Free-air CO2 enrichment (FACE) enhances biomass production in a short-rotation poplar plantation (POPFACE)

Article *in* Tree Physiology · September 2003

DOI: 10.1093/treephys/23.12.805 · Source: PubMed

8 authors, including:

Carlo Calfapietra
Italian National Research Council
116 PUBLICATIONS **3,366** CITATIONS
SEE PROFILE

Martin Lukac
University of Reading
59 PUBLICATIONS **1,828** CITATIONS
SEE PROFILE

Paolo De Angelis
Tuscia University
123 PUBLICATIONS **4,795** CITATIONS
SEE PROFILE

M.C. Moscatelli
Tuscia University
41 PUBLICATIONS **1,061** CITATIONS
SEE PROFILE

Tree Physiology 23, 805–814

Free-air CO_2 enrichment (FACE) enhances biomass production in a short-rotation poplar plantation

C. CALFAPIETRA,[1,2] B. GIELEN,[3] A. N. J. GALEMA,[4] M. LUKAC,[5] P. DE ANGELIS,[1] M. C. MOSCATELLI,[6] R. CEULEMANS[3] and G. SCARASCIA-MUGNOZZA[1]

[1] *Università degli Studi della Tuscia, Department of Forest Environment and Resources (DISAFRI), Via S. Camillo de Lellis, I-01100 Viterbo, Italy*

[2] *Author to whom correspondence should be addressed (carlocalf@unitus.it)*

[3] *University of Antwerpen, UIA, Department of Biology, Universiteitsplein 1, B-2610 Wilrijk, Belgium*

[4] *Wageningen University and Research Centre, Department of Environmental Sciences, Forest Ecology and Forest Management Group, P.O. Box 342, 6700AH Wageningen, The Netherlands*

[5] *School of Agricultural and Forest Sciences, University of Wales, Bangor, Deiniol Road, Bangor, LL57 2UW, UK*

[6] *Università degli Studi della Tuscia, Department of Agrobiology and Agrochemistry (DABAC), Via S. Camillo de Lellis, I-01100 Viterbo, Italy*

Received September 20, 2002; accepted January 24, 2003; published online July 15, 2003

Summary This paper investigates the possible contribution of Short Rotation Cultures (SRC) to carbon sequestration in both current and elevated atmospheric CO_2 concentrations ($[CO_2]$). A dense poplar plantation (1 × 1 m) was exposed to a $[CO_2]$ of 550 ppm in Central Italy using the free-air CO_2 enrichment (FACE) technique. Three species of *Populus* were examined, namely *P. alba* L., *P. nigra* L. and *P.* × *euramericana* Dode (Guinier). Aboveground woody biomass of trees exposed to elevated $[CO_2]$ for three growing seasons increased by 15 to 27%, depending on species. As a result, light-use efficiency increased. Aboveground biomass allocation was unaffected, and belowground biomass also increased under elevated $[CO_2]$ conditions, by 22 to 38%. *Populus nigra*, with total biomass equal to 62.02 and 72.03 Mg ha^{-1} in ambient and elevated $[CO_2]$, respectively, was the most productive species, although its productivity was stimulated least by atmospheric CO_2 enrichment. There was greater depletion of inorganic nitrogen from the soil after three growing seasons in elevated $[CO_2]$, but no effect of $[CO_2]$ on stem wood density, which differed significantly only among species.

Key words: elevated CO_2, light-use efficiency, POPFACE, Populus, root/shoot ratio, SRC, wood density.

Introduction

Much progress has been made in recent decades toward maximizing woody biomass production in poplar through the introduction of new clones and improved cultural techniques (Stettler and Heilman 1984, Hansen 1991). Short Rotation Cultures (SRC) have been introduced to produce biomass for energy and industry in the USA (Hohenstein and Wright 1994) and in Europe (Grassi et al. 1990), but the impact of climate changes on SRC is not well known. Numerous studies on the impact of increasing CO_2 concentration ($[CO_2]$) on tree productivity, i.e., carbon sequestration capacity, are underway (Karnosky et al. 2001). Initially, elevated $[CO_2]$ studies were conducted with small trees under controlled environmental conditions (Ceulemans and Mousseau 1994, Saxe et al. 1998). More recently, the focus has been on ecosystem-level responses, the study of which requires exposing an area of natural vegetation to elevated $[CO_2]$ without otherwise altering the environmental conditions (Norby et al. 1999). This can be achieved by the free-air CO_2 enrichment (FACE) technique (Hendrey et al. 1993). Although FACE is widely applied to herbaceous plants, few experiments have been carried out with trees because of the cost of the large installations that such experiments require (Karnosky et al. 2001).

Elevated $[CO_2]$ usually enhances both above- and belowground productivity, particularly in fast-growing species such as poplars (Gielen and Ceulemans 2001). Increases in total biomass of between 22 and 90% in response to atmospheric CO_2 enrichment have been reported in poplar (Gielen and Ceulemans 2001), although no significant effect on aboveground biomass was found in *Populus deltoides* Bartr. ex Marsh (Wait et al. 1999), *Populus tremuloides* Michx. (Kubiske et al. 1997) or *Populus grandidentata* Michx. (Curtis et al. 1994). Recently, it was reported that aboveground biomass of one *P.* × *euramericana* Dode (Guinier) and one *P. nigra* L. genotype, grown within a single small FACE ring for 5 months, increased in response to elevated $[CO_2]$ by 47 and 32%, respectively (Tognetti et al. 1999). Little is known about the effect of elevated $[CO_2]$ on belowground growth of poplar.

Although a number of experiments have shown increased growth of poplars in response to elevated $[CO_2]$, these were mostly short-term studies with plants in pots (Radoglou and Jarvis 1990, Curtis and Teeri 1992, Dickson et al. 1998, Loewe et al. 2000). However, a study with six *P. tremuloides* clones found a 113% increase in fine root biomass in response to ele-

vated [CO_2] (King et al. 2001).

Estimates of the response of forest ecosystems to elevated [CO_2] have assumed the absence of an effect of [CO_2] on the allometric relationships used to estimate biomass within treated plots (DeLucia et al. 1999, Norby et al. 2001). Norby et al. (2001) have justified this based on an analysis of the effect of elevated [CO_2] on stem taper and wood density.

To gain insight into the growth responses of forest trees to elevated [CO_2], the light-use efficiency model introduced by Monteith (1972, 1977) may be applied. This model predicts that net primary productivity (NPP) is linearly related to absorbed photosynthetically active radiation (APAR), assuming that light-use efficiency (ε) remains constant. Widespread use of this model has been made in estimating productivity over large spatial scales (Gower et al. 1999), and possible effects of rising atmospheric [CO_2] on ε need to be taken into account. Results for a *Pinus taeda* L. ecosystem showed a FACE-induced stimulation of ε of 27% as a result of increased biomass production (DeLucia et al. 2002).

In the POPFACE experiment, three poplar species were grown in an SRC plantation for three growing seasons and exposed to a [CO_2] of 550 ppm using the FACE technique, i.e., in open field conditions with otherwise unchanged environmental conditions. Because canopy closure in this system occurred in the second year (Gielen et al. 2001), it provided an opportunity to assess realistically the effect of future elevated [CO_2] on biomass productivity in forest plantations. Based on previous research at this site (for details see Calfapietra et al. 2001, Gielen et al. 2001, 2002), we hypothesized that (1) allometric relationships between stem cross-sectional area and tree biomass are unaffected by an increase in atmospheric [CO_2], (2) biomass allocation is slightly affected by the FACE treatment through increased investment of biomass in branches and roots, (3) biomass production is stimulated by the FACE treatment, and (4) the FACE treatment increases light-use efficiency of this plantation.

