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Impact of elevated CO_2 concentration under three soil water levels on growth of *Cinnamomum camphora**

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Abstract: Forest plays very important roles in global system with about 35% land area producing about 70% of total land net production. It is important to consider both elevated CO_2 concentrations and different soil moisture when the possible effects of elevated CO_2 concentration on trees are assessed. In this study, we grew *Cinnamomum camphora* seedlings under two CO_2 concentrations (350 μmol/mol and 500 μmol/mol) and three soil moisture levels [80%, 60% and 40% FWC (field water capacity)] to focus on the effects of exposure of trees to elevated CO_2 on underground and aboveground plant growth, and its dependence on soil moisture. The results indicated that high CO_2 concentration has no significant effects on shoot height but significantly impacts shoot weight and ratio of shoot weight to height under three soil moisture levels. The response of root growth to CO_2 enrichment is just reversed, there are obvious effects on root length growth, but no effects on root weight growth and ratio of root weight to length. The CO_2 enrichment decreased 20.42%, 32.78%, 20.59% of weight ratio of root to shoot under 40%, 60% and 80% FWC soil water conditions, respectively. And elevated CO_2 concentration significantly increased the water content in aboveground and underground parts. Then we concluded that high CO_2 concentration favours more tree aboveground biomass growth than underground biomass growth under favorable soil water conditions. And CO_2 enrichment enhanced lateral growth of shoot and vertical growth of root. The responses of plants to elevated CO_2 depend on soil water availability, and plants may benefit more from CO_2 enrichment with sufficient water supply.

Key words: *Cinnamomum camphora*, CO_2 concentration, Soil moisture, Plant growth, Root to shoot ratio
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INTRODUCTION

Current atmospheric carbon dioxide (CO_2) concentration has increased by about 100 μmol/mol since the industrial revolution and is predicted to continue rising approximately 1~2 μmol/mol each year (Keeling *et al*., 1995). During this century CO_2 levels could be doubled or tripled compared to pre-industrial revolution levels (IPCC, 2001). And there is about 35% of land area covered with forest ecosystems producing about 70% of total land net production (Kramer, 1981; Melillo *et al*., 1993; Meyer and Turner, 1992). Forest plays very important roles in the global system than we have always thought. So it is important to consider both elevated CO_2 concentrations and the differences in soil moisture when the possible effects of elevated CO_2 concentration on trees are assessed.

Numerous experiments showed that high atmospheric CO_2 concentration leads to increases in photosynthetic rate and whole-plant growth in many C_3 species, while in C_4 species the increasing effects were much lower (Bowes, 1993; Finzi *et al*., 2001; Ghannoum *et al*., 1997; 2000; Gifford, 1992; Griffin *et al*., 2000; Gunderson *et al*., 2000; Idso and Idso, 1994; Hymus *et al*., 2001a; 2001b; Jach and Ceulemans, 2000; Watling *et al*., 2000). The effect of CO_2 enrichment on plants was limited by soil fertility levels (Coruzzi and Zhou, 2001; Cotrufo *et al*., 1998;

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Deng and Woodward, 1998; Loladze, 2002; Poorter, 1998; LaDeau and Clark, 2001; Oren *et al*., 2001; Walch-Liu *et al*., 2001) and varies under different soil moisture regimes (Wu *et al*., 2002; 2004). Most studies were carried out under favorable water conditions. However, data on the interactive effects of CO_2 and soil moisture on plants are scarce and often contradictory. Some authors claim that the percentage increase in plant growth due to elevated CO_2 concentration is generally not reduced by water stress (Idso and Idso, 1994; Kang *et al*., 2002) whereas the results of many other theoretical projections and field or greenhouse experiments suggest that the relative effects of CO_2 enrichment on plants are constrained by less than optimal levels of soil moisture (Poorter, 1993; 1998; Wu and Wang, 2000). Experiments on broad bean (*Vicia faba*), spring wheat under elevated CO_2 concentration of different soil water contents had been conducted formerly by our group (Wu and Wang, 2000; Lin and Wang, 2002; Wu *et al*., 2002; 2004).

Our hypothesis is that plant morphology of shoot or root would vary to adapt to environment changes, and that the responses to elevated CO_2 concentration may be controlled by soil water availability and experiments with growing seedlings of *Cinnamomum camphora* under two CO_2 concentrations (350 μmol/mol and 500 μmol/mol) and three soil moisture levels [80%, 60% and 40% field water capacity (FWC)] were conducted to observe the effects of exposure of tree seedlings to elevated CO_2 concentration on the morphology and biomass of underground and aboveground plant parts, and their dependence on soil moisture.

