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Natural CO₂ Springs in Japan: A Case Study of Vegetation Dynamics

By

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Summary

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To study the effects of elevated atmospheric CO₂ concentration on vegetation dynamics in the natural environment, we measured ground cover across CO₂ gradients at a natural CO₂ spring. Two hollows, one emitting CO₂ and a similarly shaped non-emitting one, were used. Both hollows had been covered with mature beech and oak trees with a sparse understory. In 2000 the vegetation within and around the Hollows was removed, and revegetation began.

After four years of revegetation, we established 213 quadrats in the hollows, and measured the ground cover of seven target species (*Fagus crenata*, *Salix bakko*, *Sasa kurilensis*, *Carex albata*, *Carex oxyandra*, *Scirpus wichurui* and *Miscanthus sinensis*) at each quadrat. The ground cover of each species was analysed as a function of atmospheric CO₂ levels that were interpolated from actual measurements at six locations and depths from the top of the hollow. The abundance of *Carex albata* and *Salix bakko* was higher in high CO₂ areas, and *Sasa kurilensis* was more abundant in the ambient CO₂ area. No significant effect of CO₂ was observed in other species. These results suggest that elevated CO₂ favours the growth and dynamics of some species, and consequently may modify the process of vegetation succession.

Introduction

Although increase in atmospheric CO₂ concentration generally enhances plant growth, the extent of growth stimulation varies considerably from species to species (POORTER 1993). Elevated CO₂ may thus affect the relative abundance of plant species, and modulate the structure of vegetation (KÖRNER 2000).

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Vegetation around natural CO₂ springs is valuable to study the long-term effect of elevated CO₂ on plant communities (MIGLIETTA & RASCHI 1993). A number of studies have been published on plants growing around CO₂ springs (see review by BADIANI & al. 2000). However, there are few studies on the community response to elevated CO₂ (SELVI 1997, KALIGARIC 2001), and to our knowledge, no studies on community succession under elevated CO₂.

In Aomori Prefecture (northern Japan), there is a CO₂ emitting hollow with a nearby non-emitting hollow. Until 2000, the plant community in these hollows consisted of mature trees with sparse vegetation in the understory. Plants inside and around the hollows were cut down in 2000, and secondary succession has been in progress since then. This regrowth gave us a unique opportunity to study the effects of elevated CO₂ on secondary succession of vegetation.

We measured CO₂ concentrations and ground cover of seven plant species in the hollows and analysed whether elevated CO₂ modulated the relative abundance of each species during revegetation.

Material and Methods

The study hollows are located at Tashiro, Aomori Prefecture, Japan (40° 40' N, 140° 55' E, a.s.l. 610 m). This region has a cool temperate climate with relatively high rainfall throughout the growing season (annual mean temperature 9.4 °C, annual rainfall 904 mm, Towada Meteorological station, 40° 35' N, 141° 15' E, a.s.l. 42 m). Hollow A (22 long x 20 wide x 7 deep m) has CO₂ vents located near the bottom, while Hollow B (18 x 18 x 4 m) has no vents. The distance between the two hollows is about 60 m. Because of a fatal accident in Hollow A in 1997, almost all trees and ground vegetation in and around both hollows were cut down in 2000 except for a few beech (*Fagus crenata*) trees (4 trees at Hollow A and 1 tree at Hollow B). The original vegetation in the hollows consisted of mature beech and oak trees with bamboo (*Sasa kurilensis*) as a dominant vegetation on the forest floor. After the original vegetation was removed, the light intensity at ground level increased and more than 50 species naturally started to grow (data not shown).

For six days in July and September 2003, atmospheric CO₂ concentrations were measured with a CO₂ monitoring system (LI-820 and LI-1400, Li-Cor, Lincoln, NE & air sampling system, Meiwa co. Ltd. Tokyo, Japan) every 30 seconds at 1m height from the ground at six points at Hollow A and one point at Hollow B. H₂S and SO₂ concentrations were determined with H₂S- and SO₂ detecting tubes (No. 4LT and No. 5Lb, respectively, Gastec, Ayase, Japan).

