

# Atmospheric Dust Accumulation on Native and Non-Native Species: Effects on Gas Exchange Parameters

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Plants are continuously exposed to atmospheric particulate matter (dust), and their leaves are the main receptors of deposited dust. The objective of this study was to assess the effects of dust deposition on leaf gas exchange parameters of 17 native and non-native tree and shrub species growing in Gran San Miguel de Tucumán in northwestern Argentina. Maximum assimilation rate ( $A_{\max}$ ), stomatal conductance ( $g_s$ ), transpiration rate ( $E$ ), internal  $\text{CO}_2$  concentration ( $C_i$ ), and instantaneous water-use efficiency (WUE) were measured in cleaned leaves (CL) and dusted leaves (DL) of different species on November 2010, July 2011, and September 2011. In almost all studied species, gas exchange parameters were significantly affected by dust deposition. Values for  $A_{\max}$ ,  $E$ , and  $g_s$  of DL were significantly reduced in 11, 12, and 14 species compared with CL. Morphological leaf traits seem to be related to  $A_{\max}$  reduction. Indeed, *Mespilus germanica* L. and *Mespilus germanica* species with pubescent leaves and thick ribs showed the highest reduction percentages. Contrarily,  $C_i$  and WUE were increased in DL but were less responsive to dust deposition than other parameters. Increases of  $C_i$  and WUE were significant in 5 and 11 species, respectively. Correlation analyses between  $A_{\max}/g_s$ ,  $A_{\max}/E$ , and  $E/g_s$  pairs showed significant positive linear correlations in CL and DL of many studied species, including small and tall plants. These results suggest that leaf stomatal factors and shade-induced effect by accumulated dust are primarily responsible for the observed reductions in photosynthesis rate of DL.

**A**TMOSPHERIC PARTICULATE MATTER (often called dust) consists of a complex mixture of particles of varying size and chemical composition. It originates from a wide variety of natural and anthropogenic sources, such as windblown soil and dust, volcanic eruptions, road traffic, biomass burning, combustion of fossil fuels, wind-driven biological materials (plant fragments, micro-organisms, pollen, spores, etc.), and fugitive emissions from processing materials or from on-site stored materials (Grantz et al., 2003). Biomass burning and combustion of fossil fuels produces about 25% of the global emission of atmospheric particulate matter (Bond et al., 2007). In many developing countries, the burning of trash biomass in large cropping areas is applied as a low-cost harvest technology (Rehman et al., 2011). Particulate matter released from biomass burning and other aerosols allow the formation of a dense layer of atmospheric brown clouds (ABC) over many world areas (Auffhammer et al., 2006). Suspended particles can be classified by their morphological characteristics (e.g., shape or phase, size, and physical behavior in air), chemical species, or biological activity. However, the most common classification of dust is based on the aerodynamic diameter that governs their transport and deposition speed (Kempainen et al., 2003). Dust deposition is a continuous process controlled by air flow and gravity, which act in the lower atmosphere to bring dust back to the ground (Grantz et al., 2003). Deposition of particulate matter on leaf surface mainly depends on macro- and micro-surface roughness and particle diameter (Fowler, 2002). However, it also depends on climatic conditions, such as air temperature, wind speed, and rainfall intensity (Beckett et al., 2000). In this regard, dust accumulation is typically higher at the onset of a precipitation event and declines with its duration (Grantz et al., 2003). Rainfall is responsible for

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**Abbreviations:** ABC, atmospheric brown clouds; AI, aerosol index;  $A_{\max}$ , maximum assimilation rate;  $\text{AOD}_{550}$ , aerosol optical depth for 550 nm wavelength;  $C_i$ , internal  $\text{CO}_2$  concentration; CL, cleaned leaves; DL, dusted leaves;  $E$ , transpiration rate;  $g_s$ , stomatal conductance; GSMT, Gran San Miguel de Tucumán; IRGA, infrared gas analyzer; PAR, photosynthetically active radiation; TSI, total solar irradiance; WUE, water-use efficiency.

both dust deposition and redistribution of deposited dust. Moreover, dust deposition depends on the plant height, leaf surface geometry, plant phyllotaxy, and external leaf structures (e.g., hairs, wax, and cuticle thickness) (Neinhuis and Barthlott, 1998; Maletsika and Nanos, 2011). Depending on physical properties or chemical composition, or on the combination of both, particulate matter can affect external and internal leaf morphological parameters (e.g., wax deposition, stomata length, stomatal index, leaf area, trichome length, trichome density, epidermis thickness, growth, reproductive output, and fruit set) as well as physiological and biochemical parameters (e.g.,  $\text{CO}_2$  diffusion, leaf temperature, transpiration, photosynthetic pigments, photosynthesis rate, carbohydrate partitioning, and protein content) (Psaras and Christodoulakis, 1987; Samal and Santra, 2002; Prusty et al., 2005; Prajapati and Tripathi, 2008; Seyyednejad et al., 2011; Abdel-Rahman and Ibrahim, 2012). Leaves can be indirectly affected by dust deposition through secondary stresses, such as drought or pathogen attack (Farmer, 1993).

