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Testing the suitability for coastal green areas of three ornamental shrub species through physiological responses to the saline nebulization

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ABSTRACT

Besides abiotic constraints, plants along the coastal urban areas must face additional cues such as saline aerosol. which impact net plant CO₂ assimilation (P_n), reducing biomass and influencing their aesthetic features. In this study, three species (Photinia \times fraseri, P; Escallonia rubra, E; and Feijoa sellowiana, F) were subjected to saline nebulization (SN) with a 100 mM NaCl solution. Analyses were performed at 0, 10, and 20 days by monitoring the ion accumulation in plant organs, leaf osmotic potentials, gas exchange, chlorophyll a fluorescence parameters, and chlorophyll contents. Overall, E-SN plants absorbed more Na^+ and Cl^- in leaves than P-SN and F-SN ones. This phenomenon was influenced by leaf 'wettability' features such as the contact angle of water droplets, droplet retention, and water storage capacity, and the effectiveness of translocating these ions on twig tissues. SN increased the leaf osmotic potential (regardless of species). At 10 days (i.e., moderate stress conditions), P_n declined in all SN species, but more severely (-82 %) in E-SN plants. The observed P_n reductions were due to different limiting factors according to the plant species: P_n was reduced by non-stomatal limitations in P-SN plants, stomatal closure in F-SN, and a combination of both in E-SN individuals. At 20 days (i.e., severe stress conditions), in all SN-plants, lower values in all the physiological parameters than controls were observed, indicating a low tolerance to prolonged SN. The work shows that non-destructive physiological measurements provide a reliable assessment of plant tolerance to SN, which can help growers to select ornamental species suitable for coastal green areas.

1. Introduction

In the last decade, a substantial enhancement of green infrastructures has been observed in Mediterranean cities due to the development of socio-economic and environmental policies by local governments. Parks, gardens, tree-lined avenues, and flowerbeds can i) ameliorate the urban air quality (Nowak et al., 2013), ii) act as a sink of CO₂ from the atmosphere (Baraldi et al., 2019), (iii) mitigate heat island effect (Solecki et al., 2005), and iv) provide a series of other benefits to public health (e.g., improvement of the aesthetic value of urban areas; van den Berg et al., 2015; Ferrini et al., 2020). However, the effectiveness of the ecosystem services provided by plants depends on their health status (Savi et al., 2015). Urban plants often have to face severe limiting factors due to their location and land use at the site, e.g., compacted and contaminated soils, nutrient deficiency, and water deficit (Gray and

Brady, 2016; Lo Piccolo and Landi, 2021), which can negatively influence plant CO_2 fixation by resulting in low primary productivity and reduced biomass (Gilbertson and Bradshaw, 1985; Nowak, 1990; Roman et al., 2014).

Ornamental plants along the coastal areas must face additional abiotic stress such as saline aerosol (Ferrante et al., 2011; Farieri et al., 2016), which can severely deplete the provided ecosystem services (Toscano et al., 2022). The ability of plants to tolerate saline aerosol mainly depends on their morpho-anatomical characteristics, such as leaf architecture, size, orientation, and the presence of a thick cuticle or waxes over the leaf lamina (Du and Hesp, 2020). However, though leaf barriers can limit the absorption of sodium and chloride ions (Na⁺ and Cl⁻, respectively), once unavoidably absorbed, those ions cause severe metabolic alterations (Du and Hesp, 2020; Mereu et al., 2011). The saline aerosol causes osmotic stress by inducing stomatal closure,

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reduction in net CO_2 assimilation and maximal PSII efficiency, overproduction of reactive oxygen species, and severe damage to the entire photosynthetic machinery (Mereu et al., 2011; Sarabi et al., 2019). At a macroscopic level, the saline aerosol provokes visible injuries (e.g., leaf necrosis and burns), alters buds and stems structure, and reduces the whole plant growth (Griffiths and Orians, 2003). Although the detrimental effects of the saline aerosol on vegetation are well documented (as previously reported), there are still few experimental studies that have evaluated the tolerance/resistance of different ornamental species to this stressor (Farieri et al., 2016; Ferrante et al., 2011; Mereu et al., 2011; Toscano et al., 2020, 2021).

Urbanized coastal places are very attractive to tourists, and ornamental plants play a pivotal role in improving the pleasantness of these areas. Given the above, the research and the selection of plant species are crucial in the context of a wise urban greening of coastal areas. Toscano et al. (2020), documented that physiological analyses (e.g., gas exchange and chlorophyll *a* fluorescence parameters) can be used as an effective and rapid screening methodology to select plant species suitable for green areas along the coast about their tolerance to saline aerosol.

