

Effect of Elevated CO₂ on the Growth of Two Different Climate-origin Forbs in Four Levels of Nitrogen Nutrition

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ABSTRAK

Dua jenis tumbuhan dari iklim yang berbeza, *Chenopodium album* L. (tumbuhan asli dari kawasan iklim sederhana) dan *Amaranthus patulus* Bertol (tumbuhan asli dari kawasan neo-tropika), telah dibesarkan didalam "growth chamber" pada dua paras CO₂, iaitu 350 dan 700 ppm di bawah empat paras pembajaan nitrogen. Ketinggian paras CO₂ menyebabkan kenaikan jumlah jisim dan pengurangan keamatan nitrogen di dalam daun dalam *C. album* yang diperkayakan CO₂nya, tetapi tidak dalam *A. patulus*. Kesan CO₂ keatas tumbesaran *A. patulus* adalah tidak ketara tetapi kesan CO₂ keatas tumbesaran *C. album* adalah sangat ketara. Tidak terdapat pertukaran yang ketara didalam alokasi diantara tunas dan akar didalam kedua dua spesies berbandingkan CO₂ yang dibekalkan. Pada masa ini dua spesies tersebut tumbuh bersama sama di tanah "eutrophic" pada fasa awal suksesi, seperti dalam bahan buangan atau lapangan yang ditinggalkan. Bagaimanapun, dibawah keadaan CO₂ yang diperkayakan, *C. album* mungkin akan bertambah dominan relatif serta distribusinya sementara *A. patulus*, tidak. Keputusan menunjukkan bahawa kesan paras CO₂ keatas tumbuh-tumbuhan adalah berkaitan dengan iklim asalnya.

ABSTRACT

Two different climate-origin forbs, *Chenopodium album* L. (native to temperate regions) and *Amaranthus patulus* Bertol (native to neo-tropical regions), were grown in growth chambers at two CO₂ levels, 350 and 700 ppm, under four levels of nitrogen nutrition. Elevated CO₂ resulted in increased total biomass and decreased leaf-nitrogen concentration in *C. album*. A decrease in specific leaf area (SLA) was observed with *C. album* in enriched CO₂, but not in *A. patulus*. There were no apparent CO₂ effects on the growth of *A. patulus*, but CO₂ effects on the growth of *C. album* were amplified as the nutrient level increased. There was no significant change in allocation between the top (shoot) and root of either species in relation to CO₂ enrichment. At present, the two species are co-existing in the eutrophic soil conditions of early successional stages, such as in waste or abandoned fields. However, under elevated CO₂ conditions, *C. album* will probably increase its relative dominance and distribution while *A. patulus* will not. The results imply that the effects of CO₂ level on the plants will depend on their climatic origins.

Keywords: *Amaranthus patulus*, *Chenopodium album*, CO₂ elevation effect, nitrogen supply, temperate and tropical origin annuals

INTRODUCTION

The steady increase in atmospheric CO₂ concentration has inspired many biologists to study how this global change affects plant growth and ecosystems (Strain and Bazzaz 1983; Strain and Cure 1985; Hogan *et al.* 1991). However, most of these studies concern the response of crops to the enriched CO₂ (Curtis *et al.* 1989; Lawlor and Mitchell 1991). This is primarily because physiological and allocation responses of plants to CO₂ enrichment were first discovered in agricultural crops (Bazzaz 1990) and of course, such a global change could have serious effects on agricultural production (Kimball 1983; Lawlor and Mitchell 1991). It is well known that higher CO₂ concentration induces greater plant production, such as "CO₂ fertilization" in greenhouse cultivation. Therefore, studies on plant species from natural ecosystems have lagged behind those on crops. However, information on such wild species has now become available (Bazzaz 1990). Early successional stages of plant communities, which mostly consist of herbaceous species, may be more vulnerable to global climate changes than mature stages of succession. Some reports describe faster growing or pioneer species showing greater enhancement of growth by elevated CO₂ than slower growing or climax species (Tolley and Strain 1984; Oberbauer *et al.* 1985). Although there is an exceptional case of shade-tolerant and late successional species showing larger biomass increases with elevated CO₂ (Bazzaz 1990), changes in early successional assemblages by CO₂ enrichment definitely influence the subsequent development process of the communities in terms of composition and structure. Thus, the study of regenerating ecosystems is crucial to assessing the possible impact of global change (Bazzaz 1990).