The province of Tucumán ( $26^{\circ}49'60''$  S,  $65^{\circ}13'00''$  W, 420 m asl), situated in northwestern Argentina, is devoted mainly to cultivation and industrialization of sugarcane and citrus (www.tucuman.gov.ar). Burning of trash biomass during sugarcane harvest and citrus pruning has become in a common agricultural practice in this province (Tonatto et al., 2008). In the western region of Tucumán province, between the central plain and west mountains, is located the Gran San Miguel de Tucumán (GSMT), an area of 142 km<sup>2</sup> with a dense population of approximately 700,000 inhabitants (INDEC, 2010). It has two contrasting seasons: one that is rainy and hot (summer) and one that is dry with sparse rainfall (late autumn, winter, and early spring). Harvest and industrialization of sugarcane and citrus take place between June and November; thus, increased emission of particulate matter occurs during the dry season. Truck movement and machinery use during sugarcane and citrus harvesting and industrialization also produce emissions of atmospheric particulate matter, which contributes to formation of a dense ABC layer over the GSMT (Fig. 1). The effects of dust deposition on plant leaves have been poorly studied in the GSMT area. Indeed, only one leaf anatomical study has been conducted (Cabrera et al., 2009). Because there are no available data on photosynthesis, we hypothesized that the physiological parameters of plants related to photosynthetic  $\text{CO}_2$  assimilation must be affected by dust deposition occurring in the GSMT. The aim of this study was evaluate the effect of atmospheric dust deposition on leaf gas exchange parameters (i.e., maximum assimilation rate [ $A_{\text{max}}$ ], stomatal conductance [ $g_s$ ], transpiration rate [ $E$ ], internal  $\text{CO}_2$  concentration [ $C_i$ ], and water-use efficiency [WUE]) of 17 native and non-native shrub and tree species growing at the field.

## Materials and Methods

### Study Area and Plant Species

The study site is located at the Miguel Lillo Foundation, 15 km from the nearest sugarcane factory. There is little road traffic, and the study site is a tree-open area to permit free wind circulation and adequate dust deposition. Ten native species [*Rapanea laetevirens* Mez, *Tabebuia chrysotricha* (Mart. ex



**Fig. 1.** Atmospheric brown clouds over the Gran San Miguel de Tucumán area. The photograph was taken on 15 July 2011 (winter, Southern Hemisphere) in the afternoon at 1200 m asl.

DC.), *Bauhinia candicans* Benth., *Psychotria carthagenensis* Jacq., *Coccoloba cordata* Cham., *Justicia oranensis* N.De Marco & Teresa Ruiz, *Eugenia uniflora* L., *Lonchocarpus liloi* (Hassl.) Burkart, *Myrcianthes pseudomato* (Legr.) McVaugh, and *Cupania vernalis* Cambess.] and seven non-native species [*Ricinus communis* L., *Fragaria chiloensis* (L.) Mill., *Saccharum officinarum* L., *Hibiscus rosasinensis* L., *Alocasia macrorrhiza* (L.) Schott., *Rosa rubiginosa* (Coss. ex. Déségl), and *Mespilus germanica* L.] were selected for this study. Plants were selected on the basis of their wide distribution in Tucumán province and comprise 16 dicotyledonous species and one monocotyledonous species. Selected species include big-leaved (*R. communis* and *A. macrorrhiza*) and small-leaved (*E. uniflora*, *F. chiloensis*, and *M. pseudomato*) plants.

### Experimental Design

Thirteen randomly field-grown plants and four pot-grown plants were selected. Field-grown plants were grown in a large open field with 4- to 5-m interplant space. Pot-grown plants were from seedlings (*R. laetevirens*, *R. communis*, and *T. chrysotricha*) and two-leaf plantlets (*F. chiloensis*) provided by the Botany Department (Fundación Miguel Lillo, Tucumán, Argentina). Seedlings and plantlets were grown in 30-cm-diameter plastic pots filled with well-manured garden soil in a greenhouse for 6 mo. In February 2010, pots were transferred to the field with 2- to 3-m interplant space. Pot-grown species were used to study the dust deposition on small plants. During the experimental period, field- and pot-grown plants were well-watered to prevent drought stress, and no fertilizer was provided. The height of selected plants and leaf morphological traits are given in Table 1. Starting on 1 June 2010, field- and pot-grown plants were randomly divided into two groups: dusted leaves (DL) and cleaned leaves (CL) (Fig. 2a,b). Plants in the DL group were maintained without leaf-cleaning treatment. For plants in the CL group, selected leaves were cleaned carefully using a fine-bristle brush to eliminate deposited dust on the leaf surface every 2 d during the experimental period. A wooden ladder was used to reach the leaves of tallest trees.

### Gas Exchange Measurements

According to leaf life span (deciduous, evergreen) of studied species, gas exchange measurements were performed

Table 1. Characteristics of selected plants with their leaf morphological traits and the date of gas exchange measurements.