In this study, three high-value and widely-used ornamental species (*Photinia* × *fraseri*, P; *Escallonia rubra*, E; and *Feijoa sellowiana*, F) were exposed to saline nebulization. P and E have been reported in the literature to be moderately tolerant to saline nebulization or sprinkle irrigation (Toscano et al., 2020; Wu et al., 2001), while F appears to be sensitive to saline nebulization in terms of biomass accumulation and high leaf damage (Farieri et al., 2016). Plants were analyzed from a physiological point of view by testing the saline aerosol effects in terms of alterations in gas exchanges and chlorophyll *a* fluorescence parameters, ion accumulation/translocation in leaves and woody organs, and symptoms appearance over the leaf. This multilevel analysis generates new information about the suitability of these three ornamental shrub species for coastal green areas.

2. Materials and methods

2.1. Plant material

In October 2021, thirty plants (two years old) of *Photinia* \times *fraseri* 'Red Robin' 100 cm high, Escallonia rubra 50 cm high, and Feijoa sellowiana 100 cm high, propagated from cuttings, were used for the experiments conducted in polyethylene tunnels (13.0 \times 3.0 \times 1.9 m in length, width and height, respectively) at the field station of the Department of Agriculture, Food and Environment, University of Pisa, Italy (43°42'N, 10°25'E). Plants were purchased from an Italian nursery (Vannucci Piante, Pistoia, IT). Plants were grown in 6.5 L pots containing a mixture of peat/perlite (80:20, v:v). Fertilization was performed using a slow-release (8-month lasting) 3 g L^{-1} Osmocote® (N:P: K, 12:12:30). Plants were divided into two groups of 15 individuals for each species. One group was daily nebulized (1 min of nebulization) through water mist nozzles, with a solution of 100 mM NaCl (~18 % of averaged NaCl concentration in seawater) (SN), while the second group did not receive any nebulization (Cnt). An additional third group was daily nebulized with H₂O, but no relevant differences were found vs Cnt group and therefore data were not shown in the present paper. All plant species were regularly well-watered using an automated irrigation system, till the end of the experimental trials. During the cultivation period, minimum and maximum air temperatures averaged 11.4 ± 3.4 and 21.9 \pm 1.8 °C, respectively. Non-destructive and destructive analyses were performed at the beginning of the trials, and after ten (moderate stress conditions) and twenty days (severe stress conditions) on fully expanded leaves. The sampling times were chosen based on the first reduction of physiological parameters such as net CO₂ assimilation rate and loss of photosystem II (PSII) performance. At each sampling time, samples for biochemical analysis were collected at midday, immediately frozen in liquid nitrogen, and stored at - 80 °C until investigation.

2.2. Leaf gas exchange and chlorophyll a fluorescence analyses

Leaf gas exchange parameters were measured (n = 5) using a portable infrared gas analyzer LI-6400 system (Li-Cor, Lincoln, NE, USA). All gas exchange measurements were conducted on fully expanded leaves of the selected plant species from 10:00–13:00. Inside the leaf chamber, the CO₂ concentration was set to 400 µmol mol⁻¹ by using the CO₂ mixer, the flow rate was 500 µmol s⁻¹, and light intensity inside the chamber was set at similar levels to the previously measured ambient light (~800 µmol m⁻² s⁻¹). Once the steady-state was reached, net photosynthetic rate (P_n), stomatal conductance (g_s) and intercellular CO₂ concentration (C_i) were recorded.

Chlorophyll *a* fluorescence parameters were measured using PAM-2000 fluorometer (Walz, Effeltrich, Germany). All measurements (n = 5) were conducted simultaneously as gas exchange analyses in leaves similar to those used for gas exchange. After 30 min of dark adaptation, the maximum quantum yield of PSII (F_v/F_m) was measured. Analysis was performed on the central leaf section by avoiding midrib.

2.3. Leaf chlorophyll content

The leaf chlorophyll content (Chl; $\mu g \text{ cm}^{-2}$) was measured using a leaf clip sensor DUALEX® (Force-A, Orsay, France). At every sampling time, ten randomly chosen fully expanded leaves of the selected plant species were measured at 12:00 pm.

