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Interactive Effects of Ozone and Light Intensity on *Platanus occidentalis* L. Seedlings

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Abstract : Sycamore (*Platanus occidentalis* L.) seedlings were grown under low light intensity and ozone treatments to investigate the role of the light environment in their response to chronic ozone stress. One-year-old seedlings of *Platanus occidentalis* L. were grown in pots for 3 weeks under low light (OL, 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and high light (OH, 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$) irradiance in combination with 150 ppb of ozone fumigation. After three weeks of ozone and light treatment, seedlings were placed in ozone free clean chamber for 3 weeks for recovery from ozone stress with same light conditions to compare recovery capacity. Ozone fumigation determined an impairment of the photosynthetic process. Reduction of leaf dry weight (14%) and shoo/root ratio (17%) were observed in OH treatment. OL treatment also showed severe reductions in leaf dry weight and shoot/root ratio by 48% and 36% comparing to control, respectively. At the recovery phase, OH-treated plants recovered their biomass, whereas OL-treated plant showed reduction in leaf dry weight (52%) and shoot/root ratio (49%). OH-treated plants reached similar relative growth rate (RGR) comparing to control, whereas OL-treated plants showed lower RGR in stem height. However, there were no significant differences in response to those treatments in stem diameter RGR at the recovery phase. Ozone treatment produced significant reduction of net photosynthesis in both high and low light treatments. Carboxylation efficiency and apparent quantum yield in OL-treated plants showed significant reductions rate to 10% and 45%, respectively. At the recovery stage, ozone exposed seedlings under high light had similar photosynthetic capacity comparing to control plants. Antioxidant enzymes activities such as superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) were increased in ozone fumigated plants only under low light. The present work shows that the physiological changes occur in photosynthesis-related parameters and growth due to ozone and low light stress. Thus, low light seems to enhance the detrimental effects of ozone on growth, photosynthesis, and antioxidant enzyme responses.

Key words **:** Platanus occidentalis, *sycamore, low light, O_3, net photosynthesis, carboxylation efficiency, antioxidant enzyme*

Introduction

The phytotoxicity of ozone (O_3) has been demonstrated for forest tree species since more than 50 years and is now considered to be the most important air pollutant affecting vegetation in both rural and urban areas (Karnosky *et al.*, 2007; Matyssek *et al.*, 2007; Paoletti *et al.*, 2007).

Over the past several decades it has confirmed that O_3 is the major pollutant responsible for visible foliar injury and reduced growth in trees (Karnosky *et al.* 2007; Matyssek *et al.*, 2007; Wittig *et al.*, 2007). The most frequent effect linked to ozone exposure is the reduction of plant biomass, which is caused by alteration of the photosynthetic process (Topa *et al.*, 2001; Topa *et al.*, 2004; Wittig *et al.*, 2007). O_3 is a strong oxidant, and significant damage to photosynthesis occurs when O_3 enters the leaf through the stomata. This leads to a progressive loss of ribulose 1.5-bisphosphate carboxylase/oxygenase (Rubisco) activity (Dizengremel, 2001). Wittig *et al.* (2007) reported that based on the 348 measurements of photosynthesis from 61 studies, this could drive a further 8-16% decrease in photosynthesis caused by rising O_3. Reduced photosynthesis results in decreased growth rate either volume or biomass. In addition, physiological effects of ozone exposure include reduced photosynthesis and increased turn over of antioxidant systems.

Trees respond to O_3 stress through mechanisms of avoidance and defense (i.e. stress tolerance; Wieser and

