

# Phyto-Cleaning of Particulate Matter from Polluted Air by Woody Plant Species in the Near-Desert City of Jodhpur (India) and the Role of Heme Oxygenase in Their Response to PM Stress Conditions

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## Research Article

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# Abstract

Particulate matter (PM) is one of the most dangerous pollutants in the air. Urban vegetation, especially trees and shrubs, accumulate PM and reduce its concentration in ambient air. The aim of this study was to examine 10 tree and shrub species common for the Indian city of Jodhpur (Rajasthan) located on the edge of the Thar Desert and determine: (1) the accumulation of surface and in-wax PM (both in three different size fractions), (2) the amount of epicuticular waxes on foliage, (3) the concentrations of heavy metals (Cd and Cu) on/in the leaves of the examined species, and (4) the level of heme oxygenase enzyme in leaves that accumulate PM and heavy metals. Among the investigated species, *F. religiosa* and *C. myxa* accumulated the greatest amount of total PM. *F. religiosa* is a tall tree with a lush, large crown and leaves with wavy edge, convex veins and long petioles, while *C. myxa* have hairy leaves with convex veins. The lowest PM accumulation was recorded for drought resistant *S. persica* and *A. indica*, which is probably due to their adaptation to growing conditions. Heavy metals (Cu and Cd) were found in the leaves of almost every examined species. The accumulation of heavy metals (especially Cu) was positively correlated with the amount of PM deposited on the foliage. A new finding of this study indicated a potentially important role of HO in the plants' response to PM-induced stress. The correlation between HO and PM was stronger than that between HO and HMs. The results obtained in this study emphasise the role of plants in cleaning polluted air in conditions where there are very high concentrations of PM.

## 1. Introduction

Atmospheric particle pollution is among the greatest challenges faced in urban areas. One of the most dangerous pollutants in the air is particulate matter (PM) (OECD 2012; WHO 2020), which is microscopic particles of different composition and origin (Han et al. 2020; Weuve et al. 2012). In the northern part of the Indian subcontinent, the most common PM is mineral dust from the Thar Desert, around half of which is large PM (50 %) (Gobbi et al. 2000; Sarkar et al. 2019). These particles are also known to be rich in nitrates that a photo-induced "re-nitrosification" process converts into NO<sub>x</sub> (Ndour et al. 2009). Nevertheless, in this region, the most problematic and dangerous PM is generated by human activity in the form of energy production, vehicular transportation and construction (Chernysheva et al. 2018). It comprises a mixture of trace elements, black carbon, dibenzofurans, polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (Alghamdi 2016; Lukowski et al. 2018). PM of all types is often suspended in the air for weeks and travels great distances, even between continents (Lin et al. 2014).

PM can enter the human body via the respiratory tract and is harmful to human health (Jędrychowski et al. 2015). Long-term exposure to airborne PM causes severe respiratory disorders, such as breathing difficulties, worsening asthma symptoms and chronic bronchitis, as well as diseases that affect all segments of the community such as cardiopulmonary diseases and lung cancer (Hsu et al. 2015; Kim et al. 2015; Saravia et al. 2013). Outdoor air pollution, mainly PM<sub>2.5</sub> (PM particles less than 2.5 µm) caused 4.2 million premature deaths worldwide in 2016 (WHO 2017). After Bangladesh, India is the country with the most polluted air. New data reveal that air pollution shortens the average Indian lifespan by 5.2 years and average PM concentration in the country has risen by approximately 42 % since 1998 (Greenstone and Fan 2020). Today, almost the entire Indian population is exposed to levels of PM that exceed WHO guidelines (WHO 2020).

Plants, especially trees and shrubs, play an important role in the adsorption and reduction of PM concentrations in the air (Lukowski et al. 2020; Popek et al. 2015; Pugh et al. 2012). They are effective at accumulating PM on the surface of leaves, stems and bark, while being eco-friendly and in line with public needs (Popek et al. 2017). However, the ability to capture PM on leaves is strongly linked to the characteristics of the species (Jouraeva et al. 2002; Sæbø et al. 2012). Plant shape and porosity (Leonard et al. 2016), leaf surface morphology, the complexity of the layer of cuticular waxes, the arrangement of stomata and the presence of trichomes on leaves (Dzierżanowski et al. 2011; Haynes et al. 2019; Prusty et al., 2005) are very important. Urban greenery is able to remove significant amounts of pollutants from the air in cities (Kroeger et al. 2018; Pugh et al. 2012; Vailshery et al. 2013; Yang et al. 2005), and therefore air phytoremediation is becoming increasingly popular worldwide, especially as it does not involve any tangible costs (Paton-Walsh et al. 2019).

Unfortunately, the accumulated PM has a negative impact on plants, including trees and shrubs (Li et al. 2019; Mina et al. 2018; Popek et al. 2018a; Siqueira-Silva et al. 2016; Singh et al. 2019; Zhou et al. 2018). The PM aerosols can exert climatic effects by absorption and scattering of solar radiation, and cloud condensation nuclei activity (Luo et al. 2019). PM accumulated on the surface of foliage changes its optical properties due to the absorption/reflection of photosynthetic active radiation (PAR) or clogging/damage to stomata (Li et al. 2019; Singh et al. 2019). Jin et al. (2021) report that PM adsorbed on leaves is usually concentrated in the stomata or the corrugated areas around the stomata, and PM up to 2 µm can enter or block the stomata. As a result, gas exchange and the intensity of photosynthesis and transpiration are much less efficient (Li et al. 2019; Mina et al. 2018; Popek et al., 2018b). The PM may include toxic substances, such as heavy metals (HM) or organic pollutants, which can penetrate from the leaf surface to the inner plant tissues (Luo et al. 2019; Przybysz et al. 2019). There are growing reports that PM induces oxidative stress (Ghorbanli et al. 2007; Mudway et al. 2020; Piacentini et al. 2019). Prolonged exposure to higher concentrations of PM may cause different morphoanatomical (decreased plant biomass and height, disturbance in plant development, leaf chlorosis and necrosis, leaf thickness alteration, modification of the structure and chemical composition of waxes, cell turgor loss and cellular collapse) and physiological (decreased photosynthetic pigments and leaf water content, increased leaf temperature, nutritional alteration in leaflets, and early leaf senescence and abscission) alterations in foliage (Mina et al. 2018; Siqueira-Silva et al. 2016; Zhou et al. 2018). In addition, PM can change the pH and chemical composition of the soil and indirectly affect plant performance (Luo et al. 2019; Piacentini et al. 2019; Siqueira-Silva et al. 2016).

Plants growing in an environment with a polluted atmosphere are characterised by various modifications that enable them to survive in difficult growing conditions. Changes may relate to the frequency, density, location and size of the stomata (Gostin 2009; Kiyomizu et al. 2019). In order to protect gas exchange from the adverse effects of PM, smaller stomata are located on the abaxial side of the leaf (Gostin 2009; Li et al. 2019). Some species increase mesophyll thickness at sites with high pollution, which may decrease the flux of air pollutants inside leaves and thus the uptake of air pollutants by leaf tissues (Kiyomizu et al. 2019). Leaf trichomes and grooves appear to have a role in protecting plants from PM exposure (Li et al. 2019). The higher groove

proportion and presence of trichomes on the leaf surface absorbs some PM and buffers its negative effect on stomata (Li et al. 2019). Air pollutants accumulated on plant foliage may also be mitigated by phyllosphere microbes (Wei et al. 2017). To counteract the oxidative stress induced by PM, plants increase the activity of the antioxidant system, including enzymes such as peroxidase and catalase (Ghorbanli et al. 2007; Mudway et al. 2020).