2.4. Leaf and twig Na^+ and Cl^- contents

Leaves (similar in size, age, and canopy position to those selected for physiological measurements) and relative twig samples, taken at the different sampling times (0, 10, and 20 days; n = 3), were dried using a laboratory electric thermostatic oven (Memmert GmbH + Co. KG Universal Oven UN30, Schwa-bach, Germany) at 60 °C until constant weight (7 days). Na⁺ and Cl⁻ were determined according to Pompeiano et al. (2017) and Cataldi et al. (2003), respectively. About 7 mg of powdered sample material was suspended in 2 mL of Milli-q H₂O, shaken for 15 min, and finally centrifuged at 1200 g for 10 min. Then, extracts were filtered through 0.2 µm Minisart SRT 15 filters and stored at 4 °C until the determination by ion-exchange chromatography with Dionex[™] Aquion[™] (Thermo Fisher Scientific, USA). For cation elution, an aqueous solution containing CH₄O₃S was used at a flow rate of 1 mL min⁻¹. For anions, an eluent consisting of 2.7 mM Na₂CO₃ and 0.3 mM NaHCO₃ was used at a flow rate of 2.0 mL min⁻¹ (Cataldi et al., 2003). For cation quantification, this IC system is equipped with a Dionex IonPacTM CS12A analytical column (4 \times 250 mm), and a Dionex Ion-PacTM CG12A pre-column (4 \times 50 mm), and a Dionex Cation Self-Regenerating Suppressor CDRS™ 600 4 mm. The translocation factor (TF) from leaves to twigs for Na⁺ and Cl⁻ was represented in percent according to Ali et al. (2013), using the following equation:

$$TF = \frac{ions_{twig}}{ions_{leaf}} \times 100$$

2.5. Leaf osmotic potential

To extract cell sap (n = 3), leaves were thawed in sealed microtubes for 20–30 min and centrifuged at 21,000g for 10 min. Then, 10 μ L of extracted cell sap was loaded into a Vapor Pressure Osmometer (VAPRO, EliTech Group, Puteaux, France) to determine osmolality at room temperature. Osmolality was converted to leaf osmotic potential by using the Van't Hoff equation ($\Psi_{\pi} = -CsRT$, in which Ψ_{π} is the osmotic potential, Cs the osmolality, R the gas constant, and T the temperature expressed in K; Stanton and Mickelbart, 2014).

2.6. Contact angle of water droplets, leaf droplet retention and leaf water storage parameters

The contact angle and the droplet retention of both adaxial and abaxial leaf surfaces were measured according to Aryal and Neuner (2010). Sample leaves (n = 20) were placed horizontally on a plane using double-sided tape. A 5 µL droplet of 100 mM NaCl solution used for the nebulization was placed on the leaf surface with a micropipette. Then a photographic side-view image of the droplet on the leaf surface was taken by a digital camera. The photographs were further processed with imaging software (Image J software) to calculate the contact angle (θ): $\theta > 150^{\circ}$ means superhydrophobic surfaces, $130-150^{\circ}$ highly non-wettable; $110-130^{\circ}$ non-wettable; $90-110^{\circ}$ wettable; $40-90^{\circ}$ highly wettable; and $< 40^{\circ}$ superhydrophilic. The droplet retention was determined as follows. A 50 µL droplet was placed on a leaf placed horizontally on a plane of a tilting platform. Then the angle of leaf inclination was steeply increased, and when the droplet began to move, the actual inclination angle was recorded.

Leaf water storage capacity (mg of water per cm⁻² of leaf area) was quantified in the laboratory. Fresh leaf (n = 10) was weighed ($Mass_{dry}$) and subjected to saturation with a 100 mM NaCl solution for 1 min (the same time used for the nebulization treatment). When the leaf stopped dripping, it was again reweighed ($Mass_{sat}$). Leaf water storage capacity (LWSC) was calculated by using the following equation:

 $LWSC = \frac{Mass_{sat} - Mass_{dry}}{LA \times 2}$

in which LA is the leaf area of sampled leaves.

2.7. Statistical analyses

The normality of data was tested using Shapiro-Wilk test, while the homoscedasticity was tested using Bartlett's test. Data obtained from physiological (gas exchange, chlorophyll *a* fluorescence, and Dualex parameters), hydric status (leaf osmotic potential), and leaf/twig Na⁺ and Cl⁻ concentrations were analyzed by two-way analysis of variance (ANOVA) using the treatments and time as the sources of variation. Leaf/twig Δ Na⁺ and Δ Cl⁻ concentrations, and leaf 'wettability' parameters among species were analyzed by one-way ANOVA using species as the sources of variation. All the means were separated by Fisher's least significant difference (LSD) post-hoc test ($P \leq 0.05$). All statistical analyses were conducted using GraphPad (GraphPad, La Jolla, CA, USA). Heatmap was generated using GraphPad software, using data obtained from the ratio between controls and salt-nebulized plants, in which values near 0 mean low tolerance to saline aerosol, whereas values near 1 mean high tolerance.

