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ARTICLE

High-voltage electrostatic fields increase nitrogen uptake and improve growth of tomato seedlings

Meiqing Li, Yanyou Wu, Mingming Zhang, and Jianyun Zhu

Abstract: High-voltage electrostatic fields (HVEFs) can increase the nitrogen uptake of plants. An ammonium cation inhibitor, tetraethylammonium chloride, and a nitrate ion inhibitor, 5-nitro-2-(3-phenylpropylamino)-benzoate, were added to ammonium and nitrate growing solutions with and without exposure to HVEFs to investigate the effects of these fields on tomato seedlings. The seedlings were exposed to HVEFs with field intensities of 2.25 and 2.5 kV cm^{-1}, respectively, for 8 h and the dynamic absorption of nitrogen ions was comparatively analyzed. The seedlings exposed to HVEFs were planted in a greenhouse, the diameter and length of their stems were measured after a 20-d growth period, and their fruit yield was recorded after harvest. Results demonstrated that HVEFs with field intensities of 2.25 and 2.5 kV cm^{-1} could respectively improve the dynamic absorption of NH_4^+ and NO_3^- by the hydroponically grown tomato seedlings. Many channel proteins were also activated by HVEFs as nitrogen uptake increased. HVEF treatment in the seedling stage is a potential mechanism to enhance nitrogen uptake, cultivate shorter and stockier seedlings, and increase yield.

Key words: hydroponic tomato plant, nitrogen absorption, high-voltage electrostatic field.

Résumé : Les champs électriques à haute tension (CEHT) peuvent amener les plantes à absorber plus d'azote. Les auteurs ont ajouté un inhibiteur des cations ammonium, le chlorure de tétraéthylammonium, et un inhibiteur des ions nitrate, le 5-nitro-2-(3-phénylpropylamino)-benzoate, à des solutions de croissance contenant de l'ammonium et du nitrate pour étudier les effets des CEHT sur les plantules de tomate. Ces dernières ont été exposées à un CEHT d'une intensité de 2,25 ou de 2,5 kV par cm pendant huit heures, puis les auteurs ont comparé l'absorption dynamique des ions azote. Les plantules exposées à un CEHT ont ensuite été repiquées dans une serre et on a mesuré le diamètre ainsi que la longueur de la tige après vingt jours de croissance. Le calibre des fruits a également été noté à la récolte. Les résultats indiquent qu'un CEHT d'une intensité de 2,25 ou 2,5 kV par cm pourrait rehausser respectivement l'absorption dynamique des ions NH_4^+ et NO_3^- par les plantules de tomate cultivées de façon hydroponique. Le CEHT active aussi de nombreuses protéines de transport, parallèlement à la plus grande absorption d'azote. Soumettre les plantules à un CEHT pourrait contribuer à améliorer l'absorption d'azote et à obtenir des plantules plus courtes et plus robustes, susceptibles de donner un meilleur rendement. [Traduit par la Rédaction]

Mots-clés : tomate hydroponique, absorption de l'azote, champ électrostatique à haute tension.

Introduction

Attaining a high yield is one of the main goals of crop production and is often restricted by many factors such as types of nutrients and amount of absorbed nitrogen (N). Nitrogen is an essential nutrient that directly affects yield. Nitrogen nutrients are mainly absorbed through particular channels of roots and utilized by crops (Tester 1990). Ion absorption channels play an important role in plant growth and adaptation to poor external environments. Different absorption pathways and N concentrations directly influence the absorption of special ion channels and the affinity of different channels (Wang et al. 1993; Touraine and Glass 1997; Kronzucker et al. 1998). The amount of nutrients

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absorbed by crops is correlated with their open ion channels; however, channels, which are activated or inhibited by either chemical or electrical methods, can affect final crop yield (Kronzucker et al. 1998). Anion channels are the main gateway of NO_3^- absorption, and 5-nitro-2-(3-phenylpropylamino)-benzoate (NPPB) is a typical inhibitor of anion channels in plant cells (Brochiero et al. 1995). The main absorption channels of NH_4^+ are K^+ channels and these absorption channels can be blocked by tetraethylammonium chloride (TEA) (Tester 1988; Wehner et al. 2003).

Electric cultivation techniques involve the application of magnetic fields, sound waves, pulse electric fields, and electrostatic fields in agriculture (Nelson 2005). Suitable pulse magnetic fields and sound waves promote seed germination and nutrient absorption and increase the yield of crops (Qin and Lee 2003; Belyavskaya 2004; Yao et al. 2005; Dhawi et al. 2009; Radhakrishnan and Ranjitha Kumari 2012). Electrostatic fields can also stimulate seed germination (Sidaway and Asprey 1966; Yang and Shen 2011) and plant growth (Diprose et al. 1984). High-voltage short-duration electrical pulses support the growth of protoplast-derived cells and the regeneration of the shoot from protoplast-derived tissues (Davey et al. 1996). Murr (1963) found that high-voltage electrostatic fields (HVEFs) increase the dry weight of orchard grass but considerably strong electric fields cause lethal electrotropism in plants (Murr 1964*a*) and damage plant cells (Murr 1964*b*). Moon and Chung (2000) observed that the percent germination rates of tomato seeds treated with alternating current electric fields (4–12 kV cm^{-1}) increased by approximately 1.1–2.8 times as much as those of untreated seeds. However, germination is inhibited when the electric field is more than 12 kV cm^{-1} and the exposure time is longer than 60 s. These results indicate that HVEFs with an appropriate field intensity can improve the germination rate of seeds and promote nutrient absorption and the growth of seedlings.

The factors contributing to the increased N uptake by plants exposed to HVEFs are unclear. Considering that the mineral nutrient uptake of plants occurs mainly via ion channels in roots, we hypothesized that the increased N absorption is attributed to many HVEF-activated channel proteins and this condition favors the opening of the corresponding ion channels. This work aimed to investigate the mechanism by which HVEFs induce NH_4^+ promotion and NO_3^- absorption of tomato seedlings. This study also determined the possible involvement of HVEF pretreatment in increasing the diameter and height of stems and the yield of tomato.

Materials and Methods

Study site

The experiments were conducted in a Venlo-type greenhouse and laboratory (32°12′N, −119°27′E) of the Agricultural Engineering Institute of Jiangsu University in China.

Tomato seedling cultivation

The tomato seeds (hybrid 908) were obtained from a native seed company in Zhenjiang City, China. Healthy, uniform, dry seeds were selected, sterilized with 0.5% (*w*/*v*) aqueous formalin for 30 min, washed, and allowed to imbibe distilled water for 24 h. Afterward, surface-sterilized seeds were propagated in plug seedling trays with a substrate that contained perlite and vermiculite (at a 2:1 ratio) in a greenhouse. When the seeds germinated and grew out of the second euphylla (i.e., about 20 d), robust seedlings with the same size (4 cm in height) were carefully selected and gently washed. Experimental units that consisted of six seedlings were transplanted into pots with tomato Yamazaki nutrient solution formula in a controlled laboratory. The Yamazaki solution consisted of the following nutrients and concentrations (mg L^{-1}): $Ca(NO_3)_2{\cdot}4H_2O$, 354; KNO_3, 404; $(NH_4)H_2PO_4$, 77; $MgSO_4{\cdot}7H_2O$, 246; Na_2Fe-EDTA, 25; H_3BO_3, 2.13; $MnSO_4{\cdot}4H_2O$, 2.86; $ZnSO_4{\cdot}7H_2O$, 0.22; $CuSO_4{\cdot}5H_2O$, 0.08; and $(NH_4)_6Mo_7O_2{\cdot}4H_2O$, 0.22. The light intensity of both the greenhouse and laboratory was 800–1000 μmol m^{-2} s^{-1} under a 12 h day —12 h night natural light cycle. The day and night temperatures of the greenhouse and laboratory were 25 °C ± 2 °C and 22 °C ± 2 °C, respectively.

