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MODULATIONS OF STOMATAL DENSITY, LEAF PHYSIOLOGY, AND BIOCHEMICAL MARKERS IN 'SERAFIM' BASIL CULTIVAR INDUCED BY SALINITY

Elena-Iren OLARU (HÂNCU)[1*], Maria-Magdalena ZAMFIRACHE[1]

[1]Faculty of Biology, „Alexandru Ioan Cuza" University of Iași, Carol I Bd., no. 20A, 700505, Iași, Romania

Abstract: The anthocyanin pigmentation of the leaves, a distinctive trait of the Romanian purple basil cultivar 'Serafim' (*Ocimum basilicum* L.), raises the question of whether this genotype responds to salt stress through different mechanisms compared to green basil varieties. To answer this, plants were exposed to 100, 150, and 200 mM NaCl under laboratory and semi-open greenhouse conditions, while simultaneously evaluating their micromorphological, physiological, and biochemical responses. Results reveal a rapid non-enzymatic antioxidant response; polyphenols and antioxidant activity (DPPH) increased significantly from the lowest salinity level. Carotenoid content remained negligible, suggesting their photoprotective role is substituted by existing foliar anthocyanins. Stomatal behaviour diverged by environment: elevated NaCl decreased stomatal area while maintaining stable density in the lab, contrasting with dynamic density remodelling in the greenhouse. Ultimately, these data outline a unique salinity adaptation strategy built entirely upon the plant's innate anthocyanin resources.

Keywords: *Ocimum basilicum L.,* 'Serafim' purple, salt stress, stomatal density, physiological and biochemical response.

INTRODUCTION

Excessive soil salinity is one of the most severe abiotic challenges facing modern agriculture, leading to ionic toxicity, nutritional imbalances and osmotic stress, with direct negative effects on the growth, development and productivity of crops (Silva et al., 2011; Balasubramaniam et al., 2023).

Basil (*Ocimum basilicum* L.), an aromatic species of the Lamiaceae family, is of great economic and scientific importance due to its high content of phenolic compounds and bioactive volatile oils. Within the species, varieties with violet-purple pigmentation exhibit a distinct metabolic profile, differing from that of green varieties, with direct implications for their strategies in responding to abiotic stress (Salles Trevisan et al., 2006; Koroch, Simon and Juliani, 2017; Nassar et al., 2020; Azizah et al., 2023).

The Romanian variety 'Serafim', approved by the Buzău Research and Development Institute for Vegetable Crops in 2017, is a semi-early variety of purple basil, with leaves that are serrated at the edges and intensely pigmented, valued both for its ornamental and culinary qualities, as well as a natural source of food colourings (Vînătoru et al., 2019; Balanescu et al., 2020). In this context, characterising this genotype's response to salinity stress is essential for developing cultivation strategies suited to areas in Romania prone to salinisation.

The aim of this study was to assess how stomatal density and size, physiological parameters associated with the photosynthetic apparatus (chlorophyll fluorescence, assimilatory pigment content) and the biochemical profile (phenolic compounds, total and enzymatic antioxidant activity) of the test plants of the 'Serafim' variety change under experimentally induced salt stress with NaCl, under two distinct cultivation conditions - laboratory and semi-open greenhouse.

MATERIALS AND METHODS

Biological material

The biological material consisted of seeds of the indigenous purple basil variety (*Ocimum basilicum* L.) 'Serafim' (batch no. 1BZ3231-1BZ01), sourced from the Buzău Research and Development Institute for Vegetable Growing (SCDL Buzău). The plant forms a semi-erect, densely branched bush of an intense violet-purple colour, due to its high content of anthocyanin pigments, and is classified within the Linalool or Linalool-Eugenol chemotype (Burducea et al. 2015).