3. Results and discussion

The saline aerosol can strongly influence plant physiology and growth due to the accumulation of high amounts of Na⁺ and Cl⁻ into plant tissues, which are massively translocated (i.e., tips of leaves and twigs) leading eventually to plant death (Ferrante et al., 2011; Spanò and Bottega, 2016). Once the salt accumulates on the leaf surface, it can enter the leaf through stomata or the cuticle (rapid and slow absorption, respectively; Du and Hesp, 2020; Kim et al., 2011). As expected, Na⁺ and Cl⁻ accumulated in the leaves of all SN plants at 10 and 20 days according to the time of the treatment (Fig. 1), except for E-SN plants, which strongly accumulated Cl⁻ even at 10 days (59 times higher than



Fig. 1. Leaf Na⁺ and Cl⁻ contents. Na⁺ and Cl⁻ accumulation (expressed as mg g⁻¹ of dry weight; DW) in leaves of *Photinia* × *fraseri* (P-; a,d), *Escallonia rubra* (E-; b, e) and *Feijoa sellowiana* (F-; c,f). Treatments applied were control (-Cnt) and nebulization with a solution of 100 mM NaCl (-SN). Means (\pm SD; n = 3) with the same letter are not significantly different after two-way ANOVA using nebulization treatment and time as source of variations, followed by LSD post-hoc test ($P \le 0.05$).

relative control; Fig. 1e).

The plant morphological characteristics, such as plant architecture, leaf morphology, and wettability can determine the amount of NaCl effectively trapped by the plant and therefore, potentially absorbed by leaf (Ahmad and Wainwright, 1976; Du and Hesp, 2020; Farieri et al., 2016). Among SN plants, E-SN absorbed higher amounts of Na⁺ and Cl⁻ in leaves than P- and F-SN plants at both sampling times (Fig. 2). On the contrary, P-SN plant leaves had the lowest Na⁺ concentrations at both sampling times.

The contact angle of water droplets on leaves and leaf water droplet retention parameters can be good indicators to assay how the drop impact occurs on leaves (Aryal and Neuner, 2010; Roth-Nebelsick et al., 2022). According to the judgment criteria for leaf wettability, F-SN leaves were the least wettable for both adaxial and abaxial leaf surfaces, showing the lowest values in the water droplet retention for the abaxial leaf surface (Table 1). An opposite situation was observed for E-SN leaves with the highest wettability values (i.e., lowest contact angle) for the abaxial leaf surface and in the water droplet retention for both surfaces (65.1° and around 36.5°, respectively). In view of the above, the E-SN leaves can absorb high amounts of Na⁺ and Cl⁻ due to their morphological characteristics that made their abaxial surface more wettable than F-SN and P-SN ones. According to the abovementioned results, F-SN leaves should have shown the lowest Na⁺ and Cl⁻ accumulation, but this was not the case for Na⁺ (Fig. 1c). The reason for the Na⁺ contents observed in F-SN plants can be partially explained by the fact that F-SN leaves showed the highest leaf water storage capacity values among the analyzed plant species (Table 1). Probably, in the unwettable abaxial F-leaf surface (rich in trichomes), after 1 min of nebulization, the water managed to penetrate the surface structures, squeezing out the air contained and making the abaxial surface more wettable.

In twig tissues, higher Na⁺ and Cl⁻ concentrations were detected in SN plants compared to controls, both at 10 and 20 days of SN (Fig. 3). However, no differences in Na⁺ and Cl⁻ contents in P-SN, and only for Cl⁻ in F-SN plants were observed between 10 and 20 days (Fig. 3a,d,f). Furthermore, among SN treatment, at 10 days no differences in Na⁺ concentrations were observed between E- and F-SN plants, with E- that also had the highest Cl⁻ concentration followed by F- and P- plants (Fig. 4a). At 20 days a pattern comparable to leaves were observed in twigs (Fig. 4b). The presence of higher contents of Na⁺ and Cl⁻ on twig tissues in SN plants than in respective controls, indicates that the foliage took up these ions and then translocated them throughout the plant, possibly via the phloem (Lohaus et al., 2000). The TF analysis highlighted that F-SN leaves translocated more Na⁺ and Cl⁻ in twigs than other species at 10 days. Conversely, E-SN leaves showed a low propensity to translocate Na⁺ and Cl⁻ in twigs, as confirmed by the lowest values of TF (Fig. 4c). An opposite trend was observed at 20 days, in which TF values were highest in E-SN leaves for Na⁺. No statistical differences among species were observed for Cl⁻ (Fig. 4d) in relation to the treatments.

