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Effect of ambient ozone at the somma of Lake Mashu on growth and leaf gas exchange in *Betula ermanii* and *Betula platyphylla* var. *japonica*

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ABSTRACT

We examined the effects of ambient ozone, at the somma of Lake Mashu in northern Japan, on the growth and photosynthetic traits of two common birch species in Japan (mountain birch and white birch). Seedlings of the two birch species were grown in open-top chambers and were exposed to charcoal-filtered ambient air (CF) or non-filtered ambient air (NF) at the somma of Lake Mashu during the growing season in 2009. For the mountain birch, ambient ozone significantly increased the ratio of aboveground dry mass to belowground dry mass (*T*/*R* ratio), although no difference in the whole-plant biomass was observed between the treatments. For the white birch, in contrast, ozone exposure at ambient level did not decrease in growth and photosynthesis. These results suggest that ambient O_3 at the somma of Lake Mashu may shift the allocation of biomass to above-ground rather than below-ground in the mountain birch.

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1. Introduction

Tropospheric ozone (O_3) is a major secondary air pollutant and causes damage to plants (Bytnerowicz et al., 2007; Serengil et al., 2011; Yamaguchi et al., 2011). In Japan, the ground surface O_3 concentration has been increasing since the late 1980s, and this trend is expected to continue (Yamaji et al., 2008). Ohara et al. (2001) reported that this increase in O_3 concentration may be influenced by trans-boundary air pollution. The present O_3 concentration in Japan may have a negative effect on the growth of forest tree species (Watanabe et al., 2010, 2012).

Lake Mashu is located in Akan National Park in northern Japan. This lake was formed in the caldera of a potentially active volcano, and has been called the clearest lake in the world. Mountain birch (*Betula ermanii*) forest covers the somma at Lake Mashu. Birches are typical light demanding species (Koike, 1988; Mao et al., 2010), and these species comprise 12% of the total forest stock in northern Japan (Kawaguchi et al., 2012). Birch forests are natural resources that also constitute tourist attractions as a result of the beautiful scenery of northern Japan. A serious decline or dieback of mountain birch has recently been observed in the somma of Lake Mashu (Yamaguchi and Noguchi, 2011). Ozone might be one factor involved in this decline, as a relatively high O_3 concentration of at least 60 nmol mol^{-1} (monthly average) is recorded in spring in northern Japan, including the Lake Mashu area (Watanabe, 2011; Yamaguchi and Noguchi, 2011). At the somma of Lake Mashu, there is a spring peak in O_3 concentration while O_3 concentration in summer is relatively low (about 20 nmol mol^{-1}) (Yamaguchi and Noguchi, 2011). This implies that relatively high O_3 concentrations are recorded at the beginning of growing season of birches.

Ozone is known to cause a reduction in photosynthetic rate (e.g., Reich, 1987; Matyssek and Sandermann, 2003). Ozone-induced compensatory leaf growth may be initially stimulated in birch to prevent O_3-induced decline of whole-plant carbon gain, although subsequent O_3 exposure may cause reductions in leaf and stem biomass (Pääkkönen et al., 1996). Also, O_3 may limit photosynthate allocation to roots (Anderson, 2003). We hypothesized that compensatory leaf growth and limitation of root growth may occur simultaneously under O_3 stress in birch at this location, and thus may shift the allocation of biomass to above-ground rather than below-ground in the birch species grown in the somma of Lake Mashu. To test this prediction, we examined the effects of ambient O_3 at the somma of Lake Mashu on the growth and photosynthetic traits of the mountain birch (*B. ermanii*, the dominant tree species in the somma of Lake Mashu), and another common birch species in Japan (the white birch, *Betula platyphylla* var. *japonica*).

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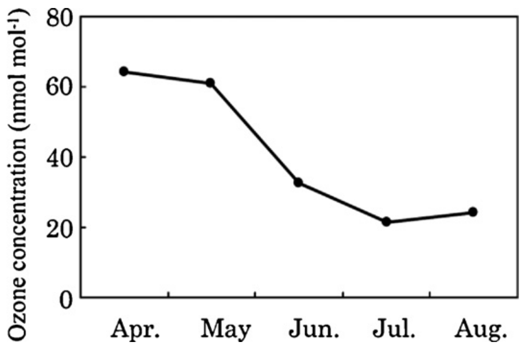

Fig. 1. Monthly mean ambient O_3 concentration (nmol mol^{-1}) at somma of Lake Mashu in 2009.

2. Materials and methods

2.1. Plant materials

We studied 2-year-old seedlings of mountain birch (*B. ermanii*) and white birch (*B. platyphylla* var. *japonica*) obtained from the nursery at Naganuma town in central part of Hokkaido, i.e., main part of distribution for these birches, in order to adjust the acclimation of day length for these birches (e.g., Evans, 1963; Larcher, 2004). The seedlings were grown outdoors in the nursery. The seeds were collected around central Hokkaido, northern Japan. In May 2009 these birch seedlings were planted in 7-l pots filled with 1:1 (v/v) mixture of Kanuma pumice soil and clay soil. These soils are nutrient poor, and originate from volcanic ash that is very common in Japan. Diluted liquid fertilizer (N:P:K = 6:10:5, Hyponex, OH, USA) was supplied to all potted soils, for a total nitrogen (N) application of 96 mg N pot^{-1}. Watering was carried out at 3–7 day intervals to prevent desiccation.