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Matyssek, 2007) such as restriction of O_3 uptake by stomatal closure and metabolic detoxification in the leaf, respectively. Wieser *et al.* (2002) reported that the extent of O_3-induced injury can be related to the amount of available antioxidants vs. stomatal flux or uptake. Constitutive detoxification is already operative in the apoplast and symplast when O_3 enters the leaf. O_3 reacts with antioxidants in the apoplast and includes the production of reactive ozygen species (ROS). As a first line of defense, the reduced ascorbate in the apoplast determines the amount of ROS that can reach the plasmalemma, where ROS will initiate stress signaling and will set the metabolism. Thereafter, self-amplification of the oxidative stress represents a component of the intrinsic redox system of the plant and may induce a wide range of metabolic changes and responses to various oxidative stressors (Kangasjärvi *et al.*, 2005; Nunn *et al.*, 2005; Wieser and Matyssek, 2007). Hence, plants manage its performance under oxidative stress, in particular O_3 stress, through the internal regulatory redox mechnisms. Therefore, an increse of the antioxidative enzyme activities under air pollution stresses could also be indicator for a build-up of a protective mechanism to reduce oxidative damages by stress (Han *et al.*, 2007). Thus, several researches adopted antioxidant levels as biomarkers of ozone sensitivity that could be used screening of great diversity of tree species' potential sensitivity to ozone (Paoletti *et al.*, 2003; Han *et al.*, 2006).

Even though sensitivity to O_3 vary among species and among genotypes, environmental factors such as light intensity, temperature, and nutrient availability may also play an important role in determining plant sensitivity of O_3 exposures. In study of responses to O_3 of several trees, more foliar injury was observed in the lower and interior crowns than upper crowns (Fredericksen *et al.*, 1996). Shade grown leaves also had lower net photosynthesis than sun-exposed leaves when grown under high O_3 exposures compared to control grown plants (Tjoelker *et al.*, 1995, Wei *et al.*, 2004; Novak *et al.*, 2005). These authors reported that when the O_3 exposures were prolonged, stomatal conductance became uncoupled from light saturated photosynthetic rates that introduce growth inhibition

Sycamore (*Platanus occidentalis* L.) is the second abundant tree species as roadside tree in urban area of Korea and they are known as a relatively tolerant species to air pollutants. There were several researches on the physiological responses and antioxidant changes to ozone fumigation under ideal environmental conditions in chamber system (Lee *et al.*, 2005; Woo, 2006) and they had been identified as extremely sensitive species that exhibiting above 50% of symptoms (Neufeld *et al.*, 1992). However, there were no studies reported about combination effect of ozone and light on physiological and biochemical responses in sycamore.

In the current study, we hypothesize that stress in low light under ozone fumigation is more severe than the stress in proper light condition under ozone fumigation. Consequently, antioxidant enzyme activities as a defense mechanism could be higher in low light condition than in proper light condition under ozone stress.

The objectives of this research were to determine the influence of low light on growth, photosynthetic capacity and antioxidant enzyme activity of ozone exposed plant. We also examined the degree of repair capacity after ozone treatment under high and low light conditions involved in post-stress repair.

Materials and Methods

1. Plant materials and treatments

Seeds of *Platanus occidentalis* were sown in sand. Seedlings were transplanted into plastic pots (H 20×W 15 cm) containing artificial soil, which consisted of 1:1:1 sand: peat moss: vermiculite (volume basis). Five seedlings per treatment were transferred into the chamber and were arranged in two blocks. One-year-old *Platanus occidentalis* seedlings were grown in chambers with two different ozone level and light intensity. Control plants were grown at 5±1 ppb (control chamber) of ozone with light condition of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 12 hours day^{-1}. Ozone fumigation was conducted at 150±10 ppb (8 hours per day) for 3 weeks under high (300 $\mu mol\ m^{-2} \cdot s^{-1}$, 12 hours day^{-1}) and low (150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) light conditions. The fumigation system has been described in detail by Lee *et al.* (2003). After 3 weeks of O_3 fumigation, seedlings were placed in an ozone free clean chamber for 3 weeks for recovery from ozone stress under the identical light conditions.

