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Effects of exogenous salicylic acid on physiological response and DNA damage in tomato under double stress of salt and cadmium

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Keywords: Salicylic acid; salt stress; cadmium stress; tomato; physiological response; DNA damage

Abstract: In order to alleviate the adverse effects of soil salinity and cadmium pollution on the quality of tomato production, the present study was conducted to investigate the effects of SA on the physiological response and DNA damage of tomato under different salt and cadmium stress conditions in the control, cadmium, salt and cadmium groups, using the "Cooperative 908" tomato as the test material, with the control, cadmium, salt and cadmium groups set up, and with the application of a series of exogenous SA solutions in a series of concentration gradient, at 7d, 14d, and 21d. The effects of SA on the physiological response and DNA damage of tomato under different salt and cadmium stress conditions were investigated after 7d, 14d and 21d. The results showed that a certain concentration of salt and cadmium stress would inhibit the normal growth and development of tomato, causing damage to the membrane system, photosynthetic system and DNA damage in the root system. And the application of SA can effectively reduce the symptoms of tomato poisoning: plant height, root length and leaf area increased; antioxidant enzyme activities increased significantly, and the maximum increase of POD, SOD and CAT activities under double stress was 90.22%, 4.78% and 40.30%, respectively; the decrease of MDA content was 49.01%; and the maximum growth rates of proline content, chlorophyll content were 168.60% and 32.69%, respectively; fluorescence parameters were significantly improved; and the degree of DNA trailing was significantly reduced. In conclusion, the application of exogenous SA can effectively enhance the resistance of tomato under salt and cadmium stress and promote the good growth of tomato, which lays the foundation for further exploring the application of SA in agriculture.

1. Introduction

In recent years, the problems of salinisation and heavy metal pollution in agricultural soils have become increasingly serious due to over-fertilisation and irrational emissions[1] . Saline soils cover an area of 954 million hectares globally, 99.13 million hectares in China, and the area and salt content are still increasing[2] . High salinity soil affects the physiological activities related to plant growth and development through osmotic effects, ionic toxicity, nutrient deficiencies and oxidative effects[3] . Cadmium, as one of the top heavy metal pollutants, has exceeded 7.0% in soil, affecting more than 13,300,000 hectares of arable land[4] , leading to a serious threat to intracellular enzyme activities in plants, substance transport processes, redox regulation, etc.[5] . Cadmium accumulates in plants and can be ingested through food, causing harm to the human body[6] . Tomato (*Solanum lycopersicum* L.) has become a vegetable consumed in large quantities in daily life due to its rich nutrition, outstanding food and medicinal value, and high adaptability[7] . However, soil salinity and cadmium pollution can hinder the normal growth and development of tomato, so it is necessary to find suitable methods to reduce the harm of salt stress and cadmium toxicity to the tomato industry.

Salicylic acid (SA) is involved in the regulation of plant physiology and development of metabolism, in a variety of stress response (temperature stress, saline and alkaline stress, heavy metal stress, etc.) in the induction process has been confirmed[8] , but its mitigation of the effects of salt and cadmium double stress in tomato has not been reported in the relevant research. Therefore, in this paper, we took "Cooperation 908" tomato as experimental material, sprayed a series of SA with concentration gradient under single stress of salt and cadmium as well as under double stress, compared with the control group, and detected and analysed the changes of growth and physiological indexes as well as the DNA damage of tomato, with a view to exploring the mitigating effect of SA on tomato under salt and cadmium adversity and the prospect of its comprehensive utilisation. In order to explore the mitigation effect of SA on tomato under salt and cadmium adversity and the prospect of its comprehensive use, and to provide theoretical guidance for improving the quality and yield of tomato.

