PHOTOSYNTHETICA 37 (1): 61-70, 1999

The effect of CO_2 enrichment on the growth of nodulated and non-nodulated isogenic types of soybean raised under two nitrogen concentrations

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Abstract

To find the effects of CO_2 enrichment on plant development and photosynthetic capacity of nodulated (line A62-1) and non-nodulated (line A62-2) isogenic lines of soybean (*Glycine max* Merr.), we examined the interactions among two CO_2 treatments (36±3 Pa = AC and 70±5 Pa = EC), and two nitrogen concentrations [0 g(N) m^{-2}(land area) = 0N; 30 g(N) m^{-2}(land area) = 30N]. Nodules were found in both CO_2 treatments in 0N of A62-1 where the number and dry mass of nodules increased from AC to EC. While the allocation of dry mass to root and shoot and the amount of N in each organ did not differ between the growth CO_2 concentrations, there was larger N allocation to roots in 0N than in 30N for A62-2. The CO_2-dependence of net photosynthetic rate (P_N) for A62-1 was unaffected by both CO_2 and N treatments. In contrast, the CO_2-dependence of P_N was lower in 0N than in 30N for A62-2, but it was independent of CO_2 treatment. P_N per unit N content was unaffected by CO_2 concentrations. The leaf area of both soybean lines grown in 30N increased in EC. But in 0N, only the nodulated A62-1 showed an increase in leaf area in EC. Nitrogen use efficiency of plants, NUE [(total dry mass of the plant)/(amount of N accumulated in the plant)] in 30N was unaffected by CO_2 treatments. In 0N, NUE in EC was lower than in AC in A62-1, and was higher than

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Received 8 March 1999, *accepted* 13 September 1999.

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Acknowledgement: We sincerely thank Dr. Mitsuru Osaki, Hokkaido University, Japan, for his invaluable comments on this study. This study was supported in part by the funds of Ministry of Education, Science, Sports, and Culture.

that at AC in A62-2. Hence, the larger amount and/or rate of N fixation with the increase of the sink-size of symbiotic microorganisms supplied adequate N to the plant under EC. In EC, N deficiency caused the down-regulation of the soybean plant.

Additional key words: genetic differences; *Glycine max*; leaf; net photosynthetic rate; nitrogen accumulation; nitrogen use efficiency; nodule and plant dry mass; stem; root.

Introduction

Growth rate of plants grown under enriched CO_2 frequently does not increase in proportion to the increasing CO_2 concentration. For instance, the N concentration of plants grown in elevated CO_2 concentration decreased (Wong 1979, Norby *et al.* 1986, O'Neill *et al.* 1987, Hocking and Meyer 1991), and CO_2 enrichment did not always down-regulate photosynthetic capacity (Delucia *et al.* 1985, Bazzaz 1990, Koike and Tabuchi 1992, Koike *et al.* 1996a,b). One cause of these responses is sink-limitation brought about by a restricted pot volume on root growth (Arp 1991, Thomas and Strain 1991, McConnaughay *et al.* 1993a,b). On the other hand, the nutritional status in the culture regulates the effects of CO_2 enrichment on photosynthesis and tissue N concentration (Conroy 1992, McConnaughay *et al.* 1993a,b, Sage 1994). In rice plants grown under high CO_2, a decrease in photosynthetic capacity was ascribed to the decrease of N concentration in leaves (Nakano *et al.* 1997). Moreover, the photosynthetic reduction was larger for the plants grown in low N regime with CO_2 enrichment. The growth response of hydroponically cultured rice plants to elevated CO_2 is mainly regulated by leaf area and the N concentration in leaf blades or sheath (Makino *et al.* 1997). Radoglou *et al.* (1992) reported that P_N in leaves of *Phaseolus vulgaris* grown in high nutrient levels did not show a down-regulation in enriched CO_2. These results provide that physiological acclimation of plants to high CO_2 seems to be controlled by the nutritional status in the culture.