2.2. O_3 treatments

The experiment was carried out in open-top chambers (OTC) located in the somma of Lake Mashu, in northern Japan (43°56′N, 144°51′E, 683 m a.s.l., annual mean temperature: 5.0 °C, total precipitation: 1393 mm in 2009). The snow-free period is from late May to late September. The hourly mean ambient O_3 concentration has been continuously monitored by commercial O_3 analyzer (Dylec, model 1150, Japan) at the measurement site. Fig. 1 shows seasonal variation of ambient O_3 concentration in measurement site. Monthly mean concentration of nitrogen dioxide (NO_2) and sulfur dioxide (SO_2) were 0.7 nmol mol^{-1} and 0.2 nmol mol^{-1} from May to October, respectively (T. Yamaguchi, personal comm.). All birch seedlings were exposed to the following treatments, from June 2nd to September 1st, 2009: charcoal-filtered ambient air (CF, O_3 = 14.1 nmol mol^{-2} as monthly average value during the experimental period) and non-filtered ambient air (NF, O_3 = 18.5 nmol mol^{-2} as monthly average value during the same period). We measured the monthly mean O_3 concentrations in OTCs by passive sampler (Ogawa Co., Kobe, Japan) and estimated the daytime mean O_3 concentration in both treatments as (a ratio between monthly mean O_3 concentration in OTCs and those in the ambient condition) × (daytime hourly mean O_3 concentration in the ambient condition) (Table 1). The CF or NF air was supplied into the chambers from the chamber bottom. Sirocco fan (Mitsubishi, BF23-S, Tokyo, Japan) was attached to OTCs to provide an air of 0.216 m^3 s^{-1}, so that the air in the OTC changed 7.5 times a minute. The theoretical wind speed was 0.15 m s^{-1} at the top of chamber. There were 6 OTCs (1.2 m × 1.2 m × 1.2 m) with three replicate OTCs for both gas treatment. The OTCs were made of a steel frame covered with polyvinyl chloride film in the side panel. The resulting transmittance of sunlight was 88%. Five potted plants per each birch species were set in each OTC.

Table 1
Daytime hourly mean O_3 concentrations (nmol mol^{-1}) in charcoal filtered air (CF) and non-filtered air (NF) open-top chambers at somma of Lake Mashu during the experiment.

	CF	NF
Month		
June	27.4 (8.8)	18.4 (5.9)
July	14.5 (5.4)	10.1 (3.7)
August	17.0 (5.5)	12.6 (4.1)

Each value is the mean (±SD).

2.3. Measurement of plant growth

The seedling height at the beginning of the experiment was 12.3 ± 3.4 cm in CF and 12.9 ± 3.7 cm in NF for mountain birch, and 24.3 ± 4.3 cm in CF and 23.2 ± 4.1 cm in NF for white birch. The initial stem basal diameter was 2.9 ± 0.6 mm in CF and 3.1 ± 0.7 cm in NF for mountain birch, and 3.7 ± 0.4 cm in CF and 3.7 ± 0.6 cm in NF for white birch. There was no statistically difference in height and diameter between CF and NF for mountain birch and white birch at the beginning of the experiment (*t*-test, p = 0.76 in height and p = 0.53 in diameter for mountain birch, p = 0.28 in height and p = 0.92 in diameter for white birch). At each month (July 14th, August 6th and September 2nd, 2009), we measured the height and diameter of the seedlings. At the end of the experiment (September 2nd, 2009), all seedlings were harvested and separated by organ (i.e., stem, branch, leaf and root). The plant organs were dried at 70 °C for 1 week and weighed. Although the roots reached the bottom of the pot and circled a little, we did not find intertwining roots at the end of the experiment.

2.4. Measurement of leaf gas exchange

To assess the accumulative effect of O_3 on leaf photosynthesis, gas exchange was measured for fully expanded sun leaves at the end of the experimental period (September 1st, 2009) before the first frost came. The measurements were carried out using a portable infra-red gas analyzer (Model 6400, Li-Cor Instruments, Lincoln, NE, USA), at controlled values of the leaf temperature (25 °C) and the leaf-to-air vapor pressure deficit (VPD, 1.2 kPa); details are the same as in Watanabe et al. (2011a). For the measurements, three seedlings per treatment-chamber combination were randomly selected for the measurements. The intercellular CO_2 concentration (C_i) response curve of the net photosynthetic rate (A), i.e., the A/C_i curve, was obtained by measurements over 12 steps of CO_2 concentration in the leaf chamber (C_a, 50–1700 μmol mol^{-1}). We determined A at growth CO_2 concentration (i.e., 380 μmol mol^{-1} for CF and NF treatment, A_{growth}) and at 1700 μmol mol^{-1} (A_{max}), and determined the stomatal conductance at growth CO_2 concentrations (G_s). The maximum rate of carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) were calculated from the A/C_i curve (Farquhar et al., 1980; Long and Bernacchi, 2003). The Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) Michaelis constants for CO_2 (K_c) and O_2 (K_o), and the CO_2 compensation point in the absence of dark respiration (Γ^*) for the analysis of the A/C_i curve were derived as according to Bernacchi et al. (2001). All gas exchange measurements were carried out on a day between 9:00 and 15:00 CET.

2.5. Measurement of leaf traits

After the measurement of the gas exchange rate, the leaves were collected to determine the leaf mass per area (LMA). The

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