MATERIALS AND METHODS

Plant materials and growth conditions

Cinnamomum camphora is a dense broadleaved evergreen that can grow to 15~46 m tall and 5 m in diameter. The shiny foliage is made up of alternate 2~10 cm oval leaves dangling from long petioles with each leaf having three distinct yellowish veins and with the area of whole adult leaf being about 3000~6000 mm^2. The flowers come out in the spring on branching, followed by large crops of fruit comprised of round pea sized berries. It comes from China, Japan, Korea and adjacent parts of East Asia, where it grows in mesic forests at well-drained sites.

An experiment was conducted at Huajiachi campus, Zhejiang University, Hangzhou, China. Plants were grown in two identical controlled greenhouses (Conviron, Controlled Environments Ltd., Canada), one supplied with ambient CO_2 concentration ((350±30) μmol/mol), and another with elevated CO_2 concentration ((500±30) μmol/mol). There were three water level treatments [80%, 60% and 40% field water capacity (FWC)] with ten replicate pots per water level in each greenhouse.

The environmental variables including CO_2 concentration, temperature and light intensity inside the two greenhouses were continuously monitored. Temperature and light intensity were the same in both greenhouses. Only CO_2 concentration was varied in the two greenhouses, one with ambient CO_2, the other with elevated CO_2. The environmental sensors and controlling systems of the two greenhouses were carefully calibrated before start of the experiment, and the environmental factors in the greenhouses were periodically monitored during the entire course of experiment in order to minimize the variance induced by the station in the greenhouses and between greenhouses heterogeneity of environmental conditions.

Air-conditionings inside the greenhouses facilitated the circulation and thorough mixing of air. The temperature inside the greenhouses was controlled at 25~30 °C during daytimes, and to that of the atmosphere during nighttimes. Average relative humidity inside the greenhouses was about 40% during the growth seasons and was measured but not controlled. The environmental variables such as CO_2 concentration, and daytime temperature inside the greenhouses were continuously monitored and controlled by a computer.

Before sowing, the soil was irrigated to 80% FWC. Then, soil samples were taken and analyzed at the laboratory. The results of analysis revealed that soil properties were: pH 7.0, organic matter 1.61%, available N 85.38 mg/kg, available P 31.01 mg/kg, available K 46.58 mg/kg, and FWC 35.6%.

Three soil water levels, 40%, 60% and 80% FWC, were applied to each greenhouse (ten pots per treatment), and kept constant throughout the entire experiment period by simply weighing each pot every 2 d and adding the water lost accordingly (Wu *et al*., 2004). At the late growth phase, when total biomass of plant accounted for more than 0.5% of the total pot weight (plastic pot+soil+soil water+biomass), that fraction of biomass was taken into account.

Growth measurements

Shoot height and root length were measured at first, then six seedlings were randomly selected to determine the wet and dry weight of shoot and root before transplanting, and all the plants were harvested at the end of the experiment. All component dry weights were measured following oven-drying to constant weight at 85 °C. And the water content of shoot and root was calculated by (wet weight–dry weight)/(dry weight). Plants were finally harvested on 20 July, 3 months (92 d) after transplanting.

Experimental design and statistical design

Our experiment consisted of two CO_2 levels (350 μmol/mol and 500 μmol/mol) and three soil water levels (40%, 60% and 80% FWC). A factorial design was used with a total of six treatments, which were designated as HC, HD, MC, MD, LC and LD, respectively, where H, M and L represented high (80% FWC), medium (60% FWC) and low soil moisture (40% FWC), C and D represented current (350 μmol/mol) and elevated CO_2 concentration (500 μmol/mol), respectively. Each treatment had ten replicate pots in the greenhouses. Since the environment was the same in the two greenhouses throughout the plant growth period, pot replication was adequate. Thirty pots were placed in each greenhouse and controlled to three soil moisture levels. H, M and L pots were placed alternately in the greenhouses and randomly changed every 2 d after weighing for soil moisture control, and the greenhouses were changed every week to minimize the variance induced by the station in the greenhouses and by the between-greenhouses heterogeneity of environmental conditions.

