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Effect of CO_2 Enrichment on Growth of two Poplar Clones, I-214 (*Populus euramericana*) and Peace (*P. koreana* × *P. trichocarpa*)

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環境條件에 대해 氣孔의 反應이 相異한 두 種의 포플라 生長에 미치는 高濃度 CO_2의 影響

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ABSTRACT

Two poplar clones, I-214 (*Populus euramericana*) and Peace (*P. koreana* × *P. trichocarpa*), were grown for 21 days in growth chambers at different CO_2 concentrations (350, 700 and 2,000 $\mu L \cdot L^{-1}$). I-214 has stomata responding to environmental conditions in normal ways and Peace has unresponsive stomata to environmental factors including light, ABA, water stress and CO_2. In both plants, elevated CO_2 stimulated the growth of plant parts, especially leaf dry weight. And a CO_2 enrichment of 700 $\mu L \cdot L^{-1}$ CO_2 caused increment of net assimilation rate (NAR). The growth responses of these plants to CO_2 enrichment were different especially at high CO_2 condition (2,000 $\mu L \cdot L^{-1}$ CO_2). The total dry weight in Peace increased up to 2,000 $\mu L \cdot L^{-1}$ CO_2 but not in I-214. A CO_2 enrichment of 2,000 $\mu L \cdot L^{-1}$ CO_2 had little effect on NAR of I-214 but enhanced NAR of Peace. Although it is uncertain whether the different responses to CO_2 enrichment between I-214 and Peace resulted from the different properties of stomatal responses to long-term CO_2 treatment, the decrease in NAR is probably due in part to CO_2-induced stomatal closure in I-214 but not in Peace.

Key words: CO_2 enrichment, Net assimilation rate, Poplar species, Unresponsive stomata

INTRODUCTION

The mean global atmospheric CO_2 concentration has been steadily increasing (Bacastow *et al.* 1985) and is predicted to reach nearly double the present concentration by the end of the next century. Many reviews have discussed the possible effects of increasing anthropogenic atmospheric CO_2 concentration on global climate and several scientists have considered possible direct and indirect effects of increased atmospheric CO_2 concentration on the biosphere and, in particular, on photosynthesis, plant growth and productivity. Kramer (1981) and Bazzaz (1990) clearly indicated in their reviews that plant responses to CO_2 enrichment are dependent on plant species, exposed CO_2 concentration, and length of exposure to elevated CO_2. It is also well known that CO_2 enrichment frequently cause an increase in stomatal resistance to gas exchange (Raschke 1975, 1979). However, there are conflicting reports in evaluating the plant growth in enriched CO_2 environment that the rate of photosynthesis is limited chiefly by CO_2-induced stomatal closure, resulting in the depression of dry weight growth, and that a low potential rate of photosynthesis characteristic to plant species is chiefly reflected to the lower dry matter production. Previous studies have shown that elevated CO_2 concentration enhances dry matter production of several woody species (Rogers *et al.* 1983, Tolley and Strain 1984, Radoglou and Jarvis 1990, Bazzaz *et al.* 1993, Callaway *et al.* 1994). These data suggest that the continued increase in atmospheric CO_2 concentration may result in greater biomass production within the forested ecosystems of the world, since forest tree species contribute up to 70% of terrestrial carbon fixation (Waring and Schlesinger 1985). In addition, if tree species respond differentially to this changing environmental factor, the composition of woody communities may be altered via CO_2-related changes in early stand development and subsequent succession of plant communities.

To assess possible effects of increasing atmospheric CO_2 concentration on woody plants, the individual responses of two poplar species to CO_2 enrichment was investigated. Two poplar clones, I-214 (*Poplus euramericana*) and Peace (*P. koreana* × *P. trichocarpa*), were chosen because they have different stomatal responses to environment. Stomata of Peace poplar are insensitive to environmental conditions such as light, CO_2, water stress, ABA and O_3 (Furukawa *et al.* 1990), which have been known to induce stomatal closure (Zeiger 1983). Because CO_2 enrichment frequently results in partial stomatal closure and consequently, an increase in stomatal resistance to gas exchange (Raschke 1979), it is interesting to compare the growth response in two poplar species with very different stomatal behavior. Growth analysis techniques have been used to determine the effects of CO_2 enrichment on growth dynamics and biomass partitioning of poplar species with responsive and unresponsive stomata.