During the culture period in the laboratory, the culture solution of the seedlings was replaced with fresh nutrient solution every 2 d. The culture solution was adjusted to the same target pH value between 6.0 and 6.5 by using a dilute aqueous solution of NaOH once a day. After a 20-d growth period, the seedlings were transferred in a solution lacking N for 2 d until they were ready for the N absorption test.

N absorption when exposed to HVEF

$(NH_4)_2SO_4$ and $NaNO_3$ were purchased from Shanghai Sinopharm Chemical Reagent Co., Ltd. (Shanghai, China). The ion channel blockers $(C_2H_5)_4NCl$ (TEA) and NPPB were purchased from Sigma (Shanghai Changjiangkou Chemical Technology Co., Shanghai, China). The following solutions were prepared: (*i*) 1.0 mmol L^{-1} NH_4^+, (*ii*) 20 μmol L^{-1} TEA and 1.0 mmol L^{-1} NH_4^+, (*iii*) 1.0 mmol L^{-1} NO_3^-, and (*iv*) 20 μmol L^{-1} NPPB and 1.0 mmol L^{-1} NO_3^-. Approximately 100 mL of each solution was placed in individual beakers and covered with black paper to avoid the effect of light on roots. Three strong and same-sized tomato seedlings were immersed in each beaker as an experimental unit. Each beaker with both the culture solution and test seedling was weighed to calculate the volume change in the culture solution in subsequent N absorption. Samples were quickly transferred in the HVEF crop treatment chamber with a temperature of 25 °C ± 2 °C and light intensity of 200 μmol m^{-2} s^{-1}.

The field intensities of the HVEF crop treatment chambers were adjusted to 2.25 or 2.5 kV cm^{-1} depending on the treatment.

Ion depletion was used to investigate the N absorption of the culture solution during the eight-hour exposure to HVEF. The NH_4^+ and NO_3^- experiments (*T* and *S*, respectively) were both performed with five treatments and four replicates arranged in a split-plot design. The detailed treatments are presented in Table 1.

Treatments were arranged in a split-plot design with four NH_4^+ or NO_3^- treatments to determine the interactive effect of both the HVEF and the inhibitor on N absorption. The details are shown in Table 2. Control treatments with NH_4^+ or NO_3^- but without the blocker or applying the HVEF (Con_0 and Con_1, respectively) were not included in the split-plot analysis for the interaction of the HVEF and inhibitor on N absorption. The N absorption of tomato seedlings for Con_0 and Con_1 was determined under the same conditions except for HVEF application.

Construction of the experimental equipment

A schematic illustration of the HVEF experimental device is shown in Figs. 1*a* and 1*b*. The experimental device (Fig. 1*b*) was composed of a BGG 100 kV/2 mA high-voltage electrostatic generator (Beijing Electrical and Mechanical Institute, Beijing, China) and the crop treatment chamber. The output voltage of the high-voltage generator can be continuously adjusted with a digital controller to a value between 0 and 100 kV. The crop treatment chamber was a cuboid frame that measured 900 mm × 900 mm × 1000 mm with high voltage insulated boards at the top and the bottom. The chamber contained two parallel electrode plates, a supplementary lighting device, and a mirror glass. The two parallel electrode plates (each 300 mm wide, 600 mm long, and 1.5 mm thick) were made of stainless steel. The two electrode plates were shaped into a rectangle with round edges to reduce point discharging and placed parallel to the chamber. One electrode plate, acting as the negative plate, was placed on four insulation columns of the same size on the bottom surface of the chamber. On the upper surface of the positive electrode, a nut was welded in the center that was connected to an insulating screw rod. The insulating screw rod passed through the transverse section of the high-voltage insulation board on top of the HVEF crop treatment chamber. The upper terminal of the screw consisted of a welded handle that was used to regulate voltage. Rotating the handle ensured that the distance between the two electrode plates could be adjusted by raising the positive plate up and down while the negative plate was kept still.

The supplementary lighting device was composed of two rows of plant growth lamps (Shanghai Heming Lighting Electric Appliance Co., Ltd., Shanghai, China). Each row consisted of four blue 60 W LED (Shanghai Heming Lighting Electric Appliance Co.) lamps. Two pieces of reflective mirror glass of the same size (90 cm × 50 cm) were installed on the left and right sides of the chamber to enhance the light intensity of the tomato seedlings. Two glass windows were placed on two opposite sides at the top of the chamber to improve ventilation. A moveable glass door was placed on the front side of the crop treatment chamber to facilitate placement of the tomato seedlings for testing. A residual charge, which was eliminated using a discharge rod to complete the HVEF treatment, existed between the two electrode plates. The rod was made of stainless steel; one terminal was protected by an insulated sleeve and the other was connected to the ground of the high-voltage electrostatic generator.

The electric field intensity between the two parallel plates can be expressed as follows:

$$E = U/d \quad (1)$$

where *E* is the electric field intensity, *U* is the voltage, and *d* is the distance between the two parallel plates.

E can be acquired by tuning *U* and *d*. In this work, *d* was 25 cm. During testing, the beakers with seedlings were symmetrically arranged into two rows and placed at the bottom of the electrode plate to keep the seedlings under similar conditions (Fig. 1*c*). The experimental devices of the no-HVEF and HVEF treatments were the same, except for the presence of the HVEF, and the treatments were under identical environmental conditions, such as temperature and light intensity.

Methods of determination

N net absorption rate of seedling roots

The volume change in the culture solutions of the seedlings exposed to HVEF and no-HVEF was calculated. After each hour of absorption, the high-voltage power was turned off and the test samples were carefully discharged by using the discharging rod. Each beaker with the absorption solution and seedlings under no-HVEF and HVEF treatments were removed quickly from their respective chambers and weighed. About 2 mL of absorption solution was extracted from each beaker. Subsequently, the beakers were placed back in the treatment chambers and the HVEF was turned on. The field intensities of HVEF treatments were readjusted to the experimental level. When the absorption test was completed, the seedling roots were cut and weighed. The NH_4^+ and NO_3^- contents in the sampling solution were analyzed using a continuous flow analyzer (AutoAnalyzer3, SEAL Analytical, Southampton, United Kingdom). The root net absorption rate (NAR) of NH_4^+ and NO_3^- can be transformed into the following expression according to the following formula (Lu and Barber 1985):

$$I_n = k \times (C_1V_1 - C_2V_2)/(T\mathrm{RW}) \quad (2)$$

where I_n is the NAR in μmol h^{-1} g^{-1} fresh weight; C_1 and C_2 are the concentrations of the N solution before and

Table 1. Treatments for NH_4^+ and NO_3^- absorption tests.

