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Tomato yield enhancement with plasma-activated water as an alternative nitrogen source

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Abstract

Background Non-thermal plasma has recently gained popularity in agriculture for their potential applications in pre-cultivation, cultivation, and postharvest processes. Plasma-treated seeds exhibit enhanced plant growth, and their fruits can be stored for extended periods. However, limited research has been conducted to confirm the effects of plasma-activated water (PAW) treatment on plant cultivation from germination to harvest. In this study, we aimed to investigate the use of PAW, generated using a surface dielectric barrier discharge (SDBD) device, for tomato cultivation from germination to harvest.

Results PAW irrigation significantly improved seedling development, increasing cotyledon area by up to 4-times and seedling biomass by up to 3.6-times compared to the untreated control. During the reproductive phase, PAW treatment doubled the number of flowers and increased chlorophyll content and leaf area. At harvest, PAW irrigation led to a 3-times increase in fruit number and up to a 3.9-times increase in plant biomass. Moreover, the characteristics of fruits produced by PAW-treated plants were normal.

Conclusion These results highlight the potential of PAW in future agricultural practices as an alternative ecofriendly nutrient source for plant irrigation under nutrient-limiting conditions, during all developmental stages.

Keywords Non-thermal plasma, Sustainable agriculture, Alternative fertilizer, Crop productivity

Background

The use of non-thermal plasma (NTP) technology, also known as cold atmospheric-pressure plasma (CAP), particularly in agriculture, has gained considerable attention owing to its broad applications ranging from seed treatment to postharvest preservation [1, 2]. Plasma-activated water (PAW) has emerged as a novel technique for promoting plant growth and enhancing agricultural productivity.

NTP technology can enhance seed germination, increase plant vigor, and extend the shelf life of agricultural products [3, 4]. Specifically, the application of PAW, a derivative of NTP technology, has shown promising results in improving the germination and growth of various plants, such as lettuce and Chinese cabbage,

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by altering growth parameters and increasing biomass [5, 6]. A recent study has also demonstrated that PAW improved yield and nutritional quality in soilless lettuce systems, reinforcing its utility in modern agriculture [7]. PAW is generated through the interaction of plasma with water, where the energy and reactive species produced by the plasma enrich the water with reactive nitrogen species (RNS) and reactive oxygen species (ROS). These reactive species play crucial roles in modulating plant physiological responses that are vital for enhancing plant growth and resilience [8–10]. During the plasma–water interaction, peroxyxynitrite acts as a short-lived RNS, while the generated nitrate and nitrite serve as long-lived RNS, significantly increasing the nitrate concentration in the solution [9, 11]. This nitrate is crucial as it serves as the primary nitrogen source for plants, influencing key physiological processes such as seed germination, root architecture development, and overall plant health [12, 13].

PAW treatment can substantially improve the growth parameters of seedlings, enhancing both vegetative growth and reproductive development. For example, in lettuce and basil, treatment with PAW increases the chlorophyll content, dry weight, and overall yield, highlighting its potential as an alternative to traditional nutrient solutions [14, 15]. This treatment can also alter the growth and development of specific tissues in seedlings, such as cotyledon, stem, root, and flower, resulting in increased growth and biomass [16–20]. However, to date, these studies have primarily been conducted on seeds, seedlings, and plants in vegetative stages, raising questions about the applicability of PAW treatment to crop plants. To effectively use the NTP technology in agriculture, it is crucial to understand not only the mechanism underlying the promotion of plant germination and growth but also its effectiveness throughout the cultivation process, from the vegetative stage to harvest.

In this study, we explore the use of PAW as a sustainable input for tomato cultivation, evaluating its effects from seed germination to fruit harvest. By systematically assessing the influence of PAW on key developmental traits, including early growth, flowering, and fruit yield, we elucidate the application of PAW irrigation throughout the plant life cycle. Our results demonstrate that different PAW treatment conditions can modulate root, vegetative, and floral traits, leading to measurable improvements in productivity. Unlike previous studies that focused primarily on early-stage development, this study highlights the broader applicability of PAW across all growth stages. These findings underscore the practical potential of PAW as a sustainable, chemical-free alternative to conventional

fertilization, offering a promising approach for enhancing crop yield while minimizing environmental impact.

Methods

Experimental setup of plasma device and PAW production

PAW was produced using SDBD in gas-tight containers (Fig. 1a), as described in our previous reports [16, 17]. The SDBD device consists of two parallel plate electrodes separated by a dielectric barrier. The electrodes, made of stainless steel, were used for power supply and grounding. An aluminum oxide plate (1-mm thick) was placed between the electrodes to serve as the dielectric barrier. The SDBD reactor, equipped with two electrodes at the top, operated at an input power of 10 W and a driving frequency of 17 kHz. Commercial fans (15-LED 120; Aone, China) were used to dissolve the plasma gas in deionized water (DW). The production of PAW ranged from PAW100 to PAW1000, following the protocol established in our prior studies [16–18, 21]. Specifically, 1 L of DW was treated with SDBD for 10, 40, 60, 80, and 100 min to generate PAW100, PAW400, PAW600, PAW800, and PAW1000, respectively.

The experimental groups were defined as follows: a control DW (without additional chemicals) group and two groups, PAW-400 and PAW-1000, treated with PAW containing nitrate at concentrations of 400 and 1000 mg/L, respectively. While PAW was initially prepared at five different concentrations (PAW100–PAW1000), PAW400 and PAW1000 were selected for comprehensive analysis in the main experiments, based on the outcomes of preliminary screening (Figure S1). The preliminary screening indicated that PAW at these concentrations (within the range commonly used in hydroponic solutions for optimal plant growth) had the most biologically relevant and distinct effects [22]. PAW was then stored in airtight containers at room temperature ($25\text{ }^{\circ}\text{C} \pm 2\text{ }^{\circ}\text{C}$) to minimize the risk of microbial contamination, thus ensuring stability and purity.