Materials and methods

Site description and plantation layout

The experimental plantation and FACE facility are located in an agricultural region of Central Italy, near Viterbo (Tuscany; 42°22′ N, 11°48′ E, altitude 150 m). In late spring 1999, a 9-ha field was planted with 25-cm-long hardwood cuttings of *Populus* × *euramericana* (*P. deltoides* × *P. nigra*) genotype I-214 at a density of 5000 trees ha^{-1} (2 × 1 m). Six experimental plots (30 × 30 m) with homogeneous soil and microclimatic conditions were selected within the plantation. Plots were planted at a density of 10,000 trees ha^{-1} (1 × 1 m) with hardwood cuttings of three different species: *P.* × *euramericana* genotype I-214, *P. nigra* (genotype Jean Pourtet) and a local selection of *P. alba* L. (genotype 2AS11). This planting density is common in SRC poplar plantations (Hansen 1991, MacPherson 1995). For further information on the descriptive species properties, see Calfapietra et al. (2001).

In each of three plots, a 22-m diameter PVC ring was mounted on telescopic poles, and pure CO_2 was released through laser-drilled holes in the ring (FACE treatment). Trees within a 22-m diameter area in the center of each of the three remaining plots served as controls. In order to avoid cross-contamination between FACE and control plots, plots were a minimum of 120 m apart. The [CO_2] was monitored with an automatic monitoring station at the center of each ring. Directional release of gas around the ring was controlled, according to wind direction, by shut-off valves located before the point of injection. The released quantity of gas was established, according to wind speed, with an algorithm developed for the facility based on a three-dimensional gas dispersion model (Miglietta et al. 2001). The computer-controlled system was set to maintain a [CO_2] of 550 ppm inside the FACE plots. The mean [CO_2] within the FACE plots was 544 ± 48 ppm during the first year of treatment, 532 ± 83 ppm during the second year, and 554 ± 95 during the third year (F. Miglietta, CNR-IATA, Florence, Italy, unpublished results). Unexpected internal corrosion of the CO_2 bulk container caused performance problems in the autumn of the second year. However, the CO_2 concentrations, measured at 1-min intervals at the center of the ring and at the top of the canopy, were within 20% of the target concentration more than 80% of the time. The [CO_2] in the canopy space was controlled and monitored throughout the season by two additional independent infrared gas analyzers. Despite considerable short-term [CO_2] fluctuations within the canopy space, mean daily values differed only slightly from those measured at the top of the canopy (F. Miglietta, unpublished results). Daytime CO_2 enrichment was provided from bud burst to leaf fall (March to November). A detailed description of the set-up and performance of this FACE facility has been provided by Miglietta et al. (2001).

The 20-cm-deep topsoil layer had a silt loam texture and a pH (KCl) of 5.04. Total carbon and nitrogen were 0.98 and 0.12%, respectively, and bulk density was 1.34 g cm^{-3}. There were no relevant differences between experimental plots (M. Hoosbeek, Wageningen University, The Netherlands, unpublished results).

A drip irrigation system was installed both in the field and in the experimental plots to avoid drought stress during plantation establishment and the dry summer period. Irrigation was monitored to ensure equal application in each experimental plot. The amount of water supplied to trees increased from spring to summer, and from the first to the third growing season, in order to match transpiration, reaching a maximum of 10 mm day^{-1} in the summer of the third growing season. Weeds were removed manually or mechanically, and insecticides was applied as necessary during the establishment year.

Harvests

In November and December 2000, the first biomass harvest was made of 2-year-old trees selected from the external rows of the plots, i.e., beyond the CO_2-enriched area, thus leaving the experimental plots undisturbed until the end of the 3-year treatment period. The experimental trees were divided into four classes according to basal area at breast height (BA). Two trees of each species were selected from each plot (n = 12)

such that, from each BA class, a number of trees proportional to the total number of trees in that class was selected. All aboveground components were dried for 5 days at 70 °C and weighed.

In November and December 2001, the second biomass harvest was made of 3-year-old trees selected within the experimental area. Eight trees of each species were selected from each plot ($n = 48$) such that, from each BA class, a number of trees proportional to the total number of trees in that class was selected. For half of the harvested trees, branch biomass was separated from stems. For the remaining trees, branches were sorted into: sylleptic branches on HGI 1 (height growth increment of the first growing season), HGI 2 (height growth increment of the second growing season) and HGI 3 (height growth increment of the third growing season); proleptic branches on HGI 1 and HGI 2; and second-order branches. Only live biomass components were sampled. Some proleptic branches developed early in the spring but died and fell before the end of the growing season, and thus were not sampled during our harvests.

Fresh stem volume was measured by water displacement, and all aboveground components were weighed after drying for 5 days at 70 °C. Wood density was calculated as fresh stem volume divided by stem dry mass. In contrast with the first (second-year) harvest, each stem was divided into three parts according to the three HGIs to determine the volume and density of each component. Two trees per species per plot (36 trees in total) were selected from those harvested to determine belowground biomass. A 1 × 1 m square centred around the tree was excavated to a depth of 70 cm for belowground biomass assessments. We assumed that roots of surrounding trees within the sample area compensated for roots of the measured tree that were outside the sampled area. Only coarse roots (diameter > 2–3 mm) were collected, and the stump was separated from the roots. Fine root biomass was excluded, as were dead coarse roots, which make up only a small fraction of the biomass. Roots were washed, dried for 3 days at 70 °C and weighed.

Scaling up to the ecosystem level

Allometric relationships between BA and total aboveground biomass of harvested trees were established for each harvest and species (subsample of 12 and 48 trees for the first and second harvests, respectively) (Table 1). The FACE treatment did not affect allometric relationships between BA and aboveground biomass, as shown by analysis of covariance for the third growing season ($P = 0.12$ and 0.93 for the slope and the intercept comparison, respectively). This justified the use of a single regression line to estimate biomass for both treatments. Data were pooled by species, which differed significantly ($P < 0.0001$) in both regression slope and intercept. Allometric relationships were used to estimate aboveground biomass from the BA of 48 experimental trees (main sample) per plot per species. Aboveground biomass per tree was estimated with the general equation (Corona 2000):

$$\bar{y}_p = \bar{y}_{ss} + b_1(\bar{x} - \bar{x}_{ss})$$

where x is BA and y is aboveground biomass; $\bar{y}_p$ = mean y estimated for the population; $\bar{y}_{ss}$ = mean y of the subsample; $\bar{x}_{ss}$ = mean x of the subsample; $\bar{x}$ = mean x of the main sample; and b_1 = the coefficient of the linear regression between y and x (i.e., $y = b_0 + b_1 x$; see Table 1).