As mentioned above, atmospheric PM often contains heavy metals (Ghasemi et al. 2020). A considerable quantity of atmospheric heavy metals is absorbed via the foliar organs of plants after the wet or dry deposition of atmospheric fallouts on the plant canopy (Liu et al. 2019; Przybysz et al. 2019; Shahid et al. 2017). Heavy metal uptake from the air greatly depends on a number of factors, including the physico-chemical characteristics of the cuticle and metals, the chemical and physical forms of the adsorbed metal, the morphology and surface area of the plant leaves, the surface texture of leaves (pubescence and roughness), exposure duration, environmental conditions, plant gas exchange, concentrations of atmospheric PM, and PM size, load and composition (Shahid et al. 2017; Sharma et al. 2020). Not all airborne heavy metals are immobilised on the foliage surface; some heavy metals linked to PM can enter plant leaf tissues and can be translocated to the stem below and roots through the vascular sap (Sharma et al. 2020; Uzu et al. 2010). The concentrations of heavy metals in the foliage of plants growing close to the emission source are usually high (Mori et al. 2015; Noh et al. 2019; Zhu et al. 2019). The considerable accumulation of heavy metals derived from PM is due to the direct transfer of contaminants from the atmosphere to foliar organs but also due to the atmosphere-soil-root transfer (Liu et al. 2019). Heavy metals accumulated by plants disturb most physiological, metabolic and biochemical processes (Shahid et al. 2017).

One of the enzymes involved in plant responses to abiotic stress (including salt, UV light, drought and particularly oxidative stress and heavy metals) is heme oxygenase (HO) (Hancock and Russell 2021; He and He 2014; Mahawar et al. 2021; Wegiel et al. 2014). In plants (*Arabidopsis thaliana* L.), the HO family comprises four members that fall into two subfamilies: the HO1 subfamily (HO-1, HO-3, HO-4) and the HO2 subfamily (HO-2) (Fang et al. 2021). The catalytic action of HO-1 is the breakdown of heme. This is an oxygen-dependent reaction that uses NADPH as a cofactor and generates biliverdin, carbon monoxide (CO) and iron (Hancock and Russell 2021; Wilks 2002). This reaction is essential in physiological processes as diverse as iron reutilisation and cellular signalling in mammals, synthesis of essential light harvesting pigments (e.g. phytochrome chromophore formation) in cyanobacteria and higher plants, and the acquisition of iron by bacterial pathogens (Lecube et al. 2014; Wilks 2002). In plants, HO-1 is also associated with root development and crosstalk between NO, CO and hydrogen peroxide (Lecube et al. 2014). According to Lawal et al. (2015), in a human HO-1 protects endothelial cells from the toxicity of air pollutant chemicals.

Until now, city planners have selected plants for urbanised areas primarily on the basis of their decorative value and tolerance to urban abiotic stresses. Recent findings have led to consideration starting to be given to the ability of plants to purify ambient air from PM. Research on the phytoremediation properties of urban plants is being conducted worldwide. However, to date there is no universal formula for assessing whether a given species is useful for air phytoremediation and thus experiments should cover the widest possible number of species occurring under different climatic conditions. Therefore, the aim of this study was to examine 10 tree and shrub species recommended for planting in the Indian city of Jodhpur (Rajasthan) on the edge of the Thar Desert and determine: (1) the accumulation of surface and in-wax PM (both in three different size fractions), (2) the amount of epicuticular waxes on foliage, (3) the concentrations of heavy metals (Cd and Cu) on/in the leaves of the examined species, and (4) the level of heme oxygenase enzyme in leaves that accumulate PM and heavy metals.

## 2. Materials And Methods

### 2.1. Study location

The study took place in the city of Jodhpur in the botanical garden of Jai Narain Vyas University (JNVU). Jodhpur is the second largest city in the Indian state of Rajasthan and has a population of approximately 1.5 million people (Fig. 1). It is called the Gateway to Thar as it is located on the edge of the Thar Desert. Its many palaces, forts and temples make the city a popular tourist destination. The climate of Jodhpur is hot and semi-arid during its almost year-round dry season. The short rainy season runs from late June to September (average rainfall of around 362 millimetres). Temperature is routinely very high at around 40 to 45 °C from March to October. During the rest of the year, it oscillates between 25 °C and 30 °C.

Jodhpur is the most polluted city in the Rajasthan and has very poor air quality. According to the latest WHO data (2016), the annual mean concentrations of PM<sub>10</sub> and PM<sub>2.5</sub> are 180 ug/m<sup>3</sup> and 98 ug/m<sup>3</sup> respectively, and these are growing significantly each year. In critical situations, the concentrations of both fractions may even exceed 300 ug/m<sup>3</sup> (WHO, 2020).

### 2.2. Plant material and sample collection

For the experiment, ten tree, shrub and climber species common to the Thar Desert region were selected: *Azadirachta indica* Juss., *Bougainvillea spectabilis* Willd., W. T. Aiton, *Colophospermum mopane* Kirk ex J. Léonard, *Cordia myxa* L., *Eucalyptus globulus* Labill., *Ficus religiosa* L., *Polyalthia longifolia* (Sonn.) Thwaites, *Salvadora persica* L., *Tinospora cordifolia* (Willd.) Hook. f. & Thomson, and *Vachellia nilotica* (L.) P.J.H. Hurter & Mabb. The plants had already been growing *in-vivo* in the JNVU's botanical garden. The location is in an area with few buildings and very little traffic. The nearest, very well-maintained road is about 500 metres from the garden's edge. The plants selected for the experiment were in good condition, i.e. healthy and free from pests.

The harvest of plant samples was preceded by several months of rainless weather, which limited the amount of PM washed off the foliage. Leaves were sampled in four biological replications (biological replication was individual tree/shrub/climber) in November 2017 (n = 4 samples x 10 species). A single sample consisted of leaves harvested from different parts of the plant. Samples were composed of three to seven leaves, depending on their size. In order to avoid the clogging of filters during the PM filtering process, the total area of each sample did not exceed 300 cm<sup>2</sup>. Each sample was placed in a paper envelope, labelled and transferred to a constant temperature and humidity test room where they were stored until analysis.