Data were analyzed using SPSS 11.5 software for two-way ANOVA and standard deviation. Two-way ANOVA was carried out on shoot height/ root length, shoot/root weight, water content of shoot/ root, as well as length/weight ratio of root to shoot, and ratio of shoot/root weight to height/length to determine the effects of CO_2 level, soil moisture level and their interactions. Because ANOVA and most other statistical tests of significance do not work very well with ratio in very high or very low numbers, the data on ratio of shoot weight to height (WH) and ratio of root weight to length (WL) whose values were less than 0.3 were arcsine transformed with the equation of $y=\arcsin x$ (where y is the data for ANOVA analysis, and x is the original data) before the analyses. Mean values and error bars are calculated on the ten replicate pots of each treatment. And the standard errors are shown with error bars in the figures, respectively.

RESULTS

Impacts on plant shoot growth of higher CO_2 concentration under three soil water levels

Although there were no significant differences between the CO_2 concentrations, higher CO_2 concentration increased shoot height by 6.39%, 6.92% and 1.72%, and shoot weight by 1.45%, 27.04%, 36.25% under 40%, 60% and 80% field water capacity (FWC) soil moisture, respectively (Table 1). The positive effect of high CO_2 concentration on shoot biomass growth of *Cinnamomum camphora* was greater under high soil moisture conditions. As a result, the difference in shoot weight among the three soil moisture levels was greater under elevated CO_2. Elevated CO_2 concentration strongly affected shoot water content (SWC) (Table 2). SWC was increased greatly under 40% and 60% FWC soil moisture, and decreased by 7.38% under 80% FWC soil moisture. Plants grown under elevated CO_2 concentration had larger ratio of shoot weight to height (WH), while plant height was no different between the two CO_2 concentrations (Table 1). The WH exposed to the higher CO_2 concentration increased by 39.58% and 20.45% under 80% and 60% FWC soil moisture, respectively. However, under 40% FWC soil water level, the ratio decreased by 3.37% (Fig.1, $P<0.05$). On the other hand, water deficit significantly decreased plant WH under both ambient and elevated CO_2 concentration (Fig.1, $P<0.01$).

Effects of elevated CO_2 concentration on plant root growth under different soil moisture

Root length was increased by 5.57%, 28.37% and 3.40% by the higher CO_2 concentration under 40%,

Table 1 Effects of elevated CO_2 on shoot height (*SH*), shoot weight (*SW*), root length (*RL*) and root weight (*RW*) under three soil moisture levels

		350 μmol/mol	500 μmol/mol	*P*
SH (cm)	40% FWC	30.83±2.24 a	32.80±1.57 a	NS
	60% FWC	33.11±1.46 ab	35.40±1.69 a	NS
	80% FWC	37.66±3.22 b	38.31±2.30 a	NS
SW (g)	40% FWC	4.15±0.64 a	4.21±0.57 a	NS
	60% FWC	4.59±0.67 a	5.83±0.59 a	NS
	80% FWC	5.90±1.02 a	8.04±0.97 b	NS
RL (cm)	40% FWC	37.18±1.65 a	39.25±2.25 a	NS
	60% FWC	34.22±3.91 a	43.93±1.39 ab	**
	80% FWC	46.24±1.91 b	47.81±0.80 b	NS
RW (g)	40% FWC	4.48±1.00 a	3.69±0.63 a	NS
	60% FWC	5.11±0.73 a	4.94±0.67 a	NS
	80% FWC	4.48±0.71 a	5.44±0.84 a	NS

Significance between 350 μmol/mol and 500 μmol/mol CO_2 concentration (NS: $P>0.05$, $^{**}P<0.01$, $n=10$); for each element, values in the same list followed by different letters are significantly different ($P<0.05$, $n=10$), and the data are shown with mean value±*SE*

Table 2 Effects of elevated CO_2 on shoot and root water content (*SWC* and *RWC*) under three soil moisture levels

		350 μmol/mol	500 μmol/mol	*P*
SWC	40% FWC	1.89±0.04 a	2.06±0.08 a	*
	60% FWC	1.96±0.03 a	2.52±0.04 b	**
	80% FWC	2.14±0.02 b	1.99±0.05 a	*
RWC	40% FWC	1.46±0.06 a	1.69±0.20 a	NS
	60% FWC	1.22±0.03 a	1.93±0.03 a	**
	80% FWC	1.81±0.03 b	1.93±0.07 a	NS

Significance between 350 μmol/mol and 500 μmol/mol CO_2 concentration (NS: $P>0.05$, $^{*}P<0.05$, $^{**}P<0.01$, $n=10$); for each element, values in the same list followed by different letters are significantly different ($P<0.05$, $n=10$), and the data are shown with mean value±*SE*