Recent studies have stressed the importance of elucidating the effects of CO₂ enrichment on the competitive interaction of plants and on feeding rates in herbivores. Nitrogen content altered by elevated CO₂ (Johnson and Lincoln 1990) will possibly affect feeding rates of herbivores (Mattson, 1980; Lincoln and Courvet 1989; Fajer *et al.* 1989, 1991). Furthermore, effects on the yield of plants grown in competition are known to be different from those grown individually (Bazzaz and Carlson 1984; Bazzaz *et al.* 1989). However, in spite of this improved understanding of the physiological response of plants to elevated CO₂, it has been difficult to transfer this work to natural plant ecosystems (Curtis *et al.* 1989), due to the great diversity in plant responses to elevated CO₂ (Carlson and Bazzaz 1980; Kimball 1983; Morgan *et al.* 1994). In addition, effects of elevated CO₂ on plant growth are dependent on other environmental factors (Patterson and Flint 1982; Bowman and Strain 1987; Eamus 1991; Hogan *et al.* 1991; Morgan *et al.* 1994). In this context, the information on plant responses to CO₂ enrichment is still limited and more case studies are needed, particularly to predict the vegetation changes in a local area.

In the present study, using two naturalized annual forbs, *Chenopodium album* (temperate origin) and *Amaranthus patulus* (neotropical origin), we studied the effects of elevated CO₂ (700 ppm) on their growth at four different nutrient levels. Both species are commonly found, sometimes co-existing, in disturbed ecosystems or abandoned agricultural fields. Recent modelling studies predict changes in regional plant productivity and the distribution pattern of plants as a result of increased temperature associated with increased CO₂ and other greenhouse gases (Davis and Botokin 1985; Emanuel *et al.* 1985; Shugart and Emanuel 1985; Davis 1989; Hogan *et al.* 1991; Bush *et al.* 1992). Some suggest a northward shift in plant distribution (e.g. Davis 1989; Sasek and Strain 1990). Thus, it is also important to study the effect of CO₂ on different climate-origin species in order to predict the direction of plant migration with global climate changes.

MATERIALS AND METHODS

Seeds of *Amaranthus patulus* and *Chenopodium album* were collected from abandoned fields in Tsukuba, Japan. They were germinated in quartz sand and transplanted in plastic cups filled with peat moss. Each cup was placed in a pot (5 cm diameter x 18 cm depth) and raised in hydroponic medium (Modified Rorison Nutrient Solution, Hewitt, 1966). Nitrogen concentration was controlled with NH₄NO₃ at four different levels; standard strength (4 mM NH₄NO₃), five-fold strength, 1/5 strength and 1/25 strength. The nutrient solution was changed once a week.

On day 10 after germination, seedlings of each species were placed in separate growth chambers and exposed to two different CO₂ levels (350 and 700 ppm). The temperature and relative humidity in both chambers were controlled at 30/25°C (12 h day/ 12 h night) and 70% respectively. A photon flux density of 450 μmol m⁻² s⁻¹ was controlled with metal halide lamps in both chambers.

Every 10 days from the start of carbon dioxide treatment until day 30 seven plants from each species and from each of the four different nitrogen levels were sampled and separated into three parts: shoot, leaf, and root. The leaf area (LA) was measured and the plant parts were dried in an oven (80°C) for two days and the weight measured. These variables permitted determination of leaf weight ratio (LWR), top root ratio (T/R), leaf area ratio (LAR) and specific leaf area (SLA) (Hunt 1990). Total nitrogen content was measured for each plant part sampled 30 days after the experiment was started, using Sumi-graph (Sumica).