The accuracy of the estimation of $\bar{y}_p$ depends on the variability of y in the subsample and of the predicted values of y in the main sample. The variance of $\bar{y}_p$ can be estimated as:

$$s^2_{\bar{y}_p} = \frac{n - n_{ss}}{n} s^2_{y,x} \left(\frac{1}{n_{ss}} + \frac{(\bar{y} - \bar{y}_{ss})^2}{(n_{ss} - 1) s^2_{x_{ss}}} \right) + \frac{N - n}{N} \frac{s^2_y}{n}$$

where $s^2_{y,x}$ = variance of the residual estimated for the subsample:

$$s^2_{y,x} = \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{n_{ss} - 2}$$

where y_i = the ith value of the parameter y measured in the subsample; $\hat{y}_i$ = the ith value of the parameter y estimated by using the linear regression corresponding to the ith value of the parameter x in the subsample; n_{ss} = the number of values in the subsample; n = the number of values in the main sample; $\bar{y}$ = mean y of the main sample; s^2_y = variance of y in the subsample; $s^2_{x_{ss}}$ = variance of x in the subsample; and N = the number of values in the population.

A similar procedure was used to obtain a regression between BA and coarse root biomass with a subsample of 12 trees per species (Table 1).

The root/shoot ratio (R/S) was calculated from values of total below- and aboveground biomass of the harvested trees, i.e., six trees per species per treatment. There were no differences in R/S ratio among stem diameter classes, and therefore belowground biomass was estimated for trees of the main sample from R/S ratio and aboveground biomass. Stump biomass was calculated as the difference between total belowground biomass and coarse root biomass.

Branch/stem ratio (B/St) was calculated for the 24 harvested trees per species per treatment. With this ratio, branch and stem biomass were estimated from aboveground biomass values. Finally, branch biomass was separated into the different types (see above) based on relative ratios calculated for 12 trees per species per treatment.

Assessments at the physiological level

In the third growing season, leaf production was collected in control and FACE treatments in six litter traps (0.13 m^2) per plot per species. Litter was determined after pooling the three replicated traps per half-plot per species to account for spatial heterogeneity. Traps were placed in the projected area of a tree or the intersection of the projected areas of four adjacent trees. Litter was dried at 80 °C for 48 h and weighed. Annual litterfall was calculated as the sum of each periodic collection (g m^{-2}). Total leaf area produced was estimated by multiplying annual litterfall by specific leaf area values for each species.

Table 1. Allometric relationships used to determine aboveground biomass after two (first harvest) and three (second harvest) growing seasons and coarse root biomass after three growing seasons for three *Populus* species. Values of control and FACE plots were merged, as no significant differences in allometric relationships between treatments were observed. Abbreviations: n is the number of trees (subsample) used for each fit; b_0 and b_1 are parameters of a linear fit with the equation $y = b_0 + b_1 x$; r^2 is the coefficient of determination; and P is the probability value.

	n	b_0	b_1	r^2	P
P. alba					
Aboveground biomass (first harvest)	12	–319.36	241.41	0.971	< 0.0001
Aboveground biomass (second harvest)	48	–1504.7	332.21	0.946	< 0.0001
Coarse roots (second harvest)	12	116.53	22.64	0.718	0.0005
P. nigra					
Aboveground biomass (first harvest)	12	–273.38	240.02	0.979	< 0.0001
Aboveground biomass (second harvest)	48	–569.53	260.55	0.951	< 0.0001
Coarse roots (second harvest)	12	50.2	22.88	0.648	0.0016
P. × *euramericana*					
Aboveground biomass (first harvest)	12	–391.35	196.98	0.954	< 0.0001
Aboveground biomass (second harvest)	48	–549.81	207.47	0.967	< 0.0001
Coarse roots (second harvest)	12	180.58	14.82	0.757	0.0002

The CPI (Canopy Productivity Index, Norby 1996) was calculated as stem biomass produced per unit leaf area (g m^{-2}) during the third growing season. The HI (Harvest Index) was calculated as the ratio of total aboveground merchantable biomass to total biomass of the 36 completely harvested trees.

Light-use efficiency (ε = biomass produced per unit absorbed photosynthetically active radiation (APAR)) during the third year was calculated for aboveground production, i.e., woody biomass and total leaf production. Accumulated APAR between bud burst and third-year biomass determination was estimated from accumulated incoming PAR (JYP 1000, SDEC, Tours, France) and canopy absorption (B. Gielen et al., unpublished data) where litter traps were placed. Canopy absorption of all species in all plots was estimated in August of the third year by measuring canopy transmittance with a ceptometer (AccuPAR, Decagon Devices, Pullman, WA), assuming reflectance = 0.036 (Zavitkovski 1982).

For soil nitrogen content determination, two soil cores per plot per species (10 cm diameter, 20 cm long) were taken from the top 20-cm-deep soil layer at both the beginning and the end of the third growing season (spring and fall 2001). Samples were immediately sieved (2 mm), and the water content adjusted to 60% of water holding capacity. The soil samples were then left to equilibrate at room temperature for 1 week. Ammonium was extracted in 1 M KCl and determined by steam distillation and titration according to Keeney and Nelson (1982). Nitrate was extracted in 0.5 M K_2SO_4 and determined colorimetrically with salicylic acid according to Cataldo et al. (1975). Total soil inorganic nitrogen content was calculated as the sum of NH_4-N plus NO_3-N.

Statistical analysis

Analysis of variance (ANOVA) was performed to evaluate the main effects of FACE and species on tree biomass production and biomass partitioning. Data were tested for normality with the Shapiro-Wilk statistic. A randomized, complete-block design was applied, with treatment, species and treatment × species interaction as fixed factors, and block as the random factor. Plot (three FACE plots versus three control plots) was the unit of replication. All statistical analyses were performed with the SAS statistical software package (SAS Version 8.1, SAS Institute, Cary, NC) using the mixed procedure. Satterthwaite's procedure was applied to obtain the denominator degrees of freedom (Littell et al. 1996). Where the ANOVA F-test showed an interaction between CO_2 treatment and species, *a posteriori* comparison of means was performed by the Bonferroni method for the multiple comparisons. Differences between means were considered significant when the P-value of the ANOVA F-test was < 0.05.

Results

After two growing seasons, *Populus nigra* had the greatest aboveground biomass: 23.6 and 27 Mg ha^{-1} in the control and FACE treatments, respectively (Figure 1). Values for *P. alba* and *P.* × *euramericana* were, respectively, 17.3 and 16.5 Mg ha^{-1} in the control treatment, versus 20.9 and 22.7 Mg ha^{-1} in the FACE treatment (Figure 1). At the end of the third growing season, *Populus nigra* again had the greatest aboveground biomass: 53.58 and 61.73 Mg ha^{-1} in the control and FACE treatments, respectively (Table 2). Three-year aboveground biomass values were 40.32 and 51.38 Mg ha^{-1} for *P. alba*, and 38.16 and 48.39 Mg ha^{-1} for *P.* × *euramericana*, in control and FACE treatments, respectively. Significant differences in belowground biomass and in total biomass between treatments were confirmed in all species (Table 3). The highest total biomass values after 3 years were observed in *P. nigra*, with 62.02 and 72.03 Mg ha^{-1} in the control and FACE treatments, respectively (Table 2). In contrast to aboveground biomass, differences in belowground biomass among species were small relative to the range of belowground biomass values of 7.5–10.5 Mg ha^{-1} for all species in both control and FACE treat-

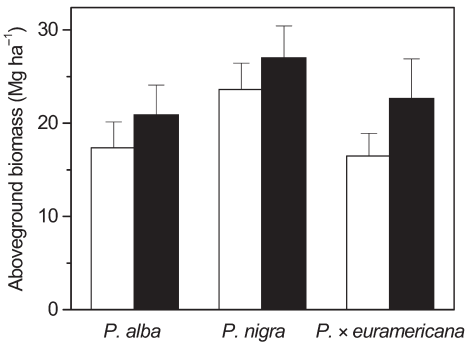

Figure 1. Total aboveground biomass measured after two growing seasons in three *Populus* species in control and FACE treatments. Mean values (+ standard error) of the control (open bars) and FACE (closed bars) treatments are presented. Each bar represents the mean of 144 trees for which biomass was estimated from basal area with allometric relationships.

ments (Table 2). Given these above- and belowground biomass values, the R/S ratio was not significantly influenced by the FACE treatment; R/S ratios ranged from 0.16 in *P. nigra* to 0.23 in *P. alba* and *P.* × *euramericana* (Figure 2).

