Physiological and biochemical responses of two tree species in urban areas to different air pollution levels

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Abstract

We investigated the physiological and biochemical differences in *Pterocarpus indicus* and *Erythrina orientalis* grown in four sites at different pollution levels in the Philippines: Makati, Pasig and Quezon (high pollution levels; HP) located in Metro Manila, and La Mesa Watershed (a non-polluted area; NP). Among these four areas, HP sites had higher net photosynthetic rates (P_N) than NP sites, except for Makati. Among HP sites, Makati and Quezon had the lowest P_N for *P. indicus* and *E. orientalis,* respectively. Chlorophyll (Chl) contents were significantly lower in HP than in NP sites. Trees in Makati had the lowest Chl contents among HP sites, and *P. indicus* had higher Chl contents than did *E. orientalis*. In addition, the chloroplasts in HP trees had small starch grains with numerous dark, large plastoglobuli. Furthermore, antioxidant enzymes, indicative of the defense mechanism, showed a significantly higher activity in HP than in NP trees.

Additional key words: antioxidant enzyme; chlorophyll content; chloroplasts; photosynthetic rate; plastoglobuli.

Introduction

Plants can be indicators of air pollution (Neufeld *et al*. 2006), and the relationship between photosynthesis and Chl content is very important for understanding air pollution-induced injury (Woo *et al.* 2004). Changes at the cellular level, affecting the size and number of chloroplasts, starch grains, and plastoglobuli, can be used as pollution stress indicators (Anttonen and Kärenlampi 1996). When pollutants enter the intercellular leaf space through the stomata, various antioxidants participate in detoxification. Therefore, measuring this activity will increase our understanding of antioxidative stress-related defense mechanisms and air pollution-induced leaf injuries.

Air pollution (heavy metals, sulfur dioxide and ozone) in Manila, Pasig, Makati, and Quezon (Philippines) has become a serious problem in recent years due to the increasing number of human activities. Emissions have not been successfully restricted: ambient SO_2 and NO_x concentrations rose by 4–5% by the end of 2004 (Woo *et al*. 2007). Few studies have examined the effect of pollutants on plants in the Philippines (Sabalvaro 2004). *P. indicus* (Thomson 2006) and *E. orientalis* (Woo *et al*. 2007) are the most important trees in the Philippines, as they are nitrogen-fixing species. The objective of this study was to investigate the effects of the air pollution-induced injuries on these two tree species in the Manila region.

Materials and methods

Study site and plant species: The experiment was conducted in the cities of Pasig, Makati and Quezon, which were classified as having high levels of air pollution (HP), and La Mesa, which was classified as a non-polluted area (NP) (Fig. 1). Field measurements were carried out with two 10-year-old species: *P. indicus* and *E. orientalis*. *P. indicus* is well known in the Philippines and is well adapted to harsh soils and strong winds (Thomson 2006). *E. orientalis* is cultivated throughout the tropics, particularly as an ornamental tree and as a shade- and soil-improvement tree due to its ability to fix nitrogen (Whistler and Elevitch 2006).

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Abbreviations: APX – ascorbate peroxidase; Chl – chlorophyll; DHAR – dehydroascorbate reductase; EtOH – ethanol; GR – glutathione reductase; g_s – stomatal conductance; HP – high levels of air pollution; MDHAR – monodehydroascorbate reductase; NP – non-polluted area; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; ROS – reactive oxygen species; SCB – sodium cacodylate buffer; TEM – transmission electron microscopy.
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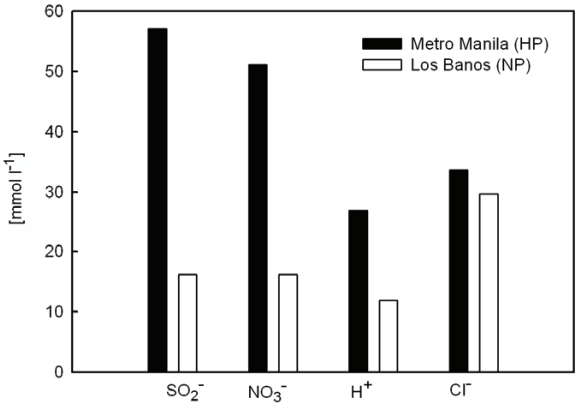

Fig. 1. Air pollution levels in Metro Manila (HP) and La Mesa (NP).

