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Polyamines mitigate the harmful effects of salt stress on the growth and gas exchange of nasturtium

Poliaminas atenuam os efeitos nocivos do estresse salino no crescimento e trocas gasosas de capuchinha

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ABSTRACT

Abiotic stresses are one of the major reasons for low crop productivity owing to the disturbances caused by them. Polyamines can be applied to mitigate the harmful effects of stress in plants. Nasturtium (*Tropaeolum majus* L.) is an ornamental, medicinal, and edible plant that is found in many countries. The objective of this work was to evaluate the effect of polyamines application and salt stress on the growth and leaf gas exchange of *T. majus*. The treatments to induce salt stress were as follows: 0 mM NaCl (no stress), 40 mM NaCl (moderate stress), 80 mM NaCl (severe stress), 40 mM NaCl + spermine (Spm), 40 mM NaCl + spermidine (Spd), 40 mM NaCl + putrescine (Put), 80 mM NaCl + Spm, 80 mM NaCl + Spd, and 80 mM NaCl + Put. Polyamines were applied every week for four weeks. The applications of Spd and Spm attenuated the harmful effects of moderate salt stress on plant height and leaf fresh mass. The application of Spm attenuated the harmful effects of moderate salt stress on stem diameter. The application of Spd attenuated the harmful effects of moderate salt stress on the number of buds, the stem fresh mass, and total fresh mass. The application of Spm attenuated the harmful effects of severe salt stress on stomatal conductance and transpiration rate and attenuated the harmful effects of moderate salt stress on stomatal conductance, net photosynthesis, and transpiration. The application of Spd attenuated the harmful effects of moderate salt stress on instantaneous water use efficiency and intrinsic water use efficiency. The applications of Spm and Spd application can attenuated the harmful effects of moderate salt stress on the growth and leaf gas exchange of nasturtium.

Index terms: *Tropaeolum majus*; edible flowers; abiotic stress; phytohormones.

RESUMO

Os estresses abióticos são uma das principais razões para a baixa produtividade das culturas devido aos distúrbios causados por eles. As poliaminas podem ser aplicadas para mitigar os efeitos nocivos do estresse nas plantas. A capuchinha (*Tropaeolum majus* L.) é uma planta ornamental, medicinal e comestível encontrada em muitos países. O objetivo deste trabalho foi avaliar o efeito da aplicação de poliaminas e estresse salino no crescimento e nas trocas gasosas foliares de *T. majus*. Os tratamentos para induzir o estresse salino foram os seguintes: 0 mM NaCl (sem estresse), 40 mM NaCl (estresse moderado), 80 mM NaCl (estresse severo), 40 mM NaCl + espermina (Spm), 40 mM NaCl + espermidina (Spd), NaCl 40 mM + putrescina (Put), NaCl 80 mM + Spm, NaCl 80 mM + Spd e NaCl 80 mM + Put. As poliaminas foram aplicadas semanalmente durante quatro semanas. As aplicações de Spd e Spm atenuaram os efeitos nocivos do estresse salino moderado na altura de plantas e na massa fresca das folhas. A aplicação de Spm atenuou os efeitos nocivos do estresse salino moderado no diâmetro do caule. A aplicação de Spd atenuou os efeitos nocivos do estresse salino moderado sobre o número de botões, massa fresca do caule e massa fresca total. A aplicação de Spm atenuou os efeitos nocivos do estresse salino severo na condutância estomática e na taxa de transpiração e atenuou os efeitos nocivos do estresse salino moderado na condutância estomática, fotossíntese líquida e taxa de transpiração. A aplicação de Spd atenuou os efeitos nocivos do estresse salino moderado na eficiência instantânea do uso da água e na eficiência intrínseca do uso da água. As aplicações de Spm e Spd podem atenuar os efeitos nocivos do estresse salino moderado no crescimento e nas trocas gasosas foliares de capuchinha.

Termos para indexação: *Tropaeolum majus*; flores comestíveis; estresse abiótico; fitormônios.

INTRODUCTION

Nasturtium (*Tropaeolum majus* L.-Tropaeolaceae), also known as capuchinha, chaguinha, or nastúrcio in Brazil, is an ornamental, edible, and medicinal plant with showy, simple, or double flowers (Melo et al., 2018). The flowers of nasturtium are rich in colors such as red, orange, or yellow. The orange phenotype is predominantly found and has a spicy flavor; therefore, it is used in salads,

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sauces, grilled dishes, and stuffed food items (Koike et al., 2015). Nasturtium originated from the region of Peru to Mexico. Owing to its rusticity and high adaptability, it can grow in various parts of the world (Brondani et al., 2016). Previous phytochemical studies on nasturtium have reported the presence of flavonoids (isoquercitrin and kaempferol glycoside), fatty acids (linoleic and oleic), and benzyl thiocyanate in *T. majus* leaves (Butnariu; Bostan, 2011; Gasparotto Junior et al., 2011). This plant has been used in the form of tea in traditional medicine to treat cardiovascular diseases, urinary tract infections, asthma, and constipation (Gomes et al., 2012).

Flowers have been important in religion, health, art, and food since ancient times. Edible flowers gained importance in the late 1980s due to the increase in the number of cookbooks, magazine articles, and interest in the nutritional value of these flowers (Pires et al., 2019). Compared with ornamental flowers, edible flowers are more vulnerable because their stems are cut too short and are stored without additional water supply (Fernandes et al., 2019). Petals are used to decorate desserts, ice cream, and salads, whereas the inflorescences are used for garnishes or decorations for many food preparations (Mlcek; Rop, 2011). Presently, most edible flowers are sold fresh, packed in small plastic packages, and kept in the refrigeration sections of stores (Rop et al., 2012).

The salinity of soil and water is a major environmental factor that limits agricultural production. Saline soil is frequent in arid, semi-arid, and coastal regions and is more widespread in irrigated areas because of improper management of irrigation and soil drainage (Phour; Sindhu, 2020). Salinization of soil is caused by natural or human activities that increase the amount of sodium chloride (NaCl) in the soil (Isayenkov; Maathuis, 2019; Silva et al., 2021). High levels of Na^+ and Cl^- ions in plant cells can affect photosynthesis, damage leaves, reduce water and nutrient absorption, cause osmotic stress, nutritional imbalance, ion toxicity, and chlorosis (Shavrukov, 2013). Salt stress has harmful effects on stomatal conductance, transpiration rate, and intercellular CO_2 concentrations by decreasing the rate of photosynthesis (Xu; Lu; Tong, 2018). NaCl inhibits net photosynthesis because the osmotic stress increases, which decreases the water potential and stomatal conductance (Khoshbakht; Asghari; Haghighi, 2018). Plants respond to salt stress by synthesizing biochemical substances and activating molecular mechanisms that act at cellular and plant-wide levels (Li et al., 2019). At the cellular level, the plant strategies include selective uptake or exclusion of ions, ion compartmentalization in the vacuole, and the synthesis and accumulation of organic solutes in the cytoplasm (Mishra; Tanna, 2017). At the whole plant level, the strategies include controlling the absorption of ions by the roots, controlling the transport of ions from the roots to the shoots, altering the photosynthetic pathway, modifying the activity of antioxidant enzymes, and altering the levels of phytohormones (Mishra; Tanna, 2017).

