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Effect of low temperature plasma on the growth and nutrients of lettuces under salt stress

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Abstract

The effects of helium plasma seed treatment on lettuce growth under salt stress were studied. Lettuce seeds were treated with an atmospheric dielectric barrier discharge (DBD) helium plasma at different discharge voltages and then planted in different concentrations of salt solution hydroponic tanks. The results show that under the same NaCl concentration (6 g/L), with the increase of the treatment voltage, the growth and quality of the lettuces gradually improved, as confirmed by the measurement of seedling height, root length, the contents of chlorophyll and nitrogen in the leaves. Similarly, under the same treatment voltage (45 kV), with an increase in NaCl concentration, the promotion effect of plasma treatment gradually strengthens, as verified through significance analysis. These results indicate that plasma seed treatment could improve the salt resistance of lettuces.

Keywords

low temperature plasma; lettuce; salt tolerance

Introduction

Saline-alkali soil is a kind of poor-quality soil that contains a large amount of soluble salt and harms the growth of agricultural crops. According to incomplete statistics from UNESCO, the global saline-alkali land area has reached about 9.54×10^9 ha and is still growing at the rate of about 1 million ha every year (1). Salinization not only directly harms crops and reduces agricultural products, but also damages the land and reduces soil fertility. Saline-alkali soil has become a serious problem for ecological, environmental construction and economic development.

Lettuce is one of the most widely planted and consumed vegetables in the world. There are many kinds of lettuces all over the world. In order to reduce the impact of saline-alkali soil on the growth of lettuces, it is necessary to explore some effective techniques to enhance the salt tolerance of lettuces.

Low temperature plasma (LTP) is capable of producing a huge number of ions, electrons, free radicals, ground- and excited- state molecules and so on, which readily react with the contacted materials. LTP is also a highly efficient and environmentally friendly agriculture green technique. Due to the fact that the overall gas temperature of LTP could be as low as room temperature (2), it could be applied for agriculture practices including seed treatment. Direct seed treatment with atmospheric plasma, which contains large amounts of active components (O_3, ·OH, O_2^-, NO, NO_2, N_2O, HNO_2 , and so on) (3) could positively affect the physical and chemical properties of the seed coat by either etching the seed envelope or promoting polar groups grafting on the seed surface, leading to a significant increase in hydrophilic interactions. Therefore, water and oxygen permeability, which are essential factors for root activity and seed germination (4-7), could be accelerated. In addition, the activity of some enzymes in seeds and the efficiency of photosynthesis in the process of growth could be enhanced by plasma treatment (8). The effects of plasma which can promote seed germination and plant growth, have been verified in rice (9), Coriandrum sativum (10), quinoa (11), Mimosa caesalpiniifolia (12), pumpkin (13), Erythrina velutina (14) and sunflower (15) by shortening germination time and increasing plant height and dry weight. Plasma seed treatment could also avoid the damage of pathogenic bacteria in soybean (16), improve drought tolerance of oilseed rape and wheat seeds (17, 18) or improve cold tolerance of tomato (19) by relieving negative effects (20-22).

Up to now, studies on the stress tolerance of plasma application in agricultural crops mainly focus on the cold or drought tolerance of plants and there is a lack of salt tolerance research on plasma seed treatment. In this paper, lettuce seeds were chosen for plasma treatment with different discharge voltages and then the effects of plasma seed treatment on salt stress under different NaCl concentrations were investigated.

Materials and Methods

Lettuce seeds originated from Beijing Academy of Agricultural Sciences. Healthy lettuce seeds with no obvious defects were selected for the experiment. Lettuce seeds were treated in a DBD plasma generator (Fig. 1) which included a power supply, a voltage regulator, 2 discharge electrodes (with a thickness and diameter of 16 and 56 mm and a spacing of 12 mm) and a quartz container (with a diameter and height of 60 and 8 mm and a covering plate) containing lettuce seeds. Plasma was produced at atmospheric pressure in a helium flushed (5 L/min) chamber. The voltage peak-to-peak amplitude was measured with a high voltage probe connected to the digital oscilloscope (Tektronix TBS 1102B). In this experiment, the applied voltage to the electrodes has amplitudes of 30, 45 and 60 kV and a frequency of 8.6 kHz. Fig. 2 shows the discharge voltage and current waveforms with V_{pp} of 30, 45 and 60 kV. It can be seen that the discharge voltage applied to the electrodes is a sine waveform. The current waveforms show the typical filamentary ac discharge and there are more discharges in half of the voltage cycle. The higher the applied voltage, the stronger the discharge current intensity and the more discharge times in one cycle.

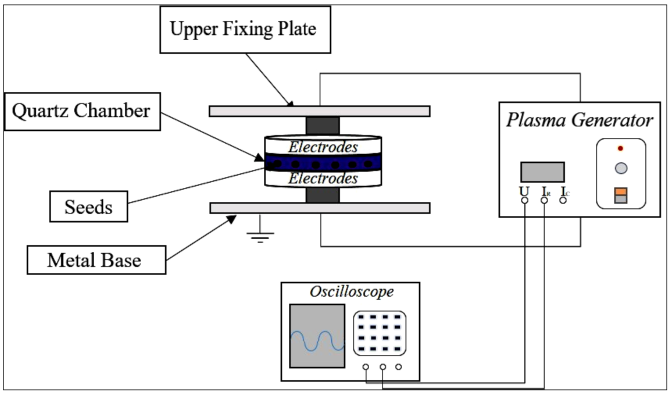

Fig. 1. Experimental setup.

