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Strategies of urban trees for mitigating salt stress: a case study of eight plant species

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Abstract

Key message Some species synthesize larger amounts of polyphenols, which probably increase the plant's ability to mitigate salt stress. Salt stress does not cause macronutrient deficiency in the leaves of urban trees. Ionic imbalance in the leaves caused by soil salinity worsens the health status of sensitive species.

Abstract Street trees are exposed to relatively high stress levels, and the average lifespan of street trees is shortened compared to those of trees living under controlled natural conditions. Soil salinity adversely affects trees at all stages of growth and development. This study attempts to determine how the urban environment, with particular emphasis on salt stress, affects tree species with different levels of salinity sensitivity. The aim of this study was to identify the strategies of eight tree species for mitigating salt stress based on the determination of the chemical composition of the macroelements in the leaves, the ionic imbalance, and the ability of the trees to synthesize and accumulate polyphenols in the leaves. The obtained results suggest that individual species implemented different strategies in response to salt stress. The low sensitivity species: *Q. rubra*, *R. pseudoacacia*, *G. triacanthos* and *A. campestre* blocked the uptake of Cl and Na to the leaves. The medium-sensitivity species: *P. x hispanica* blocked the uptake of Cl and Na and *G. biloba* maintained very high contents of Cl and Na in its leaves without leaf damage and synthesized large amounts of polyphenols. *G. triacanthos* and *A. campestre* synthesized large amounts of polyphenols. The high-sensitivity species (*T. x euchlora* and *A. platanoides*) exhibited very high contents of Cl and Na in their leaves, which were significantly damaged and had a pronounced ionic imbalance. These effects were not compensated for by the increased synthesis of polyphenols. In conclusion, the accumulation of polyphenols in leaf tissue may be one of the strategies that increase the resistance of plants to salt stress. Plants have many other methods of mitigating salt stress.

Keywords Urban trees · Salt stress · Polyphenol · Ionic balance · Macronutrients

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Introduction

Sustainable cities depend on urban green infrastructure and its ecological functions. Urban green infrastructure, such as parks, forests, street trees, green roofs, gardens, and cemeteries, is especially important in the urbanized

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world, as it is the main carrier of ecosystem services and improves the quality of life for urban residents (Breuste et al. 2013; Lee and Song 2019). However, trees remain the largest component of urban greenery in most cities. Trees not only beautify the landscape but often play a major role in moderating the environmental impact of urban settlements (Seamans 2013). The Economics of Ecosystems and Biodiversity report identifies 16 types of ecosystem services associated with urban greenery (TEEB 2011). The benefits and uses of urban forests and trees are: (i) cultural, (ii) social, (iii) esthetic and architectural, (iv) climatic and physical, (v) related to carbon storage and sequestration, (vi) ecological, and (vii) economic (Dadvand et al. 2016; Ekkel and de Vries 2017; Nowak et al. 2013; Tyrväinen et al. 2005). Trees in cities are important for their ability to provide ecosystem services. Only healthy and living trees can fulfill these needs. Urban trees, especially those growing along streets, are exposed to many stresses limiting their possibility of performing ecosystem services (Martin et al. 2016; Hallett et al. 2018).

Street trees are exposed to relatively high stress levels, and the average lifespan of these trees is short. The stresses include different agents (Paludan-Müller et al. 2002; Pauleit 2003; Sæbø et al. 2003; Sieghardt et al. 2005; Vogt et al. 2017): aspects of the urban climate, air pollution, constraints and peculiarities of urban hydrological cycles, unfavorable physical soil properties, unbalanced nutrient supply, soil pollution, high pH, limited soil volume, and development of pests and diseases.

Deicing salt, mainly NaCl, has been used on streets and sidewalks in most European countries and in the USA, Canada and Southeast Asia since the 1960s (Pauleit et al. 2002). This treatment not only increases the content of Cl and Na ions in the soil, but also causes a number of adverse soil changes that are unfavorable to trees, such as: alkalization, alteration of soil structure, decreased soil permeability and aeration, intensive erosion, and disturbance of mycorrhizae (Equiza et al. 2017; Ordóñez-Barona et al. 2018). Alternative deicing chemicals, such as potassium formate (KFO; KCOOH) and calcium magnesium acetate (CMA; $\text{Ca}_3\text{Mg}_7(\text{CH}_3\text{COO})_{20}$), may have a less negative impact on the soil, but they are more expensive and may also have an adverse effect on plants (Hanslin 2011).

Soil salinity adversely affects plants at all stages of growth and development. However, assessment of this impact is difficult due to interactions with other environmental factors. The response of woody plants to salinity also depends on the plant's development phase, mainly on the species and variety (Sieghardt et al. 2005). Salinity reduces the osmotic potential in the soil–plant water system and hinders the uptake of water by the roots. This increases the plant energy expenditure associated with osmotic adjustment and results in the inhibition of root

growth and development. Salt stress has been shown to induce a strong reduction in stems and leaves and, ultimately, in the aerial biomass of trees. It also interferes with nutrient uptake, ion transport and metabolites. It is the cause of a reduction in photosynthetic pigment contents and an increase in proline and malondialdehyde (MDA) concentrations (Dąbrowski et al. 2013; Green et al. 2008; Grote et al. 2017; Munns and Tester 2008; Laffray et al. 2018; Plesa et al. 2018; Zhou et al. 2019).

The response to salt stress is a complex process that includes changes in trees at physiological, histological, cellular and molecular levels, as it limits nutrient uptake and disrupts the ionic balance (Cekstere et al. 2008; Dąbrowski et al. 2017; Equiza et al. 2017; Jimenez-Casas and Zwiasek 2014; Kalaji et al. 2018; Malik et al. 2011; Mansour 2013; Mousavi et al. 2019; Munns 2002; Ordóñez-Barona et al. 2018). Salt stress can also increase the susceptibility of trees to pathogen attack (Munck et al. 2010), but Sienkiewicz-Paderewska et al. (2017) have shown that salt stress reduces the number of aphids on the leaves of linden. Chlorine ions are considered more toxic to trees than sodium ions. The Cl content of the leaves is more correlated than the Na content with the degree of leaf damage (Alaoui-Sosse et al. 1998; Kayama et al. 2003; Paludan-Müller et al. 2002). Munns and Tester (2008) found that in the case of trees, sodium ions are retained in the roots and shoots, and only part of the charge reaches the leaves. However, some researchers believe that chlorine and sodium exhibit a similar degree of toxicity to trees (Thornton et al. 1988). According to Cekstere et al. (2008), the main reason for the appearance of leaf necrosis was the additive effect of high concentrations of Na and Cl in leaves; however, it was difficult to separate the Na^+ and Cl^- effects.

