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Response of growth, photosynthesis, dry matter partition and roots to combined nitrogen–potassium stress in cucumber

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ORIGINAL ARTICLE

Abstract

In order to improve the yield of cucumber and ensure food safety by investigating the response of cucumber to nutrient stress, especially compound stress, gas-exchange and growth parameters, biomass, and root development were measured and compared. The results showed that compared with control (CK), different treatments had different effects on these parameters, and under short-term nitrogen (N) or potassium (K^+) stress, the development of lateral roots and root hair was promoted. The research on the response of cucumber to nutrient stress provided a basis for establishing reasonable irrigation strategies as well as improvement of fertilizer utilization rate and cucumber yield, which was of great significance for maintaining national food security. In addition, this was beneficial to reveal the stress response mechanism of crops under NK stress and conduct in-depth research on the phenotypic information characteristics of cucumber under compound stress. It provided a theoretical basis for the subsequent construction of a comprehensive evaluation system for greenhouse cucumber health status.

Keywords: greenhouse cucumber; compound stress; growth; photosynthetic; dry matter partition

Introduction

Cucumber is considered as one of the healthiest vegetables with important biological and economic significance because of its rich nutritious value and unique flavor (Mao *et al.*, 2022; Pan *et al.*, 2022). In the past 5 years, China, being the largest cucumber producer, has accounted for more than 75% of the world's total annual cucumber production (Gebretsadik *et al.*, 2021). However, the characteristics of difficult soil renewal and the sensitivity of cucumbers to the environment in protected cultivation have led to frequent nutrient deficiency and excessive application of fertilizers (Pan *et al.*, 2022); these are the main factors restricting yield and quality of cucumber. Hence, it was necessary to investigate the response of cucumber to nutritional stress to maintain its yield and quality.

Nitrogen (N) and potassium (K^+) are essential for crop growth and fruit harvesting. As a life element, N is the basis of protein and chlorophyll synthesis (Li *et al.*, 2021a), while K^+ has a fundamental role in stomata, osmotic regulation and carbohydrate transport (Zhu *et al.*, 2020). According to the description provided by Hou *et al.* (2021), N has a significant effect on the photosynthetic response and leaf growth of sorghum. Research has demonstrated that both excess and deficiency of N destroy leaf structure and adversely affect the length, width and density of stomata, plant height and dry biomass of rice (Khan *et al.*, 2021). Plant height, leaf area and biomass accumulation of K-deficient crops are significantly reduced, and photosynthesis is inhibited (Fontana *et al.*, 2020). Adequate supply of N and K^+ promotes the growth of root system (Li *et al.*, 2010; Shah *et al.*, 2017). However, short-term nutrient deficiency can also promote the growth of root system so that the crop absorbs more water and nutrients and reduces the damage caused by stress (Gao *et al.*, 2015; Ma *et al.*, 2020). Poor root development hinders the absorption of water and nutrients, resulting in the inhibition of leaf growth and chlorophyll synthesis, and subsequent reduction of photosynthesis (Ma *et al.*, 2020).

The amount of N fertilizer applied to crops in China has increased substantially in the past few decades, and the amount of K^+ fertilizer applied accounts for 20% of the annual consumption in the world (Gao *et al.*, 2015; Li *et al.*, 2021b). Nevertheless, since utilization efficiency of nutrients in the soil is too low for crops to have normal plant growth, additional application of N and K^+ is still the current mainstream method to ensure crop yield (Esfahani *et al.*, 2021). In addition, owing to the mutual effect of N and K^+, such as higher application of N increases the demand of K^+ in crops (Shah *et al.*, 2017), crops under combined NK stress have become more common. However, the current research on the response of crops to combined stress lags behind the stress of individual stress, and the rational application of NK also requires more theories about response to this adversity (Zhu *et al.*, 2020). Therefore, investigating the response of cucumber to nutrient stress, especially compound stress, is of great significance for formulating reasonable irrigation strategies for improving fertilizer utilization rate and cucumber yield and quality; this is also the fundamental factor for maintaining national food security. Moreover, the research of the stress response mechanism of crops under NK stress can not only promote further study of the phenotypic characteristics of cucumber under compound stress but can also help to provide a basis for the construction of subsequent comprehensive evaluation system in greenhouse.

Materials and Methods

Test location and details

The experiment was carried out in a Venlo greenhouse (32.11° N, 119.27° E) of Jiangsu University in October 2021. The “Jinyou 1” cucumber from Tianjin Academy of Agricultural Sciences, Tianjin, China, was used in the experiment. The length and width of the greenhouse were 100 m and 40 m, respectively, and both shoulder height and span were 2.4 m (data from the “Introduction of the Greenhouse” published by Jiangsu University). This location was affected by circulation of the monsoon, the total annual radiation being 111.3 kcal/cm^2, the annual average relative humidity being 76%, and the annual average actual sunshine period was 2051.7 h. Seeds were sowed and cultivated in plastic plug trays, and sprouts of the cucumber broke out from the perlite on the third day. When sprouts developed true leaves on the 7th day of sowing, cucumber seedlings were transplanted into a pot having a diameter of 29.5 cm and a height of 19.3 cm; the pot was filled with 8-L rinsed perlite. Water and nutrients were provided by Kawasaki nutrient solution, and the cucumbers were watered with 600 mL once every morning from 8:00 to 9:00 am. The standard concentration of the nutrient solution is shown in Table 1. During the flowering period, data of the representative plants were collected.

