



# The importance of prenol lipids in mitigating salt stress in the leaves of *Tilia × euchlora* trees

Aneta H. Baczevska-Dąbrowska<sup>1</sup> · Wojciech Dmuchański<sup>2</sup> · Dariusz Gozdowski<sup>3</sup> · Barbara Gworek<sup>2</sup> · Adam Jozwiak<sup>4,5</sup> · Ewa Swiezewska<sup>4</sup> · Piotr Dąbrowski<sup>3</sup> · Irena Suwara<sup>3</sup>

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## Abstract

**Key message** Plants use multiple mechanisms to deal with salt stress. Salt stress increases the content of polyprenols in *Tilia*'s leaves, which may mitigate stress.

**Abstract** De-icing salt has been used on streets and pavements in most northern countries since the 1960s. Salt stress limits all vital functions of trees. *Tilia × euchlora* is planted in many cities given its unique decorative qualities. The aim of this study was to determine the tree strategy to mitigate salt stress due to the synthesis of polyprenols in leaves. Many years of observations have demonstrated that trees of the same species growing in the same street conditions may have extremely different health statuses. The study consisted of two experiments: a field experiment with urban street trees growing in saline soils and a controlled pot experiment with young trees exposed to increasing doses of salt. The differences between the young trees from the pot experiment and older trees from the field experiment were expressed in their ability to synthesize polyprenols. In urban conditions, the tree leaves with less damage contained significantly more polyprenols than did those with more damage. The salt stress mitigation strategy may be related to the ability to synthesize polyprenols. This ability can be acquired through adaptation by older trees. The mechanism involves limiting the transport of Cl<sup>-</sup> and Na<sup>+</sup> to leaves. In the pot experiment, the young trees did not exhibit this ability.

**Keywords** Urban trees · Salt stress · Polyprenols · Ionic balance · *Tilia*, deicing

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✉ Aneta H. Baczevska-Dąbrowska  
a.baczevska-dabrowska@obpan.pl

<sup>1</sup> Polish Academy of Sciences Botanical Garden, Center for Conservation of Biological Diversity, Warsaw, Poland

<sup>2</sup> Institute of Environmental Protection, National Research Institute, Warsaw, Poland

<sup>3</sup> Warsaw University of Life Sciences, SGGW, Warsaw, Poland

<sup>4</sup> Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw, Poland

<sup>5</sup> Present Address: Department of Plant and Environmental Sciences, Weizmann Institute of Science, 7610001 Rehovot, Israel

## Introduction

Urban trees provide a variety of uncountable ecosystem services, such as health, economic, psychological, social, and esthetic services (Dadvand et al. 2016; Livesley et al. 2016). Only healthy trees in good condition can perform these functions to improve the living conditions of city dwellers (Martin et al. 2016; Hallett et al. 2018). Based on many years of research, McPherson (2004) calculated that statistically one tree growing in an urban area in 40 years of life confers benefits totaling \$3.117.

De-icing of streets and sidewalks has been common in countries of the Northern Hemisphere since 1960s (Pauleit et al. 2002). The amount of salt used during the winter is not determined by negative temperatures but by the frequency of the transition from temperatures above zero to negative values. Salt stress affects the health of trees at the molecular, cellular, and histological levels. These changes are caused by the combined osmotic stress, which is related to the high osmotic pressure in the salinized soils, and the

toxicity stress due to the excessive tissue concentrations of  $\text{Na}^+$  and  $\text{Cl}^-$  ions. Salt stress disrupts most of the key metabolic processes in trees, including photosynthesis, enzyme synthesis, lipid metabolism, and energy processes (Equiza et al. 2017; Sarker and Oba 2018; Nikolaeva et al. 2019; Zhou et al. 2019; Łuczak et al. 2021).

In response to salinity, plants have developed a variety of defense mechanisms. Resistance can include avoidance, tolerance and a combination of these two methods of defense against the stress factor (Blomqvist 1998). The following methods can be used to relieve salt stress by trees: inhibition of  $\text{Cl}$  and  $\text{Na}$  uptake and redistribution of elements from leaves to other parts of plants (Shelke et al. 2019), the storage of  $\text{Na}^+$  and  $\text{Cl}^-$  in cell structures (Baetz et al. 2016), the induction of antioxidant enzymes and hormones (Zhao et al. 2019; Sarker and Oba 2020), the presence of ectomycorrhizal fungi (Zwiazek et al. 2019; Olchowik et al. 2021), the accumulation of compatible compounds, the increased conversion of xanthophyll pigments (Baraldi et al. 2019), and the presence of genes that can increase salt tolerance (Parihar et al. 2015).

Polyprenols belong to the group of compounds known as plant secondary metabolites (PSMs). Polyprenols play important defense functions against environmental stresses and attacks by pathogens (Satish et al. 2020). Polyisoprene alcohols are macromolecular polymers with different carbon chain lengths ranging from 5 to more than 100 isoprene units connected together according to the “head-to-tail” mechanism. (Swieżewska et al. 1994). Although prenols are common in plants, their role has not been fully explained thus far.

The qualitative composition and share of individual homologues in the total pool of these compounds has a gausoidal system unique for a given species, and in the case of plants, is characteristic of the genus and botanical family (Swieżewska and Danikiewicz 2005). Polyprenols occur most often in the cell membrane, probably affecting its fluidity and stability (Gutkowska et al. 2004; Skorupińska-Tudek et al. 2008). Polyprenols influence plant photosynthetic performance by modulating the dynamics of the thylakoid membrane (Akhtar et al. 2017). Presumably, polyprenols act as free radical scavengers in membranes (Bergamini 2003; Bajda et al. 2009). According to Bajda et al. (2005), polyprenols can play a special role in the adaptation of plants to adverse environmental conditions. Zhang et al. (2008) showed that dolichols, which are long-chain saturated polyisoprenoids, affect the plant response to drought and darkness-induced aging in *Arabidopsis*.