2. Materials and Methods

2.1 Experimental design

The experiment was carried out using "Co-op 908" tomato as the material. Through a series of pre-tests, NaCl concentration (150 mmol-L^{-1}), cadmium ion concentration gradient (0.6, 0.9, 1.2 mmol-L^{-1}), and SA concentration gradient (0.0, 0.5, 1.0, 2.0 mmol-L^{-1}) were determined to treat tomato seedlings germinated in soil culture until the four-leaf-one-heart stage. Five experimental groups were set up: S T_{01} ($Salt_0$ $Cadmium_{0.6}$), S T_{02} ($Salt_0$ $Cadmium_{0.9}$), S T_{03} ($Salt_0$ $Cadmium_{1.2}$), S T_{10} ($Salt_{150}$ $Cadmium_0$), S T_{12} ($Salt_{150}$ $Cadmium_{0.9}$), and SA at concentrations of 0.0, 0.5, 1.0, and 2.0 mmol-L^{-1} were added to co-cultivate with the tomato seedlings under the three types of stresses (single salt stress, single cadmium stress, and double salt and cadmium stresses), and CK ($Salt_0$ $Cadmium_0$ SA_0) was used as the blank control group, and each set up with 3 replicates. During the experimental period, the solution was sprayed once a day at 20:30, and the third to fourth leaves (functional leaves) were taken at 0d, 7d, 14d and 21d for the determination of antioxidant enzymes and chlorophyll content, and in the last cycle, the plant height, root length and leaf area were measured, and 1 g of root tip was cut for the detection of DNA damage in the root system.

2.2 Experimental Methods

Plant height and main root length were measured using a 20-cm ruler; leaf area was measured using a CanoScan 4400F scanner and image analysis software (WinRHIZO); chlorophyll fluorescence parameters of tomato leaves were determined by a portable pulse modulated chlorophyll fluorometer (PAM-210)[9] ; superoxide dismutase (SOD) activity was determined by the photochemical reduction method of NBT, peroxidase activity of leaves by the guaiacol method, and catalase (CAT) activity by UV absorption method ; malondialdehyde (MDA) activity was determined by thiobarbituric acid method; and catalase (CAT) activity by UV absorption method ; and malondialdehyde (MDA) activity by thiobarbituric acid method was determined by the POD method. (POD) activity by NBT photochemical reduction method, leaf peroxidase (POD) activity by guaiacol method, catalase (CAT) activity by UV-absorbance method[10] ; malondialdehyde (MDA) content by thiobarbituric acid method[11] ; proline content by ninhydrin colour development method[12] ; chlorophyll content by acetone leaching colorimetric method[13] ; DNA damage in roots by single-cell gel electrophoresis and comet images obtained under fluorescence microscope (Axio Scope A1)[14] .

2.3 Data processing

The experimental data were collated using Microsoft Excel 2019, and significant differences were analysed using SPSS 25.0 by calculating the mean and standard error through one-way ANOVA (one-way ANOVA) and Least Significant Difference (LSD) method, and Origin 2022 software for graphing. CASP was used to derive data related to the comet experiment.

3. Results and analyses

3.1 Effect of exogenous SA on growth characteristics of tomato under salt and cadmium stresses

Changes in plant growth indexes are the most intuitive reflection of salt and cadmium toxicity[15,16] . As can be seen in Fig 1- Fig 3, all five stress groups caused significant decreases in plant height and root length, most notably under double stress, and all three growth indexes increased after SA treatment compared with the stress groups: in plant height and leaf area, 1.0 mmol-L^{-1} SA treatment had the strongest mitigating effect on most of the stress conditions, with a maximum increase of 76.79% and 83.17%, respectively; for root length, the mitigating effect increased with the increase of SA concentration, reaching a peak at 2.0 mmol-L SA treatment with a maximum increase of 65.81%. concentration increased continuously, reaching a peak at 2.0 mmol-L^{-1} SA treatment with a maximum increase of 65.81%. The maximum increase of 65.81% was achieved at 2.0 mmol-L SA treatment, and the leaf area and root length of the plants at the optimal SA concentration increased compared with that of the CK group, indicating that the appropriate concentration of SA not only alleviated the damage caused by the stress, but also promoted the further growth and development of the plants.