P_N, Chl contents, and several antioxidant enzyme activities were surveyed for trees grown along streets in these four sites. These areas have two pronounced seasons: the dry months from January to May and the wet months from June to December. The mean annual rainfall is 2,700 mm and the mean annual temperature is 23.8–30.0°C.

P_N and g_s values were measured on fully expanded leaves (n = 3 per tree) on the third branch from the ground (n = 3 per site) between 9th and 16th h with the *Li-6400* photosynthesis system (*LI-6400, Li-Cor*, Lincoln, NE, USA). Artificial irradiation was produced by red-blue light-emitting diodes on top of *LI-6400* cuvettes. Leaves were acclimated for 2 min prior to measurement at the following photosynthetic photon flux densities (PPFD): 0; 30; 50; 100; 300; 500; 800; 1,000; 1,500; and 2,000 μmol m^{-2} s^{-1}. Ambient CO_2 partial pressure was supplied by a 400 μmol mol^{-1} CO_2 mixer. The temperature and humidity were 28ºC and 40 ± 10%, respectively, which represented average environmental conditions in the Philippines.

Chl content: Leaves (n = 5 per tree) were collected and stored at 4°C. Leaf tissues (0.05 g) were homogenized in chilled 80% acetone solution for 7 days at 4ºC in the dark and their absorbances were measured. The contents were read at wavelengths of 663 nm and 645 nm by spectrophotometer. Arnon's equation (Arnon 1949) was used to calculate Chl content (*a* and *b*). Total Chl content and the Chl *a*/*b* ratio were calculated.

Transmission electron microscopy (TEM): Leaf disks (n = 10 per tree) were fixed in 2% paraformaldehyde and 2% glutaraldehyde in 0.05 M sodium cacodylate buffer (SCB, pH 7.2) at 4ºC for 2–4 h and then washed three times with 0.05 M SCB at 4ºC for 10 min. The leaves were fixed in 1% osmium tetroxide in 0.05 M SCB at 4ºC for 2 h and then briefly washed twice in distilled water at room temperature. They were then placed in 0.5% uranyl acetate at 4°C for 30 min for en bloc staining. The disks were dehydrated in an EtOH series (30, 50, 70, 80, 90, 100, 100, and 100% EtOH, room temperature, 10 min each) and then transferred two times to 100% propylene oxide at the room temperature for 15 min. They were infiltrated for 2 h with propylene oxide:Spurr's resin (1:1), transferred to Spurr's resin for 4 h or overnight, and then transferred again to Spurr's resin for 2 h. To eliminate humidity, disks were polymerized with Spurr's resin at 70ºC for 24 h. After sectioning using an ultramicrotome (*MT-X, RMC*, Tucson, AZ, USA), they were observed by light microscopy (*HM 505 E, Microm*, Germany) and *TEM* (*LIBRA 120, Carl Zeiss*, Germany).

Enzyme assays: Leaves (n = 3 per tree) were collected and stored at 4°C. The leaf material was homogenized with a pestle in an ice-cold mortar, and a small quantity (0.7 g) was added to 8 ml ice-cold 50 mM HEPES-KOH buffer (pH 7.0) containing 1% (w/v) polyvinylpyrrolidone and 0.2 mM EDTA. The mixture was centrifuged at 4°C for 20 min at 15 000 × g. Crude enzyme extracts were prepared by collecting supernatants as described (Cakmak *et al.* 1993) for the following assays: ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). Absorbances used for determining activities were taken from Nakano and Asada (1981) for APX and DHAR, and from Cakmak *et al.* (1993) for GR and MDHAR.

Statistical analyses: Data were submitted to *ANOVA* and *Duncan*'s multiple range tests. Differences were considered significant at p<0.05.

Results

Photosynthesis, stomatal conductance, total Chl contents, and Chl *a*/*b* ratios: The two tree species grown at HP sites (except Makati) showed a significantly higher P_N and g_s than those grown at the NP site (Table 1). The largest difference in P_N between Quezon (HP) and La Mesa (NP) trees was 320% for *P. indicus*. Among HP sites, *P. indicus* had the lowest P_N at Makati, while *E. orientalis* had the lowest P_N in Quezon (Fig. 2).