Cultivation conditions and saline treatment applied

The experimental design was structured into two distinct research stages. Experiment I was conducted under strictly controlled laboratory conditions, ensuring a constant temperature of 22–24°C and a photoperiod of 17 hours of light (LED light source) alternating with 7 hours of darkness. Experiment II was carried out under field conditions, inside a semi-open greenhouse located in the village of Popricani, Iași County (coordinates: 47.278°N, 27.524°E). The microclimatic conditions within the greenhouse involved daytime temperatures of 22–23°C and nighttime temperatures of 18–20°C, with the plants receiving natural light, attenuated by the covering film.

To assess stress tolerance, salinity was artificially induced by applying progressive concentrations of sodium chloride (NaCl) of 100, 150 and 200 mM. The saline solutions were administered in three successive stages, spaced at 14-day intervals. The plants' response was analysed by continuous comparison with a control group, maintained under optimal conditions (0 mM NaCl) (Arif et al., 2020; Balasubramaniam et al., 2023).

***Correspondence**: Elena-Iren OLARU (HÂNCU), „Alexandru Ioan Cuza" of Iași University, Faculty of Biology, Carol I Bd., no. 20A, 700505, Iași, Romania, email: elenairenh@gmail.com*

Micromorphometric analyses

Micromorphological analysis of the abaxial leaf epidermis, aimed at determining stomatal density and area, was carried out using scanning electron microscopy (SEM) with a Tescan Vega II - SBH system. Preparation of the plant samples began with chemical fixation in 2.5% glutaraldehyde (prepared in 0.1 M phosphate buffer, pH 7.4), followed by gradual dehydration in acetone baths with a concentration gradient. Subsequently, the samples were subjected to critical-point drying (using the EMS K850) and coated with a conductive gold film, 5–15 nm thick (EMS 550x sputter coater), in accordance with established protocols (Xu and Zhou, 2008; Pathan, Bond and Gaskin, 2010).

Physiological measurements

In vivo analysis of chlorophyll fluorescence was carried out using a portable fluorimeter (Hansatech FMS II), with the aim of assessing the φPSII parameter. The measurements were taken on mature, fully developed leaves taken from the middle node of the stem, with 10–15 measurements recorded for each experimental treatment. The quantification of assimilatory pigments (chlorophyll a, chlorophyll b and carotenoids) was carried out using the spectrophotometric method, based on extracts in 96% ethanol (Wellburn, 1994; Norazah et al., 2020). Absorbance values were measured at wavelengths of 664, 649 and 470 nm using a Shimadzu 1240 UV-mini spectrophotometer.

Biochemical analyses

Total polyphenol content was assessed spectrophotometrically by means of the Folin-Ciocâlteu procedure (Herald, Gadgil and Tilley, 2012), reading sample absorbance at 765 nm against a gallic acid calibration curve. Flavonoid levels were quantified through an aluminium chloride colourimetric assay (Herald, Gadgil and Tilley, 2012), with absorbance recorded at 510 nm and values expressed as quercetin equivalents. To evaluate overall antioxidant capacity, the DPPH (2,2-diphenyl-1-picrylhydrazyl) assay was applied, relying on the extracts' capacity to scavenge the DPPH free radical; this was quantified via solution decolourisation, with absorbance read at 517 nm (Sharma and Bhat, 2009; Behrendorff et al., 2013).

In the case of laboratory-grown plants (Experiment I), an additional set of biochemical determinations was performed, covering the activity of the antioxidant enzymes superoxide dismutase (SOD, assessed via the NBT method) and peroxidase (POD, assessed through ortho-dianisidine oxidation), together with total protein content, quantified using the Bradford method (Bradford, 1976; Artenie, Ungureanu and Negură, 2008).

Statistical analysis

The experimental results, obtained from three independent determinations (in triplicate), are presented as the mean ± standard deviation (SD). Data analysis was carried out using GraphPad Prism software. To determine statistical significance, analysis of variance (ANOVA) was used, supplemented by a post-hoc test, with a significance level of $p<0.05$.

