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Photosynthetic Acclimation of Birch, Maple, and Oak Seedlings to Elevated CO₂ and the Mediating Effect of Low Growth Irradiance

By

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Key words: *Acer*, *Betula*, *Quercus*, irradiance, elevated CO₂, photosynthetic induction, leaf nitrogen.

S u m m a r y

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Potted seedlings of *Acer mono* (maple), *Betula maximowicziana* (birch) and *Quercus mongolica* var. *grosseserrata* (oak) were grown in phytotron chambers under two light levels (open and shaded at 20% of open) and two CO₂ concentrations (36 Pa and 72 Pa). Maximum photosynthetic rate ($A_{\max}$) showed no down regulation for plants grown in shade under elevated CO₂ for 13 weeks, particularly in oak and birch. In contrast, the open-grown seedlings in high CO₂ showed an initial rise in $A_{\max}$ but then declined to a level similar to those in the ambient CO₂ treatment. Concurrent with $A_{\max}$, leaf nitrogen decreased in elevated CO₂ suggesting a reduction in Rubisco concentration but there was no evidence of increasing the light harvesting components even for shade plants. Lightfleck responses in oak were typical of sun (open-grown) and shade (shade-grown) leaves where the latter attained full photosynthetic induction quicker and declined in induction more slowly in the shade. Shade-grown plants also consistently outperformed those grown in the open with higher transient and steady-state photosynthesis; and these enhancements are greater in elevated CO₂. These results imply that because plants growing in forest shade can keep excessive carbohydrate accumulation in check, thereby circumventing the strong demand for carbon sink experienced by high light plants and sustain the photosynthetic enhancement under elevated CO₂. We predict from these findings that in forest environment with enriched CO₂, there will be better growth and survival of understory seedlings, especially for oak.

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Introduction

The anticipated doubling in atmospheric CO₂ concentration is expected to bring about dramatic ecophysiological responses in plants (BAZZAZ 1990, CEULEMANS & MOUSSEAU 1994). Elevated CO₂ has the effect of increasing photosynthetic rate, reducing stomatal conductance, and improving water-use efficiency (ZISKA & al. 1991, EAMUS & al. 1993, HIBBS & al. 1995, TSCHAPLINSKI & al. 1995) and nitrogen-use efficiency (NORBY & al. 1986a, b, WANG & al. 1994). Photosynthetic acclimation is another aspect of plant response to elevated CO₂ where the predicted enhancement in photosynthesis for some plants was temporary, lasting only weeks before declining (DELUCIA & al. 1985, STITT 1991, CEULEMANS & MOUSSEAU 1994). Such down regulation of photosynthesis has been attributed to causes including negative feedback of photosynthesis from high starch accumulation, physical disruption of chloroplasts by starch granules, limitation of RuBP and Pi-regeneration capacity, and nutrient limitation leading to a reduction of N or P to the photosynthetic machinery resulting from an accelerated shoot growth or a shift in allocation to root growth (BOWES 1991, STITT 1991, POORTER 1993, CEULEMANS & MOUSSEAU 1994, SAGE 1994).

If excessive carbohydrate production coupled with the lack of a strong carbon sink can counteract the effect of an enriched CO₂ environment, then one way to maintain the enhancement is by reducing carbon gain through lower growth irradiance. With lower photosynthesis, shaded plants are less susceptible to "sink-regulation" (STITT 1991) and, therefore, the down regulation of photosynthesis even when nutrients or root growth are limited. Under moderate light levels, BAZZAZ & al. 1990 concluded that elevated CO₂ may enhance shade-tolerant tree species more than intolerant ones. But under high light, shade-intolerant species showed better growth performance under elevated CO₂ (ROCHEFORT & BAZZAZ 1992, SIONIT & PATTERSON 1984, TOLLEY & STRAIN 1984). The significant interaction among species, irradiance and growth CO₂ levels found in the growth of annual plants (ZANGERL & BAZZAZ 1984) and temperate tree species (BAZZAZ & al. 1993) suggests that enhancement under elevated CO₂ in low light is closely linked to the physiological properties of shade tolerance in species.

In this study, we will address the question: can shading prevent the down regulation of photosynthesis in three Japanese tree species grown in elevated CO₂? Using seedlings of one early successional species (birch, *Betula maximowicziana* Regel) and two late successional species (maple, *Acer mono* Maxim. and oak, *Quercus mongolica* Fisch. var. *grosseserrata* Rehd.), we predict that under elevated CO₂ and moderate shading, oak and maple will show greater enhancement of photosynthesis than the early successional birch. We will also examine the pattern of light pulse (sunfleck) responses and seasonal growth of these species. These traits have significant bearing on the regenerative success of these seedlings in an elevated CO₂ forest environment.

