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

Wojciech Dmuchowski1 · Paulina Brągoszewska2 · Dariusz Gozdowski2 · Aneta H. Baczewska-Dąbrowska3 · Tadeusz Chojnacki4 · Adam Jozwiak4,5 · Ewa Swiezewska4 · Irena Suwara2 · Barbara Gworek1

Received: 3 December 2019 / Accepted: 1 October 2020 / Published online: 16 October 2020
© The Author(s) 2020

Abstract

Key message Some species synthesize larger amounts of polyprenols, 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 polyprenols 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 polyprenols. G. triacanthos and A. campestre synthesized large amounts of polyprenols. 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 polyprenols. In conclusion, the accumulation of polyprenols 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 · Polyprenol · Ionic balance · Macronutrients

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...
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. 2018; Eckel 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: alkalinization, 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; Ca3Mg7(CH3COO)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 (Sieghart 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 Zwiazek 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 with 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 involvement of polyamines in modulating antioxidative enzymes (Zhong et al. 2020).

- The induction of hormones, including: auxins (Hu et al. 2019), abscisic acid and salicylic acid (Farhangi-Abriz 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 antioxidative 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 (Zhong et al. 2019); 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., Gingko biloba L., Gleditsia triacanthos L., Platanus hispanica Mill, Quercus rubra L., Tilia x euchlora 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):

(a) 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:

\[
\text{organic acids} \left( \sum_\text{K} - \sum_\text{A} \right) = R - \text{COO}^-, \\
\text{sum of cations} \sum_\text{K} = Ca^{2+} + Mg^{2+} + K^+ + Na^+, \\
\text{sum of anions} \sum_\text{A} = H_2PO_4^- + SO_4^{2-} + Cl^-.
\]

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 (NO$_3^-$) 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 polyprenols

For the polyprenol 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/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. x euchlora and A. platanoides. In mid-September, T. x euchlora 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. x hispanica 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. x euchlora (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. x euchlora—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

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

Table 1 Polyprenols identified in the leaves and the leaf damage index of the tree species studied were calculated in mid-September.
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*, *Q. rubra* and *R. pseudoacacia*, the group with the moderate Cl content included *R. pseudoacacia*, *A. campestre* and *P. x hispanica*, and the group with the largest Cl content included *T. x euchlora*, *G. biloba* and *A. platanoides*.

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 mg kg⁻¹ | R- COO⁻/∑ Anions SD | ∑ prenyl lipids mg g⁻¹i SD |
|------------------|----------|--------|-------------|----------------------|---------------------------|
| *A. campestre*   | Street   | 0.43b  | 41.7b       | 3.80a 1.44           | 5.62b 1.07                |
|                  | Control  | 0.22a  | 26.6a       | 7.27a 0.18           | 0.53a 0.13                |
| *A. platanoides* | Street   | 1.43b  | 88.4b       | 1.89a 0.51           | 3.12b 0.16                |
|                  | Control  | 0.26a  | 29.0a       | 7.88b 0.99           | 0.23a 0.06                |
| *G. biloba*      | Street   | 1.48b  | 1088b       | 3.80a 1.44           | 11.80b 1.48               |
|                  | Control  | 0.08a  | 20.6a       | 13.65b 3.35          | 4.25a 0.58                |
| *G. triacanthos* | Street   | 0.13b  | 45.1b       | 9.90a 1.21           | 12.78b 3.33               |
|                  | Control  | 0.08a  | 26.0a       | 9.98a 0.73           | 8.96a 1.31                |
| *P. x hispanica* | Street   | 0.93b  | 55.9b       | 2.01a 0.43           | 0.58a 0.14                |
|                  | Control  | 0.09a  | 18.8a       | 9.72b 0.94           | 1.96b 0.46                |
| *Q. rubra*       | Street   | 0.08b  | 63.4b       | 2.50a 0.03           | 1.14b 0.16                |
|                  | Control  | 0.06a  | 21.8a       | 3.28b 0.06           | 0.76a 0.17                |
| *R. pseudoacacia*| Street   | 0.35b  | 45.9b       | 6.72a 1.42           | 0.27a 0.05                |
|                  | Control  | 0.08a  | 18.9a       | 6.77a 1.35           | 1.11b 0.29                |
| *T. x euchlora*  | Street   | 1.49b  | 1294b       | 3.07a 1.90           | 9.99b 2.31                |
|                  | Control  | 0.28a  | 59.2a       | 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 Tukey’s test and p-values based on ANOVA (different letters mean statistically significant differences between locations)

