Growth and leaf gas exchange in three birch species exposed to elevated ozone and CO_2 in summer

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Abstract

We examined the effects of ozone and elevated CO_2 concentration in summer on the growth and photosynthetic traits of three representative birch species in Japan (mountain birch, Monarch birch and white birch). Seedlings of the three birch species were grown in 16 open-top chambers and were exposed to two levels of ozone (6 nmol mol^{-1} and 60 nmol mol^{-1} for 7 h per day) in combination with two levels of CO_2 (370-380μmol mol^{-1} and 600 μmol mol^{-1} for daytime) from July to October. No adverse effects of ozone were found in the Monarch birch or the white birch, but elevated ozone in summer reduced branch biomass and net photosynthesis, and accelerated leaf abscission, in the mountain birch. Elevated CO_2 promoted root development and thereby reduced the ratio of shoot dry mass (stem + branch) to root dry mass (S/R ratio) in the mountain birch and white birch. In contrast, there was no difference in dry mass between ambient and elevated CO_2 for the Monarch birch, due to down-regulation of photosynthesis. Studies of the combined effect of CO_2 and ozone revealed that elevated CO_2 did not ameliorate the effect of ozone on mountain birch in late summer. In considering the ameliorating effect of CO_2 on ozone damage, it is necessary to take account of the species and the season.

***Key words*:** compensative effects; tropospheric ozone; elevated CO_2; birch; photosynthesis

1. INTRODUCTION

Tropospheric ozone (O_3) is a widespread phytotoxic air pollutant, and also a significant greenhouse gas (Bytnerowicz et al. 2007; Serengil et al., 2011). Ground surface O_3 concentrations are increasing in East Asia because of rapidly increasing emission of the main O_3 precursors, nitrogen oxides and volatile organic compounds (Naja and Akimoto, 2004). Ohara and Sakata (2003) reported that the annual average concentrations of photochemical oxidant, mainly O_3, increased in Japan at the large rate of 0.33 nmol mol^{-1} $year^{-1}$ from 1985 to 1999, and are still increasing (Yamaji et al., 2008). Ohara et al. (2001) reported that the increase in O_3 concentration may also be influenced by trans-boundary air pollution. Since the 1990s, many experimental studies using open-top chambers have studied the sensitivity to O_3 of various Japanese forest tree species (Yamaguchi et al., 2011).
Watanabe et al. (2010a, 2012) suggested that the present O_3 concentration in Japan may have a negative impact on the growth of forest tree species.

The effect of O_3 on tree species depends on the atmospheric conditions (e.g., Karnosky et al., 2003; Watanabe et al., 2010b). One of the topical subjects is whether elevated CO_2 concentration expected in future can ameliorate the adverse effect of O_3 on tree species (Karnosky et al., 2001). Some studies found the ameliorating effect of CO_2 on O_3-induced growth reduction and photosynthetic impairment (e.g., Grams et al., 1999; Lütz et al., 2000; Matsumura et al., 2005), but others reported no compensatory effects of CO_2 on the impact of O_3 (e.g., Barnes et al., 1995; King et al., 2005). Elevated CO_2 is generally known to induce stomatal closure (Paoletti and Grulke,

2005). A plausible mechanism for the ameliorating effect of CO_2 is stomatal closure induced by elevated CO_2, thereby limiting O_3 uptake by stomata (e.g., Broadmeadow et al., 1999).