2. Photosynthesis

At the end of ozone treatment and recovery phase, net photosynthesis of fully expanded leaves was measured with an infrared gas analyzer (Li-6400, Li-COR, USA). Environmental parameters were maintained stably for measuring (mean temperature: 24.0±0.1°C; relative humidity: 68.2±3.2%; leaf-to-air vapour pressure deficit: 1.2±0.2 kPa). All determinations were performed at 1000 $\mu mol\ m^{-2} \cdot s^{-1}$ photon flux density (PFD). Net photosynthesis ($\mu mol\ CO_2\ m^{-2} \cdot s^{-1}$) was determined at light saturation level between 10 a.m. and 3 p.m. The *ACi*-curve and light response curve were made to calculate carboxylation efficiency and apparent quantum yield (Farquhar *et al.*, 1980; Kim and Lee, 2001). The carboxylation efficiency and apparent quantum yield were determined from the initial slope of a linear regression using the lin-

ear portion of the *ACi*-curve (0-150 ppm intercellular CO_2) and light response curve (0-100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD), respectively.

3. Antioxidant enzyme activities

Fresh leaves (0.1 g) were homogenized under ice-cold condition with 5 mL of 50 mM phosphate buffer (pH 7.0), 10 mM ascorbic acid (AsA) and 1.0% (w/v) polyvinylpyrrolidone. The homogenate was centrifuged at 20,000×g for 30 min, and the supernatant was collected for enzyme assays. Superoxide dismutase (SOD) was assayed based on the inhibition of reduction of nitroblue tetrazolium in the presence of xanthine at 530 nm according to the method of Beauchamp and Fridovich (1971). Ascorbate peroxidase (APX) activity was determined by the method of Nakano and Asada (1981). The assay was carried out in a reaction mixture containing 50 mM phosphate buffer (pH 7.0), 0.5 mM AsA, 0.1 mM EDTA, 0.1 mM H_2O_2, and 0.1 mL enzyme extract. The change in A_{290} was recorded for 1 min after the addition of H_2O_2. Activity of glutathione reductase (GR) was assayed as described in Carlberg and Mannervik (1985). The assay was carried out in a reaction mixture containing 50 mM phosphate buffer (pH 7.8), 0.1 mM NADPH, 0.5 mM GSSH and 0.1 mL enzyme extract. The change in A_{340} was recorded for 5 min after the addition of enzyme extract. Catalase (CAT) activity was determined by following a two-step procedure (Fossati *et al.*, 1980). The rate of dismutation of H_2O_2 to water and molecular oxygen is proportional to the concentration of catalase. Therefore, the sample containing catalase was incubated in the presence of a known concentration of H_2O_2. After incubation for exactly one minute, the reaction was quenched with sodium azide. The amount of H_2O_2 remaining in the reaction mixture was then determined by the oxidative coupling reaction of 4-aminophenazone (4-aminoantipyrene) and 3,5-dichloro-2-hydroxybenzenesulfonic acid (DHBS) in the presence of H_2O_2 and catalyzed by horseradish peroxidase (HRP). The resulting quinoneimine dye was measured at 520 nm. All the activities of enzyme were measured using UV-120 (SHIMADZU, Japan).

4. Growth

The relative growth rate (RGR), as indicated by main stem height and basal diameter, were calculated as: $RGR=[\ln(X_2)-\ln(X_1)]/(t_2-t_1)$, where X_1 was the height or diameter at time t_1 (start of the experiment) and X_2 was the height or diameter at time t_2 (termination of the experiment). For biomass measurements, shoots and roots were carefully removed, and then thoroughly rinsed twice with distilled water. Shoot and root dry weights were recorded after drying the tissues at 70°C.

5. Statistical Analysis

To compare the effect on O_3 and low light treatment, ANOVA was performed on experimental data (statistical significance, $P \leq 0.05$). Statistical analyses were performed using the statistical package SAS System for Windows, Version 8.01 (SAS Institute, USA).

