

Article

Impact Assessment of Ozone Absorbed through Stomata on Photosynthetic Carbon Dioxide Uptake by Japanese Deciduous Forest Trees: Implications for Ozone Mitigation Policies

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Abstract: Photosynthesis by trees is expected to contribute to preventing climate change including global warming. However, the current levels of tropospheric ozone (O_3) reduce the uptake of photosynthetic carbon dioxide (CO_2) by forest trees in Japan, which is a concern. Furthermore, it is unknown how much O₃ should be reduced to prevent plants' O₃-induced damage. The objective of the present study was to assess the negative effects of the current levels of O_3 absorbed via stomata and the impact of its mitigation on the CO_2 uptake by trees in Japanese forests. Impact assessment, targeted in 2011–2015, was performed for four deciduous broad-leaved trees: Fagus crenata, Quercus serrata, Q. mongolica var. crispula, and Betula platyphylla var. japonica. The assessment was based on species-specific cumulative stomatal O₃ uptake (COU) and species-specific responses of annual photosynthetic CO₂ uptake to COU. Annual COU differed between the four trees; the average COU of F. crenata, Q. serrata, Q. mongolica var. crispula, and B. platyphylla var. japonica across Japan was 41.7, 26.5, 33.0, and 29.1 mmol m⁻², respectively, and the reductions in CO₂ uptake by the four trees were 14.0%, 10.6%, 8.6%, and 15.4%, respectively. Further analysis revealed that reducing the atmospheric O₃ concentration by approximately 28%, 20%, 17%, and 49% decreased the O₃-induced reductions in photosynthetic CO₂ uptake to 5% in *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. japonica, respectively. In the near future, implementing mitigation measures for the O₃ damage in plants is expected to enhance the photosynthetic capacity of Japanese forest tree species.

Keywords: ozone; stomatal ozone uptake; photosynthetic carbon dioxide uptake; impact assessment; mitigation; Japanese deciduous forest trees

1. Introduction

Climate change, including rising air temperatures and changes in precipitation, is recognized globally as a serious environmental problem [1]. Atmospheric carbon dioxide (CO_2) is one of the major factors causing climate change [1]. The CO_2 concentration has increased to approximately 400



 μ mol mol⁻¹ (ppm) from 280 ppm in 1750 with the increasing consumption of fossil fuels and burning of biomass [2,3]. In general, forest trees absorb atmospheric CO₂ by leaf photosynthesis, which is expected to attenuate climate change [4–6].

Tropospheric ozone (O_3) exhibits direct radiative forcing for climate change [1]. O_3 also has a potential for indirect radiative forcing, as it reduces the photosynthetic CO_2 uptake because of its high phytotoxicity [7,8]. Sitch et al. [9] suggested that indirect radiative forcing, which is the O_3 -induced reduction in the photosynthetic CO_2 fixation, could also contribute to global warming. Thus, an impact assessment of O_3 on photosynthetic CO_2 uptake is needed to support countermeasures, such as adaptation and mitigation, against the detrimental impact of O_3 .

Accumulated exposure over a threshold of 40 nmol mol^{-1} (AOT40) has been utilized to evaluate the effects of O₃ on tree species [10,11]. Although such an exposure-based O₃ index is useful for impact assessment of O₃ on plants because of the ease in calculation and fewer required parameters, stomatal O₃ uptake is more related to leaf O₃ damage than the exposure-based O₃ index [7,12]. In Europe, the impact of O₃ on trees has been assessed based on cumulative stomatal O₃ uptake (COU) [13]. However, the impact assessment on trees based on stomatal O₃ uptake is extremely limited in Asia. The tropospheric O₃ concentration in Asia is relatively high in the world [14], indicating remarkable damage of O₃ on plants grown in Asia. Therefore, it is necessary to assess the impact of O₃ on the photosynthetic CO₂ uptake of forest tree species in Asia.

