conditions' resulted, at least partly, from the increase in temperature. The observation of lower leaf conductance due to mild water shortage in *T. durum* and *V. faba* is in line with other studies (e.g., Mitchell et al 2001). More severe reductions were observed with 'elevated grown' plants (*T. durum* −41%, *V. faba* −26%) as a result of the higher saturation deficit and the low water potential in air.

Van Oijen et al (1999) reported a decrease in HI due to the influence of growth at elevated [CO_2], Wheeler et al (1996) did not observe any changes in HI and McKee and Woodward (1994) found an increase in HI under the influence of elevated [CO_2] which corresponds with the present study. HI of well watered plants increased compared to drought stressed plants where HI decreased under 'elevated conditions'. Wu and Wang (2000) also found an increase of HI in well watered plants of *V. faba* compared to a decrease in drought stressed plants grown under elevated [CO_2]. Water stress is reported to have either positive (Sánchez et al 1998) or negative effects (Mwanamwenge et al 1999) on HI. In the present study a decrease of HI in drought stressed plants was observed in 'ambient' grown plants compared to an increase in 'elevated' grown plants. It was concluded that drought stress resulted in an intensified carbon allocation to roots, which was partly compensated by elevated CO_2.

Calorific values are mirroring the source sink relations, which are determined by the photosynthetic rates and the possibility to grow. Thus, high photosynthetic rates combined with temporally limited growth will lead to higher calorific values of the organ. The analysis of calorific values (J/g) of plants tissue at final harvest showed only small differences between plant material grown at 'ambient' or 'elevated' conditions. Significant differences were only observed in kernel of *T. durum* and in pods, straw and roots of *V. faba*. This leads to the assumption that most of the assimilated carbon was invested in faster growth and not in the production of higher energy consuming processes and/or substances. Significant changes in calorific values of total biomass were only observed in *V. faba* (decrease). Moderate drought stress increased calorific values of roots, straw and seeds of *T. durum* and *V. faba* irrespectively of growth [CO_2].

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ELEVATED CO_2 DIFFERENTIALLY EFFECTS PHOTOSYNTHESIS AND CARBON BALANCE IN POPLAR STANDS, A FOUR YEAR STUDY

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Keywords: Stand-level CO_2 exchange, soil carbohydrates, soil nutrient depletion, poplars

INTRODUCTION

There has been a long-standing discussion of direct and indirect effects stimulated photosynthetic CO_2 influx in elevated [CO_2] on respiratory activities in plants and ecosystems. Although most tree species have shown a stimulation of CO_2 influx and leaf respiration (Davey et al 2004) in response to elevated [CO_2], and of above- and belowground biomass production (Bosac et al 1995, Hungate et al 1997, Norby et al 1999, DeLucia et al 2002), fewer studies have examined the longer-term effects of elevated CO_2 on plant biomass production and the influence that might have on belowground processes and feed-back responses, i.e. root exudation, mineralization, and depletion of soil nutrients (Wang et al 1998, Ceulemans et al 1999).

MATERIALS AND METHODS

Site and stand characteristics. This experiment was conducted at the Biosphere 2 Laboratory (B2L) within the Intensively-managed Forest Mesocosm (IFM). Each of the 3 bays contained 29–32 trees from cuttings of an eastern cottonwood (*Populus deltoides* Bartr.) clone planted in May 1998. The 3 separated bays had growing areas of 34×18 m and a soil volume of 550 m^3 (Murthy et al 2003). The 1 m-deep constructed soil approximates a rich agricultural loam, with approximately 30% sand, 36% silt, and 24% clay has evolved in place over 12 years, and now shows normal bulk density distribution with depth, a N concentration of 2–3 mg g^{-1}, a C/N ratio of 9, and microbial flora typical of agricultural and natural soils (Lipson et al 2004, in review).

Experimental protocol. Growing season air temperature was monitored continuously and was maintained at 30/25 °C (day night) throughout each growing season. The bays were operated in

a closed state during the day and an open-flow mode during the night so that ambient (~400 ppm) or elevated (800 and 1200 ppm) [CO_2] were maintained automatically by CO_2 injection in the day, and by managing fan speeds to stabilize respiratory CO_2 build up at night. System Net CO_2 Exchange (SNCE, $\mu mol\, m^{-2}\, s^{-1}$, soil surface area basis) was calculated from changes in the mesocosm CO_2 concentrations measured at 15 min intervals in the light ($SNCE_L$) and dark ($SNCE_D$). Spot-measurements of soil respiration were also made monthly at 28 locations within each bay using a closed-chamber gas exchange system. Aboveground biomass was determined by collecting litter at frequent intervals, and coppicing the trees at the end of each growing season (except 2002–3). Belowground biomass was determined by excavating nine trees in each bay in 2002, and all roots in a 1.5 m radial area around the stem were divided into >20 mm, 2–20 mm, and <2 mm fractions.