Treatments	NH_4^+ (mmol L^{-1})	NO_3^- (mmol L^{-1})	Tetraethylammonium chloride (TEA) blocker (μmol L^{-1})	5-Nitro-2-(3-phenylpropylamino)-benzoate (NPPB) blocker (μmol L^{-1})	High-voltage electrical field (kV cm^{-1})
Con_0	1.0	0	0	0	0
$T_{2.25}$	1.0	0	0	0	2.25
$T_{(2.25+TEA)}$	1.0	0	20	0	2.25
$T_{2.5}$	1.0	0	0	0	2.5
$T_{(2.5+TEA)}$	1.0	0	20	0	2.5
Con_1	0	1.0	0	0	0
$S_{2.25}$	0	1.0	0	0	2.25
$S_{(2.25+NPPB)}$	0	1.0	0	20	2.25
$S_{2.5}$	0	1.0	0	0	2.5
$S_{(2.5+NPPB)}$	0	1.0	0	20	2.5

Table 2. Treatments for NH_4^+ and NO_3^- absorption with HVEF and inhibitor tests.

N solution	HVEF (kV cm^{-1})	TEA (μmol L^{-1})	NPPB (μmol L^{-1})
NH_4^+	2.25	0	0
		20	0
	2.5	0	0
		20	0
NO_3^-	2.25	0	0
		0	20
	2.5	0	0
		0	20

after absorption in mmol L^{-1}, respectively; V_1 and V_2 are the corresponding volumes of the N solution before and after absorption in mL, respectively; T is the absorption time in hours; RW is the root weight in g fresh weight; and k is the conversion coefficient.

Kinetic parameters

The kinetic parameters K_m and I_{max} were calculated using the following expression deduced from the Michealis–Menten equation (Michealis and Menten 1913):

$$(3) \qquad 1/I_n = (K_m/I_{max}) \times (1/C) + 1/I_{max}$$

where I_{max} is the largest absorption rate in μmol h^{-1} g^{-1} fresh weight, $1/K_m$ is the affinity of the root for ion absorption, and C is the absorption solution concentration in mmol L^{-1}.

Determination of physiological indexes and yields

Seedlings were cultivated in a Venlo-type greenhouse after being subjected to HVEFs with field intensities of 0, 2.25, and 2.5 kV cm^{-1} for 8 h to determine the duration of the effect of the HVEF treatments on tomatoes. Seedlings were cultivated in plastic pots (30 cm in height and 30 cm in diameter) with perlite and watered by a standard solution and subsequent Yamazaki formula (Wang et al. 2013). The seedlings for each treatment were replicated four times and arranged in a completely randomized design. The stem diameter and length of the seedling were measured after the 20-d growth period. Other plants were grown to maturity and tomato yields from three treatments were recorded at harvest.

Statistical analysis

The mean values of the NAR of each of the five treatments were calculated every hour. Data from four treatments with HVEF were subjected to analysis of variance (ANOVA) using SPSS v19.0. A probability level of $p < 0.05$ was used. Linear regression was performed using SigmaPlot 10.0 to calculate I_{max} and affinity. The tomato seedling growth data were also analyzed by one-way ANOVA using the SPSS v19.0 statistical package.

Results

Absorption rates of NH_4^+

There were differential effects at various durations of exposure to HVEF (Table 3). The absorption rates of NH_4^+ for all the treatments showed two different trends during the 8-h exposure time (Fig. 2*a*). The absorption rates of the HVEF treatments increased at the field strengths of 2.25 and 2.5 kV cm^{-1} throughout the exposure time, except in the second hour. In the first hour, the $T_{2.25}$ treatment improved the NAR, whereas $T_{2.5}$ had no evident effect. In addition, the absorption rates of $T_{2.25}$ remarkably declined with continued absorption. However, the absorption rates in the presence of the inhibitor for $T_{(2.25+TEA)}$ and $T_{(2.5+TEA)}$ showed a similar leveling-off during the 8-h exposure time. The NH_4^+ absorption amount of these two treatments was lower than that of Con_0 at each hour. Nevertheless, the absorption rate of $T_{(2.5+TEA)}$ was still higher than that of $T_{(2.25+TEA)}$.

The absorption rates of NH_4^+ at different exposure times were affected by the field intensity of the HVEF and the presence of TEA as indicated by the two-way

Fig. 1. HVEF experimental device. (A) Schematic illustration of HVEF experimental device. 1, stainless steel electrode plates; 2, supplementary lighting device; 3, seedlings; 4, high-voltage insulation board; 5, insulation columns; 6, mirror glass; and 7, plate spacing adjusting device. (B) Experimental device. (C) Seedlings under exposure inside the device. [Colour online.]

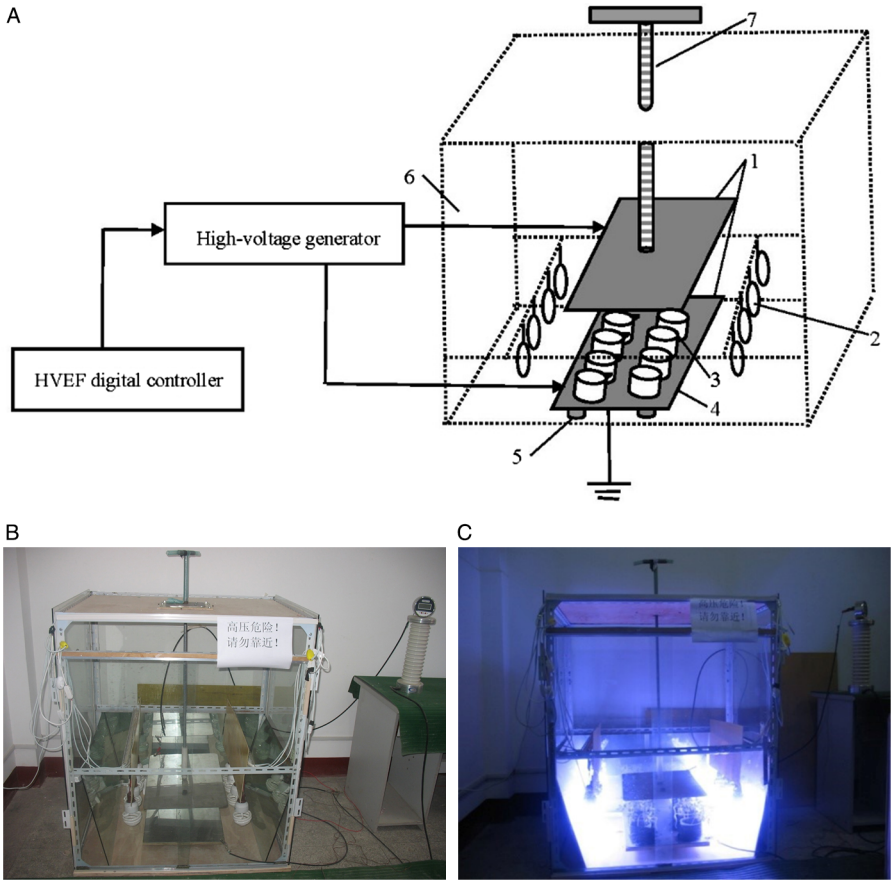


Table 3. Analysis of variance of the NH_4^+ absorption of tomato seedlings exposed to HVEFs and inhibitors under different times.