Branch biomass was similar in *P. nigra* and *P. alba*, but lower in *P.* × *euramericana*, in both treatments. Moreover, branch biomass was significantly higher in the FACE treatment than in the control treatment (Tables 2 and 3). Values after three growing seasons ranged from 6.45 to 11.57 Mg ha^{-1} in the control treatment, and from 8.56 to 13.95 Mg ha^{-1} in the FACE treatment, depending on species. In contrast, the B/St ratio was unaffected by FACE treatment in *P. nigra* and *P.* × *euramericana*, whereas it was higher in the control treatment for *P. alba* (Figure 2).

The partitioning of branch biomass among different branch types was not greatly affected by the FACE treatment. Nevertheless, in *P. nigra*, sylleptic branches on HGI 1 represented 16 and 23% of total branch biomass in the control and FACE treatments, respectively, whereas proleptic branches on HGI 2 represented 25 and 18% of total branch biomass in the control and FACE treatments, respectively (Figure 3). Species differed considerably in their allocation of biomass. For instance, *P.* × *euramericana* invested mainly in proleptic branches (69% of total branch biomass in the control treatment versus 70% in the FACE treatment), whereas *P. alba* and *P. nigra* invested more in sylleptic branches (between 50 and 60% of total branch biomass). No significant interactions between CO_2 treatment and species were found for any of the biomass parameters.

Annual litterfall during the third growing season was unaffected by treatment, but a significant difference among species emerged. Values ranged between 533 and 769 g m^{-2}, depending on species and treatment (Table 4). Canopy Productivity Index was increased by the FACE treatment ($P = 0.08$) during the third growing season, especially in *P. alba*, where values were 236 and 327 g m^{-2} in the control and FACE treatments, respectively (Figure 2). Lower values were observed in *P. nigra* and *P.* × *euramericana*. For the latter species, differences between treatments were limited. As for CPI, ε was higher in the FACE treatment for all species. The highest ε values were observed in *P. nigra* (2.25 and 2.54 g MJ^{-1} in the control and FACE treatments, respectively) (Figure 4). The Harvest Index was unaffected by both treatment and species, with values ranging from 0.81 to 0.86 (Figure 2).

Wood density was unaffected by the FACE treatment in all species, but a significant difference was observed among species (Tables 3 and 5). Mean values for whole stem wood density ranged from 0.348 g cm^{-3} in *P.* × *euramericana* to 0.409 g cm^{-3} in *P. nigra* (Table 5). Differences were evident among the three HGIs. Wood density was always highest in HGI 3, with values ranging from 0.422 to 0.470 g cm^{-3}.

Inorganic soil nitrogen content was similar among species and between treatments in the spring of the third growing season, whereas a significant treatment effect emerged in the fall (Tables 3 and 4). A depletion of soil nitrogen was evident for all species in both treatments, except for *P. nigra* in the control treatment (Table 4).

Table 2. Biomass distribution (Mg ha^{-1}) of three *Populus* species after three growing seasons in control and FACE treatments. Values are means with standard errors in parenthesis; n =144. Abbreviation: HGI = height growth increment.

Component	*P. alba*		*P. nigra*		*P.* × *euramericana*	
	Control	FACE	Control	FACE	Control	FACE
Sylleptic branches on HGI 1	1.52 (0.39)	1.70 (0.31)	1.89 (0.32)	3.21 (0.28)	0.60 (0.13)	0.88 (0.30)
Proleptic brances on HGI 1	1.58 (0.24)	1.94 (0.35)	1.48 (0.15)	1.62 (0.27)	1.79 (0.29)	2.45 (0.29)
Sylleptic branches on HGI 2	3.57 (0.52)	3.53 (0.40)	2.52 (0.35)	3.37 (0.64)	0.12 (0.04)	0.44 (0.30)
Proleptic brances on HGI 2	1.43 (0.24)	2.04 (0.37)	2.94 (0.37)	2.45 (0.38)	2.66 (0.55)	3.49 (0.73)
Sylleptic branches on HGI 3	1.33 (0.24)	1.71 (0.42)	1.83 (0.21)	2.08 (0.31)	1.04 (0.32)	1.02 (0.24)
Second-order branches	2.03 (0.42)	2.24 (0.48)	0.91 (0.19)	1.22 (0.23)	0.25 (0.08)	0.28 (0.13)
Total branches	11.45 (2.30)	13.15 (1.93)	11.57 (1.35)	13.95 (1.39)	6.45 (1.21)	8.56 (1.36)
Stem	28.87 (3.65)	38.23 (3.28)	42.01 (2.58)	47.78 (2.57)	31.71 (2.68)	39.82 (2.93)
Stump	2.65 (1.16)	4.78 (1.10)	2.73 (0.66)	3.87 (0.73)	2.95 (0.82)	4.46 (0.98)
Coarse roots	4.93 (1.71)	5.68 (1.84)	5.71 (2.46)	6.43 (1.46)	4.92 (1.27)	5.65 (1.37)
Total aboveground biomass	40.32 (4.31)	51.38 (3.81)	53.58 (2.91)	61.73 (2.93)	38.16 (2.94)	48.39 (3.23)
Total belowground biomass	7.58 (2.80)	10.46 (2.96)	8.44 (2.79)	10.30 (2.07)	7.87 (2.07)	10.11 (2.40)
Total biomass	47.90 (6.41)	61.84 (5.78)	62.02 (4.57)	72.03 (4.39)	46.03 (4.41)	58.50 (4.88)

Table 3. Analysis of variance (ANOVA) of biomass parameters for three *Populus* species grown for three growing seasons in control and FACE treatments. The aboveground biomass value (first harvest) is from data obtained after two growing seasons. Significance (*P*-values of the ANOVA *F*-test) of the effects of CO_2 treatment, species and their interaction are indicated as: ns = not significant; * = $P < 0.05$; ** = $P < 0.01$; and *** = $P <$ 0.001. Almost significant values, where *P* was between 0.05 and 0.1, are indicated.