Results

1. Growth

Ozone exposure induced visible foliar injury with dark pigmented stipples on *Platanus occidentalis*. The OL treatment resulted in greater biomass reduction than control and OH treatment in leaf biomass at the end of ozone fumigation. Although it was not statistically significant, stem and root biomass were increased in OL treatment. Shoot/root ratios of OL treatment decreased by 30% comparing to control at the end of ozone fumigation, mostly due to the damages of leaves (Table 1). At the recovery phase, OL treatment showed more

Table 1. Effects of light intensity on biomass of O_3-exposed *Platanus occidentalis* seedling under high light (OH) and low light (OL) for 3 weeks (A: the end of ozone fumigation). After the end of ozone fumigation, seedlings had recovery stage without ozone fumigation for 3 weeks (B: recovery phase). Each value represents the mean of five replicates±SD. Means for the same stage with the same letter are not significantly different at P < 0.05 (Duncan's multiple test).

Treatment	Dry weight (g)				
	Leaf	Stem	Root	Total	Shoot/root ratio
	(A) The end of ozone fumigation				
Control	2.67±0.77[a]	2.89±0.44[a]	3.81±0.88[a]	9.37±2.02[a]	1.48±0.19[a]
OH	2.29±0.39[a]	2.77±0.40[a]	4.28±1.09[a]	9.34±1.54[a]	1.23±0.25[ab]
OL	1.40±0.33[b]	3.07±0.37[a]	4.53±1.24[a]	9.00±1.45[a]	1.03±0.23[b]
	(B) Recovery phase				
Control	4.97±0.86[a]	4.98±1.06[a]	3.80±0.70[a]	13.75±2.25[a]	2.65±0.39[a]
OH	4.58±1.37[a]	4.84±1.37[a]	3.91±1.26[a]	13.33±3.22[a]	2.57±0.96[a]
OL	2.41±0.33[b]	3.68±1.06[a]	4.93±1.86[a]	11.02±2.82[a]	1.34±0.40[b]

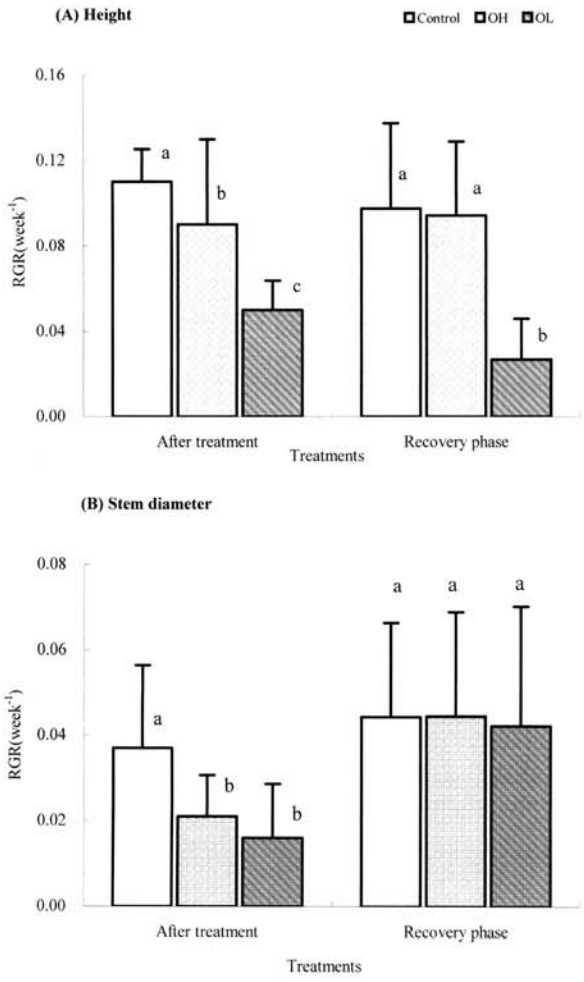

Figure 1. Effect of light intensity on relative growth rate (RGR) of height (A) and stem diameter (B) of *Platanus occidentalis* seedlings that were exposed to 150 ppb ozone under high light (OH) and low light (OL) for 3 weeks. After ozone treatment, seedlings had recovery phase without ozone fumigation for 3 weeks. Each bar represents the mean of five replicates±SD. Means for the same stage with the same letter are not significantly different at P<0.05 (Duncan's multiple test).

severe reductions in leaf dry weight by 52% comparing to control. However, OH-treated plants represented no significant differences in leaf dry weight with control plant. In addition, stem and root biomass showed no significant differences among treatments. The significant reduction in shoot/root ratio of OL-treated plants (by 49% comparing to control) at the recovery phase suggests that OL treatment significantly affected not root part but the aerial part of plant as much as they could not recover damages.