We measured ground cover of seven species (Table 1) in 2 x 2 m quadrats (132 quadrats for Hollow A and 81 for Hollow B) on 15 September 2004 four years after the trees were cut down (Fig. 2ab). Cover was evaluated using the Braun-Blanquet method (0, +, 1, 2, 3, 4, 5, for 0, 0-1, 1-10, 10-25, 25-50, 50-75, 75-100% ground cover, respectively).

The cover values for each species was analysed with an ordinal logistic regression model (R, statistical programming language). The cover values greater than 0 were standardized to 1 (i.e. 0, 0.04, 0.2, 0.4, 0.6, 0.8, 1) (with the rank of "+" being given 0.2) and analyzed as a binomial distribution. Effect of CO₂ on the cover was possibly confounded with effects of topography in Hollow A because CO₂ concentrations were correlated with depth from the top of the hollow. To remove this possibility, data in Hollow A were pooled with data in Hollow B where CO₂ was independent of topography (TSURUMI & al. 1999). Data were analyzed with multiple regression to evaluate effects of CO₂ and depth on the ground cover. CO₂ values at each quadrat in Hollow A were interpolated from actual measurement at six locations. CO₂ concentration in Hollow B was assumed to be constant (370 ppm), because there were no vents in Hollow B (TSURUMI & al. 1999) and CO₂ concentration was about 370 ppm even at the bottom where highest concentration was expected (Kigrowth experiment under competitive conditions (*Carex albata* vs *Carex oxyandra*)).

was carried out in both hollows in 2004. Two individuals x two species (each individual was 2-3 g in fresh weight) were planted together in a 4L pot that was filled with a 3:1 mixture of soil and vermiculite on 27 June. A slow-release commercial fertilizer (10g, N:P:K:Mg = 6:40:6:15) was added to each pot. Three pots were placed at the bottom of each hollow. 82 days after planting, the plants were harvested (17 September). Total dry mass (shoot + root) was measured after drying in an oven at 75 °C for one week. Effects of hollow and species on the dry mass were tested with ANOVA.

Results and Discussion

Despite strong fluctuations, the CO₂ concentrations in Hollow A were consistently higher than those in Hollow B (Fig. 1a). CO₂ was emitted from the vents (2 tons day⁻¹) and the maximum CO₂ concentration of the source gas was 24% (240,000 ppm) (TSURUMI & al. 1999). The high concentrations of CO₂ were quickly mixed with ambient air and diffused to the wide area in Hollow A. Other gases in the vents were N₂ (65-70%), O₂ (15-17%) and Ar (0.7-0.9%) (TSURUMI & al. 1999). Hydrogen sulfide and SO₂, which are toxic for plants, were not detected (< 0.1 ppm) even in the vents where maximum concentration was expected. No groundwater was detected at the ground surface of either Hollow. CO₂ concentration was highest at the bottom and lowest at the edge of Hollow A (Fig. 1b), and there was no gradient in CO₂ in Hollow B (c. 370 ppm) (TSURUMI & al. 1999). At night, CO₂ concentration tended to increase (sometimes >2%, data not shown).

In this study, we focused on seven species (see Table 1). *Sasa kurilensis* (shade-tolerant C3 perennial grass) was the most dominant species in the understorey both before and after tree cutting in 2000. *Fagus crenata* (a common species of the forest in this region) and *Salix bakko* (a fast growing C3) were two of the most representative woody species, which are expected to be tall and dominant at the hollows in the future. *Carex albata*, *Carex oxyandra* and *Scirpus wichurai* are all C3 grass species and commonly observed in this region. *Miscanthus sinensis* was also a common grass species, but its response to CO₂ was expected to be low because of its C4 type photosynthesis (POORTER 1993).