Two-way ANOVA was employed to examine the effects of CO₂ doubling and nitrogen levels on the biomass, the measured parameters mentioned above, and the nitrogen content of the plants. The 0.05 level of probability was employed for the test of significance.

RESULTS AND DISCUSSION

The growth of *Chenopodium album* was significantly affected by CO₂ doubling, while *Amaranthus patulus* did not show such a consistent response to the CO₂ enrichment. The difference in whole plant biomass of *Chenopodium* between 350 and 700 ppm levels was the most apparent in nutrient-rich conditions (standard and 5-fold strength nutrient solution) (Fig. 1). These results correspond to studies demonstrating that the response to enriched CO₂ levels is more pronounced under higher levels of nutrients, and that the CO₂ fertilization effects become indistinct under nutrient-limited conditions (Wong 1979; Goudriaan and de Ruiter 1983; Zangerl and Bazzaz 1984; Brown and Higginbotham 1986; Bazzaz 1990; Arp 1991; Hogan *et al.* 1991; Bazzaz and Fajer 1992; Patterson and McDonald 1994; Kirschbaum *et al.* 1994). Thus, the CO₂ fertilization effects are not consistent unless other resources reach sufficient levels.

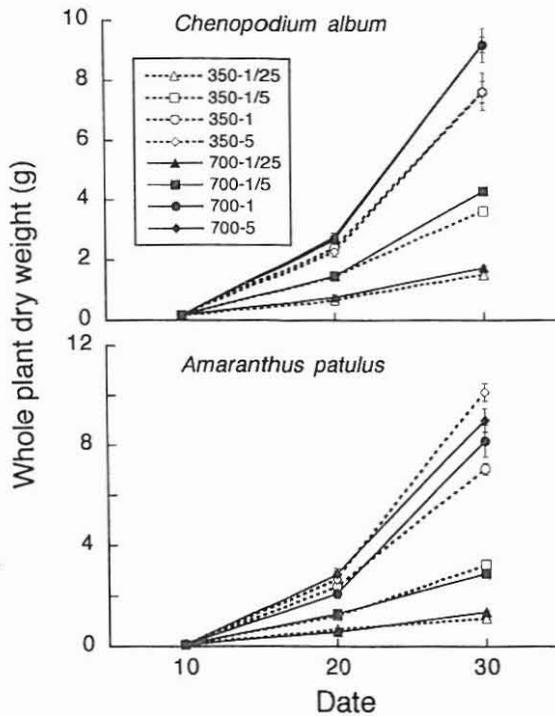


Fig. 1. Changes in whole plant dry weight (g) of *Chenopodium album* and *Amaranthus patulus* in two levels of CO₂ (350, 700 ppm) and four levels of nitrogen nutrient. Nutrient solutions were based on Modified Rorison Nutrient Solution (Hewitt, 1966), with nutrient levels of five-fold-strength (5), 1/5 strength (1/5), 1/25 strength (1/25) and of standard strength (1), containing 4 mM NH₄NO₃. Vertical bars represent 1±SE.