Polyamines are phytohormones that can be used to mitigate the harmful effects of abiotic stresses and to promote flowering in plants (Liu et al., 2015). Putrescine diamine (Put), spermidine triamine (Spd), and spermine tetramine (Spm) are arginine/ornithine-derived low-molecular-weight aliphatic polycations that are found in almost all living organisms (Lin et al., 2021). Polyamines play a role in many development processes of plants, such as cell division, embryogenesis, floral, and reproductive organ development, fruit ripening, root growth, leaf senescence, and response to biotic and abiotic stresses (Sarwat et al., 2013). Polyamines help in the tolerance and improvement of stress response in plants by interacting with macromolecules such as RNA, DNA, translation, and transcription complexes, and cell membranes as signaling molecules in the abscisic acid (ABA)-regulated stress response pathway and by generating H_2O_2, scavenging hydroxyl radicals, and increasing the production of antioxidants enzymes and metabolites (Minocha; Majumdar; Minocha, 2014).

Previous studies based on the salt stress and foliar polyamines in ornamental plants such as gladiolus (*Gladiolus gandavensis*) and frankenia (*Frankenia pulverulenta*) reported that salinity is a limiting factor for plant development. The foliar application of Spm mitigated the harmful effect of salt stress by increasing photosynthetic rates and the activity of antioxidant enzymes (Qian et al., 2021; Bueno; Cordovilla, 2021). The effects of polyamines application on the growth and physiology of *T. majus* has not yet been determined, and a detailed study on the acclimatization of this plant to abiotic stress has not been performed. The hypothesis of this work is that polyamines application reduces the harmful effects of salt stress in nasturtium. Thus, the objective of this work was to evaluate the effect of polyamines application and salt stress on the growth and leaf gas exchange of *T. majus*.

MATERIAL AND METHODS

The experiment was performed in a greenhouse of the Floriculture Sector (UEPE Belvedere), Department of Agronomy, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil. The maximum and minimum temperature and humidity during the experiment were 16 °C and

38%, 35 °C and 84%, respectively. The experiment was distributed into a completely randomized design with nine treatments and five replications. The treatments were: 0 mM NaCl (no stress), 40 mM NaCl (moderate stress), 80 mM NaCl (severe stress), 40 mM NaCl + spermine (Spm), 40 mM NaCl + spermidine (Spd), 40 mM NaCl + putrescine (Put), 80 mM NaCl + Spm, 80 mM NaCl + Spd ,and 80 mM NaCl + Put.

Nasturtium seeds (Semi-dobrada variety) were sown in a 128-cell polystyrene tray with a commercial substrate, (Tropstrato – (composition: pinus bark, vermiculite, PG mix 14.16.18, potassium nitrate, simple superphosphate, and peat; EC = 0.5 ±0.3 dS m^{-1}; pH = 5.8 ±0.3). Seedlings were transplanted in 1 L pots along with a commercial substrate (Tropstrato) after 10 days of sowing. Polyamines were diluted with deionized water to prepare the treatment solutions. Polyamines (Sigma-Aldrich®) were used at a concentration of 1 mM (Silva et al., 2022). Tween 20 (0.05%, Sigma-Aldrich®) was used as a surfactant to increase the uptake by the plant. The control treatment included deionized water and Tween 20 (0.05%). Plants were sprayed with around 10 mL of each solution or until they were completely wet. Polyamines applications were performed after every seven days for four weeks. Sodium chloride (NaCl – ACS reagent, ≥ 99.0%) was used to prepare the saline water treatments. NaCl was diluted using deionized water and applied daily to the plants. The plants were irrigated daily with saline water based on the plant's need to avoid drainage. The first application of polyamines was performed on the first day of salt stress (irrigation with saline water), which was 20 days after sowing. Plants were fertigated with 4 g L^{-1} of NPK 20–20–20 + micronutrients (Peters® Professional) once a week.

The plant height, stem diameter, the number of leaves, the number of flowers, the number of buds, and leaf area were determined after 60 days from the start of salt stress (DAS). The leaf area was measured using a leaf area integrator meter (LI-3100, Li-COR, Inc., Lincoln, NE, USA). To obtain the dry mass of each part of the plant, root, stem, and leaves were kept in an oven with forced air circulation at 70 °C for 72 h. Leaf area ratio (LAR) was determined using the following formula: leaf area (LA)/total dry mass (TDM). Specific leaf area (SLA) was determined using the following formula: LA/leaf dry mass (LDM). Leaf mass ratio (LMR) was determined using the following formula: leaf dry mass/TDM. Stem mass ratio was determined using the following formula: stem dry mass/TDM. Root mass ratio (RMR) was determined using the following formula: root dry mass/TDM. Growth rates were calculated based on the method given by Peixoto and Peixoto (2009).

Leaf gas exchange was evaluated at 60 DAS. An infrared gas analyzer (IRGA – LCPro model, ADC BioScientific Ltd.) was used to evaluate leaf gas exchange, and the readings were taken between 8:00 A.M. and 10:00 A.M. Net photosynthesis (A = μmol m^{-2} s^{-1}), stomatal conductance ($g_{s=}$ mol m^{-2} s^{-1}), internal carbon concentration (Ci = μmol mol air^{-1}), transpiration rate (E = mmol m^{-2} s^{-1}), instantaneous water use efficiency (WUE = A/E) and intrinsic water use efficiency (iWUE = A/g_s) were evaluated.

Data were analyzed by analysis of variance (ANOVA). For significant data (F test), a Scott-Knott test (p ≤0.05) was performed using the ScottKnott package (Jelihovschi; Faria; Allaman, 2014). A canonical variables analysis with confidence ellipses (p ≤0.01) was performed to determine the interrelationship between variables and factors using the candisc package (Friendly; Fox, 2021). An analysis of Pearson's correlation was performed using the corrplot package (Wey; Simko, 2021). All statistical analyses were performed using the Statistical program R (R Core Team, 2021).

RESULTS AND DISCUSSION

The application of polyamines mitigated the harmful effects of salt stress in nasturtium plants. The application of Spd and Spm mitigated the harmful effects of moderate salt stress on plant height. The application of Spm mitigated the harmful effects of moderate salt stress on stem diameter. Polyamines did not mitigate the harmful effects of salt stress on the leaf area and the number of leaves and flowers. Spd application mitigated the harmful effects of salt stress on the number of buds. Moderate salinity affected the plant shoot, leaf area, and the number of leaves and flowers more intensely (Figure 1).

The increase in salt stress reduced the shoot growth of nasturtium plants because salt stress inhibited plant growth by altering the activity of antioxidant enzymes and the level of free radicals in the leaves (Kamiab et al., 2014). Polyamines, especially Spd and Spm, mitigated the negative effects of salt stress and increased growth rates. This result was consistent with the results of previous studies that used frankenia (*Frankenia pulverulenta* L.) (Bueno; Cordovilla, 2021). Even though Put is efficiently absorbed and translocated to the shoots and has a positive effect on the discrimination of monovalent cations, its use in this study did not help the plants to mitigate the harmful effects of salt stress and even reinforced the negative effect of NaCl on shoot growth. This result was consistent with previous studies that used Indian tea (*Camellia sinensis* (L.) O. Kuntze) (Xiong et al., 2018).