To delineate the effects of nitrates and establish comparative baselines, two additional control groups were prepared: a KNO_3 group, reflecting the molarity of nitrate concentration based on PAW-400, and a KCl group, adjusted to match the molarity of potassium in the KNO_3 condition but without the nitrate, thereby establishing both nitrogen-rich and nitrogen-deprived conditions. The potential effect of Cl^- and K^+ ions on plant growth was considered, but the concentration used in our study is unlikely to have a major effect on plant growth [23, 24]. Five treatment conditions were tested in this experiment: DW, PAW400, PAW1000, KNO_3 , and KCl.

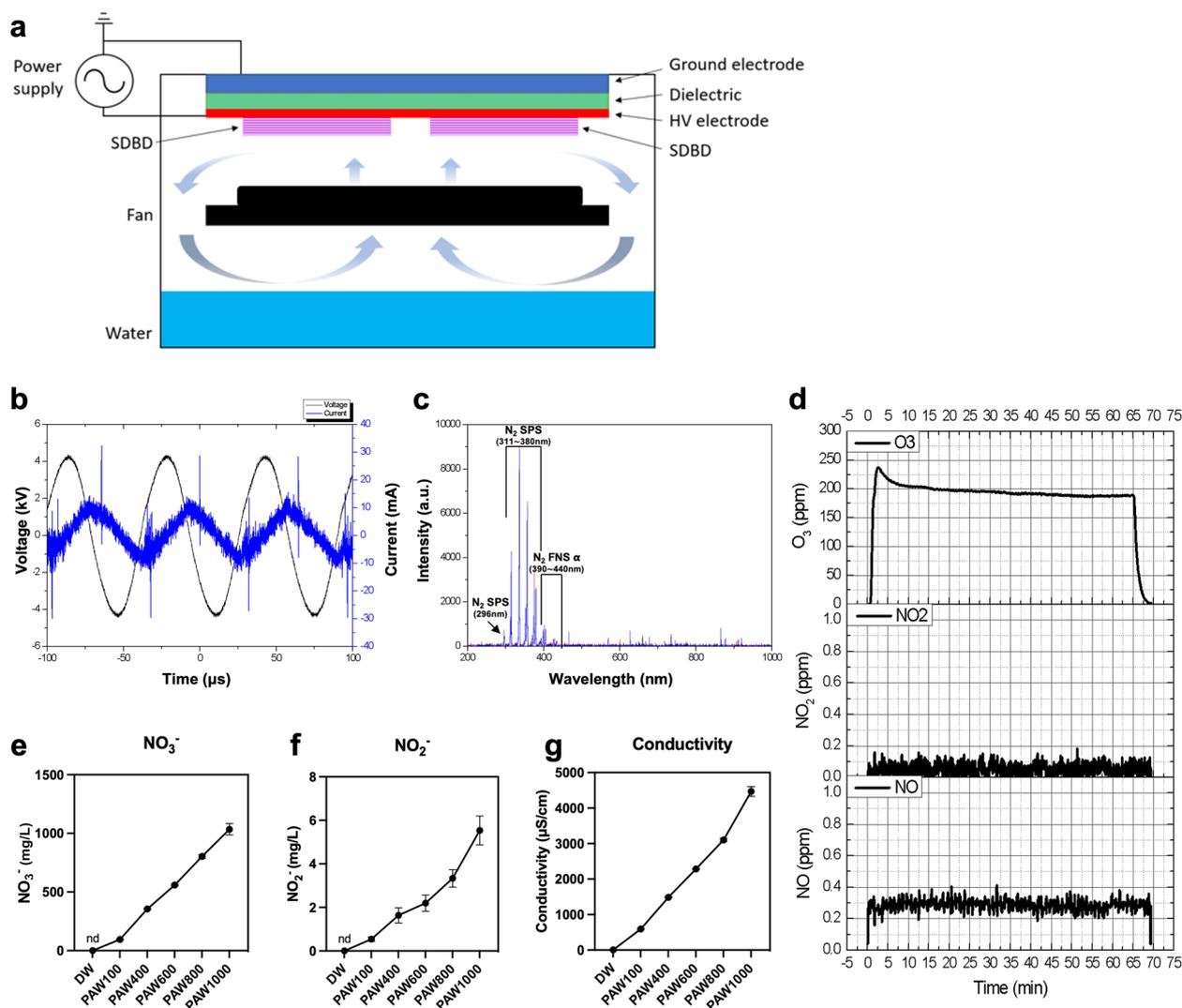


Fig. 1 Plasma-activated water (PAW) generation using surface dielectric barrier discharge (SDBD) reactor and its physicochemical properties. **(a)** Schematic of the SDBD device used for PAW generation. **(b)** Voltage and current waveforms of the SDBD during plasma operation. **(c)** Optical emission spectrum of the SDBD plasma ranging from 200 to 1000 nm. **(d)** Monitoring of reactive gas species during plasma running time. **(e–g)** PAW chemical content: **(e)** NO₃⁻ concentration, **(f)** NO₂⁻ concentration, and **(g)** conductivity

Physicochemical analysis

The optical emission spectrum (OES) of the plasma was recorded using a UV–VIS spectrometer (Ocean Optics, Maya 2000 Pro; Wonwoo Systems, Seoul, Republic of Korea) in the 200–600 nm range. The emission was collimated using an optical lens (Ocean Optics, UV-74) placed 1.5–2.0 cm from the SDBD device in the absence of DW and ventilation. OES data were collected with a 1-s integration time, averaged over 50 measurements.

The chemical characteristics of PAW were analyzed. The anion content was measured using ion chromatography (ICS-2100; Thermo Dionex, Sunnyvale, CA, USA), following a previously reported method [25]. For anion

quantification, a four-point calibration curve was established using standard solutions at 5, 10, 50, and 100 mg/L (Dionex Seven Anion Standard II [in DW]). The pH and conductivity were determined using Orion™ Versa Star Pro™ (Thermo Scientific, Waltham, MA, USA) [26]. The pH of PAW used in all experiments was adjusted to 5.6–5.8 using 0.1 and 1 N KOH solution to ensure that it is suitable for plant growth. Chemical properties were analyzed at least 24 h post-PAW generation, after which PAW stabilizes and can be stored without considerable changes in composition [27]. To maintain consistency in PAW properties across batches, PAW was generated every week, and its chemical properties were assessed;

each batch was entirely used within the same week. All measurements were conducted using three technical replicates at each time point, and a standard deviation was used to estimate the data variation.