Symbiotic microorganisms sometimes act as a carbon sink and can enhance photosynthetic capacity of the host plants that might otherwise be limited by excessive assimilate accumulation in the leaves (Arnone and Gordon 1990, Koike *et al.* 1997). The activity of these microorganisms in the plant rhizosphere is strongly dependent on the plant's nutritional condition (*i.e.*, activities are lower when the host plant is grown under high nutrient levels). Therefore, high nutritional status could indirectly contribute to down-regulation under high CO_2 through a reduced carbon sink (nodules). It is still unclear whether sink-source balance and/or nutrient status will become the limiting factor for plant growth and photosynthetic capacity under elevated CO_2. It is thought that plants with large sink organs (*e.g.*, fruit, tuber, *etc.*) are hardly facing to the photosynthetic down-regulation. Is there any big change in the allocation pattern of photosynthates and nitrogen in plant with symbionts under enriched CO_2? Thus, we postulate that the plants are not down-regulated in sufficient nutrient status under high CO_2. In legume plants such as soybean, nodules play an important role of sink in high CO_2 condition (Masuda *et al.* 1989, Ryle *et al.* 1992).

For testing the role of nodulation, we used nodulated and non-nodulated isogenic line of soybean and examined the sink effect in elevated CO_2 condition. We grew two cultivars of soybean under two CO_2 levels at two nitrogen regimes and measured growth, P_N, and N concentration in plants during vegetative growth stage.

Materials and methods

Plants: The seeds of isogenic lines of soybean A62-1 (nodulated) and A62-2 (non-nodulated) were sown in 2000 cm^3 pots filled with brown lowland soil in nursery of the Hokkaido University (two plants per pot). Superphosphate [equivalent to 10 $g(P_2O_5)\ m^{-2}$] and potassium sulfate [equivalent to 10 $g(K_2O)\ m^{-2}$] were applied as basal dressing in each pot. Each plant also received either no nitrogen (0N) or the equivalent of 30 $g(N)\ m^{-2}$ ammonium sulfate (30N).

CO_2 treatments began 25 d after sowing in a phytotron (*Koito KG, Koito Co.*, Yokohama, Japan) where the plants were grown in the Forestry and Forest Products Research Institute. Plants were grown under natural irradiance at either 36±3 $Pa(CO_2)$ (= AC) or 70±5 $Pa(CO_2)$ (= EC) at 26/16 °C (day/night) and 75-80 % relative humidity for three weeks. The pots were kept moist by watering at approximately two-day intervals. There was no CO_2 replication because of the limited number (two) of growth cabinets. Therefore, test crops were switched between cabinets (Potvin and Tardif 1988, Dutilleul 1993, Koike *et al.* 1995) at 8 and 14 d after treatments started. To reduce the position effects in the cabinet, potted plants were randomly rotated in the cabinet once a week (Miao *et al.* 1992, Koike *et al.* 1995). Because the whole plant metabolism changes greatly from the vegetative growth phase to the reproductive one (Shinano *et al.* 1991), we limited our study to the vegetative growth phase only. Plants were sampled for biomass of leaves, stem, roots, and nodules at 0 and 21 d after the CO_2 treatments began. Samples were dried at 80 °C in an air-forced oven for 72 h, weighed, and ground for N analysis.

Leaf scale measurements: After a 3-week exposure under AC or EC, P_N of mature, fully expanded leaves (4th or 5th leaf from the base) was measured at the end of CO_2 treatment using a CO_2 gas analyzer [open gas exchange system *IR59-07*, *Yokokawa Denki*, Tokyo, Japan) with thermocouples. The photon flux density (PFD) used during the measurements, higher than 1200 $\mu mol\ m^{-2}\ s^{-1}$, was supplied by halogen lamps (technical light model *KTS-100R*, *Kenko Co.*, Tokyo, Japan). Leaf temperature was kept at 25±1 °C. The gas exchange values were collected under a steady state condition (Nakamura *et al.* 1997). After determining P_N, the measured leaf was collected for leaf area determination with an area meter (*Hayashi AAM-5*, Tokyo, Japan), and oven-dried at 80 °C for 72 h. Specific leaf area (SLA) was calculated as leaf area per dry mass. Nitrogen concentration in each organ was determined by semi-micro Kjeldahl method. Differences in values were analysed by the randomization test. NUE (nitrogen use efficiency) of the whole plant was calculated as total dry mass of the plant per nitrogen accumulated in the plant.