Plants use three general strategies for coping with salinity stress: avoidance, tolerance and resistance. The ability to resist stress can be an effect of either avoidance or tolerance or a combination thereof; the general term for this is resistance (Blomqvist 1998). Plant strategies to mitigate salt stress rely on the following:

- The accumulation of compatible compounds, e.g., amino acids (Reddy et al. 2015), mannitol and sorbitol (Wu et al. 2015), glycine betaine (De la Torre-Gonzalez et al. 2018), and polyol (Kobayashi et al. 2013) in the cytoplasm, which, despite reaching high concentrations, do not adversely affect plant metabolism;
- The sequestration of Na^+ and Cl^- into the vacuole (Baetz et al. 2016);
- The induction of antioxidant enzymes (Farhangi-Abriz and Torabian 2017);
- The induction of hormones, including auxins, cytokinins, jasmonate, gibberellins, and gibberellins (Ryu and Cho 2015);

- The participation of phytohormones in many aspects of the plant life cycle, including responses to abiotic stresses such as salt stress. They play a key role in plant responses to the environment with direct bearing on a plant's fitness for adaptation and reproduction. Salinity-induced plant responses can be alleviated or enhanced by exogenous applications or genetic modifications of phytohormone levels through biotechnological tools (Ryu and Cho 2015; Llanes et al. 2018).
- The induction of hormones, including: auxins (Hu et al. 2019), abscisic acid and salicylic acid (Farhangi-Abri and Ghassemi-Golezani 2018), cytokinins (Feng et al. 2018), ethylene (Silva et al. 2014), jasmonate (Moreira et al. 2009), and gibberellins (Al-Taey 2018);
- The involvement of polyamines in modulating antioxidant enzymes (Zhong et al. 2020)
- The increased conversion of xanthophyll pigments for absorption and dissipation of heat, which protects the photosynthetic apparatus against damage caused by salt stress and drought (Baraldi et al. 2019);
- The ability to block Cl and Na uptake and redistribute elements from leaves to other parts of plants (Tester and Davenport 2003; Shelke et al. 2019);
- The presence of ectomycorrhizal fungi, which improve tolerance to salt stress (Zwiazek et al. 2019);
- The presence of genes that can increase salt tolerance by: (i) controlling salt uptake and transport, (i) having an osmotic or protective function, and (i) making a plant grow more quickly in saline soil (Munns 2005; Parihar et al. 2015);
- The synthesis of secondary metabolites that mitigate salt stress, e.g., polyprenols (Milewska-Hendel et al. 2017).

It is believed that polyprenols, representatives of prenyl lipids, can play a particular role in the adaptation of plants to adverse climatic and habitat conditions, thus demonstrating protective action in response to biotic and abiotic stresses (Bajda et al. 2009). Baczevska et al. (2014) suggest a protective role of polyprenols in limiting Cl uptake to tree leaves.

The effect of stressors on the polyprenol biosynthetic machinery has also been elucidated at the molecular level in model *Arabidopsis* plants. To date, three out of nine putative *cis*-prenyltransferases (CPT1-9) identified in the *Arabidopsis* genome have been characterized (Surowiecki et al. 2019). Both in silico and experimental gene expression analyses have revealed an upregulation of AtCPT1 and AtCPT6 transcript levels in *Arabidopsis* seedlings during various environmental stresses (Zimmermann et al. 2004). Further detailed analyses revealed that in *Arabidopsis* hairy roots cadmium chloride decreased the expression of four CPT-encoding genes, CPT1, -2, -6 and -9 and elevated the expression of CPT3 and -7. Additionally, sorbitol caused diverse changes in the expression of CPT-encoding genes;

namely, the expression of CPT3, CPT6, and CPT7 was induced, while that of CPT1, CPT2, and CPT9 was reduced considerably (Jozwiak et al. 2017). These data suggest that environmental clues might modulate the content of polyprenols by affecting the biosynthesis of polyisoprenoid at transcriptional level".

Milewska-Hendel et al. (2017) suggest that tree defensive strategies against salt stress may rely on increasing the synthesis of polyprenols, which might act as scavengers of reactive oxygen species and/or modulate the transport and deposition of chloride and sodium in the leaf cells and change the chemical composition of pectin and AGPs in the cell walls. These results may be associated with the health status of trees, which suggests that the adaptation of trees to salinity can be characterized by different chemical compositions of the cell walls.

This study attempts to determine how the urban environment, with particular emphasis on salt stress, affects tree species with different levels of salinity sensitivity. City trees are exposed to much stress. It is difficult to include many of them in one experiment but there are publications in which it succeeds (e.g. Laffray et al. 2018; Baraldi et al. 2019). Literature data and own research indicate that soil salinity caused by winter slipperiness is an important stress factor for street trees in cities of northern Europe and America. The aim of this study was to identify the strategies of eight tree species for mitigating salt stress based on the determination of the chemical composition of leaves, ionic imbalance, and the ability of the trees to synthesize and accumulate polyprenols in the leaves.

Materials and methods

Eight tree species commonly planted in European and North American cities were included in the study: *Acer campestre* L., *A. platanoides* L., *Ginkgo biloba* L., *Gleditsia triacanthos* L., *Platanus xhispanica* Mill., *Quercus rubra* L., *Tilia xeuclora* K. Koch., and *Robinia pseudoacacia* 'Umbraculifera'. Hereafter, the abbreviated name *R. pseudoacacia* will be used.

Study area

The research was performed in two types of locations: in center of Warsaw (a: between 52°15'26" N 20°59'03" E and 52°12'10" N 20°59'16" E) and the suburbs of Warsaw (b: 52°06'27" N 21°05'42" E):

- The street trees were located in the city center on main streets with a very high intensity of traffic. The roads were intensely deiced in the winter. The soils at all locations were anthropogenic and showed alkaline

reactions and a high abundance of Cl and exchangeable Ca, K and Na (Dmuchowski et al. 2011b). Warsaw was almost completely destroyed during World War II; therefore, the soil is largely mixed with building rubble. This and the fact that the areas surrounding the trees were covered with concrete slabs made it impossible to take a representative soil sample. The trees grew in areas covered with pavement at a distance of 1.5 m from the street. The space occupied by one tree, separated from the next tree by pavement, was only 1.5 m².