Plant materials and growth conditions

To investigate the effects of PAW on crop yield and biomass, we used Micro-Tom, a dwarf cultivar of *Solanum lycopersicum* L., as the model crop. Owing to its compact size and short life cycle, Micro-Tom offers advantages similar to those of *Arabidopsis thaliana* for plant growth studies. Tomato seeds were obtained from TOMATOMA (<https://tomatoma.nbrp.jp>) propagated in a greenhouse (Gyeongsang National University, Jinju, Republic of Korea). Seed propagation was carried out according to common agricultural practices and were conducted in compliance with relevant institutional regulations. To ensure uniformity of seed size as a potential variable affecting our results, any visibly damaged or irregular seeds were discarded. The sorted seeds were imaged, and their areas were measured using ImageJ software [28]. Only seeds with a seed area of 0.45–0.65 mm² were selected. From these, 50 seeds were randomly chosen for the experiment (Figure S2a). The experiment was conducted in a growth chamber (GC-S, Jeiotech, Seoul, Republic of Korea) under 16-h light/8-h dark and 60%–70% relative humidity conditions at 26 °C. For the examination of seed germination and seedling phenotype, a minimum of 30 seeds were tested under each treatment condition. The seeds were placed on filter paper and exposed to specified treatment conditions: DW, PAW, KNO₃, and KCl. Phenotypes were subsequently assessed 12 days after sowing. To ensure the reliability and reproducibility of the results, all experiments were conducted in three biological replicates, that is, the entire experiment was repeated three times, each with a new set of 30 seeds.

For the yield test, seeds were germinated on filter paper layered on a plate and irrigated with 5 mL of the solution for each condition. On day 7 after germination, uniformly germinated seeds were transplanted into commercial horticulture soil (Hanulbio; Shinsung Mineral Inc., Buan-gun, Republic of Korea) on a tray measuring 54 cm × 26 cm × 5 cm (width, length, and depth, respectively), with individual plant holes sized 5 cm × 5 cm × 5 cm (width, length, and depth, respectively). Throughout the experiment, day and night temperatures and relative humidity were maintained at 26 °C and 60%, respectively. The plants were cultivated in the chamber for approximately 3 months until harvest, receiving regular irrigation with PAW at all growth stages. In the 1st month, the plants were irrigated once every 2 days with approximately 200 mL of solution, which was increased to 500 mL per batch

from the 2nd month until harvest. The experiment was conducted with three biological replicates, each consisting of at least 20 individual plants per treatment condition. For the final quantification of biomass, plants that were damaged or did not germinate during the experiment were not included.

Analysis of agronomical and physiological characteristics

Mature tomato plants with a minimum of 80% fruit ripening were harvested for quantification of the final plant biomass, fruit yield, and other agronomic characteristics. After manually uprooting the plants, plant weight and fruit yield were recorded. Fruits were randomly selected for the measurement of average weight and total soluble sugar content (Brix) and for textural analysis. The weight of the fruit harvested from each plant was used to determine the total fruit yield per plant. The Brix value (%) was determined using a digital refractometer (PAL-1; ATAGO Co., Ltd., Tokyo, Japan). Fruit firmness was measured using a fruit penetrometer (FR-5120; Lutron Electronic Enterprise Co., Ltd., Taipei, Taiwan).

Total chlorophyll content in fully grown leaves, collected from 4-week-old plants, was quantified using a spectrophotometer (Hach DR6000; Hach, Loveland, CO, USA) by measuring the absorbance of chlorophyll extract at 665 and 648 nm, following a previously reported method [29]. For each treatment condition, five biological replicates and three technical replicates were used for chlorophyll measurements.

Statistical analyses

Statistical analyses were performed using the GraphPad Prism 9.0 software (GraphPad Software, Inc., San Diego, CA, USA). Unless described in the figure legend, the statistical analysis and comparison among samples were performed using one-way ANOVA followed by Tukey's honestly significant difference (HSD) correction for multiple comparisons. Differences were considered statistically significant at $P < 0.05$; different uppercase letters denote significant differences among samples. The results are presented as mean ± SD.

Results

Physicochemical characterization

Figure 1b shows the voltage–current waveform during discharge. The root mean square voltage and current were measured at 3.03 kV and 3.08 mA, respectively, at a discharge frequency of 15.35 kHz. The total power dissipated in the plasma was 3.22 W. Optical emission spectroscopy (OES) detected prominent nitrogen second positive (N₂ SPS) and first negative (N₂ FNS) systems in the 296–280 and 390–440 nm ranges, respectively,

indicating the generation of nitrogen ions during air discharge (Fig. 1c). These nitrogen species interact with OH radicals, O_2 , and H_2O to produce NO_2^- and NO_3^- , which were detected in PAW.

To further characterize gaseous intermediates, the concentrations of ozone (O_3), nitrogen dioxide (NO_2), and nitrogen monoxide (NO), which are important intermediates in the formation of NO_2^- and NO_3^- in PAW, were measured by a gas analyzer (Fig. 1d). Plasma exposure increased nitrate and nitrite concentrations in a time-dependent manner, consistent with our previous findings (Fig. 1e, f) [16–18]. Previously, we reported that PAW with nitrate at concentrations ranging from 25 to 100 mg/L was optimal for Arabidopsis, with suppression effects observed at 100 mg/L [16, 17]. On the basis of this finding, PAW treatments in the present study were standardized using nitrate at concentrations of 400 mg/L (PAW400) and 1000 mg/L (PAW1000). Additionally, PAW conductivity increased with longer plasma treatment durations (Fig. 1g).

PAW affects vegetative and root growth in the seedling stage

We examined the vegetative and root phenotypes of 12-day-old tomato seedlings, including cotyledon area, hypocotyl length, primary root length, lateral root number, lateral root length, and seedling biomass.