Results

Number and dry mass of the nodules: No nodules of non-nodulated line (A62-2), and nodulated line (A62-1) grown in 30N in AC and EC were found. Significant differences in numbers (72.0±8.2 and 38.5±1.1) and dry masses (471±27 and 283±5 mg per plant) of nodules of plants grown in 0N mean an approximate 1.8 and 1.7 times increase in EC than in AC, respectively.

N concentration and SLA: In the 0N treatment, leaf N concentration of A62-1 grown in EC was higher in AC (Fig. 1), but in A62-2 it was not affected by CO_2 treatments. At 30N, leaf N of EC plants was lower than that of AC plants in both soybean lines.

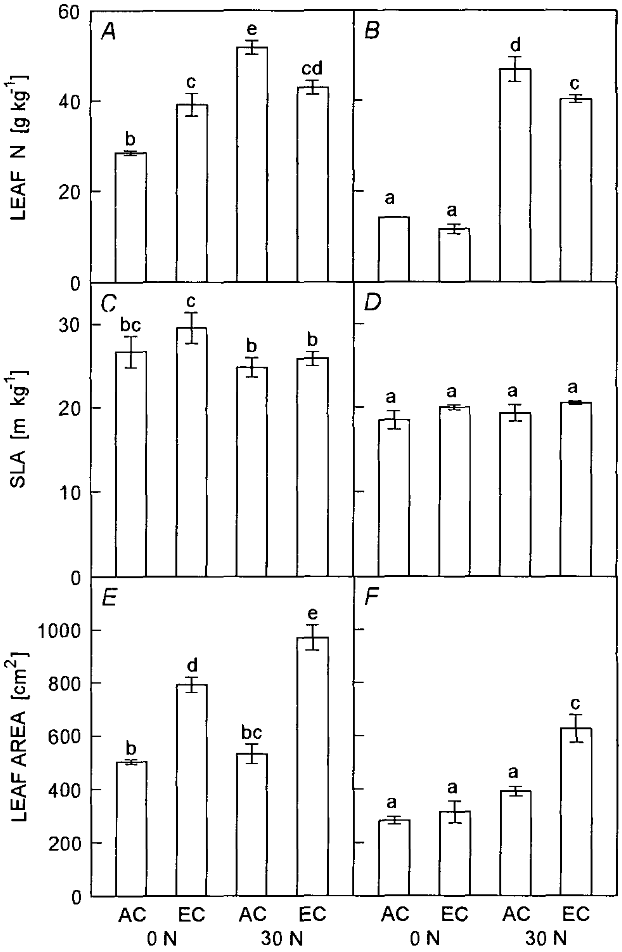

Fig. 1. Leaf nitrogen concentration (leaf N, *A*, *B*), specific leaf area (SLA, *C*, *D*), and leaf area (*E*, *F*) of whole nodulated A62-1 (*A*, *C*, *E*) and non-nodulated A62-2 (*B*, *D*, *F*) plants at two CO_2 treatments (ambient AC and enriched EC) and two N concentrations (0N and 30N). Vertical bars indicate ±SE ($n = 3$). Bars with the same letter indicate no significant difference ($p<0.05$).

SLA of A62-1 plants was higher than that of A62-2 (Fig. 1). SLA of leaves was not much affected by N and CO_2 treatments in both soybean lines. Leaf area of A62-1 plants increased with growth CO_2 concentration in both N-treatments (Fig. 1). Leaf area of A62-2 plants in 0N was unaffected by CO_2 treatment but in 30N it was significantly higher in EC than in AC.