MATERIALS AND METHODS

I-214 (*Populus euramericana*) and Peace (*P. koreana* × *P. trichocarpa*) were propagated by cuttings. Cuttings were cultivated for 3 weeks in a greenhouse by hydroponic culture (Hyponex Japan, N : P_2O_5 : K = 6 : 40 : 5). One week before the treatment of enriched CO_2, the plants were transferred into the controlled environment room at day/night temperature regime of 25/25℃ with a light/dark period of 14/10 hr and 70% RH (relative humidity). Light was provided by metal halide lamps giving PFD (photon flux density) of 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the level of pot surface. After one-week pre-conditioning, plants were transferred to small growth chambers (0.9m × 0.6m × 2.2m) in which CO_2 concentrations were kept at 350, 700 and 2,000 $\mu L \cdot L^{-1}$, respectively. Each chamber was made of transparent acrylite and contained two fans to mix internal air and a cooling device to maintain consistent air temperature in the chamber. Chamber temperatures were maintained at 27~28℃. In each chamber, CO_2 was injected automatically through a mass-flow-controller and continuously monitored by an infrared gas analyzer (Fuji, Model ZAP).

At 7, 14 and 21 days after the initiation of the CO_2 treatment, three plants were selected at random for the determinations of biomass from each CO_2 treatment, stem length and leaf area. At each harvest date, leaf, stem and roots were sorted out and dried to consistent weight at 80℃. Prior to drying the leaf area was measured with an area meter. The relative growth rate (RGR) was calculated by regressing the whole plant dry weight with time of treatment. Net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) and specific stem length (SSL) were estimated (Chariello *et al.* 1989).

$$RGR = g \cdot g^{-1} \text{ [plant weight] } \cdot day^{-1}$$
$$NAR = g \cdot m^{-2} \text{ [leaf area] } \cdot day^{-1}$$
$$LAR = m^2 \text{ [leaf area] } \cdot g^{-1} \text{ [plant weight]}$$
$$LWR = g \text{ [leaf area] } \cdot g^{-1} \text{ [plant weight]}$$
$$SLA = m^2 \text{ [leaf area] } \cdot g^{-1} \text{ [leaf weight]}$$
$$SSL = m \text{ [stem length] } \cdot g^{-1} \text{ [stem weight]}$$

RESULTS

The effects of CO_2 enrichment on dry weight of plants of I-214 and Peace poplar clones are shown in Fig. 1. Data are shown only for plants grown for 21 days under three CO_2 concentrations. Leaf, stem and root dry weight of the two poplar clones showed the growth-enhancing effect of elevated CO_2 concentrations to the level of 700 $\mu L \cdot L^{-1}$. Exposures to 2,000 $\mu L \cdot L^{-1}$ had little further effect on leaf dry weight of I-214, though

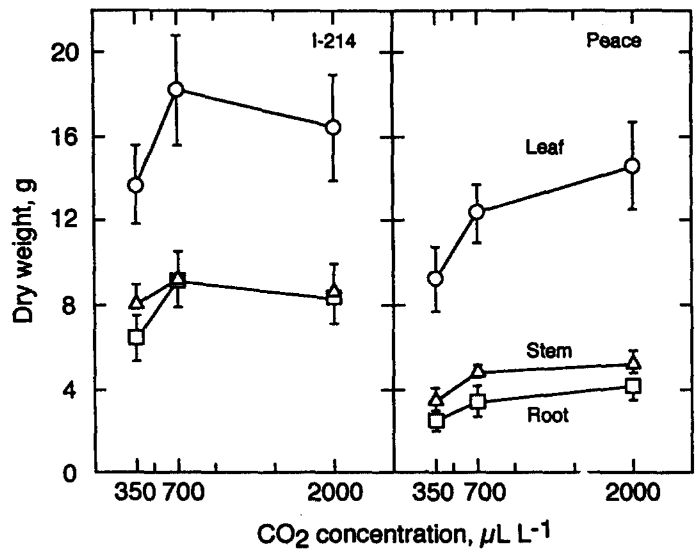

Fig. 1. Dry weight of plant parts of I-214 and Peace poplar clones grown for 21 days under three CO_2 concentrations. Vertical bars indicate standard errors of the means.