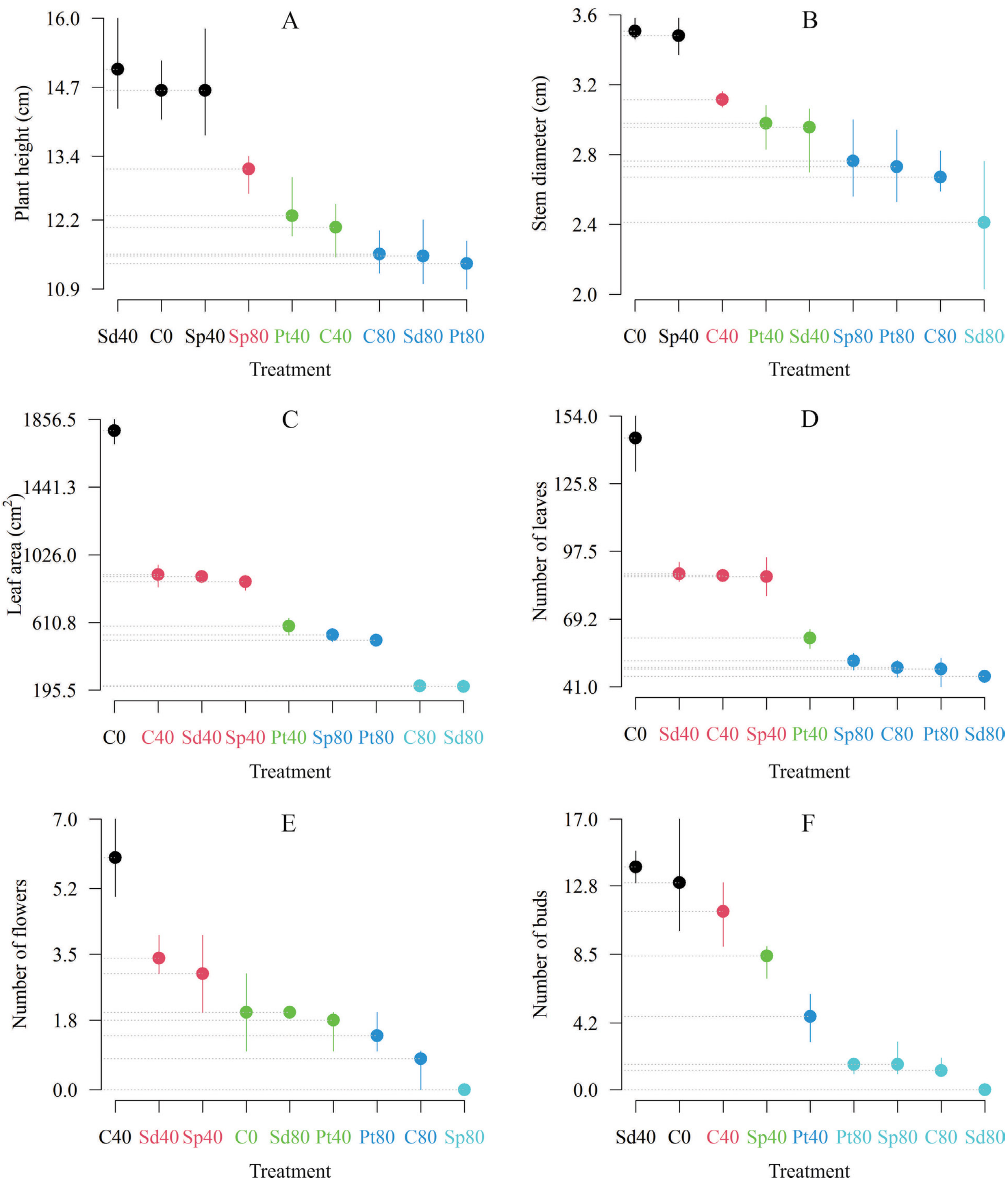

Figure 1: Plant height (A), stem diameter (B), leaf area (C), number of leaves (D), number of flowers (E), and number of buds (F) of *Tropaeolum majus* under salt stress and polyamine application. Bars are standard deviations for a mean of 5 replications. C0 = 0 mM NaCl; C40 = 40 mM NaCl; C80 = 80 mM NaCl; Sp40 = 40 mM NaCl + Spm; Sd40= 40 mM NaCl + Spd; Pt40 = 40 mM NaCl + Put; Sp80 = 80 mM NaCl + Spm; Sd80 = 80 mM NaCl + Spd; Pt80 = 80 mM NaCl + Put.

Leaves fresh mass, stem fresh mass and total fresh mass were higher in plants without stress. However, the application of Spd reduced the harmful effects of saline stress compared with the other treatments. Fresh masses were greatly affected by both moderate and severe salinities (Figure 2).

The reduction in plant fresh mass was higher in plants under stress because the water uptake was reduced due to the decrease in the osmotic potential in plant cells (Negrão; Schmöckel; Tester, 2017). Polyamines, especially Spm and Spd, mitigated the harmful effects of salt stress on the fresh mass of nasturtium plants because of the positive effect of polyamines on the various osmolytes present in plants under stress, which increased salt tolerance (Serna et al., 2015).

Leaf dry mass, stem dry mass, and total dry mass were higher in plants without stress. However, the applications of Spd and Spm mitigated the harmful effects of moderate salt stress compared with other treatments. The application of Put had a similar effect compared with the control on root dry mass (Figure 3).

Plants treated with polyamines are more acclimatized to salt stress. This is due to changes in ROS production, regulation of activity, and increase in oxidative enzymes caused by polyamine metabolism, which prevents lipid peroxidation and decreases H_2O_2 content, and neutralizes oxidative damage (Talaat, 2015). Similar results were found in a study performed on bougainvillea plants (*Bougainvillea buttiana* Wild.) (Lin et al., 2021).