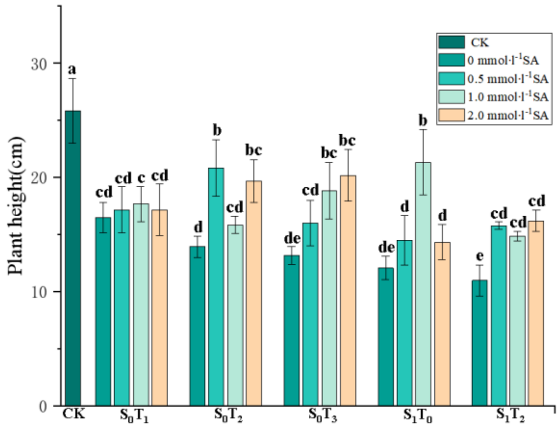


Figure 1: Variation of tomato plant height under each treatment

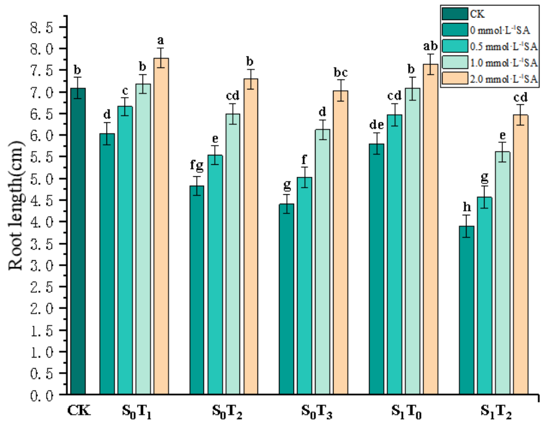


Figure 2: Variation of tomato root length under each treatment

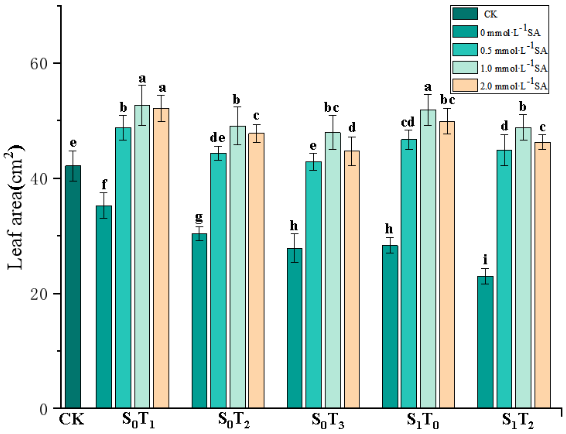


Figure 3: Variation of tomato leaf area under each treatment

3.2 Effect of exogenous SA on antioxidant enzyme system of tomato under salt and cadmium stresses

The antioxidant enzyme system can effectively resist the damage caused by reactive oxygen radicals (ROS) under stress, which is closely related to plant stress tolerance[17,18] . As can be seen from Fig 4- Fig 6, the antioxidant enzyme activities of tomato under different concentrations of SA treatments were increased to different degrees. Taking 21d as an example, under salt stress, 1.0 mmol-L^{-1} SA played the best mitigating effect, and the POD, SOD, and CAT activities of tomato were elevated by 27.16%, 45.88%, and 22.45%, respectively; under cadmium stress, the changes of the POD, CAT, and SOD activities were most obvious in the treatment groups of S T_{01}, S T_{02}, and S T_{03}, which were elevated by 30.28%, 28.74%, respectively, 35.43%. The activities of the three antioxidant enzymes under double stress increased after the application of SA, and the activities of POD, SOD, and CAT increased by 90.22%, 4.78%, and 40.30%, respectively, compared with CK. In summary, a certain concentration of exogenous SA could effectively reduce cell damage and alleviate the toxic effects of salt and cadmium by increasing the activities of antioxidant enzymes and reducing the accumulation of reactive oxygen species.