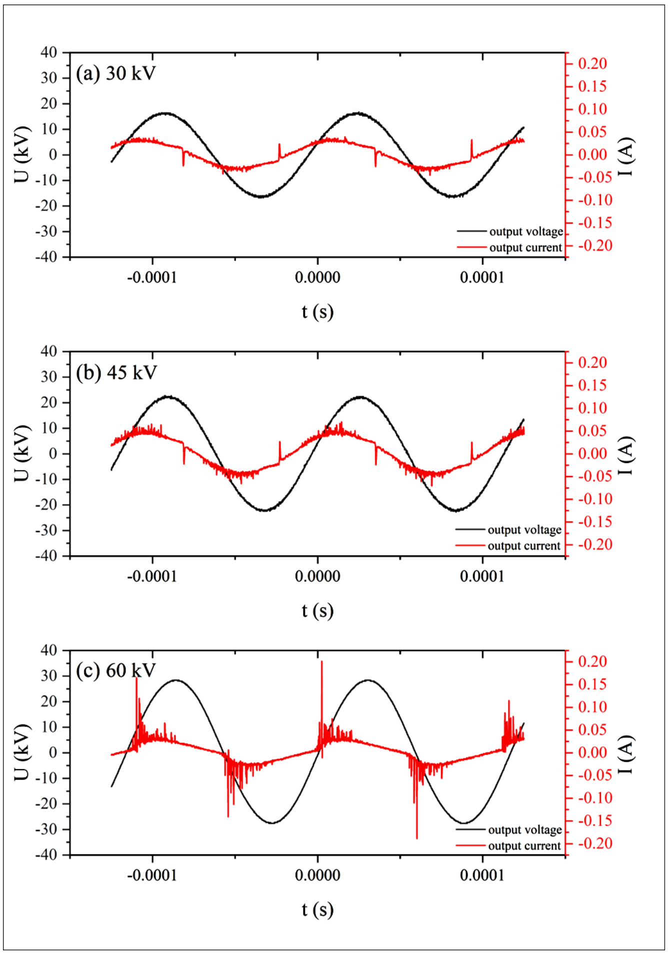

Fig. 2. Typical voltage and current waveforms with the discharge voltages of 30 kV(a), 45 kV(b) and 60 kV(c) in the DBD plasma system.

According to the discharge voltage of 0, 30, 45 and 60 kV with a treatment time of 60 s, the lettuce seeds were divided into 4 groups (200 seeds in each group), i.e., group CK (Control Check, without plasma treatment), group P30, P45 and P60. During seed germination (23, 24), the environmental humidity and temperature remained unchanged and the seeds in each group were put into a petri dish with watering 10 mL tap water every day at 25 °C. On the 7th day of germination, each group of seedlings were transplanted into a series of 40 L water planting tanks in a plant factory with illumination for 12 h per day. The salt stress experiment started on the 6th day after transplanting to the water tanks. In order to investigate the responses of the lettuces with different treatment voltages to salt stress, a fixed salt concentration was chosen for the experiment. Table 1 shows the groups with different discharge voltages and the same salt concentration. For example, group P30C6 means the seeds were treated with 30 kV and the NaCl solution concentration was 6 g/L. In order to investigate the effects of plasma on the growth of lettuces

Table 1. Groups with different discharge voltages and the same salt concentration.

Group	Discharge voltage (kV)	Concentration of NaCl (g/L)
CKC6	0	6
P30C6	30	6
P45C6	45	6
P60C6	60	6

under different NaCl concentrations, the treatment voltage was kept constant at 45 kV and different concentrations of salt solution were added into the water tanks to compare the salt resistance of lettuce with the seeds treated and untreated. Table 2 shows the 6 groups with different NaCl solution concentrations (3, 6 and 9 g/L). For example, group P45C3 means the seeds were treated at 45 kV and the NaCl solution concentration was 3 g/L. The average plant height and root length of lettuces were measured from randomly selected 21 lettuces and the chlorophyll and nitrogen content were analysed from randomly selected 10 lettuces on the 40th day after adding salt stress.

Table 2. Groups with different salt concentrations.

