Interactive Effects of CO₂ and Nitrogen Resources on Shoot Development of *Chenopodium album* L. and *Amaranthus patulus* Bertol.*

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Abstract: The interactive effects of CO₂ enrichment and nitrogen supply on several attributes of shoot development were examined for two annual weeds, *Chenopodium album* L. and *Amaranthus patulus* Bertol., appearing at an early stage of secondary succession. The elevated CO₂ increased the number of branches at high nitrogen levels in *C. album* and plant height at low nitrogen levels in *A. patulus*. The larger number of branches may increase the number of potential flowering and fruiting sites. Basal diameter was larger at high nitrogen levels in *C. album* and at low nitrogen levels in *A. patulus*. The enlargement of leaf size by CO₂ enrichment required a larger amount of nitrogen in *C. album* than in *A. patulus*. These results show that the interactive effects of CO₂ and nitrogen depend on the species-specific nitrogen requirement. In *A. patulus*, elevated CO₂ and nitrogen supply slightly delayed the beginning of flower bud initiation. The slight delay, however, does not seem to affect the reproductive success of this species considering its reproductive behavior. In addition, there is no morphogenetic effect of CO₂ on leaf initiation per shoot, at least in herbaceous species. The present study suggests that future doubling of CO₂

may not cause the two species to lose their domination potential at an early stage of secondary succession.

Key words: *Amaranthus patulus*, *Chenopodium album*, CO₂ enrichment, nitrogen supply, shoot development

Introduction

The increasing atmospheric CO₂ concentration and associated climatic changes offer an opportunity to study the effects of long-term environmental shifts on ecosystem dynamics²²⁾. Ecologists do not fully know how the increasing CO₂ will affect succession, because there are only a few reports concerning CO₂ effects on the ecological characteristics of species appearing at each successional stage.

The main aim of the present study was to examine the potential responses of shoot development in *Chenopodium album* L. (C₃) and *Amaranthus patulus* Bertol. (C₄) to higher CO₂ concentration. Each species often dominates in the first herbaceous stage of secondary succession^{12,34)}. Their seedlings can burst into growth and occupy growth space, allowing both species to dominate at the early stage of secondary succession¹³⁾. Previous studies have shown that growth or development of shoots is affected by increased CO₂ concentration^{1,22)}. Continuing increase in CO₂ concentration may therefore affect their future status in successional components.

The effects of elevated CO₂ on plant growth

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and reproductive events differ by species and interact with those of other environmental factors, such as nutrients^{23,24}, soil moisture^{2,4} and light³⁶). *C. album* and *A. patulus* differ not only in photosynthetic pathway but also in nitrogen requirement for growth (Hayashi, personal communication). The present study compares the interactive effects of CO₂ and nitrogen resources on shoot development of these two species with different nutrient requirements. The effect of CO₂ enrichment on flower bud initiation is also reported, one of the reproductive events of *A. patulus* plants.

Materials and Methods

Germination of seeds and hydroponic culture of the seedlings were performed in a phytotron in which the environment was controlled at a CO₂ concentration of 350 or 700 $\mu\text{l l}^{-1}$, 30/25°C (12 h day/12 h night), a photon flux density of 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with metal halide lamps during the day-time, and a relative humidity of 70%. Seeds of *C. album* and *A. patulus* were germinated on wet quartz sand. A five-day-old seedling was transplanted into a small cup (5 cm in diameter, 6 cm deep) filled with peat moss. The cup was placed in a pot (11.3 cm in diameter, 18 cm deep) filled with modified Rorison nutrient solution¹⁵) in which nitrogen concentration was adjusted with NH₄NO₃ to obtain 5-fold, 1-fold (a standard, 4 mM NH₄NO₃), 1/5 and 1/25 nitrogen levels. The nutrient solution was renewed every week. Seven replicates were made of each treatment.

The length and basal diameter of main stem, the number of branches, and the length of some individual leaves on the main shoot were measured for 59-day-old *C. album* seedlings and 45-day-old *A. patulus* seedlings. Only branches over 5 mm in length were counted. The total number of nodes (n) with leaves greater than or equal to the reference leaf length (λ , 0.5 cm) was counted, and the length of the leaves (Ln and Ln') on the " n "th and " $n+1$ "th nodes from the bottom

was measured. To assess the developmental stage of a seedling, a plastochron index (PI) was calculated using the following equation⁸):

$$\text{PI} = n + \frac{\ln Ln - \ln \lambda}{\ln Ln - \ln Ln'}$$

In *A. patulus*, the number of seedlings that produced inflorescences larger than 5 mm in length was counted when the seedlings were 23, 31 and 35 days-old.