Source		Type III of SS	df	MS	F	Sig.
1 h exposure						
Intercept	Hypothesis	412.090	1	412.090	633984.62	0.000
	Error	0.002	3	0.001a		
HVEF	Hypothesis	0.265	1	0.265	6365.400	0.000
	Error	0.003	3	4.167E-5c		
TEA	Hypothesis	99.301	1	99.301	193758.488	0.000
	Error	0.003	6	0.001b		
Replicates	Hypothesis	0.002	3	0.001	15.600	0.025
	Error	0.000	3	4.167E-5c		
Replicates (HVEF)	Hypothesis	0.000	3	4.167E-5	0.081	0.968
	Error	0.003	6	0.001b		
HVEF × TEA	Hypothesis	0.548	1	0.548	1068.488	0.000
	Error	0.003	6	0.001b		
2 h exposure						
Intercept	Hypothesis	369.312	1	369.312	68949.789	0.000
	Error	0.016	3	0.005b		
HVEF	Hypothesis	0.092	1	0.092	2.638	0.203
	Error	0.104	3	0.035c		
TEA	Hypothesis	81.045	1	81.045	4463.752	0.000
	Error	0.109	6	0.018b		

Table 3 (*continued*).

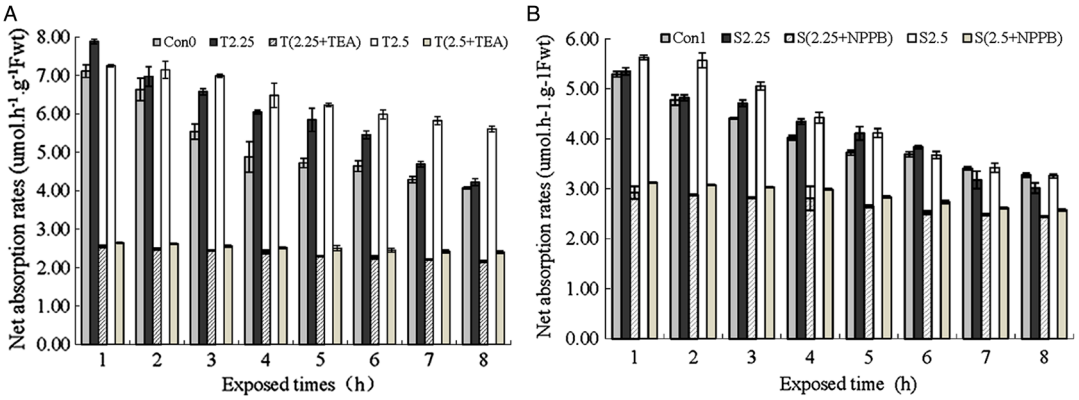
Source		Type III of SS	df	MS	F	Sig.
Replicates	Hypothesis	0.016	3	0.005	0.154	0.920
	Error	0.104	3	0.035c		
Replicates (HVEF)	Hypothesis	0.104	3	0.035	1.911	0.229
	Error	0.109	6	0.018b		
HVEF × TEA	Hypothesis	0.001	1	0.001	0.077	0.790
	Error	0.109	6	0.018b		
3 h exposure						
Intercept	Hypothesis	344.566	1	344.566	601425	0.000
	Error	0.002	3	0.001a		
HVEF	Hypothesis	0.284	1	0.284	2306.898	0.000
	Error	0.000	3	0.000c		
TEA	Hypothesis	73.231	1	73.231	96834.124	0.000
	Error	0.005	6	0.001b		
Replicates	Hypothesis	0.002	3	0.001	4.661	0.119
	Error	0.000	3	0.000c		
Replicates (HVEF)	Hypothesis	0.000	3	0.000	0.163	0.918
	Error	0.005	6	0.001b		
HVEF × TEA	Hypothesis	0.089	1	0.089	117.033	0.000
	Error	0.005	6	0.001b		
4 h exposure						
Intercept	Hypothesis	304.328	1	304.328	16209.216	0.000
	Error	0.056	3	0.019a		
HVEF	Hypothesis	0.314	1	0.314	16.405	0.027
	Error	0.057	3	0.019c		
TEA	Hypothesis	58.046	1	58.046	3991.824	0.000
	Error	0.087	6	0.015b		
Replicates	Hypothesis	0.056	3	0.019	0.982	0.506
	Error	0.057	3	0.019c		
Replicates (HVEF)	Hypothesis	0.057	3	0.019	1.314	0.354
	Error	0.087	6	0.015b		
HVEF × TEA	Hypothesis	0.087	1	0.087	5.983	0.050
	Error	0.087	6	0.015b		
5 h exposure						
Intercept	Hypothesis	287.303	1	287.303	14571.555	0.000
	Error	0.059	3	0.020a		
HVEF	Hypothesis	0.281	1	0.281	25.043	0.015
	Error	0.034	3	0.011c		
TEA	Hypothesis	51.984	1	51.984	3128.431	0.000
	Error	0.100	6	0.017b		
Replicates	Hypothesis	0.059	3	0.020	1.758	0.327
	Error	0.034	3	0.011c		
Replicates (HVEF)	Hypothesis	0.034	3	0.011	0.675	0.598
	Error	0.100	6	0.017b		
HVEF × TEA	Hypothesis	0.058	1	0.058	3.466	0.112
	Error	0.100	6	0.017b		
6 h exposure						
Intercept	Hypothesis	263.088	1	263.088	33729.282	0.000
	Error	0.023	3	0.008a		
HVEF	Hypothesis	0.442	1	0.442	272.138	0.000
	Error	0.005	3	0.002b		
TEA	Hypothesis	44.556	1	44.556	14014.875	0.000
	Error	0.019	6	0.003b		
Replicates	Hypothesis	0.023	3	0.008	4.800	0.115
	Error	0.005	3	0.002b		
Replicates (HVEF)	Hypothesis	0.005	3	0.002	0.511	0.689
	Error	0.019	6	0.003b		
HVEF × TEA	Hypothesis	0.160	1	0.160	50.328	0.000
	Error	0.019	6	0.003b		

Table 3 (*concluded*).

Source		Type III of SS	df	MS	F	Sig.
7 h exposure						
Intercept	Hypothesis	231.725	1	231.725	121560.4	0.000
	Error	0.006	3	0.002a		
HVEF	Hypothesis	1.607	1	1.607	1054.921	0.000
	Error	0.005	3	0.002c		
TEA	Hypothesis	33.669	1	33.669	7389.631	0.000
	Error	0.027	6	0.005b		
Replicates	Hypothesis	0.006	3	0.002	1.252	0.429
	Error	0.005	3	0.002c		
Replicates (HVEF)	Hypothesis	0.005	3	0.002	0.334	0.802
	Error	0.027	6	0.005b		
HVEF × TEA	Hypothesis	0.995	1	0.995	218.383	0.000
	Error	0.027	6	0.005b		
8 h exposure						
Intercept	Hypothesis	209.164	1	209.164	3.347E7	0.000
	Error	1.875E-5	3	6.250E-6a		
HVEF	Hypothesis	2.457	1	2.457	1214.611	0.000
	Error	0.006	3	0.002c		
TEA	Hypothesis	26.962	1	26.962	12504.142	0.000
	Error	0.013	6	0.002b		
Replicates	Hypothesis	1.875E-5	3	6.250E-6	0.003	1.000
	Error	0.006	3	0.002c		
Replicates (HVEF)	Hypothesis	0.006	3	0.002	0.938	0.479
	Error	0.013	6	0.002b		
HVEF × TEA	Hypothesis	1.458	1	1.458	676.200	0.000
	Error	0.013	6	0.002b		

Note: Means within a column not sharing a lowercase letter differ significantly at the $p < 0.05$ level. SS, sum of squares; df, degrees of freedom; MS, mean square; F, value from the *F* test; Sig., significance; a, data are means of four replicates per treatment; b, standard error of the mean; c, standard mean of replicates for HVEF.