Group	Discharge voltage (kV)	Concentration of NaCl (g/L)
CKC3	0	3
CKC6	0	6
CKC9	0	9
P45C3	45	3
P45C6	45	6
P45C9	45	9

Results and Discussion

Effects of different discharge voltages on the growth and nutrients of lettuces grown with the same NaCl concentration

Fig. 3 shows the growth state of the lettuces with different seed treatment voltages at fixed NaCl concentration of 6 g/L (the same black cloth was used as the background for taking the photos). It could be seen that, under a certain NaCl concentration, the lettuces with plasma seed treatment grow more vigorously than the untreated lettuces (group CK). Fig. 4 shows the comparison of average height and average root length of the lettuces with different treatment voltages grown with a NaCl concentration of 6 g/L. It can be seen that under the same NaCl concentration stress, both the average lettuce height and average root length of plasma treated lettuces are larger than those of untreated lettuces. For example, when the treatment voltage is 30 kV, the average lettuce height increases by 12.13 % and the average root length increases by 9.23 % compared with the untreated lettuces. When the treatment voltage increases to 45 kV, the average lettuce height increases by 22.56 % and the average root length increases by 16.77 %. When the treatment voltage increases to 60 kV, the plant height of the treatment group only increases by 22.77 %, and root length even slightly decreases. It shows that when the treatment voltage increases by the same value (such as from 30 to 45 kV and from 45 to 60 kV), the plasma promotion effect first increases and then weakens. For example, the average lettuce height increases by 10.43 % from 30 to 45 kV, but only increases by 0.21 % from 45 to 60 kV. The average root length increases by 7.55 % from 30 to 45 kV, but decreases by 6.66 % from 45 to 60 kV. It indicates the existence of an optimized processing voltage to achieve optimal efficiency on lettuce growth with the salt resistance effect of plasma treatment for promoting lettuce production.

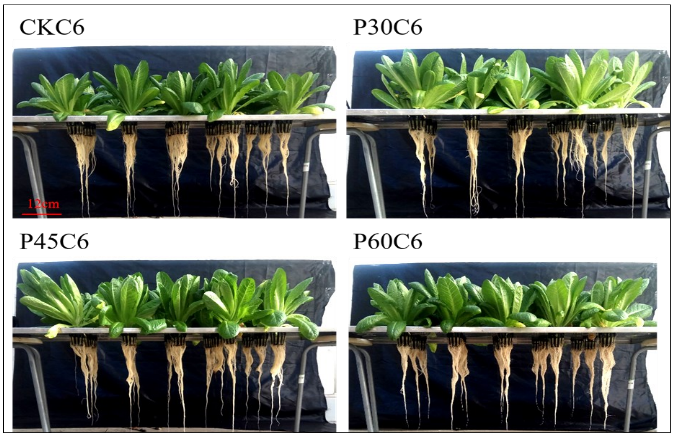

Fig. 3. The comparison of the lettuce growth with the NaCl concentration of 6 g/L and different treatment voltages.

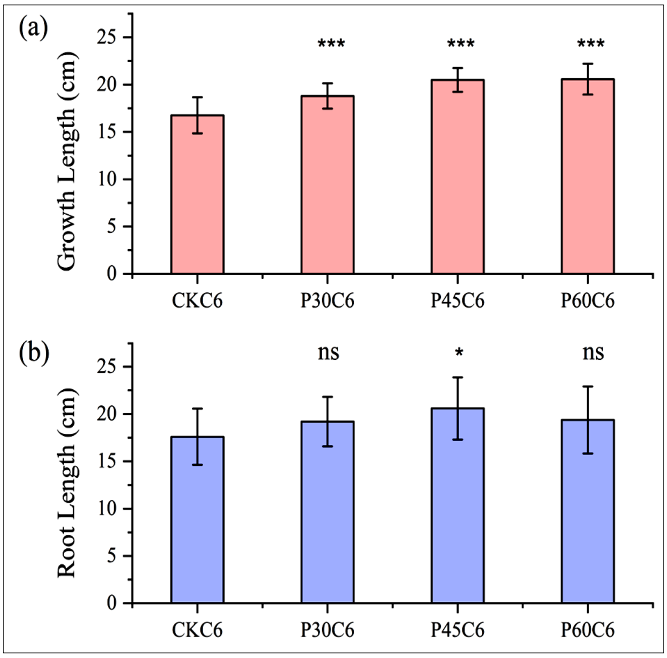

Fig. 4. Comparison of average lettuce height and average root length of twenty-one replicates under 6 g/L salt concentration with different plasma discharge voltages. Asterisks denote statistically significant difference from CK group, where ******* means the strongest significance with $p < 0.001$, ****** means the significance difference with $0.001 < p < 0.01$, ***** means the significance difference with $0.01 < p < 0.05$ and **ns** means no significant difference.

The promotion of salt resistance by plasma treatment can be understood as follows: soil salinization can change the biomass of soil microorganisms, plant respiration and enzyme activity. Therefore, land salinization has a negative impact on plant growth and is a major risk factor for obtaining low-quality agricultural products. It is mainly due to the osmotic stress of plants can be affected by the high salt concentration in water. Thus, the excess soluble salts could reduce the water's osmotic potential on the root surface, reducing plant water uptake (25), which leads to water lacking in plants. When the seeds were treated with plasma, a large amount of active ingredients in the plasma can result in the micro-damage in the seed coat and the breaking of seed dormancy and can enhance the permeability of water and oxygen of seeds as well as the activity of some enzymes in seeds, which accordingly improves seed germination accompanied by physiological and biochemical activities (26, 27). That is, the water uptake and oxygen absorption, which are essential factors for seed germination (4), are improved. Thus, root activity (8) and plant growth are improved (28). However, the promotion of excessive plasma treatment on plant growth will become weakened. According to previous studies (29, 30), this may be due to excessive erosion of the seed epidermis by excess plasma and ultraviolet radiation in the plasma. These results indicate that appropriate DBD plasma seed treatment could overcome the degree of salt damage to seedling roots and promote the growth of plants (31).