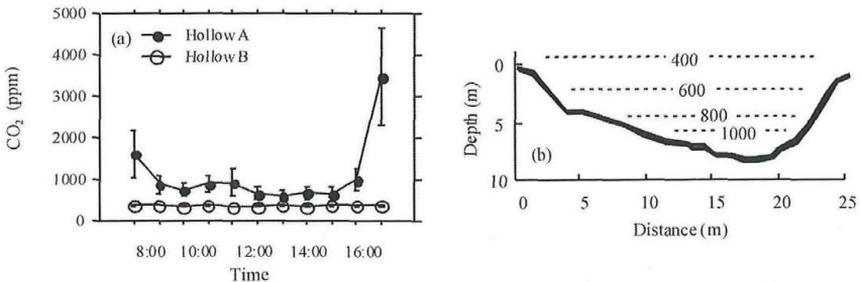


Fig. 1. (a) CO₂ concentration at 1 m height above the soil surface at the bottom of Hollow A and B for six days in July and September. Means with 95% confidential limits are shown. (b) Topography of Hollow A (thick line) with distribution of mean daytime concentration of CO₂ (µmol mol⁻¹).

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Table 1. Effects of CO₂ and depth from the top of the Hollow on the ground cover of seven species at Tashiro, Aomori, Japan. Regression coefficients and their significance in ordinal logistic regression model. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, + $P < 0.1$, ns: $P > 0.1$.

Species (functional type)	Coefficients		
	(intercepts)	CO ₂	Depth
<i>Carex albata</i> (C3 grass)	-8.19 ***	1.03×10^{-2} *	-0.497 ns
<i>Carex oxyandra</i> (C3 grass)	-1.53 **	8.15×10^{-4} ns	-0.111 ns
<i>Fagus crenata</i> (C3 tree)	-1.22 *	8.38×10^{-5} ns	-0.254 ns
<i>Miscanthus sinensis</i> (C4 grass)	-2.64 ***	-2.96×10^{-3} ns	0.516 *
<i>Salix bakko</i> (C3 shrub)	-5.75 ***	5.31×10^{-3} +	-0.188 ns
<i>Sasa kurilensis</i> (C3 grass)	14.5 ***	-2.22×10^{-3} *	-0.080 ns
<i>Scirpus wichurai</i> (C3 grass)	-17.7 ns	1.92×10^{-2} ns	-0.661 ns