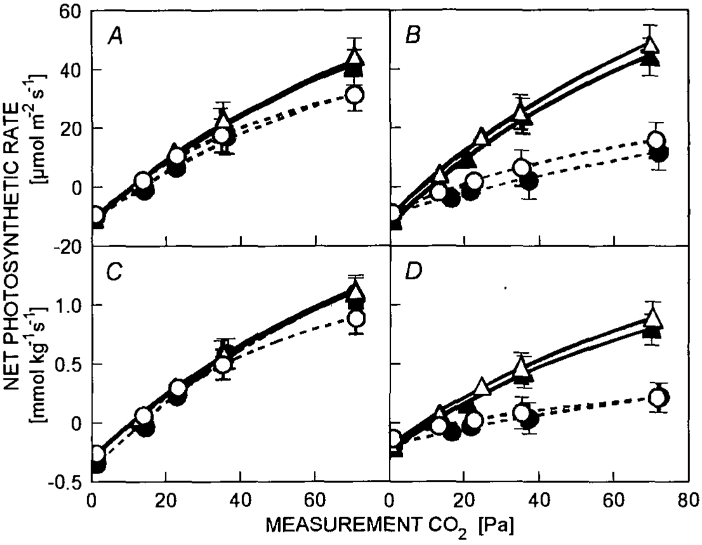

Fig. 2. Relationship between CO_2 concentration and net photosynthetic rate on leaf area (*A*, *B*) and leaf dry mass (*C*, *D*) bases of nodulated A62-1 (*A*, *C*) and non-nodulated A62-2 (*B*, *D*) plants grown at two nitrogen doses, 0N and 30N. Measurements on mature expanded leaves at ambient (AC) and enriched (EC) CO_2 concentration: ○ AC, 0N; ● EC, 0N; △ AC, 30 N; ▲ EC 30 N. Vertical bars indicate ±SE (n = 3 to 5).

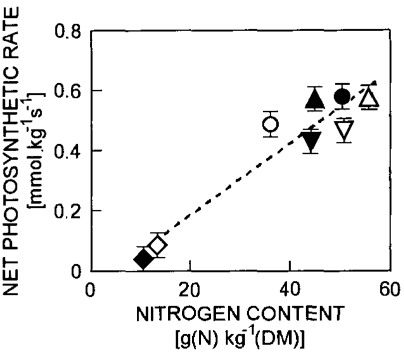

Fig. 3. Relationship between net photosynthetic rate (P_N) measured under 36 Pa CO_2 per unit dry mass of mature leaves of nodulated A62-1 and non-nodulated A62-2 soybean plants grown in ambient (AC, *open symbols*) and enriched (EC, *closed symbols*) CO_2 concentration and leaf nitrogen content. ○ A62-1, 0N; △ A62-1, 30N; ◇ A62-2, 0N; ▽ A62-2, 30N. The regression slope is represented by $P_N = 0.012\ N_c - 0.052$ ($r^2 = 0.950$, $p<0.01$), where N_c is leaf N content. Vertical bars indicate ±SE (n = 3 to 5).

Photosynthetic characteristics: The CO_2-dependence of P_N on a leaf area and dry mass bases for fully expanded leaf of A62-1 was less affected by N and CO_2 treatments (Fig. 2) than in A62-2, where P_N at both AC and EC was larger in 30N than in 0N, and was less affected by CO_2 at the same N treatment. A positive correlation between N concentration and P_N in fully expanded leaf of each soybean line was expressed as a similar linear regression line in the analysis of covariance (significant level was 1 %) (Fig. 3). Therefore, P_N per unit N of these two soybean lines was similar irrespective of CO_2 treatments.

Patterns of allocation of dry mass and nitrogen were similar in plants raised in both CO_2 concentrations (Fig. 4). In A62-1 they were unaffected by N treatments. The allocation of dry mass to roots and nitrogen in roots of A62-2 was higher in 0N than in 30N (a 2-5 % difference for dry mass and a 12-15 % difference for nitrogen).