The statistically significant analysis from group CK was also performed on the plant height and root length of the lettuces with salt stress in Fig. 4, where *** means was the strongest significance with $p < 0.001$, ** means the significance difference with $0.001 < p < 0.01$, * means the significance difference with $0.01 < p < 0.05$ and ns means no significant difference. It shows that there was the strongest significant difference in plant height between the plasma treated group and the untreated group. However, compared with the untreated lettuces, only the root length of the lettuces treated with 45 kV shows a slightly significant difference.

Chlorophyll is not only the main pigment of green plants, but also an important substance for plant photosynthesis. Nitrogen content has a direct impact on the conceptual photosynthesis of crops and affects crop products and yield. The level of chlorophyll content in leaves directly indicates the nutritional and growth status of plants. The SPAD (soil and plant analyser development) value of plant leaves is a dimensionless value used to characterize relative chlorophyll content by measuring the ratio of absorption of 650 nm red light and 940 nm infrared light by the chlorophyll analyser, i.e., the SPAD value of plant leaves is positively correlated with the chlorophyll content in leaves. Different from the conventional extraction methods, the chlorophyll analyzer can realize the non-destructive and rapid determination of plant leaves. Therefore, the measurement of SPAD has been widely used in the monitoring of plant growth status and nutrient content (32-34).

In this experiment, chlorophyll and nitrogen content were measured by a chlorophyll analyser. The influence of the DBD treatment voltage on the SPAD value and nitrogen content of lettuce seedlings growing with a 6 g/L salt concentration is shown in Fig. 5. It shows that both the SPAD value and nitrogen contents of plasma treated lettuces are higher than those of untreated lettuces and increase with the treatment voltage. For example, when the discharge voltage increases from 30 to 45 kV, the average SPAD value and nitrogen contents accordingly increase by 9.07 % (from 15.03 % to 24.10 %) and 9.06 % (from 14.96 % to 24.02 %) respectively. When plasma voltage was increased to 60 kV, the SPAD value and nitrogen contents in lettuces only slightly increased by 5.22 % and 5.12 % compared with 45 kV. It also shows that when the treatment voltage increases by the same value, the plasma promotion effect on SPAD and nitrogen content is similar to that of plant height. It indicates there is an optimized voltage to achieve the best efficiency on lettuce nutrients with the salt resistance effect of plasma treatment for improving lettuce quality. The promotion of plasma treatment on lettuce nutrients may be due to that during plasma treatment on lettuce seeds, the activity of some essential enzymes in seeds were enhanced (8), the efficiency of photosynthesis in the process of lettuce growth was also increased and the accumulation of nutrients could be accordingly improved (35), which could be shown from the chlorophyll and nitrogen contents in lettuces. This result indicates that plasma seed treatment could also promote the nutrient contents of the lettuces under salt stress. The significant differences in SPAD value and nitrogen content between the plasma treated groups and group CK shows the treatment voltage of 45 kV with strong significance. Overall, in this experiment, 45 kV is a relatively optimized parameter, which not only promotes lettuce growth but also improves the nutrients. Therefore, in the following experiments, we choose 45 kV as the fixed treatment voltage to study the growth of lettuces under different salt solution concentrations.

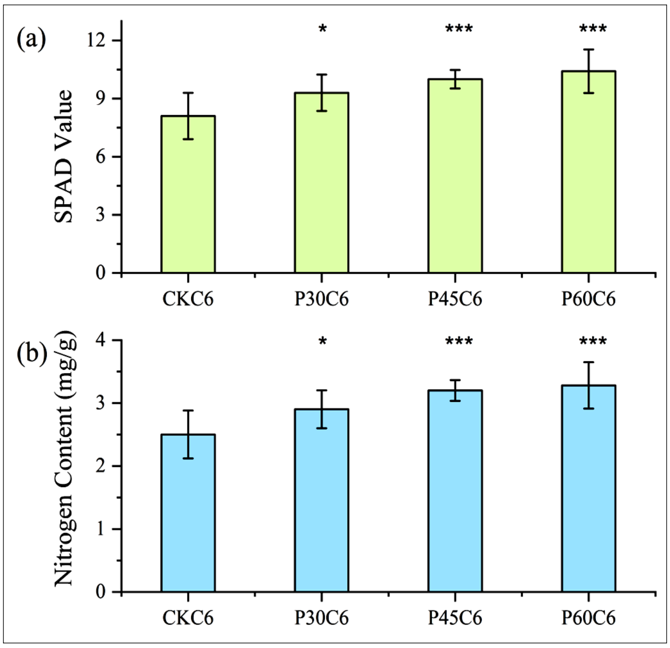

Fig. 5. Comparison of SPAD and nitrogen content in lettuce leaves grown with 6 g/L salt concentration and different treatment voltages. Data are the means of ten replicates. Asterisks denote statistically significant difference from CK group, where ***** signifies $0.01 < p < 0.05$ and ******* means $p < 0.001$.