- (b) The control trees were growing in the Botanical Garden of the Polish Academy of Sciences in Powsin, Warsaw. This region includes agro-forest areas on the southern outskirts of Warsaw, away from local emission sources and traffic routes.

Sampling

The leaf samples from all the locations were separately collected in mid-July from eight 25- to 30-year-old trees. The leaves were collected from the outer belt of the tree crown around its full perimeter at a height of approximately 3–4 m. Forty leaves were collected from each side of the trees and mixed to make one sample.

Health condition of the leaves

The health condition of the trees was assessed in the same way for all the species at all locations tested. Each tree was assessed separately, based on a health assessment of the leaves. Leaf damage was evaluated on a six-level scale where “0” indicates that the leaves had no damage; “1” indicates that damage covered up to 10% of the leaf surface; “2” indicates that damage covered 10–25%; “3” indicates that damage covered 25–50%; “4” indicates that damage covered 50–75%; and “5” indicates that damage covered over 75%. The observations were made in mid-September. During the collection of samples for chemical analyses in mid-July, the damage to the leaves was still insignificant; therefore, the later date was chosen, at which point there were clear differences between the studied tree species.

Chemical analyses of the leaves

The harvested leaves were placed in linen sacks, brought to the laboratory and dried for 12 h at 70 °C. The dried leaves were ground to powder using an impact mill (Fritsch 14,702, Germany).

After mineralization of the dry leaves in a muffle furnace (Naberthern L40/11/P320, Germany) (Allen et al.

1974), metals (Ca, K, Mg, Na) and P were determined by atomic spectrophotometry using a Perkin Elmer 1100B (Perkin Elmer, Germany). The weight of the leaf sample was 2 g. Cl was determined by potentiometric titration using an ion-selective electrode and Orion Star Plus ion meter (Thermo Scientific, USA) (LaCroix et al. 1970). S was determined using a LECO 132 elemental analyzer (Leco Corporation, USA). N was determined by the Kjeldahl method using a Foss Tecator (Foss Polska). When determining N, Cl, and S, the sample weight was 0.5 g.

The content of organic acids was calculated in accordance with the method proposed by Tuil et al. (1964) as the difference between the sum of the cations and the sum of the anions. The results were expressed in mEq/100 g of dry weight of leaves and calculated according to the following formulas:

$$\text{organic acids} \left(\sum_K - \sum_A \right) = R - \text{COO}^-,$$

$$\text{sum of cations} \sum_K = \text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+ + \text{Na}^+,$$

$$\text{sum of anions} \sum_A = \text{H}_2\text{PO}_4^- + \text{SO}_4^{2-} + \text{Cl}^-.$$

The indicator of the ionic balance in the leaves of the trees was calculated as the ratio of the sum of the organic acid to the sum of the mineral anions expressed in chemically equivalent values (De Wit et al. 1963; Tuil et al. 1964; Brogowski et al. 2000).

The N content was omitted in the calculations due to the traces of nitrates (NO₃⁻) in the tree leaves.

This ratio is considered a good indicator of ion balance in plants (De Wit et al. 1963; Devitt et al. 2014).

To provide quality control (QC), the elemental content in the plant samples was determined using certified reference materials, including apple leaves (1515) from the National Institute of Standards and Technology (USA) and beech leaves (ERM100) from the European Reference Materials. The obtained results were in close agreement with the certified values. The recovery range (comparisons of measured and certified concentrations of elements in the plants in the certified reference material) was 94.1–107.1% for all the elements.

Qualitative and quantitative analysis of polyphenols

For the polyphenol determination, samples of the dry leaf powder were subjected to extraction, and the extracts were supplemented with an internal standard (Pren-12 for *G. biloba* and Pren-15 for the rest of the studied tree

species). The lipids were purified as previously described by Skorupinska-Tudek et al. (2008). We used a combination of linear gradient mixtures of solvent A (90% methanol in water, v/v) and solvent B (50% methanol, 25% hexane and 25% isopropanol, v/v/v) at a flow rate of 1.5 mL min⁻¹; the analysis time was 25 min. Other HPLC/UV conditions were consistent with those of the previously described methods of Skorupinska-Tudek et al. (2008) and Jozwiak et al. (2013). Polyprenols were identified by comparing their retention times and absorption spectra with the corresponding parameters of standard substances (by the use of an external standard). The quantitative and qualitative analyses of the polyprenols were performed using HPLC/UV with a Waters UV detector (Waters 2487) as previously described (Baczewska et al. 2014). The separated polyprenols were identified by comparison of the retention times and absorption spectra with external standards of a polyprenol mixture from the Collection of Polyprenols, Institute of Biochemistry and Biophysics of the Polish Academy of Sciences, Warsaw. Chromatograms were integrated via the program Empower Pro. The content of the identified compounds was estimated with the aid of an internal standard (Prenol-15) and expressed as milligrams per gram of dry weight of plant tissue. The results are the means of three independent analyses.

To provide quality control, additional analyses were performed for plant material with well-characterized polyprenol content and spectra (photosynthetic tissue of *Sorbus intermedia*, *Nicotiana tabacum* and *Picea abies*). The obtained results were consistent with previously published data (Jozwiak et al. 2013).

Statistical analysis

For the studied variables, the means and standard deviations were calculated. Statistical comparisons of the means were conducted using two-way analysis of variance (factors: species and location) and Tukey's post hoc test. The correlation coefficients were used for the evaluation of the relationships between pairs of variables. Moreover, principal component analysis (PCA) was conducted for the evaluation of the multivariate relationships between the variables and for the multivariate evaluation of the objects (species and locations). For all the analyses, the significance level was set at 0.05. The analyses were performed using Statistica 13 software.

Results

The assessment of the health condition of the trees was made on the basis of the health evaluation of the leaves (Table 1). The leaves of the trees of all the examined species growing

in the control area had no damage during the entire growing season. During the leaf sample collection for chemical analysis in mid-July, only slight damage to the leaves was evident in *T. xeuchlora* and *A. platanoides*. In mid-September, *T. xeuchlora* leaves had a most damage index of 5.0 and *A. platanoides*, with a damage index of 2.8. Both of these species were also found to be sensitive to soil salinity due to NaCl by other authors (see Table 5). In mid-September, *P. xhispanica* and *G. biloba* had slightly damaged leaves (damage indexes of 0.47 and 0.23, respectively), and in *A. campestre*, *G. triacanthos*, *Q. rubra* and *R. pseudoacacia*, the leaves were undamaged.