In Japan, the tropospheric O_3 concentration has been increasing although the concentration of its precursors, such as nitrogen oxides (NO_x) and volatile organic compounds (VOCs), has decreased [15]. The increasing trend of O_3 concentration is mainly caused by the reduction in the titration effect of nitric oxide (NO) and partly increasing transboundary transportation of O_3 and/or its precursors from the Asian continent [15]. Current levels of O_3 are related to growth inhibition of plants and forest decline in Japan [16,17]. Thus, countermeasures may need to be implemented against O_3 damage to plants. Mitigation, which refers to the reduction of the atmospheric O_3 concentration here, is a fundamental and effective countermeasure against the damage of O_3 to plants. To date, however, limited information is available on the effects of the mitigation of O_3 on plants and on how much surface O_3 concentration should be reduced.

Recently, Yamaguchi et al. [18] evaluated the species-specific responses of cumulative photosynthetic CO₂ uptake to COU of the leaves in four Japanese forest tree species: *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*. Using these species-specific responses, we aimed (1) to evaluate the effects of the current levels of O_3 absorbed into the leaves via stomata on the photosynthetic CO₂ uptake by the four representative Japanese deciduous broad-leaved tree species and (2) to assess the impact of the mitigation of O_3 , i.e., reducing surface O_3 concentration, on the CO₂ uptake by the tree species.

2. Materials and Methods

2.1. Overview of Procedure for Simulating Impact and Mitigation Effects of O_3 on Photosynthetic CO₂ Uptake

In the present study, the impact and mitigation effects of O_3 on the annual photosynthetic CO_2 uptake per area of sunlit first-flush or early leaves of four Japanese deciduous broad-leaved trees—*Fagus crenata, Quercus serrata, Quercus mongolica* var. *crispula*, and *Betula platyphylla* var. *japonica*—were simulated in 2011–2015. First, environmental data and phenological data, such as leaf emergence date and leaf senescence date, for estimating stomatal O_3 uptake were collected from the databases of Japan Meteorological Agency (https://www.data.jma.go.jp/obd/stats/etrn/index.php), National Institute for Environmental Studies (https://www.nies.go.jp/igreen/), and Moderate Resolution Imaging Spectroradiometer (MODIS) product (https://doi.org/10.5067/MODIS/MCD12Q2.006). Second, COU at the O_3 monitoring stations was estimated for the four tree species using species-specific parameters of the stomatal O_3 uptake model developed by Kinose et al. [19]. The meteorological and phenological data to calculate the COU were obtained from nearby meteorological stations and nearby areas where

the trees were distributed, respectively. Third, COU in the tree distribution areas (Ministry of the Environment, http://www.biodic.go.jp/index.html) was estimated by interpolating the COU at the monitoring stations of O_3 using ordinary kriging. Fourth, according to species-specific responses of annual CO₂ uptake to COU reported by Yamaguchi et al. [18], O₃-induced reductions in CO₂ uptake for the four trees were calculated. Finally, the effects of O₃ mitigation, i.e., impact of reducing the surface O_3 concentration, on CO₂ uptake were calculated for the four tree species by simulating the input O₃ concentrations. A summary of information on simulation settings, required data, and data sources is provided in Table 1.

Parameter	Value or Source
Targeted year	2011–2015
Targeted leaves	Sunlit leaves
Calculation time step	1 h
Latitude	From 24° to 46°
Longitude	From 122° to 154°
Meteorological factors	Japan Meteorological Agency (https://www.data.jma.go.jp/obd/stats/etrn/index.php)
Ozone concentration	National Institute for Environmental Studies (https://www.nies.go.jp/igreen/)
Tree distribution ($45'' \times 30''$ mesh)	Ministry of the Environment (http://www.biodic.go.jp/index.html)
Parameters of stomatal conductance model	Kinose et al. [19]
Phenology (leaf emergence date, leaf senescence date, and f_{phen})	Friedl et al. [20] (https://doi.org/10.5067/MODIS/MCD12Q2.006)
Response of annual photosynthetic CO ₂ uptake to COU	Yamaguchi et al. [18]

Table 1. Simulation setting and data sources for the impact assessment of O_3 on annual CO_2 uptake.