RESULTS AND DISCUSSION

Micromorphometric responses of the stomatal apparatus

Under laboratory conditions, the 'Serafim' variety did not exhibit any significant changes in stomatal density in response to salt stress, with the number of stomata remaining stable regardless of the concentration of NaCl applied. The stomatal area, however, showed a progressive reduction: a dramatic decrease at 100 mM NaCl, a partial recovery at 150 mM NaCl (remaining significantly below the control level) and the lowest level at 200 mM NaCl.

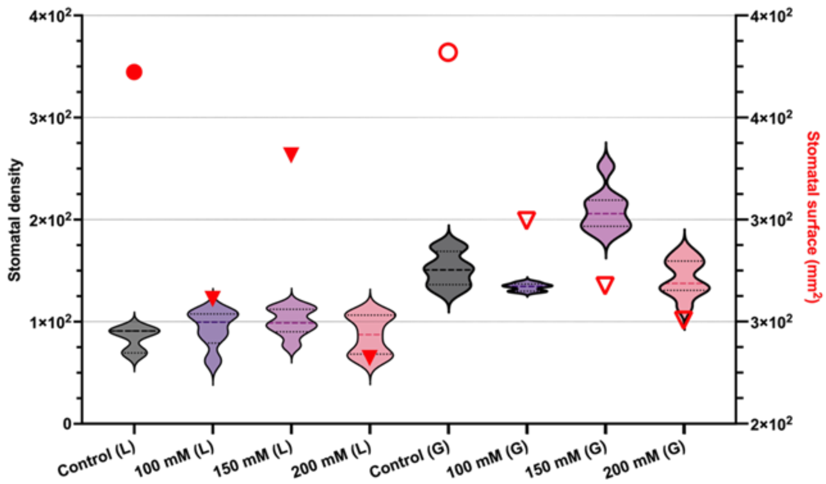

Fig. 1. Stomatal density of *Ocimum basilicum* L. 'Serafim' plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; (L) – Laboratory conditions, (G) – Semi-open greenhouse conditions. On the secondary axis (in red) is marked the stomatal surface area (●-Control, ▼- significant decrease in stomatal surface area).

In the semi-open greenhouse, stomatal density increased progressively, peaking at 150 mM NaCl, followed by a decrease at 200 mM NaCl (though the values remained significantly higher than the control) – a phenomenon interpreted as a possible strategy employed by the test plants to maintain gas exchange, supported by the antioxidant capacity of the anthocyanin pigments in their leaf mesophyll (Kovinich et al., 2015;

Cirillo et al., 2021). Stomatal area followed a specific pattern: an increase at 100 mM NaCl (acclimatisation phase, with fewer, but larger ones), a sharp decrease at 150 mM NaCl (remodelling phase, with more numerous and smaller stomata) and a return to values close to the control at 200 mM NaCl (possible late stabilisation phase).

Compared with green basil varieties, the ‘Serafim’ variety appears, under laboratory conditions, to rely more on a reduction in stomatal area whilst maintaining density, whilst in the semi-open greenhouse, stomatal remodelling predominates through the combined adjustment of density and size - a more pronounced micromorphological plasticity under conditions close to those of natural cultivation (Barbieri et al., 2012; Chaplin, Merchant and Salter, 2025).

Chlorophyll fluorescence

Under laboratory conditions, plants of the ‘Serafim’ variety demonstrated remarkable resistance to moderate salt stress, with significant differences in φPSII compared with the control only becoming apparent at 200 mM NaCl. At 100 mM NaCl, increased variability in the values was observed, possibly representing an early adaptive response phase, in which anthocyanin pigments may contribute to the protection of photosystem II by absorbing potentially photoinhibitory light radiation (Gould, McKelvie and Markham, 2002; Steyn et al., 2002).