Several germination tests were performed to confirm the differences in seed germination under various conditions; however, no significant differences were found (Figure S2b). In the vegetative tissue, the morphology of the cotyledons and hypocotyls was considerably improved (Fig. 2a–d). The cotyledon area and hypocotyl length, particularly in the PAW400 and PAW1000 groups, increased compared with those in the control group (DW). Specifically, the cotyledon area was 3 and 4-times larger in the PAW400 and PAW1000 groups than in the control group, and the hypocotyl length in the PAW1000 group was 1.3-times greater than that in the DW group (Fig. 2b–d). Primary root length was significantly greater under PAW treatments—1.6- and 2.2-times higher in the PAW400 and PAW1000 groups than in the DW group, respectively (Fig. 2e). Notably, the number of lateral roots was the highest in the PAW400 group, exhibiting an 11.1-times increase compared with that in the DW group, along with a significant increase in lateral root length (Fig. 2f, g). Seedling biomass significantly increased under PAW400 (by 3.1 times), PAW1000 (by 3.6 times), and KNO_3 conditions (by 2.5 times)—compared with that observed under the control (DW) (Fig. 2h). Furthermore, seedlings grown under DW and KCl conditions exhibited a delayed growth phenotype, whereas those treated with PAW and KNO_3 under nitrogen-replete conditions

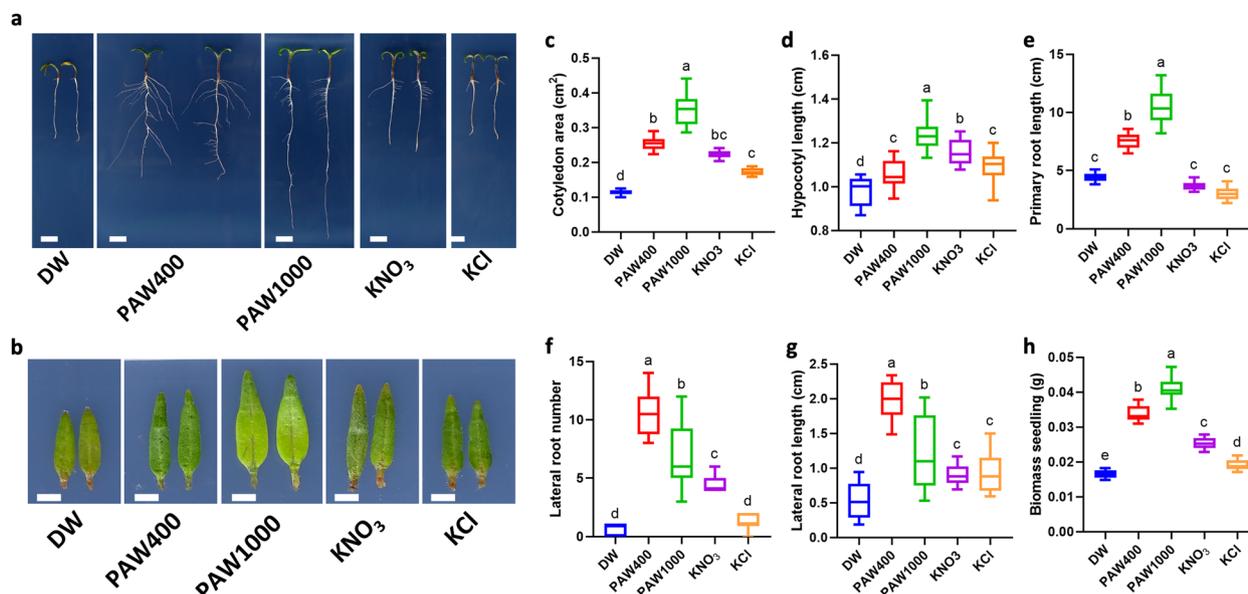


Fig. 2 Effect of PAW on vegetative and root growth during the early developmental stage of tomatoes. **(a)** Representative picture showing the seedling phenotype under PAW and DW treatments. **(b)** Phenotype of cotyledons in tomato seedlings grown on PAW. Scale bar: 3 mm. **(c–h)** Quantification of seedling phenotype and biomass: **(c)** area of cotyledons, **(d)** hypocotyl length, **(e)** primary root length, **(f)** lateral root number, **(g)** lateral root length, **(h)** biomass during the seedling stage. Boxplots indicate the 25 th and 75 th percentiles, and different letters indicate statistically significant differences (ANOVA, Tukey's honestly significant difference, $P \leq 0.05$). The seedlings were grown on filter paper supplied with appropriate solution for 12 days. All phenotypes were recorded at 12 days after sowing

demonstrated an accelerated growth phenotype during the vegetative stage (Figure S3).

PAW increases the number of flowers and fruit set

PAW treatment enhanced vegetative and root growth during early development. Therefore, we further examined whether continuous PAW irrigation would influence tomato morphology during the reproductive stage. The overall morphology under PAW400, PAW1000, and KNO_3 conditions improved, with an increase in plant size compared with the DW condition (Fig. 3a). Among all conditions, plant height was the maximum under PAW400 condition. Eight weeks post-sowing, the number of flowers increased significantly under PAW400, PAW1000, and KNO_3 conditions, but it decreased under nitrogen-depleted KCl condition (Fig. 3b). Flower counts were conducted every 2 days from days 38 to 46 after

sowing. No flowers were observed under any condition on day 38. However, by day 46, the number of flowers under PAW and KNO_3 conditions had at least doubled compared to that under DW and KCl conditions (Fig. 3c).

Following the observation of increased plant size during the reproductive stage under PAW irrigation, we evaluated leaf area and chlorophyll content. Nine weeks after sowing, the leaf area in the PAW and KNO_3 groups considerably increased, but there was no change in the DW and KCl groups (Fig. 3d). In addition, mature plants under DW and KCl conditions had pale green leaves, whereas mature plants under PAW and KNO_3 conditions had intense dark-green leaves (Figure S4). The chlorophyll measurements further validated these observations. The leaves of plants treated with PAW and KNO_3 exhibited higher chlorophyll content than those of plants treated with DW and KCl (Fig. 3e). These findings