| Species          | Location | N (%) | S (%) | P (%) | K (%) | Ca (%) | Mg (%) |
|------------------|----------|-------|-------|-------|-------|--------|--------|
| *A. campestre*   | Street   | 1.68a | 0.17  | 0.17a | 0.01  | 0.16a  | 0.02  |
|                  | Control  | 2.36b | 0.14  | 0.20b | 0.01  | 0.32b  | 0.08  |
| *A. platanoides* | Street   | 2.12a | 0.13  | 0.19a | 0.01  | 0.22a  | 0.06  |
|                  | Control  | 1.91a | 0.30  | 0.18a | 0.03  | 0.31b  | 0.04  |
| *G. biloba*      | Street   | 2.25b | 0.14  | 0.17b | 0.01  | 0.25b  | 0.02  |
|                  | Control  | 1.47a | 0.16  | 0.13a | 0.03  | 0.16a  | 0.02  |
| *G. triacanthos* | Street   | 3.29b | 0.20  | 0.23b | 0.02  | 0.35b  | 0.05  |
|                  | Control  | 2.16a | 0.33  | 0.19a | 0.04  | 0.24a  | 0.05  |
| *P. x hispanica* | Street   | 2.64b | 0.19  | 0.21b | 0.02  | 0.29c  | 0.02  |
|                  | Control  | 2.08a | 0.26  | 0.16a | 0.03  | 0.23b  | 0.03  |
| *Q. rubra*       | Street   | 2.14a | 0.20  | 0.18a | 0.02  | 0.23a  | 0.02  |
|                  | Control  | 2.12a | 0.24  | 0.18a | 0.02  | 0.23a  | 0.03  |
| *R. pseudoacacia*| Street   | 3.97a | 0.18  | 0.27a | 0.03  | 0.44a  | 0.02  |
|                  | Control  | 4.54b | 0.20  | 0.32b | 0.02  | 0.50b  | 0.02  |
| *T. x euchlora*  | Street   | 2.60a | 0.41  | 0.21a | 0.02  | 0.26a  | 0.04  |
|                  | Control  | 3.17b | 0.29  | 0.24b | 0.03  | 0.38b  | 0.07  |
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/\(\sum\)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. pseudoacacica), 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 found in 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/\(\sum\)anions were observed for G. triacanthos and R. pseudoacacia, while the lowest values were observed for A. platanoides, a very sensitive species.

### Table 4

| Species | Location | N/P SD | N/K SD | N/Ca SD | N/Mg SD |
|---------|----------|--------|--------|---------|---------|
| A. campestre | Street | 10.71b | 1.93 | 1.89a | 0.34 | 14.09b | 3.04 |
| A. platanoides | Street | 10.18a | 2.34 | 1.71a | 0.28 | 15.17b | 3.74 |
| G. biloba | Street | 9.10a | 0.12 | 1.05a | 0.17 | 13.25b | 2.04 |
| G. triacanthos | Street | 9.53a | 1.26 | 1.70b | 0.31 | 7.03a | 1.25 |
| P. xhispanica | Street | 9.11a | 0.08 | 2.41b | 0.36 | 13.83a | 2.86 |
| Q. rubra | Street | 9.29a | 0.28 | 1.71a | 0.12 | 18.88a | 4.64 |
| R. pseudoacacia | Street | 9.07a | 0.13 | 2.26b | 0.34 | 17.35a | 3.70 |
| T. x euchlora | Street | 10.54a | 1.93 | 1.89a | 0.39 | 14.09b | 3.04 |
| Control | Street | 8.45a | 1.56 | 1.81a | 0.46 | 9.26a | 1.62 |

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).
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 in cities, especially soil salinity. In contrast, A. platanoïdes and T. x euchlora 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. 2013; 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.

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

| Species            | Tolerance to soil salt | Sensitive | Intermediate | Tolerant |
|--------------------|------------------------|-----------|--------------|----------|
| A. campestre       |                        | 7         | 8,9,12       |          |
| A. platanoïdes     |                        | 1,4,6,7,11,13 | 2,7         |          |
| G. biloba          |                        | 1,5       | 10           | 3,6,7,8,9,14 |
| G. triacanthos     |                        | 1,2,3,6,7,8,9,10,11,12 |          | 12       |
| P. xhispanica      |                        | 1,5       |              | 3,7,8,9,11,12 |
| Q. rubra           |                        | 1,2,6,7,8,9,11,12 |          |          |
| R. pseudoacacia    |                        | 1,2,5,6,7,8,9,11,12 |          |          |
| T. x euchlora      |                        | 2,8,13    |              |          |