RESULTS

System Carbon Exchange. Seasonal patterns of canopy development in response to elevated CO_2 are evident in the increasing average monthly $SNCE_L$ measured at peak light 12:00 to 14:00 h (Fig. 1A, C) throughout 2002–3. Stands in 800 ppm and 1200 ppm treatments took up an average of 21 and 83%, respectively, more CO_2 than the ambient 400 ppm treatment. Throughout the 2002 growing season, $SNCE_D$ was clearly greater in elevated CO_2 treatments (Fig. 2A; $P = 0.002$). *In situ* soil respiration measurements from soil collars averaged over the entire growing season in 2002 were significantly greater in the elevated CO_2 treatments, on average 45 and 102% greater in 800 and 1200 ppm treatments, respectively (Fig. 2B; $P < 0.001$). As observed previously (Murthy et al 2003), whole system respiration rates were lower than those of *in situ* soil respiration from soil collars. Substrate (glucose) induced soil respiration (SIR) *in vitro* was also significantly increased by increasing [CO_2] (Fig. 2C), 42 and 80% greater in the 800 and 1200 ppm treatments, respectively.

Stand Biomass Distribution. Four years of growth under elevated CO_2 resulted in increased cumulative root, foliar, and total aboveground biomass (Table 1). Stem and branch biomass production in the coppiced plantation increased each year. By the end of the four-year experiment the 800 and 1200 ppm CO_2 treatments produced 26.8% and 27.5% respectively, more total biomass than the 400 ppm treatment. Trees in the 800 and 1200 ppm CO_2 treatments produced an average of 27% and 37%, respectively, more cumulative root biomass per tree than the 400 ppm control treatment, and most root biomass was found in the upper 25 cm of the soil profile. Although only a small proportion of total root biomass was in the 0–2 mm size class, fine roots also increased 48–68% in response to 3 years of growth in elevated CO_2 (Barron-Gafford et al 2004, in press).

DISCUSSION

The study is distinctive in that it was carried out using stands of trees grown in nutrient-rich soil in a closeable flow-through system. This model field laboratory permitted direct and precise estimates of net CO_2 exchange, especially of system respiratory efflux at night, which is less easily measured in flux tower studies. Four years of growth under elevated CO_2 increased plant biomass production above- and

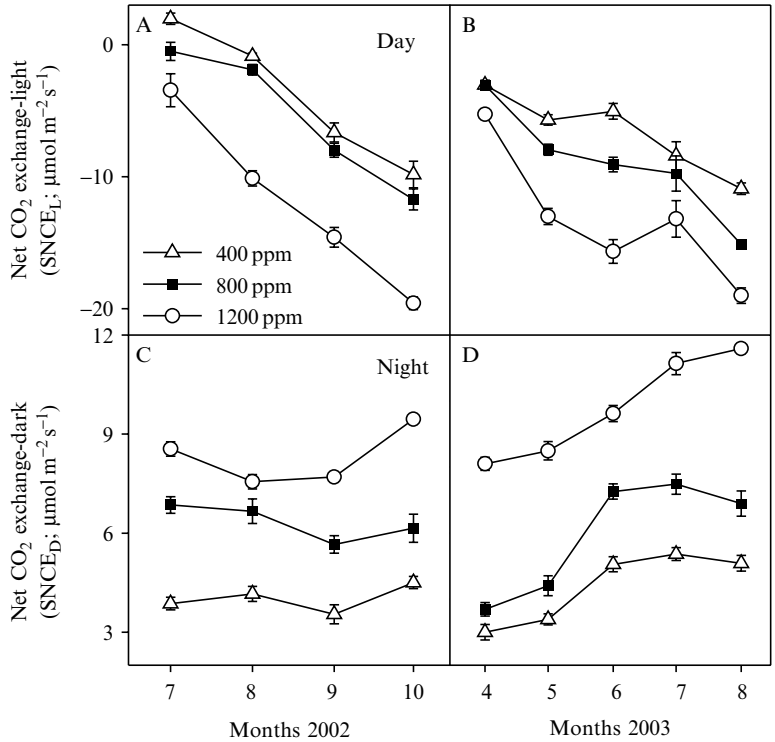

Figure 1: Stand CO_2 exchange in the light ($SNCE_L$) and dark ($SNCE_D$) ($\mu mol\, m^{-2}\, s^{-1}$) for *Populus deltoides* under ambient and elevated atmospheric [CO_2]. Data are means of five representative days per month, ±SE.