Fig. 2. Net absorption rates with exposure time from different treatments: (A) NH_4^+ and (B) NO_3^-.



interaction (Table 3). The effects among HVEF, TEA, and HVEF × TEA on absorption rates were different. TEA exerted an apparent inhibitory effect on absorption rates at all exposure times. HVEF also increased the absorption rates except during the second hour of exposure. However, in the second and fifth hours of exposure, the interaction effect of HVEF × TEA on absorption rates was not different.

Kinetic parameters of NH_4^+

The responses of NH_4^+ absorption kinetic parameters to the field intensity and inhibitor are illustrated in Table 4. Compared with that of Con_0, the I_{max} of $T_{2.25}$ increased by 154.7%, whereas that of I_{max} of $T_{2.5}$ decreased by 2.3% (Table 4). However, the I_{max} values of $T_{(2.25+TEA)}$ and $T_{(2.5+TEA)}$ were apparently lower than that of Con_0, and that of $T_{(2.5+TEA)}$ was slightly higher than that of $T_{(2.25+TEA)}$.

Table 4. I_{max} and affinity of NH_4^+ absorption of seedlings from different treatments.

Treatment	Regression equation	R^2 (n = 8)	I_{max}	$1/K_m$
Con_0	$y = 0.2618X - 0.11$	0.9405	9.09	0.42
$T_{2.25}$	$y = 0.0854X + 0.432$	0.9615	23.15	0.51
$T_{(2.25+TEA)}$	$y = 0.6551X - 0.282$	0.9884	3.55	0.43
$T_{2.5}$	$y = 0.0264X + 0.1126$	0.9574	8.88	4.27
$T_{(2.5+TEA)}$	$y = 0.1263X + 0.2549$	0.9469	3.92	2.02

The affinity values of $T_{2.25}$ and $T_{(2.25+TEA)}$ were almost the same as that of Con_0. Nevertheless, the affinity values of both $T_{2.5}$ and $T_{(2.5+TEA)}$ clearly increased. It appeared that the $1/K_m$ of $T_{2.5}$ was the highest among the five treatments.

Absorption rates of NO_3^-

The various treatments affected nitrate uptake differently (Table 5). The NAR of NO_3^- in $S_{2.25}$ was almost the same as that for Con_1 in the first hour (Fig. 2*b*). However, a noticeable increase was observed from the second hour to the sixth hour. In the last 2 h, the absorption rate was lower than that of Con_1. The absorption rates of $S_{2.5}$ apparently increased than that of with Con_1 in the first 5 h. No difference was observed during the remaining exposure time. The net absorption of NO_3^- in $S_{(2.25+NPPB)}$ and $S_{(2.5+NPPB)}$ evidently decreased compared with that of Con_1. Although the change in the NAR of $S_{(2.25+NPPB)}$ and $S_{(2.5+NPPB)}$ was slight throughout the entire exposure time, the rates of $S_{(2.5+NPPB)}$ were still higher than those of $S_{(2.25+NPPB)}$.

For the entire exposure time, the NAR of NO_3^- in the four treatments with HVEF and NPPB was affected differently by field intensity and inhibitor (NPPB), as indicated by the two-way interaction (Table 5). The effects of HVEF and NPPB on NAR were different at various exposure times.

Kinetic parameters of NO_3^-

The responses of I_{max} to the different treatments are shown in Table 6. The I_{max} of NO_3^- for $S_{2.25}$ and $S_{2.5}$ increased. Moreover, the I_{max} of $S_{2.25}$ was obviously higher than that of $S_{2.5}$ and exhibited a value of 11.47 μmol h^{-1} g^{-1} fresh weight. Both the I_{max} values of NO_3^- in $S_{(2.25+NPPB)}$ and $S_{(2.5+NPPB)}$ were lower than that of Con_1. The kinetics of the affinity of NO_3^- absorption decreased slightly for $S_{2.25}$ and reached a maximum of 0.60 for $S_{2.5}$. Nonetheless, the values of NO_3^- absorption in $S_{(2.25+NPPB)}$ and $S_{(2.5+NPPB)}$ were almost the same as that in Con_1.

Effect of HVEF on physiological indexes and yields

After the 20-d growth period in the greenhouse, the stem diameter of seedlings subjected to HVEF with 0, 2.25, and 2.5 kV cm^{-1} increased by 51.7%, 73.1%, and 65.7%, respectively (Fig. 3*a*). While the stems were visually thicker after treatment with HVEFs, there was no statistical difference ($p < 0.05$). The stem length of tomato seedlings treated with HVEFs with field intensities of 2.25 and 2.5 kV cm^{-1} showed an evident (not significant) decrease (Fig. 3*b*). The fruit yield of seedlings treated with 2.25 and 2.5 kV cm^{-1} increased by 1.14 and 0.31 kg per plant, respectively (Fig. 3*c*). Yield from the 2.25 kV cm^{-1} treatment was higher than that of the control or 2.5 kV cm^{-1} treatment.

Discussion

According to the foundational theory of cell membranes (Bezanilla and White 1987), the plasma membrane of the plant cell is a selectively permeable barrier that ensures the entry of essential ions and metabolites into the cell. Membranes contain different types of transport proteins: ATPases or ATP-powered pumps, channel proteins, and cotransporters (Chrispeels et al. 1999). Channel proteins are communication gateways between intracellular and external environments and provide a special path for charged ions and molecules. Channel proteins exhibit two kinds: one kind is open and ions can pass through freely at any time and the other kind is commonly closed, opening when external factors such as voltage, chemical, and mechanical actions are induced (Bezanilla and White 1987). The ionic compositions of the solutions on either side of both plasma membrane and tonoplast are considerably different, which causes charge imbalance. Thus, an electric potential ranging from −80 to −180 mV at the plasma membrane (negative inside) is established. This plasma membrane creates a very strong electric field that provides energy for biochemical processes at the plasma membrane, such as the opening and closing of ion channels (voltage-gated channels) (Chrispeels et al. 1999).

The voltage-gated ion channels can exist in three functionally distinct states or groups of states: resting, active, and inactivated (Lalonde et al. 1999; Sze et al. 1999). Both resting and inactivated states are nonconducting; nevertheless, channels that are inactivated by prolonged depolarization are refractory, unless the cell is repolarized to allow them to return to the resting state (Catterall 1995). Therefore, when field intensities of 2.25 and 2.5 kV cm^{-1} are applied to seedlings, the NH_4^+ absorption of the seedlings is accelerated because of the activation of many NH_4^+ absorption channels. However, inhibitors hinder the opening of ion absorption channels. Thus,

Table 5. Analysis of variance of the NO_3^- absorption of tomato seedlings exposed to HVEFs and inhibitors under different times.