Table 1

Contact angle of water droplets on leaves, leaf water droplet retention, and leaf water storage capacity parameters of *Photinia* \times *fraseri* (P), *Escallonia rubra* (E) and *Feijoa sellowiana* (F) plants using a 100 mM NaCl solution.

Species	Contact angle (°)		Water droplet retention (°)		Leaf water storage capacity (mg cm ⁻²)
	Adaxial	Abaxial	Adaxial	Abaxial	Whole leaf
Р	$\begin{array}{c} 64.2 \\ \pm \ 7.9^{b} \end{array}$	$\begin{array}{c} 69.7 \\ \pm \ 5.7^{b} \end{array}$	$\begin{array}{c} 32.2 \\ \pm \ 3.8^{\mathrm{b}} \end{array}$	$\begin{array}{c} 23.2 \\ \pm \ 4.2^{\mathrm{b}} \end{array}$	1.8 ± 0.1^{c}
Е	$\begin{array}{c} 62.8 \\ \pm \ 6.9^{\mathrm{b}} \end{array}$	$\begin{array}{c} 65.1 \\ \pm \ 7.4^{c} \end{array}$	$\begin{array}{c} 36.3 \\ \pm \ 5.6^{\rm a} \end{array}$	$\begin{array}{c} 36.6 \\ \pm \ 3.6^{\rm a} \end{array}$	$\textbf{2.9}\pm\textbf{0.4}^{b}$
F	$73.0 \\ \pm 8.3^{\rm a}$	$\begin{array}{c} 134.6 \\ \pm \ 6.7^{\mathrm{a}} \end{array}$	$\begin{array}{c} 31.2 \\ \pm \ 3.4^{b} \end{array}$	$\begin{array}{c} 17.5 \\ \pm \ 3.2^{\rm c} \end{array}$	3.9 ± 0.5^a

Contact angle of water droplets on leaves and leaf water droplet retention values are the mean \pm SD (n = 20), while leaf water storage capacity values are the mean \pm SD (n = 10). Means with the same letter are not significantly different following the one-way ANOVA test using the species as variability factor; means were separated by Fisher's least significant difference (LSD) post-hoc test.

Several authors consider the translocation of potentially harmful ions from leaves to other plant organs (e.g., twigs and roots) via the phloem as a convenable mechanism to prevent excessive ion accumulation (Lima et al., 2021; Lohaus et al., 2000; Munns, 2005; Zhang et al., 2020).

The different Na⁺ and Cl⁻ accumulation in leaves of the selected species, influenced by their extent of 'wettability' and translocation mechanisms, have altered the plant physiological parameters. A typical effect linked to the excessive accumulation of Na⁺ and Cl⁻ in the leaf tissue is the onset of cell osmotic imbalances (Calzone et al., 2020; Mereu et al., 2011; Sánchez-Blanco et al., 2004; Tezara, 2003). In our experiment, all SN-plant species showed a decline of osmotic potential compared to Cnt at both 10 (-18, -163 and -54 %; P, E and F, respectively) and 20 days (Fig. 5); but only in E- and F-SN plants was observed a further decrease at 20 days (-257 and -141 %; for E and F, respectively; Fig. 5b,c).

Once Na⁺ and Cl⁻ are inevitably absorbed, cellular osmotic adjustments are necessary to increase the cell turgor potential to balance the osmotic pressure of Na⁺ and Cl⁻ sequestered into the vacuole (Calzone et al., 2019; Guidi et al., 2016; Munns and Tester, 2008). The increase in the leaf osmotic potential is usually associated with a rapid and drastic stomatal closure to reduce water losses, which, together with the phytotoxic effect of ions, have consequences on g_s , CO₂ assimilation, and maximal efficiency of the PSII (Calzone et al., 2021; Tezara, 2003; Zhang et al., 2022). In our study, P_n declined in all SN species at 10 days (–58, –82, and –34 % compared with Cnt, for P-, E-, and F- species, respectively; Fig. 6a,b,c). A parallel decline in g_s was also observed in E- and F-SN plants (–85 and –44 %, respectively; Fig. 6e,f), while C_i values severely increased only in P-SN plants (+25 %; Fig. 6 g).