The difference in growth response to elevated CO₂ between *C. album* and *A. patulus* may be due to the difference in photosynthetic pathway, as *C. album* belongs to the C₃ plant group and *A. patulus* belongs to C₄. Since the C₃ photosynthetic pathway is more inhibited by photorespiration in ambient CO₂ level than C₄, it is assumed to be more favourably enhanced by CO₂ enrichment (Bowes 1991; Long 1991; Mooney *et al.* 1991). The results in the present study correspond to previous reports, which have commonly found that C₃ plants increase growth with increased CO₂ concentration. On the other hand, the response of C₄ plants is generally lower than C₃ plants and varies widely among the species within the C₄ group (Ford and Thorne 1967; Carlson and Bazzaz 1980; Rogers *et al.* 1983; Potvin and Strain 1985; Downton *et al.* 1987; Smith *et al.* 1987; Mooney *et al.* 1991). However, there are some exceptions; Garbutt *et al.* (1990) studied the effect of the differential responses of five annuals (C₃ forbs, one C₃ grass and two C₄ forbs) to elevated CO₂, and reported that there were biomass increases in one C₃ and one C₄ forb but no significant increase in any of the other species. Moreover, *Amaranthus retroflexus* (a closely related C₄ species to *A. patulus*) showed a more positive response to elevated CO₂ than its counterpart C₃ species, *Abutilon theophrasti* and the competitive balance between them shifted in favour of *A. retroflexus* (Bazzaz *et al.* 1989). Therefore, the response of any species to CO₂ is unlikely to be simple (Garbutt *et al.* 1990). It may be species specific, rather than being caused by the C₃/C₄ dichotomy.

In *C. album*, leaf area (LA) showed slightly higher values in elevated CO₂ only at the 5-fold nitrogen level (Fig. 2), but it was mostly unaffected by CO₂ enrichment. The T/R ratio in both species did not show consistent changes in relation to CO₂ enrichment (Table 1), although many previous studies had shown increases in allocation to roots (Tolley and Strain 1985; Luxmoore *et al.* 1986; Norby *et al.* 1986; Larigauderie *et al.* 1988; Mousseau and Enoch 1989; Lawlor and Mitchell 1991). Similarly, leaf weight ratio (LWR) in both species did not show significant changes between ambient and enriched CO₂ levels.

In *C. album*, SLA (cm² g⁻¹) and LAR (cm² g⁻¹) showed lower values at 700 ppm than at 350 ppm (Fig. 3, 4), indicating that leaf-thickening had occurred and the plants had become less leafy in the elevated CO₂ conditions which partly agree with previous work (Lieth *et al.* 1986; Leadley and Reynolds 1988). Moreover, the lower value of LAR in 700 ppm suggests that *C. album* had increased its biomass with less carbon investment in its leaves (increased production efficiency). Decreased SLA in elevated CO₂ has also been reported in other studies (e.g. Garbutt *et al.* 1990). The decrease in SLA is often associated with a decrease in nitrogen content (Bazzaz 1990); this trend was shown in the present study.

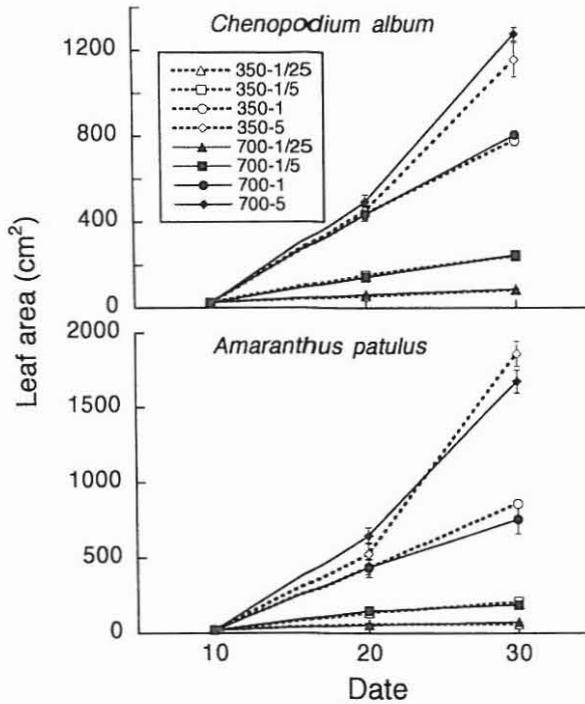


Fig. 2. Changes in leaf area (cm^2) of *Chenopodium album* and *Amaranthus patulus* in two levels of CO_2 and four levels of nitrogen nutrient. Notation is same as in Fig. 1.