2.2. Simulating Cumulative Stomatal O₃ Uptake

COU is given by

$$COU = \Sigma F_{st} \tag{1}$$

$$F_{\rm st} = [O_3]/(R_{\rm s_O3} + R_{\rm b_O3})$$
(2)

$$R_{\rm s_O3} = 1/(0.663 \times g_{\rm s}) \tag{3}$$

$$R_{\rm b\ O3} = 1.3 \times 150 \times (L_{\rm d}/u)^{0.5} \tag{4}$$

where F_{st} is the stomatal O₃ uptake, [O₃] is the atmospheric O₃ concentration, R_{s_O3} and R_{b_O3} are the stomatal resistance and leaf boundary layer resistance to O₃, respectively, g_s is the stomatal conductance to H₂O, L_d is the crosswind leaf dimension, and u is the wind speed.

The g_s was estimated according to the g_s model provided by Kinose et al. [19], originally developed by Jarvis [21]:

$$g_{\rm s} = g_{\rm max} \times f_{\rm phen} \times f_{\rm light} \times \max(f_{\rm min}, f_{\rm temp} \times f_{\rm VPD} \times f_{\rm SWC} \times f_{\rm O3conc}) \tag{5}$$

where g_{max} is the maximum g_s ; f_{min} is the ratio of minimum g_s to g_{max} ; and f_{phen} , f_{light} , f_{temp} , f_{VPD} , f_{SWC} , and f_{O3conc} represent responses of g_s/g_{max} to leaf phenology, photosynthetic photon flux density (PPFD), air temperature, vapor pressure deficit, volumetric soil water content, and atmospheric O₃ concentration, respectively. These parameters are species-specific and were essentially based on our previous results (see details in Kinose et al. [19]). The leaf emergence date and leaf senescence date

were provided by MODIS Land Cover Dynamics Product, MCD12Q2 v. 006, in 500-m grids in the world. Seasonal changes in enhanced vegetation index (EVI) of the MCD12Q2 were substituted for the f_{phen} . These phenological data were obtained considering tree distribution using vegetation raster data (45'' × 30'' mesh) of the National Survey on the Natural Environment (Ministry of the Environment), indicating the distribution of dominant species, although uncertainties exist in the dataset because the forest is not necessarily pure. In the present study, g_s was considered to be unchanged according to soil water content, i.e., $f_{SWC} = 1$, because the amount of precipitation was relatively high in Japan (annual mean precipitation: approximately 1700 mm).

The concentrations of photochemical oxidants are officially monitored at approximately 1200 monitoring stations across Japan (National Institute for Environmental Studies). In the present study, the concentration of photochemical oxidants was considered as the concentration of O_3 [10]. The meteorological data such as air temperature and wind velocity officially monitored at approximately 1300 monitoring stations throughout Japan (Japan Meteorological Agency) were used for the calculation of COU. PPFD was estimated based on the study by Masaki et al. [22]. The vapor pressure deficit (VPD) was estimated regarding the vapor pressure during the daytime as the saturated vapor pressure at the minimum temperature on the day, as the relative air humidity is almost 100% at the minimum temperature. The distribution of monitoring stations of photochemical oxidants and meteorological factors and regional partition in Japan is shown in Figure 1.



Figure 1. Distribution of monitoring stations of photochemical oxidants (red circle) and meteorological factors (green circle) and regional division in Japan.

The gaussian model was used as a semi-variogram model in the ordinary kriging to interpolate the annual COU at the O_3 monitoring stations, which was clipped by the tree distribution. As in a previous study [23], we did not interpolate the input data for calculating COU, i.e., meteorological data and O_3 data, because the interpolation is extremely difficult due to enormous calculation time. Kriging interpolation was performed using SAGA GIS v. 6.4.0 [24].

2.3. Impact Assessment of O₃-induced Reduction in Annual Photosynthetic CO₂ Uptake

The responses of annual photosynthetic CO_2 uptake to COU were fitted by the Weibull function, and the O_3 -induced reduction in annual CO_2 uptake was calculated as follows:

O₃-induced reduction in annual photosynthetic CO₂ uptake = $100 - 100 \times \exp[-(COU/\omega)^{\lambda}]$ (6)

where ω and λ are species-specific parameters of the Weibull function. ω and λ were originally proposed by Yamaguchi et al. [18] and were modified to make the intercept 100 (Figure 2).



