^{-2}) for the three harvests. Values are given ± 1 SE (for A_l/A_s SE is given for the slope of the relationship). *P*-values are given for *t*-tests of ambient and +30 Pa CO_2 treatments

	November 1994			January 1995			September 1995		
	Ambient	+30 Pa	*P*	Ambient	+30 Pa	*P*	Ambient	+30 Pa	*P*
A_l	13.5 ± 1.0	21.4 ± 2.8	0.02	26.2 ± 3.9	28.2 ± 4.5	0.7	31.4 ± 6.6	57.0 ± 8.6	0.04
A_s	11.7 ± 1.3	20.5 ± 2.6	0.01	37.2 ± 5.1	43.0 ± 5.8	0.5	33.7 ± 6.7	57.3 ± 7.4	0.04
A_l/A_s	1.0 ± 0.1	1.1 ± 0.1	0.4	0.6 ± 0.1	0.7 ± 0.1	0.7	1.0 ± 0.1	0.9 ± 0.1	0.6

shown in Fig. 3. Although the variance is high, both treatments exhibit almost identical behavior. However, it should be noted that stomatal closure as a result of soil moisture depletion is not evident, so that the lack of precipitation during this period did not appear to provide conditions dry enough to evaluate CO_2 effects under drought conditions.

Discussion

There have been few studies on the effects of elevated CO_2 on water use in whole crowns, and these have primarily focused on non-woody species (Dugas et al. 1994; Senock et al. 1996). The results of these studies are inconsistent, sometimes contradicting reductions in water use hypothesized from leaf-level studies on these same species (Akita and Moss 1972; Bhattacharya et al. 1994). In this study, no CO_2 effect on J_s was found. As J_s represents flux on a sapwood area basis, a treatment effect on water use per unit leaf area may still be present if elevated CO_2 increased the ratio of leaf area to sapwood area (A_l/A_s) so as to compensate for a reduction in average canopy stomatal conductance (G_s). In fact, Eq. 1 may be simplified to:

$$J_sA_s = G_sA_lDc \qquad (2)$$

where c is a constant for a limited range of ambient air temperatures (Phillips and Oren 1998). Thus, reductions in G_s may be present if A_l/A_s is higher in CO_2 treatments without a noticeable effect on J_s.

Reductions in water use in response to elevated CO_2 have generally been discussed in terms of stomatal closure. However, alterations in water use may also result from changes in wood structure and anatomy following long-term exposure to high CO_2. Conroy et al. (1990) found that increases in wood density occurred due to thickening of tracheid walls in *Pinus radiata* grown under high CO_2. If such changes reduce the permeability of pit membranes, A_l/A_s may be expected to decrease (Schulte and Gibson 1988) and affect whole-tree water relations independent of direct effects of CO_2 on g_s. In this study, wood anatomy and hydraulic conductance were not affected inasmuch as the proportion of leaf area to cross-sectional wood area did not change in the elevated CO_2 treatment (Table 1). Such information on the effects of CO_2 on hydraulic architecture is necessary for predictions of whole-stand water relations under future climate scenarios. In Table 2, previously reported CO_2 effects on A_l/A_s in tree species are reviewed. In all species, effects on A_l/A_s are muted in comparison to effects on A_l and/or A_s alone. In general, relative changes in A_l/A_s in response to elevated CO_2 were often similar to those reported for g_s (Field et al. 1995), and thus could double (negative changes) or cancel (positive changes) the effects of g_s responses on J_s.

In the absence of CO_2 effects on J_s and A_l/A_s, no effect on G_s can be expected. Leaf-level g_s was previously reported to be reduced as much as 40% under high CO_2 in this same study (Tissue et al. 1997). However, gas exchange measurements were performed under saturating light conditions, such that g_s represented maximum values. Even under these conditions, the CO_2 effect on gas exchange was large only under summer conditions when photosynthetic rates were highest. During autumn and spring, leaf-level effects were sometimes undetect-

Table 2 Percent changes in cross-sectional area (%ΔA), leaf area or mass (%ΔL), and leaf to cross-sectional area ratios (A_l:A_s) under elevated CO_2. For %ΔA and %ΔL, differences were significant at $P \leq 0.05$ unless marked as not significant (*ns*). In the absence of raw data, it was not possible to test differences between treatments in A_l:A_s except in the current study, but it was assumed not to be different when no effects were found in both leaf area and/or biomass and diameter