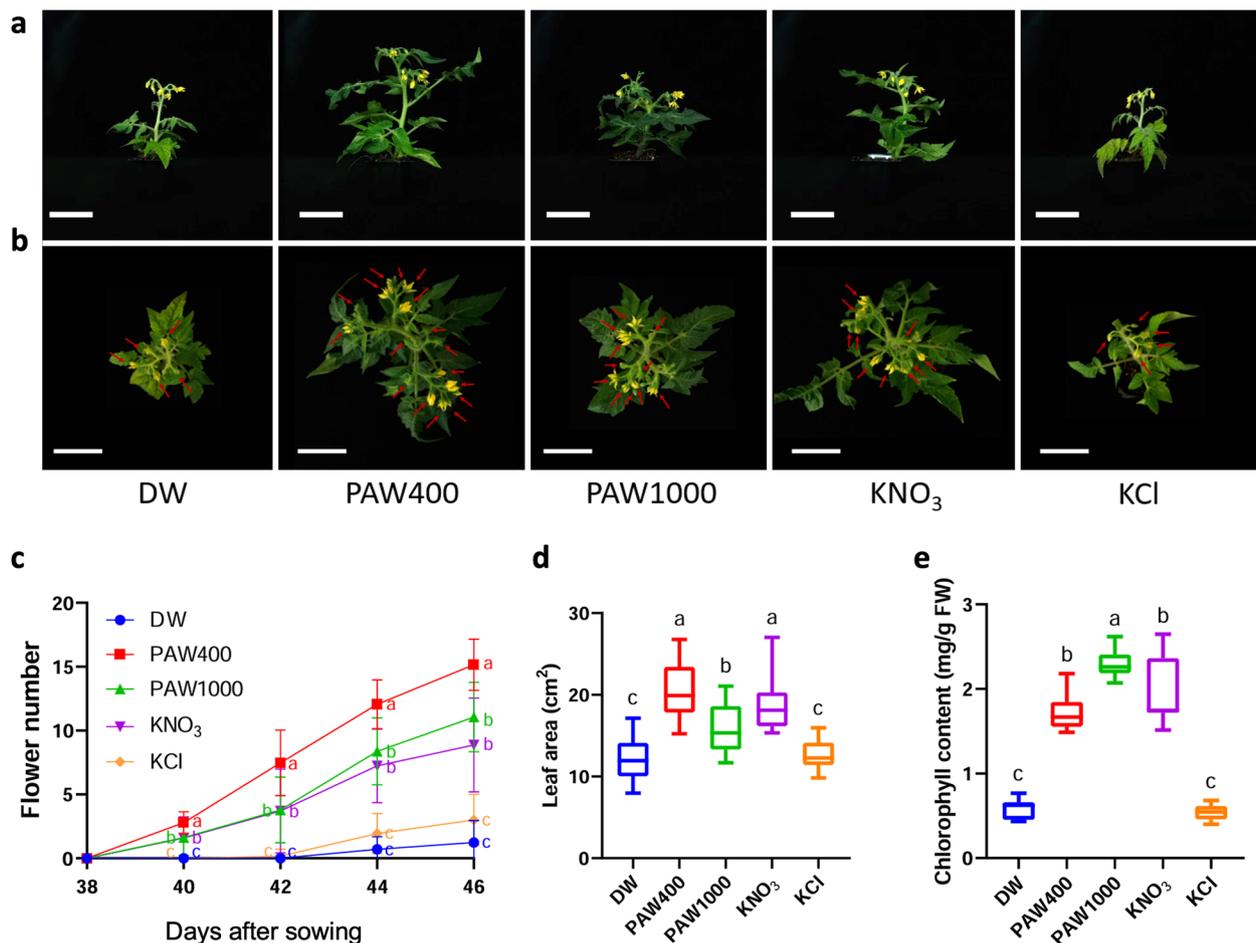


Fig. 3 Effect of PAW irrigation on flower emergence. (a) Plant phenotype during the flower-emergence stage. (b) Aerial view of the plants showing the flower number. Red arrows indicate an emerging flower. (a) and (b) Photographs were taken at 8 weeks after sowing. Scale bar: 5 cm. (c) Quantification of floral number during the flower-emergence stage at 38–46 days after sowing. (d, e) Quantification of leaf area and chlorophyll content at 9 weeks after sowing. Boxplots indicate the 25 th and 75 th percentiles, and different letters indicate statistically significant differences (ANOVA, Tukey's honestly significant difference, $P \leq 0.05$)

underscore the substantial effect of nitrogen-replete conditions on flower production, leaf area, and chlorophyll content, highlighting the potential of PAW as a sustainable non-chemical nitrogen source.

Fruit number and weight per fruit under PAW irrigation conditions

Given its early growth-promoting effects, we evaluated the influence of PAW on tomato fruit yield at harvest. In addition, we measured the number, weight, and firmness of fruits to determine the effect of PAW. The phenotypes of the fruits under DW, PAW400, PAW1000, KNO₃, and KCl conditions are shown in Fig. 4a-b. PAW400 led to the greatest increase in fruit number (the number of red and green fruits increasing by approximately 2- and 3-times, respectively) compared to the DW control. This was the highest

enhancement observed across all treatments (Fig. 4c). KNO₃ treatment also increased fruit number, but to a less extent—approximately 1.7 times higher than that of the control. In contrast, PAW1000 increased the fruit number, not exceeding 1.5 times that of the control. In addition, KCl, representing nitrogen-depleted conditions, resulted in the lowest fruit counts, closely matching the baseline set by DW.

The average fruit weight (calculated as total fruit weight divided by fruit number) increased under PAW400 and KNO₃ treatments, but no changes were observed under DW and KCl conditions. Despite increasing the nitrate content, PAW1000 did not improve the average fruit weight (Fig. 4d). Fruit firmness remained unaffected across all treatments (Fig. 4e). These findings suggest that PAW irrigation, particularly PAW400 irrigation, effectively increased both fruit number and weight.