## 2.3. Analysis of PM accumulation and amount of epicuticular waxes on leaves

Accumulation of PM and the amount of epicuticular waxes on foliage were determined gravimetrically. The amount of PM was determined in two categories: surface PM ( $s$ PM), which was washed off with water (in natural conditions it can be washed off from the foliage by rain), and in-wax PM ( $w$ PM), which was washed off with chloroform (PM immobilised in waxes). Both categories were analysed in three size fractions: 0.2–2.5, 2.5–10 and 10–100  $\mu\text{m}$ . Leaf samples were first washed with distilled water and then with chloroform. The solutions obtained were then passed through a 100- $\mu\text{m}$  mesh sieve (to remove particles larger than 100  $\mu\text{m}$  from the solution) and were then sequentially filtered using pre-weighed filters of type 91 (paper filter with a pore size of 10  $\mu\text{m}$ ), type 42 (paper filter with a pore size of 2.5  $\mu\text{m}$ ) and polytetrafluoroethylene (PTFE) membrane filters (a pore size of 0.2  $\mu\text{m}$ ) (all Whatman, UK). After filtration, all the filters were weighed again. The quantity of epicuticular waxes was weighed after evaporation of the chloroform collected in pre-weighed beakers. The area of leaves from each sample was determined using a Plant Leaf Area Meter (Petiole, Ukraine). The amounts of PM from filters and waxes were then recalculated to give the  $\mu\text{g cm}^{-2}$  of leaves (Dzierzanowski et al. 2011).

## 2.4. Quantitative analysis of heavy metals in leaves

Quantitative assessments of cadmium (Cd) and copper (Cu) were performed for all the examined species. Amounts of HMs were measured in two replicates ( $n = 2$  samples  $\times$  10 species). Foliage, including accumulated PM (these samples were not used for PM analysis), was collected in the same way as previously described in 2.2. After harvest, the samples were dried at 105°C for 48 h, then ground into a fine powder and placed in paper bags until analysis. Powdered plant material (500 mg) was digested with 9 mL of 65 % v/v  $\text{HNO}_3$  in Titan MPS (PerkinElmer, Waltham, USA) and diluted to 50 mL. Samples were then analysed with the high-resolution ICP-OES technique using an Optima 8000 spectrometer (PerkinElmer, Waltham, USA).

## 2.5. Extraction and assay of heme oxygenase

The catalysis of the heme oxygenase (HO) enzyme was evaluated according to the method of Balestrasse et al. (2005). Freshly harvested leaves were homogenised in a cold  $\text{KPO}_4$  buffer (50 mM, pH 7.4) with PMSF (1 mM), EDTA (0.2 mM) and sucrose (0.25 M). Homogenates were centrifuged for 20 minutes at 10,000  $\times$  g at 4°C and supernatants were employed for HO analysis. The concentration of HO ( $\mu\text{M}$  biliverdin reduced  $\text{mg}^{-1}$  protein) was estimated by documenting the optical density of biliverdin (the main product of HO catalysis) formed by the reaction between an assay compound [ $\text{KPO}_4$  buffer (50 mM, pH 7.4) + haemin (200 nM) + NADPH (60 nM)] and HO extract at 37°C for one hour at 650 nm (molar absorption coefficient 6.25  $\mu\text{M}^{-1} \text{cm}^{-1}$ ).

## 2.6. Statistical analysis

Statistical analysis was performed using Statistica (StatSoft, USA). Before all analyses, normal distributions were verified using the Shapiro-Wilk test. Analysis involved ANOVA and Tukey's test at the significance level of  $\alpha = 0.05$  for comparisons of means in order to determine the impact of factors such as plant species, amount of accumulated PM fractions and categories, amount of waxes, amounts of Cd and Cu, and amount of heme oxygenase. Non-parametric Spearman's correlation coefficients were calculated between different measured variables. The significance of correlation was determined using  $\alpha = 0.05$ .

## 3. Results

### 3.1 The amount of particulate matter on leaves

The species examined in this study differed significantly in their potential to accumulate PM on their leaves. Significant differences were recorded for total PM ( $\text{PM}_T$ ) accumulation and different PM size fractions (0.2–2.5, 2.5–10, 10–100  $\mu\text{m}$ ) and categories ( $s$ PM and  $w$ PM).

The significantly highest  $\text{PM}_T$  accumulation was recorded for *F. religiosa*, *C. myxa* and *T. cordifolia* (Fig. 2). The differences in  $\text{PM}_T$  between these species ranged from 117.8  $\mu\text{g cm}^{-2}$  (*F. religiosa*) to 88.6  $\mu\text{g cm}^{-2}$  (*T. cordifolia*), therefore *F. religiosa* accumulated 15 % more  $\text{PM}_T$  than *T. cordifolia*. Plants of *B. spectabilis*, *V. nilotica*, *P. longifolia*, *C. mopane*, *A. indica* and *E. globulus* ( $\text{PM}_T$  accumulation in the range of 59.4 to 39.2  $\mu\text{g cm}^{-2}$ ) turned out to be average  $\text{PM}_T$  accumulators, while *S. persica* accumulated significantly the least  $\text{PM}_T$  (17.1  $\mu\text{g cm}^{-2}$ ). *S. persica* accumulated 85 % less  $\text{PM}_T$  than *F. religiosa*, which accumulated  $\text{PM}_T$  most efficiently (Fig. 2).

The studied species also differed statistically in the accumulation of different PM size fractions (Table 1). On average for all species, the share of large PM was 65 %, coarse PM 28 % and fine PM 9 %. The species with the highest share of large PM were *C. mopane* and *A. indica* (both about 72 %), while the lowest were *C. myxa* and *F. religiosa* (56 % and 54 % respectively). *F. religiosa*, *C. myxa* and *V. nilotica* were characterised as having the highest share of coarse PM (35 % for *F. religiosa* and 34 % for *C. myxa* and *V. nilotica*). In the case of this fraction, the lowest share was found for *C. mopane* and *A. indica* (20 % and 16 % respectively). The smallest fraction represented the highest share in the  $\text{PM}_T$  accumulated by *A. indica* (13 %), *B. spectabilis* (13 %) and *F. religiosa* (10 %), while the lowest was recorded in *S. persica* (7 %), *E. globulus* (6 %) and *T. cordifolia* (6 %) (Table 1).

Table 1

Accumulation of different PM fractions by the leaves of 10 plant species. Data are mean  $\pm$  SE, n = 4. Different letters indicate statistical significance for each fraction (P < 0.05)

Species	PM size fraction [ $\mu\text{g cm}^{-2}$ ] (mean $\pm$ SE)		
	10–100 [ $\mu\text{m}$ ]	2.5–10 [ $\mu\text{m}$ ]	0.2–2.5 [ $\mu\text{m}$ ]
<i>Ficus religiosa</i>	63.5 $\pm$ 0.8 a	42.2 $\pm$ 0.8 a	12.1 $\pm$ 0.1 a
<i>Cordia myxa</i>	59.8 $\pm$ 1.7 a	36.4 $\pm$ 1.0 b	9.9 $\pm$ 0.4 ab
<i>Tinospora cordifolia</i>	53.5 $\pm$ 1.9 b	29.8 $\pm$ 1.3 c	5.3 $\pm$ 0.3 c
<i>Bougainvillea spectabilis</i>	37.8 $\pm$ 0.2 c	13.6 $\pm$ 0.6 de	8.0 $\pm$ 0.2 b
<i>Vachellia nilotica</i>	32.0 $\pm$ 0.3 cd	19.0 $\pm$ 1.0 d	4.4 $\pm$ 0.1 cd
<i>Polyalthia longifolia</i>	32.4 $\pm$ 1.0 cd	15.4 $\pm$ 0.6 de	4.4 $\pm$ 0.3 cd
<i>Colophospermum mopane</i>	35.5 $\pm$ 0.3 cd	9.7 $\pm$ 0.3 ef	3.9 $\pm$ 0.2 cd
<i>Azadirachta indica</i>	31.6 $\pm$ 0.2 d	7.0 $\pm$ 0.3 f	5.5 $\pm$ 0.3 c
<i>Eucalyptus globulus</i>	25.0 $\pm$ 1.1 e	11.7 $\pm$ 0.4 ef	2.5 $\pm$ 0.2 d
<i>Salvadora persica</i>	11.2 $\pm$ 0.1 f	4.7 $\pm$ 0.3 g	1.2 $\pm$ 0.0 e
Average	38.2 $\pm$ 4.4 A	19.0 $\pm$ 2.5 B	5.7 $\pm$ 1.2 C