Nitrogen content in leaves (LNc , mg g^{-1}) of *C. album* was significantly lowered by the elevated CO_2 (Table 1, Fig. 5). The difference in this value in *A. patulus* was significant ($P < 0.05$), but it was not as apparent as in *C. album*, and its response to CO_2 levels was inconsistent (Fig. 5). This finding partly corresponds to the finding that most plants unaccountably reduce the nitrogen concentration in their leaves (Wong, 1979; Strain and Bazzaz 1983; Johnson and Lincoln 1990; Newton 1991; Conroy 1992). However, *A. patulus* did not necessarily follow this trend. Decrease in leaf-nitrogen content is probably due to the increased starch levels in leaves of plants that increase their biomass in an enriched CO_2 atmosphere (Bazzaz 1990). Therefore, the decrease in LNc may not be found in C_4 plants such as *A. patulus*, which shows no increase in biomass with the enriched CO_2 . The nitrogen content of other parts of the plant body, the stem and root, was not distinctly different between the two CO_2 levels in both species (Table 1).

Although the nitrogen content in leaves was significantly higher in 350 ppm than in 700 ppm in *C. album*, nitrogen content per unit area (LNc/LA) showed no significant difference between the two CO_2 levels (Table 1). Therefore, increased biomass and production efficiency in elevated CO_2 probably result from increased photosynthetic ability on the basis of leaf

TABLE 1

ANOVA table showing F-value for whole plant dry weight (WD), Leaf weight ratio (LWR), top and root ratio (T/R), leaf area (LA), leaf area ratio (LAR), specific leaf area (SLA), leaf nitrogen content (LNc), stem nitrogen content (SNc), root nitrogen content (RNc) and leaf nitrogen content per unit area of leaf (LNc/LA) in *Chenopodium album* and *Amaranthus patulus* at 30 days from the start of experiment. Factors are CO₂ concentration (A) and nitrogen nutrient level (B).

Factors	A	B	A x B
df	1	3	3
<i>Chenopodium album</i>			
WD	17.008**	193.320**	1.873
LWR	3.503	9.584**	0.363
T/R	1.471	81.210**	2.811*
LA	2.947	510.439**	1.415
LAR	26.335**	417.479**	0.974
SLA	22.163**	213.441**	0.503
LNc	16.865**	646.651**	1.103
SNc	2.502	2498.125**	1.174
RNc	3.742	326.371**	3.845**
LNc/LA	0.004	240.790**	0.064
<i>Amaranthus patulus</i>			
WD	1.373	422.191**	3.234**
LWR	0.143	586.197**	0.260
T/R	2.440	221.795**	0.851
LA	3.034	678.477**	2.301
LAR	0.087	459.778**	0.857
SLA	0.348	105.204**	0.536
LNc	5.995*	1873.199**	2.635
SNc	0.258	2474.758**	6.600**
RNc	0.497	2754.520**	6.463**
LNc/LA	1.428	3.019	0.874

* $P < 0.05$, ** $P < 0.01$

area in this species. Such increased photosynthesis implies that *C. album* leaves have higher nitrogen use efficiency under the elevated CO₂. This is because elevated CO₂ increases intercellular CO₂ in leaves and as a result, its increase allows RuBp carboxylase to capture more CO₂.

CONCLUSION

Both *A. patulus* and *C. album* are components of early successional plant communities in abandoned fields, where the soil is rich in nutrients due to the large amount of fertilizer used during crop cultivation. Changes in