Biomass parameter	Treatment	Species	Treatment × species
Total aboveground biomass (first harvest)	0.05	***	ns
Total aboveground biomass (second harvest)	*	**	ns
Sylleptic branch biomass on HGI 1	*	***	ns
Proleptic branch biomass on HGI 1	ns	ns	ns
Sylleptic branch biomass on HGI 2	ns	***	ns
Proleptic branch biomass on HGI 2	ns	**	ns
Sylleptic branch biomass on HGI 3	ns	0.1	ns
Second order branch biomass	*	***	ns
Total branch biomass	**	***	ns
Stem biomass	**	**	ns
Stump biomass	**	ns	ns
Coarse roots biomass	*	**	ns
Total belowground biomass	**	ns	ns
Total biomass	*	**	ns
Wood density whole stem	ns	**	ns
Wood density (HGI 1)	ns	***	ns
Wood density (HGI 2)	ns	***	ns
Wood density (HGI 3)	ns	ns	ns
Canopy productivity index	0.08	ns	ns
Harvest index	ns	*	ns
Branch/stem ratio	ns	*	ns
Root/shoot ratio	ns	***	ns
Light-use efficiency (ε)	*	*	ns
Annual litterfall	ns	**	ns
Soil N content (spring)	ns	ns	ns
Soil N content (fall)	*	ns	ns

Discussion

Averaged across three species, a 24% stimulation of total woody biomass production in SRC poplar was observed after 3 years of atmospheric CO_2 enrichment. The FACE treatment increased aboveground woody biomass after 2 years by 15 to 37%, depending on species. The effect was slightly less after the third year, i.e., +27% (*P. alba*), +15% (*P. nigra*) and +18% (*P.* × *euramericana*). Comparable results were observed in a sweetgum stand where the effect of FACE treatment on stand-level aboveground biomass production was 33% in the first year and 15% in the second (Norby et al. 2001). Differences in yearly increments of wood, including coarse roots, and foliage in a 15-year-old loblolly pine forest were increased by 27% in FACE compared with control treatments (Hamilton et al. 2002).

Elevated [CO_2] usually stimulates plant biomass production, particularly in plants such as poplars with indeterminate growth, presumably because of differences in sink strength (Oechel and Strain 1985), although this question is still strongly debated (Poorter 1998, Lloyd and Farquhar 2000). Different poplar species exposed to elevated [CO_2] for some months showed increased stem biomass production ranging from 31 to 55% (Bosac et al. 1995, Ceulemans et al. 1996). In our experiment, trees grew larger in the FACE treatment, particularly during the first growing season, when stem volume index was on average 70% higher in the FACE than in the con-

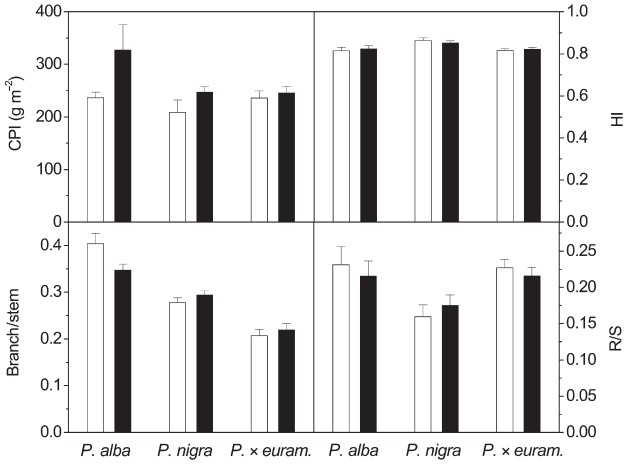

Figure 2. Canopy Productivity Index (CPI; stem mass per unit leaf area (g m^{-2}), *n* = 3), Harvest Index (HI, *n* = 6), branch/stem ratio (branch biomass per unit stem biomass, *n* = 24) and root/shoot ratio (R/S; belowground biomass divided by aboveground biomass, *n* = 6) of three *Populus* species after three growing seasons in control (open bars) and FACE treatments (closed bars). Values are means + S.E.

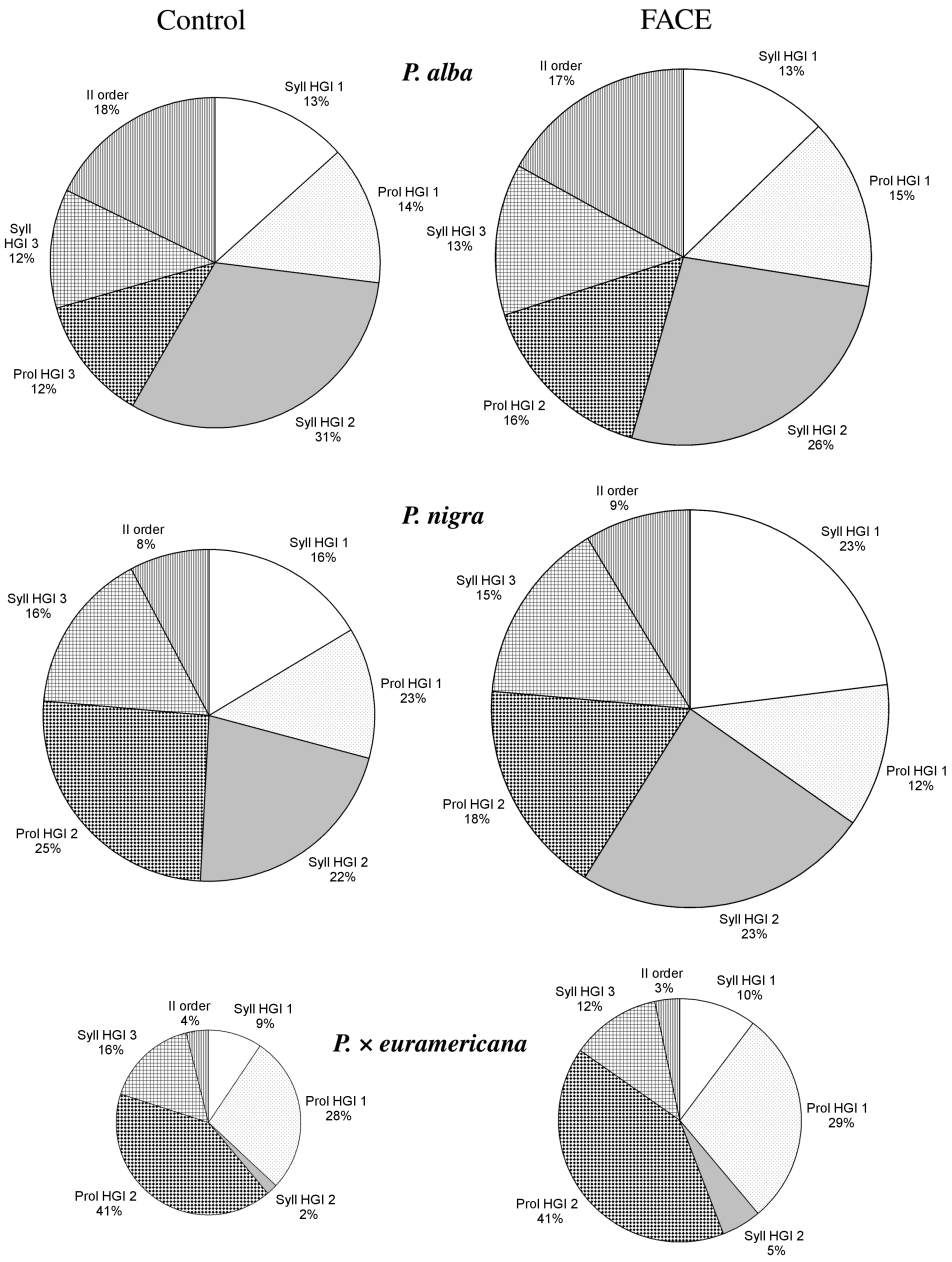

Figure 3. Relative partitioning of branch biomass among different branch categories for three *Populus* species after three growing seasons in control and FACE treatments. Values were determined from a sample of 12 trees selected according to the frequency distribution of stem cross-sectional area at breast height of the entire main sample. All values are percentages. The diameter of each pie graph is proportional to the total branch biomass for each species and treatment. Abbreviations: Syll = sylleptic branches; Prol = proleptic branches; II order = second-order branches; and HGI = height growth increment.

trol treatment (Calfapietra et al. 2001). Leaf area index (LAI) also consistently increased in the FACE treatment, especially during the first growing season before canopy closure (Gielen et al. 2001). Growth in elevated [CO_2] resulted in an increase in daily integrated carbon uptake for upper canopy leaves ranging from 35 to 77%, depending on species and measurement date (Bernacchi 2002). Leaf gas exchange measurements indicated no physiological acclimation to elevated [CO_2] (Bernacchi 2002). Relative stimulation of stem volume index by elevated [CO_2] decreased after the first growing season to a mean of 22% for the three species at the end of both the second and third growing seasons.