In the semi-open greenhouse, the inhibitory effects of NaCl on φPSII were statistically significant as early as the 100 mM concentration and intensified progressively, reaching a highly significant difference compared with the control at 200 mM NaCl, with no recovery in values at higher NaCl concentrations. This pattern of progressive inhibition suggests a higher photosynthetic sensitivity in plants of the ‘Serafim’ variety to the interaction between salinity and variable environmental factors in the greenhouse. (Fig. 2).

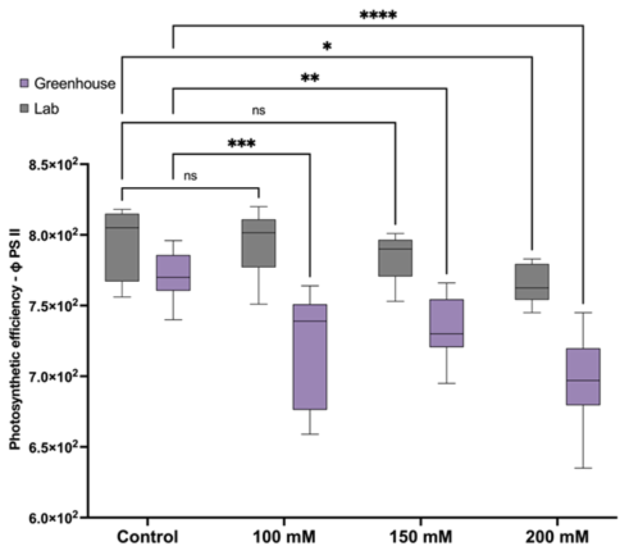

Fig. 2. Photosynthetic efficiency of *Ocimum basilicum* L. ‘Serafim’ plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; * - Statistically significant differences.

Assimilatory pigment content

In the laboratory, the chlorophyll a content remained relatively stable, with a slight decrease at intermediate concentrations (100 and 150 mM NaCl) and a recovery at 200 mM NaCl. Chlorophyll b, present at a very high baseline level, exceeding that of chlorophyll a in all treatments, showed a marked increase at 100 mM NaCl and a peak at 150 mM NaCl, followed by a reduction at 200 mM NaCl, suggesting active stimulation of the antenna system as a compensatory mechanism, until the tolerance limit was reached (Ashraf and Harris, 2013; Asrar et al., 2017).

The carotenoid pigment content was extremely low throughout the experiment, tending towards zero at 150 and 200 mM NaCl. The negligible level of this pigment fraction suggests that, in this purple variety, the plants’ photoprotective function is taken over by vacuolar anthocyanin pigments, which act as antioxidants and provide light screening (Xu et al., 2012; Mancarella et al., 2016; Zhang et al., 2025).

In the semi-open greenhouse, chlorophyll a level decreased moderately at 100 mM NaCl, with a slight recovery at 150 mM NaCl and a significant decline at 200 mM NaCl. Chlorophyll b increased noticeably at 100 and 150 mM NaCl, slightly exceeding chlorophyll a, before returning to the control level at 200 mM NaCl. Carotenoid pigments collapsed even at the lowest concentration tested (100 mM NaCl), remaining at a critically low level at higher NaCl concentrations. (Fig. 3).