Species	Gas exchange measurements date	Growth condition		Habit	Leaf shape	Leaf surface	Phyllotaxy	Sampling height	Origin	Species codet†	
		Pot	Soil							CL	DL
								m			
<i>Tabebuia chrysotricha</i>	Nov. 2010	X		tree	oblong, elliptic	rough with hairs	opposite	0.40	native	1	1'
<i>Fragaria chiloensis</i>	Nov. 2010	X		shrub	trifoliolate	rough with hairs	alternate	0.10	non-native	2	2'
<i>Ricinus communis</i>	Nov. 2010	X		shrub	palmatilobate	smooth	alternate	0.50	non-native	3	3'
<i>Rapanea laetevirens</i>	Nov. 2010	X		tree	obovate to elliptic	smooth	alternate	0.40	native	4	4'
<i>Saccharum officinarum</i>	Nov. 2010		X	shrub	elongate	smooth, a thick midrib	alternate	2.0–3.0	non-native	5	5'
<i>Hibiscus rosa-sinensis</i>	July 2011		X	shrub	ovate to lanceolate	smooth, prominent ribs	alternate	1.50	non-native	6	6'
<i>Alocasia macrorrhiza</i>	July 2011		X	shrub	broadly ovate	smooth, thick ribs	spirally	1.50	non-native	7	7'
<i>Rosa rubiginosa</i>	July 2011	X		shrub	ovate	smooth, glandular hairs	opposite	1.50	non-native	8	8'
<i>Mespilus germanica</i>	July 2011	X		tree	elliptic	rough, densely hairy	opposite	5.0–6.0	non-native	9	9'
<i>Bauhinia candicans</i>	Sept. 2011	X		tree	ovate to oblong	rough	alternate	1.50	native	10	10'
<i>Psychotria carthagenensis</i>	Sept. 2011	X		shrub	lanceolate to elliptic	smooth	opposite	1.50	native	11	11'
<i>Coccoloba cordata</i>	Sept. 2011		X	shrub	orbiculate	smooth	alternate	2.00	native	12	12'
<i>Justicia oranensis</i>	Sept. 2011		X	shrub	ovate to elliptic	rough slight pubescence	opposite	1.50	native	13	13'
<i>Eugenia uniflora</i>	Sept. 2011	X		tree	ovate	smooth	opposite	4.00	native	14	14'
<i>Lonchocarpus lilloi</i>	Sept. 2011		X	tree	elliptic to lanceolate	smooth	opposite	3.00	native	15	15'
<i>Myrcianthes pseudomato</i>	Sept. 2011	X		tree	oblong	smooth	opposite	4.0–5.0	native	16	16'
<i>Cupania vernalis</i>	Sept. 2011	X		tree	lanceolate	smooth	alternate	3.00	native	17	17'

† CL, cleaned leaf; DL, dusted leaf.

at different times during the winter–spring period (June–November, Southern Hemisphere). Measurements were made in November 2010, July 2011, and September 2011. On the first date, harvest and burning of sugarcane and citrus trash had already been completed. In this condition, dust deposition on upper leaf epidermis of deciduous perennial species reaches a maximum. On the second date, harvest and burning of sugarcane trash began, and the burning of citrus pruning was already completed. In this period, soot from sugarcane factories is the minor component of particulate matter deposited on leaf surfaces of winter-grown species. On the third date, harvest and burning of sugarcane trash reached maximum intensity. Citrus harvest had already finished. Pollen grains were an important component of deposited dust on this date. Gas exchange measurements were made in fully expanded leaves of the upper canopy (two leaves per plant, four plants per species). For plants taller than 1.5 m, upper branches were cut using an aluminum pole pruner; two branches were cut per plant. After cutting, branches were immediately placed in containers with the cut ends submerged in distilled water for 2 h under shaded conditions to rehydrate the leaves. Preliminary gas exchange measurements did not reveal significant differences between branch-excised leaves and branch–non-excised leaves. Values for  $A_{\max}$ ,  $g_s$ ,  $C_i$ , and  $E$  were determined with a portable open-system infrared gas analyzer (IRGA) (LI-6400 Portable Photosynthesis System XT, LI-COR, Inc.). Measurements were performed between 0900 and 1200 h (local time) under a constant photosynthetically active radiation (PAR) light intensity of  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  provided by a red-blue LED light source attached to the sensor head. Under this PAR

value, photosynthesis rate reached at least 99% saturation. Carbon dioxide concentration and temperature inside the leaf chamber were controlled automatically by adjusting the IRGA system to  $340 \mu\text{mol mol}^{-1}$  and  $25^\circ\text{C}$ , respectively. Leaves were acclimated to the chamber for 3 min before measurements. For each established date, a total set of gas exchange measurements was completed in 2 to 3 d. Before starting gas exchange measurements, the IRGA system was calibrated using a known  $\text{CO}_2$  concentration according to Li-Cor manual protocol. The leaf chamber was kept in the shade when not in use to keep it at ambient temperature and to avoid overheating. The WUE was calculated as the ratio between  $A_{\max}$  and  $E$  (Centritto et al., 2009).

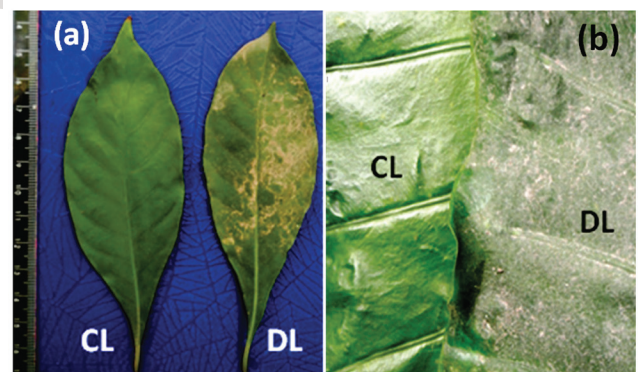


Fig. 2. (a) Cleaned leaves (CL) and dusted leaves (DL) of *Psychotria carthagenensis*, a small-leaf species; (b) CL and DL of *Alocasia macrorrhiza*, a large-leaf species.



## Atmospheric Aerosol and Solar Irradiance Data

Data on aerosol optical depth for 550 nm wavelength ( $AOD_{550}$ ), aerosol index (AI), and total solar irradiance (TSI) over the GSMT were obtained from the satellite observation database of the National Aeronautics and Space Administration.