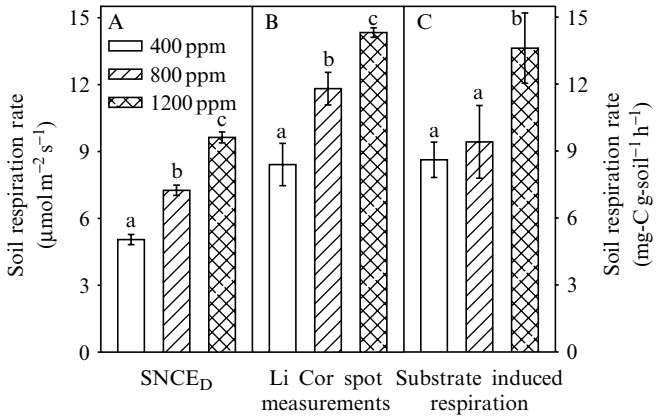

Figure 2: (A) Whole system respiration $SNCE_D$ ($\mu mol\,m^{-2}\,s^{-1}$), (B) respiration of soil collars ($\mu mol\,m^{-2}\,s^{-1}$) and (C) substrate induced soil respiration ($\mu g\text{-}C\,g\text{-}soil^{-1}\,h^{-1}$) after 4-years growth of *Populus deltoides* under ambient and elevated atmospheric [CO_2]. Data are treatment means for the 2003, ±SE.

Table 1: Average stem, branch, and foliar biomass production (kg $tree^{-1}$) in each [CO_2] treatment in the first and last years of the experiment

	2000			2003		
Treatment	Stem	Branch	Foliage	Stem	Branch	Foliage
400	4.64	6.58	8.91	3.8	8.42	12.22
800	7.51	10.71	14.34	5.79	11.91	17.39
1200	8.78	12.36	16.46	5.85	11.6	18.97

belowground (Table 1). In the first growing season, 2000, much of the stimulation in growth in response to elevated CO_2 was due to increased woody biomass production, particularly in the stem. Foliar biomass was stimulated more by elevated [CO_2] than the other components in 2003, presumably because the stand was not coppiced in 2002. The stimulation in $SNCE_L$ was thus due to increased foliar biomass under elevated growth CO_2.

Four years of growth of eastern cottonwoods under elevated [CO_2] also increased system CO_2 efflux, at least in part due to elevated foliar biomass. However, $SNCE_D$ was uncoupled from $SNCE_L$ early in the growing season before canopy development had responded to elevated [CO_2] (Fig. 1), and presumably was dominated at the time by soil respiration, that was also responding to prior growth in elevated [CO_2]. The system temperature was lowered each winter to precipitate leaf fall prior to coppicing, and this would be expected to lead to death of fine-roots. Indeed, the more detailed analyses of soil fractions by Truemann and Gonzalez-Meler (2005, in press) show a strong annual cycle of stimulated fine root production by elevated [CO_2] in Spring, and decline in this fraction in Fall as expected from the studies of Matamala and Schlesinger (2003). We believe that this [CO_2] dependent soil-C fraction was responsible for the [CO_2] stimulated system CO_2 efflux prior to canopy development. Consistent with the girdling studies of Högberg et al (2001), our analyses showed that although total soil-C declined over the 4-year experiment, elevated [CO_2] transiently stimulated soil carbohydrate levels, and these also contributed to stimulated system CO_2 efflux at elevated [CO_2] (Barron-Gafford et al 2004, in press). Furthermore, stable isotope analyses of soil CO_2 efflux by Trueman and Gonzalez-Meler (2005, in press), showed that elevated [CO_2] also stimulated the oxidation of old soil-C (Cardon et al 2001).

Our studies do not provide evidence for increased C-sequestration in this soil by these rapidly growing plantations under elevated [CO_2]. Rather, even though stimulation of aboveground CO_2 influx by elevated [CO_2] lead to increased aboveground and belowground biomass, it also promoted increased system CO_2 efflux through stimulation of respiratory activities in all above- and belowground components of the system. In addition, removal of increased foliar, branch and stem biomass in the elevated [CO_2] treatments from the coppiced system studied here led to rapid depletion of soil phosphorus, potassium and magnesium level. These comprehensive large-scale experiments reveal the complexities and feedbacks in stand and ecosystem-level responses following the stimulation of photosynthetic CO_2 influx at elevated atmospheric [CO_2].

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