The total Chl contents of both species grown at HP sites were significantly lower than those at NP sites. The largest difference in total Chl contents between Makati (HP) and La Mesa (NP) trees was 24% for *P. indicus*. Among HP sites, both species grown in Makati had the lowest Chl content. *P. indicus* had significantly higher Chl contents than did *E. orientalis* (Fig. 3). The Chl *a*/*b* ratio of both species grown at HP sites was significantly lower than those at NP sites. The largest difference in the Chl *a*/*b* ratio between Makati (HP) and La Mesa (NP) was 13% for *P. indicus* (Fig. 3).

Table 1. Stomatal conductance (g_s) and net photosynthesis (P_N) at saturation levels of *P. indicus* and *E. orientalis* grown in four sites. Letters indicate significant differences of means at $p<0.05$ ($n = 3$). Means ± SD are shown.

Feature	Plant	Site La Mesa	Pasig	Makati	Quezon
g_s [mol m^{-2} s^{-1}]	*P. indicus*	0.01±0.001^{e}	0.11±0.01^{c}	0.004±0.001^{f}	0.14±0.01^{bc}
	E. orientalis	0.04±0.01^{d}	0.28±0.02^{a}	0.17±0.005^{b}	0.05±0.001^{d}
P_N [μmol m^{-2} s^{-1}]	*P. indicus*	1.9±0.1^{f}	5.3±0.2^{c}	0.7±0.01^{g}	5.7±0.2^{bc}
	E. orientalis	3.8±0.2^{e}	12.7±0.4^{a}	6.2±0.2^{b}	4.3±0.1^{d}

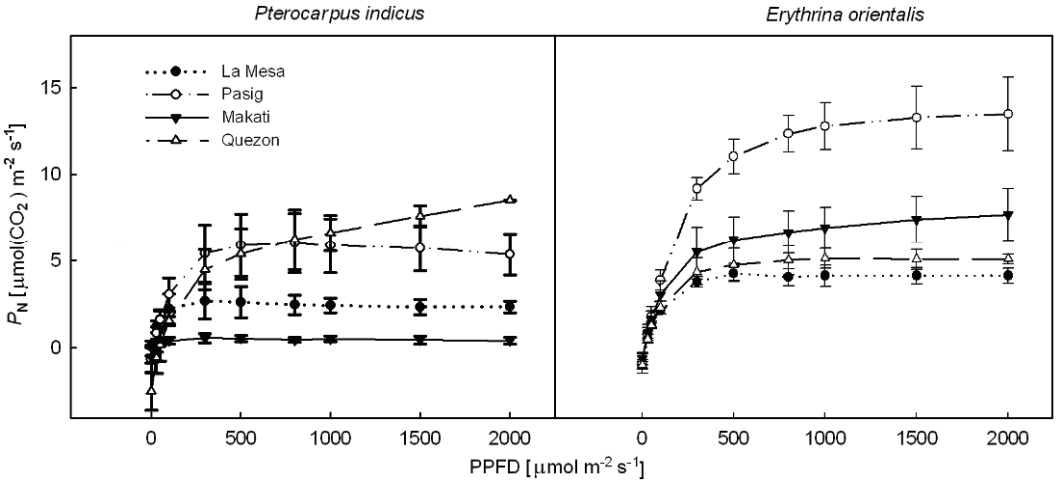

Fig. 2. Photosynthetic photon flux density (PPFD) response curves of net photosynthetic rates (P_N) in *P. indicus* and *E. orientalis* grown in four sites: La Mesa (●), Pasig (○), Makati (▼) and Quezon (Δ). Means ± SD are expressed ($n = 3$).

Ultrastructural changes: The chloroplasts of plants at NP sites were intact and contained large starch grains with no plastoglobuli. In contrast, the chloroplasts of plants at HP sites contained small starch grains with numerous plastoglobuli (Fig. 4). The largest difference in starch grain size between Quezon and La Mesa trees was 78% for *P. indicus***.**

Among the sites, *P. indicus* grown in Pasig had the highest cell wall thickness (285.2 nm) and greatest number of plastoglobuli per chloroplast (13.3). However, the Length of *E. orientalis* chloroplast did not significantly differ between HP and NP sites. For the two species, *P. indicus* had a significantly higher number of plastoglobuli per chloroplast than did *E. orientalis* (Fig. 4 and Table 2).

Antioxidative enzymes: *P. indicus* exhibited the highest activity of APX, MDHAR, DHAR and GR in Quezon, while the same enzymes of *E. orientalis* had the highest activity in Pasig, except for GR, which had the highest activity in Makati (Fig. 5).