The increase in the synthesis of polyprenols is postulated to be a defensive strategy developed in *T. × euchlora* trees to salt stress (Milewska-Hendel et al. 2017). It cannot be excluded that polyprenols are involved in the regulation of chloride and sodium deposition in leaves. Baczevska et al.

(2014) suggested that polyprenols have an effect on reducing the accumulation of  $\text{Cl}^-$  in urban street trees in *Tilia*, and Dmuchowski et al. (2019) found similar results for *Ginkgo biloba*. Polyprenols play a special role in mangrove trees. Basyuni et al. (2017, 2019) suggested their significant role in withstanding salt stress and/or water stress.

The literature review showed a relationship between the content of prenols and sodium and chlorine in leaves and the health condition of trees. It was noted in the study that *Tilias* growing under comparable conditions significantly differed in the degree of damage to the leaves and the content of  $\text{Cl}$ ,  $\text{Na}$  and prenol in them. Observations conducted for many years have indicated the existence of Crimean linden trees with a healthy appearance and trees that have visible symptoms of damage in the same habitat. The aim of this study was, therefore, to answer the question of whether they trees can develop a defensive strategy based on the ability to synthesize larger amounts of polyprenols in the leaves to alleviate salt stress. The research presented in this publication is an extension of the preliminary work published by Baczevska et al. (2014). As an additional model, young trees were tested with controlled increases in soil salinity.

## Materials and methods

The study was performed on trees belonging to one species, *T. × euchlora* K. Koch. This tree has been known since the mid-nineteenth century and is cultivated in many countries of Central and Western Europe, where it grows in the wild and is commonly used for urban vegetation in public parks and along streets (Weryszko-Chmielewska et al. 2019).

In the field experiment, research was localized in the center of Warsaw (Poland). The trees grew on the lawn between the streets of Żwirki and Wigury Avenue (134 trees). The control trees (8 trees) grew in a green area 150 m from the avenue. No more suitable trees were found in the control area, but the leaves of all control trees showed no damage at all throughout the growing season. Żwirki and Wigury Avenue connect the main airport with the city center, which results in heavy vehicle traffic. In winter, black ice on the street is removed using  $\text{NaCl}$ . There is no reason why any parts of the street would receive a higher or lower dose of salt.

Street and park trees (control) were also of the same age and from the same nursery and were planted simultaneously. The only difference was the salinity of the soil. The distance between the street trees was 10 m and the trees were 4 m from the roadway. Basic methodological information about the conditions of the experiment with *T. × euchlora* street and control trees as well as a pot experiment with young trees treated with different amounts of  $\text{NaCl}$  are presented in Table 1.

**Table 1** Basic methodological information about the conditions of the experiment with *Tilia × euchlora* street and control trees as well as a pot experiment with young trees treated with different amounts of NaCl

	Field experiment		Pot experiment	
	Control		Control	
Number of trees	134	8	2 × 8	8
Age of trees	80	80	5	5
Date of salt addition	Winter	Winter	March 2018	March 2018
Date of samples collection	Middle of July 2018			
Number of leaves collected from single tree	120	120	All (~ 80)	All (~ 80)
Trunk diameter	~20 cm	~20 cm	3–3.5 cm	3–3.5 cm

In the field experiment, the leaves were cut from the twigs from a height of 2–4 m. The sampling date was mid-July, which is when the first damage occurred. Mid-July is recommended for collecting leaves for chemical analysis because at a later date, significantly magnified damage will distort the results of chemical analyses.

The field tests were supplemented with experiments performed on the same species under controlled conditions in pots. The experiment was organized in a park on the outskirts of the city. Five-year-old *T. × euchlora* trees were placed in 10-L containers directly on the ground and filled with soil consisting of light loamy silt under the mud. The containers were covered with soil to protect the roots of the trees from overheating and over drying. The linden seedlings were treated once in mid-March with salt at 0 (control), 15 and 30 g of NaCl dissolved in 250 mL of water. The containers were placed outside and watered by rain. During the experiment, seedlings were watered twice, supplementing the natural watering. Fertilization was not applied. In mid-July, all the leaves were torn off, and the experiment ended.

### Health condition of the leaves

The health condition of trees was assessed on the basis of the degree of leaf damage. This classification consists of six categories of leaf damage index: where “0” indicates that the leaves had no damage; “1” indicates that damage covered up to 10% of the leaf surface; “2” damage covered 10–25%; “3”—25–50%; “4”—50–75%; and “5” indicates a seriously damaged (damage to more than 75% of the leaf surface). The damage index was based on the assessment of combined leaf necrosis and chlorosis. The assessment of chlorosis and necrosis separately turned out to be practically impossible due to the large number of trees. Damage observations were carried out in mid-July. Determination of the leaf damage index in both experiments was carried out in mid-July. In the field experiment, damage index of the leaves was also assessed in mid-September, and such an assessment was impossible in the pot experiment because the experiment was completed.

### Chemical analysis of the leaves

After collection, washing the leaves was abandoned due to the possibility of rinsing, especially P but also to a lesser extent  $\text{Na}^+$  and  $\text{Cl}^-$ , which would have an impact on the result. The samples were dried in the laboratory at 70 °C and ground in a Fritsh 14702 grinder.

Then, mineralization of the dry leaves was performed in a muffle furnace. The ash was dissolved in 30% HCl. Metals and P were determined by atomic spectrophotometry using a Perkin Elmer 1100B apparatus.  $\text{Cl}^-$  was determined by potentiometric titration with an ion-selective electrode and the Orion Star Plus apparatus. N was determined by the Kjeldahl method using a Foss Tecator, and the LECO 132 apparatus was used to determine the content of S.