Effects of plasma seed treatment on the lettuce growth with different NaCl concentrations

High salinity induces osmotic and ionic stress in plants, leading to decreased plant photosynthesis capacity, growth inhibition and even plant death (36-38). In order to explore the influence of plasma treatment on lettuce growth with different salt concentrations, the treatment voltage was kept at 45 kV. Fig. 6 shows the growth photos of the lettuces under the different NaCl concentrations (3, 6 and 9 g/L) and with the seed treatment at 45 kV. It is seen that with the increase in NaCl concentrations, the lettuce growth was suppressed for certain NaCl concentration. For a certain NaCl concentration, plasma treatment obviously promotes lettuce growth.

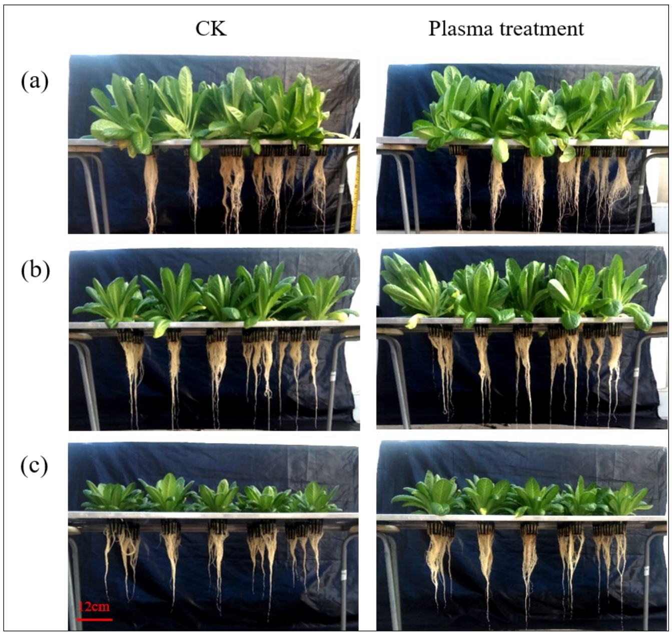

Fig. 6. The growth photos of lettuces with seed treatment by 45 kV and with different NaCl concentrations of (a) 3, (b) 6 and (c) 9 g/L.

Fig.7 shows the lettuce height and root length under the different NaCl concentrations and with plasma seed treatment at 45 kV, which shows the growth inhibition caused by the salt concentrations as well as plasma promotion on the growth of lettuces in salt solutions. Under the same seed treatment voltage, with the increase of NaCl concentration, both the lettuce height and root length gradually decreased, showing that the growth was gradually suppressed by the increasing concentration of salt solution. It's due to that high salt content that stress compromises the dynamic balance of water potential and ion distribution in plant roots. This disruption of the homeostasis caused by high salt content occurs at the cellular level and compromises balanced plant osmosis. Dramatic changes in ion and water homeostasis due to high salt concentrations could lead to molecular damage, growth stunts and even death (1). The modulation of homeostasis was evoked by plasma treatment, with the key role of reactive oxygen and nitrogen species in some applications (39, 40). In this experiment, under the same plasma treatment voltage, the promotion effect of plasma varies at different concentrations of salt solutions. For example, when the NaCl concentration is 3 g/L, the lettuce height increases by about 4.09 % compared with the untreated lettuce. When the NaCl concentration is increased to 6 and 9 g/L, the lettuce height increases by 22.56 % and 53.37 % respectively. A similar changing trend is also found in the comparison of root length, i.e., as the NaCl concentration increases from 3 to 6 and 9 g/L, the root length increases from 4.95 % to 16.77 % and 40.52 % respectively. Fig.7 shows that at the highest NaCl concentration of 9 g/L, there are the strongest significant differences in plant height and root length between the plasma treated group and the untreated group. When the NaCl concentration is low (for example, 3 g/L), there is no significant difference between the plasma treated group and the untreated group. The detailed increase in plant height and root length of the lettuces with plasma treatment at different salt concentrations is shown in Table 3. It is obviously true that the higher the concentration of salt solution, the more significant the promoting effect of plasma.

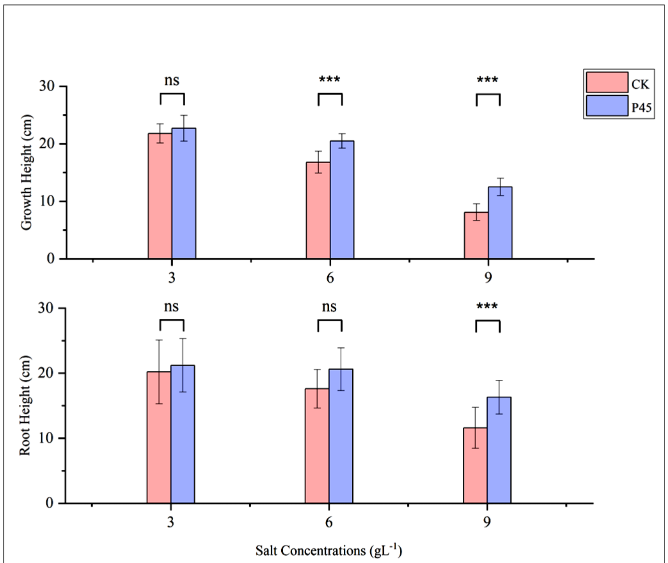

Fig. 7. The lettuce height and root length under different NaCl concentrations (3, 6 and 9 g/L) with 45 kV plasma seed treatment. Data are the means of twenty-one replicates. Asterisks denote statistical significance where ******* signifies $p < 0.001$, while **ns** means non-significant differences.