Discussion

The results of this study showed a significantly higher P_N in HP sites than in NP sites, except for Makati, which was attributed to the plant response to the dry season (Fig. 2). When photosynthesis was measured in the dry season, the soil in NP sites had dried and many trees were defoliated. The lower P_N of the tree species grown in NP sites was attributed to the mechanism of stomata closure, a defense against water loss (Table 2). These study sites have a severe dry season from January to April. Dry conditions generally reduce stomatal conductance. It has been suggested that many species that close their stomata in response to dry conditions have less water loss and thus are protected from wilt (Kozlowski and Pallardy 1997). Rapid transpiration on sunny days can be very significant and could cause loss of turgor in cells of young leaves, especially in dry sites. This results in stomatal closure, leading to a reduction in photosynthesis and eventually growth (Woo *et al*. 2004).

The higher P_N of trees at different pollution levels suggests different compensation abilities. The two species had very high P_N rates under HP conditions and were able to maintain high P_N rates in HP sites. Their response may be an example of the ability to adjust to or to compensate for air pollution (Winner 1994). *P. indicus*

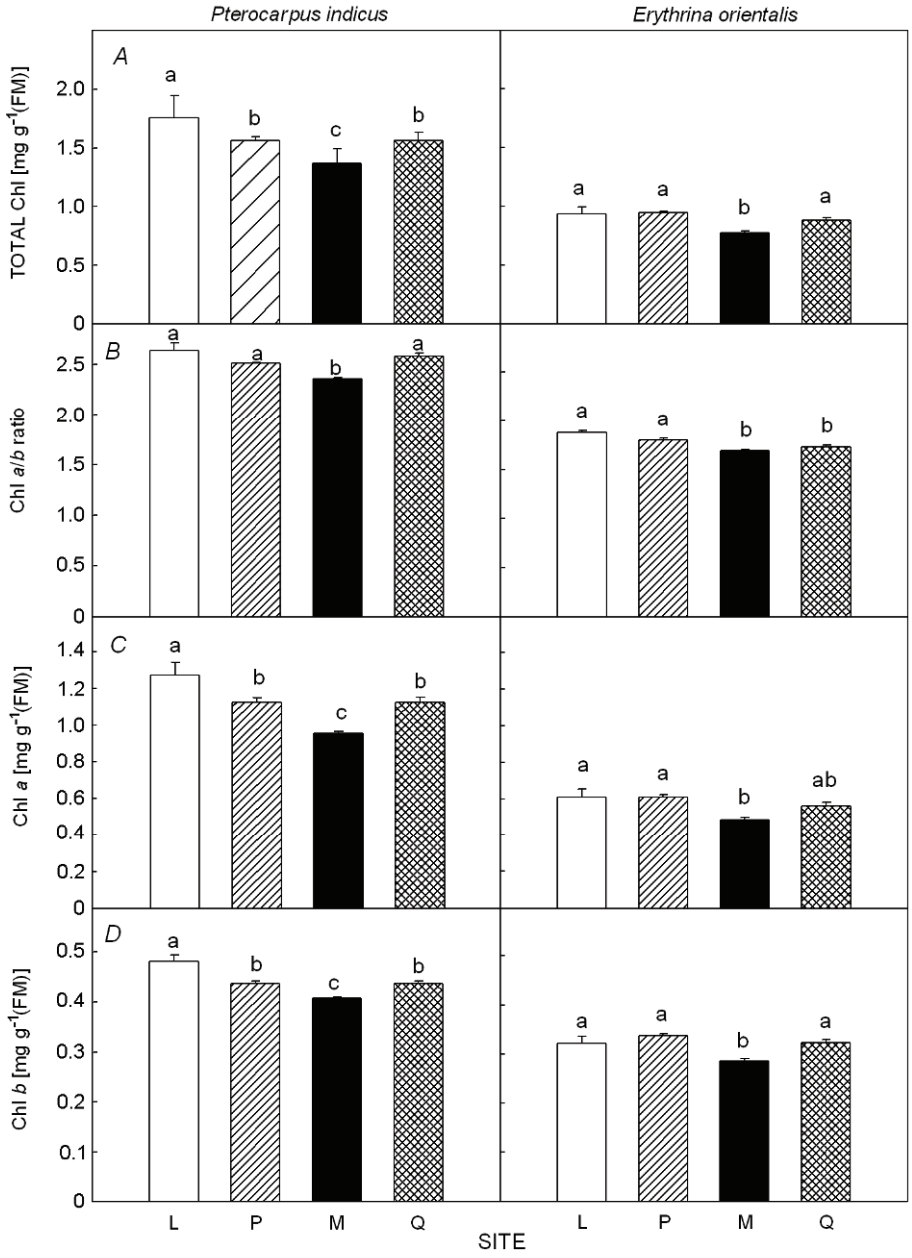

Fig. 3. Changes in total chlorophyll contents (*A*), the Chl *a*/*b* ratio (*B*), and the Chl *a* (*C*) and Chl *b* (*D*) levels of *P. indicus* and *E. orientalis* grown in four sites [L: La Mesa (NP), P: Pasig, M: Makati, Q: Quezon (HP)]. Data were analyzed using one-way *ANOVA* between the four different sites. Letters indicate significant difference at $P<0.05$. Means ± SD are shown ($n = 5$).

and *E. orientalis* can make physiological adjustments to environmental stresses, which appears to enable them to minimize damage from air pollution. Increases in the photosynthetic rate in these species caused by air pollution result from biological compensation. Winner (1994) reported increased photosynthetic rates under ozone stress. These two species may be suitable for phytoremediation in air-polluted areas such as urban regions.