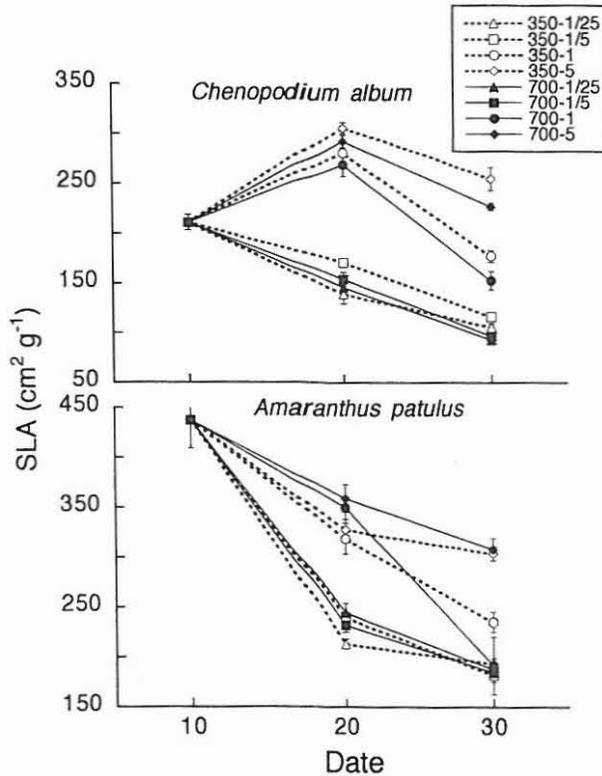


Fig. 3. Changes in specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) of *Chenopodium album* and *Amaranthus patulus* in two levels of CO_2 and four levels of nitrogen nutrient. Notation is same as in Fig. 1

the proportions of two major components in such an assemblage in elevated CO_2 atmospheres, together with eutrophic environments, will influence the subsequent alternation of a plant community.

Furthermore, the results of the present study imply that the enriched CO_2 level possibly causes the changes in species composition, between cool climate origin species like *C. album* and warm climate origin species like *A. patulus*. The former may increase the proportional dominance while the latter may decrease when they are coexisting. However, C_3 species are generally categorized as cool-growing species, while C_4 species are warm-growing species (e.g. Akin and Burdick 1977; Fribourg *et al.* 1982). Warm-growing species generally increase in importance as the temperature increases, while the reverse is true for cool-growing species (Monson *et al.* 1983; Pearcy and Ehleringer 1984; Hunt *et al.* 1991). Thus if the C_3 species consistently responds more vigorously than the C_4 species under enriched CO_2 , as has been stated in the previous studies, then a competitive superiority of C_3 over C_4 may possibly be offset by global warming (Ling 1991).

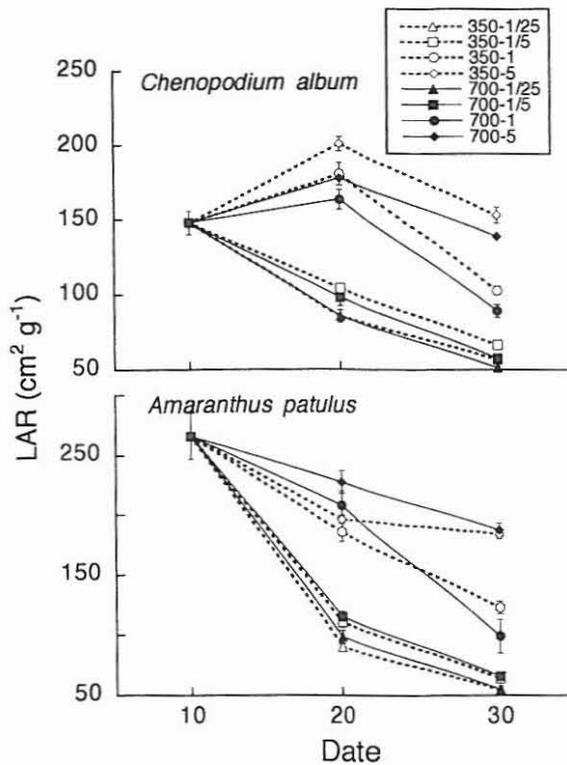


Fig. 4. Changes in leaf area ratio (LAR, cm² g⁻¹) of *Chenopodium album* and *Amaranthus patulus* in two levels of CO₂ and four levels of nitrogen nutrient. Notation is same as in Fig. 1.