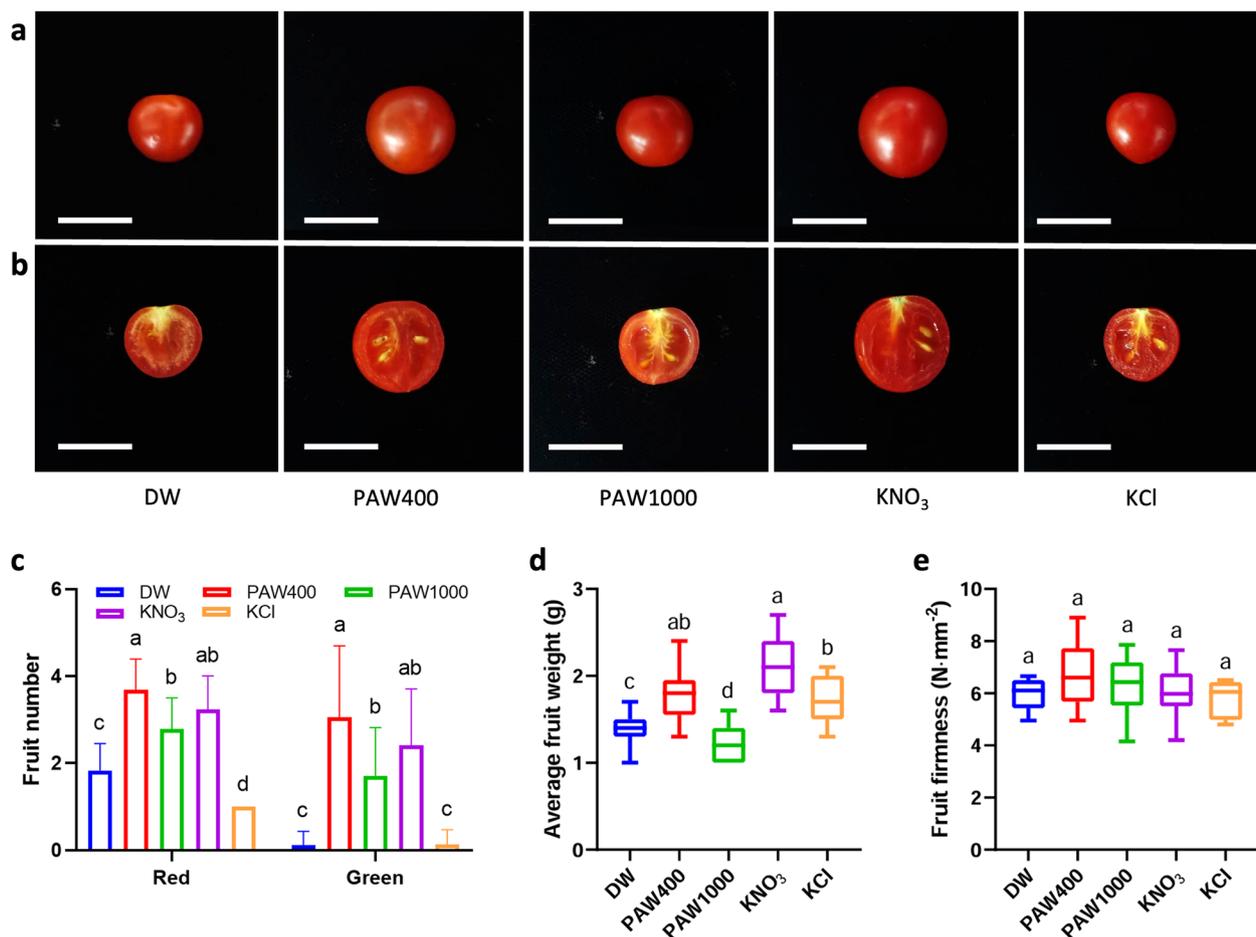


Fig. 4 Effects of PAW irrigation on the number and weight of fruits. **(a-b)** Fruit morphology in PAW-irrigated plants: **(a)** Representative whole fruit from plants irrigated with deionized water (DW), PAW400, PAW1000, KNO₃, and KCl, **(b)** Longitudinal section of a representative fruit from plants irrigated with DW, PAW400, PAW1000, KNO₃, and KCl. Scale bar: 1.5 cm. **(c-e)** Quantification of fruit number, weight, and firmness: **(d)** average fruit weight (total fruit weight/total fruit number), **(e)** fruit firmness. Boxplots indicate the 25 th and 75 th percentiles, and different letters indicate statistically significant differences (ANOVA, Tukey's honestly significant difference, $P \leq 0.05$). **(a-e)** All data were collected at 14 weeks after sowing

PAW increases tomato biomass

Plant height, stem thickness, total fruit weight, and biomass were measured to investigate the effects of PAW on fruit yield and biomass. The measurements were conducted under all the conditions (Fig. 5). All plants were grown under identical climatic conditions (see Methods). Plant height increased under PAW400 treatment but tended to decrease under PAW1000 treatment (Fig. 5a-b). Stem thickness increased compared to DW under PAW400 and KNO₃ treatments 14 weeks after sowing (Fig. 5c).

To evaluate fruit yield, we measured the total fruit weight and plant biomass 14 weeks after sowing. Total fruit weight was the highest under PAW400 treatment, followed by that under other nitrate-supplemented conditions (Fig. 5d). Plant biomass followed a similar trend, with PAW400 increasing the biomass by 3.9 times compared to DW. This was followed by KNO₃, which increased the biomass by approximately 3.1 times, and PAW1000, which increased the biomass by 2.7 times. KCl resulted in the lowest increase (Fig. 5e). These results indicate that PAW irrigation improves both fruit yield and biomass production.

Discussion

In our previous study, we examined the effects of PAW generated via the SDBD device during the early developmental stages of plants [16, 17]. In the present study, we extend our investigation to the effects of continuous PAW irrigation on tomato cultivation. We examined the effects of PAW on germination, seedling development, overall morphology, floral characteristics, and fruit yield.

The SDBD device efficiently generates PAW enriched with RNS, which promote germination and plant growth. This approach is also cost-effective, as gaseous RNS are readily dissolved in DW [30, 31]. The OES data for the SDBD system, showing the presence of N₂ FNS and SPS, correlated with a high concentration of RNS, particularly NO₃⁻, in water. Consistently, the concentration of NO₃⁻ significantly increased in DW exposed to the SDBD plasma device (Fig. 1).

Plasma treatment, both directly and indirectly, positively affects germination [8, 32]. In our study, although there was no marked difference in germination rates between the DW and PAW treatments (Figure S2b), significant variations in phenotypic development were observed during the seedling stage. PAW1000 notably enhanced shoot system development early during growth, whereas PAW400 most effectively increased the number and length of lateral roots.