## Statistical Analysis

Student's  $t$  test was used to compare mean values of gas exchange parameters. Significance was assessed at  $P < 0.05$  unless otherwise stated. Relationships among  $A_{\max}/g_s$ ,  $A_{\max}/E$ , and  $E/g_s$  pairs were evaluated by linear regression analysis using the SAS/STAT version 8.0 statistical package (SAS Institute Inc.).

## Results

### Aerosol Optical Depth, Aerosol Index, and Total Solar Irradiance over the Gran San Miguel de Tucumán

Figure 3 shows monthly variation of  $AOD_{550}$ , AI, and TSI for the GSMT obtained from the NASA satellite database. The  $AOD_{550}$  measurements during the period 1998 to 2010 showed a similar interannual variability (Fig. 3a). The lowest values of  $AOD_{550}$  ( $<0.05$ ) recorded during the first months of the study correspond to a very clear sky, but  $AOD_{550}$  increases significantly from the period June to July until the end of the year. The maximum monthly value ranged between 0.2 and 0.3 throughout the period. Fitting data correspond to a steady linear increase of  $AOD_{550}$  mean values with a slope of 0.026 per decade. Figure 3b shows monthly mean values of AI for the period 2005 to 2008. Significant increases of AI during the winter–spring period with some events overpassing the reference AI value (1.5) are observed. The reference value indicates a large atmospheric contamination event. The numbers of overpassed events during the 2005–2008 period were 5, 8, 10, and 9, respectively. The AI allows one to discriminate between absorbing aerosols, mainly black carbon type, and nonabsorbing aerosols. In general, absorbing aerosols show high positive values, whereas nonabsorbing aerosols acquire very low positive values or negative values. Monthly variation of daily TSI reaching the GSMT area during the period 1983 to 2005 is shown in Fig. 3c. The annual mean value of daily TSI was  $5.43 \text{ kW m}^{-2} \text{ d}^{-1}$ , and the minimum and maximum values were  $3.76 \text{ kW m}^{-2} \text{ d}^{-1}$  (July) and  $6.70 \text{ kW m}^{-2} \text{ d}^{-1}$  (November), respectively. Increased trash biomass burning during the winter season contributes highly to low values of TSI recorded on the GSMT during June and July. A maximum TSI value was not recorded in the summer months even though the Southern Hemisphere is closer to sun. This apparent anomalous feature of solar irradiance can be explained by denser cloud cover, which occurred frequently over the GSMT during December and January compared with November (not shown).

### Effect of Dust Deposition on Gas Exchange Parameters

Data of  $A_{\max}$ ,  $g_s$ ,  $E$ ,  $C_i$ , and WUE of CL and DL for all studied species are summarized in Table 2. Regardless of whether plants are native or non-native species, reductions in  $A_{\max}$  produced by dust deposition were evident. Depending on leaf morphological traits and measurement date, significant reductions of  $A_{\max}$  in DL leaves of 11 species were observed. Decreases of  $\text{CO}_2$

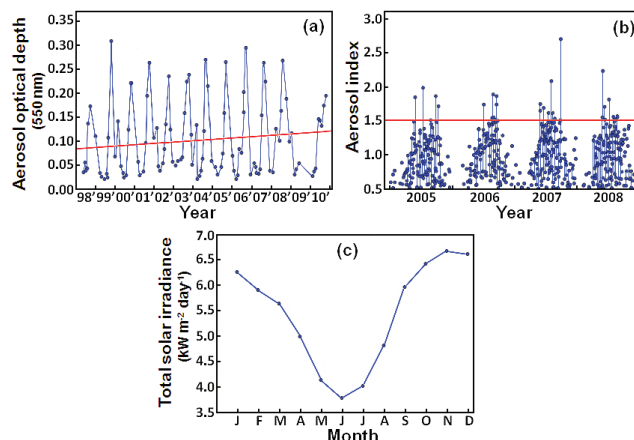


Fig. 3. Atmospheric data. (a) Mean monthly aerosol optical depth for 550 nm wavelength ( $AOD_{550}$ ) over the Gran San Miguel de Tucumán (GSMT) calculated with the Deep Blue Level 3 algorithm from data of the 1998–2010 period. Land surface resolution was  $0.5 \times 0.5$  degree<sup>2</sup>. The straight red line is a linear fit to the data  $y = 0.000221x + 0.08149$ , where  $x$  = time (month) (NASA, 2012). (b) Mean monthly aerosol index (AI) (level 3) recorded over the GSMT during the 2005–2008 period. The straight red line is a reference for determination of greater contamination events with  $AI \geq 1.5$  (GES DISC, 2012). (c) Annual mean of daily total solar irradiance (TSI) over the GSMT during the 1983–2005 period ( $1^\circ \times 1^\circ$  surface extension). Data were obtained from the SSE/NASA web page and were from more than 200 satellites records (Atmospheric Science Data Center, 2012).