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⁻/∑anions and sum of prenyl lipids (values for street were divided by values for control)

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

(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) Dmuchowski et al. (2013); (12) Šerá (2017); (13) Baczewska et al. (2017); (14) Dmuchowski et al. (2019)
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. x euchlora 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; Durr 1976; Kopinda and Van den Burg 1995; Mellert and Göttlein 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 Rodríguez-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. x euchlora 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. xhipanica, 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 polyrenols (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 polypropenols. Eight polypropenols (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 polypropenols 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 polypropenols 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 polypropenols in tree leaves are quite limited (Baczewska et al. 2014; Milewska-Hendel et al. 2017). These studies suggest that polypropenols 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. xhispica*, contained fewer polypropenols 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 polypropenols than were found in the control. This may indicate a certain, but not decisive, property in mitigating salt stress.

*Gingko biloba* leaves from the street trees contained very high levels of polypropenols (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 polypropenols 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 polypropenols, 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; Zahradníková et al. 2007).

The comparison of the polypropenol 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 polypropenol 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 polypropenols, which probably have the ability to mitigate salt stress. The leaves of *T. euchlora* street trees were found to be sensitive to salt stress and contained higher levels of polypropenols than those of the control trees. Baczewska et al. (2014) studied *T. euchlora* and suggested that polypropenols may reduce the uptake of Cl to leaves. This study suggests that an increase in polypropenol content in the leaves of street trees of this species is not able to mitigate salt stress. *T. euchlora* 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 polypropenols 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 polypropenol 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 polypropenol synthesis/accumulation.
- *Acer campestre* has a relatively low content of Cl and Na. The street trees of this species synthesize significant amounts of polypropenols.
- *Gingko biloba* has very high content of Cl and Na in its leaves but does not show leaf damage. This species synthesizes large amounts of polypropenols. Some disturbance of the ionic balance does not lead to a reduction in resistance.
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 *hispanica 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 x euchlora* 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 euchlora* 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.

Acknowledgements This investigation was partially supported by the grant from the National Science Centre of Poland [UMO-2018/29/B/NZ3/01033].

Compliance with ethical standards

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

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

---

### Table 6 Response of tested trees species to salt stress

| Species          | Blocking leaf transport Cl | Blocking leaf transport Na | Polyprenol content | Deficiency essential nutrients | Ionic balance |
|------------------|-----------------------------|-----------------------------|--------------------|--------------------------------|---------------|
| Q. rubra         | + + +                       | +                           | 0                  | 0                              | 0             |
| R. pseudoaccacia | + +                         | +                           | 0                  | 0                              | 0             |
| G. triacanthos   | + + +                       | +                           | 0                  | 0                              | 0             |
| P. × hispanica   | +                           | +                           | 0                  | 0                              | 0             |
| G. biloba        | - - -                       | -                           | 0 +                | 0                              | 0             |
| A. campestre     | -                           | -                           | 0 +                | 0                              | 0             |
| A. platanoides   | - - -                       | -                           | 0 +                | 0                              | 0             |
| T. x euchlora    | - - -                       | -                           | 0 +                | 0                              | 0             |

0: no effect

*a* Blocking leaf transport-“+”, intensive transport—“- -” blocking

*b* High ability to synthesize and accumulate polyprenols-“+”

*c* Ionic imbalance expressed by the ratio of organic acids to the sum of anions-“+”
References

Alaoui-Sosse B, Sehmer L, Barnola P, Diezengremel P (1998) Effect of NaCl salinity on growth and mineral partitioning in Quercus robur L., arhythmically growing species. Trees 12:424–430. https://doi.org/10.1007/PL00009726

Allen SE, Grimsha WHN, Parkinson JA, Quarmby C (1974) Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford

Allen JA, Chambers JL, Stine M (1994) Prospects for increasing the yield of forest trees. Tree Physiol 14:843–843. https://doi.org/10.1093/treephys/14.7-8.9.843

Al-Taey DK (2018) The role of GA and organic matter to reduce the salt tolerance of forest trees. Trees 15:186–194. https://doi.org/10.1007/s00468-018-1031-5

Allen SE, Grimsha WHN, Parkinson JA, Quarmby C (1974) Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford

Allen JA, Chambers JL, Stine M (1994) Prospects for increasing the yield of forest trees. Tree Physiol 14:843–843. https://doi.org/10.1093/treephys/14.7-8.9.843

Baczewska AH, Dmuchowski W, Jóźwiak A, Gozdowski D, Baetz U, Eisenach C, Tohge T, Martinoia E, De Angeli A (2016) Tilia ‘Euchlora’). Dendrobiology 72:177–186. https://doi.org/10.12657/denbio.072.015