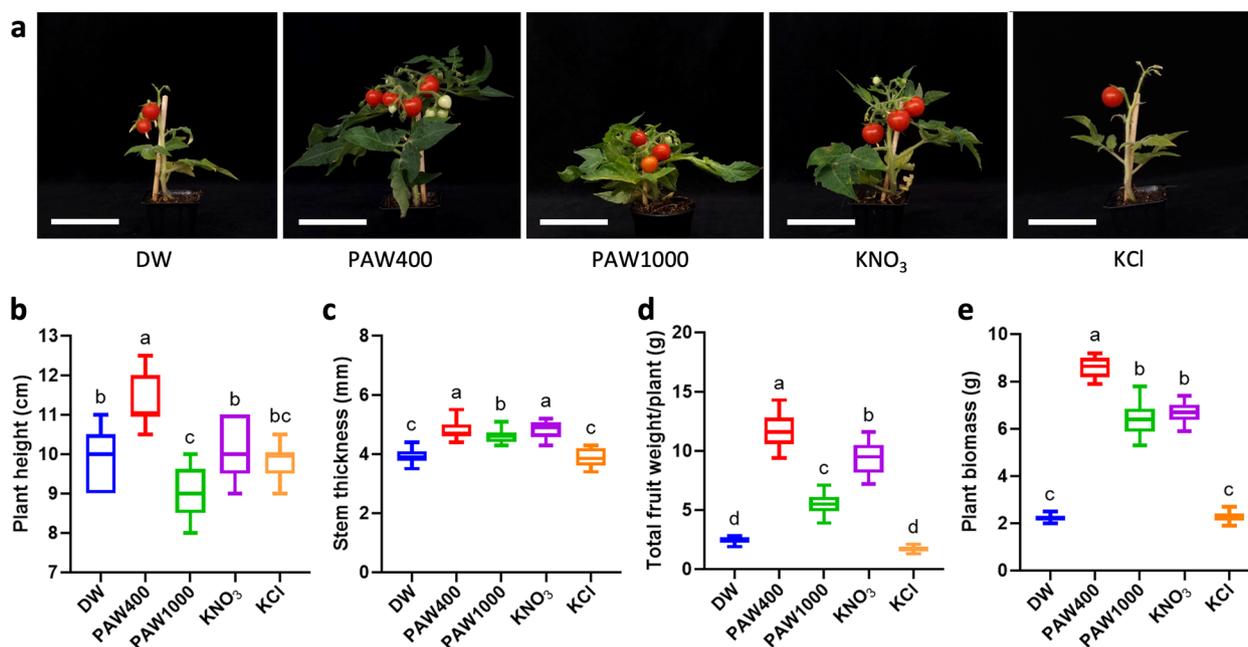


Fig. 5 Effects of PAW irrigation on agronomic characteristics of tomato plants under nutrient-limiting conditions. (a) Plant phenotype during the harvest stage. Scale bar: 5 cm. (b) Plant height during the harvest stage. (c) Stem thickness during the harvest stage. (d) Total fruit weight/plant during the harvest stage. (e) Fruit weight during the harvest stage. (b–e) Boxplots indicate the 25 th and 75 th percentiles, and different letters indicate statistically significant differences (ANOVA, Tukey's honestly significant difference, $P \leq 0.05$). (a–e) All data were collected at 14 weeks after sowing

Seedlings grown under PAW and KNO_3 conditions developed larger cotyledons than those under KCl and DW conditions, with similar phenotypes. Notably, while PAW400 had a negligible effect on the hypocotyl length of seedlings, PAW1000 had a considerable effect (Fig. 2). Cotyledons, the first leaves that emerge post-germination, are critical for the early energy supply through photosynthesis. The observed enlargement of the cotyledon area under PAW treatment not only supports seedling vitality but also suggests potential improvement in overall plant growth and development, which may improve overall plant health and productivity. Damage to cotyledons at this stage could impede further growth, thereby reducing the biomass of mature plants [33].

Both PAW400 and PAW1000 treatments led to an increase in the number and length of lateral roots compared to the control (Fig. 2a). However, PAW1000 resulted in fewer lateral roots than PAW400, indicating that excessive nitrate may inhibit lateral root formation during early development. This inhibitory effect of high nitrate levels is consistent with prior findings in *Arabidopsis* and maize, where elevated nitrate level suppresses lateral root meristem activation [34–36].

Plant hormones play a crucial role in plant growth, development, and interaction with the environment. PAW promotes seedling growth by upregulating the production of endogenous reactive oxygen and nitrogen species and phytohormones (auxin, cytokinin, salicylic acid, jasmonic acid, and other plant hormones) via hormone biosynthesis and signal transduction and expression of key pathogenesis-related (PR) genes [10, 37]. Increased concentrations of nitrite and nitrate ions in PAW serve as not only effective nitrogen fertilizers—enhancing germination, growth, and overall biomass [31]—but also signaling molecules that promote floral induction during extended photoperiods [38]. A well-established relationship exists between nutrient availability and plant reproductive success; studies have shown that nitrate availability can considerably influence the timing and quantity of flower and fruit production. For instance, grapevines exhibit a nitrate dose-dependent increase in the number of both flowers and fruits, likely due to nitrate's role in modulating the expression of genes related to fruit maturation and nutrient assimilation, thereby enhancing overall plant yield. Similarly, increased nitrogen supply significantly increased the chlorophyll content in olive leaves and expanded the leaf area in *Leymus chinensis*, demonstrating nitrate's broad effect on plant physiology [39, 40].

While PAW treatments increased leaf area and chlorophyll content, comparable with those in the KNO_3 control group (Fig. 3), the most notable difference was observed in the flowering stage. As plants transitioned

from the vegetative stage to the flowering stage, the number of flowers from the 40th to 46th day of seedling growth considerably differed from that under the nitrogen-deficient condition (Fig. 3). This finding suggests that PAW may promote reproductive success under nitrate-supplemented conditions. Future research including transcriptomic analysis during the reproductive stages and analysis of hormonal regulation by PAW could elucidate the specific molecular pathways influenced by PAW.