Material and Methods

Bare root seedlings of *Acer mono* Maxim. (maple), *Betula maximowicziana* Regel (birch) and *Quercus mongolica* Fisch. var. *grosseserrata* Rehd. (oak) were obtained from Kuriyama, Hokkaido Japan. Seedlings of each species originated from a single tree. Seedlings were planted in 2.6-L vinyl pots filled with Kanuma pumice soil (Konoen, Sapporo, Japan). On June 1, 1994, the potted plants were placed in two adjacent phytotron chambers at the Forestry and Forest Products Research Institute, Sapporo, Japan (42°58'N, 141°23'E, 140 m above sea level). In each chamber, 5 seedlings each of the three species were allowed to receive full sunlight (open treatment) while a same number of plants were covered by neutral density shade cloth, reducing the irradiance to 20% full sunlight (shade treatment). We found a close correspondence in the light regimes of the two chambers under both open and shade treatments. Plants are positioned in the centre 1/3 portion of the chambers such that environmental heterogeneity is assumed to be minimal. Budbreak and leaf expansion took place under the two light regimes and ambient CO₂. On July 16, six weeks after the initiation of the light treatments, CO₂ concentration in one chamber was increased to and maintained at 72 Pa CO₂ using a flow controller (Daiwa Air Regulation Co. Ltd. Sapporo, Japan) and a CO₂ monitor (Model ZDF DF23, Fuji Electric Co. Tokyo, Japan). The concentration in the ambient CO₂ chamber varied between 32 and 36 Pa during daylight and rose to 46 Pa during the night from respiration of the experimental plants. Temperature in the chambers fluctuated continuously daily reaching a maximum of 23°C at 1400 hr and a minimum of 14°C at 0400 hr. All seedlings were watered regularly and fertilized once weekly with Hyponex (N-P-K, 5:10:5; M. Scott & Son Co., Maryville, Ohio) at 10 mg N in 200 ml of tap water.

Five weeks after the seedlings were placed in the two phytotron chambers and prior to the initiation of CO₂ treatments, maximum photosynthetic rates ($A_{\max}$) of all species in the two chambers were determined. We found no significant chamber effect (3-way ANOVA, $F=0.32$, $P=0.58$) but a significant light ($F=10.2$, $P=0.003$) and species ($F=57.6$, $P<0.001$) effect. There was also a significant light x species effect ($F=5.57$, $P=0.007$), which indicates an ecological difference species response to growth irradiance levels.

Maximum photosynthetic rates ($A_{\max}$) were measured for all experimental plants at weekly intervals beginning one week after the initiation of the CO₂ treatment. One leaf per plant was randomly chosen and tagged for repeated gas exchange measurement (Li-Cor 6200, Li-Cor Ltd. Co. Lincoln, NB). Leaves were allowed to acclimate for 30 min in a light cabinet (16 metal halide, 6 mercury, 8 incandescent and 16 fluorescent lamps; Koito KG, Yokohama) at 20°C and photosynthetic photon flux density (PPFD) between 700 and 900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. At these light levels, leaves all species and treatments were photosynthetically saturated (cf. Fig. 1). Repeated measurements of the same leaves continued until the leaf is harvested for morphological and biochemical analyses 19 days and 52 days after the initiation of the CO₂ treatment. A new leaf was selected after each harvest. For *Betula* with an indeterminant shoot growth, a new mature leaf was selected prior to visible signs of senescence appeared in the existing tagged leaf. The CO₂ treatments were continued for 13 weeks.

Seven weeks after the initiation of the CO₂ treatment, a set of lightfleck measurements were taken on oak seedling to examine their photosynthetic induction response. This species was selected because it showed the strongest enhancement in photosynthesis to both light and CO₂ treatments. In the light cabinet, 5 seedlings were acclimated to dim light (30 - 50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for 40 - 60 min, then a dim light photosynthetic rate (A_{dim}) was taken. Individual plants were then placed under saturating light (700 - 900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) where transient photosynthetic rate was measured at 20 s, 2 min 20 s, 4 min 20 s, 6 min 20 s, 8 min 20 s (A_t), and 22 min 20 s which is designated as the steady-state photosynthesis ($A_{\max}$). After the last measurement, the plants were placed back in dim light for 4 min 30 s to initiate loss of photosynthetic induction. To measure the loss of induction and the subsequent re-acquisition of induction, the plants were brought under saturating light again and measured at 20 s and 2 min 20 s.