To calculate the ion balance index, the content of elements in leaves was converted into equivalent values (meq/100 g dry mass of leaves) by dividing the obtained result in a mass unit by atomic weight and valence. By calculating the data in this manner, it is possible to calculate the equilibrium state in plants and thus to compare electrochemically equivalent data. The organic acid content was calculated according to the method proposed by Van Tuil et al. (1964) as the difference between the sum of cations and the sum of anions ( $\text{R-COO}^- = (\sum_{\text{K}} - \sum_{\text{A}})$ ). The ratio of the sum of organic acids to the sum of mineral anions  $-\sum_{\text{A}}$  was calculated as an indicator of the ionic balance in the leaves. The  $\text{NO}_3^-$  content was not included in the calculations due to the presence of trace amounts in the leaves. Four ions were used to calculate the sum of cations  $-\sum_{\text{K}}$  (De Wit et al. 1963; Brogowski et al. 2000):  $\sum_{\text{A}} = \text{H}_2\text{PO}_4^- + \text{SO}_4^{2-} + \text{Cl}^-$ ;  $\sum_{\text{K}} = \text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+ + \text{Na}^+$ .

The quality control (QC) of the results of the chemical determinations was performed with certified reference materials: apple leaves (1515) from the National Institute of Standards and Technology (USA). The recovery range was from 90 to 95%.

## Qualitative and quantitative analyses of polyprenols

To the dried and milled ground leaves (50 mg), 1 mL of an acetone:methanol mixture (1:1, v/v) and internal standard (prenol 15, 50  $\mu\text{L}$ ,  $C - 1 \mu\text{g}/\mu\text{L}$ ) from the Collection of polyprenols, Institute of Biochemistry and Biophysics, PAS were added and then incubated at 37 °C for 30 min. The sample was centrifuged, and the supernatant was decanted. The pellets were re-extracted in 1 mL of acetone–hexane mixture (1:1) in an ultrasound bath and centrifuged again. The combined supernatant residues were evaporated in a nitrogen stream. The hydrolysing mixture was added (0.5 mL) and heated for 1 h at 95 °C (Jozwiak et al. 2013). After hydrolysis, the lipids were purified as described earlier by Skorupinska-Tudek et al. (2008).

The lipids were isolated by column chromatography on silica gel in hexane. The latter fraction was evaporated in a nitrogen stream, dissolved in 200  $\mu\text{L}$  of IPA-EtOH mixture and analyzed by HPLC/UV detector (Waters 2487) according to the methodology of Skorupinska-Tudek et al. (2008) using a combination of linear gradients of solvent mixtures A (90% methanol in water, v/v) and B (50% methanol, 25% hexane and 25% isopropanol v/v/v) at a flow of 1.5 mL/min.

The signal from the Waters photodiode detector (2487) was recorded in the form of a series of chromatograms in the wavelength range 210–254 nm. Separated compounds were identified on the basis of comparison of their retention times and absorption spectra with appropriate parameters of an external standard polyprenol mixture. The results were integrated at 210-nm wavelength in the Empower Pro program. The content of identified prenols was calculated considering the internal standard and administered in mg per 1 g of plant tissue dry matter. In the leaves, the contents of four polyprenols, pren-9, pren-10, pren-11 and pren-12, were identified and determined. Only the sum of polyprenols was used during further studies.

## Soil analysis

Soil samples were obtained from nine randomly selected trees from each category of leaf damage index and control area. Four samples were collected in four directions at 1.5 m from each randomly selected tree. The mixed sample for each tree was separately analyzed. Soil samples for testing were obtained from depths of 0–20 cm and 20–40 cm.

Air-dried soil samples weighing 100 g were saturated with redistilled water to 150% of their full water capacity and then incubated at room temperature for 66 h to achieve ionic equilibrium between the solid and liquid phases. The solutions were filtered through blotting paper filters into polyethylene bottles and then frozen and stored for chemical analysis (Allen et al. 1974). Na determination was performed

with a flame AAS (Perkin Elmer 1100 A). Cl was determined by potentiometric titration with an ion-selective electrode, and pH was determined by potentiometry using an Orion Star Plus apparatus (Thermo Scientific, USA) (LaCroix et al. 1970).

## Statistical analysis

The results for all variables are presented as the means and standard deviations. Comparisons of means between groups (various NaCl levels or various damage indices) were based on one-way analysis of variance and Tukey's HSD test at the 0.05 significance level. Relationships between variables were evaluated using Pearson's correlation coefficient. For multivariate evaluation of the relationships between variables and multivariate characteristics of the groups, principal component analysis (PCA) was conducted. All analyses were performed using Statistica 13 software.

## Results and discussion

In the field experiment, 134 street trees of *T. × euchlora* and 8 park trees (control) were examined to determine the damage index of leaves and their chemical composition. In mid-July, during leaf sample collection for chemical analysis, observations of leaf health status revealed only slight damage to a small number of trees. Therefore, this observation date was not included in further analyses. Observations from mid-September revealed a very large variation in leaf damage index values despite growing in practically the same soil. The following number of trees was detected in each category of leaf damage: “0”—10.1% trees, “1”—30.1%, “2”—20.1%, “3”—24.6%, “4”—9.0%, and “5”—6.0%. In mid-September, 60% of street trees had damage to more than 25% of the leaf surfaces, which indicates the high sensitivity of this species to street conditions. The control (park) trees did not have any leaf damage on either observation date. In the pot experiment, in mid-July, only a few trees had slight leaf damage at the highest salt dose.

The publications describing *T. × euchlora* as sensitive were found (Roloff et al. 2009; Dmuchowski et al. 2020). In Warsaw, in 1973, *T. × euchlora* constituted 38% of street plantings in the city center; by 2007, 62% had died and had been removed (Dmuchowski et al. 2011b). Our current research confirms the high sensitivity of *T. × euchlora* to street conditions in the urban environment.