Chl content of leaves can be a useful diagnostic parameter (Neufeld *et al.* 2006), as it is affected by a wide variety of environmental stresses including air pollution. One symptom of stress injury is a reduction of Chl content (Lawson *et al.* 2001). Numerous studies have shown that Chl contents are strongly associated with net photosynthesis (Reich *et al*. 1983, Lascano *et al*. 2001, Neufeld *et al*. 2006). Air pollution decreases Chl levels and induces senescence (Finnan *et al.* 1998, Ojanperä *et al.* 1998, Lawson *et al.* 2001). In this study, the tree species grown at HP sites had low Chl contents under conditions of air pollution. The largest difference in total Chl contents between Makati (HP) and La Mesa (NP) trees was 24% for *P. indicus*.

In response to air pollution, mesophyll cells become disorganized, the ellipsoid structure of chloroplasts disintegrates, and cell walls appear to thicken (Günthardt-Goerg *et al.* 1993). Gravano *et al.* (2003) reported that air pollution-induced cytological damage could be influenced mainly by alterations in palisade tissue and leaf area. The decreased size of starch grains of HP site trees may indicate the consumption of carbon assimilates. The

Table 2. Mean cell wall thickness, chloroplast length, and number and size of plastoglobuli per chloroplast cross section of *P. indicus* and *E. orientalis* grown in four sites. Statistical significances of the two-way interactions between city and plant in leaf palisade tissue. Data were analyzed using multifactor two-way *ANOVA*. Letters indicate significant differences at $p<0.05$. n.s., *, ** and *** indicate non-significant, significant at $p<0.05$, 0.01, and 0.001, respectively. Means ± SD are expressed ($n = 10$).

Feature	Plant	Site				Main effects		
		La Mesa	Pasig	Makati	Quezon	City	Plant	Interaction
Thickness of cell wall [nm]	*P. indicus*	174.0 ± 10.3^{c}	285.2 ± 22.5^{a}	262.8 ± 16.3^{ab}	154.4 ± 8.66^{c}	***	n.s.	*
	E. orientalis	169.9 ± 8.14^{c}	181.9 ± 20.0^{c}	230.0 ± 20.7^{b}	165.4 ± 11.6^{c}			
Length of chloroplast [μm]	*P. indicus*	4.37 ± 0.29^{d}	4.92 ± 0.29^{b}	5.43 ± 0.27^{ab}	4.95 ± 0.30^{bc}	*	n.s.	**
	E. orientalis	6.16 ± 0.39^{a}	4.71 ± 0.31^{cd}	5.76 ± 0.23^{ab}	4.61 ± 0.12^{cd}			
Number of plastoglobuli per chloroplast	*P. indicus*	7.22 ± 0.77^{e}	13.3 ± 0.74^{a}	10.5 ± 1.04^{bc}	12.8 ± 1.20^{ab}	n.s	***	***
	E. orientalis	8.83 ± 0.94^{cd}	8.81 ± 0.61^{cd}	10.9 ± 0.93^{bc}	7.82 ± 0.86^{de}			
Size of plastoglobuli [nm]	*P. indicus*	152.4 ± 8.68^{d}	205.3 ± 12.7^{c}	543.8 ± 19.2^{a}	124.3 ± 7.21^{d}	n.s	*	***
	E. orientalis	117.9 ± 6.38^{d}	201.8 ± 14.2^{c}	463.4 ± 34.3^{b}	226.1 ± 6.74^{c}			