Three-way ANOVA (Proc GLM, SAS 1988) was used to analyze the chamber and light treatment effects on seedlings prior to the initiation of the CO₂ treatment.

Results and Discussion

Similar to other temperate herbs and trees (ZANGERL & BAZZAZ 1984, WILLIAMS & al. 1986), we found a strong mediating effect of light on plant responses to elevated CO_2 (Fig. 1). For all three species, light response of photosynthesis was substantially higher when grown under high CO_2 , in the case of oak, doubling that of plants in ambient CO_2 .

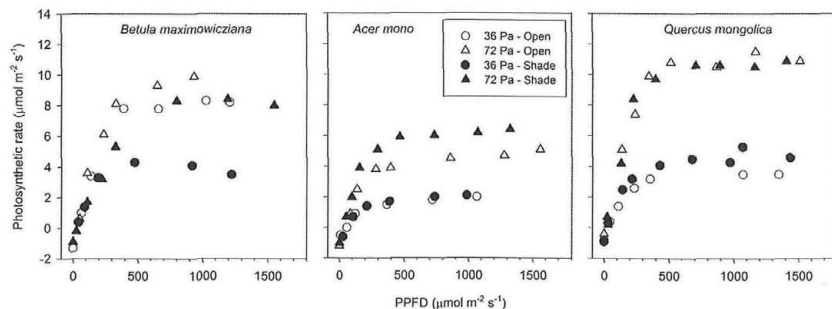


Fig. 1. Light response curves of photosynthesis for the three tree species grown under the two light regimes and two CO_2 levels. Photosynthesis was measured in the same CO_2 concentration as the growth CO_2 . Measurements were taken on July 27, 1994, 11 days after the initiation of the CO_2 treatment.

Another significant finding of this study is that by reducing carbon uptake through shading, we observed a pronounced and sustained response to elevated CO_2 in both the pioneer birch and the late successional oak (Fig. 2). Those seedlings grown under high light responded poorly to elevated CO_2 by down regulating photosynthesis within several weeks even though adequate water and nutrients were supplied. The initial gain in A_{max} in the open treatment declined after 3 - 7 weeks to levels similar to seedlings growing in ambient CO_2 (Fig. 2). The photosynthetic enhancement of all three species grown in the shade under elevated CO_2 continued through the entire measurement period until the onset of senescence in birch at 13 weeks (Fig. 2). Senescence appeared to be delayed by shading in oak where no decline in A_{max} was evident even after 13 weeks. The enhancement of A_{max} in the shade + elevated CO_2 seedlings was strongest in oak, followed by birch and maple. Shade also had the effect in raising A_{max} under ambient CO_2 in oak but not in birch and maple.

Oak, the species with the greatest photosynthetic response to CO_2 and light treatments, was examined in more detail for its pattern of photosynthetic induction to transient light exposure (sunflecks). More rapid responses to sunflecks can contribute to significant carbon gains in forest understory plants (CHAZDON & PEARCY 1986). Shade-grown oak seedlings did show the expected rapid photosynthetic induction (Fig. 3). While this behavior is typical of shade-adapted plants (e.g. CHAZDON & PEARCY 1986, KÜPPERS & SCHNEIDER 1993), the higher by

CHAZDON & PEARCY 1986, KÜPPERS & SCHNEIDER 1993), the higher by shade-grown oaks is not. Furthermore, shade plants were able to retain higher levels of induction during a dim light phase and regain lost induction with the return of high light more quickly than open-grown plants. Therefore, it appears that, oak seedlings grown in the shade not only retained their superior response to sunflecks, this response was further enhanced by its a higher A_{max} when grown under elevated CO_2 .

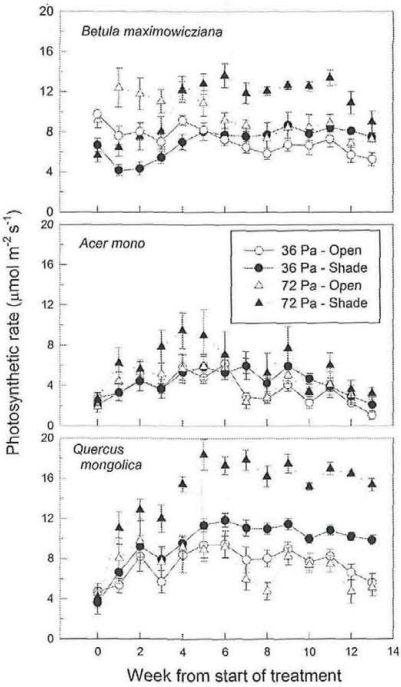


Fig. 2. The time course of maximum photosynthetic rate under the light and CO_2 treatments in the three tree species. Measurements were taken at weekly at the growth CO_2 concentrations. Photosynthesis was measured under saturating light and in the same CO_2 concentration as the growth CO_2 . The values at 0 week was taken prior to the start of the CO_2 treatment five weeks after the seedlings were placed under the shade and open treatments. Each data point is the mean (± 1 SE) of 5 plants.