Table 2 presents the results of soil analyses: the pH and Cl and Na contents of randomly selected trees from individual leaf damage categories with nine samples from each category and the contents of  $\text{Cl}^-$  and  $\text{Na}^+$  in the leaves of the trees in the field study. All other analyses included the results of leaf analyses from all 134 trees. The pH of street

**Table 2** The content of Cl and Na in the leaves of street trees *Tilia × euchlora* and control trees and in two layers of soil (0–20 cm and 20–40 cm) from under these trees with depending on the value of the leaf damage index

Leaves-damage index	Leaves		Soil				
	Cl (%)	Na mg kg <sup>-1</sup>	pH	0–20 cm		20–40 cm	
				Cl (mg dm <sup>-3</sup> )	Na (mg dm <sup>-3</sup> )	Cl (mg dm <sup>-3</sup> )	Na (mg dm <sup>-3</sup> )
Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
0	0.90 ± 0.07b	179 ± 50a	7.45 ± 0.28b	3073 ± 801b	2101 ± 301b	2673 ± 1637b	1136 ± 225ab
1	1.15 ± 0.16c	222 ± 25a	7.52 ± 0.18b	3264 ± 1135b	1899 ± 620ab	2252 ± 464ab	1314 ± 421b
2	1.52 ± 0.09d	250 ± 42a	7.44 ± 0.18b	3445 ± 1135b	2133 ± 676b	2703 ± 858b	1410 ± 447b
3	1.54 ± 0.08d	541 ± 217a	7.59 ± 0.18b	3544 ± 503b	2908 ± 2061b	2741 ± 1005b	1520 ± 859b
4	1.82 ± 0.10e	1217 ± 317b	7.54 ± 0.28b	3014 ± 1014b	2238 ± 965b	2636 ± 359b	1326 ± 301b
5	1.95 ± 0.21e	3479 ± 935c	7.61 ± 0.27b	3385 ± 1014b	2658 ± 1099b	2696 ± 359b	1458 ± 301b
Contr.	0.35 ± 0.21a	86 ± 10a	6.35 ± 0.72a	1334 ± 1014a	47 ± 149ab	1333 ± 359a	359 ± 301a

Based on analysis of variance and Tukey's test different letters mean statistically significant differences between trees treated with different doses of NaCl

soil ranged from 7.44 to 7.61 and was significantly higher than the park soil pH (6.35). Statistical analysis showed no significant differences in the soil pH of street soils in each variant (Table 2). The trends obtained are consistent with the literature data. Soil contamination with NaCl increases soil pH, which has adverse effects on trees (Park et al. 2010; Zhang et al. 2012). The contents of Cl<sup>-</sup> and Na<sup>+</sup> in street soil from the two depths were significantly higher than those in park soil. However, no significant differences were found among individual street soil variants. Moreover, no relationship was found between the content of Cl<sup>-</sup> and Na<sup>+</sup> in the leaves and their content in the soil collected from under the same trees. Moreover, the content of Cl<sup>-</sup> and Na<sup>+</sup> in the soil was accompanied by a very high standard deviation, which demonstrates large variability in the degree of soil salinity consistent with the literature data (Cekstere and Osvalde 2010). Determination of the content of elements in the leaves of trees provides important information, especially about the threat of pollution but also about their vitality, nutrition, growth conditions, and other threats, and this information may be more important than determining the chemical composition of the soil in urbanized areas (Cekstere et al. 2010; Mellert and Göttlein 2012; Dmuchowski et al. 2013). For these reasons, only the chemical composition of the leaves is discussed in the following sections.

Figure 1 presents the results of the leaf contents of Cl<sup>-</sup> and Na<sup>+</sup>, the ionic balance indicator and the sum of polyphenols based on the value of the leaf damage index. The content of Cl<sup>-</sup> increased with increasing degree of leaf damage from 0.98% at damage index “0” to 1.88% at damage index “5”, and the content was 0.35% in control trees. The corresponding contents of Na were 184 mg kg<sup>-1</sup>, 3479 mg kg<sup>-1</sup>, and 86 mg kg<sup>-1</sup>, respectively. Statistical analysis of the results showed that leaf damage index values was strongly positively correlated with the contents of Cl<sup>-</sup> and