Birch is a pioneer species that is rapidly established following fire or other site disturbance in cool temperate region in Northeast Asia including northern Japan (Linder, 1987; Koike, 1995b). These species are commercially important because of their high growth rate, great timber quality (Koike, 1988; Mao et al., 2010), and comprise 12% of total forest stock in northern Japan (Hokkaido prefecture, 2011; Kawaguchi et al., accepted). Recently declining or die-back birch has been observed in northern Japan (Ohno et al., 2010; Noguchi et al., 2011) and near Tokyo, capital of Japan (the Oku-Nikko region) (Shimizu and Feng, 2007). Ozone might be one of the factors related to these declines. Shimizu and Feng (2007) suggested that dry mass and photosynthesis of mountain birch were reduced by exposure to O_3 at a concentration of 50 nmol mol^{-1} (daily average) as recorded in the Oku-Nikko region of Japan, a mountainous area. The effects of elevated O_3 and elevated CO_2 on tree growth and on physiological traits were determined by OTC experiments over the entire growing season (April to October) in Japan for two kinds of birch species in central Japan (Matsumura et al., 2005). They reported compensatory effects of CO_2 on the impact of O_3 in white birch (*Betula platyphylla* var. *japonica*).

This ameliorating effect of CO_2 may also depend on seasonal influences (Grams et al., 1999; Lütz et al., 2000). Lütz et al. (2000) suggested that the amelioration of O_3-induced reduction in photosynthesis was attenuated in late summer for European beech

(*Fagus sylvatica* L.). High O_3 peak concentrations, exceeding 100 nmol mol^{-1}, were frequently recorded during summer in suburban and mountainous areas of Japan (Shimizu and Feng, 2007; Takeda and Aihara, 2007; Takigawa et al., 2007). Moreover, the peak photosynthetic rate in birch leaves in Japan occurs in late summer (Koike and Sakagami, 1985, Koike 1995b). Late-season's photosynthesis contributes large biomass increment in poplar clone in north-central U.S.A. (Nelson and Isebrands, 1983). The effect of late summer exposure to O_3 is a key to develop our knowledge of the realistic effects of O_3 on birch species native to Japan. Therefore, it is a matter of discussion if elevated CO_2 may provide no compensatory effect on O_3 impacts in late summer for birch species of Japan.

To test this prediction, we examined the effects of elevated O_3 in combination with elevated CO_2 on the growth and photosynthesis of three birch species from late July to October. Based on the data, we discuss the interaction of the effects of O_3 and CO_2 on growth.

2. MATERIALS AND METHODS

2.1 Plant materials

We used 2-year old seedlings of mountain birch (*B. ermanii*), Monarch birch (*B. maximowicziana*) 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 seeds were collected around central Hokkaido, northern Japan. The height and stem basal diameter at the beginning of the experiment were 35.6±4.5 cm and 4.3±0.4 mm for

mountain birch, 65.1±4.8 cm and 6.3±0.5 mm for Monarch birch, and 53.3±4.5 cm and 5.7±0.6 mm for white birch. Before bud break, these bare rooted birch seedlings were planted in late May 2010 in 7-liter pots filled with 1:1 (v/v) mixture of the Kanuma pumice soil and clay soil (infertile plant culture material). After leaf initiation, diluted liquid fertilizer (Nutrient balanced fertilizer, N:P:K=6:10:5, Hyponex, Ohio, U.S.A.) was supplied to all potted soils, amounting to total nitrogen (N) application of 192 mg N pot^{-1}. All plants were supplied with water at 3-7 day intervals to avoid water stress.

2.2 O_3 and CO_2 treatments

The experiment was carried out in open-top chambers (OTC) in the Sapporo Experimental Forest of Hokkaido University, in northern Japan (43°04' N, 141°20' E, 15 m a.s.l., annual mean temperature: 11.5 ˚C, total precipitation: 1325 mm in 2010). All birch seedlings were exposed to the following treatments from July to October 2010: control (CO_2= 370-380 μmol mol^{-1}; O_3 =6 nmol mol^{-1}, charcoal filtered air), elevated O_3 (62 ± 17 nmol mol^{-1}: 7 hours, 10:00-17:00 CET), elevated CO_2 (600 μmol mol^{-1} during daytime) and a combination (elevated O_3 and CO_2). Ozone was generated from pure oxygen by an O_3 generator (Model PZ-1C, Kofloc, Kyoto, Japan). A propotional-integrative-differential (PID) control algorithm was applied to maintain the desired concentration of O_3. The 16 open-top chambers (1.2m × 1.2m × 1.2m) were set in the experimental forest. Each treatment was replicated four times. The chambers were made of steel frame with polyvinyl chloride film having a transmittance of 88% of full sunlight. Four potted plants per each birch species were set in

each OTC. The plant position was changed every 2-weeks within each OTC and every month between the OTCs in each treatment because of the elimination of positional and chamber effects (Koike et al., 1995a).