### 3.2 Amount of surface PM, in-wax PM and waxes on leaves

The examined trees also differed statistically in terms of the amount of surface PM (sPM) and PM immobilised in waxes (wPM) (Table 2). Most of the studied species accumulated the majority of PM as sPM (an average 68 % and 32 % for sPM and wPM respectively). The species with the highest share of sPM were *S. persica* (86 % of sPM in PM<sub>T</sub>), *A. indica* (80 % of sPM in PM<sub>T</sub>) and *B. spectabilis* (75 % of sPM in PM<sub>T</sub>), while those with the lowest share were *V. nilotica* (56 % of sPM in PM<sub>T</sub>), *E. globulus* (57 % of sPM in PM<sub>T</sub>) and *F. religiosa* (59 % of sPM in PM<sub>T</sub>) (Table 2). Plants of *E. globulus*, *F. religiosa* and *C. myxa* had foliage covered with significantly the largest amount of waxes and almost three times greater than that of *P. longifolia* and *B. spectabilis* (Table 2).

Table 2

The percentage share of sPM and wPM in PM<sub>T</sub> and the amount of epicuticular waxes on the foliage of 10 plant species. Data are mean  $\pm$  SE, n = 4. Different letters indicate statistical significance between the species (P < 0.05).

Species	<i>Ficus religiosa</i>	<i>Cordia myxa</i>	<i>Tinospora cordifolia</i>	<i>Bougainvillea spectabilis</i>	<i>Vachellia nilotica</i>	<i>Polyalthia longifolia</i>	<i>Colophospermum mopane</i>	<i>Azadirachta indica</i>	<i>Eucalyptus globulus</i>	<i>Salvadora persica</i>
PM types and waxes										
sPM %	59	65	63	75	56	70	70	80	57	86
wPM %	41	35	37	25	44	30	30	20	43	14
Waxes [ $\mu\text{g cm}^{-2}$ ]	53.5a	51.1a	48.7a	17.3d	40.9b	17.d	30.2c	33.4c	58.9a	32.9c
(mean $\pm$ SE)	$\pm$ 2.3	$\pm$ 4.2	$\pm$ 3.5	$\pm$ 3.4	$\pm$ 3.8	$\pm$ 2.0	$\pm$ 0.8	$\pm$ 2.0	$\pm$ 2.2	$\pm$ 2.9

### 3.3 Amounts of Cd and Cu on/in leaves

The examined tree and shrub species differed in their ability to accumulate heavy metals (Cd and Cu) in leaves (Fig. 3). *B. spectabilis*, *F. religiosa* and *P. longifolia* turned out to be the species with the highest accumulation of Cu. These three species accumulated 35 % more Cu than *E. globulus*, *A. indica* and *T. cordifolia*, and 65 % more than *C. myxa*, *V. nilotica* and *S. persica*. Statistically the highest concentrations of Cd were noted in the leaves of *C. myxa*, *F. religiosa* and *V. nilotica*. A very low accumulation of Cd was recorded in *T. cordifolia*, *A. indica*, *E. globulus* and *S. persica*, while in *B. spectabilis*, *P. longifolia* and *C. mopane* the amount of Cd was below the detection level. In all species, the accumulation of Cu was considerably higher than that of Cd (Fig. 3).

### 3.4. Activity of heme oxygenase (HO)

The examined species differed in the activity of HO (Fig. 4). Significantly the highest activity of this enzyme was recorded in *F. religiosa*, which was twice as intense as in *C. myxa* and *A. indica*. Significantly the lowest activity of HO was noted in the leaves of *S. persica*, at almost 95 % lower than in *F. religiosa* (Fig. 4).

### 3.5. Correlations

For all examined species, a strongly significant positive correlation was found between HO and all types of PM accumulated on foliage (Table 3). The highest correlation (0.92) was found between HO and the smallest PM fraction (0.2–2.5 µm). A significant positive correlation was also recorded between HO and Cu concentration in leaves, while for Cd concentration the correlation was not significant. There were no statistically significant correlations between the amount of Cu in leaves and all types of PM,

Table 3  
Non-parametric Spearman's correlation coefficients calculated between different categories of particulate matter (PM) and the amount of heavy metals (Cu and Cd) and HO enzyme analysed for 10 plants species. Bold values indicate a statistical significance ( $P < 0.05$ )

Types of PM	Heavy metals							
	Total 0.2–100 µm	Large 10–100 µm	Coarse 10 – 2.5 µm	Fine 0.2–2.5 µm	Surface <sub>s</sub> PM	In-wax <sub>w</sub> PM	Cu	Cd
HO	<b>0.82</b>	<b>0.81</b>	<b>0.78</b>	<b>0.92</b>	<b>0.80</b>	<b>0.82</b>	<b>0.77</b>	0.63
Cu	0.44	0.46	0.40	0.50	0.41	0.47		0.04
Cd	0.73	0.67	<b>0.76</b>	<b>0.79</b>	0.68	<b>0.76</b>	0.04	

## 4. Discussion

Urban vegetation plays an extremely important role in the urbanised environment (Pugh et al., 2012; Popek et al., 2017). In addition to its undeniable aesthetic values, it also fulfils important ecological functions in stabilising and shaping the climate. The presence of plants in cities can lead to reduced temperatures, higher air humidity and better water retention (Rai and Panda, 2014; Yang et al., 2005; Kroeger et al., 2018). Urban vegetation also reduces the negative impact of air pollutants (e.g. PM) on the environment and human health (Popek et al., 2017; Paton-Walsh et al., 2019). This is particularly important in areas where air pollution limits are often exceeded. An important function of this kind is usually played by trees and shrubs, which have a large, biologically active biomass to purify the air and play the role of an urban "green liver".