The ozone exposure and low light treatment resulted in low height and diameter growth increments of seedlings (Figure 1). Ozone affected growth more under low light treatment than under high light treatment, possibly due to low light intensity. Compared to control, O_3 treatment resulted in 18% and 55% less height relative growth rate (RGR) under high and low light treatments, respectively. At the recovery stage, OH resulted in similar RGR comparing to control, whereas OL resulted in much less height RGR (72% of control). The OL treatment resulted in significantly smaller height growth under equal O_3 exposure; and the differences in height growth were due to light differences. Main stem diameter expressed a similar trend to height growth. The ozone exposure resulted in significantly less diameter growth than control under both high and low light treatments. Compared to control, OH and OL treatment resulted in 50% less diameter RGR increment. However, OH and OL treatment showed fully recovered results in diameter RGR increment during recovery period. There was a trend for the seedlings grown under high light treatment to have high stem height and diameter increment during recovery stage. The seedlings grown under low light had the least diameter increment, which was significantly smaller than high light treatment at recovery phases.

Table 2. Effects of light intensity on net photosynthesis, carboxylation efficiency, and apparent quantum yield of O_3-exposed *Platanus occidentalis* seedling under high light (OH) and low light (OL) for 3 weeks (A: the end of ozone fumigation). After the end of ozone fumigation, seedlings had recovery stage without ozone fumigation for 3 weeks (B: recovery phase). Each value represents the mean of five replicates±SD. Means for the same stage with the same letter are not significantly different at P<0.05 (Duncan's multiple test).

Treatment	Net photosynthesis (μmol CO_2 m^{-2} s^{-1})	Carboxylation Efficiency (mmol CO_2 mol^{-1})	Apparent quantum yield (mol CO_2 mol^{-1})
(A) The end of ozone fumigation			
Control	10.9±1.62^a	0.062±0.017^a	0.051±0.003^a
OH	6.1±1.31^b	0.049±0.013^{ab}	0.045±0.004^{ab}
OL	6.0±2.23^b	0.035±0.009^b	0.042±0.006^b
(B) Recovery phase			
Control	7.21±1.03^a	0.053±0.019^a	0.041±0.007^a
OH	7.66±2.56^a	0.067±0.011^a	0.046±0.005^a
OL	6.40±1.90^a	0.029±0.017^b	0.037±0.007^b

Table 3. Effects of light intensity on antioxidant enzyme activities of O_3-exposed *Platanus occidentalis* seedling under high light (OH) and low light (OL) for 3 weeks (A: the end of ozone fumigation). After the end of ozone fumigation, seedlings had recovery phase without ozone fumigation for 3 weeks (B: recovery phase). Each value represents the mean of five replicates±SD. Means for the same stage with the same letter are not significantly different at P<0.05 (Duncan's multiple test).

Treatment	SOD (unit g^{-1})	APX (μmol g^{-1})	GR (nmol g^{-1})	CAT (unit g^{-1})
	(A) The end of ozone fumigation			
Control	308±83[a]	421±63[b]	507±123[b]	1813±239[a]
OH	216± 49[b]	567±123[a]	462±21[b]	1955±268[a]
OL	360±104[a]	533±55[a]	740±167[a]	1908±200[a]
	(B) Recovery phase			
Control	333±58[b]	429±112[b]	779±240[b]	979±238[b]
OH	336±59[b]	750±322[a]	1139±232[a]	897±230[b]
OL	454±99[a]	603±96[a]	617± 59[b]	1390±393[a]

2. Photosynthesis

The O_3 and light were significant sources of differences for net photosynthesis, carboxylation efficiency, and apparent quantum yield (Table 2). Ozone exposures greatly suppressed photosynthesis and resulted in high reduction (44%) of net photosynthesis. The average carboxylation efficiency and apparent quantum yield of seedlings grown under OL were much lower than those of the seedlings grown under OH. OL-treated plants had more severe reduction rate to 44% of control in carboxylation efficiency. The apparent quantum yield decreased significantly in OH and OL leaves to 12% and 18% comparing to control plants. Low light intensity resulted in significantly lower carboxylation efficiency and apparent quantum yield than control and high light treatment.

