Comparison of the photosynthetic capacity of Siberian and Japanese birch seedlings grown in elevated CO$_2$ and temperature

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Summary The effects of increased CO$_2$ and temperature on the photosynthetic capacity of Siberian white birch and Japanese white birch (Betula platyphylla Sukatch. and B. platyphylla Sukatch. var. japonica Hara) were measured. Birch seedlings were raised with a CO$_2$ partial pressure of 36 ± 0.3 Pa (i.e., ambient) or 70 ± 0.6 Pa at day/night temperatures of either 30/16 °C or 26/12 °C. Siberian birch leaves were smaller and thicker than Japanese birch leaves. Water use efficiency and nitrogen use efficiency of Siberian birch grown in the CO$_2$-enriched air were higher than those of Japanese birch. Both species showed a physiological adjustment to the growth CO$_2$ partial pressure. Carboxylation efficiency and quantum yield of both species grown in CO$_2$-enriched air were lower than those of seedlings grown in ambient CO$_2$. The adaptation of Siberian and Japanese birch to elevated CO$_2$ and temperature are discussed in relation to predicted climate change.

Keywords: carboxylation efficiency, climate change, eastern Siberia, foliar nitrogen concentration, photosynthetic adjustment, quantum yield, water use efficiency.

Introduction White birch is a pioneer species that quickly becomes established following fire or other site disturbance (Koike and Sakagami 1985, Kuusela 1990, Ohta et al. 1993a). The species is broadly distributed in northeastern Asia (Tabata 1966, Gorchakovsky and Shiyatov 1978), but precipitation and temperature appear to be important factors affecting the distribution of white birch varieties. The Siberian variety grows in regions with low precipitation (200 mm per year), especially during the growing season (Ohta et al. 1993b, Ivanov 1994). The Japanese variety of white birch grows in regions with an annual precipitation of 1200–2000 mm (JFTA 1981). Models of global climate change (Cubasch and Cess 1990) predict an increase in ambient temperature of 3 to 5 °C around mid and high latitudes (e.g., Woodward 1991, Oikawa 1993). Associated with this warming trend, the pattern and amount of precipitation in eastern Asia may change (Ohta et al. 1993b). Because Siberian birch is better adapted to dry sites than Japanese birch, and the northern and southern limits of this broad ranging species are closely related to the cumulative temperature during the growing season, we postulated that a drier climate resulting from the predicted increases in atmospheric CO$_2$ and temperature may increase the range of Siberian birch.

To test this hypothesis, we compared (1) the photosynthetic acclimation of Siberian and Japanese white birch to ambient and elevated CO$_2$ during growth, and (2) the physiological and growth responses of these birch varieties to elevated CO$_2$ and temperature.

Materials and methods

Plant materials

Seeds of Siberian birch (Betula platyphylla Sukatch.) and Japanese birch (B. platyphylla Sukatch. var. japonica Hara) were collected at Spasskaya Pad field station of the Yakut Institute of Biology (63° N, 129° E) and Hitsujigaoka experimental forest of the Forestry and Forest Products Research Institute (FFPRI, 43° N, 132° E), respectively. All seeds were germinated on vermiculite in ambient CO$_2$ at day/night temperatures of 25/20 °C and a 22-h photoperiod. When seedlings were 8 cm in height, each was transplanted to a vinyl pot (diameter 15 cm, depth 12 cm) containing a 5/1 (v/v) mix of clay loam and pumice, and placed in the FFPRI phytotron in one of four treatment regimes.

Treatments

Ten seedlings were assigned to each CO$_2$ × temperature treatment regime. The treatments were 36 ± 3 Pa CO$_2$ (ambient) or 70 ± 5 Pa CO$_2$ (elevated) at a day/night temperature of 30/16 °C (high temperature) or 26/12 °C (low temperature). The CO$_2$ partial pressure was regulated with a CO$_2$ controller (DAIWA Air Co. Ltd., Sapporo, Japan). The low temperature regime was based on the mean maximum and minimum temperatures from June to August at Spasskaya Pad and from June to September at Hitsujigaoka. The high temperature regime was set at 4 °C above these mean maximum and minimum tem-
temperatures. Day length was extended to 20 h with supplemental lighting (SOD metal-halide lamps, 500 W, Hitachi, Japan) to simulate the photoperiod of early spring. Liquid fertilizer (5/10/5 N,PK, HyponeX, O.M. Scott & Sons Co., Marysville, USA) was supplied at the rate of 25 mg N l⁻¹ week⁻¹ pot⁻¹. The trays containing the potted plants were filled with water to a depth of 1.5 cm each day.