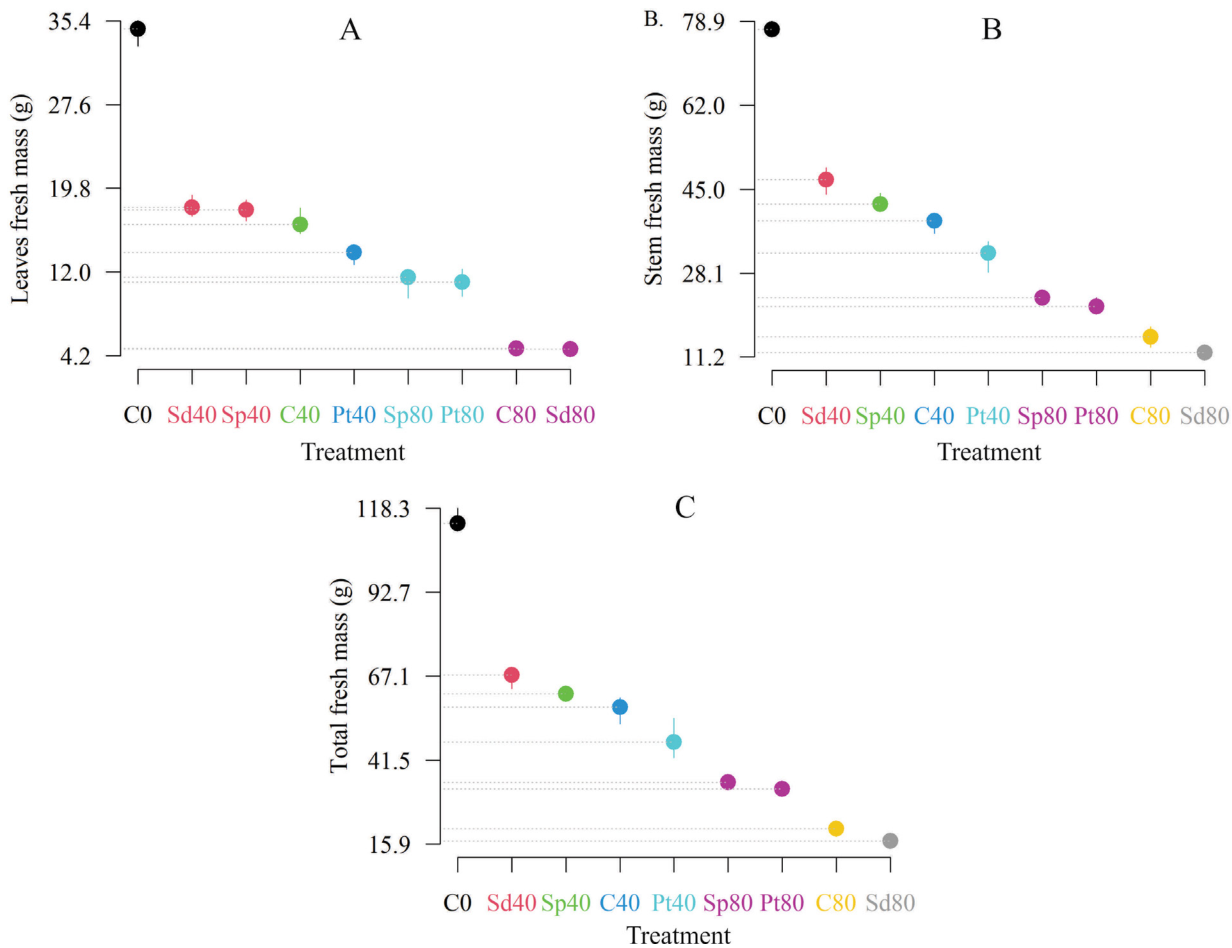

Figure 2: Leaves fresh mass (A), stem fresh mass (B) and total fresh mass (C) of *Tropaeolum majus* under salt stress and polyamine application. Bars are standard deviations for a mean of 5 replications. C0 = 0 mM NaCl; C40 = 40 mM NaCl; C80= 80 mM NaCl; Sp40 = 40 mM NaCl + Spm; Sd40 = 40 mM NaCl + Spd; Pt40 = 40 mM NaCl + Put; Sp80 = 80 mM NaCl + Spm; Sd80 = 80 mM NaCl + Spd; Pt80 = 80 mM NaCl + Put.

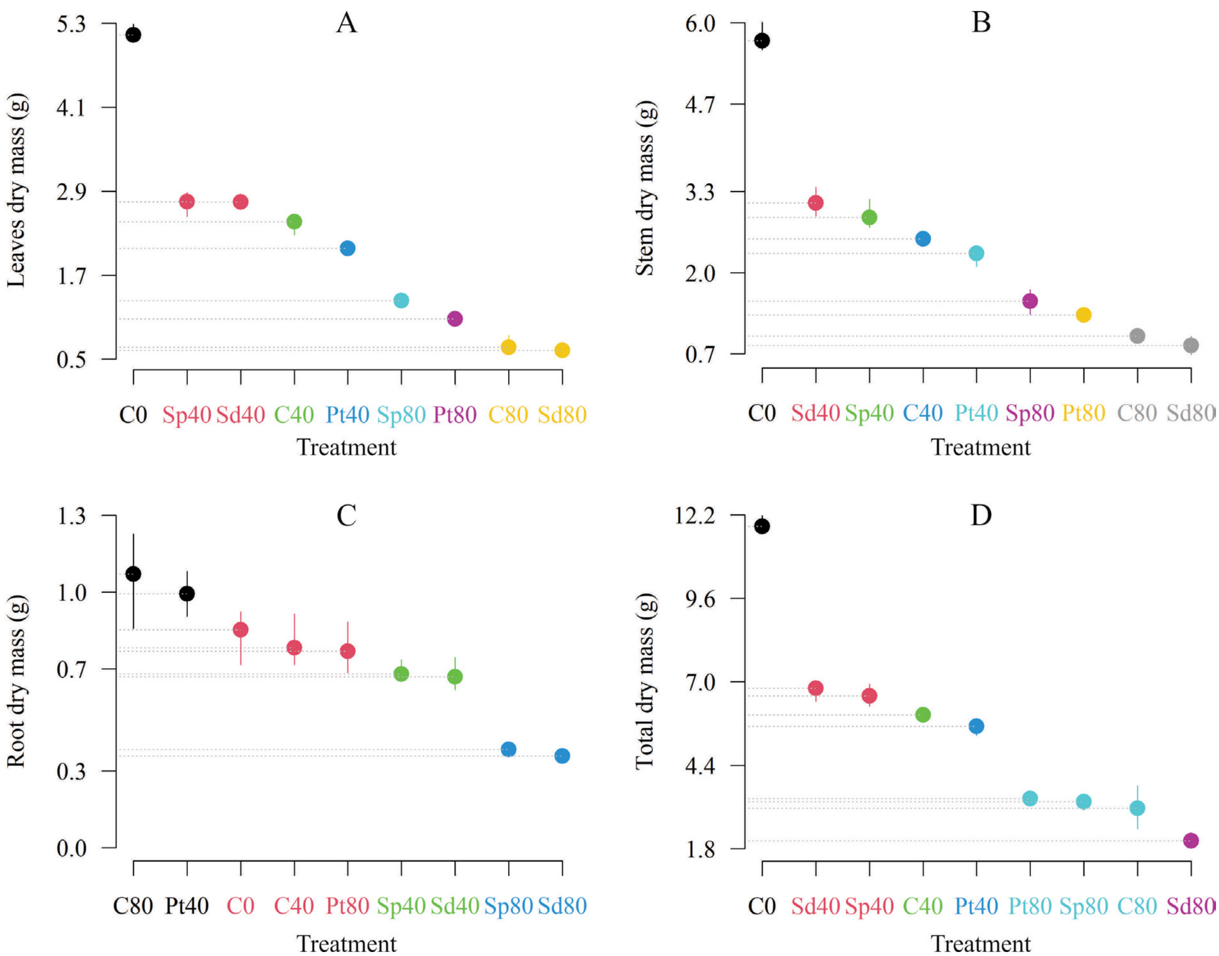

Figure 3: Leaves dry mass (A), stem dry mass (B), root dry mass (C) and total dry mass (D) of *Tropaeolum majus* under salt stress and polyamine application. Bars are standard deviations for a mean of 5 replications. C0 = 0 mM NaCl; C40 = 40 mM NaCl; C80= 80 mM NaCl; Sp40 = 40 mM NaCl + Spm; Sd40 = 40 mM NaCl + Spd; Pt40 = 40 mM NaCl + Put; Sp80 = 80 mM NaCl + Spm; Sd80 = 80 mM NaCl + Spd; Pt80 = 80 mM NaCl + Put.

Spm application mitigated the harmful effects of severe salt stress on leaf area ratio. On the contrary, the application of Put reduced the harmful effects of severe salt stress on specific leaf area of nasturtium plants. The applications of Spd and Spm mitigated the harmful effects of moderate and severe salt stress on the stem and leaf mass ratio. Polyamines application did not mitigate the harmful effects of salt stress on root mass ratio. However, the application of Put mitigated the harmful effects of severe salt stress compared with other treatments (Figure 4).

One of the major effects of salinity on *T. majus* plants was the reduction in vegetative growth. The results obtained in the present study showed that excess salt compromised the characteristics related to the growth in terms of plant height, the number of leaves, leaf area, and shoot dry mass. Moreover, the reduction in plant growth affected the production of flowers and buds. This may be due to the inhibition of protein synthesis and excessive accumulation of Na^+, which changed the content and activity of polyamine catabolic enzymes and increased lipid peroxidation and H_2O_2 production (Jain et al., 2015). Similar results were also reported in previous studies that were performed on wheat (*Triticum aestivum* L.) (Talaat; Shawky, 2012) and gladiolus (*Gladiolus gandavensis* Van Houtte) (Quian et al., 2021).