Soil inorganic nitrogen decreased considerably during the third growing season (Table 4), particularly in the FACE treatment, presumably because of greater biomass production. The more rapid depletion of soil nitrogen in the FACE treatment may have reduced the effect of elevated [CO_2] on productivity.

Mean annual aboveground biomass production was 17.86 and 20.58 Mg ha^{-1} year^{-1} in the control and FACE treatments, respectively. For the same parameter, Heilman et al. (1994) observed values between 11.40 and 24.30 Mg ha^{-1} year^{-1} in a 4-year-old plantation (1 × 1 m spacing) of *P. trichocarpa* Tott. & Gray, *P. deltoides* and their hybrids. After 3 years of growth, four *Populus* clones had a mean total aboveground woody biomass of 48.0, 45.0 and 39.1 Mg ha^{-1} at 0.5-m, 1.0-m and 1.5-m spacings, respectively (DeBell and Harrington 1997). These values agree with those found for *P. alba* and *P.* × *euramericana* in our experiment (Table 2).

The stimulation of belowground biomass production (fine roots excluded) by elevated [CO_2] ranged from 22 to 38%, de-

Table 4. Soil inorganic nitrogen content (μg N (NH_4-N + NO_3-N) g^{-1} dry soil) at the beginning (spring) and end (fall) of the third growing season, and cumulative annual litterfall (grams litter per m^{-2} of ground) during the third growing season for three *Populus* species grown for three growing seasons in control and FACE treatments. Values are mean values ($n = 6$) with standard errors in parenthesis.

	Inorganic soil N		Annual litterfall
	Spring	Fall	
P. alba			
Control	35.0 (1.8)	30.1 (5.7)	533 (23)
FACE	33.2 (4.2)	11.0 (2.4)	564 (27)
P. nigra			
Control	35.9 (2.3)	36.2 (6.7)	709 (45)
FACE	38.0 (1.4)	8.8 (2.2)	769 (55)
P. × *euramericana*			
Control	40.1 (1.9)	20.6 (1.3)	679 (20)
FACE	35.6 (4.0)	9.9 (2.1)	711 (34)

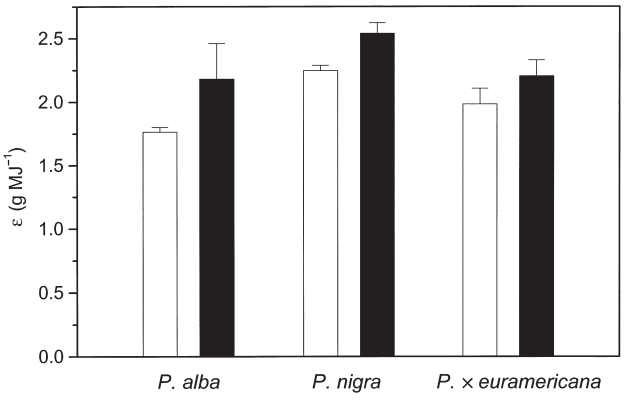

Figure 4. Light-use efficiency (ε = aboveground biomass produced divided by accumulated absorbed photosynthetically active radiation) of three *Populus* species in the third growing season. Mean values (+ standard error) of the control (open bars) and FACE (closed bars) treatments are presented; $n = 3$ plots.

pending on species. These results are in agreement with those obtained with an 8-cm diameter corer (Lukac et al. 2003), although the magnitude of stimulation that we observed was smaller. The effect of elevated [CO_2] on belowground biomass production was comparable with its effect on aboveground biomass so that the R/S ratio was unaffected, in agreement with findings for other poplar genotypes (Radoglou and Jarvis 1990, Pregitzer et al. 1995).

Enquist and Niklas (2002) derived general biomass relationships among plant parts, and showed that those allocation rules are conservative and relatively insensitive to environmental conditions. In most field experiments, there has been no significant effect of elevated [CO_2] on R/S ratio in either broadleaf or coniferous trees (Norby et al. 1995, Rey and Jarvis 1997, Tissue et al. 1997, Crookshanks et al. 1998).

Canopy Productivity Index was stimulated ($P = 0.08$) by the FACE treatment, with a mean increase for the three species of 20%; the stimulation was greatest in *P. alba* (38%). These values agree with those of Norby et al. (1999), who calculated a mean increase in CPI of 26% from 13 different experiments with field-grown trees in elevated [CO_2]. This stimulation was sustained after canopy closure, and the third-year CPI was higher in the FACE treatment, which supports the premise of Norby et al. (1999) that an increase in CPI would be a robust response even in closed canopies. Similarly, the largest stimulation of ε occurred in *P. alba*. In agreement with results from a pine forest exposed to FACE (DeLucia et al. 2002), stimulation of ε was caused by increased woody biomass production ($P = 0.02$) with no significant effect on accumulated APAR ($P = 0.4$) or leaf litter production (Tables 3 and 4). The absence of significant effects on LAI in a closed canopy (mid-second year onward) support these findings (Gielen et al. 2001). Our values of ε in the control treatment compare closely with those reported in the literature for poplar species and hybrids (Cannell et al. 1988, Green et al. 2001). Moreover, we found no evidence of an increase in branch mortality in elevated [CO_2], which can occur when shading increases in response to elevated [CO_2] (Gielen et al. 2002). For this reason, only long-lived aboveground components were sampled.

Wood density was unaffected by elevated [CO_2] in all of the HGIs, in agreement with the observations of Ceulemans et al. (2002) for Scots pine seedlings grown in open-top CO_2 fumigation chambers for 3 years. In contrast, there was a significant species effect on both HGI 1 and HGI 2, which agrees with the results of Jourez et al. (2001), who reported values from 0.353 to 0.426 g cm^{-3} for the bottom of young stems of a *P.* × *euramericana* clone, whereas Chantre and Chaunis (1992) re-

Table 5. Stem wood density (g cm^{-3}) of three *Populus* species grown for three growing seasons in control and FACE treatments. Values are means ($n = 12$) with standard errors in parenthesis for stem portions corresponding to the three height growth increments (HGIs). A mean value ($n = 36$) for the whole stem with standard error in parenthesis is also indicated.