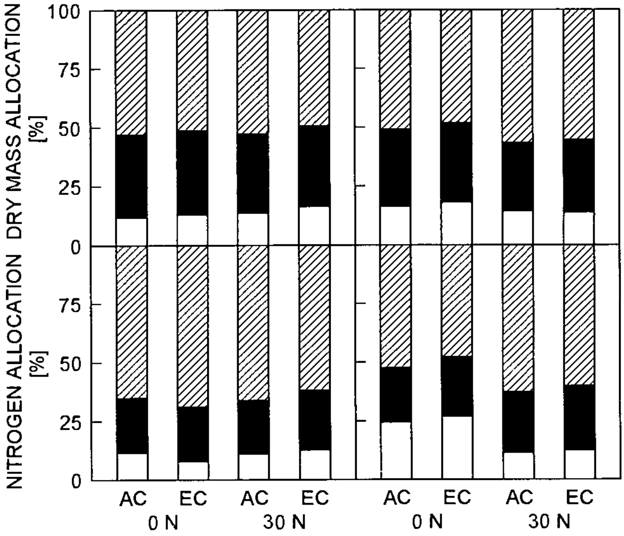

Fig. 4. Allocation of dry matter (*top*) and accumulated nitrogen (*bottom*) in each plant organ in soybean lines A62-1 (*A*, *C*) and A62-2 (*B*, *D*). *Hatched areas*: leaves, *closed areas*: stems, *empty areas*: roots. The values of max. SE are the highest ones in the data set ($n = 3$). LSD are 3.1 for dry matter and 3.4 for N allocation.

Total dry mass and nitrogen use efficiency (NUE) of the plant: In A62-1, total dry mass of the plant in EC was higher than that in AC in both N treatments (Fig. 5). In A62-2, total dry mass of the plant in EC was higher than that in AC at 30N treatment. In the 0N treatment, the total dry mass of plants was not affected by CO_2 treatments.

NUE in 30N was unaffected by CO_2 treatments in these two soybean lines (Fig. 5). In 0N treatment, NUE in EC was lower than in AC in A62-1 and was higher than that in AC in A62-2. NUE was relatively higher in 0N than in 30N in both lines.

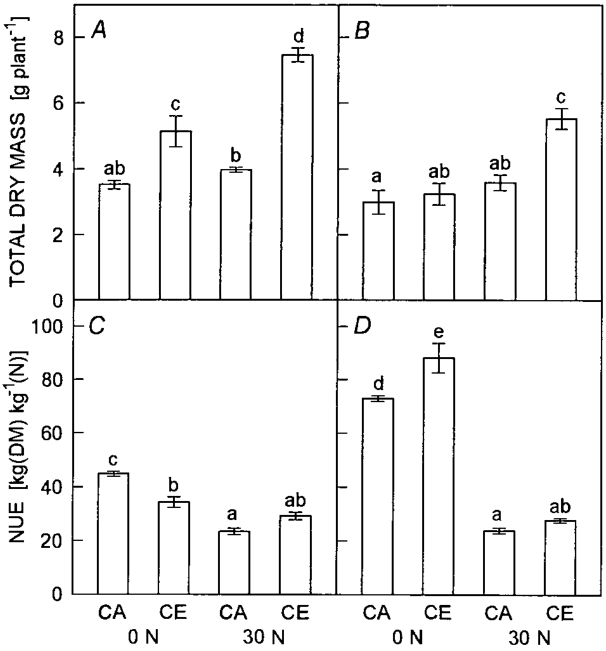

Fig. 5. Total dry mass (*A*, *B*) and N use efficiency (NUE, *C*, *D*) of soybean lines A62-1 (*A*, *C*) and A62-2 (*B*, *D*) after CO_2 treatment. For symbols see Fig. 1.