Nevertheless, because of the limited knowledge of CO₂ effects and of the complexity of interactive effects between CO₂ and other factors, such as level of available resources, herbivores and pathogens, and species-specific response to the elevated CO₂, predictions about the future impact of the rising CO₂ and associated climate changes are very tenuous (Bazzaz 1990).

Moreover, it is well known that photosynthetic capacity tends to decrease after long-term exposure to elevated CO₂ (Arp 1991; Kirschbaum *et al.* 1994; Morgan *et al.* 1994). This photosynthetic acclimation may be due to the feedback inhibition resulting from an imbalance between supply and demand of carbohydrates. Aspects of experimental conditions, such as volume of pots, may affect the sink size by restricting root growth (Arp 1991). The plants with reduced photosynthetic capacity under elevated CO₂ often show lower leaf nitrogen concentrations and/or partition less of their nitrogen into photosynthetic enzymes (Newton 1991; Conroy 1992). The fact that nitrogen content in *C. album* decreases under elevated CO₂ indicates that photosynthetic acclimation may occur when

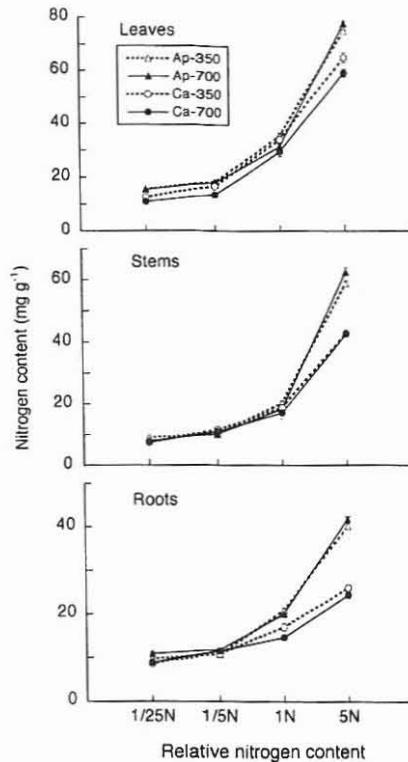


Fig. 5. Changes in nitrogen content (mg g^{-1}) in leaves, stems and roots of *Chenopodium album* and *Amaranthus patulus* in relation to the CO_2 enrichment and nitrogen nutrient treatment at 30 days after the experiment. Ap: *Amaranthus patulus*, Ca: *Chenopodium album*. 350: 350 ppm in CO_2 concentration, 700: 700 ppm.

this species is exposed to long-term elevated CO_2 . In this sense, competitive balance between the two annual forbs chosen for the present study may not necessarily shift in favour of *C. album* under elevated CO_2 . However, in natural conditions where sufficient nutrients are available, such a reduced photosynthetic capacity may not occur as Arp (1991) suggested, and competitive superiority of *C. album* may not be constrained.

Decrease in foliar nitrogen content with increased CO_2 will result in lower nutrients in the litter and ultimately influence the nutrient cycle in the soil (Bazzaz 1990; Bazzaz and Fajer 1992). Furthermore, it has been noted that the consumption rate of insect herbivores feeding on plants grown in elevated CO_2 is higher than of those feeding on the plants grown in ambient CO_2 (Fajer 1989; Lincoln and Couvet 1989; Johnson and Lincoln 1990). This is probably due to insect herbivores compensating for lower nitrogen uptake in nitrogen poor foliage (Bazzaz 1990). Therefore, positive responses to increased CO_2 in some plants do not

necessarily lead to increases in production of the entire ecosystem. The changes in nitrogen content caused by elevated CO₂ may, in the long term, be more important in changing community structure than more obvious differences such as biomass and morphological characteristics (Garbutt *et al.* 1990).

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