The application of Spm mitigated the harmful effects of severe salt stress on stomatal conductance (g_s), net photosynthesis (A), and transpiration (E). This observation was higher in plants without stress. However, the application of Spm mitigated the harmful effects of salt stress compared with other treatments. Instantaneous water use efficiency (WUE) was also higher in plants without stress. However, the application of Spd mitigated the harmful effects of salinity compared with other treatments. The application of Spd attenuated the harmful effects of moderate salt stress on intrinsic water use efficiency (iWUE), which surpassed the control plants. The application of Spd mitigated the harmful effects of severe salt stress on internal carbon concentrations (Figure 5).

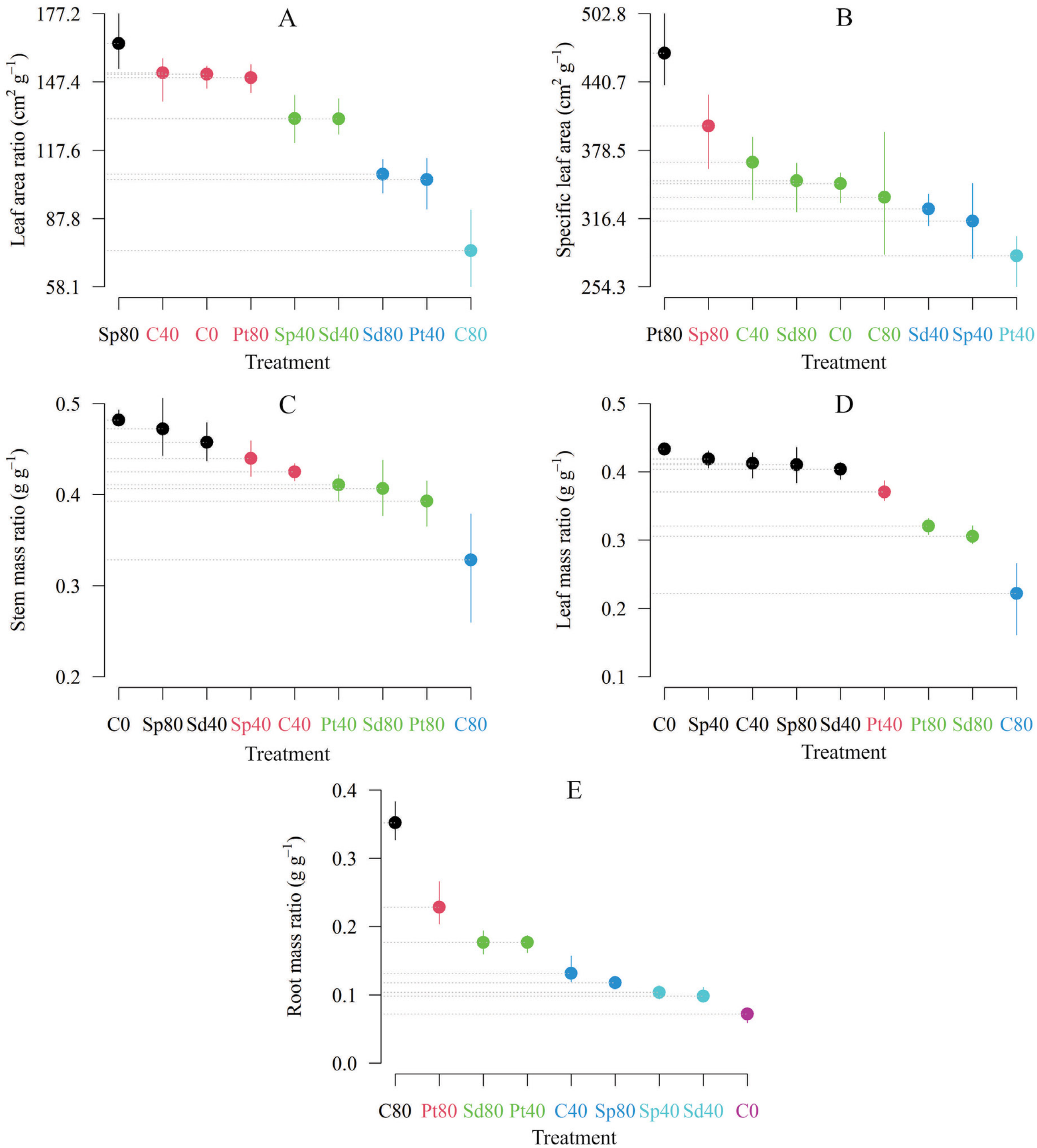

Figure 4: Leaf area ratio (A), specific leaf area (B), stem mass ratio (C), leaf mass ratio (D) and root mass ratio (E) of *Tropaeolum majus* under salt stress and polyamine application. Bars are standard deviations for a mean of 5 replications. C0 = 0 mM NaCl; C40 = 40 mM NaCl; C80= 80 mM NaCl; Sp40 = 40 mM NaCl + Spm; Sd40 = 40 mM NaCl + Spd; Pt40 = 40 mM NaCl + Put; Sp80 = 80 mM NaCl + Spm; Sd80 = 80 mM NaCl + Spd; Pt80 = 80 mM NaCl + Put.