Table 3. The increase in lettuce height and root length between seed treatment with 45 kV and untreated at different salt concentrations.

Salt concentrations (g/L)	**3**	**6**	**9**
Average height promoted by plasma	4.09 %	22.56 %	53.37 %
Average root length promoted by plasma	4.95 %	16.77 %	40.52 %

The more significant promotion of plasma seed treatment at higher salt concentrations is due to the fact that the excess soluble salt will reduce water absorption potential on the root surface, leading to plant water shortage. The high concentration of Na^{+} in the cytoplasm destroys the absorption of other ions, affecting many metabolic pathways. In addition, osmotic and ionic stresses caused by salt stress led to plant secondary metabolite stress, including the accumulation of toxic compounds and the destruction of nutritional balance. Plasma treatment could promote the growth of lettuces under high concentration NaCl stress. After plasma activating the enzyme protection system, the activity of SOD, POD, CAT and soluble protein content could be increased, decreasing the relative permeability of the membrane, leading to improved NaCl tolerance at high concentrations in plants. In addition, different genes activated by plasma can help plants respond to high salt stress and promote plant growth (31, 41) and the optimal duration of plasma treatment time is expected to be different for various plant varieties (42).

Conclusion

A high concentration of salt will cause plant ion imbalance and hyperosmotic stress, making plant growth slow or even stagnant. In this paper, the salt stress of the lettuces with DBD plasma seed treatment with different NaCl concentrations was investigated. The plant height and root length of lettuces were used to characterize the growth speed. The chlorophyll and leaf nitrogen contents of lettuces were used to characterize the growth quality. The results show that under NaCl concentration, DBD plasma seed treatment could reduce the damage of NaCl on lettuces, promote growth and improve the quality of the lettuces. Plasma treatment at 45 kV shows a more optimized promoting effect and at a high NaCl concentration of 9 g/L plasma promotion shows more significance than at other concentrations.

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Authors' contributions

Conceptualization, XL and FH; methodology, XL and FH; software, SB, AL and BL; validation, DZ, JG and CY; formal analysis, XT and QG; investigation, DZ and XT; resources, FH; data curation, XL and LL; writing—original draft preparation, XL, FH; writing—review and editing, FH and XL; visualization, JG and CY; supervision, project administration, funding acquisition, FH and WL. All authors have read and agreed to the published version of the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None.