2.3 Measurement of plant growth

The height, diameter and number of leaves of the seedlings were measured at the beginning and end of the experiment. Height and diameter increment was calculated as absolute difference between the final and initial diameters. The number of defoliated leaves was estimated by counting the leaf traces. In October 2010 all seedlings were harvested, and were separated into each organ (i.e., stem, branch, leaf and root). The plant organs were dried at 70˚C for 1 week and weighed.

2.4 Measurement of leaf gas exchange

At the beginning of September 2010, leaf gas exchange was measured for fully expanded sun leaves, 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 vapour pressure deficit (VPD, 1.2 kPa), according to Watanabe et al. (2011a). One or two seedlings per treatment-chamber combination were selected randomly 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 CO_2 steps (C_a, 380, 300, 220, 140, 60, 300, 380, 600, 800, 1100, 1400, 1700 μmol mol^{-1} for the seedlings grown in ambient CO_2 treatments and C_a=600 380, 300, 220, 140, 60, 380, 600, 800, 1100, 1400, 1700 μmol mol^{-1} for

the seedlings grown in elevated CO_2 treatments). The wait-time for stability of net photosynthesis at each level of CO_2 concentration was followed the procedure by Long and Bernacchi (2003). We determined A at the long-term CO_2 concentration (380 and 600 μmol mol^{-1} in the control and elevated treatment, respectively, A_{growth}), and also at 1700 μmol mol^{-1} (A_{max}), and the stomatal conductance at the long-term 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 values of 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 analysis of the A/C_i curve, were derived according to the methodology of Bernacchi et al. (2001). All gas exchange measurements of A/C_i curve were carried out on days with clear sky between 9:00 and 15:00 CET.

2.5 Statistics

Statistical unit was single OTC. Data were checked for normal distribution (Kolmogorov-Smirnov D test) and homogeneity of variance (Levene's test). The effects of O_3 and CO_2 on leaf gas exchange, and on plant biomass, were tested via two-way analysis of variance (ANOVA). Result were considered significant at $p<0.05$; a tendency toward significance was considered when $0.05<p<0.1$. All statistical analyses were performed with SPSS software (10.0, SPSS, Chicago, USA).

3. Results

3.1 Biomass and growth of seedlings

Elevated CO_2 significantly increased the diameter increments of the Monarch birch (Fig. 1). Height increments in the mountain birch were decreased with elevated CO_2. Attached leaves of mountain birch showed a tendency to be decreased by O_3 on Oct 6th (Fig. 2). The tendency to decrease in attached leaves was also found in monarch birch on Sep 29th. Defoliated leaves of the mountain birch tended to be larger with elevated O_3 (Fig. 3).

At the end of the experimental period, no significant difference in whole plant biomass was found between the elevated O_3 and/or CO_2 treatments for the mountain birch and Monarch birch (Table 1); for the white birch, whole plant mass tended to be larger with elevated CO_2. Interactive effect of O_3 and CO_2 on leaf biomass was recorded (P=0.081) in mountain birch. With elevated O_3, the branch biomass of the mountain birch tended to decrease. Elevated CO_2 increased the root biomass of the white birch. Interactive effect of O_3 and CO_2 on the ratio of shoot dry mass (stem + branch) to root dry mass (S/R ratio) of Monarch birch seedlings was found between the treatments, while elevated CO_2 reduced the S/R ratio of the mountain birch (P=0.038) and white birch (P=0.058).

3.2 Photosynthetic parameters

Leaf gas-exchange measurements showed that O_3 exposure significantly reduced A_{growth}, A_{max}, V_{cmax} and J_{max} of the mountain birch (Table 2). Elevated CO_2 significantly increased A_{growth} of the mountain birch and white birch. No significant increase in A_{growth} was

found for the Monarch birch. A decrease in V_{cmax} under elevated CO_2 was also found in the Monarch birch.