The limitation of the CO₂ assimilation rate is a typical physiological response of plants subjected to saline stress (Calzone et al., 2021; Farieri



Fig. 2. Leaf ΔNa^+ and ΔCl^- concentrations in saline nebulized plants. ΔNa^+ and ΔCl^- concentrations between saline nebulized plants (solution of 100 mM NaCl; -SN) and relative controls (expressed as mg g⁻¹ of dry weight, DW) in leaves of *Photinia* × *fraseri* (P-), *Escallonia rubra* (E-) and *Feijoa sellowiana* (F-) after 10 (moderate stress conditions; a) and 20 days (severe stress conditions; b) of nebulization. Means (\pm SD; n = 9) with the same letter are not significantly different after one-way ANOVA using species as a source of variations, followed by LSD post-hoc test ($P \le 0.05$).



Fig. 3. Twig Na⁺ and Cl⁻ concentrations. Na⁺ and Cl⁻ accumulation (expressed as mg g⁻¹ of dry weight, DW) in twigs of *Photinia* × *fraseri* (P-; a,d), *Escallonia rubra* (E-; b,e), and *Feijoa sellowiana* (F-; c,f). Treatments applied were control (-Cnt) and nebulization with a solution of 100 mM NaCl (-SN) at 10 days and 20 days. Means (\pm SD; n = 3) with the same letter are not significantly different after two-way ANOVA using nebulization treatment and time as source of variations, followed by LSD post-hoc test ($P \le 0.05$).



Fig. 4. Twig ΔNa^+ and ΔCl^- concentrations, and Na⁺ and Cl⁻ translocation factors in saline nebulized plants. ΔNa^+ and ΔCl^- concentrations between saline nebulized plants (solution of 100 mM NaCl; -SN) and relative controls (-Cnt, expressed as mg g^{-1} of dry weight, DW) in twigs of Photinia $\times \mathit{fraseri}$ (P-), Escallonia rubra (E-) and Feijoa sellowiana (F-) after 10 (moderate stress conditions; a) and 20 days (severe stress conditions; b) of nebulization. Translocation factor (TF) values, from leaves to twigs for Na⁺ and Cl⁻ in SN plants, were analysed at the same times previously reported (10 and 20 days; c and d). Means $(\pm SD; n = 9)$ with the same letter are not significantly different after one-way ANOVA using species as a source of variations, followed by LSD post-hoc test ($P \leq 0.05$).



Fig. 5. Leaf osmotic potential. Osmotic potential (Ψ_{π} ; expressed as MPa) in leaves of *Photinia* × *fraseri* (P-, a), *Escallonia rubra* (E-, b) and *Feijoa sellowiana* (F-, c). Treatments applied were control (-Cnt) and nebulization with a solution of 100 mM NaCl (-SN). Means (\pm SD; n = 3) with the same letter are not significantly different after two-way ANOVA using nebulization treatment and time as source of variations, followed by LSD post-hoc test ($P \leq 0.05$).



Fig. 6. Leaf gas exchange analysis. Gas exchange parameters of *Photinia* × *fraseri* (P-; a,d,g), *Escallonia rubra* (E-; b,e,h) and *Feijoa sellowiana* (F-; c,f,i). Net photosynthetic rate (P_n; expressed as μ mol CO₂ m⁻² s⁻¹), stomatal conductance (g_s; expressed as mol m⁻² s⁻¹) and intercellular CO₂ concentration (C_i; expressed as μ mol mol⁻¹). Treatments applied were control (-Cnt) and nebulization with a solution of 100 mM NaCl (-SN). Means (\pm SD; n = 5) with the same letter are not significantly different after two-way ANOVA using nebulization treatment and time as source of variations, followed by LSD post-hoc test ($P \le 0.05$).

et al., 2016; Guidi et al., 2016; Tezara, 2003; Toscano et al., 2020; Zhang et al., 2022). When Na⁺ and Cl⁻ accumulated in leaf tissues, the impairment of photosynthetic performance can occur due to stomatal (restriction of CO₂ uptake) and/or non-stomatal (biochemically-related alterations) limitations, caused by both the negative impacts of ion accumulation on the leaf osmotic potential (ionic imbalance), and the direct toxicity to chloroplast metabolism (Calzone et al., 2020; Sarabi et al., 2019; Zhang et al., 2022). The parallel decline of P_n and g_s values observed in E- and F-SN plants suggests a strong influence of g_s on the CO₂ assimilation rate (Fig. 6b,c,e,f).