Compared to seedlings in ambient CO_2 concentration under the same light level, plants in elevated CO_2 showed a higher leaf mass to area ratio (LMA) in all species (Table 1). While this may possibly indicate greater starch accumulation, it did not appear to have a negative feedback effect on seedlings grown in elevated CO_2 as their seasonally higher A_{max} indicates (Fig. 2). Open-grown seedlings of all

(150)

species, and birch in particularly, showed the expected higher LMA, which suggests both a greater structural acclimation to high light and a higher starch accumulation. It is surmised that, under elevated CO₂, the structural adjustments of the open-grown plants exacerbated the demand for carbon sink which facilitated a greater decline in photosynthetic down regulation (Fig. 2). Despite similarity in the apparent excess starch among species, the degree of inhibition in photosynthetic rate was different with a decreasing severity ranking of oak > birch > maple. This suggests that without an adequate carbon sink, oak, with its greater carboxylation capacity will experience the greatest suppression in A. Maple seedlings, with a lower photosynthetic capacity, will be less affected by the lack of a carbon sink.

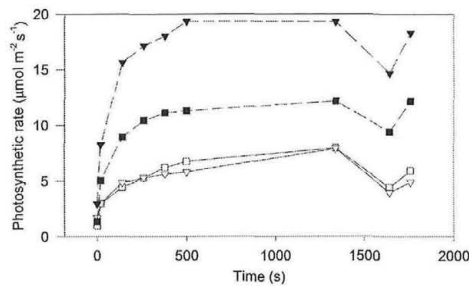


Fig. 3. Lightfleck response patterns of oak seedlings grown under two light levels (shade and open) and two CO₂ treatments (36 Pa and 72 Pa) measured 7 weeks after the start of the CO₂ treatment. Plants were first allowed to acclimate in dim light (30 - 50 μmol m⁻² s⁻¹) before being exposed to saturating light (> 700 μmol m⁻² s⁻¹) where repeated measurements were taken. Values at time= 0s were steady state A under dim light. After reaching steady state under saturating light (at 22 min), a 4.5-min darkfleck was imposed before returning to saturating light to determine the loss of photosynthetic induction. Each data point represents the mean of 5 plants at one measurement per plant.

Table 1. Leaf characters (mean±1 SE; n=5) of *Acer mono*, *Betula maximowicziana* and *Quercus mongolica* var. *grosseserrata* grown under open and shade (20% full sun) with ambient (36 Pa) and elevated (72 Pa) CO₂. Measurements were made 7.5 weeks after the initiation of the CO₂ treatments.

Light	CO ₂	LMA (g m ⁻²)			Total leaf N (mg cm ⁻²)		
		Birch	Maple	Oak	Birch	Maple	Oak
Open	Ambient	42.8±1.5	43.6±2.2	54.2±1.9	0.078±0.003	0.101±0.012	0.102±0.011
Open	Elevated	51.3±0.6	51.9±2.2	62.8±4.3	0.070±0.004	0.087±0.003	0.083±0.005
Shade	Ambient	17.5±0.6	28.6±1.1	38.7±2.3	0.070±0.003	0.091±0.004	0.127±0.007
Shade	Elevated	21.5±1.9	32.5±1.3	39.4±0.7	0.069±0.005	0.089±0.008	0.127±0.005

Acclimation to high CO₂ was different from acclimation to high light in that the former does not involve an increase in carboxylation capacity while the

latter does. In this study, all species in elevated CO₂ showed a reduced carboxylation capacity as indicated by their lower leaf N (except shade-grown oak; Table 1). Similarly, CIPOLLINI & al. 1993 reported a decrease in leaf N under elevated CO₂ for the deciduous woody shrub *Lindera benzoin*. Since a lower leaf N indicates a reduction in Rubisco (EVANS 1989), maximum photosynthetic rate is also expected to decrease.

In conclusion, this study demonstrated that even with a modest decrease in growth irradiance, some tree seedlings can dramatically alter their response to elevated CO₂ by maintaining a substantial enhancement in photosynthesis. We believe that these results have implications on predicting forest dynamics in an elevated CO₂ environment, by accounting for the mediating effect of partial shade on CO₂ acclimation.

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

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