4. Discussion

Late summer exposure to O_3 reduced branch biomass (Table 1) and accelerated leaf abscission in the mountain birch (Fig. 3). In the present study, a reduction in A_{growth} was also found under elevated O_3 for the mountain birch (Table 2). Maintenance of O_3-injured leaves may raise respiratory costs for repair of the damaged parts (Matyssek and Sandermann, 2003). As a result, leaf abscission may be accelerated. Growth of long shoots is known to result from current year assimilation (Linder, 1987; Koike, 1995b), and thus is limited by O_3-induced early defoliation (e.g., Matyssek et al., 1993).

Late summer exposure to elevated CO_2 induced down-regulation of photosynthesis in the Monarch birch (Table 2). The present result shows that the photosynthetic down-regulation was due not to stomatal closure but to a reduction in the assimilation capacity, such as V_{cmax} (Table 2). As a result, the value of A_{growth} for Monarch birch under elevated CO_2 did not differ from that under ambient conditions. Similar findings were reported from the result of a Free-Air CO_2 Enrichment (FACE) experiment on Monarch birch (Eguchi et al., 2008; Watanabe et al., 2011b). Elevated CO_2 reduced the S/R ratio of mountain birch and white birch. This implies that elevated CO_2 stimulated root growth in the mountain birch and white birch, rather than aboveground growth. In contrast, Monarch birch did not show an enhancement of root growth in elevated CO_2. Absence of stimulation of root development at elevated CO_2 may limit the acquisition of

nutrients by the Monarch birch. Although biomass production was initially accelerated by high CO_2, the excess of carbon gain and deficiency of nutrients may cause dilution of nutrients with rapid growth, and thus depressed Rubisco activity (Watanabe et al., 2011a). The insufficient sink capacity resulting from environmental and/or genetic factors may also cause acclimation of photosynthetic capacity under elevated CO_2 conditions (Long et al., 2004; Ainsworth and Rogers, 2007).

Concurrent exposure of elevated O_3 and CO_2 in late summer changed the allocation to each organ for Monarch birch (Table 1). Interactive effect of O_3 and CO_2 on S/R ratio of Monarch birch seedlings was found. Monarch birch appeared to allocate photosynthates to leaf production rather than other organs as a compensative response to O_3 under elevated O_3 and CO_2 conditions during early period of the experiment (Fig. 2). Previous study also reported that the compensative leaf growth in response to elevated O_3 was stimulated under enhanced CO_2 conditions for *Fagus crenata* seedlings (Watanabe et al., 2010b). Elevated CO_2 is expected to enhance A_{growth} during the early period of the experiment as a short-term response to elevated CO_2, and thus may develop compensatory leaf growth. The observed compensatory response to O_3 may depend on CO_2 supply (Kolb and Matyssek, 2001).

In late summer, exposure to elevated CO_2 did not ameliorate the adverse effects of O_3 on dry mass or photosynthetic parameters that were observed in the mountain birch (Table 1; 2). Previous studies by season-long exposure to O_3 and CO_2 showed the compensatory effect of elevated CO_2, and the ameliorating effect of CO_2 may be caused by

reducing G_s, i.e., limiting O_3 uptake by stomata (Broadmeadow et al., 1999; Matsumura et al., 2005). In the present study, however, late summer exposure to elevated CO_2 did not induce stomatal closure in the three birch species studied (Table 2). The result is supported by a phytotron study of European beech (*Fagus sylvatica*) (Grams et al., 1999), which found that a reduction of G_s was induced by elevated CO_2 in early summer, but the effects of CO_2 on G_s diminished in late summer. Stomatal aperture is also affected by leaf-to-air vapor pressure (VPD) in summer, because of high temperatures. Heath (1998) found that stomatal sensitivity to VPD was reduced under elevated CO_2. Moreover, O_3 is known to induce sluggish stomatal response to light (e.g., Hoshika et al., 2012), VPD (Grulke et al., 2007; Uddling et al., 2009) and CO_2 (Onandia et al., 2011). A reduction in stomatal responsiveness to CO_2 under high VPD conditions may decrease the protective effects of elevated CO_2 against O_3 damage (Heath, 1998).