References

1. Zhu J-K. Plant salt tolerance. Trends Plant Sci. 2001;6(2):66-71. https://doi.org/10.1016/S1360-1385(00)01838-0
2. Attri P, Ishikawa K, Okumura T, Koga K, Shiratani M. Plasma agriculture from laboratory to farm: A review. Processes. 2020;8(8):1002. https://doi.org/10.3390/pr8081002
3. López M, Calvo T, Prieto M, Múgica-Vidal R, Muro-Fraguas I, Alba-Elías F et al. A review on non-thermal atmospheric plasma for food preservation: Mode of action, determinants of effectiveness and applications. Front Microbiol. 2019;10:622. https://doi.org/10.3389/fmicb.2019.00622
4. Ji S-H, Choi K-H, Pengkit A, Im JS, Kim JS, Kim YH et al. Effects of high voltage nanosecond pulsed plasma and micro DBD plasma on seed germination, growth development and physiological activities in spinach. Arch Biochem Biophys. 2016;605:117-28. https://doi.org/10.1016/j.abb.2016.02.028
5. Monica V, Anbarasan R, Mahendran R. Influence of cold plasma in accelerating the germination and nutrient composition of foxtail millet (*Setaria italica* L.). Plasma Chem. Plasma Process. 2023;43(6):1843-61. https://doi.org/10.1007/s11090-023-10368-1
6. Mitra A, Li Y-F, Klämpfl TG, Shimizu T, Jeon J, Morfill GE et al. Inactivation of surface-borne microorganisms and increased germination of seed specimen by cold atmospheric plasma. Food Bioprocess Technol. 2014;7:645-53. https://doi.org/10.1007/s11947-013-1126-4
7. Wang X-Q, Zhou R-W, Groot Gd, Bazaka K, Murphy AB, Ostrikov K. Spectral characteristics of cotton seeds treated by a dielectric barrier discharge plasma. Sci Rep. 2017;7(1):5601. https://doi.org/10.1038/s41598-017-04963-4
8. El Shaer M, Mobasher M, Abdelghany A. Effect of gliding arc plasma on plant nutrient content and enzyme activity. Plasma Medicine. 2016;6(3-4). https://doi.org/10.1615/PlasmaMed.2016018649
9. Khamsen N, Onwimol D, Teerakawanich N, Dechanupaprittha S, Kanokbannakorn W, Hongesombut K et al. Rice (*Oryza sativa* L.) seed sterilization and germination enhancement via atmospheric hybrid nonthermal discharge plasma. ACS Appl Mater Interfaces. 2016;8(30):19268-75. https://doi.org/10.1021/acsami.6b04555
10. Ji SH, Kim T, Panngom K, Hong YJ, Pengkit A, Park DH et al. Assessment of the effects of nitrogen plasma and plasma-generated nitric oxide on early development of *Coriandum sativum*. Plasma Process Polym. 2015;12(10):1164-73. https://doi.org/10.1002/ppap.201500021
11. Gómez-Ramírez A, López-Santos C, Cantos M, García JL, Molina R, Cotrino J et al. Surface chemistry and germination improvement of Quinoa seeds subjected to plasma activation. Sci Rep. 2017;7(1):5924. https://doi.org/10.1038/s41598-017-06164-5
12. Da Silva A, Farias M, Da Silva D, Vitoriano J, De Sousa R, Alves-Junior C. Using atmospheric plasma to increase wettability, imbibition and germination of physically dormant seeds of *Mimosa caesalpiniafolia*. Colloids Surf B Biointerfaces. 2017;157:280-85. https://doi.org/10.1016/j.colsurfb.2017.05.063
13. Volkov AG, Hairston JS, Patel D, Gott RP, Xu KG. Cold plasma poration and corrugation of pumpkin seed coats. Bioelectrochemistry. 2019;128:175-85. https://doi.org/10.1016/j.bioelechem.2019.04.012
14. Alves Junior C, de Oliveira Vitoriano J, da Silva DLS, de Lima Farias M, de Lima Dantas NB. Water uptake mechanism and germination of *Erythrina velutina* seeds treated with atmospheric plasma. Sci Rep. 2016;6(1):33722. https://doi.org/10.1038/srep33722
15. Matra K. Atmospheric non-thermal argon–oxygen plasma for sunflower seedling growth improvement. Jpn J Appl Phys. 2017;57(1S):01AG03. https://doi.org/10.7567/JJAP.57.01AG03
16. Pérez-Pizá MC, Prevosto L, Grijalba PE, Zilli CG, Cejas E, Mancinelli B et al. Improvement of growth and yield of soybean plants through the application of non-thermal plasmas to seeds with different health status. Heliyon. 2019;5(4). https://doi.org/10.1016/j.heliyon.2019.e01495
17. Ling L, Jiangang L, Minchong S, Chunlei Z, Yuanhua D. Cold plasma treatment enhances oilseed rape seed germination under drought stress. Sci Rep. 2015;5(1):13033. https://doi.org/10.1038/srep13033
18. Guo Q, Wang Y, Zhang H, Qu G, Wang T, Sun Q et al. Alleviation of adverse effects of drought stress on wheat seed germination using atmospheric dielectric barrier discharge plasma treatment. Sci Rep. 2017;7(1):16680. https://doi.org/10.1038/s41598-017-16944-8
19. Jiang J, Lu Y, Li J, Li L, He X, Shao H et al. Effect of seed treatment by cold plasma on the resistance of tomato to *Ralstonia*

solanacearum (bacterial wilt). PLoS One. 2014;9(5):e97753. https://doi.org/10.1371/journal.pone.0097753