Figure 2. Responses of annual CO₂ uptake per unit leaf area to cumulative stomatal O₃ uptake (COU) of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* seedlings. These responses were obtained from the study by Yamaguchi et al. [18] with slight modifications. The Y-intercept was modified to 100 in the present study. Plots indicate the first-flush or early leaves (\bigcirc) or second-flush or late leaves (×). The Weibull function was fitted to the response, and its parameters, ω and λ , and the mean absolute error (MAE, %) are indicated in each figure.

Since previous studies indicated that leaf morphological and physiological characteristics, such as leaf mass per area and gross photosynthetic rate, are related to the sensitivity to O_3 [7,25], the leaf-level photosynthetic sensitivity to O_3 might be different between seedlings and mature trees due to the differences in their leaf characteristics. However, this has not been clarified to date. In the present study, therefore, we assumed that the responses of CO_2 uptake to COU obtained in the seedlings in Yamaguchi et al. [18] were the same as those in the mature trees, although this might cause estimation errors in the impact of O_3 on CO_2 uptake to some extent.

3. Results

Figure 3 shows the spatial distribution of 5-year mean annual COU per unit leaf area of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in Japan in 2011–2015. The annual COU in each year is indicated in Figure 4. The 5-year mean COU averaged across Japan differed

between the tree species, being 41.7 (2011–2015 range: 37.2–46.2), 26.5 (24.1–27.9), 33.0 (29.7–34.9), and 29.1 (27.8–30.6) mmol m⁻² in the leaves of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*, respectively. COU was relatively low in the Tohoku and Hokkaido regions, and relatively high in Kanto, Chubu, Kinki, and Chugoku regions relative to the other regions.



Figure 3. Spatial distribution of 5-year mean annual cumulative stomatal O₃ uptake (COU) per unit leaf area (mmol m⁻²) of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in 2011–2015.



Figure 4. Annual cumulative stomatal O₃ uptake (COU) per unit leaf area (mmol m⁻²) of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in 2011–2015. Horizontal solid lines show the median, boxes show the first through third interquartile ranges, and whiskers show the minimum and maximum COU.

Figure 5 shows the spatial distribution of the 5-year mean O_3 -induced reduction in annual CO_2 uptake per unit leaf area of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in Japan in 2011–2015. The O_3 -induced reduction in annual CO_2 uptake each year is shown in Figure 6. The 5-year mean O_3 -induced reduction in CO_2 uptake averaged across Japan differed between the tree species, being 14.0% (2011–2015 range: 9.5–18.7%), 10.6% (7.3–12.1%), 8.6% (6.2–10.0%), and 15.4% (14.2–16.7%) in the leaves of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*, respectively.

Figure 7 demonstrates the impact of O_3 mitigation on the annual CO_2 uptake per unit leaf area of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in 2011–2015. A curvilinear response of the reduction in the surface O_3 concentration to the O_3 -induced reduction in the annual CO_2 uptake was observed in the four tree species. To diminish the O_3 -induced reduction in the annual CO_2 uptake to a value of 5%, the surface O_3 concentrations should be reduced by 28% (2011–2015 range: 19–34%), 20% (11–23%), 17% (8–21%), and 49% (46–51%) for *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*, respectively.



Figure 5. Spatial distribution of 5-year mean O₃-induced reduction in annual CO₂ uptake per unit leaf area (%) of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in 2011–2015.



Figure 6. Ozone-induced reduction in annual CO₂ uptake per unit leaf area (%) of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in 2011–2015. Horizontal solid lines show the median, boxes show the first through third interquartile ranges, and whiskers show the minimum and maximum reductions in CO₂ uptake.



Figure 7. Effects of O_3 mitigation for the O_3 -induced reduction in annual CO_2 uptake per unit leaf area (%) of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* in Japan in 2011–2015. The range of the O_3 -induced reduction in annual CO_2 uptake in 2011–2015 is represented in gray, and the means are indicated by the solid black lines.

4. Discussion

The present study firstly evaluated the impact of the current levels of O_3 absorbed via stomata on the annual cumulative photosynthetic CO_2 uptake per unit leaf area of four Japanese forest tree

species. The O₃-induced reduction in annual CO₂ uptake averaged across Japan was 14.0%, 10.6%, 8.6%, and 15.4% in *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*, respectively (Figures 5 and 6). This result indicated that the current atmospheric O₃ concentrations have the potential to reduce the capacity of CO₂ uptake by Japanese forest tree species.