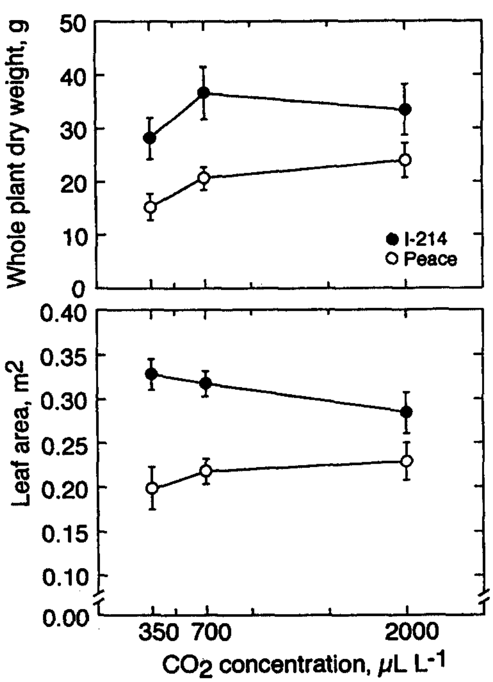

Fig. 2. Total dry weight and leaf area of I-214 and Peace poplar clones grown for 21 days under three CO_2 concentrations. Vertical bars indicate standard errors of the means.

leaf dry weight of Peace increased further.

Increasing CO_2 concentration from 350 to 700 $\mu L \cdot L^{-1}$ enhanced the growth in total dry weight of I-214 and Peace clones (Fig. 2). The growth of Peace poplar clone responed to 2,000 $\mu L \cdot L^{-1}$ to a greater extent than the growth of I-214 clone when compared with the 700 $\mu L \cdot L^{-1}$ CO_2 value.

CO_2 enrichment increased leaf area of Peace poplar, whereas depressive effect was observed in leaf area of I-214 (Fig. 2).

The effect of CO_2 enrichment on the RGR and NAR are shown in Fig. 3. The RGR, the product of NAR and LAR, was a little influenced by CO_2 enrichment in both clones. The response of NAR to the exposed concentration of CO_2 was different between I-214 and Peace clones. The NARs of both poplar clones were enhanced by 700 $\mu L \cdot L^{-1}$ CO_2. However, at the treatment of 2,000 $\mu L \cdot L^{-1}$ CO_2 NAR increased in Peace but decreased in I-214.

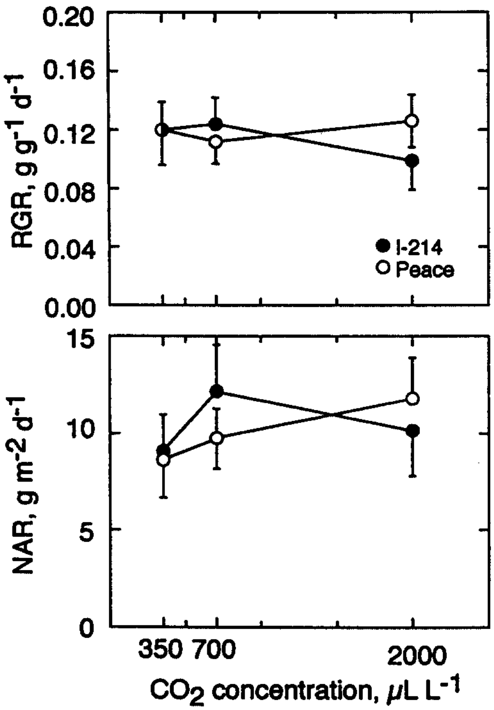

Fig. 3. RGR and NAR for I-214 and Peace poplar clones grown under three CO_2 concentrations during the interval days 14 to 21. Vertical bars indicate standard errors of the means.

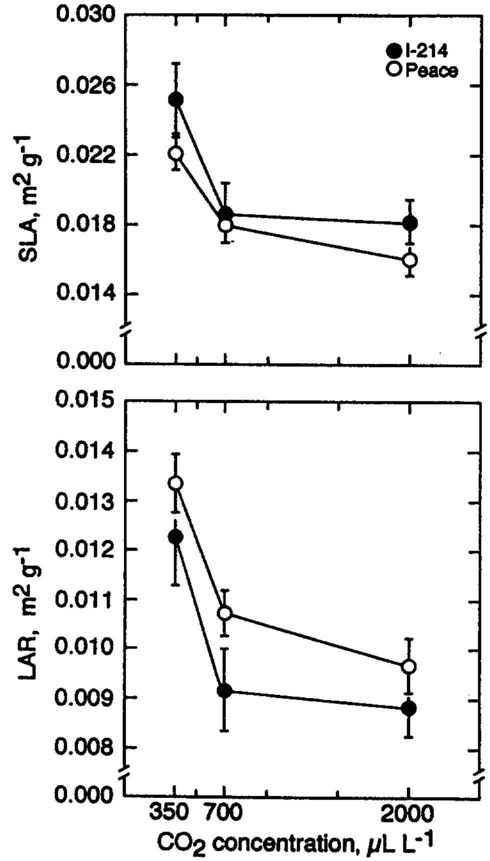

Fig. 4. SLA and LAR for I-214 and Peace poplar clones grown for 21 days under three CO_2 concentrations. Vertical bars indicate standard errors of the means.