Measurements

All measurements were made in an illuminated growth cabinet (Koito KG, Yokohama, Japan). The light source consisted of 16 metal-halide, six mercury, eight incandescent, and 16 fluorescent lamps. Light- and CO₂-dependent photosynthetic rates at a leaf temperature of 27.2 °C were measured with a portable gas analyzer (ADC H3, Hoddesdon, U.K.). A supplemental halogen lamp (Nikon, Tokyo, Japan) was used to generate irradiances above 1200 µmol m⁻² s⁻¹. The photosynthetic photon flux density (PPFD) incident on the surface of the leaf chamber was regulated with neutral density cloth filters (Kurary Co., Osaka, Japan). The CO₂ partial pressure was varied by mixing CO₂-enriched air and soda-lime filtered air with a flow meter (Kojima Sci. Co., Tokyo, Japan). Gas exchange rates were measured on the third and fourth leaves from the shoot tip. The age of measured leaves was always 25 to 30 days. Four or more replicates were used for each measurement.

Quantum yield (φ) was estimated from the initial slope of the light–photosynthesis curve determined at CO₂ saturation. Carboxylation efficiency (CE) was calculated by the initial increment of intercellular CO₂ partial pressure (C₅) and net photosynthetic rate based on the assumption of uniform stomatal responses to CO₂ (Terashima 1992). Maximum photosynthetic rate at saturating light and CO₂ (Pₚₘₐₓ) was determined to estimate the rate of ribulose-1,5-bisphosphate regeneration (Farquhar and Sharkey 1982). Water use efficiency (WUE, µmol mmol⁻¹) was calculated as the ratio of photosynthesis to transpiration at saturating light and constant water vapor pressure deficit (Field et al. 1983). Relative stomatal limitation of photosynthesis (lₛ, %) was estimated from

\[ lₛ = (A_o - A)/A_o \]

where A₀ is the net photosynthetic rate when stomatal resistance to CO₂ diffusion is zero, and A is the actual photosynthetic rate (Sharkey 1985). After the gas exchange measurement, leaf area was determined with an area meter (Hayashi AAM-5, Tokyo, Japan), and leaves were oven dried at 85 °C for 48 h. Specific leaf area (SLA) was calculated as leaf area per dry mass (cm² g⁻¹). Leaf nitrogen concentration was analyzed with a N/C analyzer (Yanagimoto MT 500W, Tokyo, Japan). Chlorophyll concentration of leaves was determined after extraction with 80% ethanol (Arnon 1949).

Results

Foliage characteristics

Cessation of leader shoot growth occurred about 45 and 65 days after leaf unfolding for Siberian birch and Japanese birch, respectively. The number of leaves per leader shoot was 10.4 ± 2.4 for Siberian birch and 17.6 ± 2.2 for Japanese birch. The mean leaf size of Siberian birch was 20% less than that of Japanese birch. The temperature treatment did not affect leaf area; however, the elevated CO₂ treatment reduced mean leaf size of both birch varieties (Figure 1A). Siberian birch had a smaller SLA than Japanese birch in the 70 Pa CO₂ plus low temperature treatment (Figure 1B). The elevated CO₂ treatment decreased leaf chlorophyll concentration and leaf nitrogen concentration of both birch varieties, and the effect on leaf nitrogen concentration was greater in Japanese birch than in Siberian birch (Figures 1C and 1D). The high temperature treatment decreased foliar chlorophyll concentration but had no effect on foliar nitrogen concentration in Siberian birch.

Photosynthetic characteristics in leaves

The elevated CO₂ treatment decreased the quantum yield (φ) of both birch varieties (Figure 2A). The value of φ was strongly linked with leaf chlorophyll concentration (cf. Figures 1C and 2A). The elevated CO₂ treatment suppressed Pₚₘₐₓ of both birch varieties, but Siberian birch had a slightly higher Pₚₘₐₓ than...
Japanese birch (Figure 2B) in the low temperature plus 70 Pa CO₂ treatment. In response to the elevated CO₂ treatment, CE was marginally reduced in Siberian birch and markedly reduced in Japanese birch (Figure 2C). Nitrogen-based photosynthetic rates were higher in seedlings grown at 70 Pa CO₂ than at 36 Pa CO₂ in both birch varieties (Figure 2D), and higher in Siberian birch than in Japanese birch.

Independent of treatment temperature, the elevated CO₂ treatment significantly enhanced WUE and stomatal limitation (lₛ) of Siberian birch, whereas in Japanese birch, the elevated CO₂ treatment had no effect on WUE (Figure 3A) but significantly increased lₛ (Figure 3B).