Ashraf MPIC, Harris PIC (2004) Potential biochemical indicators of salinity tolerance in plants. Plant Sci 166:3–16. https://doi.org/10.1016/j.plantsci.2003.10.024

Baczewska AH, Dmuchowski W, Jóźwiak A, Gozdowski D, Brągoszewska P, Dąbrowski P, Świeżewska E (2014) Effect of salinity on growth and leaves contents of elements and antioxidant in pepper. Plant Arch 18:479–488

Bajda A, Konopka-Postupolska D, Krzymowska M, Hennig J, Skorupinska-Tudek K, Szymczak L., arhythmically growing species. Trees 12:424–430. https://doi.org/10.1007/PL00009726

Bajda A, Konopka-Postupolska D, Krzymowska M, Hennig J, Skorupinska-Tudek K, Szymczak L., arhythmically growing species. Trees 12:424–430. https://doi.org/10.1007/PL00009726

Bajda A, Konopka-Postupolska D, Krzymowska M, Hennig J, Skorupinska-Tudek K, Szymczak L., arhythmically growing species. Trees 12:424–430. https://doi.org/10.1007/PL00009726

Bayuelo-Jiménez JS, Debouck DG, Lynch JP (2003) Growth, gas exchange, water relations, and ion composition of Phaseolus species grown under saline conditions. Field Crops Res 80:207–222. https://doi.org/10.1016/S0378-4909(02)00179-X

Benloch M, Arboleda F, Barranco D, Fernandez-Escobar R (1991) Response of young olive trees to sodium and boron excess in irrigation water. HortScience 26:867–870. https://doi.org/10.21273/HORTSCI.26.7.867

Blomqvist G (1998) Impact of de-icing salt on roadside vegetation: A literature review. Swedish National Road and Transport Research Institute, VTI rapport 427A

Borowski J, Latocha P (2006) Trees and shrubs suitable for street conditions in warsaw and other cities in central Poland. Rocznik Dendrologiczny 54:83–93

Breuste J, Qureshi S, Li J (2013) Applied urban ecology for sustainable urban environment. Urban Ecosyst. 16:675–680. https://doi.org/10.1007/s11252-013-0337-9

Brogowski Z, Zagórski Z, Czarnowska K, Chojnicki J, Pracz J (2000) Influence of salt stress on the chemical composition of tree leaves from the Łódź city area. Soil Sci Ann 51:17–28

Cape JN, Freer-Smith PH, Paterson IS, Parkinson IA, Wolfenden J (1990) The nutritional status of Picea abies (L.) Karst. across Europe, and implications for ‘forest decline.’ Trees 4:211–224

Carpenter ED (1970) Salt tolerance of ornamental plants. Am Nurseryman 131:12–71

Czekstere G, Nikodemus O, Osvalde A (2008) Toxic impact of the de-icing material to street greenery in Riga. Latvia Urban For Urban Green 7:207–217. https://doi.org/10.1016/j.ufug.2008.02.004

Czekstere G, Osvalde A, Vellenweider P (2016) De-icing salt impact on leaves of street trees (Tilia x vulgaris) in Riga. Latvia Acta Biol Univ Daugavpil 16:31–38

Chen Z, Wang W, Liu T (2014) Effects of chemical deicers on the growth and vitality of Lolium perenne L. International Conference of Transportation Professionals, pp 2926–2936. https://DOI:https://doi.org/10.9780784412424.298

Dąbrowski P, Pawlukiewicz B, Kalaji HM, Baczewska AH (2013) The effect of light availability on leaf area index, biomass production and plant species composition of park grasslands in Warsaw. Plant Soil Environ 59:543–548. https://doi.org/10.1016/j.jIEWS.2016.11.031

Dąbrowski P, Kalaji MH, Baczewska AH, Pawlukiewicz B, Mastalerz G, Gorawska-Jarmulowicz B, Paunov M, Golsvev T (2017) Delayed chlorophyll a fluorescence, MR 820, and gas exchange changes in perennial ryegrass under salt stress. J Lumin 183:322–333. https://doi.org/10.1016/j.jlumin.2016.11.031

Dadvand P, Bartoll X, Basaganya X, Dalmau-Bueno A, Martinez D, Ambros A, Cirach M, Truggero-Mas M, Gascon M, Borrell C, Nieuwenhuijzen MJ (2016) Green spaces and general health: roles of mental health status, social support, and physical activity. Environ Int 91:161–167. https://doi.org/10.1016/j.envint.2016.02.029