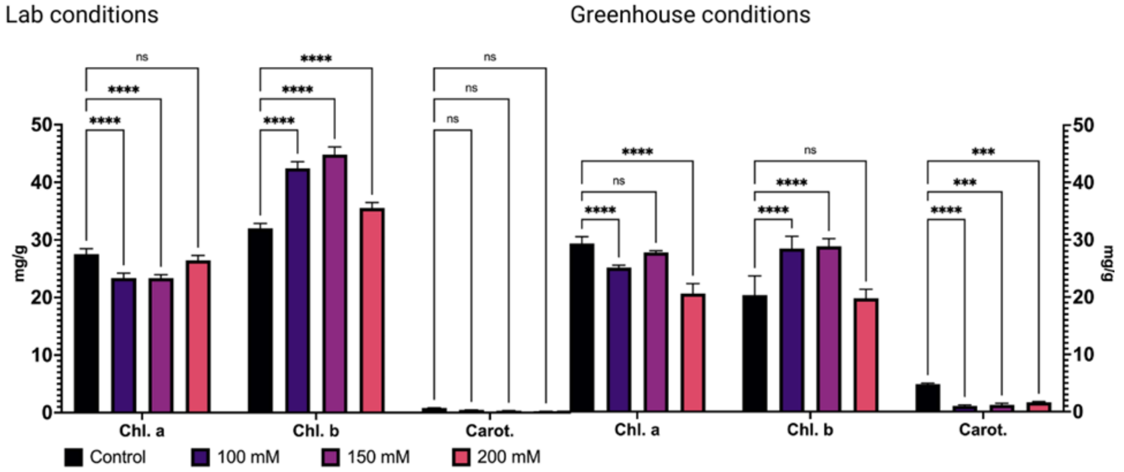

Fig. 3. Assimilatory pigments content of *Ocimum basilicum* L. 'Serafim' plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; * - Statistically significant differences.

Total polyphenol content

In the laboratory, all NaCl-treated variants recorded significantly higher polyphenol content than the control, with the highest accumulation observed at 100 mM NaCl (an increase of approximately 42 %), with a slight levelling off at higher concentrations.

In the semi-open greenhouse, the behaviour was the opposite to that observed in the laboratory: salt stress led to a significant reduction in polyphenol content compared with the control, suggesting that, under field conditions, the adaptive response capacity of 'Serafim' basil plants is limited by the possible simultaneous interaction of several stress factors (salinity, temperature fluctuations, fluctuating light intensity). The high polyphenol content recorded in the greenhouse control, compared with the laboratory control, suggests a natural stimulation of the biosynthesis of these compounds by environmental factors (UV radiation, temperature fluctuations), even in the absence of salinity stress (Ciriello et al., 2023; Meftahizadeh, Shahhoseini and Ghanbari, 2025). (Fig. 4).

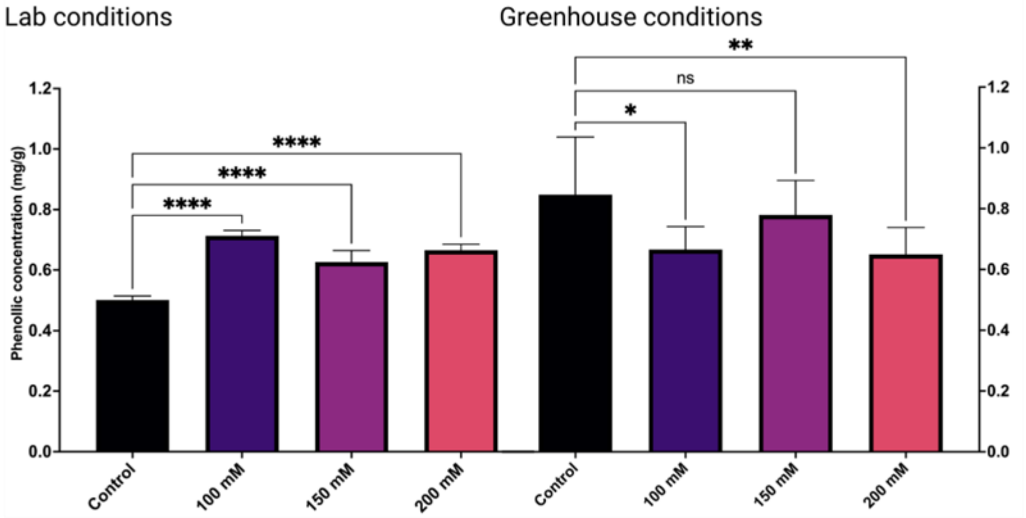

Fig. 4. Polyphenol content of *Ocimum basilicum* L. 'Serafim' plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; * - Statistically significant differences.