In conclusion, our hypothesis was supported by the results of birch responses to CO_2 and O_3 in late summer. The result presented here suggests that elevated CO_2 did not exert any ameliorating effect on the impact of late summer exposure to O_3 on birch species. Surface concentrations of O_3 are expected to increase continuously in East Asian countries (Yamaji et al., 2008). Only two reports are available on the combined effects of O_3 and elevated CO_2 on tree species native to Japan (Matsumura et al. 2005; Watanabe et al., 2010b). Our findings contribute to develop knowledge of forest dynamics of birch species in northern Japan under the atmospheric conditions expected in future, with elevated O_3 and CO_2.

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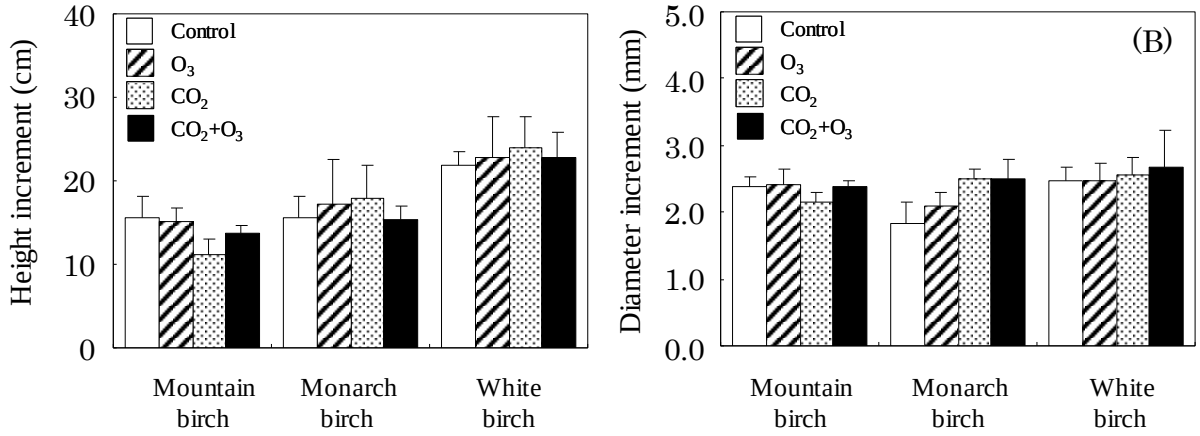
Figure captions

Fig.1 Height increments (A) and stem basal diameter increments (B) of three birch species treated with elevated O_3 (60 nmol mol^{-1} during daytime) and/or CO_2 (600 μmol mol^{-1} during daytime) during the experimental period from July to October 2010. Each value is the mean of four replications. The vertical bar indicates standard deviation.

Fig.2 Seasonal variation of number of attached leaves of three birch species (A, mountain birch; B, Monarch birch; C, white birch) treated with elevated O_3 (60 nmol mol^{-1} during daytime) and/or CO_2 (600 μmol mol^{-1} during daytime) during the experimental period from July to October 2010. Each value is the mean of four replications. The vertical bar indicates standard deviation.