### 4.1. Accumulation of particulate matter

In this study, the results clearly showed that woody plants grown in the heavily polluted Indian city of Jodhpur efficiently accumulated PM on their foliage. However, the examined species differed in the amount of PM accumulated. Among the investigated species, *F. religiosa* accumulated the greatest amount of total PM. This tree is tall with a lush, large crown. The air turbulence between the leaves and branches of its dense crown can be an efficient trap for PM, as previously demonstrated by Xie et al. (2018). Dense but porous deciduous trees and shrubs have been shown to form street canyons that can reduce air PM concentrations by as much as 60 % (Pugh et al. 2012). The morphology of *F. religiosa* leaves may also be important (Chiam et al. 2019; Muhammad et al. 2020). The leaves of this species are characterised by a wavy edge and convex veins, which can act as natural microbarriers to PM. It has been reported that PM accumulation is relatively high on the leaf margins (Mitchell et al. 2010) and/or along the main leaf nerves (Tomašević et al. 2005). In addition, the leaves of *F. religiosa* are set on long petioles, which move in the wind and actively purify the air from PM, as previously presented by Prusty et al. (2005). It is very important to note that accumulation of PM with the smallest diameter was also highest in that species, with coarse and fine PM amounting to 36 % and 10 % of the total PM accumulated by *F. religiosa*. It can be assumed that the number of particles of this fraction compared with large PM was even greater. According to Grochowicz and Korytkowski (1996), despite the low weights, the number of fine PM particles accumulated on plants can be very high. Fine and ultrafine PM fractions contribute to 30 % of total PM weight, but at the same time make up 99.9 % of the total number of particles (Grochowicz and Korytkowski 1996). Purifying air from fine fraction PM is most important because it represents the greatest threat to human health. Therefore, the great ability of *F. religiosa* to accumulate this fraction makes it a tree of great phytoremediation value in urban areas.

The species with the next greatest ability to accumulate PM was *C. myxa*. Like *F. religiosa*, its leaves have convex veins. They are also pubescent and when young tend to be hairy. Many morphological characteristics, such as surface roughness and the presence of trichomes, have been shown to increase the amount of PM on leaves (Leonard et al. 2016). According to Dzierżanowski and Gawroński (2011), leaves densely covered with hairs can act as air-cleaning brushes.

The third and fourth species that accumulated PM most efficiently were *T. cordifolia* and *B. spectabilis*, two vigorously growing climbers. The leaf edges of these species are usually curled, which may increase PM accumulation as this leaf shape creates a 'basin' into which rainwater with associated contaminants can flow. Similar conclusions were drawn by Popek et al. (2013), who found great accumulation of PM by *Syringa meyeri* 'Palibin' C.K. Schneid, which has leaves with a similar morphology. Climbers are very important for city planners because these plants occupy small areas of land and,

by climbing on the surface of buildings, can produce a huge leaf area (in relation to the land area occupied) capable of accumulating PM and other pollutants (Ottel  et al. 2010). This is especially important in cities where green areas are still limited due to a lack of space. Green walls covered with climbers can therefore be an attractive alternative to trees and shrubs. In addition, climbers are also increasingly being used to cover acoustic barriers along motorways, which are especially exposed to extremely high PM concentrations and counteract air pollution. It is noteworthy that *B. spectabilis* is another species with a very high share of the smallest PM, thus most dangerous for human health, out of total accumulated PM.

Another important species in this research turned out to be *P. longifolia*. This tree, although not characterised by very high PM accumulation, is valuable in the urban environment. It has a very dense crown and a huge mass of leaves that can filter air. This plant does not accumulate as much PM per square centimetre, but the whole tree can probably capture large amounts of PM from the air. Its narrow shape also allows this tree to be planted close to traffic routes as well as next to buildings without causing damage.

*S. persica* and *A. indica* were the plants that accumulated the least PM. Those two species are well known for their resistance to drought. They are commonly found in semi-arid and desert areas, and are sources of shade for other vegetation in these locations (Khatak et al. 2010). The morphology of their leaves is similar, with both having smooth and glossy leaves. Bakker et al. (1999) showed that the *Plantago* species with its smooth leaf surfaces accumulates less PM than densely hairy species. PM deposited on *S. persica* and *A. indica* foliage can probably easily be blown off by the wind or washed off by rain. These specific morphological features of *S. persica* and *A. indica* leaves are probably due to the places where they are found. They grow in dry and extremely dusty environments, which has probably led to the development of protective mechanisms against the deposition of particles on the leaves (not investigated in this research), otherwise PM thickly covering the leaves would impair the photosynthetic apparatus by shading the leaf blade and/or clogging the stomata (Li et al. 2019; Mina et al. 2018; Popek et al. 2018a; Siqueira-Silva et al. 2016). Moreover, both these species were characterised by a high share of coarse PM out of total accumulated PM. These results indicate that plants well adapted to drought and high air pollution are not always the most effective PM accumulators.

Low PM accumulation was also recorded for *C. mopane* and *V. nilotica*, invasive trees originating from Africa, and *E. globulus* from Australia. All three are also adapted to dry and semi-desert conditions. Low efficiency of PM accumulation in eucalyptus (unidentified species) has also been demonstrated in studies conducted on 16 tree species in Australia (Leonard et al. 2016). *E. globulus* and *S. persica* accumulated the smallest amount of the fine PM fraction, while *A. indica* was the species with a large share of this fraction out of the total mass of PM deposited on foliage.

## 4.2. Relationship between the amount of epicuticular waxes and PM accumulation

Opinions vary about whether the amount of waxes on foliage increases PM accumulation (Jouraeva et al. 2002; Popek et al. 2015; Renault et al. 2017; S eb  et al. 2012). The undeniable fact, however, is that part of the PM is immobilised on and in the wax layer. In-wax particles ( $wPM$ ), unlike those deposited directly on the leaf surface ( $sPM$ ), are strongly attached to the leaf surface and it is not easy for them to be washed away by rain or blown by the wind; they also can be removed from the environment with falling leaves (Jouraeva et al. 2002; S eb  et al. 2012). In this study, the species with the highest PM accumulation (*F. religiosa*, *C. myxa*, *T. cordifolia*) were also the ones that produced very high amounts of waxes on their leaves. Moreover, the share of PM immobilised in waxes was also highest (about 40 %) in these species. Similar results have been obtained for silver birch (*Betula pendula* L.) and Scots pine (*Pinus sylvestris* L.) on whose foliage a large amount of wax on leaves causes a high accumulation of  $wPM$  (Popek et al. 2015; S eb  et al. 2012). In contrast, a species with the highest amounts of waxes recorded in this work (*E. globulus*) was not efficient at PM accumulation. Similar results have been presented by Popek et al. (2019), who show that two Australian tree species, Sweet Pittosporum (*Pittosporum undulatum* Vent.) and Large Mock-olive (*Notelaea longifolia* Vent.), accumulate only slightly less PM than swamp gum (*Eucalyptus ovata* Labill.) despite a much thinner wax layer. As many researchers have noted, these contrasting data suggest that not only the total wax content, but also its chemical composition or structure, may be important for efficient PM accumulation (Jouraeva et al. 2002;  ukowski et al. 2018; Popek et al. 2015; Przybysz et al. 2014; S eb  et al. 2012). In this work, taking into account all the species together, the amount of wax was positively correlated with the amount of  $wPM$  ( $r = 0.66$ ;  $P < 0.0001$ ). This has also been noted in the studies of S eb  et al. (2012) and Przybysz et al. (2014), but not those of  ukowski et al. (2018) or Popek et al. (2019). It should be noted that some types of PM may affect negatively the structure and degradation of waxes, thus affecting the amount of PM accumulated (Jouraeva et al. 2002).