Kinose et al. [19] indicated that when the four tree species were grown in the same environmental conditions, the COU was ranked as follows: *B. platyphylla* var. *japonica* > *F. crenata* > *Q. mongolica* var. *crispula* > *Q. serrata*. However, the tree distributions and environmental growth conditions greatly differ between the four tree species. *Betula platyphylla* var. *japonica* is mainly distributed in the Hokkaido region, where the stomatal O₃ uptake was relatively low (Figure 3). As a result, the COU of *B. platyphylla* var. *japonica* averaged across Japan was lower than that of *F. crenata* and *Q. mongolica* var. *crispula* (Figures 3 and 4). Nevertheless, the impact of O₃ on the CO₂ uptake of *B. platyphylla* var. *japonica* was more remarkable than that of the other tree species (Figures 5 and 6). This is due to the relatively higher sensitivity of photosynthetic CO₂ uptake to COU in *B. platyphylla* var. *japonica* (Figure 2).

Several studies have assessed the effects of O_3 absorbed via stomata on gross or net primary production (GPP or NPP, respectively) in forest ecosystems [9,26]. Lombardozzi et al. [26] estimated the O_3 -induced reduction in GPP targeted at global forest based on the relationships between COU and maximum carboxylation rate and between COU and stomatal conductance derived in a specific tree species, the tulip poplar. Sitch et al. [9] evaluated the impact of O_3 on the GPP of five plant functional types, namely broad-leaved trees, conifers, C_3 grasses, C_4 grasses, and shrubs, considering different sensitivities of the net photosynthetic rate to O_3 among the plant functional types. However, the sensitivity of the photosynthetic capacity to O_3 is extremely different between tree species possibly because of the differences in the defensive ability to O_3 [18]. The advantage of our impact assessment is that we considered the species-specific responses of photosynthetic CO_2 uptake to COU, even though there was uncertainty in the evaluation of O_3 -induced reduction rates by 3.1%, 3.6%, 3.8%, and 6.2% in *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*, respectively (Figure 2).

In the present study, COU and O_3 -induced reduction rates of CO₂ uptake were relatively high in Kanto, Chubu, Kinki, and Chugoku regions (Figures 3–6). Akimoto et al. [15] reported that the contribution of the transboundary transport of O_3 from the Asian continent to its concentration in Japan seemed to be relatively small except for that in the Kyushu region. According to Nagashima et al. [27], the contribution to the O_3 concentrations in Japan from China and the Korean Peninsula were estimated to be approximately 10% and 4%, respectively, although the domestic contribution was approximately 42% in the Japanese summer. Furthermore, O_3 is recognized as a short-lived climate pollutant (SLCP). These results indicate the necessity and effectiveness of domestic countermeasures against O_3 formulation for avoiding the O_3 -induced reduction in CO₂ uptake by Japanese forest tree species.

The concept of critical level of O_3 has been discussed in Europe to prevent its damage to plants. The critical levels of O_3 for European beech and European birch were defined as 5 ppm h of daylight AOT40 to diminish the growth reduction to a value of 5% [28]. In Japan, a provisional critical level based on AOT40 is suggested for the tree species sensitive to O_3 , namely 8–15 ppm h (6 months) corresponding to a 10% growth reduction [29]. However, the critical level based on stomatal O_3 uptake has been developed because the O_3 absorbed through stomata is more physiologically related to the O_3 damage to tree growth [30]. Critical levels of the two European trees were set at 5.2 mmol m⁻² of POD₁ (phytotoxic O_3 dose above the threshold of 1 nmol m⁻² s⁻¹) corresponding to a 4% growth reduction [28]. Although this concept of the critical level of O_3 is more scientifically plausible, how much O_3 should be reduced is unclear. While the stomatal O_3 uptake concept is significantly useful to assess the impact of O_3 on plants, to create and implement mitigation measures against O_3 damage to plants, determining the atmospheric O_3 concentration is needed. To the best of our knowledge, the present study is the first to evaluate the impact of the mitigation of O_3 absorbed via stomata on the annual photosynthetic CO₂ uptake. As a result, we clarified that O_3 concentrations should be reduced by 28% (2011–2015 range: 19–34%), 20% (11–23%), 17% (8–21%), and 49% (46–51%) for *F*.