At recovery phase, ozone exposed seedlings under high light (OH) exhibited similar photosynthetic capacity comparing to control plants. No significant differences in net photosynthesis were noted among control, OH and OL treatment after recovery phase. The carboxylation efficiency and apparent quantum yield of seedlings grown under high light that showed similar pattern of control were significantly greater than those of the seedlings grown under low light. OL-treated plants showed significant reductions rate in carboxylation efficiency and apparent quantum yield to 45% and 10% comparing to control, respectively. Over the entire ozone treatment and recovery phases, low light resulted in lower carboxylation efficiency and apparent quantum yield than control and high light treatment.

3. Antioxidant enzyme

Table 3 shows the results of the antioxidant enzyme activities in leaves of *P. occidentalis* plants subjected to ozone and two different light intensities. OL treatment had significant increase of APX (26%) and GR (46%) activities after treatment comparing to control, while APX (35%) activities were increased in only OH treatment. There were no significant effects of ozone or light intensity on CAT activities.

At the recovery phase, response of enzyme activities to ozone and low light was obvious. APX activities were increased both in OH (75%) and OL (41%) treatments, while GR activities were increased only in OH treatment comparing to control. OH treatment showed no significant differences in SOD and CAT activities comparing to control, however, OL treatment had significant increase to 36% and 42%, respectively.

Discussion

The interactive effects of ozone and light intensity on sycamore (*Platanus occidentalis* L.) seedlings were examined, with an emphasis on growth response, photosynthesis and antioxidant enzyme activity. *P. occidentalis* foliar symptoms were consistent with those observed during previous studies (Lee *et al.*, 2005; Woo *et al.*, 2006). Ozone and low light significantly reduced seedling growth in leaf dry weight by 50% at the end of ozone fumigation. However, slight increases in root biomass under ozone stress were observed, although it was not statistically significant (Table 1). This trend is contradictory in respect to other studies that found a greater reduction in root biomass as compared to shoots (Paludan-Müller *et al.*, 1999; Rebbeck and Scherzer, 2002). Novak *et al.* (2008) reported that *Viburnum* root biomass affected negatively as result of ozone stress, whereas root biomass in beech tended to be stimulated under ozone stress. In unshaded poplar plants, ozone exposure reduced root dry mass, while shaded plants had no such response, by comparison, sugar maple root dry mass was reduced by ozone in shaded plants by 10%, but was unaffected by ozone in unshaded plants (Tjoelker *et al.*, 1993). Overall our results and previous studies, light environment alters response to ozone stress in depending on species and ozone sensitivity. At the recovery phase, OH-treated

plant showed adequate recovery of biomass after ozone fumigation. On the other hand, OL-treated plant was observed severe reduction in leaf dry weight and shoot/root ratio to 52% and 49% of control. Our results indicated that enough sunlight offered greater protection against ozone injury, and more carbon was available for injury repair processes like early reported in sugar maple by Topa *et al.* (2001).