The studied tree species were characterized by varied sensitivity to urban conditions, especially to soil salinity, which was reflected in the large variation in the chemical composition of the leaves (Tables 2, 3 and 4). Among all the species, the leaves of the control trees contained significantly less Cl than the street tree leaves. The highest amounts of Cl were found in the leaves of *T. xeuchlora* (1.49%), *G. biloba* (1.48%) and *A. platanoides* (1.43%) from the street, and the lowest amounts of Cl were found in *Q. rubra* (0.08%) and *G. triacanthos* (0.13%). In the control trees, the Cl content in the leaves ranged from 0.06% in *Q. rubra* to 0.28% in *T. x euchlora*. The Na content in the leaves of the control trees in all the species was not very diverse (18.6–59.2 mg kg⁻¹); however, the quantities in the street trees were different. The average Na content in the leaves of two species was much higher and more varied than that in the other species: *T. xeuchlora*—1294 mg kg⁻¹ and *G. biloba*—1088 mg kg⁻¹ (range 724–1269 mg kg⁻¹). The Na content was significantly lower in the other species in the street location, with values ranging from 41.7 mg kg⁻¹ in *A. campestre* to 88.4 mg kg⁻¹ in *A. platanoides*. The leaves of the street trees in all the studied species contained significantly more Cl and Na than those of the control trees. The differences in Cl leaf content between the locations showed significance for all species. The statistical analysis of the comparisons between

Table 1 Polyprenols identified in the leaves and the leaf damage index of the tree species studied were calculated in mid-September

Species	Leaf damage index	Polyprenol mixture composition
<i>A. campestre</i>	0	Pren-10,-11,-12,-13
<i>A. platanoides</i>	2.8	Pren-10,-11,-12,-13
<i>G. biloba</i>	0	Pren-15,-16,-17,-18,-19,-20,-21,-22,-23
<i>G. triacanthos</i>	0	Pren-10,-11,-12,-13
<i>P. xhispanica</i>	0.47	Pren-9,-10,-11,-12
<i>Q. rubra</i>	0.25	Pren-9,-10,-11
<i>R. pseudoacacia</i>	0	Pren-9,-10,-11
<i>T. xeuchlora</i>	5.0	Pren-9,-10,-11,-12

Table 2 The content of Cl, Na, ionic balance index and sum of prenyl lipids (means and SDs, $n=8$) in leaves of trees and their comparisons between different locations (separately for each species) based on analysis of variance and Tukey's test (different letters mean statistically significant differences between locations)

Species	Location	Cl		Na		R-COO ⁻ /∑Anions		∑ prenyl lipids	
		(%)	SD	mg kg ⁻¹	SD		SD	mg g ⁻¹	SD
<i>A. campestre</i>	Street	0.43b	0.07	41.7b	12.02	2.50a	0.23	5.62b	1.07
	Control	0.22a	0.05	26.6a	6.50	2.72a	0.18	0.53a	0.13
<i>A. platanoides</i>	Street	1.43b	0.12	88.4b	11.75	1.89a	0.51	1.32b	0.16
	Control	0.26a	0.04	29.0a	7.39	7.88b	0.99	0.23a	0.06
<i>G. biloba</i>	Street	1.48b	0.27	108.8b	193	3.80a	1.44	11.80b	1.48
	Control	0.08a	0.02	20.6a	5.78	13.65b	3.35	4.25a	0.58
<i>G. triacanthos</i>	Street	0.13b	0.02	45.1b	5.86	9.90a	1.21	12.78b	3.33
	Control	0.08a	0.02	26.0a	8.02	9.98a	0.73	8.96a	1.31
<i>P. xhispanica</i>	Street	0.93b	0.11	55.9b	10.06	2.01a	0.43	0.58a	0.14
	Control	0.09a	0.02	18.6a	2.40	9.72b	0.94	1.96b	0.46
<i>Q. rubra</i>	Street	0.08b	0.03	63.4b	18.85	0.25a	0.03	1.14b	0.16
	Control	0.06a	0.01	21.8a	3.55	0.32b	0.06	0.76a	0.17
<i>R. pseudoacacia</i>	Street	0.35b	0.07	45.9b	7.46	6.72a	1.42	0.27a	0.05
	Control	0.08a	0.02	18.9a	3.68	6.77a	1.35	1.11b	0.29
<i>T. x euchlora</i>	Street	1.49b	0.57	129.4b	131	3.07a	1.90	9.99b	2.31
	Control	0.28a	0.09	59.2a	26.82	10.60b	1.03	6.15a	0.90

Table 3 The macronutrients (means and SDs, $n=8$) contents in leaves of trees and their comparisons between different locations (separately for each species) based on analysis of variance and Tuk-

ey's test and p-values based on ANOVA (different letters mean statistically significant differences between locations)

Species	Location	N		S		P		K		Ca		Mg	
		(%)	SD	(%)	SD	(%)	SD	(%)	SD	(%)	SD	(%)	SD
<i>A. campestre</i>	Street	1.68a	0.17	0.17a	0.01	0.16a	0.02	0.91a	0.13	0.12a	0.02	1.43a	0.16
	Control	2.36b	0.14	0.20b	0.01	0.32b	0.08	1.14b	0.17	0.24b	0.07	1.38a	0.23
<i>A. platanoides</i>	Street	2.12a	0.13	0.19a	0.01	0.22a	0.06	1.25b	0.13	0.15a	0.04	1.66a	0.24
	Control	1.91a	0.30	0.18a	0.03	0.31b	0.04	1.25b	0.17	0.23b	0.04	1.45a	0.18
<i>G. biloba</i>	Street	2.25b	0.14	0.17b	0.01	0.25b	0.02	2.17b	0.30	0.17a	0.03	1.92b	0.23
	Control	1.47a	0.16	0.13a	0.03	0.16a	0.02	0.88a	0.13	0.21b	0.02	1.38a	0.19
<i>G. triacanthos</i>	Street	3.29b	0.40	0.23b	0.02	0.35b	0.05	1.32b	0.16	0.15b	0.02	1.95b	0.29
	Control	2.16a	0.33	0.19a	0.04	0.24a	0.05	1.11a	0.15	0.09a	0.02	0.77a	0.11
<i>P. xhispanica</i>	Street	2.64b	0.19	0.21b	0.02	0.29c	0.02	1.11b	0.15	0.20b	0.04	1.06ab	0.13
	Control	2.08a	0.26	0.16a	0.03	0.23b	0.03	0.95a	0.15	0.17ab	0.03	0.95a	0.15
<i>Q. rubra</i>	Street	2.14a	0.20	0.18a	0.02	0.23a	0.02	1.24b	0.05	0.12a	0.03	1.19a	0.22
	Control	2.12a	0.24	0.18a	0.02	0.23a	0.03	0.95a	0.10	0.13a	0.03	1.06a	0.14
<i>R. pseudoacacia</i>	Street	3.97a	0.18	0.27a	0.03	0.44a	0.02	1.92a	0.21	0.17b	0.01	1.83b	0.26
	Control	4.54b	0.20	0.32b	0.02	0.50b	0.02	1.77a	0.20	0.14a	0.02	1.03a	0.06
<i>T. x euchlora</i>	Street	2.60a	0.41	0.21a	0.02	0.26a	0.04	1.45a	0.53	0.29a	0.09	1.99a	0.40
	Control	3.17b	0.29	0.24b	0.03	0.38b	0.07	1.84a	0.46	0.35a	0.05	2.05a	0.20

