Elevated atmospheric-carbon dioxide concentration increases soil respiration in a mid-successional lowland forest

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Significant increases in both soil respiration and root biomass (50 and 30%, respectively) were detected in a mid-successional lowland forest soil exposed to elevated atmospheric [CO2] compared with soil exposed to ambient [CO2].

Many studies have focused on the way in which elevated atmospheric [CO2] will affect vegetation processes. Photosynthesis has been shown to be enhanced by elevated [CO2] in plants using the C3 pathway (Kimball et al., 1993). In many instances this can lead to an increase in dry biomass and, particularly in crop species, an accumulation of carbohydrates in the green tissues of the plant (Allen, 1990; Kimball et al., 1993). However, one area of which relatively little is known is the effect of elevated [CO2] on belowground processes. There have been a number of reports citing an increase in total root biomass which accompanies increases in total plant biomass of C3 species grown in elevated [CO2] (Curtis et al., 1989; Berryman et al., 1993). Reports of changes in the root-to-shoot ratio are less consistent, although a number of studies do show a greater allocation of biomass to roots in elevated [CO2] (Rogers et al., 1983; Hocking and Meyer, 1991). Of daily photosynthetic carbon production 30 to 60% is lost in respiration and a significant portion (between 10 and 50%) of this carbon is released from roots (Lambers, 1985) but studies on the effects of elevated [CO2] on soil and root respiration are few in number and generally based on short-term exposure. Results from these studies have shown a decrease (Callaway et al., 1994), an increase or no effect (Gifford et al., 1985), depending on species and growing conditions. Stimulation of soil respiration by elevated [CO2] has also been observed for marsh vegetation (Ball and Drake, 1998). This increase in soil respiration in swards of Scirpus olneyi was accompanied by an 83% increase in root biomass. However increased soil respiration was also observed in swards of Spartina patens, although no increase in root biomass was detected (Ball and Drake, 1998). Further work is required to establish the long-term effects of elevated [CO2] on soil and root respiration.

We have examined the effects of long-term exposure of elevated atmospheric [CO2] on in situ soil respiration and root respiration within a natural population of the temperate zone shrub Lindera benzoin (spice-bush). The study site was mid-successional lowland forest located 300 m inland from the Rhode River, a subsidiary of the Chesapeake Bay, MD, at a latitude of 36°53′N and longitude of 76°33′W. The site, which was dominated by mature L. tulipifera and L. styraciflua in the overstorey, was occupied almost exclusively by the C3 shrub, L. benzoin on Adelphia sandy loam (Kirby and Matthews, 1973). Plots at this site were exposed to elevated atmospheric [CO2] during every growing season (May to October) from 1991 until 1996.

Within this site a 60 × 30 m area was divided into three 20 × 30 m blocks arranged in parallel along a slight slope (approx. 3%). Within each block, plants were grouped into three experimental treatments: control, ambient and elevated. The control treatment is not relevant to this study. For elevated and ambient treatments, plants were enclosed within 3.4 m tall × 3.8
was calculated from CO2 accumulation rates, as bare soil surface between plants. Respiratory activity respiration chamber (dia 10 cm) over the naturally ment took about 5 min, and was made by placing the day beginning at 10.30 h. Each individual measure- ment were recorded from July–August 1995 (3 weeks, Julian days 208–230) using a portable environmental gas monitor (EGM-1, PP Systems, UK) connected to a soil respiration chamber (SRC-1, PP Systems, UK). At the same time, soil temperature at a depth of 1.5 cm was measured using a battery-operated digital thermomter (HH-25TC, Omega, USA) and a thermo-couple (Type T Cu–Cu–Ni, Omega, USA). Measurements were taken five times on each sample day beginning at 10.30 h. Each individual measurement took about 5 min, and was made by placing the respiration chamber (dia 10 cm) over the naturally bare soil surface between plants. Respiratory activity was calculated from CO2 accumulation rates, as described by the manufacturer, (Anon, 1990), and expressed as μmol CO2 m⁻² s⁻¹. For soil respiration measurements, the five readings taken from each plot were used to obtain a mean value for that field chamber. The three field chambers were treated as replicates. Repeated measures ANOVA was used to interpret the results presented in Fig. 1.