Flavonoid content

In the laboratory, the flavonoid content decreased significantly at 100 mM NaCl, recovered and slightly exceeded the control level at 150 mM NaCl, and at 200 mM NaCl it reached the maximum value observed in the experiment (an increase of approximately 26% compared with the control), data suggesting the activation of flavonoids in response to more intense salt stress, following an initial phase of inhibition (Wang et al., 2023).

In the semi-open greenhouse, variations in flavonoid content did not reach the threshold for statistical significance at any of the NaCl concentrations tested; the high dispersion of the values reflects the biological variability induced by heterogeneous growing conditions, a factor which limited the possibility of a consistent and reproducible response of the flavonoid metabolism of the test plants to salinity under field conditions. (Fig. 5).

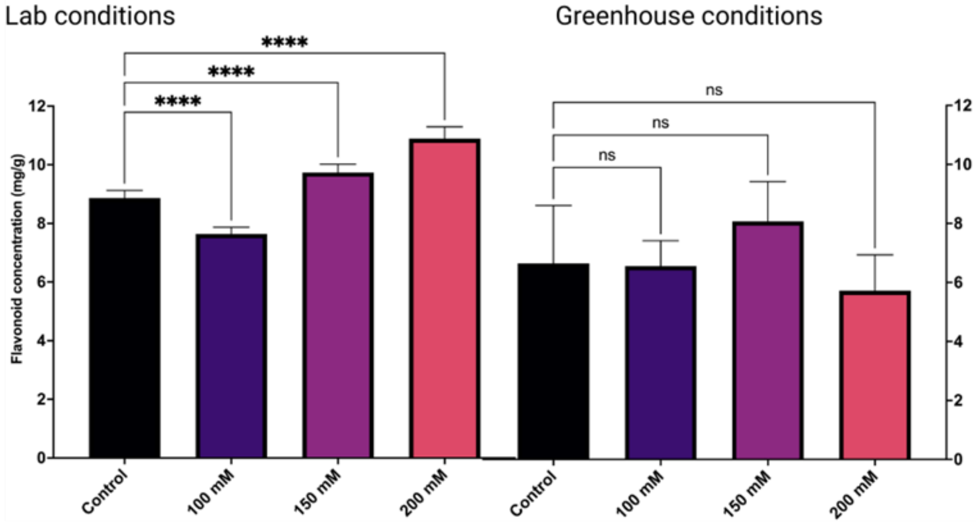

Fig. 5. Flavonoid content of *Ocimum basilicum* L. 'Serafim' plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; * - Statistically significant differences.

Total antioxidant activity (DPPH)

In the laboratory, the DPPH antioxidant activity of plants of the 'Serafim' variety increased sharply as early as a concentration of 100 mM NaCl, remaining at similar levels at 150 and 200 mM NaCl, with no significant differences between the three variants tested, indicating a rapid and robust response from the test plants, suggesting early activation of their antioxidant system once salt stress exceeds a minimum threshold (Ciriello et al., 2023; Kandil et al., 2023; Shabani et al., 2025).

In the semi-open greenhouse, the values of this biochemical parameter fluctuated, showing no dose-dependent pattern and lacking statistical significance, and the difference between the control in the greenhouse and that in the laboratory suggests that the field-grown basil plants began their growth from a pre-existing state of antioxidant alert, chronically induced by environmental factors, a reality which could explain the absence of a clear additional response to salt stress (Fig. 6).