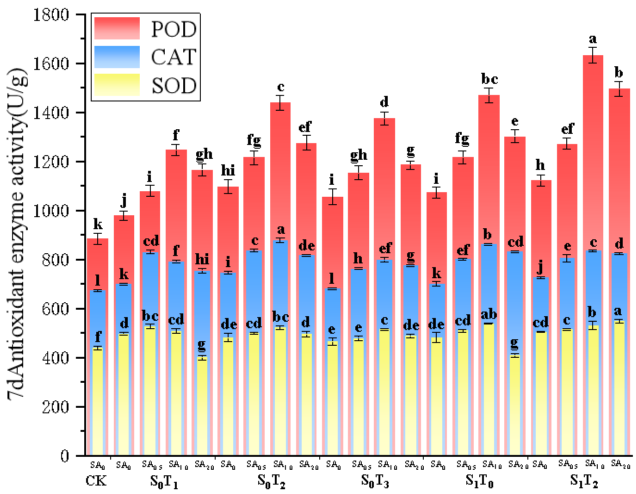


Figure 4: Tomato antioxidant enzyme activity after 7 d of treatment

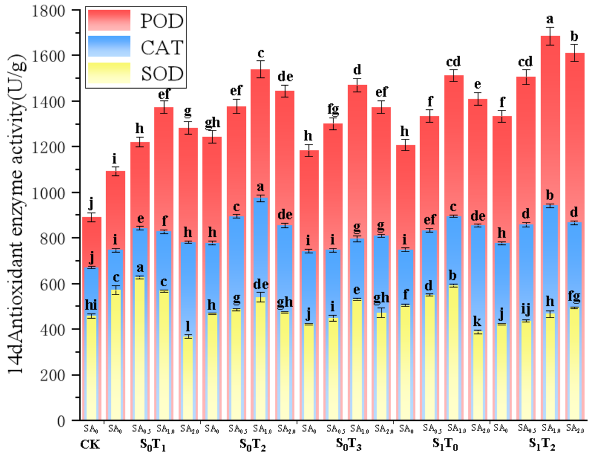
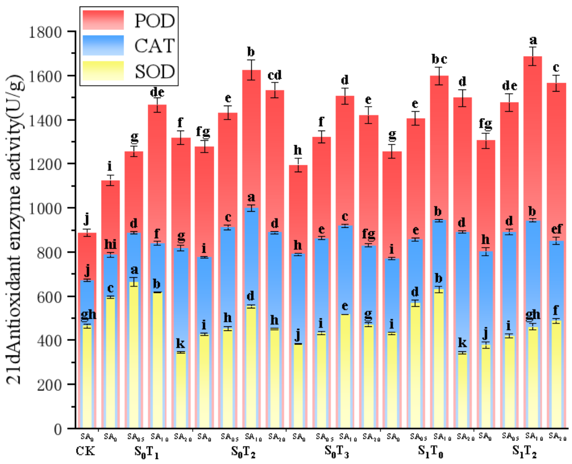


Figure 5: Tomato antioxidant enzyme activity after 14 d of treatment



(Note: 0d SOD, POD and CAT activities were 423.821±3.0856, 763.0629±92.1629 and 668.9896±6.0679 U/g respectively)

Figure 6: Tomato antioxidant enzyme activity after 21 d of treatment

3.3 Effect of exogenous SA on proline and MDA content of tomato under salt and cadmium stresses

Proline has the role of maintaining the stability of subcellular structures such as proteins and scavenging superoxide anion, and when plants suffer from injury under adversity, they can alleviate the effects of adverse environment on the osmoregulatory system and membrane system by accumulating proline[19] . And MDA as an important product of membrane lipid peroxidation reflects the degree of cell membrane damage[20] . As can be seen from Fig 7 and Fig 8, both proline and MDA contents were maintained at high levels with the extension of stress time. After the application of exogenous SA, proline was further elevated and peaked at an SA concentration of 1 mmol-L^{-1}. For the dual stress of salt and cadmium at S T$_{12}$, the maximum increase was 168.60%, which was 13.84% higher compared to the same period of single stress. Whereas, the application of exogenous SA resulted in a decrease in MDA content with a maximum decrease of 49.01% under double stress, which was 6.59% higher compared to the same period of single stress. In conclusion, exogenous SA application was more effective than single stress on double stress in terms of proline content and MDA content in tomato.