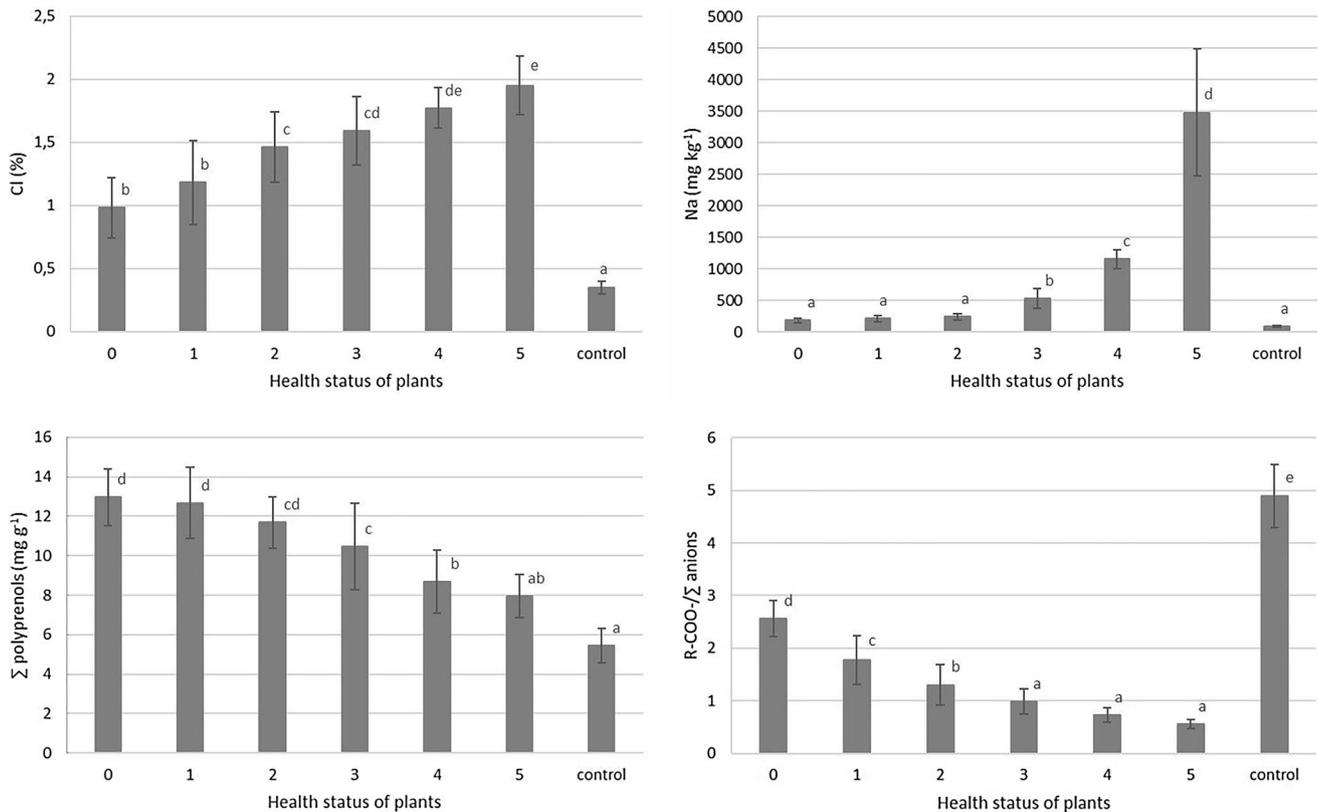
Na<sup>+</sup> (Table 3). Many studies confirm our results (Goodrich and Jacobi 2012; Jimenez-Casas and Zwiazek 2014; Calvo-Polanco et al. 2014; Helama et al. 2020).

The Cl content exceeded the level of 0.6% specified in the literature as being toxic to *Tilia* (Pauleit 1988; Chmielewski et al. 1996). For Na, a similar toxicity level was not found in the literature. Significant soil contamination with NaCl affects practically all life processes of trees. The results include physiological drought, nutrient deficiencies and eventual tree death (Chen et al. 2010; Cekstere et al. 2020; Ordóñez-Barona et al. 2018). High Na<sup>+</sup> content in the leaves is not only toxic but can also limit the absorption of macroelements (Ca, K, and Mg). Leaf damage is mainly caused by Cl<sup>-</sup> (Slabu et al. 2009; Genc et al. 2015). Salt stress can also increase the susceptibility of trees to pathogens (Munck et al. 2010; Snieškienė et al. 2016), but there have also been reports that salinity may reduce the number of aphids on linden leaves (Sienkiewicz-Paderewska et al. 2017; Bouraoui et al. 2019).

In the pot experiment, the contents of Cl<sup>-</sup> and Na<sup>+</sup> in the leaves increased significantly with increasing salt dose. Cl<sup>-</sup> increased from 0.33 to 2.08% in the control at 30 g per pot, and Na increased accordingly from 48 to 2865 mg kg<sup>-1</sup>.

Ion imbalance is considered the cause of the poor condition of street trees and their death, one of the causes of which is soil salinity (Mazher et al. 2007; Green et al. 2008). Figure 1 shows the relationship between the value of the ionic balance in the leaves and the street leaf damage index. The ionic balance indicator value decreased with the deterioration of leaf health from 2.56 at leaf damage index “0” to 0.56 at “5”, and the value in the control was 4.90.

Differences between leaf damage index categories were significant, especially between trees with a higher leaf damage index. The chloride ion content, which strongly affected the value of the ionic balance, increased with the increase



**Fig. 1** The contents of Cl, Na, and polyphenols and the ionic balance index (means and SDs) in the leaves of street and control trees depending on the value of the leaf damage index. The results are

based on analysis of variance and Tukey's test (different letters indicate significant differences)