assimilation ranged between 14.7% (*F. chiloensis*) and 43.7% (*M. germanica*). The highest reductions were found in *M. germanica* (−43.7%), *T. chrysotricha* (−40.5%), and *H. rosa-sinensis* (−27.8%). Decreased values of  $A_{\max}$  for *T. chrysotricha* and *H. rosa-sinensis* were recorded in July when a denser ABC layer stayed over the GSMT (Fig. 1). Data of  $g_s$  also showed significant decreases in DL of almost all species. Reductions ranged between 17.4% (*S. officinarum*) and 74.4% (*M. pseudomato*). By contrast, in *R. communis* the value of  $g_s$  in DL showed a significant increase (+39.3%) compared with CL. In *C. cordata* and *R. rubiginosa*, no significant variations of  $g_s$  were found. The value of  $E$ , closely related to  $g_s$ , in most species decreased significantly due to dust deposition. Reductions of  $E$  ranged between 13.9% (*B. candicans*) and 67.8% (*J. oranensis*). Some species (e.g., *R. communis*, *R. rubiginosa*, *L. lilloi*, and *M. pseudomato*) did not show significant changes in  $E$ . In contrast to other gas exchange parameters,  $C_i$  increased significantly in DL of *T. chrysotricha*, *A. macrorrhiza*, *H. rosa-sinensis*, *R. rubiginosa*, *M. germanica*, *C. cordata*, and *J. oranensis*. The highest increases were 68.4% (*C. cordata*), 62.4% (*M. germanica*), and 53.4% (*J. oranensis*). In *R. rubiginosa*,  $C_i$  increased 460.5%. Of interest,  $C_i$  was reduced significantly by dust deposition only in *S. officinarum* (−69.9%). Similar to  $C_i$ , instantaneous WUE increased significantly in most DL (Table 2). Increases ranged between 41.7% (*P. carthagenensis*) and 154.4% (*J. oranensis*). No significant variations of WUE were observed in *R. communis*, *R. rubiginosa*, *M. germanica*, *L. lilloi*, and *M. pseudomato*.

### Correlation Analysis

Data recorded in November 2010 and July 2011 show that  $A_{\max}$  was significantly positively correlated with  $g_s$  in CL and DL. Coefficients of determination ( $r^2$  for CL and  $r'^2$  for

Table 2. Effect of dust accumulation on maximum assimilation rate, stomatal conductance, transpiration rate, internal CO<sub>2</sub> concentration, and instantaneous water-use efficiency in cleaned and dusted leaves.

Species	Cleaned leaves†					Dusted leaves				
	A <sub>max</sub>	g <sub>s</sub>	E	C <sub>i</sub>	WUE	A <sub>max</sub>	g <sub>s</sub>	E	C <sub>i</sub>	WUE
	μmol m <sup>-2</sup> s <sup>-1</sup>	mmol m <sup>-2</sup> s <sup>-1</sup>	mmol m <sup>-2</sup> s <sup>-1</sup>	μmol mol <sup>-1</sup>	μmol mmol <sup>-1</sup>	μmol m <sup>-2</sup> s <sup>-1</sup>	mmol m <sup>-2</sup> s <sup>-1</sup>	mmol m <sup>-2</sup> s <sup>-1</sup>	μmol mol <sup>-1</sup>	μmol mmol <sup>-1</sup>
<i>Tabebuia chrysotricha</i>	13.79 ± 0.29a†	101.3 ± 9.4a	2.90 ± 0.30a	169.1 ± 18.2b	4.75 ± 0.30b	8.24 ± 0.45b	70.1 ± 6.4b	1.50 ± 0.12b	197.1 ± 17.3a	5.49 ± 0.41a
<i>Fragaria chiloensis</i>	14.28 ± 1.93a	169.2 ± 14.3a	8.15 ± 0.89a	258.2 ± 27.2a	1.75 ± 0.20b	12.18 ± 1.89b	139.1 ± 10.4b	4.70 ± 0.51b	251.1 ± 26.3a	2.59 ± 0.32a
<i>Ricinus communis</i>	27.03 ± 3.35a	280.2 ± 31.2b	11.21 ± 1.30a	218.1 ± 24.1a	2.41 ± 0.23a	25.91 ± 2.08a	390.4 ± 26.9a	11.79 ± 1.80a	242.5 ± 26.3a	2.20 ± 0.21a
<i>Rapanea laetevirens</i>	2.49 ± 0.20a	27.4 ± 1.43a	1.53 ± 0.12a	194.3 ± 22.0a	1.62 ± 0.13b	2.10 ± 0.17b	15.2 ± 1.6b	0.88 ± 0.11b	167.2 ± 13.6a	2.39 ± 0.24a
<i>Saccharum officinarum</i>	14.80 ± 0.85a	76.5 ± 5.5a	4.62 ± 0.33a	110.8 ± 12.4a	3.20 ± 0.28b	12.11 ± 1.42b	63.2 ± 6.5b	3.10 ± 0.40b	33.3 ± 2.6b	3.91 ± 0.40a
<i>Hibiscus rosa-sinensis</i>	10.12 ± 1.45a	240.2 ± 3.3a	1.11 ± 0.16a	66.1 ± 0.8a	9.12 ± 1.03b	7.31 ± 1.22b	128.2 ± 4.1b	0.60 ± 0.07b	70.5 ± 7.3a	12.18 ± 1.52a
<i>Alocasia macrorrhiza</i>	5.84 ± 0.23a	509.1 ± 46.8a	0.02 ± 0.00a	120.7 ± 10.4b	292.02 ± 25.22b	4.37 ± 0.56b	408.4 ± 50.1b	0.01 ± 0.00b	163.4 ± 17.6a	437.12 ± 45.35a
<i>Rosa rubiginosa</i>	20.90 ± 1.87a	1797.1 ± 165.1a	0.07 ± 0.01a	24.3 ± 1.8b	298.60 ± 30.14a	20.41 ± 1.54a	1759.1 ± 158.9a	0.07 ± 0.01a	136.2 ± 12.4a	291.63 ± 27.92a
<i>Mespilus germanica</i>	6.94 ± 0.76a	864.1 ± 89.8a	0.05 ± 0.01a	109.2 ± 9.9b	138.01 ± 12.67a	3.91 ± 0.56b	563.2 ± 58.1b	0.03 ± 0.00b	177.4 ± 15.6a	130.32 ± 13.77a
<i>Bauhinia candicans</i>	6.52 ± 0.41a	100.3 ± 12.1a	2.38 ± 0.21a	271.8 ± 28.9a	2.74 ± 0.31a	4.82 ± 0.54b	71.1 ± 5.3b	2.05 ± 0.16b	240.4 ± 26.5a	2.35 ± 0.25b
<i>Psychotria carthagenensis</i>	3.80 ± 0.32a	20.2 ± 1.8a	0.52 ± 0.02a	123.9 ± 11.1a	7.31 ± 0.68b	3.03 ± 0.25b	15.3 ± 1.4b	0.32 ± 0.01b	135.6 ± 14.2a	9.50 ± 1.24a
<i>Coccoloba cordata</i>	4.72 ± 0.24a	10.0 ± 0.8a	0.42 ± 0.03a	343.7 ± 30.1b	11.24 ± 1.42b	4.24 ± 0.35a	9.3 ± 0.2a	0.20 ± 0.00b	578.8 ± 56.3a	21.11 ± 2.39a
<i>Justicia oranensis</i>	9.51 ± 1.01a	28.3 ± 2.5a	1.21 ± 0.11a	193.1 ± 22.1b	7.86 ± 0.52b	7.80 ± 0.59b	20.4 ± 1.7b	0.39 ± 0.04b	296.2 ± 25.9a	20.00 ± 1.94a
<i>Eugenia uniflora</i>	11.33 ± 0.85a	23.1 ± 0.9a	0.49 ± 0.04a	252.9 ± 28.7a	23.12 ± 2.21b	9.53 ± 0.84b	18.3 ± 2.1b	0.28 ± 0.06b	229.1 ± 19.4a	34.04 ± 1.71a
<i>Lonchocarpus liloi</i>	12.81 ± 0.88a	40.0 ± 4.6a	1.36 ± 0.14a	178.9 ± 15.8a	9.42 ± 1.13a	12.32 ± 0.82a	27.2 ± 4.1b	1.30 ± 0.15a	162.5 ± 14.1a	9.48 ± 0.84a
<i>Myrcianthes pseudomato</i>	11.22 ± 0.90a	40.2 ± 3.6a	0.42 ± 0.02a	86.7 ± 9.4a	26.71 ± 2.80a	10.63 ± 0.53a	30.3 ± 2.9b	0.40 ± 0.02a	76.3 ± 6.2a	26.57 ± 2.82a
<i>Cupania vernalis</i>	13.30 ± 0.95a	28.4 ± 2.8a	0.56 ± 0.03a	104.2 ± 11.2a	23.75 ± 2.22b	12.55 ± 0.86a	18.1 ± 2.1b	0.33 ± 0.01b	110.3 ± 12.5a	38.03 ± 3.85a