**Homeostatic adjustment in photosynthesis**

At a given measurement CO₂ concentration, net photosynthetic rate was always lower in seedlings grown in elevated CO₂ than in seedlings grown in ambient CO₂ irrespective of growth temperature. However, as shown by the dotted lines connecting the triangles in Figure 4, net photosynthetic rates did not differ between seedlings grown and measured at 36 Pa CO₂ and seedlings grown and measured at 70 Pa CO₂, indicat-
ing homeostatic adjustment. The high temperature growth regime resulted in increased maximum photosynthetic rates for both birch varieties, and the increase was greater for Siberian birch than for Japanese birch.

Discussion

The patterns of morphological and physiological acclimation of Siberian birch and Japanese birch to elevated CO\textsubscript{2} partial pressures were similar to those reported for other tree species (e.g., Eamus and Jarvis 1989, Bazzaz 1990). We observed decreases in chlorophyll concentration and foliage nitrogen concentration and an increase in nitrogen use efficiency in response to elevated CO\textsubscript{2} (Figures 1 and 2). Sage et al. (1989) demonstrated that the photosynthetic rate of five plant species grown in elevated CO\textsubscript{2} was regulated by leaf-level nitrogen. Tissue et al. (1993) concluded that the decline in the photosynthetic rate of loblolly pine seedlings grown for 2 years in a CO\textsubscript{2}-enriched atmosphere was caused by decreases in nitrogen and Rubisco content rather than by inactivation of Rubisco.

Both the Siberian birch and Japanese birch seedlings exhibited photosynthetic adjustment, i.e., net photosynthesis of seedlings grown and assayed at 70 Pa CO\textsubscript{2} was similar to that of seedlings grown and assayed at 36 Pa CO\textsubscript{2} (Figure 4). Photosynthetic adjustment to the growth CO\textsubscript{2} partial pressure has also been reported in Alaskan perennials (Oechel and Strain 1985, Tissue and Oechel 1987) and French bean (Socias et al. 1993). Based on reciprocal transplanting experiments, it has been concluded that net photosynthetic rate adjusts to the growth CO\textsubscript{2} concentration within 3 weeks (Tissue and Oechel 1987, Grulke et al. 1990, Oechel and Billings 1992).

Because photosynthetic rate is strongly influenced by the balance of source–sink activities (Thomas and Strain 1991), it has been suggested that photosynthetic adjustment is an artifact caused by pot size (Arp 1991). In a CO\textsubscript{2}-enriched atmosphere, the depression in photosynthetic capacity is closely related to a deficiency of inorganic phosphate, which may be associated with the translocation of photosynthates (Sage et al. 1989, Sawada and Usuda 1992, Makino 1994). However, homeostatic adjustment of arctic tussock sedge occurred even though there was no root restriction (Oechel and Billings 1992). McConnoughay et al. (1993a, 1993b) concluded that growth of annual plants raised in a CO\textsubscript{2}-enriched atmosphere was controlled not by pot size but by the availability of nutrients.

Tissue et al. (1993) reported that an increased supply of nitrogen fertilizer enabled a high photosynthetic rate to be maintained in loblolly pine seedlings grown at elevated CO\textsubscript{2}. Similar results have been reported for Betula pendula Roth. (Pettersson et al. 1993). Coleman et al. (1993) suggested that the CO\textsubscript{2}-induced reduction in plant nitrogen concentration was the result of dilution caused by accelerated plant growth. Because the reductions in foliar nutrient concentrations, especially nitrogen and phosphorus, closely paralleled the reductions in CO\textsubscript{2} exchange rates in plants grown in elevated CO\textsubscript{2}, we postulate that, in white birch, reductions in foliar nitrogen and phosphorus underlie the homeostatic adjustments.

Siberian birch leaves were smaller and thicker than Japanese birch leaves and are, therefore, better adapted to the dry climate in eastern Siberia (Bewley and Krochko 1982). These morphological characteristics were more pronounced in Siberian birch seedlings grown at 70 Pa CO\textsubscript{2} and high temperature than in seedlings grown at 36 Pa CO\textsubscript{2} and low temperature. The high photosynthetic rate of Siberian birch seedlings may also confer an advantage by enabling this variety to compensate for the short growing season (< 3 months) in eastern Siberia (Ohta et al. 1993a, Ivanov 1994). The photosynthetic capacity of Siberian birch seedlings acclimated to elevated CO\textsubscript{2}, but not to high temperature. Seedlings of this birch variety did not acclimate to the high temperature regime because their phenotype includes small leaves adapted to a dry environment and so the seedlings can maintain high WUE at high temperatures. In contrast, Japanese birch seedlings showed a relatively modest degree of acclimation to elevated temperature and CO\textsubscript{2} in foliage morphology and photosynthesis. We conclude that, under infertile conditions, as a result of homeostatic adjustment in photosynthesis, growth responses of both Siberian birch and Japanese birch to elevated CO\textsubscript{2} will be small.

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PHOTOSYNTHESIS OF BIRCH IN ELEVATED CO₂


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