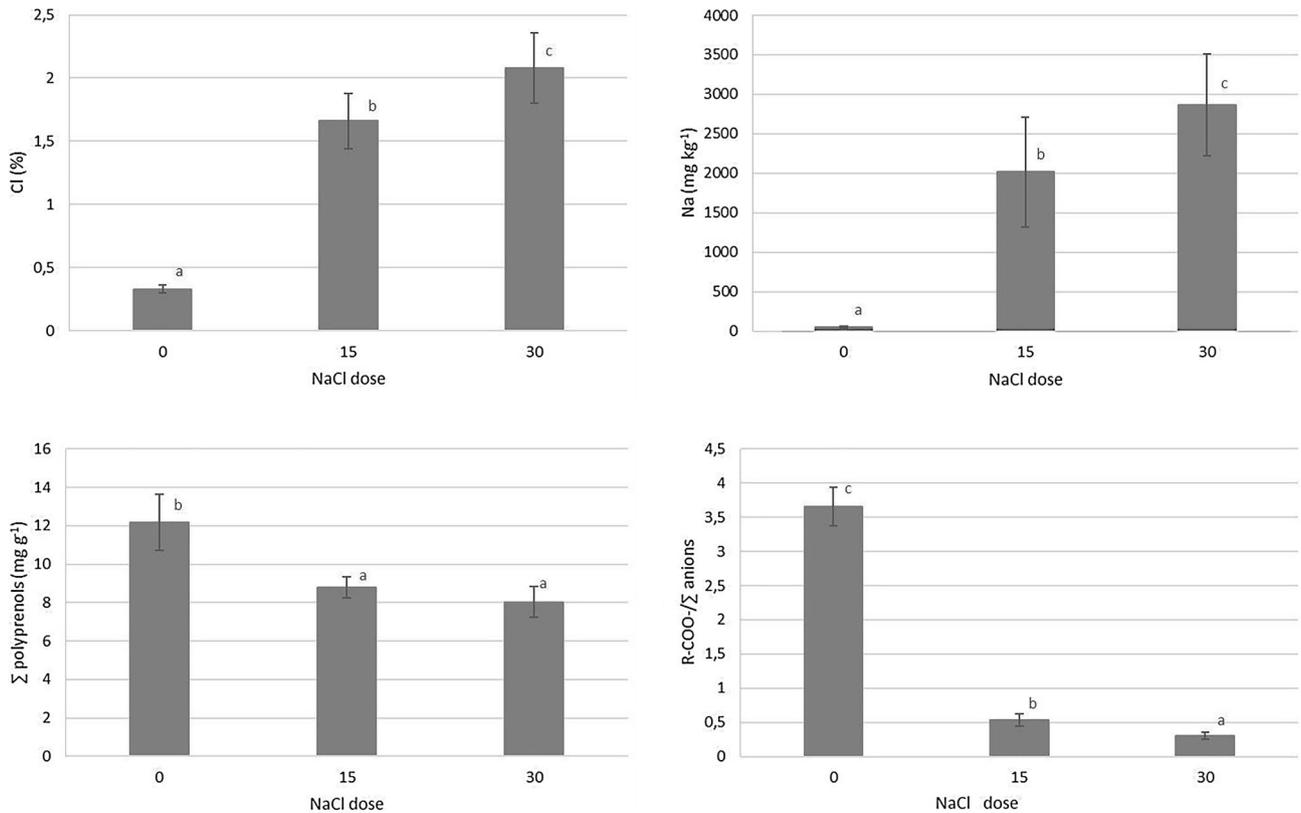
**Table 3** Correlation coefficients and *P* values between the pH and Na and Cl content in two layers of soil and leaves damage index and content of Cl and Na of the leaves of street *Tilia × euclora* trees

Soil	Leaves damage index		Cl leaves		Na leaves	
	Correlation coefficient	<i>P</i> value	Correlation coefficient	<i>P</i> value	Correlation coefficient	<i>P</i> value
pH 0–20	0.216	0.116	0.161	0.246	0.222	0.139
Cl 0–20	0.055	0.692	0.061	0.664	0.048	0.730
Na 0–20	0.203	0.140	0.131	0.344	0.137	0.324
Cl 20–40	0.069	0.620	0.018	0.900	0.026	0.853
Na 20–40	0.162	0.241	0.103	0.457	0.032	0.819

in the value of the leaf damage index. The pot experiment yielded the same trends as the field tests (Fig. 2). The differences between the experimental variants were significant, and the ionic balance indicator value decreased from 3.66. In the majority of studies, the content of elements in plants is given in units of weight (e.g., mg/kg and %), which is a gross 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 comparing our own results with those of other studies. Brogowski et al. (2000) and Dmuchowski et al. (2011a) showed that an ionic

balance indicator value less than one indicates poor conditions for street trees. In our research, trees with a damage index greater than “2” had an index of the ionic balance value less than one.

There are opinions about the role of polyphenols in mitigating biotic and abiotic stress, but the information remains very limited. The content of polyphenols in the leaves of street trees (Fig. 1) decreased from 13.0 mg g<sup>-1</sup> in leaves without damages (index “0”) to 7.9 mg g<sup>-1</sup> in those with the greatest damage (index “5”). Decreased content of polyphenols in the significantly damaged leaves comparing to that with slightly damaged most probably



**Fig. 2** The contents of Cl, Na, and polyphenols and the ionic balance index (means and SDs) in the leaves of the model pot trees depending on the dose of NaCl in the pot. The results are based on analysis of

variance and Tukey's test (different letters indicate significant differences between trees treated with different doses of NaCl)

result from the enhanced catabolic processes that occur in the former group of leaves which might lead to polyphenol decomposition. Importantly, control trees contained the lowest content of polyphenols at  $5.4 \text{ mg g}^{-1}$ . Thus, on the one hand, exposition of the urban trees to salinity resulted in the increase of the content of polyphenols while on the other hand, the content of polyphenols decreased in the leaves of trees growing in saline soil as the content of  $\text{Cl}^-$  and  $\text{Na}^+$  increased. This latter observation might also be explained by the increased level of the reactive oxygen species (ROS) generated in the leaves of the significantly damaged (index "5") since ROS are able to break down polyphenols (Komaszylo née Siedlecka et al. 2016). In the pot experiment, the relationships were different. The leaves of control trees contained significantly more polyphenols ( $12.3 \text{ mg g}^{-1}$ ) than did those of trees growing in saline soil. Between trees growing in both doses of soil salinity, the content of polyphenols in leaves did not differ significantly ( $8.8 \text{ mg g}^{-1}$  and  $8.0 \text{ mg g}^{-1}$ ). Pot experiments do not provide an unequivocal answer as to whether increases in the  $\text{Cl}^-$  and  $\text{Na}^+$  contents in leaves increase the synthesis of polyphenols again indicating the importance of the urban model. Moreover, young plants used

in the pot model might have possibly not developed the salinity-adaptive mechanisms observed for older plants.

Increasing of polyphenols in leaves of *T. × euchlora* as a reaction to salt stress has already been shown and has been interpreted as a method of adaptation to salinity, where the properties of polyphenols as free radical scavengers affect the transport of chloride and sodium to leaves (Milewska-Hendel et al. 2017). Baczevska et al. (2014) suggested that polyphenols have an effect on reducing the acclimation of Cl in *Tilia*, and Dmuchowski et al. (2019, 2021) reported similar results for *Gingko biloba* and *Acer*. Polyphenols also reported protect mangroves from salty seawater (Basyuni et al. 2017). This protective function in leaves and roots can be realized in three ways: isolation, exclusion and management of salt accumulation (Basyuni et al. 2019).