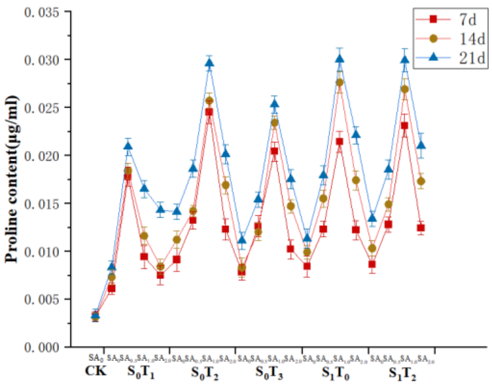
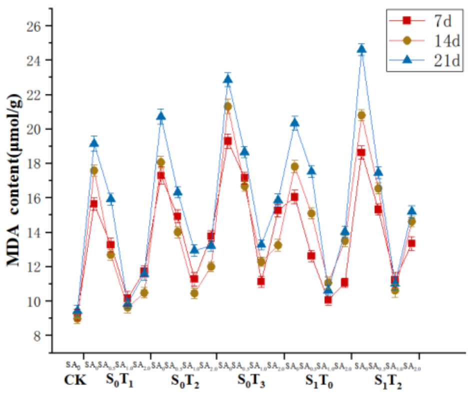


Figure 7: Changes in proline content of tomato under each treatment



(Note: 0d Proline and MDA levels were 0.0030 μg/ml and 8.1621 μmol/g, respectively)

Figure 8: Changes in MDA content of tomato under each treatment

3.4 Effect of exogenous SA on photosynthetic characteristics of tomato under salt and cadmium stresses

Chlorophyll fluorescence, as a natural probe to study photosynthesis, can rapidly, accurately, sensitively and non-destructively characterise the effects of environmental factors on the photosynthetic apparatus of plants[21] . As the material basis of photosynthesis, chlorophyll content can reflect the photosynthetic capacity and growth of plants[22] . As shown in Fig 9- Fig 12, under single salt, single cadmium and double salt and cadmium stress without SA treatment, tomato leaf Fo and qN increased significantly, while Fv/Fm and chlorophyll content decreased significantly, indicating that leaf photosystem activity was damaged and photosynthetic efficiency was reduced under the stress conditions. The degree of damage increased with the increase of stress intensity, and reached the maximum under 1.2 mmol-L^{-1} Cd stress and double stress. In terms of chlorophyll content, for example, it decreased by 42.41% in the 21d double stress group compared with 0d and 49.53% compared with CK. After the application of SA, the damaged phenomenon was effectively alleviated. Taking Fo and Fv/Fm as an example, after the optimum SA treatment, the Fo of the five treatment groups fell back by 53.24%, 35.62%, 51.87%, 43.04%, and 54.44%, and the Fv/Fm went back up by 5.29%, 17.12%, 25.64%, 5.07%, and 30.28%, respectively. It was concluded that salt and cadmium stress would reduce the photochemical conversion efficiency and chlorophyll content of tomato, and the external application of SA could effectively improve its adversity tolerance ability, and the specific effects varied according to the different degrees of stress, mostly the most obvious with double stress.