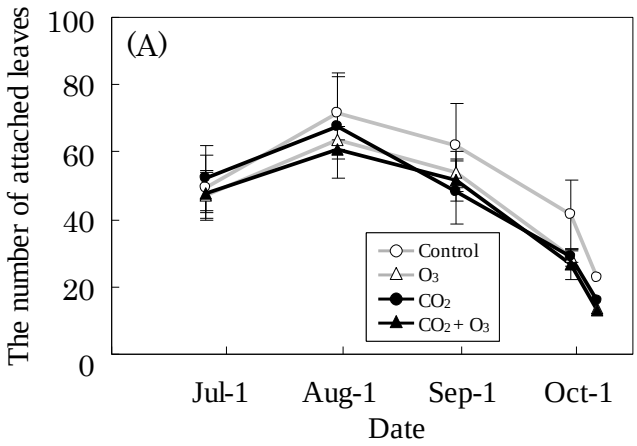
Fig.3 Number of defoliated leaves of three birch species treated with elevated O_3 (60 nmol mol^{-1} during daytime) and/or CO_2 (600 μmol mol^{-1} during daytime) during the experimental period from July to October 2010. Each value is the mean of four replications. The vertical bar indicates standard deviation.

Fig.1

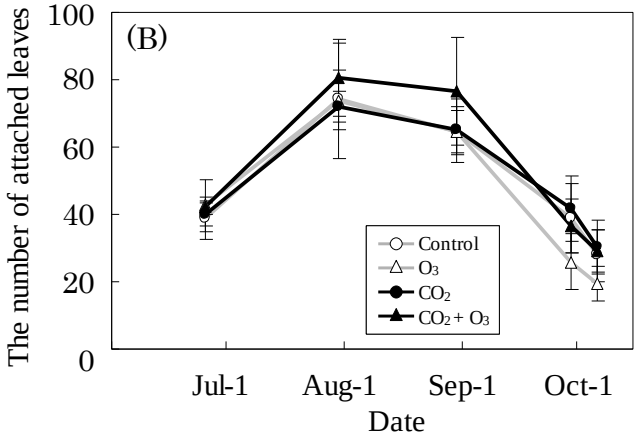


	P value for Two-way ANOVA		
	O_3	CO_2	CO_2+O_3
Height increment			
Mountain birch	0.274	**0.011**	0.136
Monarch Birch	0.848	0.901	0.260
White Birch	0.995	0.578	0.582
Diameter increment			
Mountain birch	0.191	0.123	0.223
Monarch Birch	0.369	**0.001**	0.328
White Birch	0.741	0.452	0.747

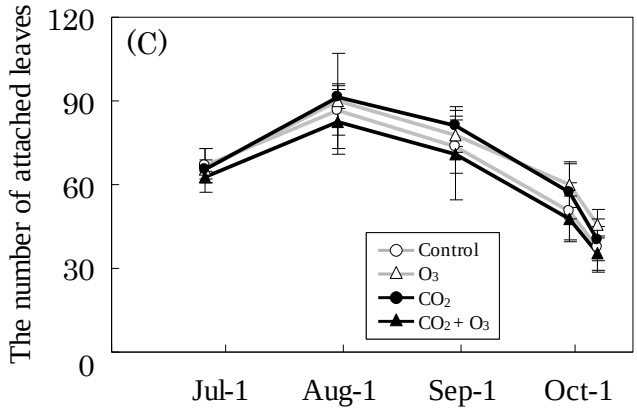
Fig.2



P value for two-way ANOVA	Jun-25th	Jul-30th	Aug-30th	Sep-29th	Oct-6th
O_3	0.251	0.119	0.654	0.118	*0.060*
CO_2	0.576	0.527	0.115	0.118	0.240
O_3+CO_2	0.733	0.946	0.283	0.261	0.319

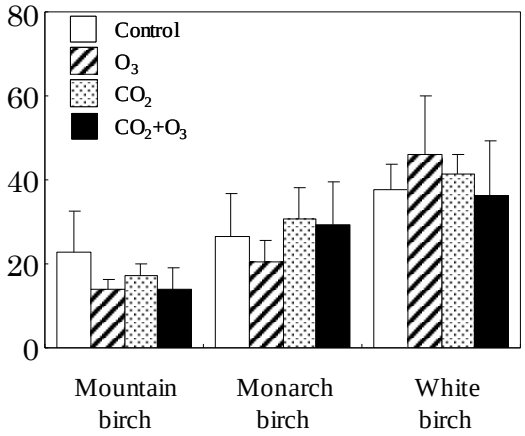


P value for two-way ANOVA	Jun-25th	Jul-30th	Aug-30th	Sep-29th	Oct-6th
O_3	0.350	0.316	0.322	*0.074*	0.181
CO_2	0.796	0.703	0.246	0.165	0.103
O_3+CO_2	0.885	0.510	0.264	0.402	0.345