Daujmer J, Chorover J, Chadwick OA, Oleksyn J, Tjoelker MG, Hobbie SE, Eissenstat DM (2007) Controls over leaf and litter calcium concentrations among temperate trees. Biogeochemistry 86:175–187. https://doi.org/10.1007/s10533-007-9153-8

De la Torre-Gonzalez A, Montesinos-Pereira D, Blasco B, Ruiz JM (2016) Influence of drought and salt stress on the photosynthetic performance of Liquidambar styraciflua L.: understanding tree ecophysiological responses in the urban context. Forests 7:203. https://doi.org/10.3390/f701011032

De Vries W, Reinds GJ, van Kerkvoorde MS, Hendriks CMA, Leeters EEJM, Gross CP, Voogd JCH, Vel EM (2000) Intensive Monitoring of Forest Ecosystems in Europe, Technical Report, EC/UN/ECE 2000. Brussels, Geneva, 191 pp.

De Wit CT, van Kerkvoorde MS, Hendriks CMA, Leeters EEJM, Gross CP, Voogd JCH, Vel EM (2000) Intensive Monitoring of Forest Ecosystems in Europe, Technical Report, EC/UN/ECE 2000. Brussels, Geneva, 191 pp.

De Wint CT, Dijkshoorn W, Nolle JG (1963) Ionic balance and mineral nutrition in tobacco resistance against biotic stresses. Physiol Plant 18:479–488

De Vries W, Reinds GJ, van Kerkvoorde MS, Hendriks CMA, Leeters EEJM, Gross CP, Voogd JCH, Vel EM (2000) Intensive Monitoring of Forest Ecosystems in Europe, Technical Report, EC/UN/ECE 2000. Brussels, Geneva, 191 pp.

De Wint CT, Dijkshoorn W, Nolle JG (1963) Ionic balance and mineral nutrition in tobacco resistance against biotic stresses. Physiol Plant 18:479–488

De Vries W, Reinds GJ, van Kerkvoorde MS, Hendriks CMA, Leeters EEJM, Gross CP, Voogd JCH, Vel EM (2000) Intensive Monitoring of Forest Ecosystems in Europe, Technical Report, EC/UN/ECE 2000. Brussels, Geneva, 191 pp.

De Wint CT, Dijkshoorn W, Nolle JG (1963) Ionic balance and mineral nutrition in tobacco resistance against biotic stresses. Physiol Plant 18:479–488
Dmuchowski W, Bazewska AH, Bragoszewska P (2011) Reaction of street trees to adverse environmental conditions in the centre of Warsaw. Ecol Quest 15:97–105. https://doi.org/10.12775/v1009-011-0041-4

Dmuchowski W, Brogowski Z, Bazewska AH (2011) Evaluation of vigour and health of street trees in Warsaw using the foliar ionic status. Pol J Environ Stud 20:489–496

Dmuchowski W, Bazewska AH, Gazdowski D, Bragoszewska P (2013) Effect of salt stress on the chemical composition of leaves of different trees species in urban environment. Fresenius Environ Bull 22:987–994

Dmuchowski W, Gozdowski D, Bazewska AH, Rutkowska B, Szulc W, Suwara I, Bragoszewska P (2014) Effect of salt stress caused by deicing on the content of microelements in the leaves of linden. J Elem 19:65–79. https://doi.org/10.5601/jelem.2014.19.1.1588

Dmuchowski W, Bragoszewska P, Gazdowski D, Bazewska-Dabrowska AB, Chojnacki T, Joziwacki A, Szwezewska E, Suwara I (2019) Strategy of Ginkgo biloba L. in the mitigation of salt stress in the urban environment. Urban For Urban Green 38:223–231. https://doi.org/10.1016/j.ufug.2019.01.003

Ekkel ED, de Vries S (2017) Nearby green space and human health: Evaluating accessibility metrics. Landsc Urban Plan 157:214–220. https://doi.org/10.1016/j.landurbplan.2016.06.008

Ellnain-Wojtaszek M, Kruczyński Z, Kasprzak J (2002) Variations in leaf ontogeny in ash and oak trees. Plant Cell Environ 28:834–842. https://doi.org/10.1046/j.1365-3090.2001.00973.x

Grassl G, Magnani F (2005) Stomatal, mesophyll conductance and biochemical limitations to photosynthesis as affected by drought and leaf ontogeny in ash and oak trees. Plant Cell Environ 28:834–849. https://doi.org/10.1111/j.1365-3040.2005.01333.x