This is supportive of previous findings on native coastal plant species (Du and Hesp, 2020; Mereu et al., 2011; Puijenbroek et al., 2017; Sánchez-Blanco et al., 2003), and ornamental species grown under saline aerosol (Farieri et al., 2016; Toscano et al., 2020, 2021), highlighting that stomatal closure represents one of the first responses to saline stress when leaf osmotic adjustments take place (Calzone et al., 2019; Puijenbroek et al., 2017; Sarabi et al., 2019). Moreover, a first decrease in F_v/F_m values was only observed in P- and E-SN plants at 10 days (Fig. 7a,b). This condition could be attributable to a reduction in the CO₂ assimilation due to stomatal limitations, which generates a surplus of excitation energy in the thylakoid membranes (Lo Piccolo



Fig. 7. Chlorophyll *a* fluorescence analysis. Maximal quantum yield of chlorophyll-*a* fluorescence (F_v/F_m) in leaves of *Photinia* × *fraseri* (P; a), *Escallonia rubra* (E; b) and *Feijoa sellowiana* (F; c). Treatments applied were control (-Cnt) and nebulization with a solution of 100 mM NaCl (-SN). Means (\pm SD; n = 5) with the same letter are not significantly different after two-way ANOVA using nebulization treatment and time as sources of variations, followed by LSD posthoc test ($P \le 0.05$).

et al., 2020) and/or a direct result of salinity effects on the functional integrity of the photochemical apparatus (Mateos-Naranjo et al., 2013).

The different physiological responses found in P-SN plants (i.e., no differences in g_s with respect to controls and increasing values in C_i), highlighted non-stomatal limitations mainly constrained to plant photosynthesis (i.e., decreased photochemical PSII activity). Accumulation of Na⁺ and Cl⁻ in leaves can hinder photosynthetic components such as chlorophylls (dissolution of pigment-protein lipid complex in chloroplasts) and related enzymes (increase in activity of chlorophyllase) and/or proteins (Khare et al., 2020; Riaz et al., 2019; Sarabi et al., 2019). Several studies have shown that saline aerosol reduced the chlorophyll contents only in some species (Calzone et al., 2020; Farieri et al., 2016; Ferrante et al., 2011; Toscano et al., 2020), whereas others were unaffected (Farieri et al., 2016; Tezara, 2003; Toscano et al., 2022). Similar observations were made in the present study, as the Chl contents were reduced at 10 days only in P-SN plants (-10% to controls; Fig. 8a), whereas no changes were observed for E- and F-SN plants. These inconsistent findings result from different sensitivities and distinct metabolic adjustments of the selected plant species.

At 20 days, P_n further decreased in P-SN and F-SN plant species (-93, and -87 %, respectively Fig. 6a,c). The further decrease in P_n could be due to the occurrence of both stomatal and non-stomatal limitations to photosynthesis (i.e., lower g_s and lower F_v/F_m ; Fig. 6d,f; Fig. 7a,c). Therefore, we suggest that the early marked reduction in CO₂ assimilation observed in E-SN plants at 10 days and maintained at 20 days were due to the early occurrence of both limitation types to the photosynthetic process (Fig. 6b,e,h; Fig. 7b).

At 20 days, both P- and F-SN plants showed reductions in leaf Chl contents (-9 and -12 % to controls, respectively; Fig. 8a,c), whereas in E-SN plants the detected Chl values increased (Fig. 8b). The Chl increase in E-SN plants was probably due to an excessive loss of the leaf turgor, increasing the concentration of chloroplasts per unit area, interfering with the Chl measurements; and/or a possible physiological compensation response due to marginal leaf necrosis (Fig. 9c).

To allow a more direct and immediate visual comparison among the selected species, a heatmap of the ratio between Cnt- and SN-plants was performed (Fig. 9a,b). Using plant physiological indicators P_n , g_s , F_v/F_m , and Chl for the heatmap visualization is a reliable method to ensure quick and accurate detection of the degree of plant tolerance to environmental stress and thus make it easier for the selection of resistant plant species to saline aerosol. This approach was successfully adopted in previous works conducted on many ornamental species subjected to saline aerosol (Mereu et al., 2011; Toscano et al., 2020, 2021).

Our results highlighted that both P and F could tolerate a period of 10 days of constant SN by adopting different physiological strategies to handle high Na⁺ and Cl⁻ contents in leaves, though CO₂ assimilation processes were better preserved in F plants.