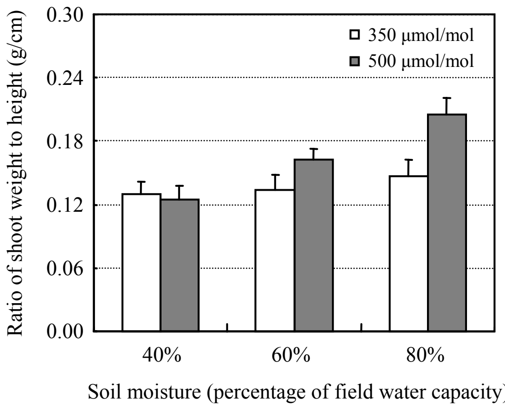

Fig.1 Effects of elevated CO_2 on ratio of shoot weight to height (WH) (g/cm) under three soil moisture levels

60% and 80% FWC soil moisture, and there was significant difference between the CO_2 concentrations ($P<0.01$, Table 1). While high CO_2 concentration decreased root weight by 21.66% under low soil moisture (40% FWC), and increased by 21.26% under high moisture (80% FWC), but there was no significant difference between them (Table 1). The positive effect of high CO_2 concentration on *C. camphora* root growth was only shown under high soil moisture conditions. Root water content (RWC) was obviously increased by high CO_2 concentration under favourable soil water condition (60% FWC, Table 2), while under 40% and 80% FWC soil moisture, there were no significant responses of RWC to CO_2 content variability. The tendency of ratio of root weight to length (WL) was similar to that of root weight, and decreased under low water levels but increased under high soil moisture conditions. However, there were no differences between the two CO_2 concentrations and three water levels of plant W/L ratio (Fig.2).

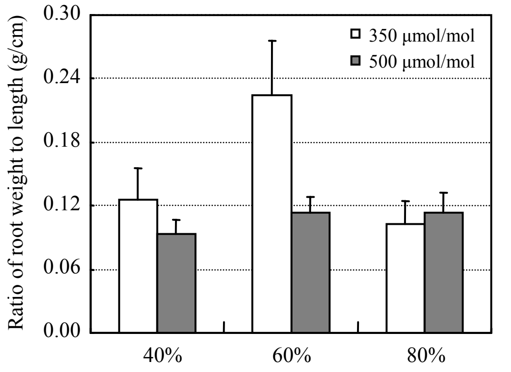

Fig.2 Effects of elevated CO_2 on ratio of root weight to length (WL) (g/cm) under three soil moisture levels

Responses of ratio of root to shoot to elevated CO_2 concentration and different water supply levels

The positive effect of high CO_2 concentration on length ratio of root to shoot of *C. camphora* was only shown under 60% FWC soil moisture, while under 40% and 80% FWC soil water levels CO_2 enrichment resulted in 5.03% and 3.53% decrease, respectively (Fig.3). ANOVA analysis indicated that the interaction between elevated CO_2 concentration, soil water levels, and CO_2 concentration×water on plant growth was not significant. The effects of CO_2 concentration enrichment and different soil water conditions on weight ratio of root to shoot of *C. camphora* are shown in Fig.4 indicating that high CO_2 concentration decreases the ratio. And high soil water content (80% FWC) decreases the ratio by 42.4% and 29.4% compared with 60% FWC under current and elevated CO_2 concentration, respectively. CO_2 concentration enrichment decreased the ratio by 20.42%, 32.78%, 20.59% under 40%, 60% and 80% FWC soil water conditions, respectively. There were significant differences between different CO_2 concentration ($P<0.01$) and soil moisture ($P<0.01$), while the interaction between CO_2 enrichment and soil water levels was not significant.

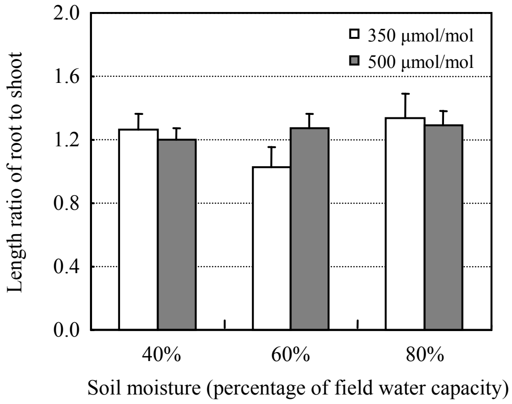

Fig.3 Effects of elevated CO_2 on length ratio of root to shoot under three soil moisture levels