The contents of macroelements in linden leaves from the field and pot experiments are presented in Table 4. In the leaves of street and control trees, the contents of Ca and Mg did not differ significantly regardless of the degree of damage to the leaves. Trees with greater leaf damage contained significantly less N and K than healthier and control trees. In the case of P, control trees contained more P compared

**Table 4** Means and SDs for the content of macronutrients in street trees depending on the value of the leaf damage index and in the leaves from the pot experiment treated with different doses of NaCl

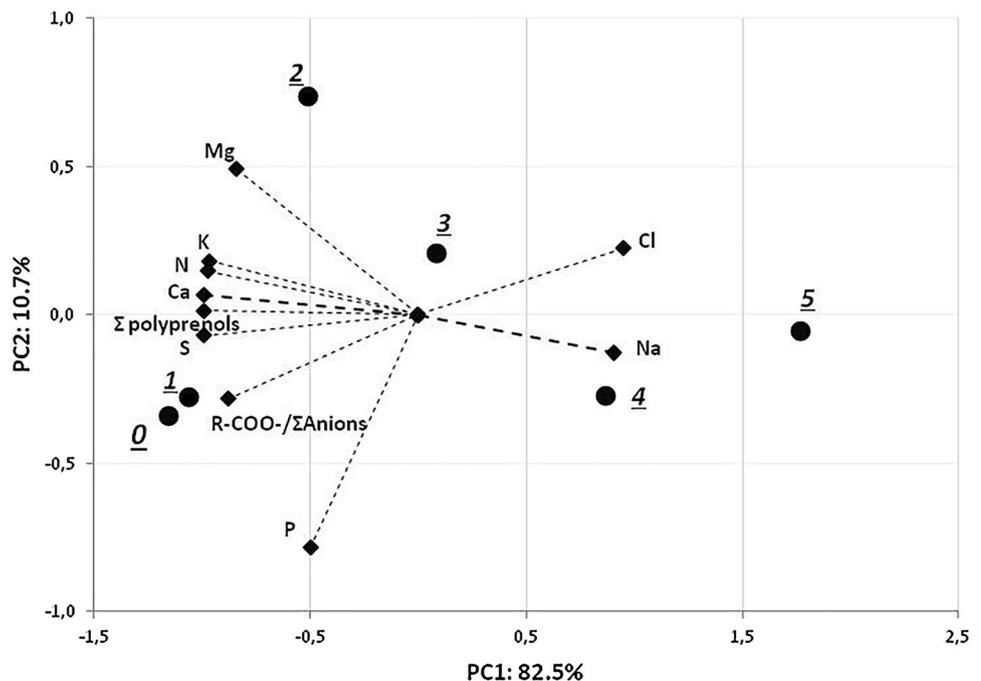
Leaf damage index	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD
Field experiment					
0	3.01 $\pm$ 0.13c	0.43 $\pm$ 0.10a	1.78 $\pm$ 0.24c	2.27 $\pm$ 0.26a	0.36 $\pm$ 0.09a
1	3.02 $\pm$ 0.24c	0.44 $\pm$ 0.06a	1.75 $\pm$ 0.30c	2.26 $\pm$ 0.41a	0.37 $\pm$ 0.09a
2	3.01 $\pm$ 0.22c	0.39 $\pm$ 0.14a	1.77 $\pm$ 0.19c	2.19 $\pm$ 0.29a	0.38 $\pm$ 0.10a
3	2.63 $\pm$ 0.24b	0.41 $\pm$ 0.06a	1.61 $\pm$ 0.19bc	2.16 $\pm$ 0.58a	0.36 $\pm$ 0.12a
4	2.49 $\pm$ 0.24ab	0.42 $\pm$ 0.12a	1.39 $\pm$ 0.19ab	1.99 $\pm$ 0.41a	0.34 $\pm$ 0.15a
5	2.31 $\pm$ 0.24a	0.40 $\pm$ 0.07a	1.05 $\pm$ 0.20a	1.87 $\pm$ 0.20a	0.33 $\pm$ 0.07a
Control	3.14 $\pm$ 0.21c	0.59 $\pm$ 0.10b	1.52 $\pm$ 0.20bc	2.24 $\pm$ 0.20a	0.38 $\pm$ 0.07a
Dose					
g NaCl/pot	N (%)	P (%)	K (%)	Ca (%)	Mg (%)
	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD
Pot experiment					
0	2.43 $\pm$ 0.17a	0.42 $\pm$ 0.06a	1.23 $\pm$ 0.10a	1.10 $\pm$ 0.13b	0.25 $\pm$ 0.10a
15	2.37 $\pm$ 0.23a	0.38 $\pm$ 0.05a	1.48 $\pm$ 0.23ab	1.09 $\pm$ 0.08b	0.27 $\pm$ 0.04a
30	2.23 $\pm$ 0.16a	0.36 $\pm$ 0.05a	1.65 $\pm$ 0.25b	0.88 $\pm$ 0.09a	0.28 $\pm$ 0.03a

Based on analysis of variance and Tukey's test different letters mean statistically significant differences between trees treated with different doses of NaCl

with all categories of street trees. In the pot experiment, soil salinity did not affect the contents of N, P or Mg in leaves.

Analysis of the contents of macronutrients in the leaves did not provide a clear answer. Previously published data indicate that the content of macroelements (N, P, K, Ca and Mg) in the leaves was at the level considered "normal" and often optimal. Deficient levels were not found in any

experimental variant (Dirr 1976; Mellert et al. 2012; Kopinga and Van den Burg 1995; De Vries et al. 2000). The same tendencies were observed by Cekserte et al. (2020) in studies on street *T.  $\times$  vulgaris* in Riga (Latvia). The relationship between soil salinity and mineral uptake is not simple. Salinity may increase, decrease or have no effect on

**Fig. 3** Results of PCA based on the first and second principal components (PC1 and PC2) presenting multivariate relationships between variables and multivariate differences between groups with various levels of the leaf damage index

the content of macronutrients in plants (Green et al. 2008; Dmuchowski et al. 2014).