crenata, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*, respectively, to diminish the O₃-induced reduction to a value of 5% (Figure 7). Because the domestic contribution of O₃ formation is 42% in the Japanese summer [27], it would be impossible to prevent the O₃ damage by 5% for *B. platyphylla* var. *japonica* by domestic control of the emission of O₃ precursors. In contrast, such a mitigation measure may be effective for the other tree species: *F. crenata*, *Q. serrata*, and *Q. mongolica* var. *crispula*. We provisionally propose that the O₃ concentration should be reduced by approximately 30% to decrease its damage on CO₂ uptake below 5% in some Japanese forest tree species. We hope our results will contribute to creating and implementing mitigation measures against the detrimental impact of O₃ on forest tree species in Japan and to enhancing their photosynthetic CO₂ uptake.

There are some uncertainties and future issues in the assessment on the impact of O_3 on the photosynthetic CO₂ uptake by forest tree species, including estimation accuracies of the stomatal conductance and errors of COU induced by the interpolation or extrapolation by kriging. One of the major issues is whether the parameterization results of the stomatal conductance model and the responses of CO₂ uptake to COU obtained in the particular environment of the experimental studies by Kinose et al. [19] and Yamaguchi et al. [18] could be applicable to the whole Japan in 2011–2015. Alonso et al. [31] reported different parameter values of the stomatal conductance model of Quercus ilex between marine-influenced sites and continental sites, indicating that the values of the model parameters depend on the environmental growth conditions of the trees. Actually, the optimum air temperature for stomatal opening depends on the growth conditions of *F. crenata* seedlings in Japan possibly because of an acclimation to the air temperature [32]. Therefore, the application of the stomatal conductance model of Kinose et al. [19] to the whole Japan may cause estimation errors of COU. Furthermore, Kinose et al. [7] indicated a higher sensitivity in the high-fertilized F. crenata seedlings due to the higher COU. In a forest area with a higher soil nutrient status, stomatal conductance may be higher via photosynthetic enhancement and be limited to some extent with shorter leaf longevity [33], indicating nutrient-dependent g_{max} and f_{phen} . In the present study, nutrient-dependent f_{phen} may be partly considered because f_{phen} was determined from the seasonal changes in EVI provided by satellite data. However, g_{max} was regarded as a constant in the present study, which could cause estimation errors of COU. The nutrient-induced modification of g_{max} in the calculation of COU is an issue to be considered in the future. On the other hand, the responses of CO_2 uptake to COU can differ depending on the growth conditions because the environmental conditions, such as atmospheric CO_2 concentration and soil drought, affect the leaf detoxification capacity to O_3 [34,35]. However, information on the effects of tree growth environment on the responses of CO_2 uptake to COU is insufficient to date. In order to perform a more accurate evaluation of the impact of O_3 on the photosynthetic CO₂ uptake by forest tree species, the effects of environmental growth conditions on COU and responses of CO₂ uptake to COU should be considered.

5. Conclusions

We evaluated the O_3 -induced reduction in annual CO_2 uptake per unit leaf area of *Fagus crenata*, *Quercus serrata*, *Quercus mongolica* var. *crispula*, and *Betula platyphylla* var. *japonica* in 2011–2015 based on the COU per unit leaf area and species-specific responses of the annual CO_2 uptake to COU. The current levels of ambient O_3 reduced the annual CO_2 uptake of *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica* by 14.0%, 10.6%, 8.6%, and 15.4%, respectively. Further analysis revealed that, to diminish the O_3 damage to a value of 5%, O_3 concentrations should be reduced by 28%, 20%, 17%, and 49% for *F. crenata*, *Q. serrata*, *Q. mongolica* var. *crispula*, and *B. platyphylla* var. *japonica*, respectively. We hope that implementing mitigation measures against O_3 damage will help increase the photosynthetic CO_2 uptake by Japanese forest tree species.

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