The response of plants to the combined treatment with light and ozone seems to confirm the presence of cooperation between two stress factors with major limitations in net photosynthesis. The present work shows changes in photosynthesis-related parameters due to low light stress under ozone treatment. Low light can modify the reaction of leaves to ozone treatment by reducing carboxylation efficiency and apparent quantum yield. Several studies suggest that if photosynthesis and leaf growth are impaired during long-term exposure to ozone, carbohydrate availability may limit root growth and other metabolic activities (Topa *et al.*, 2001). In our results, low light under ozone treatment showed significant reduction of net photosynthesis and leaf biomass, however, it was not long or high concentration of ozone exposure to produce root growth reduction by reduced net photosynthesis as much as that causes carbohydrate insufficient supply available for root growth. Environmental conditions such as the heterogeneous low light environment in a forest canopy, which results in a higher conductance than is needed to support CO_2 uptakes, are likely to exacerbated damage by O_3 uptakes (Fredericksen *et al.*, 1996). Our results showed similar results that low light treatment under ozone fumigation had more severe damages in growth and photosynthetic capacity than OH-treated plants. However, the response of trees is also likely to vary with age (Karnosky *et al.*, 2007; Wittig *et al.*, 2007) and capacity of the tree to detoxify O_3 (Matyssek *et al.*, 2007). From our results, irradiance may be a critical factor, influencing the carbon-gain response to ozone stress in a forest canopy.

O_3-induced detoxification processes require energy for the regeneration and *de novo* synthesis of antioxidants and other related chemical compounds. On a long-term scale carbon gain and carbohydrate accumulation typically decrease in parallel with the increase in antioxidants (Wieser *et al.*, 1998). At a critical level of cumulative O_3 uptake, the antioxidative defense system becomes overwhelmed. Ascorbate as well as glutathione is involved in detoxification that is known as defense against metabolic poisoning (Wieser and Matyssek, 2007). In our present research, OL-treated plant had increased in APX and GR activities, whereas, OH-treated plant did not increase at the end of ozone fumigation. However, both SOD and CAT showed no significant differences in OH and OL treatment comparing to control at the end of ozone fumigation. In contrast, at the recovery phase OL treatment had significant increase. This is in agreement with previous several studies. Cu/Zn-SOD and CAT are major targets for ozone-induced inactivation and both ascorbate and GR are very effective in protecting the enzyme from ozone. Cu/Zn-SOD and CAT are known to play an important role in defense against ozone but excess ozone inactivates these enzymes. Actually photocopying operators are exposed to ozone and found to have lower activity of Cu/Zn-SOD and CAT (Lee *et al.*, 2003; Zhou *et al.*, 2003). From our results we could hypothesis that significant increase of SOD and APX activities in OL treatment means more severe stress than OH treatment. Thus, low light seems to enhance the detrimental effects of ozone on plant protection.

Shade-tolerant species should be more sensitive to ozone when grown in shade than in full sunlight because of high stomatal conductance and ozone uptake in low light. Conversely, shade-intolerant species should exhibit a smaller ozone response when grown under low light because of reduced stomatal conductance. The importance of shade tolerance and light environment in understanding ozone sensitivity in forest trees is also complicated by tree developmental stage (Chappelka and Samuelson, 1998). Shade-tolerant species, sugar maple and red oak, showed decrease of net photosynthesis and growth in mature stage under low light to ozone; however, seedlings were not affected at the same conditions (Samuelson, 1994 a; Tjoelker *et al.*, 1995; Laurence *et al.*, 1996). Although black cherry is a shade-intolerant species, it was observed more reductions of net photosynthesis and growth in shade and lower-stem leaves in both mature tree and seedlings (Samuelson, 1994 b; Fredericksen *et al.*, 1996; Chappelka and Samuelson, 1998). Our study had also similar result. Despite sycamore is shade-intolerant species, great reductions were observed in photosynthesis and growth of O_3-exposed seedlings under low light. Therefore, species' inherent shade tolerance, tree developmental stage and light environment during ozone exposure influence ozone sensitivity (Tjoelker *et al.*, 1993; Chappelka and Samuelson, 1998)

Conclusion

The negative impacts of low light on growth were greater than those of high light. High O_3 treatment resulted in greater reductions on growth and photosynthetic capacity in OL-treated seedlings than OH-treated seedlings. Seedlings grown under high light could recover the negative impacts of ozone treatment, however, seedlings grown under low light after ozone treatment could not recover within 3 weeks. The overall results of this study suggest

that light intensity play an important role in determining plant sensitivity to O_3 exposures and environmental factors must be considered in studying plant responses to O_3 exposure.

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