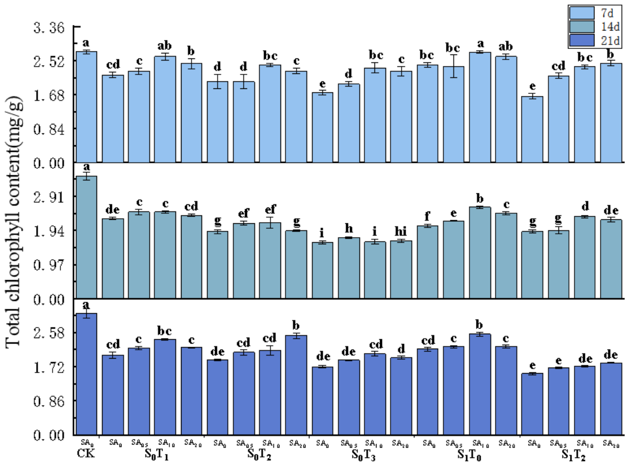


Figure 9: Changes in total chlorophyll content of tomato under each treatment

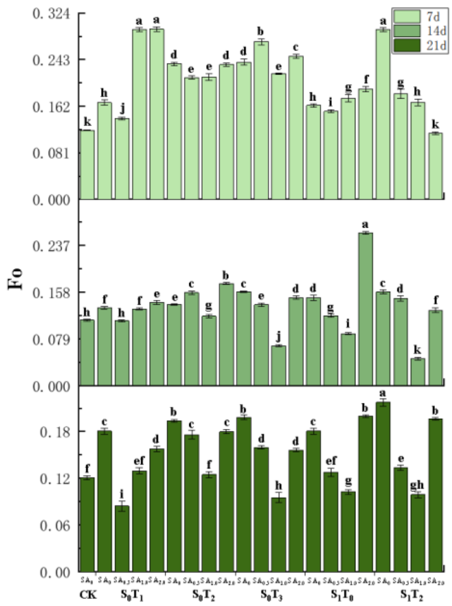


Figure 10: Variation of tomato Fo under each treatment

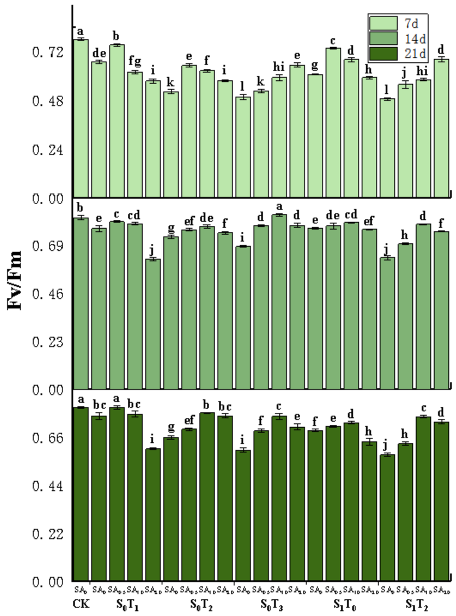
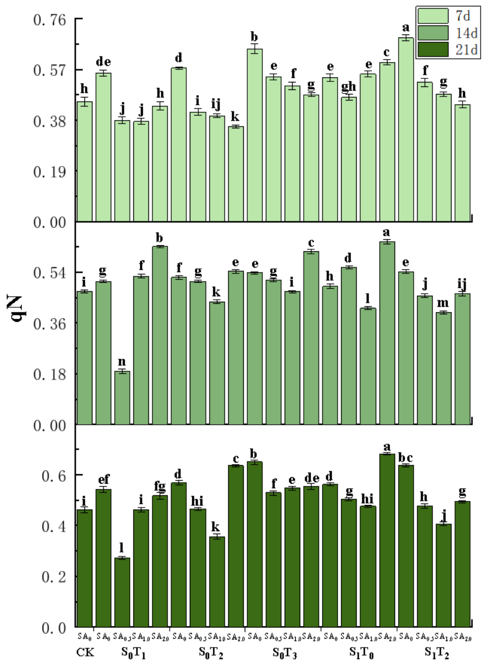


Figure 11: Variation of tomato Fv/Fm under each treatment



(Note: 0d Fo, Fv/Fm, and qN values are 0.1187±0.0192, 0.8048±0.0144, and 0.4617±0.0646, respectively)

Figure 12: Variation of tomato qN under each treatment

3.5 Effect of exogenous SA on DNA damage in tomato roots under salt and cadmium stresses

Under alkaline electrolyte electrophoresis, the damaged cellular DNA will leave the nucleus and migrate towards the positive pole to form a "comet"-like figure, and the higher degree of tail dragging indicates that the damage is more serious, and thus the comet tail length and fluorescence brightness can be used to judge the degree of DNA damage[23] . As can be seen from Fig 13, the core of the comet image in the CK group was rounded and complete without tail dragging, and the DNA was normal and undamaged; under cadmium and salt stress, the proportion of the comet head was significantly reduced, the shape was irregular, and there was an obvious comet tail. Under the lower concentration of exogenous SA treatment, the DNA damage condition was alleviated, and the proportion of the head increased and the length of the comet tail decreased compared with that of the 0 mmol-L^{-1} SA treatment group. The experimental group with the most suitable concentration of SA was basically free of tail dragging, while the tail dragging reappeared under high concentration of SA, which indicated that high concentration of SA was not conducive to the repair of DNA damage, and even exacerbated the DNA damage.