Statistical comparisons of means were made with one-way ANOVA. The effects of CO₂ and nitrogen supply on the inflorescence development were analyzed with Fisher's exact test²⁸). For all analyses the significance level was $P=0.05$.

Results

Amaranthus patulus developed inflorescences at the top of the main shoot during the experimental period, but no initiation of flower buds occurred in *C. album*. The percentage of the plants that developed the inflorescence at the ages of 23 and 31 days decreased with increasing nitrogen level (Fig. 1). None of the plants grown at the 5-fold level produced flower buds during the experimental period. The inhibitory effect of nitrogen level on flower bud initiation was greater under high than under low CO₂. These results show that the CO₂ doubling slightly delayed the beginning of flower bud initiation.

The increase in plant height (length of main stem) depending on nitrogen supply was significant for *C. album* and *A. patulus*, but no significant difference in the plant height of *A. patulus* was detected between 5-fold and 1/5 nitrogen levels (Fig. 2). The increase in plant height with elevated CO₂ was significant below 1-fold nitrogen level for *A. patulus*, but was not significant for *C. album*. The basal diameter of the main stem for both species significantly increased with rise in nitrogen level, but was not significant for *A. patulus* between levels of 1-fold and 5-fold (Fig. 2). The significant increase in

Fig. 1. Effects of elevated CO₂ and nitrogen nutrient levels on flower bud initiation (percentage of plants with flower buds, $n=7$) of *A. patulus* at 23, 31 and 35 days. Elevated, $700 \mu\text{l l}^{-1}$ CO₂; Normal, $350 \mu\text{l l}^{-1}$ CO₂. Results of statistical analyses (Fisher's exact test, $P=0.05$) are omitted (see text).

Fig. 2. Effects of elevated CO₂ and nitrogen nutrient levels on plant height and basal diameter of the main stem of *C. album* (Ca) and *A. patulus* (Ap). Closed circles, $700 \mu\text{l l}^{-1}$ (elevated CO₂); open circles, $350 \mu\text{l l}^{-1}$ (normal CO₂). Values are means and SD (bars) of seven replicates. For statistical analyses (one-way ANOVA, $P=0.05$), the same letters, denote no significant difference: capital letters, among nitrogen treatments at elevated CO₂; small letters, among nitrogen treatments at normal CO₂. Asterisks denote significant difference between elevated and normal CO₂ at each nitrogen level.

basal diameter by CO₂ enrichment was found at higher nitrogen levels for *C. album* and at lower nitrogen levels for *A. patulus*.

Plant size was defined as the value of the plant height multiplied by the basal area of the main stem⁷⁾. The increasing effect of nitrogen availability on plant size differed greatly between the two species at the comparative nitrogen level of 5-fold to 1/25 (Table 1). At this comparative level, the increase rate of plant size in *C. album* was more than 20-fold at both elevated and normal CO₂.

The nitrogen supply up to the 1-fold level increased the number of branches in both species (Fig. 3). In *A. patulus*, there was no significant effect of CO₂. *Chenopodium album* plants under high CO₂, and 5-fold and 1/5 levels produced a significantly greater number of branches than

Table 1. Increasing effect of nitrogen availability on plant size of *C. album* and *A. patulus* under elevated and normal CO₂ conditions.

Nitrogen level	<i>C. album</i>		<i>A. patulus</i>	
	Elevated	Normal	Elevated	Normal
5 N	28.4	22.0	11.9	19.2
1 N	16.9	14.6	13.9	18.8
1/5 N	4.8	5.3	4.5	5.2
1/25 N	1.0	1.0	1.0	1.0

Note: a) The plant size was defined as the value of plant height (cm) multiplied by basal area of the main shoot (cm²) calculated from its basal diameter.

b) Results are relative values to 1/25 nitrogen level (1/25 N).

c) Elevated, 700 $\mu\text{l l}^{-1}$ CO₂; Normal, 350 $\mu\text{l l}^{-1}$ CO₂.