P value for two-way ANOVA	Jun-25th	Jul-30th	Aug-30th	Sep-29th	Oct-6th
O_3	0.994	0.873	0.827	0.951	0.597
CO_2	0.318	0.350	0.407	0.716	0.832
O_3+CO_2	0.887	0.795	0.822	0.509	0.597

Fig.3



	P value for Two-way ANOVA		
	O_3	CO_2	CO_2+O_3
The number of defoliated leaves			
Mountain birch	*0.090*	0.346	0.183
Monarch Birch	0.383	0.605	0.632
White Birch	0.926	0.315	0.993

Tables

Table 1 Dry mass of plant organs per plant and the ratio of shoot dry mass (stem + branch) to root dry mass (S/R ratio) of three birch species treated with O_3 (60 nmol mol^{-1} during daytime) and/or CO_2 (600 μmol mol^{-1} during daytime) at the end of the experimental period

	Control	O_3	CO_2	CO_2+O_3	*P* value for Two-way ANOVA		
					O_3	CO_2	CO_2+O_3
Mountain Birch							
Stem biomass (g)	5.38 (0.64)	5.25 (0.54)	4.87 (0.44)	4.91 (0.27)	0.857	0.111	0.738
Branch biomass (g)	1.39 (0.11)	1.25 (0.20)	1.47 (0.20)	1.29 (0.20)	*0.095*	0.519	0.792
Leaf biomass (g)	1.80 (0.85)	1.14 (0.14)	1.05 (0.03)	1.29 (0.40)	0.388	0.239	*0.081*
Root biomass (g)	13.09 (2.45)	13.18 (1.09)	14.57 (1.52)	14.10 (1.84)	0.837	0.205	0.761
Whole plant biomass (g)	19.86 (3.12)	19.68 (1.54)	20.92 (1.33)	20.36 (2.17)	0.739	0.436	0.862
S/R ratio	0.52 (0.04)	0.49 (0.04)	0.45 (0.07)	0.44 (0.05)	0.464	**0.038**	0.713
Monarch Birch							
Stem biomass (g)	11.47 (0.36)	11.64 (1.37)	12.62 (0.88)	11.66 (1.43)	0.485	0.307	0.329
Branch biomass (g)	2.78 (0.62)	2.95 (0.30)	2.83 (0.33)	3.07 (0.28)	0.346	0.674	0.874
Leaf biomass (g)	2.71 (0.88)	2.70 (0.79)	3.39 (0.66)	3.13 (0.98)	0.754	0.208	0.778
Root biomass (g)	20.07 (3.64)	17.13 (3.00)	20.69 (4.35)	21.06 (2.93)	0.481	0.220	0.367
Whole plant biomass (g)	32.90 (6.04)	31.71 (3.89)	36.15 (5.02)	35.80 (4.55)	0.761	0.163	0.868
S/R ratio	0.72 (0.09)	0.88 (0.12)	0.80 (0.11)	0.71 (0.04)	0.460	0.355	**0.025**
White Birch							
Stem biomass (g)	9.31 (0.32)	9.11 (1.05)	9.62 (0.79)	9.80 (1.13)	0.987	0.282	0.672
Branch biomass (g)	1.88 (0.47)	1.88 (0.20)	1.93 (0.17)	1.78 (0.17)	0.596	0.870	0.600
Leaf biomass (g)	4.83 (0.61)	5.06 (0.31)	4.94 (0.65)	4.38 (1.10)	0.661	0.456	0.302
Root biomass (g)	17.39 (3.74)	17.01 (1.20)	21.50 (3.66)	20.81 (4.27)	0.757	**0.040**	0.929
Whole plant biomass (g)	28.59 (4.44)	28.00 (2.23)	31.37 (0.97)	32.39 (5.01)	0.905	*0.067*	0.660
S/R ratio	0.67 (0.10)	0.67 (0.04)	0.57 (0.06)	0.60 (0.10)	0.725	*0.058*	0.710

Each value is the mean (±SD) of 4 replicates.