Species	%ΔA	%ΔL	%ΔA_l:A_s	Source
Castanea sativa Mill	6^{ns}	-5^{ns}	8^{ns}	El Kohen et al. 1993
Fagus sylvatica L.	12ns	50	29	El Kohen et al. 1993
Liquidambar styraciflua L.	25	33*	−5	Sionit et al. 1985
Liquidambar styraciflua L.				Tolley and Strain 1985
High light treatment	44	44^{ns}	−2	
Low light treatment	25^{ns}	31	1	
Picea rubens Sarg	77	42	−17	Samuelson and Sieler 1993
Pinus pinaster Ait.				Guehl et al. 1994
Well-watered treatment	25	63*	26	
Drought treatment	17^{ns}	31^{ns}*	15^{ns}	
Pinus taeda L.	74	82	11^{ns}	This study
Pinus taeda L.	30	50*	−14	Sionit et al. 1985
Pinus taeda L.				Tolley and Strain 1985
High light treatment	-8^{ns}	-14^{ns}	8^{ns}	
Low light treatment	19^{ns}	17^{ns}	-12^{ns}	
Quercus alba L.	72	77	8	O'Neill et al. 1987
Quercus petraea Liebl.				Guehl et al. 1994
Well-watered treatment	72	112	21	
Drought treatment	69	21^{ns}	−25	

Where A_1 was not available, leaf mass was substituted, on the assumption that there were no CO_2 effects on specific leaf area (A_1 divided by leaf mass) able (Tissue et al. 1997). Canopy stomatal conductance values calculated from sap flux in this study indicate that CO_2 has no detectable effect on the mean whole-plant rates found under ambient light conditions (Fig. 3).

Ellsworth et al. (1995) suggested that stomatal closure in *P. taeda* under high CO_2, which was found to be minimal under drought conditions, may be more pronounced when soil moisture is abundant. This hypothesis was generated from the results in Ellsworth et al. (1995) and the finding that *P. taeda* is highly sensitive to soil drought, resulting in rapid stomatal closure and decreased transpiration as soil moisture declines (Oren et al. 1998; Phillips and Oren 1998). Conductance values in this study were very similar to those reported at the beginning of a drying cycle in a nearby stand taking into account the use of projected leaf area (Phillips and Oren 1998), indicating that soil moisture was highly available throughout the 12-day period without precipitation, probably due to the deep rooting zone (1 m). Thus, the hypothesis that elevated CO_2 may affect g_s of *P. taeda* only when soil moisture is not limiting is refuted in the present study.

In summary, the only effect of CO_2 enrichment on water relations of *P. taeda* found in this study was increased whole-plant water use in direct proportion to the increase in leaf and sapwood area of saplings grown at high CO_2 (Table 1). Changes in whole-plant water use under high CO_2 are of interest for predictions of large-scale water vapor fluxes, as well as stand growth and composition under future elevated atmospheric concentrations of CO_2. Results of chamber studies, however, cannot be directly extrapolated to forest-level responses. As total biomass and leaf area increase under elevated CO_2, increased rain interception by the canopy may promote the onset and increased frequency of drought as soil moisture is more rapidly depleted by higher transpiration, particularly when root:shoot ratios do not increase, as has been found for some species, including *P. taeda* (Tissue et al. 1997). Furthermore, higher light interception by larger canopies under elevated-CO_2 conditions will lower the average stomatal conductance. Thus, increased leaf area may represent an indirect mechanism by which elevated CO_2 may cause a reduction in average canopy stomatal conductance. While open-top chambers provide a means of studying mechanisms of leaf and whole-plant level responses under controlled conditions, these stand-level responses cannot be adequately tested in chambers that do not mimic the effect of increased leaf area index on rain interception and permit light penetration on all sides. Thus, extrapolations of results to the forest level will be greatly improved using a modeling approach (Baldocchi et al. 1991) or stand-level experiments.

Acknowledgements We thank Will Cook, John King, and Jeff Pippin for assistance in the field. This research was supported by the U.S. Department of Energy (DOE), CO_2 Research Division, contract DE-FG05-87ER60575, the Electric Power Research Institute Forest Response to CO_2 Program, and by an NSF grant DEB-9112571 for support of the Duke University Phytotron. The water relations study was also funded in part by the DOE through the National Institute for Global Environmental Change (NIGEC) Southeast Regional Center at the University of Alabama, Tuscaloosa (DOE Cooperative Agreement DE-FC03-90ER61010).

References

Akita S, Moss DN (1972) Differential stomatal response between C_3 and C_4 species to atmospheric CO_2 concentration and light. Crop Sci 12:789–793

Baldocchi DD, Luxmoore RJ, Hatfield JL (1991) Discerning the forest from the trees: an essay on scaling canopy stomatal conductance. Agric For Meteorol 54: 197–226

Bhattacharya NC, Radin JW, Kamball RA, Mauney JR, Hendrey GR, Nagy J, Lewin KF, Ponce DC (1994) Leaf water relations of cotton in a free-air CO_2-enriched environment. Agric For Meteorol 70: 171–182

Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO_2 on woody plants. New Phytol 127: 425–446