the species in the same locations indicated that no significant differences in the content of Cl in *G. biloba*, *G. triacanthos*, *P. x hispanica*, *Q. rubra* and *R. pseudoacacia* leaves were found in the control region. *A. campestre* leaves contained less Cl than *A. platanoides* leaves and *T. x euchlora* leaves contained the most Cl. The content of Na was significantly lower in the leaves of the control trees than in the leaves of all of the street trees species.

The same analysis for the street trees allowed us to identify the Cl content in the leaves of 3 groups. The group with the lowest Cl content included *G. triacanthos*, and *Q. rubra*, the group with the moderate Cl content included *R pseudoacacia*, *A. campestre* and *P. xhispanica*, and the group with the largest Cl content included *T. x euchlora*, *G. biloba* and *A. platanoides*.

Table 4 The ratios of macronutrients (means and SDs, $n=8$) in leaves of trees and their comparisons between different locations (separately for each species) based on analysis of variance and Tukey's test and p values based on ANOVA (different letters mean statistically significant differences between locations)

Species	Location	N/P		N/K		N/Ca		N/Mg	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>A. campestre</i>	Street	10.71b	1.93	1.89a	0.34	14.09b	3.04	1.19a	0.20
	Control	7.79a	2.17	2.12ab	0.39	10.85a	3.40	1.76b	0.40
<i>A. platanoides</i>	Street	10.18a	2.34	1.71a	0.28	15.17b	3.74	1.30a	0.19
	Control	6.21a	1.18	1.55a	0.29	8.34a	1.50	1.34ab	0.30
<i>G. biloba</i>	Street	9.10a	0.12	1.05a	0.17	13.25b	2.04	1.18a	0.11
	Control	9.53a	1.26	1.70b	0.31	7.03a	1.25	1.07a	0.16
<i>G. triacanthos</i>	Street	9.61a	1.63	2.51b	0.32	22.33a	3.60	1.73a	0.36
	Control	9.17a	0.60	1.96a	0.27	24.33b	6.50	2.86b	0.54
<i>P. xhispanica</i>	Street	9.11a	0.08	2.41b	0.36	13.83a	2.86	2.52b	0.38
	Control	9.10a	0.16	2.24b	0.47	12.27a	1.64	2.23ab	0.41
<i>Q. rubra</i>	Street	9.29a	0.28	1.71a	0.12	18.88a	4.64	1.85a	0.44
	Control	9.07a	0.13	2.26b	0.34	17.35a	3.70	2.04a	0.35
<i>R. pseudoacacia</i>	Street	9.11a	0.07	2.09a	0.21	24.05a	2.02	2.20a	0.33
	Control	9.09a	0.06	2.59b	0.27	34.02b	5.36	4.42b	0.34
<i>T. x euchlora</i>	Street	10.05a	2.04	2.04a	0.86	9.36a	2.24	1.34a	0.28
	Control	8.45a	1.56	1.81a	0.46	9.26a	1.62	1.55a	0.15

The macroelements (N, S, P, K, Mg and Ca) contents in leaves were not very diverse, and no significant trends could be identified (Tables 3, 4). There were differences between species and locations, but no overall trend could be determined. A similar situation was observed for the N/K, N/Mg and N/Ca ratios (Table 4).

The ion balance indicator in the leaves was calculated as the ratio of the organic acid to the sum of the anions (Table 2). A significant disturbance of the ionic balance caused by salt stress occurs almost exclusively in street trees. The value of this indicator was the lower in all the street tree species than in the control trees, but in the case of *G. triacanthos* and *R. pseudoacacia*, this difference was not significant. The values of this indicator for the street trees varied significantly between species, with values ranging from 0.25 for *Q. rubra* and 1.89 for *A. platanoides* to 9.90 for *G. triacanthos* and 6.72 for *R. pseudoacacia*.

Based on the chromatographic analysis, different compositions of the polyprenol mixtures were identified in the tree leaves independent of their place of growth, i.e., either with exposure to salinity in the street or in the control conditions in the Botanical Garden (Table 1). Long-chain polyprenols have been identified in *G. biloba* leaves (Pren-15–Pren-23) in agreement with the published data from Ibata et al. (1983), while only short-chain polyprenols (Pren-9–Pren-13) were identified in the leaves of the remaining species studied here.

To assess the effect of polyprenol accumulation on the trees, the total polyprenol content was estimated. Statistical analysis of the results showed that the street trees, except *R. pseudoacacia* and *P. xhispanica*, had a significantly higher content of polyprenols in their leaves than

did the controls (Table 2). In the control trees, the polyprenol content ranged from 0.23 mg g⁻¹ in the leaves of *A. platanoides*, 0.53 mg g⁻¹ in *A. campestre* and 0.76 mg g⁻¹ in *Q. rubra* to 6.15 mg g⁻¹ in *T. x euchlora* and 8.96 mg g⁻¹ in *G. triacanthos*. In the street trees, the lowest values were found in *R. pseudoacacia* (0.27 mg g⁻¹), *P. xhispanica* (0.58 mg g⁻¹) and *Q. rubra* (1.14 mg g⁻¹) leaves, and the highest values were found in *G. biloba* (11.80 mg g⁻¹) and *G. triacanthos* (12.78 mg g⁻¹) leaves.