Stem portion	*P. alba*		*P. nigra*		*P.* × *euramericana*	
	Control	FACE	Control	FACE	Control	FACE
Whole stem	0.381 (0.013)	0.388 (0.008)	0.409 (0.011)	0.408 (0.009)	0.350 (0.017)	0.348 (0.014)
HGI 1	0.379 (0.005)	0.386 (0.005)	0.367 (0.004)	0.380 (0.003)	0.311 (0.005)	0.314 (0.003)
HGI 2	0.329 (0.004)	0.365 (0.010)	0.387 (0.007)	0.381 (0.004)	0.306 (0.004)	0.303 (0.004)
HGI 3	0.441 (0.018)	0.422 (0.006)	0.470 (0.011)	0.467 (0.011)	0.434 (0.024)	0.440 (0.015)

ported lower values of between 0.257 and 0.373 g cm^{-3} for young stems of 25 different poplar clones. The wood density values of HGI 3 were considerably higher than those of HGI 1 and HGI 2. A similar increase in wood density in young poplar has been reported in specific experiments (Kellogg and Swan 1986, Singh 1986).

In conclusion, our experiment confirmed inter-specific differences in biomass production in poplar, and demonstrated that elevated atmospheric [CO_2] enhanced productivity and light-use efficiency of a poplar SRC ecosystem without changing biomass allocation. It remains an open question whether this stimulation will continue for longer periods, and how it would be affected by limitations in soil water and mineral nutrient availability. Reduced soil inorganic nitrogen as a result of increased [CO_2] in our experiment raises the possibility of reduced long-term productivity. If the amount of carbon incorporated in agroforestry systems increases with rising [CO_2], this will not necessarily result in increased ecosystem carbon sequestration because a significant fraction of this carbon is lost to heterotrophic respiration (Schlesinger 1997). Therefore, the fate of carbon in the soil–microbial–root system must be known before sound predictions of carbon sequestration potential can be made.

Acknowledgments

This research was conducted within the framework of the following programs: EU-POPFACE (ENV4-CT97-0657), Centre of Excellence "Forest and Climate" (MIUR Italian Ministry of University and Research), MIUR-COFIN 2000 (coordinated by M. Borghetti). The authors acknowledge M. Hovenden (University of Tasmania) for language revision, and P. Corona (University of Viterbo), T. Crowe (University of Southampton) and S. Van Dongen (University of Antwerpen) for statistical advice. We also thank T. Oro, B. Assissi and M. Tamantini for technical assistance, as well as G. Avino, B. Bartoli, A. Claus and I. Laureysens for their help with the harvests. B. Gielen is a Research Assistant of the Fund for Scientific Research-Flanders (F.W.O.-Vlaanderen).

References

Bernacchi, C.J. 2002. Improved temperature response functions for modeling photosynthetic carbon assimilation in the context of rising carbon dioxide. Ph.D. Thesis, University of Illinois, 136 p.

Bosac, C., S.D.L. Gardner, G. Taylor and D. Wilkins. 1995. Elevated CO_2 and hybrid poplar: a detailed investigation of root and shoot growth and physiology of *P. euramericana* 'Primo.' For. Ecol. Manage. 74:103–116.

Calfapietra, C., B. Gielen, M. Sabatti, P. De Angelis, G. Scarascia Mugnozza and R. Ceulemans. 2001. Growth performance of *Populus* exposed to "Free Air Carbon dioxide Enrichment" during the first growing season in the POPFACE experiment. Ann. For. Sci. 58:819–828.

Cannell, M.G.R., L.J. Sheppard and R. Milne. 1988. Light use efficiency and woody biomass production of poplar and willow. Forestry 61:125–136.

Cataldo, D.A., M. Haroon, L.E. Schrader and V. Young. 1975. Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. Commun. Soil Sci. Plan. 6:71–80.

Ceulemans, R. and M. Mousseau. 1994. Effects of elevated atmospheric CO_2 on woody plants. Tansley Review No. 71. New Phytol. 127:425–446.

Ceulemans, R., B.Y. Shao, X.N. Jiang and J. Kalina. 1996. First- and second-year aboveground growth and productivity of two *Populus* hybrids grown at ambient and elevated CO_2. Tree Physiol. 16: 61–68.

Ceulemans, R., M.E. Jach, R. Van de Velde, J.X. Lin and M. Stevens. 2002. Elevated atmospheric CO_2 alters wood production, wood quality and wood strength of Scots pine (*Pinus sylvestris* L.) after three years of enrichment. Global Change Biol. 8:153–162.

Chantre, G. and S. Chaunis. 1992. Etude de la variabilité des qualités papetières de 25 clones de peuplier agés d'un an. Ann. AFOCEL, pp 219–249.

Corona, P. 2000. Introduzione al rilevamento campionario delle risorse forestali. CUSL, Florence, 284 p.

Crookshanks, M., G. Taylor and M. Broadmeadow. 1998. Elevated CO_2 and tree root growth: contrasting responses in *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris*. New Phytol. 138: 241–250.

Curtis, P.S. and J.A. Teeri. 1992. Seasonal responses of leaf gas exchange to elevated carbon dioxide in *Populus grandidentata*. Can. J. For Res. 22:1320–1325.

Curtis, P.S., D.R. Zak, K.S. Pregitzer and J.A. Teeri. 1994. Above- and below-ground response of *Populus grandidentata* to elevated atmospheric CO_2 and soil N availability. Plant Soil 165:45–51.

DeBell, D.S. and A. Harrington. 1997. Productivity of *Populus* in monoclonal and polyclonal blocks at three spacings. Can. J. For. Res. 27:978–985.

DeLucia, E.H., J.G. Hamilton, S.L. Naidu et al. 1999. Net primary production of a forest ecosystem with experimental CO_2 enrichment. Science 284:1177–1179.

DeLucia, E.H., K. George and J.G. Hamilton. 2002. Radiation-use efficiency of a forest exposed to elevated concentrations of atmospheric carbon dioxide. Tree Physiol. 22:1003–1010.

Dickson, R.E., M.D. Coleman, D.E. Riemenschneider, J.G. Isebrands, G.E. Hogan and D.F. Karnosky. 1998. Growth of five hybrid poplar genotypes exposed to interacting elevated CO_2 and O_3. Can. J. For. Res. 28:1706–1716.

Enquist, B.J. and K.J. Niklas. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. Science 295: 1517–1519.

Gielen, B. and R. Ceulemans. 2001. The likely impact of rising atmospheric CO_2 on natural land and managed *Populus*: a literature review. Environ. Pollut. 115:335–358.

Gielen, B., C. Calfapietra, M. Sabatti and R. Ceulemans. 2001. Leaf area dynamics in a poplar plantation under free-air carbon dioxide enrichment. Tree Physiol. 21:1245–1255.

Gielen, B., C. Calfapietra, A. Claus, M. Sabatti and R. Ceulemans. 2002. Crown architecture of *Populus* spp. is differentially modified by free-air CO_2 enrichment (POPFACE). New Phytol. 153:91–100.

Gower, S.T., C.J. Kucharik and J.M. Norman. 1999. Direct and indirect estimation of leaf area index, fAPAR, and net primary production of terrestrial ecosystems. Remote Sens. Environ. 70:29–51.

Grassi, G., G. Gosse and G. Dos Santos. 1990. Biomass for energy and industry. Vol. I. *In* Policy, Environment, Production and Harvesting. Elsevier Applied Science, London, 697 p.

Green, D.S., E.L. Kruger, G.R. Stanosz and J.G. Isebrands. 2001. Light-use efficiency of native and hybrid poplar genotypes at high levels of intracanopy competition. Can. J. For. Res. 31:1030–1037.

Hamilton, J.G., E.H. DeLucia, K. George, S.L. Naidu, A.C. Finzi and W.H. Schlesinger. 2002. Forest carbon balance under elevated CO_2. Oecologia 131:250–260.