Fig. 3. Effects of elevated CO₂ and nitrogen nutrient levels on number of branches and plastochron index (PI) of *C. album* (Ca) and *A. patulus* (Ap). See Fig. 1 for details of symbols and letters (statistical analyses: one-way ANOVA, $P=0.05$).

Fig. 4. Effects of elevated CO₂ and nitrogen nutrient levels on elongation of individual leaves on the main shoot of *C. album* (Ca) and *A. patulus* (Ap). Open circles, 5-fold nitrogen nutrient level; closed circles, 1-fold; open lozenges, 1/5; open squares, 1/25. Elevated, 700 $\mu\text{l l}^{-1}$ CO₂; Normal, 350 $\mu\text{l l}^{-1}$ CO₂. Values are means and SD (bars) of seven replicates. Results of statistical analyses (one-way ANOVA, $P=0.05$) are omitted (see text).

those under normal CO₂. In both species, the stimulation of PI was significant for nitrogen supply up to the 1-fold level, although no stimulative effect of CO₂ was recognized (Fig. 3).

The length of individual leaves on the main shoot of *C. album* and *A. patulus* significantly increased with increasing nitrogen supply (Fig. 4), although the first leaves were almost insensitive

to nitrogen supply. The enhanced effect of CO₂ enrichment on the length of leaves on the fifth to fifteenth nodes was observed at high nitrogen levels. The positive effect of CO₂ on the size of individual leaves occurred only at the 5-fold nitrogen level for *C. album* and at the 1-fold and 5-fold levels for *A. patulus*. The vertical position of the largest leaf was shifted downward for

C. album and upward for *A. patulus* with higher CO₂.

Discussion

Flower bud formation

In most species, the beginning of the reproductive phase is delayed by the presence of extra nitrogen^{19,20}. The effect of CO₂ availability is inconsistent, or species-specific⁹. Under elevated CO₂ conditions, there is often a small decrease^{3,21} or increase^{14,32} in the time to anthesis, which has never been explained physiologically¹. In *A. patulus*, the doubling of CO₂ slightly delayed the beginning of flower bud initiation (Fig. 1); however, this delay would not seem able to affect the reproductive success since most *Amaranthus* species have anemophilous flowers for a long period.

The branching of many crops is increased by CO₂ enrichment^{5,16}. For the weeds in this study, the doubling of CO₂ stimulated the branching of *C. album*, while its effect was not significant for *A. patulus* (Fig. 3). The larger number of branches may enhance the reproductive success by increasing the number of potential flowering and fruiting sites. Sionit *et al.* (1981)²⁹ and Sionit (1983)³⁰ documented that, in some crops grown at high CO₂, the increased branching yielded a larger number of seeds. The positive effects of CO₂ on both branching and seed production may be favorable for invasive plants with respect to the following abilities: to exploit the space available for growth, and to increase the chance of seed dispersal and the richness of the seed bank.

Shoot development

In a monoculture, *C. album*, and *A. patulus* plants grown at elevated CO₂ differed in the nitrogen level where there were positive CO₂ effects on the basal diameter of main stem and plant height (Fig. 2). The effective level tended to be higher in *A. patulus* than in *C. album*. Since these attributes are the main components of biomass^{7,18}, it seems that elevated CO₂ increased

biomass at lower nitrogen levels in *A. patulus* but at higher levels in *C. album* (Table 1). In leaf size, also the enlargement by CO₂ enrichment required a greater amount of nitrogen in *A. patulus* than in *C. album* (Fig. 4).

The CO₂-induced increase in biomass and leaf size can reduce nitrogen content on a dry weight basis with time, if the nitrogen supply is constant⁶. This explains the strong nitrogen dependence of CO₂ effects in *C. album* which is nitrophilous (Table 1)¹⁹. In the case of *A. patulus*, the CO₂ effect at the lower nitrogen level may be attributable to relatively low nitrogen requirement (Table 1; Fig. 2). These results show that the interactive effects of CO₂ and nitrogen depend on a species-specific nitrogen requirement. However, Wong (1979)³⁵ and Goudriaan and de Ruiter (1983)¹¹ suggested that C₄ plants are less able than C₃ plants to take advantage of CO₂ enrichment when nitrogen is deficient. The present study indicates that their suggestion can not be generally applied.