In the field experiment (Fig. 3), PCA results showed a strong positive correlation between the contents of Na and Cl in leaves, which were negatively correlated with other elements, with the exception of P. High contents of most elements, polyphenols and indicators of ionic balance in plants were observed for low leaf damage rates (“0” and “1”). An increase in the leaf damage index was positively correlated with the contents of  $\text{Na}^+$  and  $\text{Cl}^-$  and negatively correlated with the contents of other elements and polyphenols and the indicator of ionic balance.

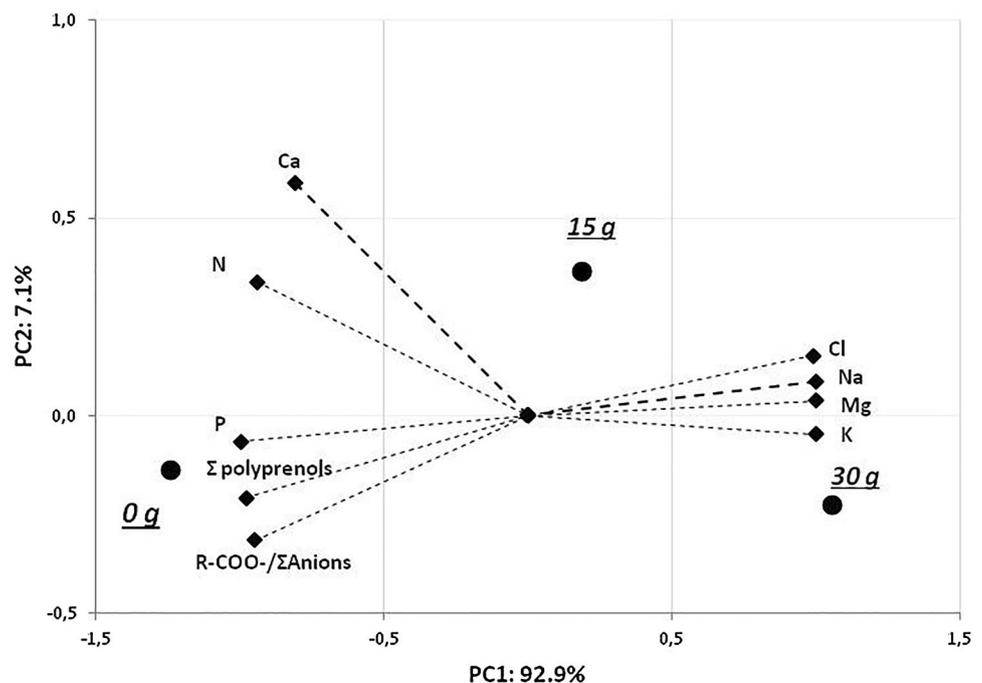
The results of PCA for the pot experiment demonstrate a strong positive correlation between Na, Cl, Mg and K, which were negatively correlated with Ca, N, P, polyphenols and ionic balance (Fig. 4). For the group without NaCl (0 g NaCl), high contents of P, N, Ca, and polyphenols and high values of ionic balance were observed. For the group with the highest NaCl dose (30 g NaCl), high contents of Na, Cl, K and Mg were observed.

## Conclusions

In accordance with previous publications, *T. × euchlora* exhibited a lack of resistance to urban street conditions. Although they grew in the same soil conditions, the health of trees was very diverse. This diversity was expressed as a strongly significant positive correlation between the contents of  $\text{Cl}^-$  and  $\text{Na}^+$  and the value of the leaf damage index,

value of ionic balance and content of polyphenols. The trees with the most damaged leaves had an ionic balance that was 4.5-fold less compared with trees with the least damage and 8.7-fold less compared with control trees. The contents of  $\text{Na}^+$  and  $\text{Cl}^-$  in the leaves were negatively correlated with N, K, Ca and Mg, indicating a disturbed ionic balance, but no deficiencies in any bioelements were found. In the pot experiment, similar relationships were found with the only difference being that negative correlations were found for P instead of K and Mg. The differences between young trees from the pot experiment and older trees from the field were expressed in their ability to synthesize polyphenols. Under street conditions, the leaves of trees with slight damage contained more polyphenols than heavily damaged leaves. The leaves of control (nonsaline) trees contained significantly fewer polyphenols. The ability to synthesize polyphenols acquired in the process of acclimation by mature trees may be a method of mitigating salt stress. In the pot experiment, the reactions of the trees were completely different. The pot experiment method allows all other factors besides salt stress that may affect the health of plants to be eliminated. Control trees contained more polyphenols compared with those treated with NaCl. The dose of salt had no significant effect on polyphenol levels. Young trees may not have had time for acclimation to develop the ability to synthesize more polyphenols. Plants have developed many methods of protection against salt stress. Our results suggest that one of these methods for the mitigation of salt stress by trees may be the ability to synthesize more polyphenols. It seems likely

**Fig. 4** Results of PCA based on the first and second principal components (PC1 and PC2) presenting multivariate relationships between variables and multivariate differences between the experimental groups (0, 15, and 30 g of NaCl per pot)



that this mitigation could be by blocking  $\text{Cl}^-$  and  $\text{Na}^+$  from entering the leaves.

**Author contribution statement** AH B-D and WD led the writing of the manuscript. AH B-D, WD, AJ, and ES conceived the hypothesis, AJ, AH B-D, and DG designed the methodology, and analyzed the data. All the authors (AH B-D, WD, IS, ES, AJ, DG, PD, and BG) contributed to data interpretation and discussion and substantially improved the final draft of the manuscript.

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## Declarations

**Conflict of interest** The authors declare no conflict of interest.

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