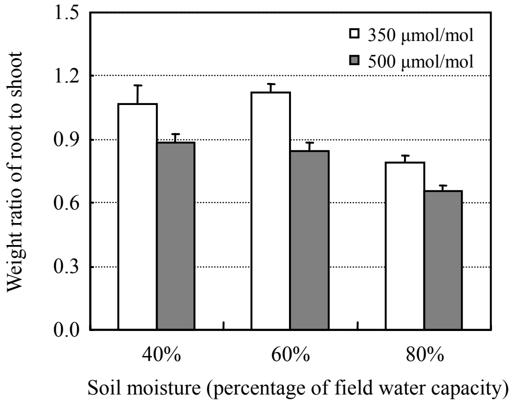

Fig.4 Effects of elevated CO_2 on weight ratio of root to shoot under three soil moisture levels

DISCUSSION

Effects of CO_2 enrichment on plant morphology of *Cinnamomum camphora*

In the present experiments, CO_2 enrichment significantly increased shoot weight as reported previously in many other studies (Curtis and Wang, 1998; DeLucia *et al*., 1999; Eichelmann *et al*., 2004; Niklaus *et al*., 2001; Norby *et al*., 1999; Smith *et al*., 2000; Tissue *et al*., 2001; Usami *et al*., 2001; Woodward, 2002) but without obvious impacts on its height, the ratio of shoot weight to height (WH) was bigger under elevated CO_2 concentration ($P<0.05$, Fig.1). While the effects of CO_2 concentration enrichment on root growth was significant on length rather than weight, especially under favorable conditions (60% FWC soil moisture), the ratio of root weight to length (WL) in higher CO_2 concentration was half of that in current concentration (Fig.2). The positive effects of high CO_2 concentration on length ratio of root to shoot of *C. camphora* was not significant, while there was significant differences between different CO_2 concentration ($P<0.01$) on weight ratio. CO_2 and soil water levels had significant effects on plant water content (Table 2, $P<0.01$). Then we concluded that CO_2 enrichment should favour plant water conservation which accords with reported positive effects of elevated CO_2 concentration on plant water use efficiency (Allen, 1990; Ellsworth, 1999; Gavazzi *et al*., 2000; Hui *et al*., 2001; Liao and Wang, 2002; Wu and Wang, 2000; Wu *et al*., 2002; 2004). Then we suggest that plant morphology could be altered under future high CO_2 concentration conditions. High CO_2 enhances plants shoot lateral growth more than vertical growth, whereas there was little effect on root growth.

Interactive effect of CO_2 concentration and soil moisture on plant growth

Observation results indicated that CO_2 concentration and soil moisture had significant interactive effects on plant growth. High CO_2 could alleviate the negative effects of water deficit on plants on the one hand, and the positive effects of high CO_2 concentration on plant growth were constrained by less favorable soil moisture conditions on the other hand. This accords with most previous reports (Conroy and Hocking, 1993; Poorter, 1998; Catovsky and Bazzaz, 1999; Ward *et al*., 1999; Wu and Wang, 2000).

Moreover, still other reports on similar experiments suggested that growth induced by high CO_2 was greater under drought stress than under high soil moisture (Gifford, 1992). This may be partly attributed to the different method of water control. In their experiments, dry treatment was realized by periodically supplying a preset amount of water (very little) or giving no water. The quantity of water added to maintain the soil moisture gradient did not give out the actual soil moisture. This may lead to actually better soil water conditions in high CO_2 treatment than in ambient treatment since plants use water more economically under high CO_2 concentration conditions. Additionally, use of different factors, such as temperature and light intensity, may alter the interaction between CO_2 concentrations and soil moisture.

Thus, based on the results of ours and those from the literature, it can be concluded that the positive effects of CO_2 enrichment on plants are greater under more suitable conditions. Depending on the life history and evolutionary traits of species, different species of wild plants and their cultivated relatives or even different cultivars of the same domesticated species may respond differently to an environmental gradient as realized by the researchers. For instance, Catovsky and Bazzaz (1999) found that under elevated atmospheric CO_2 levels, the seedling growth of paper birch often found on more xeric, well-drained soils, was enhanced more by low soil moisture treatment than by high soil moisture treatment, while yellow birch usually associated with more mesic sites, showed more improved growth under high soil moisture treatment (Catovsky and Bazzaz, 1999).

CONCLUSION

Morphologically, high CO_2 concentration enhances shoot lateral growth more than vertical growth, but the responses of root were just opposite.

That high CO_2 concentration beneficial to tree aboveground biomass is consistent with many other study results reported in the literature, but its effects on plant underground biomass growth is relatively lower.

The responses of plants to elevated CO_2 depend on soil water availability, and plants may benefit more from CO_2 enrichment under favorable environment such as sufficient water and nutrients.

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