Conroy JP, Milham PJ, Mazur M, Barlow EWR (1990) Growth, dry weight paritioning and wood properties of *Pinus radiata* D. Don after 2 years of CO_2 enrichment. Plant Cell Environ 13: 329–337

Curtis PS (1996) A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. Plant Cell Environ 19: 127–137

Dugas WA, Heuer ML, Hunsaker D, Kimball BA, Lewin KF, Nagy J, Johnson M (1994) Sap flow measurements of transpiration from cotton grown under ambient and enriched CO_2 concentrations. Agric For Meteorol 70: 231–246

Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. Adv Ecol Res 19: 1–55

El Kohen L, Venet L, Mousseau M (1993) Growth and photosynthesis of two deciduous forest species at elevated carbon dioxide. Funct Ecol 7: 480–486

Ellsworth DS, Oren R, Huang C, Phillips N, Hendrey G (1995) Leaf and canopy responses to elevated CO_2 in a pine forest under free-air enrichment. Oecologia 104: 139–146

Field CB, Jackson RB, Mooney HA (1995) Stomatal responses to increased CO_2: implications from the plant to the global scale. Plant Cell Env 18: 1214–1225

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol 3: 309–320

Guehl JM, Picon C, Aussenac G, Gross P (1994) Interactive effects of elevated CO_2 and soil drought on growth and transpiration efficiency and its determinants in two European forest tree species. Tree Physiol 14: 707–724

Monteith JL, Unsworth MH (1990) Principles of environmental physics. Arnold, London

Morison JIL, Gifford RM (1984) Plant growth and water use with limited water supply in high CO_2 concentrations. I. Leaf area, water use and transpiration. Aust J Plant Physiol 11: 361–374

Mott KA (1988) Do stomata respond to CO_2 concentrations other than intercellular? Plant Physiol 86: 200–203

Mousseau M, Saugier B (1992) The direct effect of increased CO_2 on gas exchange and growth of forest tree species. J Exp Bot 43: 1121–1130

Norby RJ, O'Neill EG (1991) Leaf area compensation and nutrient interactions in CO_2-enriched seedlings of yellow-poplar (*Liriodendron tulipfera* L.) New Phytol 117: 515–528

O'Neill EG, Luxmoore RJ, Norby RJ (1987) Increases in mychorrizal colonization and and seedling growth in *Pinus echinata* and *Quercus alba* in an enriched CO_2 atmosphere. Can J For Res 17: 878–883

Oren R, Phillips N, Katul G, Ewers BE, Pataki D (1998) Scaling xylem sap flux and soil water balance, and calculating variance: a method for partitioning water flux in forests. Ann Sci For 55: 191–216

Pataki DE, Oren R, Phillips N (1998) Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. J. Exp Bot 49: 871–878

Phillips N, Oren R (1998) A comparison of daily representations of canopy conductance based on two conditional time-averaging methods. Ann Sci For 55: 217–235

Picon C, Guehl JM, Ferhi A (1996) Leaf gas exchange and carbon isotope composition responses to drought in a drought-avoiding (*Pinus pinaster*) and a drought-tolerant (*Quercus petraea*) species under present and elevated atmospheric CO_2 concentrations. Plant Cell Environ 19: 182–190

Reekie EG, Bazzaz FA (1989) Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated CO_2. Oecologia 79: 212–222

Samuelson LJ, Seiler JR (1993) Interactive role of elevated CO_2, nutrient limitations, and water stress in the growth responses of red spruce seedlings. For Sci 39: 348–358

Saxe H, Ellsworth DS, Heath J (1998) Tree and forest function in an enriched CO_2 atmosphere. New Phytol (in press)

Schulte PJ, Gibson AC (1988) Hydraulic conductance and tracheid anatomy in six species of extant seed plants. Can J Bot 66: 1073–1079

Senock RS, Ham JM, Loughin TM, Kimball BA, Hunsaker DJ, Pinter PJ, Wall GW, Garcia RL, LaMorte RL (1996) Sap flow in wheat under free-air CO_2 enrichment. Plant Cell Environ 19: 147–158

Sionit N, Strain BR, Hellmers H, Riechers GH, Jaeger CH (1985) Long-term atmospheric CO_2 enrichment affects the growth and development of *Liquidambar styraciflua* and *Pinus taeda* seedlings. Can J For Res 15: 468–471

Tissue DT, Thomas RB, Strain BR (1997) Atmospheric CO_2 enrichment increases growth and photosynthesis of *Pinus taeda*: a 4 year experiment in the field. Plant Cell Environ 20: 1123–1134

Tolley LC, Strain BR (1985) Effects of CO_2 enrichment and water stress on gas exchange of *Liquidambar styraciflua* and *Pinus taeda* seedlings grown under different irradiance levels. Oecologia 65: 166–172

Weisberg S (1985) Applied linear regression, 2nd edn. Wiley, New York