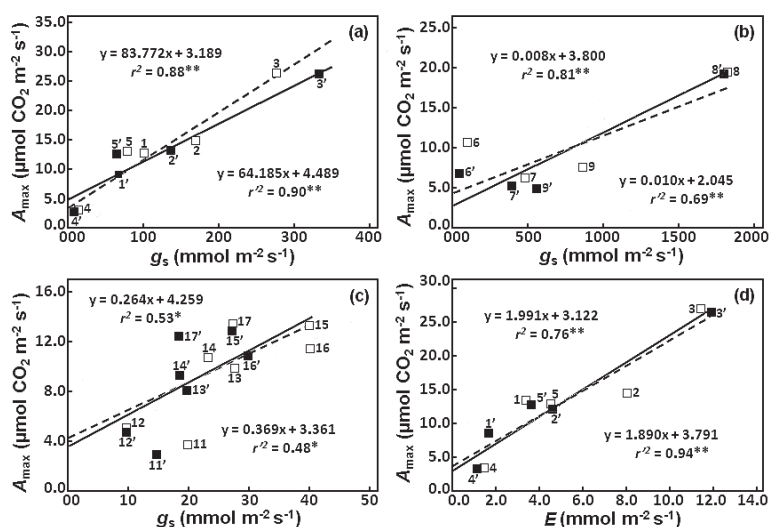
† A<sub>max</sub>, maximum assimilation rate; C<sub>i</sub>, internal CO<sub>2</sub> concentration; g<sub>s</sub>, stomatal conductance; E, transpiration rate; WUE, instantaneous water-use efficiency.

‡ For each species and a given variable, mean values followed by different letters are significantly different (P < 0.05) (n = 8).