## 4.3. HM concentration in leaves

The concentrations of HMs on/in leaves can be significantly affected by PM concentration in the air (Liu et al. 2019; Maisto et al., 2004; Przybysz et al. 2019; Shahid et al. 2017). Approximately 70 % of the As, Pb, Zn, and Cd mass is emitted to the air as PM (Bartnicki 1994). In this study, Cu and Cd were found in the leaves of almost every examined species. Probably due to the long distance from roads (or other sources of HMs), the concentrations of both HMs were low, approximately five times lower than in the research of Popek et al. (2017) on small-leaved lime trees (*Tilia cordata* L.) growing close to roads in cities with high PM pollution. Furthermore, Mori et al. (2015), Noh et al. (2019) and Zhu et al. (2019) show that the PM concentration in leaves increases with decreasing distance from the emission source. In this study, it was impossible to estimate how much of the HMs was taken up from the soil and how much was of atmospheric origin. According to Maisto et al. (2004), Cd and Cu are most often accumulated in ionic form from the soil and then translocated from the roots to the leaves; direct accumulation from the atmosphere is less likely. However, Przybysz et al. (2019) demonstrate that concentrations of Ni, Pb, Cd and Sb are higher in PM accumulated on foliage than in plant tissue, offering clear evidence that airborne PM could be an important source of HMs and that plants, if used properly, can serve as efficient green filters purifying ambient air from toxic HMs. In this study, concentrations of Cu in leaves were not correlated with accumulated PM, while concentrations of Cd were significantly correlated with fine and coarse PM deposited on foliage. These results are in agreement with Bartnicki (1994), who found that HMs on leaves are associated with PM of a diameter less than 0.95 mm, which in urban areas is mainly of anthropogenic origin. S rme et al. (2001) and Hjortenkrans et al. (2006) demonstrate that increased amounts of Cd in PM usually have their origins in traffic emissions, especially in association with abraded vehicle tires. The results of the present study also showed

a positive correlation between Cd and  $w$ PM. In contrast to the above, according to Przybysz et al. (2019) HMs are recorded in all PM size fractions accumulated by plants and are fairly equally distributed between surface PM ( $s$ PM) and in-wax PM ( $w$ PM).

#### 4.4. Heme oxygenase as the response to the PM stress

Heme oxygenase (HO) is an enzyme involved in plant responses to various abiotic stresses, including heavy metals (Hancock and Russell 2021; He and He 2014; Mahawar et al. 2021; Shekhawat and Verma, 2010; Shekhawat et al. 2011; Shekhawat et al. 2019). In this study, a positive correlation was recorded between HO and concentrations of both HMs (Cu and Cd) in and on leaves, but only significantly so in the case of Cu. Mahawar and Shekhawat (2018) show that the activity of HO increases with an increasing concentration of Cd in plants and time of exposure to this metal. The participation of HO in defensive responses against Cd has also been demonstrated by Balestrasse et al. (2008) and Noriega et al. (2012). Mahawar and Shekhawat (2018), Noriega et al. (2012), Hancock and Russell (2021) and Mahawar et al. (2021) suggest that HO may be involved in mitigating the effects of stress caused by most heavy metals. The new finding in the present study was that the activity of HO was significantly positively correlated with PM (all examined fractions and categories) accumulated on plant foliage. Moreover, the correlation between HO and PM was stronger than between HO and HMs. PM has a well-known negative effect on plants, especially on the photosynthetic apparatus (Li et al. 2019; Mina et al. 2018; Mudway et al. 2020; Piacentini et al. 2019; Popek et al. 2018a; Singh et al. 2019; Zhou et al. 2018). The high activity of HO in the leaves of plants growing in conditions of increased PM concentration in the air may indicate that the defence reactions of plants to PM are more complicated than previously thought, and that plants accumulating large amounts of PM must adapt to their unfavourable impact. HO is produced and active mainly in leaves and may be involved in alleviating the oxidative stress (Mahawar and Shekhawat 2018) induced in plants by PM (Mudway et al. 2020; Piacentini et al. 2019). Li et al. (2014), Mahawar and Shekhawat (2018), Verma et al. (2013) and Zhu et al. (2017) show that HO is related to chlorophyll biosynthesis, which may be important in plants suffering from a dysfunctional photosynthetic apparatus due to the negative effects of PM.

## 5. Conclusions

Urban residents struggle with high air pollution, especially PM, in their cities every day. The results of this study showed that woody plants can actively biofiltrate PM and HMs from the air in a heavily polluted Indian city. The phytoremediation properties of plants should be taken into account in the planning, selection, planting and maintenance of urban greenery. Some species, such as *F. religiosa*, accumulated PM more efficiently, while others, such as the semi-desert species *A. indica* and *S. persica*, avoided high PM deposition on foliage, which is probably due to their adaptation to growing conditions. PM accumulation by plants depends on various factors, such as the density and porosity of the crown, the shape and morphology of the leaf, and the presence of hairs and epicuticular waxes on foliage. The accumulation of HMs (especially Cu) was positively correlated with the amount of PM deposited on the leaves. A new finding of this study indicated a potentially important role of HO in the plants' response to PM-induced stress. The correlation between HO and PM was stronger than that between HO and HMs. The results obtained in this study emphasise the role of plants in cleaning polluted air in conditions where there are very high concentrations of PM, and shed new light on the defence responses of plants against PM.

## Declarations

**Availability of data and materials:** The data and materials from the current study are available from the corresponding author on reasonable request.

**Author contribution:** Robert Popek: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing, Visualization, Supervision, Funding acquisition. Lovely Mahawar: Investigation, Validation, Writing - review & editing, Visualization. Gyan Singh Shekhawat: Validation, Formal analysis, Resources, Writing - review & editing, Supervision. Arkadiusz Przybysz: Formal analysis, Writing - review & editing, Visualization, Supervision.