Source		Type III of SS	df	MS	F	Sig.
1 h exposure						
Intercept	Hypothesis	290.276	1	290.276	34876.77	0.000
	Error	0.025	3	0.008a		
HVEF	Hypothesis	0.243	1	0.243	60.045	0.004
	Error	0.012	3	0.004c		
NPPB	Hypothesis	24.478	1	24.478	15728.679	0.000
	Error	0.009	6	0.002b		
Replicates	Hypothesis	0.025	3	0.008	2.060	0.284
	Error	0.012	3	0.004c		
Replicates (HVEF)	Hypothesis	0.012	3	0.004	2.596	0.148
	Error	0.009	6	0.002b		
HVEF × NPPB	Hypothesis	0.009	1	0.009	5.498	0.057
	Error	0.009	6	0.002b		
2 h exposure						
Intercept	Hypothesis	267.159	1	267.159	62493.339	0.000
	Error	0.013	3	0.004a		
HVEF	Hypothesis	0.941	1	0.941	187.555	0.001
	Error	0.015	3	0.005b		
NPPB	Hypothesis	19.669	1	19.669	3443.190	0.000
	Error	0.034	6	0.006b		
Replicates	Hypothesis	0.013	3	0.004	0.852	0.551
	Error	0.015	3	0.005b		
Replicates (HVEF)	Hypothesis	0.015	3	0.005	0.878	0.503
	Error	0.034	6	0.006b		
HVEF × NPPB	Hypothesis	0.325	1	0.325	56.875	0.000
	Error	0.034	6	0.006b		
3 h exposure						
Intercept	Hypothesis	244.141	1	244.141	140176.435	0.000
	Error	0.005	3	0.002a		
HVEF	Hypothesis	0.325	1	0.325	209.613	0.001
	Error	0.005	3	0.002c		
NPPB	Hypothesis	15.406	1	15.406	6759.324	0.000
	Error	0.014	6	0.002b		
Replicates	Hypothesis	0.005	3	0.002	1.124	0.463
	Error	0.005	3	0.002c		
Replicates (HVEF)	Hypothesis	0.005	3	0.002	0.680	0.596
	Error	0.014	6	0.002b		
HVEF × NPPB	Hypothesis	0.022	1	0.022	9.872	0.020
	Error	0.014	6	0.002b		
4 h exposure						
Intercept	Hypothesis	211.994	3	211.994	139776	0.000
	Error	0.005	1	0.002a		
HVEF	Hypothesis	0.076	3	0.076	7.531	0.071
	Error	0.030	1	0.010c		
NPPB	Hypothesis	8.880	6	8.880	404.037	0.000
	Error	0.132	3	0.022b		
Replicates	Hypothesis	0.005	3	0.002	0.151	0.923
	Error	0.030	3	0.010c		
Replicates (HVEF)	Hypothesis	0.030	6	0.010	0.457	0.722
	Error	0.132	1	0.022b		
HVEF × NPPB	Hypothesis	0.009	6	0.009	0.411	0.545
	Error	0.132	1	0.022b		
5 h exposure						
Intercept	Hypothesis	188.033	1	188.033	90709.221	0.000
	Error	0.006	3	0.002a		
HVEF	Hypothesis	0.039	1	0.039	26.186	0.014
	Error	0.004	3	0.001c		

Table 5 (*concluded*).

Source		Type III of SS	df	MS	F	Sig.
NPPB	Hypothesis	7.576	1	7.576	5002.205	0.000
	Error	0.009	6	0.002b		
Replicates	Hypothesis	0.006	3	0.002	1.392	0.396
	Error	0.004	3	0.001c		
Replicates (HVEF)	Hypothesis	0.004	3	0.001	0.983	0.461
	Error	0.009	6	0.002b		
HVEF × NPPB	Hypothesis	0.026	1	0.026	17.435	0.006
	Error	0.009	6	0.002b		
6 h exposure						
Intercept	Hypothesis	162.945	1	162.945	62471.013	0.000
	Error	0.008	3	0.003a		
HVEF	Hypothesis	0.004	1	0.004	2.097	0.243
	Error	0.005	3	0.002c		
NPPB	Hypothesis	5.130	1	5.130	2910.766	0.000
	Error	0.011	6	0.002b		
Replicates	Hypothesis	0.008	3	0.003	1.519	0.370
	Error	0.005	3	0.002c		
Replicates (HVEF)	Hypothesis	0.005	3	0.002	0.974	0.465
	Error	0.011	6	0.002b		
HVEF × NPPB	Hypothesis	0.130	1	0.130	73.532	0.000
	Error	0.011	6	0.002b		
7 h exposure						
Intercept	Hypothesis	138.533	1	138.533	145824.105	0.000
	Error	0.003	3	0.001a		
HVEF	Hypothesis	0.112	1	0.112	101.256	0.002
	Error	0.003	3	0.001c		
NPPB	Hypothesis	2.465	1	2.465	1235.023	0.000
	Error	0.012	6	0.002b		
Replicates	Hypothesis	0.003	3	0.001	0.857	0.549
	Error	0.003	3	0.001c		
Replicates (HVEF)	Hypothesis	0.003	3	0.001	0.555	0.663
	Error	0.012	6	0.002b		
HVEF × NPPB	Hypothesis	0.003	1	0.003	1.516	0.264
	Error	0.012	6	0.002b		
8 h exposure						
Intercept	Hypothesis	127.013	1	127.013	177227.302	0.000
	Error	0.002	3	0.001a		
HVEF	Hypothesis	0.133	1	0.133	86.416	0.003
	Error	0.005	3	0.002c		
NPPB	Hypothesis	1.525	1	1.525	4207.517	0.000
	Error	0.002	6	0.000b		
Replicates	Hypothesis	0.002	3	0.001	0.465	0.727
	Error	0.005	3	0.002c		
Replicates (HVEF)	Hypothesis	0.005	3	0.002	4.253	0.062
	Error	0.002	6	0.000b		
HVEF × NPPB	Hypothesis	0.008	1	0.008	22.345	0.003
	Error	0.002	6	0.000b		

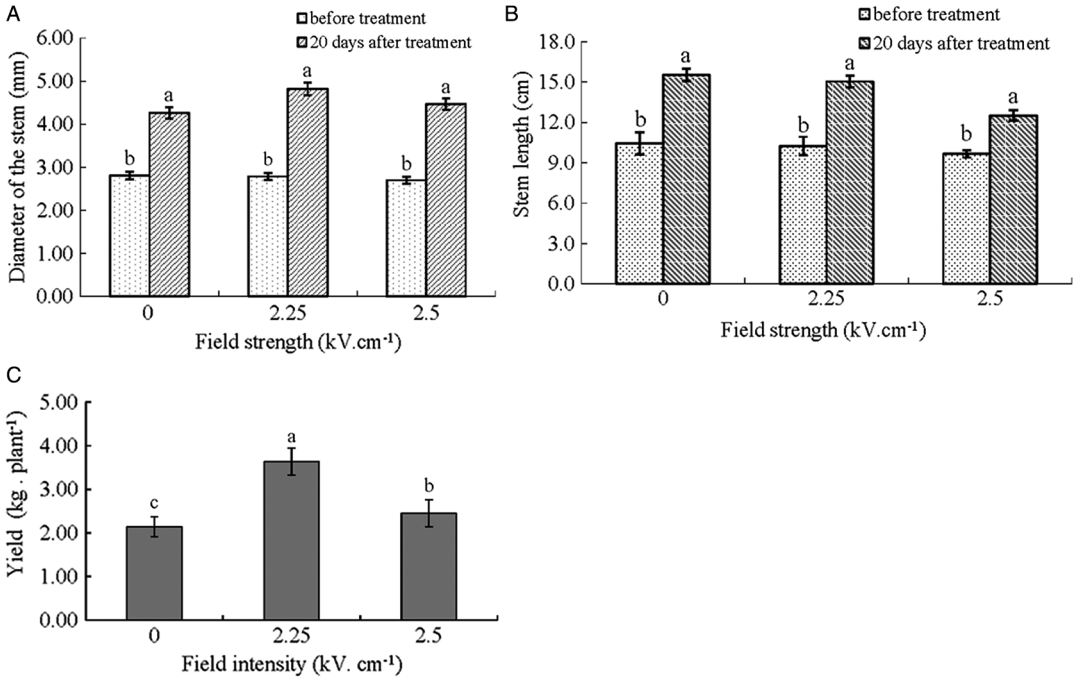
Note: Means within a column not sharing a lowercase letter differ significantly at the $p < 0.05$ level. SS, sum of squares; df, degrees of freedom; MS, mean square; F, value from the *F* test; Sig., significance; a, data are means of four replicates per treatment; b, standard error of the mean; c, standard mean of replicates for HVEF.