In this study, the benefits of PAW irrigation were significant in terms of fruit yield; PAW-treated plants had higher fruit numbers and weights than those irrigated with DW and KCl (Fig. 4). Fruit yield under PAW400 treatment was comparable to that under KNO_3 treatment, suggesting similar efficacy under controlled conditions. Notably, our findings did not indicate any significant effects of PAW on fruit firmness, which remained consistent across different treatment groups. However, further studies are needed to determine whether PAW affects the nutritional qualities of tomato, including vitamin C and antioxidant levels and other key nutritional metrics.

A previous study has shown that nitrogen supplementation positively affects fruit weight and yield, as demonstrated in muskmelon, where nitrogen-replete conditions increased biomass [41]. Consistent with these findings, our results indicate that PAW, as a nitrogen-enriched irrigation input, can support both vegetative growth and reproductive development in tomato. In particular, early PAW application improved seedling vigor and increased flower production, ultimately contributing to greater fruit set and final yield. The presence of nitrate and nitrite in PAW may facilitate nutrient uptake and improve stress tolerance, thereby creating more favorable conditions for crop development. These findings suggest that the effects of PAW can be comparable to those of conventional nitrogen fertilizers in supporting plant productivity.

During the late growth stage, plants irrigated with DW or KCl senesced earlier than those treated with PAW or KNO_3 (Fig. 5a), consistent with the findings of previous studies on nitrogen deprivation and early senescence in *Arabidopsis* [42, 43]. These findings suggest that PAW may delay senescence by providing a sufficient nitrogen supply throughout plant development. Significant differences in agronomic traits, including plant height, stem thickness, fruit yield, and total biomass, were observed across treatment groups (Fig. 5 and Figure S5). The presence of long-lived, water-soluble RNS in PAW likely contributes to improvements in both early and late growth stages.

PAW1000 treatment initially promoted shoot elongation, whereas PAW400 enhanced lateral root development. Over time, PAW400-treated plants exhibited

more balanced growth, resulting in greater structural stability and higher yield. In contrast, the early growth stimulation observed in PAW1000-treated plants did not translate to increased fruit yield, possibly because of nitrate-induced stress in later growth stages. These findings highlight the need to optimize the concentrations of nitrate and other PAW components to align with crop-specific developmental phases. Additionally, the potential applications of PAW extend beyond growth promotion. The ability of PAW to reduce pathogen contamination in irrigation water may contribute to improved seedling health and reduced inoculum pressure—critical factors in integrated disease management. This broader functionality suggests that PAW could support both plant productivity and health in sustainable cropping systems. While the results are promising, it is important to recognize that this study was conducted at a relatively small scale. Future research should evaluate the effectiveness of PAW under field conditions and across diverse agricultural systems. Additionally, the economic feasibility of scaling up PAW production for commercial use remains an important consideration. Developing energy-efficient plasma devices and integrating renewable energy sources may enhance the cost-effectiveness and sustainability of PAW application at larger scales.

Owing to its unique physicochemical composition, PAW represents a promising option for advancing sustainable agricultural practices. As a non-thermal plasma-based innovation, PAW has the potential to reduce dependence on synthetic fertilizers and pesticides, thereby facilitating a transition toward low-input, eco-friendly farming systems. PAW use may help maintain or even improve crop productivity while enhancing plant resilience, contributing to long-term food security and environmental restoration. The integration of PAW with emerging biotechnological and agroecological approaches offers a strategy for sustainable and regenerative agriculture.

Conclusions

This study provides comprehensive evidence that PAW, generated using a SDBD device, can enhance tomato growth and productivity across all developmental stages from seedling growth to fruit harvest. PAW treatment, particularly PAW400 treatment, significantly improved early seedling development, increased flower production, and ultimately led to improved fruit yield and total biomass. These effects were comparable to those observed under conventional KNO_3 fertilization, suggesting that PAW is as effective as a nitrogen source. Notably, PAW treatment also delayed senescence and improved agronomic traits such as stem thickness and chlorophyll content, without compromising fruit quality. While

PAW1000 initially stimulated shoot growth, PAW400 achieved more balanced development and superior final yield, underscoring the importance of optimizing nitrate level for targeted crop outcomes. These findings position PAW as a promising and environmentally friendly input for sustainable agriculture.

Abbreviations

CAP	Cold atmospheric-pressure plasma
DW	Deionized water
N_2 FNS	First negative
HSD	Honestly significant difference
NO_2	Nitrogen dioxide
NO	Nitrogen monoxide
N_2 SPS	Nitrogen second positive
NTP	Non-thermal plasma
OES	Optical emission spectrum
O_3	Ozone
PR	Pathogenesis-related
PAW	Plasma-activated water
RNS	Reactive nitrogen species
ROS	Reactive oxygen species
SDBD	Surface dielectric barrier discharge

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12870-025-06701-9>.

Supplementary Material 1.

Acknowledgements

Not applicable.

Authors' contributions

All authors read and approved the final manuscript. Conceptualization, RAP and YKL; experiment and data curation, HKB, RAP, ICS, and SP; writing—original draft preparation, RAP, HKB, and YKL; writing—review and editing, RAP, SP, SJP, SBK, and YKL; funding acquisition, SBK and YKL. All authors have read and agreed to the published version of the manuscript.

Funding

This work was supported by the R&D Program of "Plasma Advanced Technology for Agriculture and Food (Plasma Farming) EN2525-12" through the Korea Institute of Fusion Energy (KFE) to R.A.P, H.K.B., and Y.K.L.; a National Research Foundation of Korea (NRF) grant funded by the Korean Government (MSIT) (No. NRF-2021R1 A2 C1005650) to Y.K.L., R.A.P., H.K.B., I.C.S., and Y.K.L.; and the National Research Council of Science & Technology (NST) grant by the Korean Government (MSIT) (No. CCL23171-100). R.A.P., I.C.S., and S.B.K. were supported by grants from the NST supported by the MSIT (No. CRC-21022-340).

Data availability

All data generated and analyzed during this study are included in this published article and its Additional files. Additional datasets are available from the corresponding author on reasonable request. The materials used in this study, including PAW treatment setups, are described in detail in the Methods section, and the details are available on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 21 February 2025 Accepted: 9 May 2025

Published online: 20 May 2025

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