Hansen, E.A. 1991. Poplar woody biomass yields: a look to the future. Biomass Bioenergy 1:1–7.

Heilman, P.E., G. Ekuan and D. Fogle. 1994. Above- and below-ground biomass and fine roots of 4-year-old hybrids of *Populus trichocarpa* × *Populus deltoides* and parental species in short-rotation culture. Can. J. For. Res. 24:1186–1192.

Hendrey, G.R., K.F. Lewin and J. Nagy. 1993. Free air carbon dioxide enrichment: development, progress, results. Vegetatio 104/105: 17–31.

Hohenstein, W.G. and L.L. Wright. 1994. Biomass energy production in the United States—an overview. Biomass Bioenergy 6:161–173.

Jourez, B., A. Riboux and A. Leclerq. 2001. Comparison of basic density and longitudinal shrinkage in tension wood and opposite wood in young stems of *Populus euramericana* cv. Ghoy when subjected to a gravitational stimulus. Can. J. For. Res. 31: 1676–1683.

Karnosky, D.F., B. Gielen, R. Ceulemans, W.H. Schlesinger, R.J. Norby, E. Oksanen, R. Matyssek and G.R. Hendrey. 2001. FACE systems for studying the impacts of greenhouse gases on forest ecosystems. *In* The Impact of Carbon Dioxide and Other Greenhouse Gases on Forest Ecosystems. Eds. D.F. Karnosky, R. Ceulemans, G.E. Scarascia-Mugnozza and J.L. Innes. CABI, Wallingford, U.K., pp 297–324.

Keeney, D.R. and D.W. Nelson. 1982. Nitrogen inorganic forms. *In* Methods of Soil Analysis. Part 2. Eds. A.L. Page, R.H. Miller and D.R. Keeney. American Society of Agronomy, Madison, WI, pp 643–698.

Kellogg, R.M. and E.P. Swan. 1986. Physical properties of black cottonwood and balsam poplar. Can. J. For. Res. 16:491–496.

King, J.S., K.S. Pregitzer, D.R. Zak, J. Sober, J.G. Isebrands, R.E. Dickson, G.R. Hendrey and D.F. Karnosky. 2001. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO_2 and tropospheric O_3. Oecologia 128:237–250.

Kubiske, M.E., K.S. Pregitzer, C.J. Mikan, D.R. Zak, J.L. Maziasz and J.A. Teeri. 1997. *Populus tremuloides* photosynthesis and crown architecture in response to elevated CO_2 and soil N availability. Oecologia 110:328–336.

Littell, R.C., G.A. Milliken, W.W. Stroup and R.D. Wolfinger. 1996. SAS System for mixed models. SAS Institute, Cary, NC, 633 p.

Lloyd, J. and G.D. Farquhar. 2000. Do slow-growing species and nutrient stressed plants consistently respond less to elevated CO_2? A clarification of some issues raised by Poorter (1998). Global Change Biol. 6:871–876.

Loewe, A., W. Einig, L. Shi, P. Dizengremel and R. Hampp. 2000. Mycorrhiza formation and elevated CO_2 both increase the capacity for sucrose synthesis in source leaves of spruce and aspen. New Phytol 145:565–574.

Lukac, M., C. Calfapietra and D. Godbold. 2003. Production, turnover and mycorrhizal colonisation of root systems of three *Populus* species grown under elevated CO_2 (POPFACE). Global Change Biol. In press.

MacPherson, G. 1995. Home-grown energy from short-rotation coppice. Farming Press Books, Ipswich, U.K., 214 p.

Miglietta, F., A. Peressotti, F.P. Vaccari, A. Zaldei, P. De Angelis and G. Scarascia-Mugnozza. 2001. Free-air CO_2 enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. New Phytol. 150:465–476.

Monteith, J.L. 1972. Solar radiation and productivity in tropical ecosystems. J. Appl. Ecol. 9:747–766.

Monteith, J.L. 1977. Climate and efficiency of crop production in Britain. Philos. Trans. R. Soc. Lond. B Biol. Sci. 281:277–294.

Norby, R.J. 1996. Forest canopy productivity index. Nature 381:564.

Norby, R.J., S.D. Wullschleger, C.A. Gunderson and C.T. Nietch. 1995. Increased growth efficiency of *Quercus alba* trees in a CO_2-enriched atmosphere. New Phytol. 131:91–97.

Norby, R.J., S.D. Wullschleger, C.A. Gunderson, D.W. Johnson and R. Ceulemans. 1999. Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell Environ. 22: 683–714.

Norby, R.J., D.E. Todd, J. Fults and D.W. Johnson. 2001. Allometric determination of tree growth in a CO_2-enriched sweetgum stand. New Phytol. 150:477–487.

Oechel, W.C. and B.R. Strain. 1985. Native species responses to increased atmospheric carbon dioxide concentration. *In* Direct Effects of Increasing Carbon Dioxide on Vegetation. Eds. B.R. Strain and J.D. Cure. Department of Energy, Office of Basic Energy Sciences, Carbon Dioxide Research Division, Springfield, VA, Washington, DC, pp 117–154.

Poorter, H. 1998. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO_2? Global Change Biol. 4:693–697.

Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri and C.S. Vogel. 1995. Atmospheric CO_2, soil nitrogen and turnover of fine roots. New Phytol. 129:579–585.

Radoglou, K.M. and P.G. Jarvis. 1990. Effects of CO_2 enrichment on four poplar genotypes. I. Growth and leaf anatomy. Ann. Bot. 65:617–626.

Rey, A. and P.G. Jarvis. 1997. Growth response of young birch trees (*Betula pendula* Roth.). *In* Impacts of Global Change on Tree Physiology and Forest Ecosytems. Eds. G.M.J. Mohren, K. Kramer and S. Sabaté, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 207–212.

Saxe, H., D.S. Ellsworth and J. Heath. 1998. Tree and forest functioning in an enriched CO_2 atmosphere. Tansley Review No. 98. New Phytol. 139:395–436.

Schlesinger, W.H. 1997. Biogeochemistry and analysis of global change. 2nd Edn. Academic Press, New York, 592 p.

Singh, T. 1986. Wood density variation of six major tree species of the Northwest Territories. Can. J. For. Res. 16:127–129.

Stettler, R.F. and P.E. Heilman. 1984. Short-rotation poplar culture in the Pacific Northwest: components of a genetic program. *In* Ecology and Management of Forest Biomass Production Systems. Ed. K. Perttu. Swed. Univ. Agric. Sci. Dep. Ecol. Environ. Res. Rep. 15:217–232.

Tissue, D.T., R.B. Thomas and B.R. Strain. 1997. Atmospheric CO_2 enrichment increases growth and photosynthesis in *Pinus taeda*: a 4-year experiment in the field. Plant Cell Environ. 20:1123–1134.

Tognetti, R., A. Longobucco, A. Raschi, F. Miglietta and I. Fumagalli. 1999. Responses of two *Populus* clones to elevated atmospheric CO_2 concentration in the field. Ann. For. Sci. 56:493–500.

Wait, D.A., C.G. Jones, J. Wynn and F.I. Woodward. 1999. The fraction of expanding to expanded leaves determines the biomass response of *Populus* to elevated CO_2. Oecologia 121:193–200.

Zavitkovski, J. 1982. Characterization of light climate under canopies of intensively cultured hybrid poplar plantations. Agric. Meteorol. 25:245–255.