The LAR, one of the component growth parameters of the RGR, was inversely related to CO_2 concentration (Fig. 4). By the treatment of 700 $\mu L \cdot L^{-1}$ CO_2, the LARs in both poplar clones decreased significantly. However, the decline of the LAR was not marked under a much higher CO_2 concentration, 2,000 $\mu L \cdot L^{-1}$ CO_2, when compared with the 700 $\mu L \cdot L^{-1}$ value.

In both poplar clones the decrease in LAR under elevated CO_2 was primarily due to the substantial reduction in SLA, as changes in LWR were small (Park *et al.*, unpublished data). The SLA, an indicator of leaf thickness, was also influenced by the treated concentrations of CO_2 and the response of the SLA to CO_2 concentration was similar in the two poplar clones (Fig. 4). Significantly greater decrease of the SLA was observed when plants were grown under 700 $\mu L \cdot L^{-1}$ CO_2.

The SSL was also influenced by CO_2 enrichment (Fig. 5). Peace poplar grown under 700 $\mu L \cdot L^{-1}$ CO_2 showed a greater decline of the SSL compared with I-214. The SSLs of both poplar clones grown at 2,000 $\mu L \cdot L^{-1}$ CO_2 were not reduced further when compared

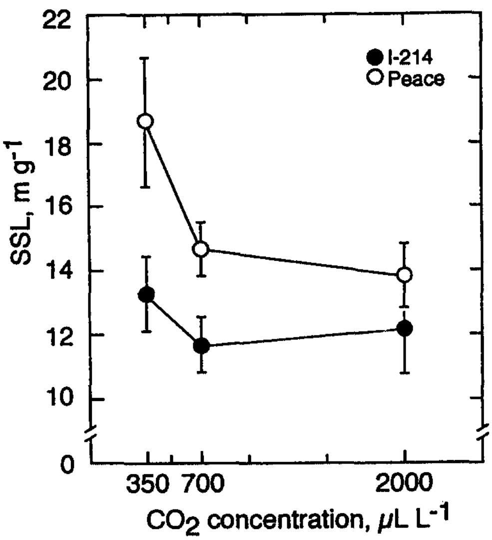

Fig. 5. SSL for I-214 and Peace poplar clones grown for 21 days under three CO_2 concentrations. Vertical bars indicate standard errors of the means.

with the 700 $\mu L \cdot L^{-1}$ values.

DISCUSSION

It is well known that many plant species grown under increased CO_2 concentration had lower photosynthetic capacity than plants grown under the ambient level of CO_2 concentration (DeLucia *et al.* 1985, Mauney *et al.* 1979). This decline of photosynthetic capacity is considered to be induced by the partial stomatal closure under CO_2 enriched condition (Peet *et al.* 1986) and/or accumulation of starch grain in chloroplasts (Mauney *et al.* 1978). These physiological responses might be the reasons why the dry matter production of plants grown under the enriched CO_2 condition is not so stimulated as expected from the relationship between net photosynthetic rates and CO_2 concentration for plants grown in ambient level CO_2 concentration. If it is possible to use plants whose stomata are unresponsive to the increased CO_2, we should be able to predict whether partial stomatal closure is a possible factor that diminishes the enhancement of plant growth under the increased CO_2 condition.