On the contrary, E plants showed high sensitivity to saline nebulization (Fig. 9a). As confirmed by the appearance of tip brown-reddish stipples, homogenously distributed in the interveinal adaxial leaf area (data not shown). At first sight, the results obtained for E and F could contrast with previous research conducted on the salt tolerance of these species, especially for E, since it is considered a moderately salt tolerant species (Valdez-Aguilar et al., 2011; Wu et al., 2001). Indeed, a previous work conducted by Cassaniti et al. (2009), shows that Escallonia plants were able to tolerate saline irrigation due to root compartmentalization of toxic ions thereby limiting their transport, and harmful effects, to the shoots. Notably, how salt water is administered (e.g. irrigation vs nebulization) and the NaCl concentrations used can strongly influence the final results (Spano and Bottega, 2016). It was reported that plants are often less tolerant to salt nebulization than irrigation (Benes et al., 1996; Spanò and Bottega, 2016), and plants which are considered tolerant to irrigation with saline water, can be more sensitive to saline nebulization, as observed for E plants in the present work. This could be due to a reduced ability of leaves to selectively exclude Na⁺ and Cl⁻ than roots causing severe metabolic alterations (Benes et al., 1996).



Fig. 8. Chlorophyll content. Chlorophyll (Chl) content of leaves (expressed as μ g cm⁻²) of *Photinia* × *fraseri* (P; a), *Escallonia rubra* (E; b) and *Feijoa sellowiana* (F; c). Treatments applied were control (-Cnt) and nebulization with a solution of 100 mM NaCl (-SN). Means (\pm SD; n = 10) with the same letter are not significantly different after two-way ANOVA using nebulization treatment and time as sources of variations, followed by LSD post-hoc test ($P \le 0.05$). When the F ratio of the interaction between the variability factors is not significant, letters indicate statistically significant differences between means over time. Significative statistical differences in Chl contents between treatments within the day of analysis were indicated by asterisks ($P \le 0.05$: *; $P \le 0.01$: **; $P \le 0.001$: ***).



Fig. 9. Control-saline nebulization ratio heatmap. Heatmap of the net photosynthetic rate (P_n), stomatal conductance (g_s), maximal quantum yield of chlorophyll-*a* fluorescence (F_v/F_m), and chlorophyll content (Chl) ratio between controls and SN plants after 10 (a) and 20 (b) days of treatment. Mean values near 0 (red) indicate low tolerance, whereas values around 1 (green) indicate tolerance to saline nebulization. Image (c) reported symptoms on the leaf surface of *Photinia* × *fraseri*, *Escallonia rubra* and *Feijoa sellowiana* leaves after 20 days of saline nebulization treatment.

At 20 days, all the analysed plants showed low ratio values in the physiological parameters and the presence of visible injuries, indicating low tolerance to prolonged saline nebulization (Fig. 9b,c). In particular, P- and F-SN plants showed visible foliar injury in the form of roundish dark-reddish necrosis and widespread chlorosis scattered among the leaf veins of the adaxial surface of completely expanded leaves. In E-SN plants, brown-reddish stipples coalesced by inducing premature leaf death. Physiological results from the present experiment suggest that the

three selected plant species are all unsuitable for areas prone to high intensity of saline aerosol (i.e., high frequency/amplitude of saline aerosol exposure), as confirmed by the macroscopic responses and ornamental quality point of view (Fig. 9c).

4. Conclusion

This study points out that Na⁺ and Cl⁻ leaf accumulation in the three

selected plant species was influenced by the extent of leaf 'wettability' and translocation mechanisms of toxic ions adopted by each plant species. From a physiological point of view, different responses to the saline nebulization stress were observed in relation to the species and the stress duration. The early reduction in net photosynthetic rate was caused by different limiting factors: P SN-plants have shown non-stomatal limitations to photosynthesis, F stomatal limitations, and E showed both factors. P and F were more tolerant than E plants under moderate stress conditions (at 10 days) while under severe stress conditions (at 20 days) all three plant species showed low tolerance to prolonged saline nebulization. This work highlights that non-destructive physiological parameters are reliable indicators to assay plant tolerance to SN, helping growers to screen ornamental species suitable for coastal green areas.

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CRediT authorship contribution statement

M. Landi: Conceptualization, Investigation, Methodology, Writing – review & editing. P. Vernieri: Conceptualization, Investigation, Writing – review & editing. E. Lo Piccolo: Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. G. Lauria: Data curation, Formal analysis, Investigation, Methodology. L. Cotrozzi: Data curation, Investigation, Methodology. M. Skoet: Formal analysis, Investigation, Methodology. D. Remorini: Writing – review & editing. R. Massai: Writing – review & editing. L. Guidi: Writing – review & editing. E. Pellegrini: Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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