As shown in Fig 14, the comet tail length (TL), comet tail DNA content (TD) and tail moment (TM) of tomato under salt and cadmium stresses were different from those of CK groups.

The degree of increase in TL, TD and TM after applying a certain concentration of SA decreased to different degrees compared with the control group and reached the minimum value under the treatment of suitable concentration of SA, which indicated that exogenous SA could reduce the DNA strand breakage and further alleviate the damage of salt and cadmium adversity on the cellular DNA of tomato root system. By comparing the magnitude of TL, TD and TM values in each treatment group, overall, 1.0 mmol-L^{-1} SA played the best treatment effect.

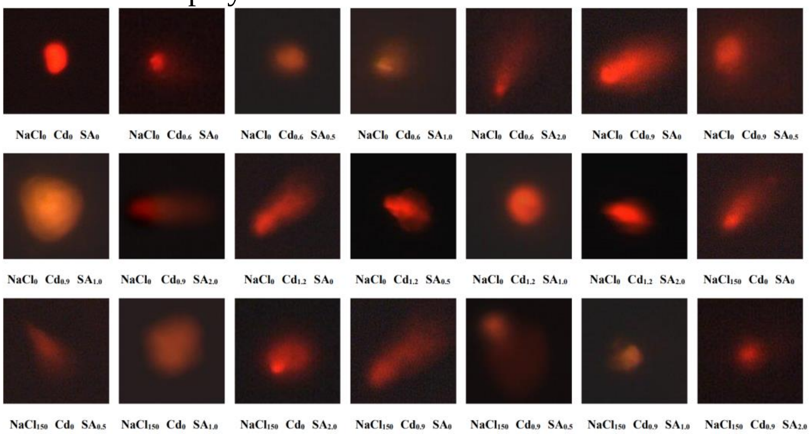


Figure 13: Effects of different concentrations of exogenous SA on DNA damage in tomato roots under salt and cadmium stress

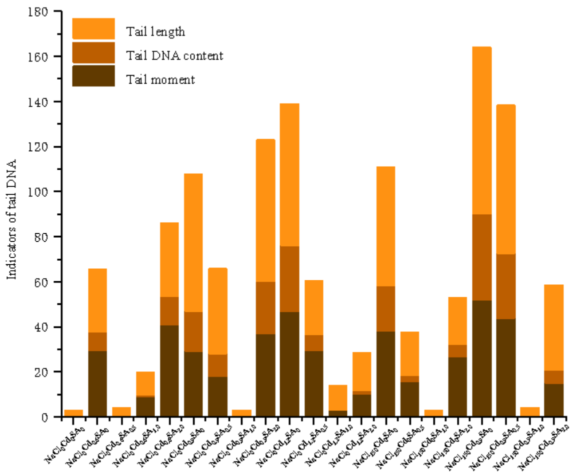


Figure 14: Results of the analysis of comet electrophoretic image indexes of tomato root DNA under each treatment

4. Conclusion

Seed germination and early growth stages are the most sensitive to environmental stresses, so the growth and photosynthetic efficiency at this stage are often used to evaluate plant stress tolerance[24] . Studies have shown that abiotic stresses lead to inhibition of seedling growth, reduction of bioaccumulation, disruption of the chloroplast membrane system, and a decrease in photosynthetic rate[25] . In this experiment, it was pointed out that elevated salt and cadmium concentrations would lead to a significant decrease in root length, leaf area and plant height of tomato seedlings, and after SA treatment, plant height and leaf area showed a tendency to increase and then decrease with the increase of SA concentration, and root length showed a tendency to increase with the increase of SA concentration. And under salt and cadmium toxicity, Fo and qN values showed an increasing trend, while Fv/Fm and chlorophyll content decreased significantly. This is basically similar to the results of the experiments of roasted tobacco (*Nicotiana tobacum* L.) under cadmium stress[26] and wheat (*Triticum aestivum* L.) under salt stress[27] etc. After SA treatment, the Fo and qN values decreased, while the Fv/Fm and chlorophyll contents gradually increased. Therefore, exogenous SA can to a certain extent attenuate the adverse effects of salt and cadmium toxicity, promote the growth of tomato seedlings, increase the accumulation of bioaccumulation, improve the efficiency of photochemical conversion, maintain the normal conduct of photosynthesis, and enhance its salt and cadmium tolerance.