The growth reasponse to the CO_2 enrichment in Peace with unresponsive stomata to environmental factors was different from that in I-214 poplar with responsive stomata. The stimulation of total dry weight after 21 days in 700 $\mu L \cdot L^{-1}$ CO_2 was comparable between I-214 (32 %) and Peace (37%). However, these poplar clones grown for 21 days at 2,000 $\mu L \cdot L^{-1}$ CO_2, the stimulation of total dry weight were 20 and 61% for I-214 and Peace, respectively. Though the dry weight in I-214 and Peace was enhanced by CO_2 enrichment, leaf area was not significantly affected by CO_2 enrichment. The leaf area of I-214 grown at 2,000 $\mu L \cdot L^{-1}$ CO_2 was reduced by 10-15% of the value in the condition of control (350 $\mu L \cdot L^{-1}$). Wong (1979) reported that leaf area in CO_2 enriched cotton plants was 60% greater than the value of plants grown at ambient CO_2 level. Tolley and Strain (1984) reported that the increase in leaf area of two woody seedlings, ***Liquidambar styraciflua*** and ***Pinus taeda***, grown under elevated CO_2 was associated with an increase in leaf number. However, in the present study, we could not detect a significant increase in leaf number of the two poplar clones. Ethylene which is warned to be contaminated in CO_2 cylinders and affects plant metabolism (Morrison and Gifford 1984), however, was not detectable in the present experiments. Thus negligible effects of CO_2 enrichment on leaf number observed in the present study should not have resulted from the contamination of ethylene and/or the defoliation of these plants but from the interspecific differences. It is noteworthy that the elevated CO_2 concentration enhanced the NARs of the two poplar clones, while the RGR was hardly affected. From the growth analysis, the increase in NAR was compensated by the decrease in LAR, and thus RGR did not change. The NARs at 700 $\mu L \cdot L^{-1}$ CO_2 were 34 and 32% higher than those of I-214 and Peace at 350 $\mu L \cdot L^{-1}$ CO_2, respectively. However, NARs at 2,000 $\mu L \cdot L^{-1}$ CO_2 was different between the two poplar clones. These different responses to CO_2 enrichment between the two poplar clones might have resulted from the different responses of SLAs, since SLA is one of the components of NAR. SLA decreased in response to increased CO_2 concentration in both poplar clones detected in the present study. The decrease in SLA was greater in I-214 poplar than in Peace at 700 $\mu L \cdot L^{-1}$ CO_2. Reekie and Bazzaz (1989) and Norby and O'Neil (1991) have observed such a response, whilst Ziska *et al.* (1991) found no response of SLA to CO_2 enrichment. The observed greater decrease in SLA of I-214 poplar than that of Peace poplar was principally due to the increase in leaf dry weight than leaf area in response to CO_2 enrichment.

Since productivity is ultimately dependent upon photosynthesis and because of the role of stomata in gas exchange, it is assumed that CO_2-induced stomatal closure in I-214 may have contributed to the reduction of NAR at 2,000 $\mu L \cdot L^{-1}$ CO_2. Unfortunately, because we do not know to what extent a partial stomatal closure influences dry matter production under the elevated CO_2 conditions, it is uncertain whether the different responses to CO_2 enrichment in I-214 and Peace were due to the different stomatal responses to CO_2 enrichment. Moreover, CO_2-induced stomatal closure alone may not be enough to explain the reduced NAR of I-214 grown at 2,000 $\mu L \cdot L^{-1}$ CO_2, since no photosynthetic reduction was detected in I-214 grown at the present CO_2 concentration (Park *et al.*, unpublished data). There are numerous reports showing that the CO_2 enrichment causes an accumulation of high level of starch which limits the rate of photosynthesis by feedback inhibition (Mauney *et al.* 1979, Herold 1989, Azocon-Bieto 1983).

적 요

環境의 여러가지 變化에 正常的으로 反應하는 氣孔을 가진 I-214와 高 CO_2 濃度條件에서도 氣孔의 反應이 거의 일어나지 않는 Peace를 350, 700, 2,000 μL $CO_2 \cdot L^{-1}$ 條件에서 21일 동안 生長시켰다. 이들 두 포플라 種들의 相異한 生長反應은 2,000 μL $CO_2 \cdot L^{-1}$ 條件에서 顯著히 나타났으며 특히, 葉乾重量에서 많은 差異를 보였다. 700 μL $CO_2 \cdot L^{-1}$ 條件하에서는 두 포플라 種 모두에서 純同化率(NAR)이 增加되었으나 2,000 μL $CO_2 \cdot L^{-1}$ 條件下에서 I-214의 NAR은 350 μL $CO_2 \cdot L^{-1}$ 條件에서와 거의 같은 값을 보였다. 그러나 Peace의 NAR은 2,000 μL $CO_2 \cdot L^{-1}$ 條件下에서도 增加되었다. 高 CO_2 條件下에서 나타나는 이 같은 結果가 두 포플라 種간의 相異한 氣孔反應으로부터 인한 것인지는 不確實하다. 그러나 2,000 μL $CO_2 \cdot L^{-1}$ 條件下에서 I-214의 NAR의 減少는 氣孔의 閉空으로부터 어느 정도 기인된다고 생각된다.

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