Grott SR, Grieve CM (1999) Salinity-mineral nutrition relations in horticultural crops. Sci Hortic 78:127–157. https://doi.org/10.1016/S0304-4238(98)00192-7

Green SM, Machin R, Cresser MS (2008) Effect of long-term changes in soil chemistry induced by road salt applications on N transformations in roadside soils. Environ Pollut 152:20–31. https://doi.org/10.1016/j.envpol.2007.06.005

Grote R, Samson R, Alonso R, Amorim JH, Carriñanos P, Churkin G, Fares S, Le Thiec D, Niinemets Ú, Norgaard Mikkelsen T, Paolotti E, Tiwary A, Callafiapetica C (2017) Functional traits of urban trees: air pollution mitigation potential. Front Ecol Environ 15:453–550. https://doi.org/10.1002/fee.1426

Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. Int J Genom. https://doi.org/10.1155/2014/701596

Hallett R, Johnson ML, Sonti NF (2018) Assessing the tree health impacts of salt water flooding in coastal cities: a case study in New York City. Landsc Urban Plan 177:171–177. https://doi.org/10.1016/j.landurbplan.2018.05.004

Hanslin HM (2011) Short-term effects of alternative de-icing chemicals on tree sapling performance. Urban For Urban Green 10:53–59. https://doi.org/10.1016/j.ufug.2010.08.001

Hermans C, Smeyers M, Rodriguez RM, Eyletters M, Strasser RJ, Delhaye JP (2003) Quality assessment of urban trees: a comparative study of physiological characterisation, airborne imaging and on site fluorescence monitoring by the OJIP-test. J Plant Physiol 160:81–90. https://doi.org/10.1016/S0176-1617(00)01306-8

Hu H, Fu Y, Yang Y, Chen S, Ning N (2019) Arabidopsis IAR4 modulates primary root growth under salt stress through ROS-mediated modulation of auxin distribution. Front Plant Sci 10:522. https://doi.org/10.3389/fpls.2019.00522

Ibata K, Mizuno M, Takigawa T, Tanaka Y (1983) Long-chain betulaprenol-type polyprenols from the leaves of Ginkgo biloba. Bioch J 213:305–311

Iyengar ERR, Reddy MP (1996) Photosynthesis in highly salt tolerant plants. In: Pessarakli M (ed) Handbook of photosynthesis. Marshall Dekar, Baten Rose, pp 897–910

Jimenez-Casas M, Zwiezak J (2014) Adventitious sprouting of Pinus leiolepis in response to salt stress. Ann For Sci 71:811–819. https://doi.org/10.1051/forest/20140379-x

Johnson GR, Sucoff E (2000) Minimizing de-icing salt injury to trees. Univ Minn, Extension Service, FO-1413-S

Jozwiak A, Brzozowski R, Bujnowski Z, Chojnacki T, Swiezewska E (2017) Application of supercritical CO₂ for extraction of polyisoprenoid alcohols and their esters from plant tissues. J Supercrit Fluids 137:64–70. https://doi.org/10.1016/j.supcritfluids.2018.06.008

Jull LG (2009) Winter salt injury and salt-tolerant landscape plants. Univ Wisconsin Coop, Ext A, p 3877

Kalaji HM, Račková L, Paganová V, Swoczyna T, Rusinowski S, Sitko A, Calafiapetica C (2017) Functional traits of urban trees: air pollution mitigation potential. Front Ecol Environ 15:453–550. https://doi.org/10.1002/fee.1426

Kayama M, Quoreshi AM, Kitaoka S, Kitahashi Sakamoto Y, Kitao M, Jull LG (2009) Winter salt injury and salt-tolerant landscape plants. Univ Wisconsin Coop, Ext A, p 3877

Koike T (2003) Effects of deicing salt on the vitality and health of street trees planted along roadsides in northern Japan. Environ Pollut 124:127–137. https://doi.org/10.1016/S0269-7491(02)00415-3
Kobayashi Y, Yoshida J, Iwata H, Koyama Y, Kato J, Ogihara J, Kasumi T (2013) Gene expression and function involved in polyl biosynthesis of Trichosporonoides megachiliensis under hyper-osmotic stress. J Biosci Bioeng 115:645–650. https://doi.org/10.1016/j.jbiosc.2012.12.004

Kopinger J, Van den Burg J (1995) Using soil and foliar analysis to diagnose the nutritional status of urban trees. J Arboric 21:17–24

LaCroix RL, Keeney DR, Walsh LM (1970) Potentiometric titration of chloride in plant tissue extracts using the chloride ion electrode. Soil Sci Plant Anal 1:1–6. https://doi.org/10.1002/62700936233