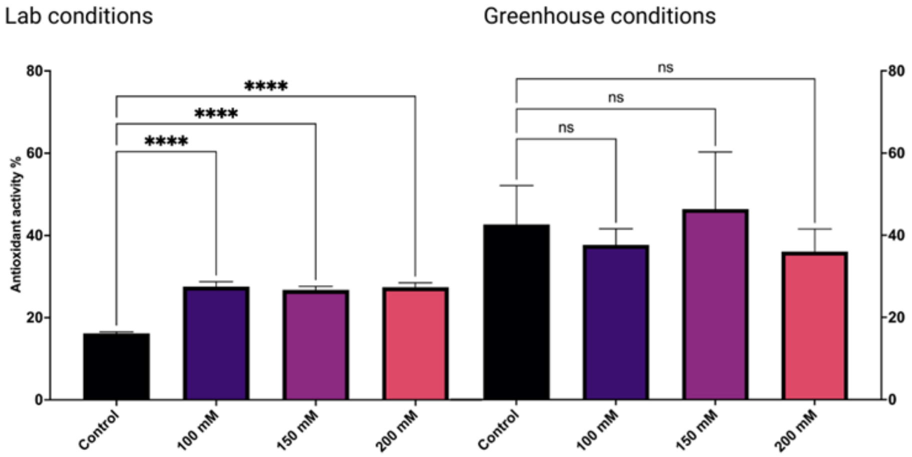

Fig. 6. Total antioxidant activity of *Ocimum basilicum* L. 'Serafim' plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; * - Statistically significant differences.

Antioxidant enzyme activity (SOD, POD)

Analyses carried out exclusively on plants grown in the laboratory showed that the control variant exhibited the highest superoxide dismutase (SOD) activity, at approximately 3.7% inhibition/g/min, with all three salt concentrations applied experimentally resulting in a significant decrease in SOD activity compared with the control, with values that were close to one another (a predominantly linear effect), with the threshold for enzymatic inhibition already reached at 100 mM NaCl, and no further notable changes observed at higher NaCl concentrations - a pattern of progressive inhibition similar to that reported for another aromatic plant, *Rosa damascena*, exposed to increasing concentrations of NaCl (Attia et al., 2020).

Peroxidase (POD) activity decreased at all tested salt concentrations, and the recovery observed at 200 mM NaCl was only partial, with values remaining significantly below the control level. This pattern suggests a limited capacity of plants of the 'Serafim' variety to fully neutralise severe oxidative stress through the re-induction of peroxidase activity, with the enzymatic mechanisms remaining inhibited throughout the salt treatment - a persistent inhibition of POD also reported in Genovese basil exposed to salinity (Tarchoune et al., 2010).

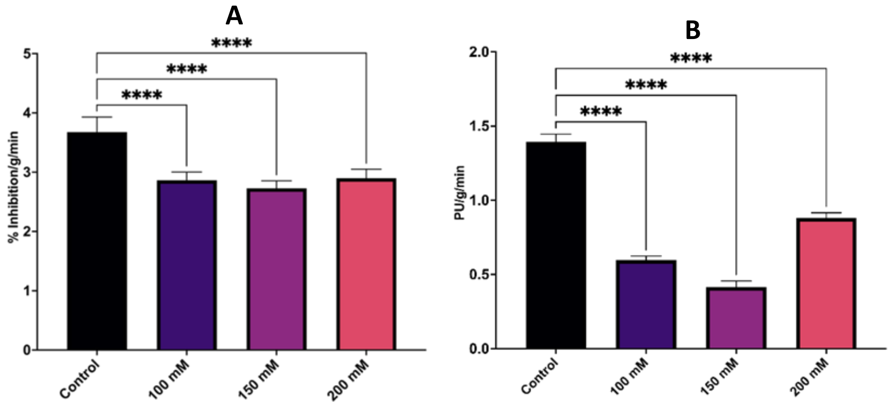

Fig. 7. SOD activity (A) and POD activity (B) of *Ocimum basilicum* L. 'Serafim' plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; * - Statistically significant differences.

Total protein content

At a concentration of 100 mM NaCl, a slight but statistically significant decrease in total protein content was observed in the test plants, reflecting an initial disruption of their protein metabolism. At 150 mM NaCl, the protein content returned practically to the control level, without any further stimulation of protein synthesis, whilst at 200 mM NaCl there was a sharp and highly significant increase in this biochemical parameter, which practically reached the maximum for the entire experimental series, a phenomenon interpreted as an active induction of defence protein synthesis, observed exclusively at the highest NaCl concentration tested, suggesting a relatively high activation threshold for the adaptive protein synthesis mechanisms of plants belonging to this variety (Vershinina et al., 2025).