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## Figures

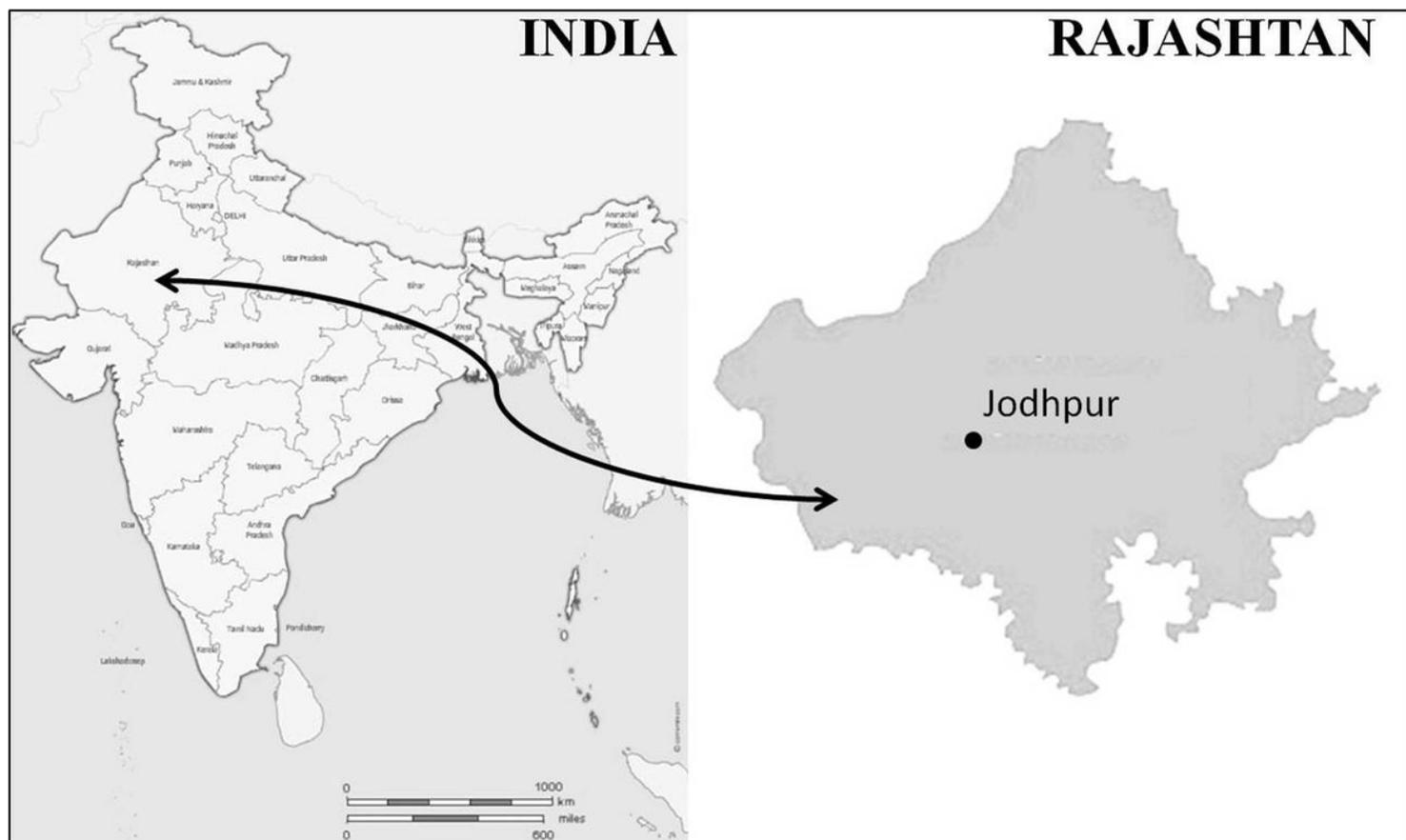


Figure 1

Map showing the location of the city of Jodhpur

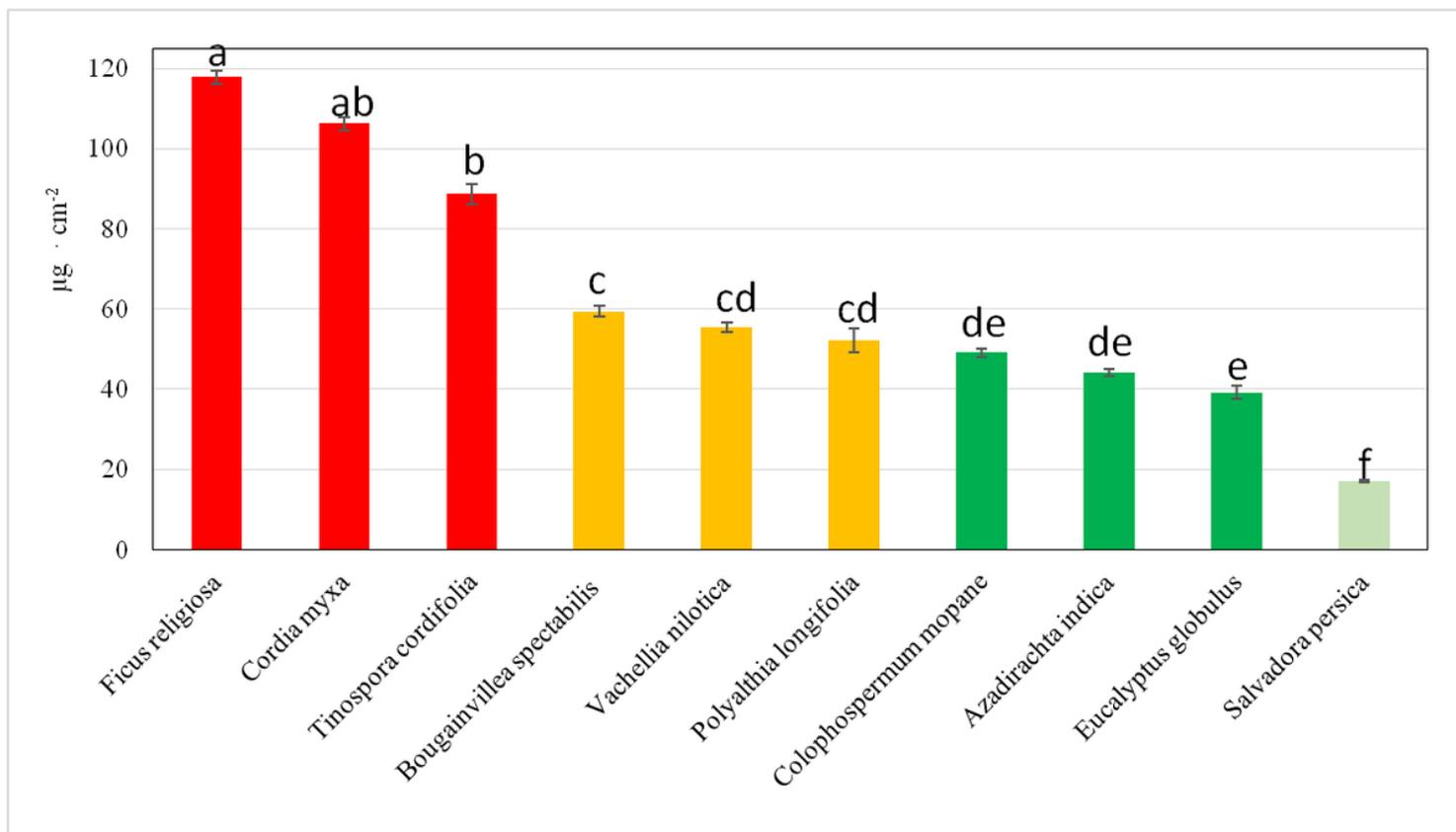


Figure 2

Total PM accumulation on the leaves of 10 plant species. Data are mean  $\pm$ SE, n = 4. Different letters indicate statistical significance ( $P < 0.05$ )