the amount of open ion absorption channels depends on the dual action from the HVEF and inhibitors. The amount of open ion absorption channels increases when the HVEF activation effect transcends over the inhibitory effect of inhibitors and vice versa. The absorption rates of $T_{2.25}$ and $T_{2.5}$ treatments clearly increase throughout the entire exposure time (Fig. 2*a*). This increase occurs because many ion absorption channels are opened by the HVEF action, thereby promoting NH_4^+ absorption. The NH_4^+ absorption rates of $T_{(2.25+TEA)}$ are lower than

Table 6. I_{max} and affinity to NO_3^- of tomato seedlings grown in different treatments.

Treatment	Regression equation	R^2 (n = 8)	I_{max}	$1/K_m$
Con_1	$y = 0.3294X - 0.1541$	0.9748	6.49	0.47
$S_{2.25}$	$y = 0.2454X - 0.0873$	0.9780	11.45	0.36
$S_{(2.25+NPPB)}$	$y = 0.5756X - 0.2509$	0.9091	4.00	0.44
$S_{2.5}$	$y = 0.2389X - 0.1443$	0.9486	6.93	0.60
$S_{(2.5+NPPB)}$	$y = 0.5435X - 0.2444$	0.9392	4.09	0.45

Fig. 3. Effect of field intensity on (A) stem diameter, (B) stem length, and (C) yield. Means (n = 4) followed by the same letters above the bar are considered different at the $p < 0.05$ level, as determined by Duncan's multiple-range test.



that of Con_0 because the HVEF activates the channel proteins, TEA deactivates the channel proteins, and the inhibition action from TEA exceeds the HVEF activation. Therefore, the amount of open NH_4^+ absorption channels decreases and NH_4^+ absorption rates are consequently reduced. Nevertheless, the HVEF exposure duration and treatment exerts a differential effect. The ammonium absorption rates in the $T_{(2.5+TEA)}$ treatment are higher than that in the $T_{(2.25+TEA)}$ treatment possibly because the HVEF treatment reduces the inhibitory action. Consequently, the amount of open NH_4^+ absorption channels increases when the field intensity increases from 2.25 to 2.5 kV cm^{-1}. Thus, the promotive effect of HVEF on N uptake is improved under the same inhibitory action of TEA.

The I_{max} of $T_{2.25}$ increases by 154.7% whereas that of $T_{2.5}$ decreases by 2.3%; these results may have been induced by the changes in the absorption solution caused by seedlings and their root activity. When the absorption test began, the NH_4^+ in the nutrient solution slowly moves to the negative plate driven by the electric field of 2.25 kV cm^{-1}. Moreover, the NH_4^+ concentration in the top-layer solutions gradually declines. The applied field can contribute to carrying positively charged hydrogen ions, a type of reaction product, to the lower parts of plants (Wu et al. 2016). Additionally, NH_4^+ in root tip zones could be quickly absorbed and assimilated by plants (Taylor and Bloom 1998). Consequently, NH_4^+, which moves to lower layer solutions, could be quickly absorbed. Moreover, the threshold voltage of channel proteins is reached when the HVEF with a field intensity of 2.25 kV cm^{-1} is applied to seedlings. Therefore, initially closed channels are opened and NH_4^+ uptake is improved. When the field intensity increases from 2.25 to 2.5 kV cm^{-1}, the threshold voltage of the channel proteins is reached and the shift of NH_4^+ to the negative plate is also rapidly accelerated. However, the glutamine synthetase activity possibly declines with increased field intensity, thereby decreasing NH_4^+ absorption. As a result, the I_{max} of 2.25 kV cm^{-1} increases and that of 2.5 kV cm^{-1} decreases because the effective absorption of NH_4^+ decreases. The I_{max} of NH_4^+ absorption in $T_{(2.25+TEA)}$ and

$T_{(2.5+TEA)}$ is lower than that in Con_0 because of the dual interaction from HVEF and TEA. On the one hand, NH_4^+ channels are opened by HVEFs with field intensities of 2.25 and 2.50 kV cm^{-1}. On the other hand, the TEA produces an inhibitory action on the opening of NH_4^+ channels. The inhibitory effect of TEA on the absorption channel prevails over the HVEF promotion action. Therefore, the I_{max} of $T_{(2.25+TEA)}$ and $T_{(2.5+TEA)}$ declines. However, the I_{max} of NH_4^+ for $T_{(2.5+TEA)}$ is slightly superior to that of $T_{(2.25+TEA)}$, which also shows that the activity of ion absorption channels protein increases (Catterall 1995) in a certain range as field intensity increases from 2.25 to 2.50 kV cm^{-1}.

The affinity of NH_4^+ for $T_{2.5}$ exhibited the best performance among the five treatments. Nonetheless, the affinity of $T_{2.25}$ is slightly higher than that of Con_0. We suggest that this result is related with field intensity. The applied HVEF intensity changes the affinity to ammonium of *Cucumis sativus* L. seedlings (Wu et al. 2016); this result is in agreement with our results. The channel proteins are activated by the field intensity of 2.25 kV cm^{-1} because the threshold voltage of the channel protein (Armstrong and Hille 1998) is reached. As the field intensity increases to 2.5 kV cm^{-1}, many gateway channel proteins are activated because the ion conductance of the activated ion channels is both highly selective and remarkably efficient (Catterall 1995). Thus, the affinity of $T_{2.5}$ is noticeably enhanced compared with that of Con_0.

The affinity of $T_{(2.25+TEA)}$ is slightly lower than that of $T_{2.25}$, which indicated that TEA inhibits only a certain type of gateway channel proteins and its inhibitory effect is not evident. When the field intensity increases to 2.5 kV cm^{-1}, the affinity of $T_{(2.5+TEA)}$ is still higher than that of $T_{(2.25+TEA)}$. This result verified that the effect of HVEF on improving affinity is apparent with increased field intensity. These results agreed with the voltage dependency of the K^+ channel (Hodgkin and Katz 1949).