There were no effects of CO₂ enrichment on PI values, which were almost equivalent to the total number of leaves on the main stem, regardless of species (Fig. 3). Similar results have been reported for *Echinochloa frumentacea*, *Hordeum hexastichum*, *Oryza sativa* and *Zea mays*^{16,17}, and *Triticum aestivum*¹⁰. Thus, at least in herbaceous species there is no morphogenetic effect of CO₂ on leaf initiation per shoot, which is of great interest as compared to the stimulative effects of nitrogen (Fig. 3). The effect of elevated CO₂ on total number of leaves per plant is species-specific in herbaceous species: effective, *Layia platyglossa*³¹; not effective, *Cucumis sativus*²⁶ and *Liriodendron tulipifera*²⁵. The increase in leaf number of *L. platyglossa* may be due to the increase in the number of lateral shoots.

Tolley and Strain (1984)³³ and Radoglou and Jarvis (1990)²⁷ demonstrated that the increase in total leaf area by elevated CO₂ is due not to an increase in the size of individual leaves but to that

in leaf number. The present study suggests that a possible contribution of leaf size to total leaf area occurs when plants are grown at high nitrogen levels (Fig. 4).

In conclusion, it seems unlikely that future doubling of CO₂ will cause *C. album* and *A. patulus* to lose their potential for dominating at an early stage of secondary succession. This is because CO₂ doubling does not retard the shoot development of *C. album* and *A. patulus*, rather, it increases their shoot growth when the nutrient condition is appropriate for their particular requirement. However, the present study was not designed to determine competitive interactions with sympatric species appearing together with *C. album* and/or *A. patulus*. To discuss with certainty whether both species really continue to dominate with future CO₂ enrichment will require mixed-culture experiments.

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シロザおよびホソアオゲイトウのシュートの発育に及ぼす二酸化炭素と窒素の影響

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摘 要

二次遷移初期に優占群落をつくる雑草2種(シロザとホソアオゲイトウ)のシュートの発育に対するCO₂と窒素の相互効果を調べた。そのために、4段階の窒素条件で水耕栽培した実生を350 ppmと700 ppmのCO₂濃度で長期暴露したのち、草丈・地際径・分枝数・主茎葉の葉身長と葉数を測定した。また、暴露期間中に花芽を着蕾したホソアオゲイトウについては、花芽形成に要する時間を調査した。

シロザとホソアオゲイトウのシュートの発育は、窒素濃度の増加によって有意に促進された。結果として、植物体のサイズ生長も高窒素条件ほど良くなった(Table 1)。しかし、高CO₂濃度に対する生育反応は両種の間で異なった。草丈はホソアオゲイトウで(Fig. 2)、分枝数はシロザで(Fig. 3)、地際径は両種で増加した(Fig. 2)。何れの促進効果も、シロザでは高窒素条件で、ホソアオゲイトウでは低窒素条件でより顕著だった。同様の傾向は葉サイズにも見

られた(Fig. 4)。ただし、高CO₂条件は主茎の葉数に影響を持たなかった(Fig. 3)。シロザは好窒素植物であるのに対してホソアオゲイトウの窒素要求性は高いことから(Table 1)、これらの差異は両種間の窒素要求性の違いによると考えられた。

ホソアオゲイトウの花芽形成は高CO₂・高窒素条件で僅かに遅れた(Fig. 3)。しかし、長期間風媒花をつくるホソアオゲイトウにとって、この程度の僅かな遅れは種子生産などへ影響を及ぼさないと考えられた。しかし、シロザで見られた分枝数の増加は花や果実の着く場所を増やす可能性があり、結果的に種子生産数の増加をもたらすかもしれない。

シロザとホソアオゲイトウのように二次遷移初期に優占群落をつくる草本植物の実生は他種よりも速くシュートを発達させ、生育空間を占有する能力がある。両草種は栄養塩環境が適切であれば、高CO₂濃度でシュートの発育は良くなるので、今後予想される高CO₂条件下でも優占種となるための潜在的能力を失うことはないと考えられる。しかし、実際に優占群落を形成できるか否かは他種との相互作用の結果であるので、これを明らかにするために今後は混植による競合実験等が必要であろう。

キーワード: ホソアオゲイトウ, シロザ, 高二酸化炭素濃度, 窒素供給, シュート生長

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