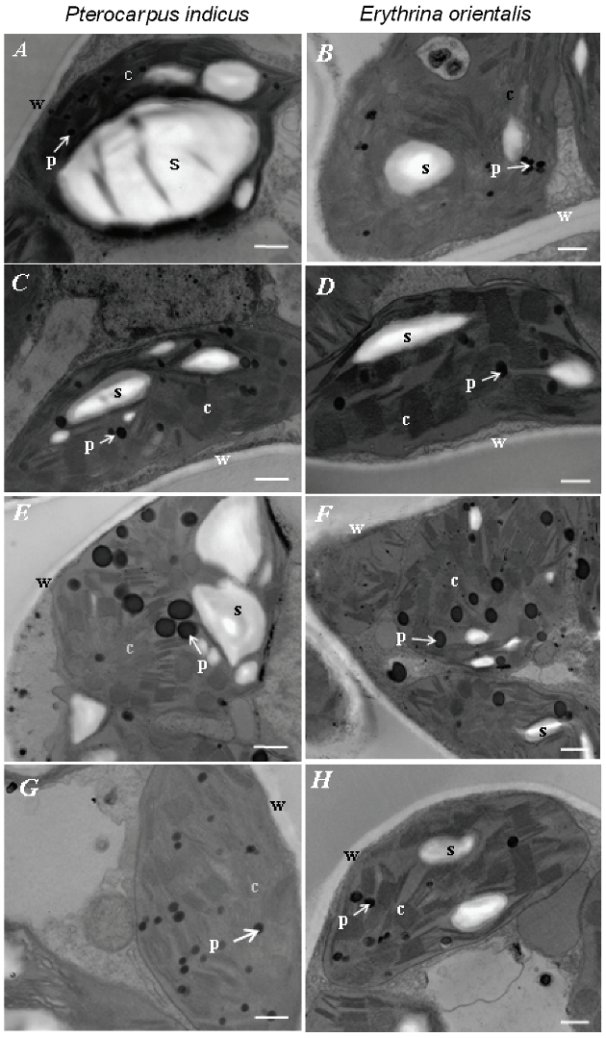

Fig. 4. Transmission electron microscopy images of mesophyll cells of *P. indicus* and *E. orientalis* grown in four sites [*A*: La Mesa (NP), *C*: Pasig, *E*: Makati, and *G*: Quezon (HP)]. Large starch grains are shown with rare plastoglobuli in (*A*) and (*B*), while small starch grains are shown with larger and more numerous plastoglobuli in (*C*), (*D*), (*E*), (*F*), (*G*) and (*H*). The bars in (*A*), (*B*), (*C*), (*D*), (*E*), (*G*) and (*H*) indicate 0.5 μm. The bar in (*F*) indicates 1 μm. (C: chloroplast, S: starch grain, P: plastoglobulus, W: cell wall).

carbon assimilates are not only reduced, but the carbon allocation is altered with increasing amount of carbon being allocated to foliage repair and replacement together with a decreasing carbon allocation to leaves and roots. The reduced translocation of carbon assimilates to leaves and roots appears to be due to the disruption of carbon partitioning after exposure to air pollution, according to Wallin and Skärby (1992) and Anttonen and Kärenlampi (1996).

The thickened cell walls observed for trees in HP sites indicate an increased defense metabolism against air pollution, according to Oksanen *et al.* (2003) and Pääkönen *et al*. (1995). The increased size of plastoglobuli measured at HP sites might be interpreted as a precocious senescence (Tevini and Steinmüller 1985, Anttonen and Kärenlampi 1996).

Many plant injuries caused by stress are associated with oxidative damage at the cellular level (Allen 1995, Meloni *et al.* 2003). Antioxidative enzymes are the most important components in the reactive oxygen species (ROS) scavenging system (Oksanen *et al*. 2003, Neto *et al*. 2006). An increase in the activity of antioxidative enzymes in plants exposed to environmental pollutant stresses could be an indicator of increased ROS production and a protective mechanism to reduce the