The PCA results showed a very strong positive correlation between the Na and Cl content (Fig. 1). These two elements were strongly negatively correlated with the ratio of R-COO⁻/∑anions (street/control). The ratio of the sum of the polyprenols (street/control) was not correlated with the contents of Na and Cl. The reason for this fact was the large variation in the Cl content in the leaves of the resistant species (*Q. rubra*, *G. triacanthos* and *R. pseudoacacia*), which had a very low content, and in the leaves of *G. biloba*, which had a very high content. The highest values of the ratio with the sum of the polyprenols were observed for *A. campestre*, a species resistant to salinity. *T. x euchlora*, a very sensitive species, had very high leaf Na and Cl contents. The highest values of the ratio of R-COO⁻/∑anions were observed for *G. triacanthos* and *R. pseudoacacia*, while the lowest values were observed for *A. platanoides*, a very sensitive species.

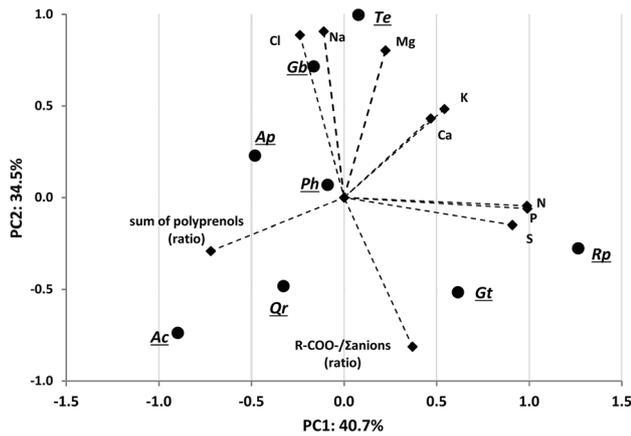


Fig. 1 Results of principal component analysis (PCA) presenting multivariate variability of species as well multivariate relationships between content of elements for street and ratio of R-COO⁻/Σanions and sum of prenyl lipids (values for street were divided by values for control)

Discussion

The reasons for the very large differences in sensitivity to salinity between species and even taxa are not clearly understood (Allen et al. 1994; Ashraf and Harris 2004). Plants have developed many biochemical and molecular mechanisms to adapt to salt stress. Recent studies have identified various adaptive responses to salinity at molecular and cellular levels and metabolic and physiological processes, although the mechanisms underlying salinity tolerance are far from completely understood (Gupta and Huang 2014; Pirasteh-Anosheh et al. 2016; Yokoi and Ray 2002). The biochemical pathways leading to the synthesis of compounds and initiating processes that increase salt tolerance can act additively and probably synergistically (Iyengar and Reddy 1996).

The state of the health of urban trees depends on many factors acting simultaneously which makes identification of the most important factors difficult. Trees in the urban environment are widely exposed to many stress factors: critical water stress, increased soil pH, limited soil volumes, soil compaction, air pollution, deicing salt and many others (Grassi and Magnani 2005; Hermans et al. 2003; Ugolini et al. 2012). However, many authors point to soil salinity as the main cause of poor health and dieback of street trees (e.g., Zimmerman and Jull 2006; Oleksyn et al. 2007; Cekstere et al. 2016; Equiza et al. 2017; Ordóñez-Barona et al. 2018). Therefore, it is important to identify the specific features of individual species that increase tree health in urban stress.

Studies have shown that six species, *A. campestre*, *G. biloba*, *G. triacanthos*, *P. xhispanica*, *Q. rubra* and *R. pseudoacacia*, are characterized by resistance to street conditions

Table 5 Sensitivity of eight studied tree species to soil salinity according to various authors

Species	Tolerance to soil salt		
	Sensitive	Intermediate	Tolerant
<i>A. campestre</i>		7	8,9,12
<i>A. platanoides</i>	1,4,6,7,11,13		2,7
<i>G. biloba</i>	1,5	10	3,6,7,8,9,14
<i>G. triacanthos</i>			1,2,3,6,7,8,9,10,11,12
<i>P. xhispanica</i>	1,5		3,7,8,9,11,12
<i>Q. rubra</i>		10	1,2,6,7,8,9,11,12
<i>R. pseudoacacia</i>			1,2,5,6,7,8,9,11,12
<i>T. x euclhora</i>	2,8,13		

(1) Shortle and Rich (1970); (2) Dirr (1976); (3) Townsend (1984); (4) Barrick and Davidson (1980); (5) Gibbs and Palmer (1994); (6) Johnson and Sucoff (2000); (7) Borowski and Latocha (2006); (8) Bassuk et al. (2009); (9) Appleton et al. (2009); (10) Jull (2009); (11) Dmuchowskiet al. (2013); (12) Šerá (2017); (13) Baczewska et al. (2017); (14) Dmuchowski et al. (2019)

in cities, especially soil salinity. In contrast, *A. platanoides* and *T. xeuclhora* are relatively very sensitive. Table 5 shows the sensitivity of the 8 studied street tree species to soil salinity due to deicing, according to various authors. Information from the table confirms our results from Warsaw. Of the studies on *A. campestre*, only 3 items found in the literature suggest the resistance of this species. *A. campestre* is the most drought resistant (Samson et al. 2017; Schumann et al. 2018), which is accompanied by its high resistance to soil salinity (Appleton et al. 2009; Šerá 2017).

Many studies have shown a positive correlation between the damage index of leaves and their Cl and Na contents (e.g., Appleton et al. 2009; Dmuchowski et al. 2014; Goodrich and Jacobi 2012; Ordóñez-Barona et al. 2018; Paludan-Müller et al. 2002). Reliable data determining the toxic limits of Cl and Na in tree leaves were not found in the literature.

A high content of Cl and Na was also found in *G. biloba* leaves (Cl: 1.48% and Na: 1088 mg·kg⁻¹), which did not have any damage. This species was also considered tolerant by most authors. Similarly, a high content of Cl in *G. biloba* leaves under saline conditions was described by Townsend (1984). Three of the species tested were characterized by extremely low Cl content in the leaves under street conditions: *Q. rubra*, 0.08%; *G. triacanthos*, 0.13%; and *R. pseudoacacia*, 0.35%. Similar values for these three species were found by Dmuchowski et al. (2013). The low content of Cl in leaves can be caused by its accumulation in roots and shoots and limited transport to the leaves (Alaoui-Sossé et al. 1998; Benlloch et al. 1991; Tattini et al. 1993), which may result in low sensitivity to salt stress.