Discussion

The CO_2-P_N curve was affected by N-treatments, but not by CO_2 treatments (Fig. 2). For the nodulated line (A62-1), this curve was unaffected by either CO_2 or nitrogen. P_N per unit N was also less affected by CO_2 treatments (Fig. 3). In CO_2 enriched atmosphere, CO_2-dependence of P_N is frequently depressed (Delucia *et al.* 1985, Koike *et al.* 1996a, Sage *et al.* 1989). This depression in photosynthetic capacity is caused by a deficiency of inorganic phosphate in chloroplast (Sage *et al.* 1989, Makino 1994) or by the inactivation of ribulose-1,5-bisphosphate carboxylase (Sage *et al.* 1989, Yelle *et al.* 1989). In our experiments, photosynthetic capacity was not suppressed by EC. Woodward and Smith (1994) showed that P_N per unit N in the plants with symbiotic associations was lower than that in non-mycorrhizal plants because of the enhancement of the sink size (Koike *et al.* 1996b, 1997). At 0N in A62-1, the reason for unaffectedness of photosynthesis by EC means that N fixation with symbionts provided adequate N to the plants in both CO_2 treatments. Hence the increase of sink size of nodules may enhance N fixation and supply enough N to the plant under EC. However, Ogawa (1987) reported that an excess increase of the sink size of the nodules caused a reduction of P_N per unit N in the plants.

An increase in the shoot/root ratio was reported for cotton and soybean at CO_2 enrichment (Vessey *et al.* 1990, Wong 1990). However, we found that dry matter and N allocation in each organ were not affected by EC, but were strongly affected by N-treatment (Fig. 4). Similar results were found in wild plants raised under elevated CO_2 (McConnaughay *et al.* 1993a,b). Stulen and den Hertog (1993) showed that at non-limiting nutrient conditions, dry mass partitioning and N allocation between shoot and roots did not change under elevated CO_2 in many plant species. Thus, N deficiency would cause a higher dry matter and N allocation per cent in roots of 0N than 30N grown A62-2 plants.

A decrease in N content (a reciprocal of NUE) is commonly found in many plants under CO_2 enrichment (Imai 1988, Eamus and Jarvis 1989, Hocking and Meyer 1991, Mousseau and Saugier 1992). In our experiment, under the high N level, NUE in both soybean lines was unaffected by CO_2 treatments (Fig. 5). In A62-2 at 0N, NUE in EC was higher than that in AC. According to the pot size criticism of Arp (1991), pot volume affects the sink size of plant, mainly root system. McConnaughay *et al.* (1993a, b) showed that the enhancement of growth under high CO_2 was not affected by sink size of roots, but was affected by nutrient status in the soil. Thus, at the enriched CO_2, these two soybean lines were not down-regulated under high N in spite of the pot size.

P_N at the same leaf N content was higher for mountain alder which had high activity of nodules of *Frankia* at high CO_2 than that at ambient CO_2 because the sink size of the nodules was increased at high CO_2 (Koike *et al.* 1997). In the present experiment, NUE was lower in EC than in AC in 0N of A62-1, and NUE in 0N of A62-1 was lower than that in 0N of A62-2 (Fig. 5). The CO_2-dependence of P_N and P_N per unit N in 0N of the nodulated line were unaffected by CO_2 treatments (Figs. 2 and 3), but the leaf area of the plant in 0N of A62-1 was higher than that in 0N of A62-2 and increased with EC (Fig. 1). The dry mass and numbers of nodules in 0N of A62-1 increased at EC. These results indicated that the enlargement of sink size of nodules stimulated leaf area growth and whole-plant photosynthesis (Arnone and Gordon 1990). Thus, nodulated soybean can respond to low N and high CO_2 with a stimulated leaf growth and an increase in dry mass production (Nakamura *et al.* 1997) through an enhanced N supply derived from the N fixation of nodules. And NUE of the nodulated line (A62-1) declined because of the higher N assimilation (Fig. 5).

Our findings showed that at sufficient N, P_N, dry mass and nitrogen distribution, and NUE were less affected by EC. Therefore, the down-regulation of soybean plants grown in EC may not be caused by root size, but by N deficiency. At low N concentration, nodule size affected down-regulation in EC.

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