The net absorption phenomenon of NO_3^- revealed that a field strength of 2.25 kV cm^{-1} improves the NAR of NO_3^- only during a part of the exposure time. However, an HVEF with a field strength of 2.5 kV cm^{-1} could increase NO_3^- NAR throughout the entire exposure time. This phenomenon can be explained as follows. Convincing evidence shows that the energy sources that contribute to stimulating nitrate uptake are derived from coupling to the proton electrochemical gradient across the plasma membrane. Particularly, two hydrogen ions are required when one nitrate ion is absorbed into the root epidermal cell (Hawkins et al. 2000; McClure et al. 1990). Moreover, the applied field contributes to the concentration of positively charged hydrogen ions surrounding the cucumber root, which benefits the cotransport of nitrate (Wu et al. 2016). In addition, only a proportion of the absorbed nitrate is assimilated into the root and the remaining part is transported upward through the xylem for assimilation into the shoot (Forde 2000). In the present study, the applied field accelerated the transport of negatively charged nitrate and nitrite. The acceleration provides sufficient reactant for glutamate synthesis and promotes nitrate absorption by the plant. Nitrate assimilation is an energy-intensive process that especially requires the transfer of two electrons per NO_3^- converted to NO_2^-, six electrons per NO_2^- converted to NH_4^+, and two electrons and one ATP per NH_4^+ converted to glutamate (Bloom et al. 1992). This implies that electrons are required for every process of nitrate absorption.

The applied electric field also provides enough electrons to reduce nitrate and assimilate ammonium and thus nitrate uptake is accelerated. Finally, with the action of the applied field, NO_3^- moves toward the direction of the positive electrode while the hydrogen ions move towards the opposite direction. Thus, the concentration of NO_3^- in the lower-layer solution is relatively low and the concentration of hydrogen ions is high. From the above analysis, the hydrogen ions and sufficient electrons are necessary in NO_3^- uptake. The NO_3^- uptake depends on the NO_3^- concentration but also on the number of electrons and the concentration of hydrogen ions in the solution. Namely, NO_3^- uptake mainly depends on the coupling between NO_3^- and the hydrogen ion and the absorption rate of nitrate is greatest within 0 to 4 cm of the maize root tip (Taylor and Bloom 1998). The height of the absorption solution in our experiments is only 4 cm, which is still in the effective uptake zone of tomato root tips, and the gradient of NO_3^- concentration is small. Therefore, the acceleration in NO_3^- uptake is mainly caused by coupling to the proton electrochemical gradient across the plasma membrane.

NPPB inhibits the net absorption of NO_3^- under 2.25 and 2.5 kV cm^{-1}. Nevertheless, this inhibitory effect decreases when the field intensity increases from 2.25 to 2.5 kV cm^{-1}. The interaction between HVEF and NPPB further verified the influence of these two factors on NO_3^- absorption with different exposure times. Thus, the NPPB reduces the NO_3^- absorption ability and the HVEF overcomes the effect of the nitrate inhibitor.

The increased I_{max} in $S_{2.5}$ is slightly higher than that in Con_1 and lower than that in $S_{2.25}$. This HVEF with a field intensity of 2.5 kV cm^{-1} may have resulted in high absorption rates from the beginning to the end. The I_{max} increase of NO_3^- in $S_{2.5}$ and $S_{2.25}$ implied that HVEFs with field intensities of 2.25 and 2.5 kV cm^{-1} promote the NO_3^- absorption of the seedlings. As a result of the inhibitory action of NPPB on channel proteins, the I_{max} of $S_{(NPPB+2.25)}$ and $S_{(NPPB+2.5)}$ is evidently reduced. The amount of opened ion absorption channels at a field intensity of 2.5 kV cm^{-1} is more than that at 2.25 kV cm^{-1}. Therefore, the I_{max} of $S_{(NPPB+2.5)}$ is slightly higher than that of $S_{(NPPB+2.25)}$ when the field intensity reaches 2.5 kV cm^{-1}. Therefore, HVEFs with field intensities of 2.25 and 2.5 kV cm^{-1} promote the increase in I_{max}.

The affinity of $S_{2.5}$ increases whereas that of $S_{2.25}$ decreases. Many active gateways are opened by the HVEF when the field strength increases to 2.5 kV cm^{-1}.

Therefore, the affinity of NO_3^- absorption increases, thereby promoting NO_3^- absorption. Furthermore, the activation of ion absorption channels, which facilitates N absorption, compensates for the decreased NO_3^- concentration in the root hair zone. Consequently, the affinity of NO_3^- absorption for $S_{2.5}$ is improved. As a result of the inhibitory effect of NPPB on NO_3^- absorption, the affinity of NO_3^- absorption in $S_{(2.25+\mathrm{NPPB})}$ and $S_{(2.5+\mathrm{NPPB})}$ is low, but its affinity in $S_{(2.5+\mathrm{NPPB})}$ is slightly higher than that in $S_{(2.25+\mathrm{NPPB})}$.

The stem diameter of seedlings subjected to 2.25 and 2.5 kV cm^{-1} HVEFs increases visually compared with those of the control. Moreover, the increase in the stem length of tomato seedlings with the three field intensities shows no difference ($p < 0.05$). However, increased stem diameter from the balanced growth between the vegetative and generative organs of the plants is important (Ozer and Kandemir 2016). Thus, balanced growth is the key in plant production (Kandemir 2005). There is a very simple, practical need for thicker stem diameters. Thin, spindly plants are more prone to damage and death during transplanting than stockier, thicker stemmed plants. Plant growers also take great care in producing such plants and harden plants off near the time of transplanting. Arenas et al. (2002) reported that the thicker stem diameter of tomato was accepted as a grower rating and the hardening of plants was important for transplantation to the field (Seifert and Shecterle 2003; Grey et al. 2012).

Plants from seedlings treated with field intensities of 2.25 and 2.5 kV cm^{-1} produce higher yields than those of the control; this result is consistent with the research results of Ozer and Kandemir (2016). This result also showed that HVEF treatment on seedlings can carry through to the harvest and increase the yield under greenhouse conditions. Results also demonstrated that HVEF treatment on seedlings may be applied to field environments to observe whether the effect can carry through to the harvest and increase yields under greenhouse and field conditions.

In conclusion, this study investigated the effect of HVEFs with field intensities of 2.25 and 2.5 kV cm^{-1} on N absorption by tomato seedlings during an 8-h exposure time by adding TEA and NPPB. The interaction of inhibitors and HVEF on the effective N absorption showed that HVEF overcomes the effect of ion channel inhibitors on N uptake. These results indicated that the improved dynamic absorption of NH_4^+ and NO_3^- induced by HVEF is attributed to many activated channel proteins, thereby improving nutrition absorption. The absorption rates for $T_{2.25}$ and $S_{2.5}$ are enhanced throughout the entire exposure period, which showed that the HVEF overcomes the effect of inhibitors. With the increased field intensity, the NH_4^+ I_{max} decreases because the NH_4^+ in the absorption solution is influenced by HVEF, whereas the affinity of NH_4^+ increases. Field intensities of 2.25 and 2.5 kV cm^{-1} help improve I_{max} and the affinity of NH_4^+ and NO_3^-, respectively. After the 20-d growth period, the stem diameter of the seedlings treated with HVEF is visually thicker than that of the control group and the fruit yields from the seedlings exposed to HVEF are higher than those from the control under greenhouse conditions. Thus, HVEF treatment has potential to increase yields and warrants such investigations in the greenhouse and field environments.

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