It showed significant differences in the content of Cl in the leaves of street trees of the same genus (*Acer*) with different sensitivity to urban conditions. The species considered to be not very sensitive (*A. campestre*) accumulated three times less Cl in its leaves than the amount that is considered to have an impact on the very sensitive species *A. platanoides*. Leh (1990) and Zimmerman and Jull (2006) classified *A. platanoides* as a sensitive species that collects large amounts of Cl (Gibbs and Palmer 1994; Marosz 2012; Rose and Weber 2011) and *A. campestre* as relatively resistant. In older publications, *A. platanoides* is classified as resistant to salinity (Carpenter 1970; Lumis et al. 1975). This research and newer publications do not confirm this fact (Dmuchowski et al. 2011a; Šerá 2017).

The variation in Na content in the leaves of various species of trees growing in comparatively saline soil is very large, and is significantly greater than that of Cl. The interpretation of the results of the Na content in the leaves of trees is difficult due to the lack of information in the literature about the threshold values of toxicity. Na is characterized by high lability in both the soil and plants, and its excess mostly causes ionic imbalance rather than a simple toxic effect (Alaoui-Sosse et al. 1998; Dmuchowski et al. 2011b). Genc et al. (2015) performed tests separating Cl^+ and Na^+ ions and showed that Na mainly affects plants osmotically and that Cl affects plants osmotically and is toxic to plants. For most trees, the action of Cl^- ions is more important than that of Na^+ in terms of health. The content of Cl in leaves is more correlated with leaf damage than the content of Na (Alaoui-Sosse et al. 1998; Dirr 1976; Storey and Walker 1999). Ziska et al. (1991) and Munns and Tester (2008) found that in the case of trees and shrubs, Na^+ ions are retained in the roots and shoots, and only part of the charge reaches the leaves. Only after exceeding the critical level in the shoots are the ions transported in larger quantities to the leaves. Zhou et al. (2019) found a higher content of Na in the roots as well as Cl mostly accumulated in leaves, suggesting a defense mechanism for Na toxicity through the compartmentalization of this element in the roots. It is possible that such a situation occurred in *T. xeuchlora* and *G. biloba* near the street in Warsaw.

Determining the (N, P, K, Mg, Ca) contents in tree leaves provides a large amount of valuable information about the tree's vitality, nutrition, growth conditions, and threats and may be more valuable than determining the chemical composition of the soil (Cape et al. 1990; Musio et al. 2007; Prietzel et al. 2008). The content of macroelements in tree leaves is shown in Table 3. The results varied, and no significant trends were noted in the content of individual elements in the leaves depending on the species and location. The relationship between salinity and mineral uptake is complex. Salinity may increase, decrease or remain unaffected by the content of elements in plants

(e.g., Bayuelo-Jiménez et al. 2003; Chen et al. 2014; Dmuchowski et al. 2014; Loupassaki et al. 2002; Marosz 2004). The observed differences may be the result of the effect of salinity on the uptake of microelements, which may be due to their availability, ion competitiveness or interferences in transport within the plant (Chen et al. 2001; Grattan and Grieve 1999). A comparison of the obtained results with previously published data indicates that macroelements (N, P, K, Ca and Mg) contents in the leaves of the studied trees was at a level considered "normal" and often optimal. Deficient levels were not found in any of the species at any locations tested (Dauer et al. 2007; De Vries et al. 2000; Dirr 1976; Kopinga and Van den Burg 1995; Mellert and Göttelein 2012; Van den Burg 1974). Similarly, the ranges of the N/P, N/K, N/Mg and N/Ca ratios in the leaves of all the tree species and locations were consistent with those in previously published literature (Flückiger and Braun 2003; Zhou et al. 2019).

Ion imbalance due to salt stress affects plant growth and development (e.g., Green et al. 2008; Loupassaki et al. 2002; Mazher et al. 2007; Serrano and Rodriguez-Navarro 2001). However, in the vast majority of studies, the content of elements in plants is given in units of weight (e.g., mg/kg and %), which is a great simplification. Chemicals and ions react with each other not in equal weight proportions but in equivalent proportions depending on the atomic or ionic mass and valence. This fact significantly limits the possibility of discussing our own results with those of other studies.

The ratio of the sum of the organic acids to the sum of the mineral anions expressed in chemically equivalent values is considered an appropriate indicator of ionic balance in the leaves of trees. Relatively low ratios may indicate ionic imbalance (Brogowski et al. 2000; De Wit et al. 1963; Tuil et al. 1964). The value of this indicator in the leaves of most of the studied species was significantly lower in the street trees than in the control trees. The largest differences were found in species sensitive to soil salinity and that had damage to the leaves (*T. xeuchlora* and *A. platanoides*), which may indicate a significant disturbance of the ionic balance, resulting in deterioration of leaf health. In the second resistant species of the genus *Acer* (*A. campestre*), the differences between locations occurred but were statistically insignificant. This may be the reason for differences in resistance between both species. The leaves of *G. biloba* and *P. xhispanica*, species resistant to soil salinity despite large differences in the balance index values between locations, were characterized by good health without significantly damaged leaves. The research program does not allow us to explain this, and additional research is needed. In the resistant species *G. triacanthos* and *R. pseudoacacia*, there were no significant differences between locations.

Short-chain polyprenols (Pren-9–Pren-13) have been identified in the leaves of various plant species, and these

mixtures usually contain 3–4 homologues (Roslinska et al. 2002; Swiezewska et al. 1994). Seven of the studied tree species except *G. biloba* had such a set of polyphenols. Eight polyphenols (Pren-15–Pren-23) have been identified in *G. biloba*. The same homologues in *G. biloba* leaves were also identified by van Beek and Montoro (2009) and Wang et al. (2015). However, we have no reason to say that this unusual set of polyphenols for trees causes the low sensitivity of this species to salt stress. This problem requires additional research. An additional criterion when determining the species response to salinity was the content of polyphenols in leaves. The role of these compounds in the adaptation to adverse habitat conditions as well as biotic and abiotic stress has been postulated (Bajda et al. 2009; Skorupińska-Tudek et al. 2008). Data on the impact of salt stress on the content of polyphenols in tree leaves are quite limited (Baczewska et al. 2014; Milewska-Hendel et al. 2017). These studies suggest that polyphenols mitigate salt stress by blocking the transport of Cl^- ions to leaves and changing the structure and the chemical composition of cell walls.