Laffray X, Alaoui-Sehmer L, Bourioug M, Bourgeade P, Alaoui-Sossé B, Aleya L (2018) Effects of sodium chloride salinity on ecophysiological and biochemical parameters of oak seedlings (Quercus robur L.) from use of de-icing salts for winter road maintenance. Environ Monit Assess 190:266. https://doi.org/10.1007/s10661-018-6645-z

Lee DK, Song Y (2019) Urban green infrastructure and the ecological functions. Landsc Ecol Eng 15:241–243. https://doi.org/10.1007/s10661-019-00384-9

Leh HO (1990) Investigations on health conditions of street trees after discontinued use of de-icing salts on streets in Berlin. Nachr Dtsch Pfanzenschutz 42:134–142

Liu CS, Cheng Y, Hu JF, Zhang W, Chen NH, Zhang JT (2006) Comparison of antioxidant activities between salvianolic acid B and Ginkgo biloba extract (EGB 761). Acta Pharmacol Sin 27:1137. https://doi.org/10.1111/j.1745-7254.2006.00378.x

Llanes A, Reginato M, Devinar G, Luna V (2018) What is known about phytohormones in halophytes? A review. Biologia 73:727–742. https://doi.org/10.2478/bs-2017-018-0093-7

Loupassaki MH, Chartzoulakis KS, Digalaki NB, Androulakis II (2002) Effects of salt stress on concentration of nitrogen, phosphorus, potassium, calcium, magnesium, and sodium in leaves, shoots, and roots of six olive cultivars. J Plant Nutr 25:2457–2482. https://doi.org/10.1081/PLN-120014707

Lumis GP, Hofstra G, Hall R (1975) Salt damage to roadside plants. J Arboric 1:14–16

Malik S, Nayak M, Sahu BB, Panigrahi AK, Shaw BP (2011) Response of antioxidant enzymes to high NaCl concentration in different salt-tolerant plants. Biol Plant 55:191–195

Mansour MMF (2013) Plasma membrane permeability as an indicator of salt tolerance in plants. Biol Plant 57:1–10. https://doi.org/10.1007/s10535-012-0144-9

Marosz A (2012) Effect of green waste compost and mycorrhizal fungi on calcium, potassium, and sodium uptake of woody plants grown under salt stress. Water Air Soil Pollut 223:787–800. https://doi.org/10.1007/s11270-011-0902-x

Martin MP, Simmons C, Ashton MS (2016) Survival is not enough: The effects of microclimate on the growth and health of three common urban tree species in San Francisco, California. Urban For Urban Green 19:1–6. https://doi.org/10.1016/j.ufug.2016.06.004

Mazher AAM, Yassen AA, Zaghloul SM (2007) Influence of foliar nutrition on potassium uptake and chemical composition of Bauhinia variegata seedlings under different irrigation intervals. World J Agric Sci 3:23–31

Mellert KH, Göttlein A (2012) Comparison of new foliar nutrient thresholds derived from van den Burg’s literature compilation with established central European references. Eur J For Res 131:1461–1472. https://doi.org/10.1007/s10342-012-0615-8

Milewska-Hendel A, Baczewska AH, Sala K, Dmuchowski W, Bragoszewska P, Godzowski D, Joziawak A, Chojnacki T, Zwiezewska E, Kurczynska E (2017) Quantitative and qualitative characteristics of cell wall components and prenyl lipids in the leaves of Tilia x euchlora trees growing under salt stress. PLoS ONE 12:e0172682. https://doi.org/10.1371/journal.pone.0172682

Moreira X, Sampedro L, Zas R (2009) Defensive responses of Pinus pinaster seedlings to exogenous application of methyl jasmonate: concentration effect and systemic response. Environ Exp Bot 67:94–100. https://doi.org/10.1016/j.envexpbot.2009.05.015

Mousavi S, Regni L, Bocchini M, Mariotti R, Culltrera NG, Mancuso S, Googlan J, Chakerolhosseimi MR, Guerrero C, Albertini E, Baldoni L, Prioit P (2019) Physiological, epigenetic and genetic regulation in some olive cultivars under salt stress. Sci Rep 9:1093. https://doi.org/10.1038/s41598-018-37496-5

Munck IA, Bennett CM, Camilli KS, Nowak RS (2010) Long-term impact of de-icing salts on tree health in the Lake Tahoe Basin: Environmental influences and interactions with insects and diseases. For Ecol Manag 260:1218–1229. https://doi.org/10.1016/j.foreco.2010.07.015