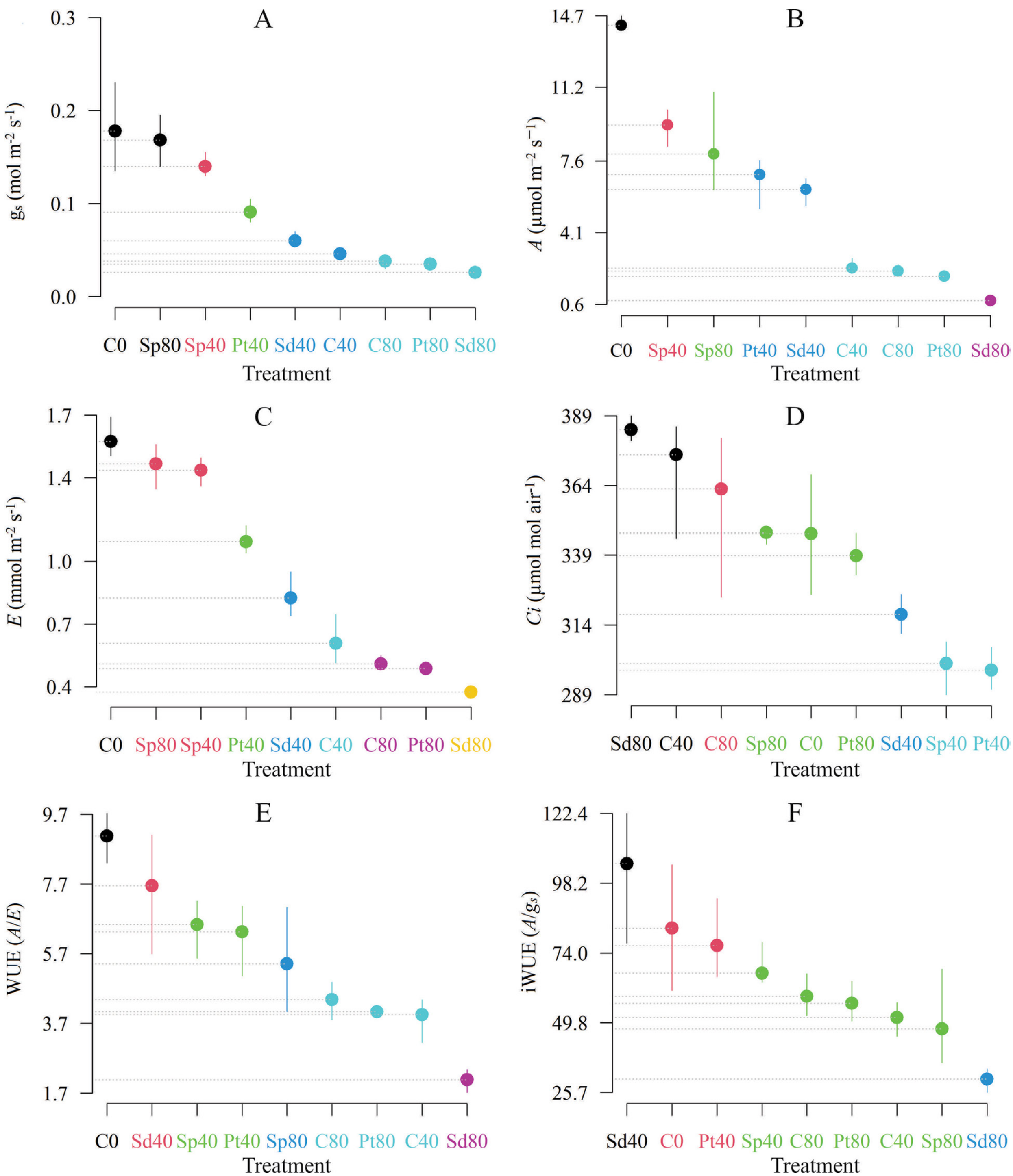

Figure 5: Stomatal conductance (A), net photosynthesis (B), transpiration rate (C), internal carbon concentration (D), instantaneous water use efficiency (E) and intrinsic water use efficiency (F) of *Tropaeolum majus* under salt stress and polyamine application. Bars are standard deviations for a mean of 5 replications. C0 = 0 mM NaCl; C40 = 40 mM NaCl; C80= 80 mM NaCl; Sp40 = 40 mM NaCl + Spm; Sd40 = 40 mM NaCl + Spd; Pt40 = 40 mM NaCl + Put; Sp80 = 80 mM NaCl + Spm; Sd80 = 80 mM NaCl + Spd; Pt80 = 80 mM NaCl + Put.

Restriction of ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) activity is one of the harmful effects of salinity because salt stress decreases the expression of *RbcL* and *RbcS* genes, which reduces photosynthesis rates (Elsayed et al., 2018). In the present study, photosynthetic reduction caused by salt stress was alleviated with the application of Spm. This can be due to the ability of Spm to regulate the expression of RbcL and RbcS genes and to act on the structure and function of RuBisCO (Alcázar; Tiburcio, 2014). Salt stress also triggers a considerable decrease in CO_2 fixation and internal carbon concentration (Shu et al., 2012). In the present study, the application of Spd and Spm in plants under stress increased internal carbon concentration, with the application of Spd being the most effective. This is because Spd can increase stomatal conductance, which results in more production of CO_2 in the cell pores, thereby improving the efficiency of carbon assimilation (Elsayed et al., 2018). Similar results were found in wheat (Elsayed et al., 2018). A reduction in water use efficiency indicated a loss of turgor in plant cells, which made compensation for water loss through transpiration difficult for the roots. The application of polyamines, especially Spd, alleviated this issue by preventing the leakage of electrolytes and amino acids, which recovered the damage to the plasma membrane of plant cells (Khajuria; Ohri, 2018). The damage caused by the salt can also be due to water stress or a type of physiological drought caused by NaCl because of the decrease in instantaneous water use efficiency and intrinsic water use efficiency observed in the present study (Belkheiri; Mules, 2013).

A canonical variables analysis with confidence ellipses was performed to determine the relationship between factors and the analyzed variables. Plant height (PH), stem diameter (SD), number of leaves (NL), number of flowers (NFl), and number of buds (NB) were less associated with polyamine application and severe salt stress, except for the Spm application. Stem fresh mass (SFM), leaf fresh mass (LFM), and total fresh mass (TFM) were strongly associated with control without salt stress. Root dry mass (RDM) had a greater relationship with the control in moderate salt stress, and stem dry mass (SDM), leaf dry mass (LDM), and total dry mass (TDM) had a greater relationship with the control without salt stress. Leaf mass ratio (LMR) and stem mass ratio (SMR) was more closely associated with the application of Spd and Spm in moderate salt stress, whereas root mass ratio (RMR) was less associated with them. Leaf area (LA) had a greater relationship with the no-stress control, leaf area ratio (LAR) had a greater relation with Spd and Spm in moderate salt stress, and specific leaf area (SLA) had a greater relation with Put and moderate salt stress (Figure 6).

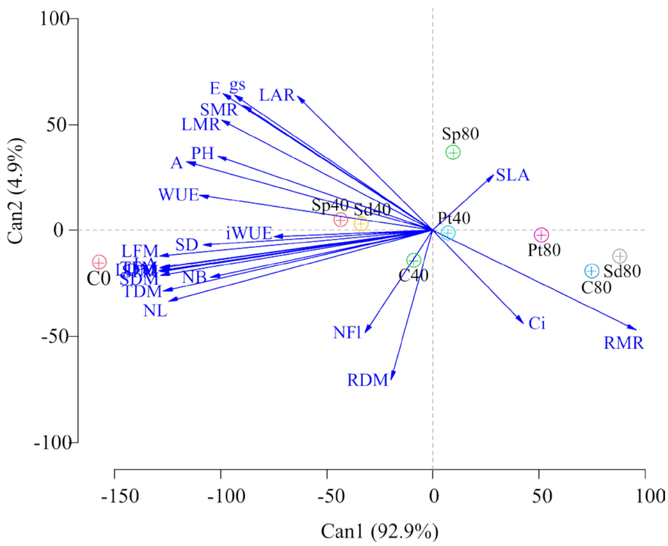

Figure 6: Canonical variables analysis and confidence ellipses between growth and leaf gas exchange variables of *Tropaeolum majus* under salt stress and polyamine application. Plant height (PH), stem diameter (SD), number of leaves (NL), number of flowers (NFl), number of buds (NB), stem fresh mass (SFM), leaf fresh mass (LFM), total fresh mass (TFM), root dry mass (RDM), stem dry mass (SDM), leaf dry mass (LDM), total dry mass (TDM), leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR), leaf area (LA), leaf area ratio (LAR) and specific leaf area (SLA). C0 = 0 mM NaCl; C40 = 40 mM NaCl; C80= 80 mM NaCl; Sp40 = 40 mM NaCl + Spm; Sd40 = 40 mM NaCl + Spd; Pt40 = 40 mM NaCl + Put; Sp80 = 80 mM NaCl + Spm; Sd80 = 80 mM NaCl + Spd; Pt80 = 80 mM NaCl + Put.

The decrease in cell growth processes is caused by dehydration that resulted from the osmotic effect of salts that accumulated in the root area and the toxic effect of Na^+ and Cl^-, which accumulated in plant tissues and impaired physiological processes and cell membrane integrity (Pizolato Neto et al., 2020). Plants under stress that are treated with Spd and Spm have increased dry mass compared with tomatoes grown without treatment (*Lycopersicon esculentum* Mill.) (Fariduddin et al., 2018). For the root dry mass, plants under salt stress treated with Put were less affected than those that did not receive the polyamine application. This is possibly due to the effect of Put on DNA replication, gene transcription, cell division, and root growth (Fariduddin et al., 2014). Similar results were also found in a study performed on Put-treated cucumber (*Cucumis sativus* L.) (Fariduddin et al., 2014).