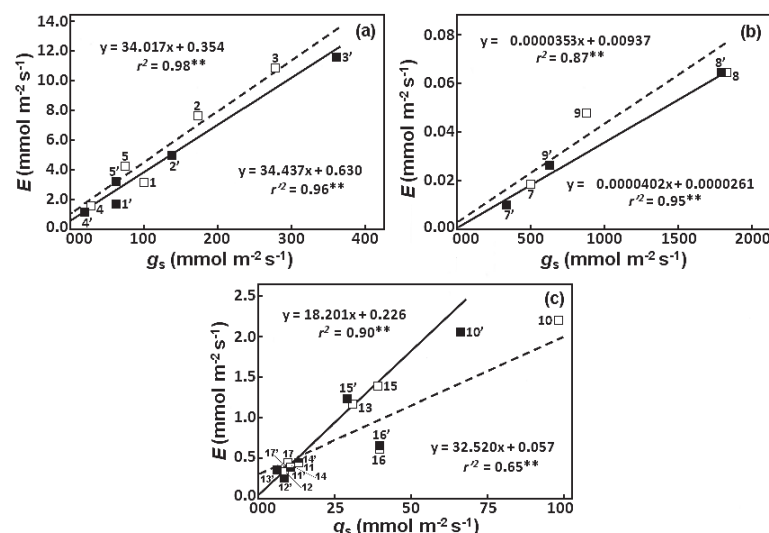
DL) were  $r^2 = 0.88$  and  $r'^2 = 0.90$  (November data) and  $r^2 = 0.69$  and  $r'^2 = 0.81$  (July data) (Fig. 4a,b). No significant correlation was observed for data recorded in September 2011 (not shown). When *B. candicans* was excluded from the data set corresponding to this measurement date, statistical analysis showed significant positive correlations in CL ( $r^2 = 0.53$ ) and DL ( $r'^2 = 0.48$ ) (Fig. 4c). For the  $A_{\max}/E$  pair in CL and DL, correlation analysis showed significant positive correlations only for data recorded in November 2010. Coefficients of determination were  $r^2 = 0.76$  and  $r'^2 = 0.94$  (Fig. 4d). Correlation analysis using data from July 2011 and September 2011 did not show significant values of  $r^2$  and  $r'^2$  (not shown). When  $E$  was correlated with  $g_s$ , significant positive correlations were observed for data recorded at the three measurement dates in CL and DL of the studied species, except *H. rosa-sinensis* (Fig. 5a–c).

## Discussion

Results of this study show that atmospheric particulate matter accumulated on leaf surfaces of native and non-native shrub and tree species produces significant changes in gas exchange parameters. In most species,  $A_{\max}$ ,  $g_s$ , and  $E$  was decreased by dust accumulation. The highest decreases of  $A_{\max}$  were found in tall and small plants, but in some tall plants no significant changes were observed (Table 2). This fact could indicate a low wind contribution to dust deposition, in opposition to the accepted assumption that wind facilitates more dust deposition on taller plants than on smaller ones (Beckett et al., 2000). Regardless of measurement date and plant size, decreases of  $A_{\max}$  show significant variations between species. This fact could indicate that morphological, physiological, and biochemical traits of leaves play key roles in photosynthetic responses of field-grown plants to dust accumulation. In this regard, structural leaf traits strongly affect dust deposition (Maletsika and Nanos, 2011). Indeed, pubescent leaves with prominent ribs on the blade (lamina) surface are more efficient at capturing dust than leaves having flat and smooth blade surfaces (Younis et al., 2013). In agreement with this finding, two of three species that exhibit the highest reductions of  $A_{\max}$  (*M. germanica* and *T. chrysotricha*) have pubescent leaves with thick ribs (Table 1). However, the high reduction of  $A_{\max}$  observed in *H. rosa-sinensis*, a nonpubescent species, may be related to the shiny and waxy coating leaf surface with prominent ribs, serrate margin, and small petiole that reduces the wind-dependent leaf movement (Joshi and Bora, 2011). Leaf size and surface texture also affect dust accumulation. Leaves having greater surface rigidity or roughness accumulate more dust than leaves without roughness (Kumar et al., 2013). Furthermore, big and horizontally arranged leaves tend to accumulate more dust than small pendulous leaves (Prusty et al., 2005). Agreeing with these findings, in this study two species (*A. macrorrhiza* and *P. carthagenensis*) with



**Fig. 4.** Relationships between maximum assimilation rate ( $A_{\max}$ ) and stomatal conductance ( $g_s$ ) in cleaned leaves (CL) and dusted leaves (DL). Data are from (a) November 2010, (b) July 2011, and (c) September 2011. (d) Relationships between  $A_{\max}$  and transpiration rate ( $E$ ) for data recorded in November 2010. Open squares: CL; closed squares: DL. Best-fit simple linear regression lines are shown. \*Significant at  $P < 0.05$ ; \*\*significant at  $P < 0.01$ . Numbers near the symbols correspond to species code (see Table 1).



**Fig. 5.** Relationships between stomatal conductance ( $g_s$ ) and transpiration rate ( $E$ ) in cleaned leaves (CL) and dusted leaves (DL). Data are from (a) November 2010, (b) July 2011, and (c) September 2011. Open squares: CL; closed squares: DL. Best-fit simple linear regression lines are shown. \*\*Significant at  $P < 0.01$ . Numbers near the symbols correspond to species code (see Table 1).

similar height and exposed to the same atmospheric pollution accumulated different amounts of dust. Higher dust accumulation was observed in *A. macrorrhiza* due to its big and rough leaves compared with *P. carthagenensis*, which has smaller sized leaves with smooth surfaces (Fig. 2). Moreover, increased dust deposition in *A. macrorrhiza* was coincident with an observed larger decrease of  $A_{\max}$  (Table 2). Decreased photosynthesis by leaf shading effect has been reported as the main effect of dust deposition onto leaf surfaces (Seyyednejad et al., 2011). However, unchanged and even increased photosynthetic  $\text{CO}_2$  assimilation have been suggested to affect dust deposition (Wijayratne et al., 2009; Yunusa et al., 2009). To explain the different photosynthetic responses of DL, Eller (1977)

proposed that the accumulation of dust on leaf surfaces increases the absorption of solar infrared radiation and PAR reflectance, leading to a temperature rise of 2 to 4°C. In this way, photosynthesis rate can increase significantly depending on its leaf temperature-dependent functionality (Hirano et al., 1995). In our study we found that six species, including small and tall plants, did not show significant variation in  $A_{\max}$  between CL and DL. In this regard, we assumed that in these species accumulated dust increases the leaf low temperature occurring in winter, and then a rise of photosynthesis rate must occur in DL. Although this assumption could explain our results, we did not measure the leaf temperature and therefore cannot confirm it. Further studies will be performed to verify our assumption.