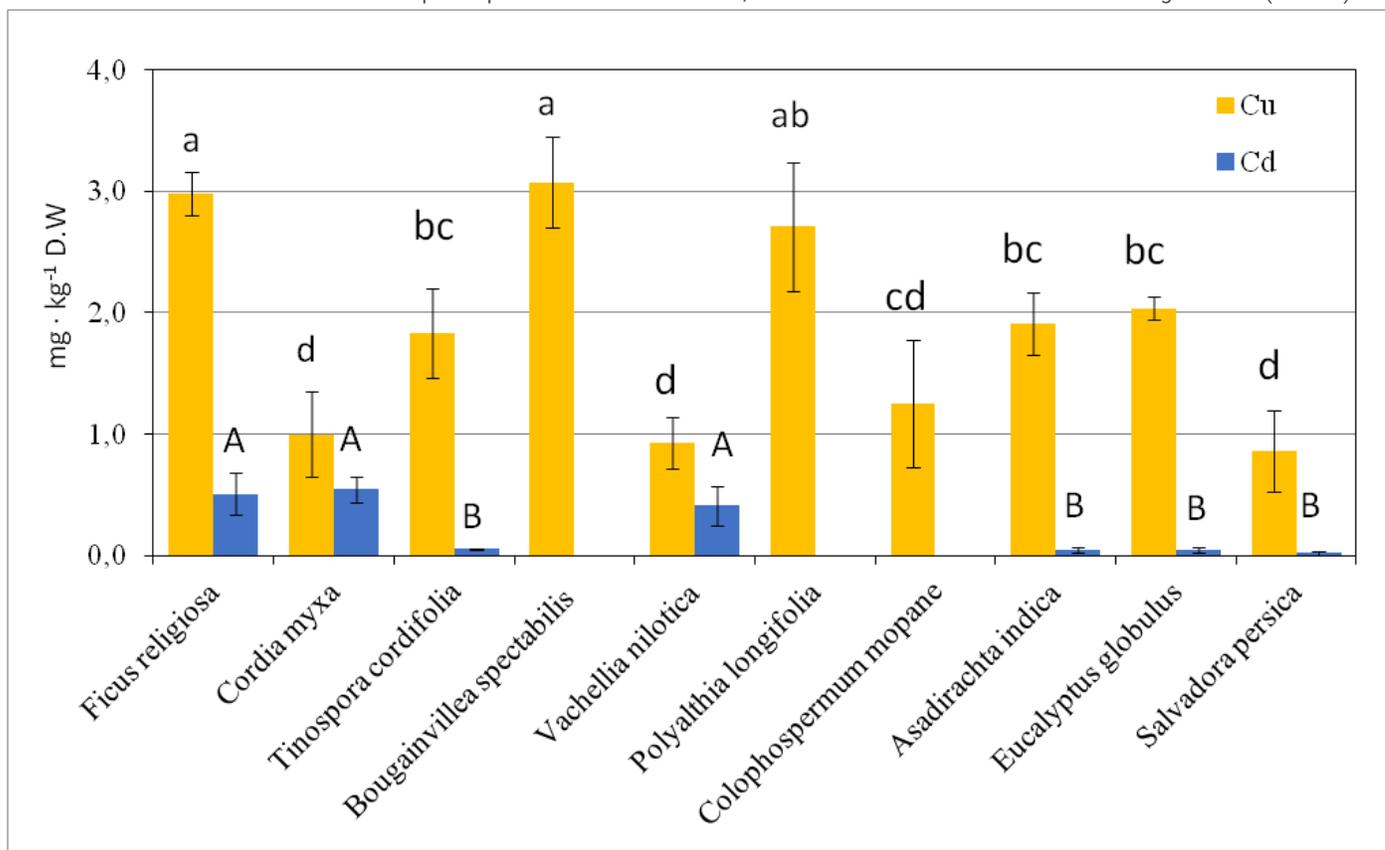


Figure 3

Concentrations of Cu and Cd in the foliage of 10 plant species. Data are mean  $\pm$ SE, n = 2. Different lowercase letters for Cu and capital letters for Cd indicate a statistical significance ( $P < 0.05$ ) between species separately for each heavy metal.

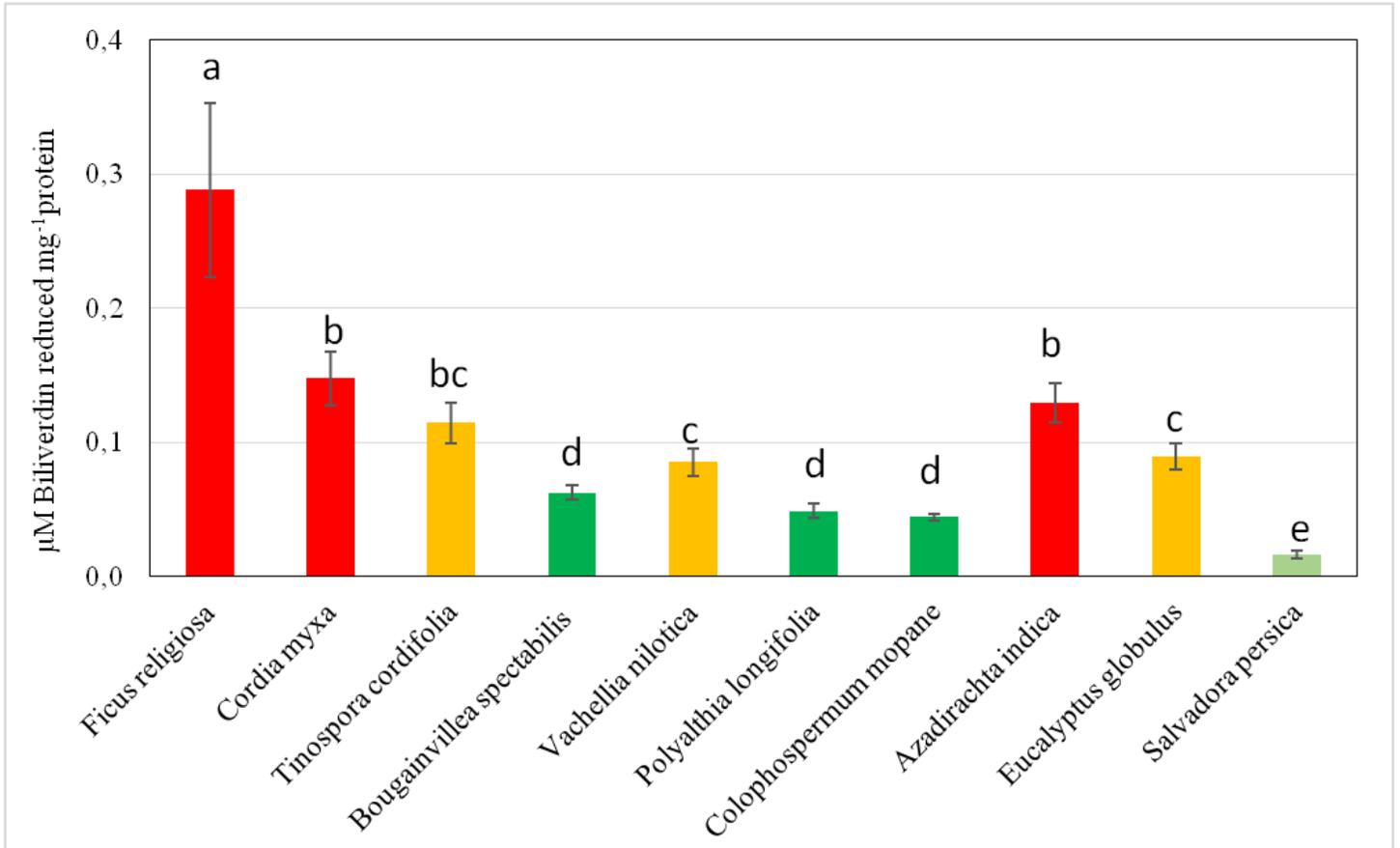


Figure 4

Heme oxygenase activity in the leaves of 10 plant species. Data are means  $\pm$ SE, n = 3. Different letters indicate a statistical significance ( $P < 0.05$ ).