20. Adhikari B, Adhikari M, Ghimire B, Adhikari BC, Park G, Choi EH. Cold plasma seed priming modulates growth, redox homeostasis and stress response by inducing reactive species in tomato (*Solanum lycopersicum*). Free Radic Biol Med. 2020;156:57-69. https://doi.org/10.1016/j.freeradbiomed.2020.06.003
21. Gierczik K, Vukušić T, Kovács L, Székely A, Szalai G, Milošević S et al. Plasma-activated water to improve the stress tolerance of barley. Plasma Process Polym. 2020;17(3):1900123. https://doi.org/10.1002/ppap.201900123
22. Kabir AH, Rahman MM, Das U, Sarkar U, Roy NC, Reza MA et al. Reduction of cadmium toxicity in wheat through plasma technology. PLoS One. 2019;14(4):e0214509. https://doi.org/10.1371/journal.pone.0214509
23. Bozhanova V, Marinova P, Videva M, Nedjalkova S, Benova E. Effect of cold plasma on the germination and seedling growth of durum wheat genotypes. Processes. 2024;12(3):544. https://doi.org/10.3390/pr12030544
24. Ling L, Jiafeng J, Jiangang L, Minchong S, Xin H, Hanliang S et al. Effects of cold plasma treatment on seed germination and seedling growth of soybean. Sci Rep. 2014;4(1):5859. https://doi.org/10.1038/srep05859
25. Yang Y, Guo Y. Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytol. 2018;217(2):523-39. https://doi.org/10.1111/nph.14920
26. Ďurčányová S, Slováková L, Klas M, Tomeková J, Durina P, Stupavská M et al. Efficacy comparison of three atmospheric pressure plasma sources for soybean seed treatment: plasma characteristics, seed properties, germination. Plasma Chem Plasma Process. 2023;43(6):1863-85. https://doi.org/10.1007/s11090-023-10387-y
27. Shapira Y, Multanen V, Whyman G, Bormashenko Y, Chaniel G, Barkay G et al. Plasma treatment switches the regime of wetting and floating of pepper seeds, Colloid Surf B-Biointerfaces. 2017;157:417-23. https://doi.org/10.1016/j.colsurfb.2017.06.006
28. Considine MJ, Foyer CH. Redox regulation of plant development. Antioxid Redox Signal. 2014;21(9):1305-26. https://doi.org/10.1089/ars.2013.5665
29. Švubová R, Slováková L, Holubová L, Rovˇnanová D, Gálová E, Tomeková J. Evaluation of the impact of cold atmospheric pressure plasma on soybean seed germination. Plants-Basel. 2021;10(1):177. https://doi.org/10.3390/plants10010177
30. Lin L, Liang R, Liu X, Zhang D, Wang M, Zhao W et al. Seed vigor of soybean treated by corona discharge plasma. Plant Sci Today. 2024;11(1):266-73. https://doi.org/10.14719/pst.2288
31. Iranbakhsh A, Ardebili NO, Ardebili ZO, Shafaati M, Ghoranneviss M et al. Non-thermal plasma induced expression of heat shock factor A4A and improved wheat (*Triticum aestivum* L.) growth and resistance against salt stress. Plasma Chem Plasma Process. 2018;38(1):29-44. https://doi.org/10.1007/s11090-017-9861-3
32. Sarinont T, Amano T, Attri P, Koga K, Hayashi N, Shiratani M. Effects of plasma irradiation using various feeding gases on growth of *Raphanus sativus* L. Arch Biochem Biophys. 2016;605:129-140. https://doi.org/10.1016/j.abb.2016.03.024
33. Yue X, Hu Y, Zhang H, Schmidhalter U. Evaluation of both SPAD reading and SPAD index on estimating the plant nitrogen status of winter wheat. Int J Plant Prod. 2020;14:67-75. https://doi.org/10.1007/s42106-019-00068-2
34. Hashizume H, Kitano H, Mizuno H, Abe A, Yuasa G, Tohno S et al. Improvement of yield and grain quality by periodic cold plasma treatment with rice plants in a paddy field. Plasma Process Polym. 2021;18(1):2000181 https://doi.org/10.1002/ppap.20200018
35. Chen Z, Li L, Zhang H, Huang Q. Stimulation of biomass and astaxanthin accumulation in *Haematococcus pluvialis* using low -temperature plasma (LTP). Bioresource Technology Reports. 2020;9:100385. https://doi.org/10.1016/j.biteb.2020.100385
36. Zhang Z, Liu H, Liu X, Chen Y, Lu Y, Shen M et al. Organic fertilizer enhances rice growth in severe saline–alkali soil by increasing soil bacterial diversity. Soil Use Manage. 2022;38(1):964-77. https://doi.org/10.1111/sum.12711
37. Van Horn DJ, Okie JG, Buelow HN, Gooseff MN, Barrett JE, Takacs-Vesbach CD. Soil microbial responses to increased moisture and organic resources along a salinity gradient in a polar desert. Appl Environ Microbiol. 2014;80(10):3034-43. https://doi.org/10.1128/AEM.03414-13
38. Fgaier S, Aarrouf J, Lopez-Lauri F, Lizzi Y, Poiroux F, Urban L. Effect of high salinity and of priming of non-germinated seeds by UV-C light on photosynthesis of lettuce plants grown in a controlled soilless system. Front Plant Sci. 2023;14:1198685. https://doi.org/10.3389/fpls.2023.1198685
39. Volkov AG, Xu KG, Kolobov VI. Plasma-generated reactive oxygen and nitrogen species can lead to closure, locking and constriction of the *Dionaea muscipula* Ellis trap. J R Soc Interface. 2019;16:(150):20180713. https://doi.org/10.1098/rsif.2018.0713
40. Cui DJ, Yin Y, Sun H, Wang XJ, Zhuang J, Wang L et al. Regulation of cellular redox homeostasis in *Arabidopsis thaliana* seedling by atmospheric pressure cold plasma-generated reactive oxygen/nitrogen species. Ecotox Environ Safe. 2022;240:113703. https://doi.org/10.1016/j.ecoenv.2022.113703
41. Priatama RA, Pervitasari AN, Park S, Park SJ, Lee YK. Current advancements in the molecular mechanism of plasma treatment for seed germination and plant growth. Int J Mol Sci. 2022;23(9)4609. https://doi.org/10.3390/ijms23094609
42. Liu B, Honnorat B, Yang H, Arancibia J, Rajjou L, Rousseau A. Non-thermal DBD plasma array on seed germination of different plant species. J Phys D-Appl Phys. 2018;52(2)025401. https://doi.org/10.1088/1361-6463/aae771