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25:239–250. https://doi.org/10.1046/j.0016-8025.2001.00808.x

Munns R (2005) Genes and salt tolerance: bringing them together. New Phytol 167:645–663. https://doi.org/10.1111/j.1469-8137.2005.00487.x

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Physiol Plant Mol Biol 59:651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911

Musio M, von Wilpert K, Augustin NH (2007) Crown condition as a function of soil, site and tree characteristics. Eur J For Res 126:91–100. https://doi.org/10.1007/s10342-006-0132-8

Nowak DJ, Greenfield EJ, Hoehn RE, Lapoint E (2013) Carbon storage and sequestration by trees in urban and community areas of the United States. Environ Pollut 178:229–236. https://doi.org/10.1016/j.envpol.2013.03.019

Oleskyn J, Kloeppel BD, Lukasiewicz S, Karolewski P, Reich PB (2007) Ecophysiology of horse chestnut (Aesculus hippocastanum L.) in degraded and restored urban sites. Pol J Ecol 55:245–260

Ordóñez-Barona C, Sabetski V, Millward AA, Steenberg J (2018) De-icing salt contamination reduces urban tree performance in structural soil cells. Environ Pollut 234:562–571. https://doi.org/10.1016/j.envpol.2017.11.101

Paludan-Müller G, Saxe H, Pedersen LB, Randrup TB (2002) Differences in salt sensitivity of four deciduous tree species to soil or airborne salt. Physiol Plant 114:223–230. https://doi.org/10.1034/j.1399-3054.2002.014020.x

Parihar P, Singh S, Singh R, Singh VP, Prasad SM (2015) Effect of salinity stress on plants and its tolerance strategies: a review. Environ Sci Pollut Res 22:4056–4075. https://doi.org/10.1007/s11356-014-3739-1

Park BS, Lee SE, Kim MK, Kim YS, Lee HS (2000) Antioxidative activity of Ginkgo biloba leaves-derived components on free radicals and active oxygen species. Food Sci Biotech 9:317–321

Pauliet S (2003) Urban street tree plantings: identifying the key requirements. Proc Inst Civ Eng Municipal Eng 156:43–50

Pauliet S, Jones N, Garcia-Martín G, García-Valdecantos JL, Rivière LM, Vidal-Beaudet L, Bodson M, Randrup TB (2002) Tree establishment practice in towns and cities–Results from a European survey. Urban For Urban Green 1:83–96. https://doi.org/10.1016/j.urbanfor.2002.11.002

Pirasteh-Anosheh H, Ranjbar H, Pakniyat H, Emamy Y (2016) Physiological mechanisms of salt stress tolerance in plants: an overview. In: Azooz MM, Ahmad P (eds) Plant-environment interaction: responses and approaches to mitigate stress. Wiley, London, pp 141–160

Plesa I, Al Hassan M, Sestras AF, Vicente O, Boscaiu M, Sestras RE (2018) Biochemical markers of salt stress in European Trees (2022) 36:899–914
Zhong M, Wang Y, Shu S, Sun J, Guo S (2020) Ectopic expression of CsTGase enhances salt tolerance by regulating polyamine biosynthesis, antioxidant activities and Na⁺/K⁺ homeostasis in transgenic tobacco. Plant Sci 296:110492. https://doi.org/10.1016/j.plantsci.2020.110492

Zhou Q, Shi M, Zhu Z, Cheng L (2019) Ecophysiological responses of Carpinus turczaninowii L. to various salinity treatments. Forests 10:96. https://doi.org/10.3390/f10020096

Zimmermann P, Hirsch-Hoffmann M, Hennig L, Gruissem W (2004) GENEVESTIGATOR. Arabidopsis microarray database and analysis toolbox. Plant Physiol 136:2621–2632. https://doi.org/10.1104/pp.104.046367

Zimmerman EM, Jull LG (2006) Sodium chloride injury on buds of Acer platanoides, Tilia cordata, and Viburnum lantana. Arbor Urban For 32:45

Ziska HL, De Jong TM, Hoffman GF, Mead RM (1991) Sodium and chloride distribution in salt-stressed Prunus salicina, a deciduous tree species. Tree Physiol 8:47–57. https://doi.org/10.1093/treephys/8.1.47

Zwiazek JJ, Equiza MA, Karst J, Senorans J, Wartenbe M, Calvo-Polanco M (2019) Role of urban ectomycorrhizal fungi in improving the tolerance of lodgepole pine (Pinus contorta) seedlings to salt stress. Mycorrhiza 29:303–312. https://doi.org/10.1007/s00572-019-00893-3

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.