Table 2 Photosynthetic parameters of three birch species treated with elevated O_3 (60 nmol mol^{-1} during daytime) and/or CO_2 (600 µmol mol^{-1} during daytime), measured at the beginning of September 2010.

	Control	O_3	CO_2	CO_2+O_3	*P* value for Two-way ANOVA		
					O_3	CO_2	CO_2+O_3
Mountain Birch							
A_{growth} (µmol m^{-2} s^{-1})	12.9 (2.5)	10.9 (1.7)	17.7 (2.3)	15.5 (1.8)	*0.069*	**0.001**	0.973
A_{max} (µmol m^{-2} s^{-1})	25.5 (3.5)	21.7 (2.4)	24.4 (3.5)	22.7 (1.5)	*0.083*	0.973	0.466
G_s (mmol m^{-2} s^{-1})	373.6 (88.5)	298.3 (85.4)	364.8 (65.0)	323.4 (23.1)	0.110	0.763	0.587
V_{cmax} (µmol m^{-2} s^{-1})	54.0 (11.4)	47.0 (5.1)	54.2 (3.9)	45.9 (6.1)	**0.047**	0.977	0.793
J_{max} (µmol m^{-2} s^{-1})	114.2 (15.1)	99.9 (12.0)	112.7 (11.8)	104.9 (5.8)	**0.044**	0.523	0.856
Monarch Birch							
A_{growth} (µmol m^{-2} s^{-1})	7.6 (1.1)	7.7 (2.3)	7.1 (1.1)	7.3 (3.1)	0.888	0.694	0.941
A_{max} (µmol m^{-2} s^{-1})	13.3 (1.9)	12.5 (5.4)	9.9 (1.2)	10.2 (2.7)	0.870	0.102	0.745
G_s (mmol m^{-2} s^{-1})	233.3 (45.5)	187.1 (42.7)	223.2 (44.4)	188.8 (102.3)	0.231	0.897	0.856
V_{cmax} (µmol m^{-2} s^{-1})	27.8 (3.9)	26.4 (10.5)	18.8 (2.7)	19.9 (7.6)	0.975	**0.045**	0.721
J_{max} (µmol m^{-2} s^{-1})	60.6 (9.2)	51.8 (19.8)	45.7 (5.0)	48.7 (12.6)	0.661	0.186	0.376
White Birch							
A_{growth} (µmol m^{-2} s^{-1})	10.3 (1.4)	10.5 (1.7)	12.7 (1.8)	13.7 (1.9)	0.588	**0.019**	0.696
A_{max} (µmol m^{-2} s^{-1})	17.6 (2.6)	17.5 (2.3)	16.0 (2.5)	18.3 (3.2)	0.368	0.759	0.351
G_s (mmol m^{-2} s^{-1})	232.5 (13.3)	219.6 (23.8)	201.6 (29.4)	233.1 (49.3)	0.568	0.593	0.188
V_{cmax} (µmol m^{-2} s^{-1})	46.3 (9.6)	43.8 (11.5)	41.0 (11.6)	39.6 (8.7)	0.633	0.259	0.893
J_{max} (µmol m^{-2} s^{-1})	82.2 (11.7)	78.1 (13.6)	77.8 (15.7)	82.6 (15.7)	0.955	0.997	0.471

A_{growth}, net photosynthetic rate at the chosen long-term CO_2 concentration;

A_{max}, net photosynthetic rate at CO_2 saturation; G_s, stomatal conductance for water vapor;

V_{cmax}, maximum rate of carboxylation; J_{max}, maximum rate of electron transport.

Each value is the mean (±SD) of 4 replicates.