Plants produce reactive oxygen species[28] that are detrimental to their growth and development under adversity, and normal physiological activities are impeded. Plants can use the antioxidant system (including protective enzymes such as SOD, POD and CAT) and proline to scavenge reactive oxygen species, and at the same time play the role of proline to alleviate the osmotic stress[19,29,30] . The content of MDA, as a product of membrane peroxidation, can be used as an important indicator for detecting the degree of damage to the plant in the presence of adversity[20] . This experiment proved that the SOD, CAT, POD activities and proline and MDA contents of tomato increased to a certain extent after being poisoned by salt and cadmium. Plant damage was significantly reduced after spraying appropriate concentrations of SA, as evidenced by enhanced antioxidant enzyme activities, increased proline content, and decreased MDA content, which is consistent with the results obtained by Ma Yonghui et al.[31] in experiments on Lycium *ruthenicum* Murray (Lycium *ruthenicum*) seedlings. The results also pointed out that, over time, the high concentration of stress would cause the dynamic balance of protective enzymes to be disrupted and the activity of antioxidant enzymes to be decreased in seedlings, which could be effectively alleviated after applying a certain concentration of SA. And it was found that the treatment effect of SA on double stress was more obvious in the proline and MDA content determination experiments. It is concluded that exogenous SA can reduce the oxidative damage and repair the membrane system under salt and cadmium adversity by inducing the antioxidant enzyme defence system in tomato, and at the same time regulate the osmotic balance to achieve a better detoxification effect, which is conducive to the maintenance of the homeostasis of the tomato plant in vivo.

Salt stress and metal ions can induce the production of reactive oxygen species, which damage DNA by breaking nucleic acid strands and modifying bases[32] . In the comet assay, the number of DNA breaks is closely related to the degree of damage. Damaged DNA was deconvoluted in alkaline electrophoresis solution and released short DNA strands and fragments, which moved to the anode during electrophoresis and formed a comet image[23] . In this study, it was found that the comet image of tomato root DNA under stress was obviously trailing, the DNA molecules were severely damaged, and the degree of damage increased with the increase of the stress concentration, which was similar to the experimental findings of Chen Suyu et al.[33] . After applying suitable concentration of SA, TL, TD, TM and OTM of tomato decreased, and DNA damage was obviously alleviated, but its improvement on the abnormal nucleic acid status of the root system was weakened when the concentration of SA exceeded a certain range, which indicated that the suitable concentration of SA could help the plant to resist salt and cadmium toxicity.

In summary, the growth, physiological, photosynthetic and molecular indexes of tomato under salt and cadmium adversity changed significantly, and the normal physiological process and growth and development were inhibited, and the application of exogenous SA could increase the antioxidant enzyme activity, photosynthetic capacity, osmoregulatory substance content of tomato seedlings, as well as repair the damage of the membrane system and the DNA of the root system, and then enhance the plant's resilience. On the basis of existing research, this experiment further broadened the idea from the perspective of salt and cadmium double stress for the current situation of tomato cultivation, and established a multi-dimensional comprehensive evaluation system to explore the effects of each stress on tomato seedlings and the optimal concentration of SA application. It was concluded that 0.5 mmol-L^{-1} SA under 0.6 mmol-L^{-1} single cadmium stress, 0.9, 1.2 mmol-L^{-1} single cadmium stress, 150 mmol-L^{-1} single salt stress, 150 mmol-L^{-1} salt, and 0.9 mmol-L^{-1} cadmium double stress, and 1.0 mmol-L^{-1} SA could effectively alleviate the damage of tomato plants, and the effect of SA on double stress was better than that of single stress. The conclusion of single stress. The results provide a reference for the high-yield and high-quality cultivation of tomato and the application of SA in agriculture to achieve the optimal production efficiency and economic value.

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