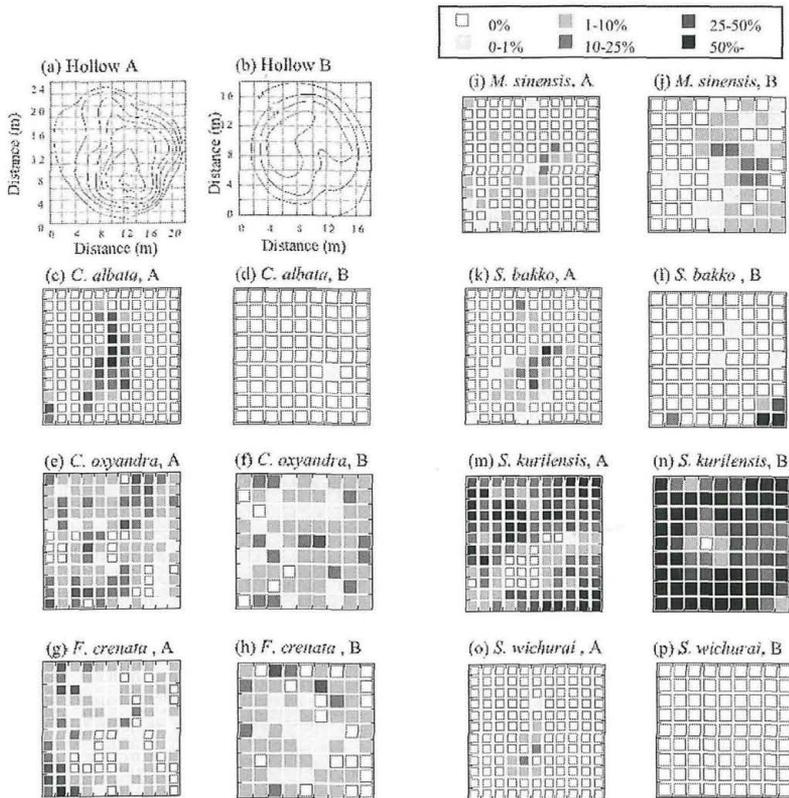


Fig. 2. (a, b) Topography and study-quadrats of Hollow A and Hollow B. (c-p) Ground cover of seven species at Hollow A (c, e, g, i, k, m, o) and Hollow B (d, f, h, j, l, n, p). Cover of each quadrat (2 x 2 m, 213 quadrats) was evaluated using the Braun-Blanquet method on 15 September 2004.

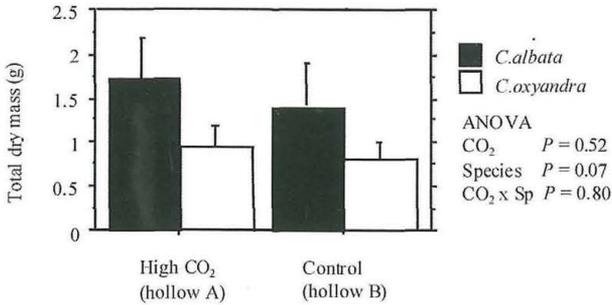


Fig. 3. Dry mass of *Carex albata* and *Carex oxyandra* that were grown under competitive conditions in 4 L pots at Hollow A (high CO₂) and Hollow B (ambient CO₂). Mean values with SE (n = 6).

Fig. 2 shows ground cover of the seven species. The effect of CO₂ and depth on the ground cover of each species is shown in Table 1. A positive CO₂ effect was observed in *Carex albata* and *S. bakko*, while a negative effect was observed in *S. kurilensis*. No effect of elevated CO₂ was observed in the other species. These results suggest a possibility that elevated CO₂ may modulate the structure of plant communities. Although *M. sinensis* is a C4 species, the cover of *M. sinensis* did not significantly decline at high CO₂ area (Table 1). This suggests that, at least in the early stages of secondary succession, this C4 species will not be outcompeted under elevated CO₂. Topographical features also affected the distribution of *M. sinensis*: it was significantly more abundant in quadrats deep in hollows.

Although differences in vegetation were observed between the two hollows, we cannot deny possible effects of initial propagule availability and other environmental factors (e.g. soil nutrients, pH), both of which are likely to affect the structure of the community after cutting. Further analyses of the vegetation change and additional experiments are necessary to determine the relative importance of these factors and of atmospheric CO₂ that determine the community structure observed today.

Two similarly-sized *Carex* species that showed markedly different levels of ground covers between hollows: *C. albata* was more abundant than *C. oxyandra* in the elevated CO₂ quadrats (Fig. 2). We hypothesised that this difference is attributable to interspecific differences in the CO₂ response of growth, reproduction, phenology or resource utilization. To test one of these possibilities, we conducted a growth experiment. Total dry mass of *C. albata* tended to be higher than that of *C. oxyandra* ($P = 0.070$), suggesting that *C. albata* grew faster than *C. oxyandra* (Fig. 3). However, no interaction between CO₂ and species was observed, implying that at least under the conditions of the present experiment, vegetative growth was not a primary factor causing different distributions of the two species. Reproductive effort might be important, because the two species show different reproduction strategies: *C. albata* continued to produce seeds from spring to late-summer, while

C. oxyandra produces seeds only in spring. The higher sink capacity of *C. albata* due to its larger reproductive output may contribute to greater carbon assimilation without sink-limitation that may cause down-regulation of photosynthesis. Consequently *C. albata* may not only increase growth but also have greater seed production under elevated CO₂.

In the present study, we investigated the succession of vegetation at a natural CO₂ spring and found a possibility that elevated CO₂ modifies the structure of the plant community. Further research is needed to clarify the mechanism that caused the different distribution of the plants in response to CO₂-enriched environment.

A c k n o w l e d g e m e n t s

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