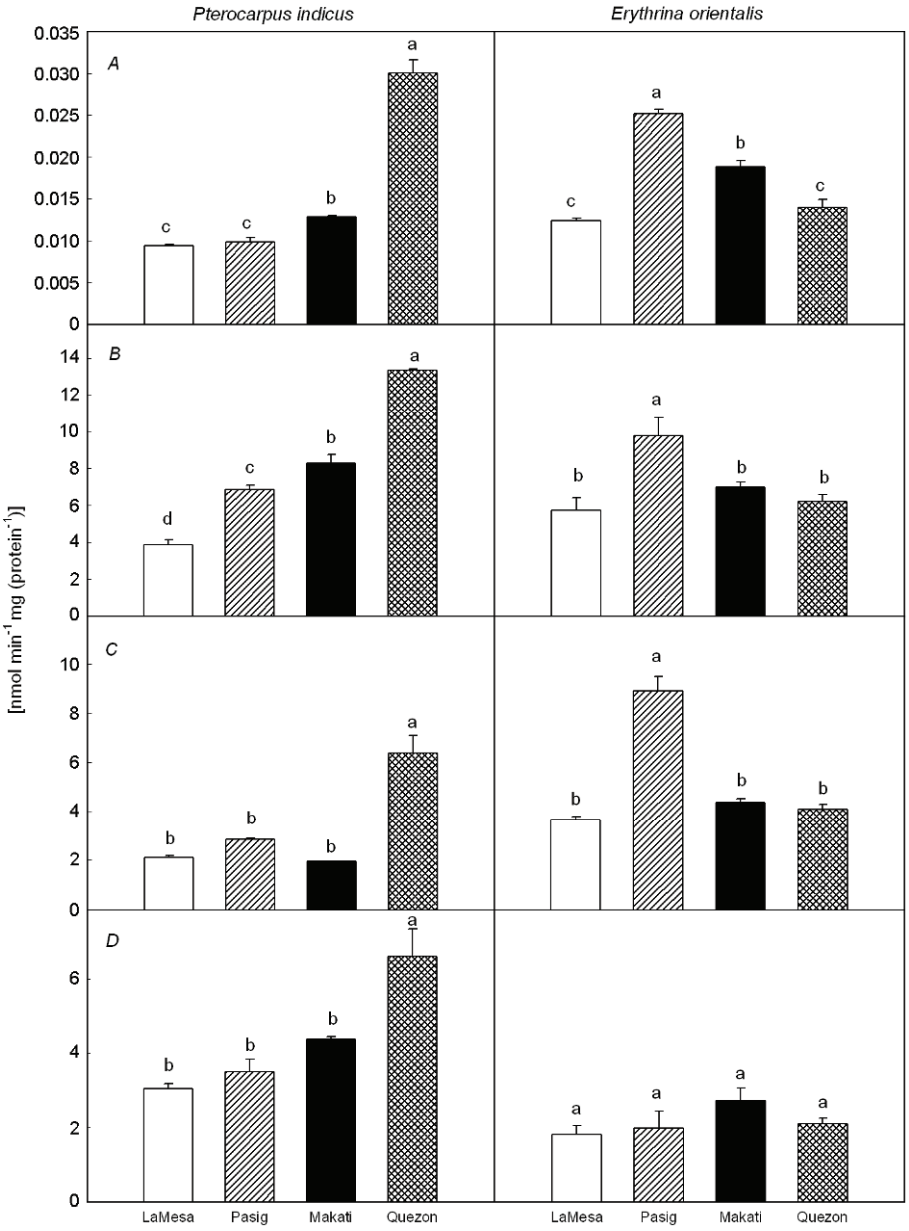

Fig. 5. Antioxidant enzyme activities of *P. indicus* and *E. orientalis* grown in four sites [La Mesa (NP), Pasig, Makati, and Quezon (HP)]. APX – ascorbate peroxidase (*A*), MDHAR – monodehydroascorbate reductase (*B*), DHAR – dehydroascorbate reductase (*C*), and GR – glutathione reductase (*D*). Data were analyzed using one-way *ANOVA* between the four different sites. Letters indicate significant differences at $P<0.05$. Means ± SD are expressed ($n = 3$).

stress-induced oxidative damage (Foyer *et al.* 1994, Meloni *et al.* 2003, Woo *et al.* 2007, Ryang *et al*. 2009).

In conclusion, the street trees in HP sites are exposed to more environmental stress than those in NP sites. Among HP sites, the street trees in Makati suffered most seriously from the stress caused by air pollution. Of the two species, *E. orientalis* showed less air pollution-induced damage and more resistance to air pollution than did *P. indicus*.

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