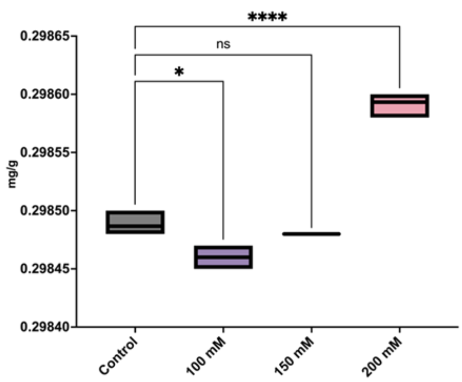

Fig. 8. Total protein content of *Ocimum basilicum* L. 'Serafim' plants under experimental conditions. Experimental variants: Control, 100 mM NaCl, 150 mM NaCl, 200 mM NaCl; * - Statistically significant differences.

CONCLUSIONS

The indigenous purple basil variety 'Serafim' exhibits an adaptive strategy based on the rapid and robust activation of non-enzymatic antioxidant defences, even at moderate concentrations of salt stress, as well as on stomatal remodelling that is strongly dependent on the growing environment: at the micromorphological level, under laboratory conditions there is a reduction in stomatal area whilst stomatal density is maintained, whereas in the semi-open greenhouse, remodelling is characterised by an increase in density and dynamic adjustment of stomatal size, suggesting that the micromorphological plasticity of the test plants is more pronounced under conditions closer to those found in nature.

At the physiological level, the photosystem II efficiency of plants of this variety remains stable up to 150 mM NaCl in the laboratory, supported by a compensatory increase in chlorophyll b content; however, at 200 mM NaCl their photosynthetic tolerance threshold is reached, marked by a simultaneous decrease in the φPSII value and chlorophyll b concentration, and the almost total disappearance of carotenoid pigments. In the greenhouse, the inhibition of φPSII is significant as early as 100 mM NaCl, following a linear-decreasing trend as the concentration of the experimentally applied NaCl solution increases. The low level of carotenoid pigment content under both cultivation conditions suggests that their photoprotective role is taken over by the vacuolar anthocyanin pigments specific to this purple variety - an effective substitution under moderate abiotic (saline) stress, but one that is overwhelmed under severe or combined stress.

From a biochemical point of view, the 'Serafim' variety triggers non-enzymatic defence mechanisms in the laboratory even at moderate concentrations of salt stress, possibly due to its pre-existing cellular pool, rich in anthocyanin pigments. Its non-enzymatic defence strategy is supported by a decrease in SOD and POD activity at all tested salt concentrations, with the difference that POD recovery at 200 mM NaCl is only partial, suggesting a limited enzymatic compensatory capacity, which is, however, offset by the abrupt induction of protein synthesis under conditions of maximum salt concentration. In the semi-open greenhouse, the plants start from a state of chronic antioxidant alert, induced by environmental factors, which explains the absence of a significant additional biochemical response to salt stress.

Overall, the research findings highlight a salinity tolerance strategy specific to plants of the ‘Serafim’ purple variety, based on the early activation of non-enzymatic antioxidant defences and the probable involvement of anthocyanin pigments in photoprotection; the data thus obtained have potential implications for the selection and agricultural utilisation of indigenous pigmented basil genotypes on land affected by salinisation.

AUTHORS CONTRIBUTIONS

Conceptualization, E.-I.O. and M.-M.Z.; methodology, E.-I.O.; data collection, E.-I.O.; data validation, E.-I.O. and M.-M.Z.; data processing, E.-I.O.; drafting – initial version, E.-I.O.; revision and editing, E.-I.O. and M.-M.Z.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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