According to Schulze and Hall (1982), in most plant species assimilation of  $\text{CO}_2$  shows either linear or curvilinear relationships with stomatal aperture. Correlation analyses between  $A_{\max}$  and  $g_s$  showed linear positive correlations in CL and DL for all measurement dates (Fig. 4a–c). Similar to  $A_{\max}$ , in almost all studied species  $g_s$  decreased in DL when compared with CL (Table 2). In many species the decrease of  $A_{\max}$  under low incident light (darkening) has been related to low  $C_i$  due to stomatal closure (Fay and Knapp, 1996), so one might assume that reductions of  $A_{\max}$  and  $g_s$  are produced by a shading effect of accumulated dust rather than by stomatal plugging. Supporting our assumption, it has been reported that adaxial stomata are more sensitive to darkening than abaxial stomata. Also, stomatal response is more intensive in mature leaves than in young, still-expanding leaves (Ceulemans et al., 1989). The requirements of photosynthetic light by light-demanding plants and shade-tolerant plants are quite different. Therefore, leaf gas exchange responses can have significant intra- and interspecies variability (Rijkers et al., 2000). Differences in light-dependent photosynthetic traits among the studied species could also contribute to explaining the observed variations in  $A_{\max}$  and  $g_s$ . However, a more detailed correlation analysis for September data revealed higher variability in DL than in CL (Fig. 4c). On the September measurement date, increased wind prevalence and some light rains were recorded at the experimental site (J.A. González, unpublished results).

These conditions might have affected the accumulation of dust, and then dust-shade-induced decrease of  $g_s$  would not be the main responsible factor of decreased  $A_{\max}$ . In this regard, it has been stated that when the decrease of  $g_s$  and increase of  $C_i$  occur simultaneously, the decrease of  $\text{CO}_2$  assimilation can also be attributed to nonstomatal limitations (Farquhar and Sharkey, 1982). Gas exchange measurements revealed that this condition can occur in four of the studied species (*T. chrysotricha*, *A. macrorrhiza*, *M. germanica*, and *J. oranensis*). Therefore, one might assume that in these species  $A_{\max}$  is limited by stomatal and nonstomatal factors. However, relationships between  $g_s$  and  $C_i$  also depend



on prevailing season (Eamus and Cole, 1997) and on the time of day at which gas exchange measurements were performed (Downton et al., 1987). Correlations between  $g_s$  and  $C_i$  are different depending on whether gas exchange measurements are performed in the morning or in the afternoon (Schulze et al., 1975). Because gas exchange measurements were only performed in the morning, a more careful analysis is required to confirm that nonstomatal factors are involved in  $A_{\max}$  reductions occurring in DL of these species.

Transpiration is a physiological process by which leaves lose water through stomata and are simultaneously cooled (Chen, 2001). According to Farquhar and Sharkey (1982), in C3 species transpiration and  $g_s$  are closely related and show a positive linear correlation. Our data show significant reductions of  $g_s$  and  $E$  in DL of many studied species (Table 2). Moreover, significant linear correlations between  $E$  and  $g_s$  were observed for all dates in DL and CL, indicating that in both leaves water loss by transpiration is mainly controlled by leaf stomatal factors (Fig. 5a–c). Gas exchange data revealed that instantaneous WUE (i.e.,  $A_{\max}/E$  ratio) also increased significantly in DL of 11 of 17 species. This indicates that higher reductions of  $E$ , compared with  $CO_2$  assimilation rate, take place at the single-leaf level (Comstock and Ehleringer, 1984). Thus, our results tend to confirm that stomatal plugging is not the main factor controlling the photosynthesis rate in these species. Overall, close relationships between  $A_{\max}$ ,  $g_s$ ,  $E$ , and WUE observed in DL of many species, including small and tall plants, could indicate that leaf stomatal factors and shade-induced effect by accumulated dust are primarily responsible for the reductions in photosynthesis rate observed in these leaves. In species that show nonclose relationships of gas exchange parameters, it could be assumed that the effect of dust accumulation is associated with other nonstomatal factors (Naidoo and Chirkoot, 2004).

In field-grown plants, extrinsic water-related factors (e.g., evaporative water demand and boundary air layer surrounding leaves) and edaphic factors (e.g., soil water content) can affect stomatal closure and transpiration rate (Martin et al., 1999). Therefore, one might conclude that differences in gas exchange parameters occurring in DL of all studied species are produced through interactive relationships among intrinsic and extrinsic plant factors, dust accumulation, and environmental conditions. Further studies performed at multiple scales are needed to better understand the effects of accumulated dust on growth and development of plants in areas with increasing emissions of atmospheric pollutants.

## Conclusions

Although plants can tolerate atmospheric pollution, severe morphological and physiological alterations can occur as result of dust deposition. Gas exchange measurements in shrubs and trees reported herein revealed that the accumulation of dust on leaf surfaces causes important physiological changes related to photosynthetic  $CO_2$  assimilation, which can affect plant development and productivity.

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