Net photosynthesis (*A*), stomatal conductance (g_s), transpiration (*E*), and instantaneous water use efficiency (WUE) were positively associated with all growth variables, except for the number of flowers and root mass ratio (RMR). Internal carbon concentration (*Ci*), RMR, and specific leaf area (SLA) were negatively associated with most variables (Figure 7).

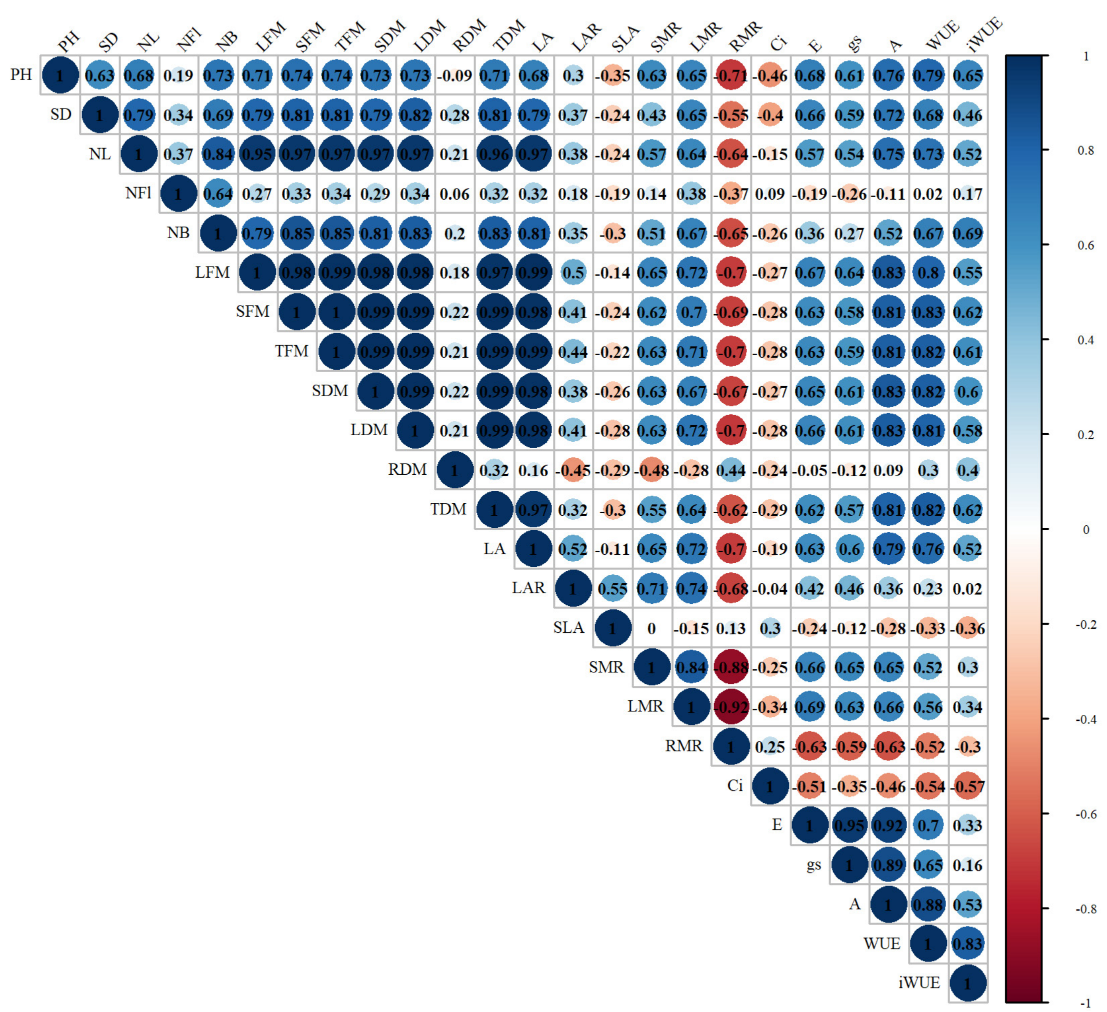

Figure 7: Pearson's correlation of growth and leaf gas exchange variables of *Tropaeolum majus* under salt stress and polyamine application. Plant height (PH), stem diameter (SD), number of leaves (NL), number of flowers (NFl), number of buds (NB), stem fresh mass (SFM), leaf fresh mass (LFM), total fresh mass (TFM), root dry mass (RDM), stem dry mass (SDM), leaf dry mass (LDM), total dry mass (TDM), leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR), leaf area (LA), leaf area ratio (LAR) and specific leaf area (SLA).

High concentrations of Na^+ and Cl^- on the leaves reduce the stomatal conductance and net photosynthesis. This leads to less increase in the development of leaves, which explains the decrease in leaf area ratio (Khoshbakht; Asghari; Haghighi, 2018). Polyamines have positive effects on the photosynthetic efficiency in plants under stress due to their acid-neutralizing and antioxidant properties and their membrane and cell wall stabilization activity (Serna et al., 2015).

CONCLUSIONS

The application of Spm and Spd mitigated the harmful effects of moderate salt stress on the growth and leaf gas exchange of nasturtium. Putrescine attenuated the harmful effects of severe salt stress on the specific leaf area of nasturtium. These polyamines can be used to mitigate the damage caused on leaf gas exchange and the growth of nasturtium cultivated under salt stress.

AUTHORS' CONTRIBUTION

Conceptual idea: Silva, T. I.; Data collection: Santos Filho, F. B.; Dias, M. G.; Silva, T. I.; Methodology design: Silva, T. I.; Grossi, J. A. S.; Data analysis and interpretation: Silva, T. I.; Santos Filho, F. B.; Writing and editing: Santos Filho, F. B.; Dias, M. G.; Silva, T. I.; Grossi, J. A. S.

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REFERENCES

ALCÁZAR, R.; TIBURCIO, A. F. Plant polyamines in stress and development: An emerging area of research in plant sciences. Frontiers in Plant Science, 5:319, 2014.

BELKHEIRI, O.; MULAS, M. The effects of salt stress on growth, water relations and ion accumulation in two halophyte *Atriplex* species. Environmental and Experimental Botany, 86:17-28, 2013.

BRONDANI, J. C. et al. Traditional usages, botany, phytochemistry, biological activity and toxicology of *Tropaeolum majus* L.-A review. Boletín Latinoamericano y del Caribe de Plantas Medicinales y Aromáticas, 15(4):264-273, 2016.

BUENO, M.; CORDOVILLA, M. D. P. Spermidine pretreatments mitigate the effects of saline stress by improving growth and saline excretion in *Frankenia pulverulenta*. Agronomy, 11(8):1515, 2021.

BUTNARIU, M.; BOSTAN, C. Antimicrobial and anti-inflammatory activities of the volatile oil compounds from *Tropaeolum majus* L. (Nasturtium). African Journal of Biotechnology, 10(31):5900-5909, 2011.

ELSAYED, A. I. et al. Enhancing antioxidant systems by exogenous spermine and spermidine in wheat (*Triticum aestivum*) seedlings exposed to salt stress. Functional Plant Biology, 45(7):745-759, 2018.

FARIDUDDIN, Q. et al. 24-epibrassinolide and/or putrescine trigger physiological and biochemical responses for the salt stress mitigation in *Cucumis sativus* L. Photosynthetica, 52(3):464-474, 2014.

FARIDUDDIN, Q. et al. Ameliorative role of salicylic acid and spermidine in the presence of excess salt in *Lycopersicon esculentum*. Photosynthetica, 56(3):750-762, 2018.