In this study, significant quantitative differences between the species and locations of the trees were noted. The leaves of the street trees of two species, *R. pseudoacacia* and *P. xhispanica*, contained fewer polyphenols than the control trees did, which indicates the lack of influence of these compounds on the mitigation of salt stress. The leaves of *G. triacanthos* and *Q. rubra* grown near the street contained only approximately 30% more polyphenols than were found in the control. This may indicate a certain, but not decisive, property in mitigating salt stress.

Ginkgo biloba leaves from the street trees contained very high levels of polyphenols (11.8 mg g^{-1}), and this amount was three times higher than that in the control. This may indicate that the ability to synthesize polyphenols under conditions of salt stress determines the high resistance of this species to soil salinity. Research by Dmuchowski et al. (2019) has shown that in urban conditions the increasing amount of Cl in *G. biloba* leaves was accompanied by an increase in the amount of polyphenols, and the leaves could remain beige without damage. In other studies, the exceptionally low sensitivity of *G. biloba* to salt stress was explained by increased photosynthetic intensity with moderate amounts of NaCl in the soil, increased free leaf proline content, and high antioxidant activity, reducing the content of free radicals and reactive oxygen species in the leaves (Ellnain-Wojtaszek et al. 2002; Liu et al. 2006; Park et al. 2000; Zahrádníková et al. 2007).

The comparison of the polyphenol content in the urban tree leaves of two *Acer* species with different sensitivities to urban conditions showed significant differences. In the leaves of the street trees, the total polyphenol content found in the leaves of the resistant species, *A. campestre*, was more than four times higher than that in the leaves of the

sensitive species, *A. platanoides*. *A. campestre* street leaves contained far lower amounts of Cl and Na than did *A. platanoides* leaves. *A. campestre* synthesized larger amounts of polyphenols, which probably have the ability to mitigate salt stress. The leaves of *T. xeuchlora* street trees were found to be sensitive to salt stress and contained higher levels of polyphenols than those of the control trees. Baczewska et al. (2014) studied *T. xeuchlora* and suggested that polyphenols may reduce the uptake of Cl to leaves. This study suggests that an increase in polyphenol content in the leaves of street trees of this species is not able to mitigate salt stress. *T. xeuchlora* is thought to be the most sensitive of the species studied.

Conclusions

The range of influence of salt stress on plants is very wide. Our research was limited to the study of the effect of salt on the contents of Na, Cl, macronutrients and polyphenols and the ion balance index in the leaves of trees. However, testing in two significantly different locations: a street environment in the city center with all possible inconveniences for trees, and a relatively favorable location for urban trees in the suburbs, allowed us to expand our knowledge about the causes of such a diverse response of different species to salt stress.

The results obtained suggest that individual species implement different strategies in response to salt stress. The study summary is presented in Table 6. In addition to the absolute values, the classification was also determined by the differences between the street locations and the control.

The species studied can be ranked in terms of sensitivity to salt stress as follows:

The least sensitive species

- *Quercus rubra* and *R. pseudoacacia* ‘Umbraculifera’ block the uptake of Cl and Na by leaves in the absence of an increase in polyphenol synthesis/accumulation and in the absence of ionic imbalance in the leaves.
- *Gleditsia triacanthos* blocks the uptake of Cl and Na by leaves, with an increase in polyphenol synthesis/accumulation.
- *Acer campestre* has a relatively low content of Cl and Na. The street trees of this species synthesize significant amounts of polyphenols.
- *Ginkgo biloba* has very high content of Cl and Na in its leaves but does not show leaf damage. This species synthesizes large amounts of polyphenols. Some disturbance of the ionic balance does not lead to a reduction in resistance.

Table 6 Response of tested trees species to salt stress

Species	Blocking leaf transport Cl ^a	Blocking leaf transport Na ^a	Polyprenol content ^b	Deficiency essential nutrients	Ionic balance ^c
<i>Q. rubra</i>	+++	+	0	0	0
<i>R. pseudoacacia</i>	++	+	0	0	0
<i>G. triacanthos</i>	+++	+	++	0	0
<i>P. × hispanica</i>	+	+	0	0	+
<i>G. biloba</i>	--	--	++	0	+
<i>A. campestre</i>	+	+	+	0	0
<i>A. platanoides</i>	--	-	+0	0	++
<i>T. xuechloa</i>	--	--	+	0	++

0: no effect

^aBlocking leaf transport- “+”, intensive transport—“-- - blocking

^bHigh ability to synthesize and accumulate polyprenols- “+”

^cIonic imbalance expressed by the ratio of organic acids to the sum of anions- “+”

Medium sensitive species

The sensitivity of trees in the medium-sensitivity category is only slightly higher than that observed for the low-sensitive species, but much lower than that of highly sensitive species.

- *Platanus xhispanica* has a relatively low content of Cl and Na and a slight disturbance of the ionic balance in its leaves. The cause of salinity resistance is not identified.
- *Gingko biloba* has a very high content of Cl and Na in its leaves but does not show leaf damage. This species synthesizes large amounts of polyprenols. Some disturbance of the ionic balance does not lead to a reduction in resistance.

Very sensitive species

Tilia xuechloa and *A. platanoides*, which have very high contents of Cl and Na in their leaves, are significantly damaged, with a pronounced ionic imbalance, and the damage is not compensated for by the increased synthesis of polyprenols.

City trees, especially street ones, are exposed to many factors affecting their health. One of these factors is soil salinity caused by winter deicing of streets and sidewalks. In many cities planted trees belong, predominantly, to saline-sensitive species, what results in their high death rate. Therefore, on the basis of the results of our research, we postulate to significantly increase the amount of trees belonging to the species *Acer campestre* L., *Gleditsia triacanthos* L., *Quercus rubra* L., *Robinia pseudoacacia* ‘Umbraculifera’, planted on the streets where deicing in winter is required. We also confirm that in some cities trees belonging to the species *Gingko biloba* L. and *Platanus x hispanica* Mill, should also be planted in higher numbers. *Tilia x euchloa* K. Koch., and

Acer platanoides L. should be eliminated from new street plantings.

Author contributions statement WD, PB and AHB-D contributed equally to this work. PB carried out the observations of health state of trees and determined the prenyl lipids content in the leaves with AJ. AHB-D and PB carried out the chemical analyses of leaves. DG participated in the statistical analysis. WD, ES, TCh, IS and BG designed and directed the study and revised the manuscript. ES and BG revised the English language of the manuscript. All authors have read and approved the final manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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