Root respiration measurements were taken on material obtained on five separate occasions (Julian dates 208, 210, 212, 216 and 230). Following soil respiration measurements, 5.5 cm dia cores (depth 10 cm, n = 5) were obtained using an auger. All root material was removed by washing the core over a fine mesh net (1 mm) with Cu2Cl (0.2 mM), to counteract membrane damage sustained during separation. Root respiration was measured using a dark-type oxygen electrode (Rank Brothers, Cambridge, UK) with a high sensi-tivity membrane (Yellow Springs Instrument Co. Inc., OH, USA). The roots were washed in distilled water prior to being placed in a buffer solution of 10 mM MES (2[N-morpholino] ethanesulphonic acid, pH 6) and the oxygen concentration monitored over time at 20°C. Following each measurement and rewashing in water, the dry weight of the root material used was assessed by placing the roots in an oven at 60°C until a constant dry weight was obtained. Root respiration was determined as μmol of O₂ utilised g dry root bio-mass s⁻¹.

The results (Fig. 1) are based on the mean daily res-piration rate. Variations in soil respiration over the 3 weeks may have been caused by changes in water availability (not determined) because, although soil temperature varied between 17 and 25°C during the taking of soil respiration measurements, no correlation could be detected between soil temperature and soil respiration ($r^2 = 0.30$).

Mean soil respiration rates measured in field chambers maintained at elevated [CO₂] ranged from 1.8 to 5.0 μmol CO₂ m⁻² s⁻¹ and were significantly greater ($P < 0.05$) on eight of the 10 sampling dates than the rates of 1.2 to 3.8 μmol m⁻² s⁻¹ in chambers containing L. benzoin exposed to ambient [CO₂] (Fig. 1). This general increase in situ soil respiration in field chambers exposed to elevated [CO₂] confirms previous findings based on other natural ecosystems (Ball and Drake, 1998) and supports the hypothesis of Zak et al. (1993) that stimulation of soil processes occurs as a consequence of the effects of elevated [CO₂] on plant physiological processes.

At this site, L. benzoin showed only a slight, non-significant enhancement of aboveground growth when exposed to elevated [CO₂] (Cipollini et al., 1993). However, the authors concluded that nitrogen limitation might have led the plants to store any increased carbon assimilated in belowground growth. Increased root biomass may therefore account for the increased soil respiration observed in Fig. 1. To examine this hypothesis, root respiration was assessed from soil cores taken from field chambers. In all cores, between 70 and 80% (by volume) of the roots were identified as being from L. benzoin, confirming the dominant nature of this plant in this soil (data not shown). When respiration was expressed per unit dried weight of roots, no significant difference was observed between the ambient and elevated [CO₂] systems ($46 \pm 6$ and $52 \pm 8$ μmol O₂ s⁻¹ g dry weight roots⁻¹ respectively), suggesting that elevated [CO₂] does not affect root res-

![Fig. 1. Mean soil respiration rate (μmol CO₂ produced m⁻² s⁻¹) from field chambers exposed to ambient (□) or elevated (●) atmospheric [CO₂] in stands dominated by L. benzoin. Results are the means of five replicates. * indicates a significant differences ($P < 0.05$) between soil respiration rates in field chambers exposed to ambient and elevated [CO₂].](image-url)
piration in \textit{L. benzoin}-dominated systems. However, when these values were expressed in terms per unit of soil, a significant increase was observed in root respiration in samples from field chambers exposed to elevated [CO$_2$] (70 ± 9 µmol O$_2$ s$^{-1}$ kg dry weight soil$^{-1}$ compared to 44 ± 8 µmol O$_2$ s$^{-1}$ kg dry weight soil$^{-1}$ for samples from field chambers exposed to ambient [CO$_2$]). This resulted from a 30% increase in the dry weight of roots present in field chambers exposed to elevated [CO$_2$]. Similar increases in root biomass in plants grown in elevated atmospheric [CO$_2$] were described by Fitter et al. (1996, 1997). Interestingly the % increase in both soil respiration and root respiration (on a soil weight basis) in samples from field chambers exposed to elevated atmospheric [CO$_2$] were both around 50%. These results imply that both an increase in root respiration per unit of soil and an increase in microbial respiration per unit area occurred in soils exposed to elevated [CO$_2$]. However root respiration did not respond to elevated [CO$_2$] on a root dry weight basis. Further work is necessary to establish the effects of elevated [CO$_2$] on the size and activity of the soil microbial community.

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**References**