FERNANDES, L. et al. Post-harvest technologies applied to edible flowers: a review: Edible flowers preservation. Food Reviews International, 35(2):132-154, 2019.

FRIENDLY, M.; FOX, J. Candisc: Visualizing generalized canonical discriminant and canonical correlation analysis. 2021. R package version 0.8-0. 2017. Available in: <https://cran.r-project.org/web/packages/candisc/index.html>. Access in: January, 03, 2022.

GASPAROTTO JUNIOR, A. et al. Diuretic and potassium-sparing effect of isoquercitrin: An active flavonoid of *Tropaeolum majus* L. Journal of Ethnopharmacology, 134(2):210-215, 2011.

GOMES, C. et al. Evaluation of subchronic toxicity of the hydroethanolic extract of *Tropaeolum majus* in Wistar rats. Journal of Ethnopharmacology, 142(2):481-487, 2012.

ISAYENKOV, S. V.; MAATHUIS, F. J. Plant salinity stress: Many unanswered questions remain. Frontiers in Plant Science, 10:80, 2019.

JAIN, V. et al. Spermine reduces salinity-induced oxidative damage by enhancing antioxidative system and decreasing lipid peroxidation in rice seedlings. Journal of Plant Biochemistry and Biotechnology, 24(3):316-323, 2015.

JELIHOVSCHI, E. G.; FARIA, J. C.; ALLAMAN, I. B. ScottKnott: A package for performing the Scott-Knott clustering algorithm in R. *Trends in Applied and Computational Mathematics*, 15(1):3-17, 2014.

KAMIAB, F. et al. Exogenous application of free polyamines enhance salt tolerance of pistachio (*Pistacia vera* L.) seedlings. Plant Growth Regulation, 72(3):257-268, 2014.

KHAJURIA, A.; OHRI, P. Exogenously applied putrescine improves the physiological responses of tomato plant during nematode pathogenesis. Scientia Horticulturae, 230:35-42, 2018.

KHOSHBAKHT, D.; ASGHARI, M. R.; HAGHIGHI, M. Influence of foliar application of polyamines on growth, gas-exchange characteristics, and chlorophyll fluorescence in Bakraii citrus under saline conditions. Photosynthetica, 56(2):731-742, 2018.

KOIKE, A. et al. Irradiation as a novel approach to improve quality of *Tropaeolum majus* L. flowers: Benefits in phenolic profiles and antioxidant activity. Innovative Food Science & Emerging Technologies, 30(1):138-144, 2015.

Li, J. et al. The role of melatonin in salt stress responses. International Journal of Molecular Sciences, 20(7):1735, 2019.

LIN, K. H. et al. Effects of plant growth regulators and polyamines on bract longevity in *Bougainvillea buttiana*. Horticulture, Environment, and Biotechnology, 62(2):149-157, 2021.

LIU, J. H. et al. Polyamines function in stress tolerance: From synthesis to regulation. Frontiers in Plant Science, 6:827, 2015.

MELO, A. C. et al. Hydroethanolic extract of *Tropaeolum majus* promotes anxiolytic effects on rats. Revista Brasileira de Farmacognosia, 28(5):589-593, 2018.

MINOCHA, R.; MAJUMDAR, R.; MINOCHA, S. C. Polyamines and abiotic stress in plants: A complex relationship. Frontiers in Plant Science, 5:175, 2014.

MISHRA, A.; TANNA, B. Halophytes: Potential resources for salt stress tolerance genes and promoters. Frontiers in Plant Science, 8:829, 2017.

MLCEK, J.; ROP, O. Fresh edible flowers of ornamental plants: A new source of nutraceutical foods. Trends in Food Science & Technology, 22(10):561-569, 2011.

NEGRÃO, S.; SCHMÖCKEL, S. M.; TESTER, M. Evaluating physiological responses of plants to salinity stress. Annals of Botany, 119(1):1-11, 2017.

PEIXOTO, C. P.; PEIXOTO, M. F. S. P. Dinâmica do crescimento vegetal: Princípios básicos. In: CARVALHO, C. A. L. et al. Tópicos em ciências agrárias. Cruz das Almas, Bahia: UFRB, v.1, p.37-53, 2009.

PHOUR, M.; SINDHU, S. S. Amelioration of salinity stress and growth stimulation of mustard (*Brassica juncea* L.) by salt-tolerant *Pseudomonas* species. Applied Soil Ecology, 149(1):103518, 2020.

PIRES, T. C. et al. Edible flowers: Emerging components in the diet. Trends in Food Science & Technology, 93(1):244-258, 2019.

PIZOLATO NETO, A. et al. Pretreatment of forage legumes under moderate salinity with exogenous salicylic acid or spermidine. Acta Scientiarum. Agronomy, 42:e42809, 2020.

QIAN, R. et al. Effect of exogenous spermidine on osmotic adjustment, antioxidant enzymes activity, and gene expression of *Gladiolus gandavensis* seedlings under salt stress. Journal of Plant Growth Regulation, 40(4):1353-1367, 2021.

R CORE TEAM. R: A language and environment for statistical computing. Viena, Austria, 2021. Available in: <https://cran.r-project.org/mirrors.html>. Access in: January, 03, 2022.

ROP, O. et al. Edible flowers: A new promising source of mineral elements in human nutrition. Molecules, 17(6):6672-6683, 2012.

SARWAT, M. et al. Phytohormones and microRNAs as sensors and regulators of leaf senescence: Assigning macro roles to small molecules. Biotechnology Advances, 31(8):1153-1171, 2013.

SERNA, M. et al. A brassinosteroid analogue prevented the effect of salt stress on ethylene synthesis and polyamines in lettuce plants. Scientia Horticulturae, 185:105-112, 2015.

SHAVRUKOV, Y. Salt stress or salt shock: Which genes are we studying? Journal of Experimental Botany, 64(1):119-127, 2013.

SHU, S. et al. Effects of exogenous spermidine on photosynthesis, xanthophyll cycle and endogenous polyamines in cucumber seedlings exposed to salinity. African Journal of Biotechnology, 11(22):6064-6074, 2012.

SILVA, A. A. R. D. et al. Salicylic acid relieves the effect of saline stress on soursop morphysiology. Ciência e Agrotecnologia, 45:e007021, 2021.

SILVA, T. I. et al. Application of phytohormones as attenuators of salt stress in *Tropaeolum majus* L. (Tropaeolaceae). Acta Botanica Croatica, 81(1):1-10, 2022.

TALAAT, N. B. Effective microorganisms modify protein and polyamine pools in common bean (*Phaseolus vulgaris* L.) plants grown under saline conditions. Scientia Horticulturae, 190:1-10, 2015.

TALAAT, N. B.; SHAWKY, B. T. 24-Epibrassinolide ameliorates the saline stress and improves the productivity of wheat (*Triticum aestivum* L.). Environmental and Experimental Botany, 82:80-88, 2012.

WEI, T.; SIMKO, V. R package "corrplot": Visualization of a Correlation Matrix. (Version 0.89), 2021. Available in: <https://cran.r-project.org/web/packages/corrplot/index.html>. Access in: January, 03, 2022.

XIONG, F. et al. The protective effect of exogenous putrescine in the response of tea plants (*Camellia sinensis*) to salt stress. HortScience, 53(11):1640-1646, 2018.

XU, H.; LU, Y.; TONG, S. Effects of arbuscular mycorrhizal fungi on photosynthesis and chlorophyll fluorescence of maize seedlings under salt stress. Emirates Journal of Food and Agriculture, 30(3):199-204, 2018.