Experiment design

The cucumbers were treated in groups on the 10th day after transplanting (DAT). Three levels of N and K^+ were set, respectively—50%, 100% and 150%—that is, a total of the following nine treatment groups were set up in the experiment, including a set of controls (600 mL × standard concentration): CK (control group, 100% N + 100% K^+), LN (50% N + 100% K^+), HN (150% N + 100% K^+), LK (100% N + 50% K^+), HK (100% N + 150% K^+), LNLK (50% N + 50% K^+), LNHK (50% N + 150% K^+), HNLK (150% N + 50% K^+) and HNHK (150% N + 150% K^+). A total of 10 cucumber plants were included in each treatment.

After 10 days of transplanting, under low-level treatment, N and K^+ were halved by replacing calcium nitrate and potassium nitrate with calcium chloride and potassium chloride, while under high-level treatment, sodium nitrate and potassium chloride were used to increase N and K^+ elements. As potassium nitrate contains both N and K^+, potassium chloride and sodium nitrate were always used to supplement N and K^+ reduced by low-level treatment. Specific details are shown in Figure 1.

Table 1. Components of standard nutrient solution.

Standard A		Standard B	
Chemical reagent	g/10 L	Chemical reagent	g/10 L
$Ca(NO_3)_2{\cdot}4H_2O$	826	$NH_4H_2PO_4$	114
KNO_3	607	$MgSO_4{\cdot}7H_2O$	429
		Fe-EDTA	7
		$MnSO_4{\cdot}4H_2O$	1.7
		$ZnSO_4{\cdot}7H_2O$	1.45
		$Na_2B_4O_7{\cdot}10H_2O$	2.45
		$CuSO_4{\cdot}5H_2O$	0.19
		$Na_2MoO_4{\cdot}2H_2O$	0.12

Note: Standards A and B were prepared separately and mixed before use. Used after diluting for 100 times.

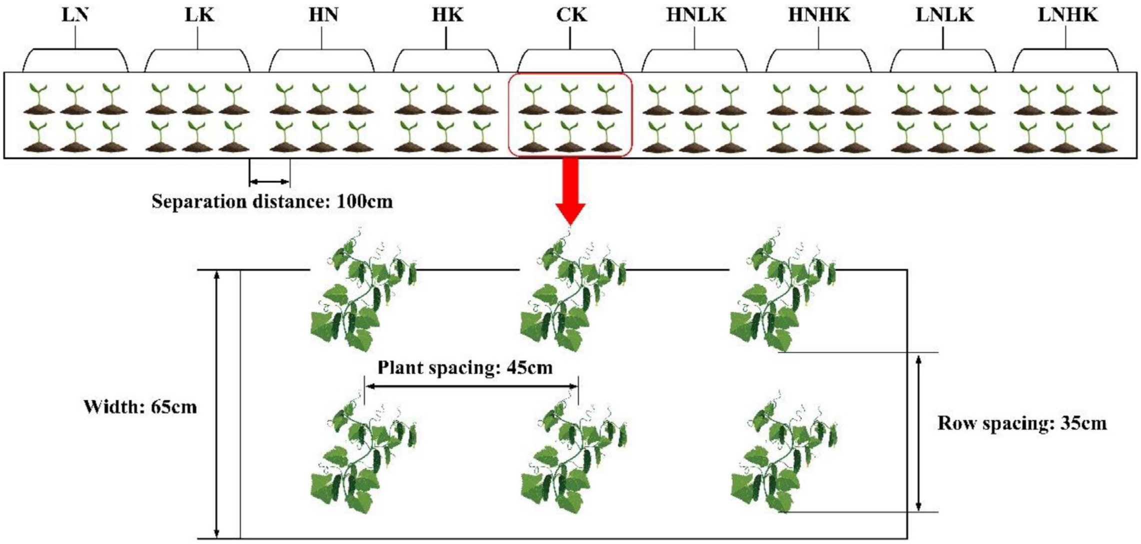

Figure 1. Diagram of experiment design.

Gas exchange parameters

The data collection of gas exchange parameters, including photosynthetic rate (Pn), intercellular CO_2 concentration (Ci), stomatal conductance (Gs) and transpiration rate (Tr), was processed at 9:00–11:30 am in the morning. Li-6400 (LI-COR Inc., Lincoln, NE, USA) was used to determine the well-grown leaves. The data were collected before group treatment (on the 10th day of transplanting) to ensure that the initial state of growth of tested plants was consistent. The data were again collected on the 7th day of treatment (on the 17th day of transplanting). Five plants were selected for each treatment, with each plant having three leaves. Stable data were recorded for five times for each leaf.

Growth parameters

After the measurement of gas exchange parameters (on the 17th day of transplanting), the plants were divided into leaves, stems and roots, and the growth parameters of cucumber were collected. Plant height (cm), distance from the bottom cotyledon to the top of the plant, was measured by a metric ruler (0.1 cm). Vernier calipers (0.01 mm) were used to determine diameter of the stem (mm), taking the average of upper, middle and lower stem. The leaf area was calculated by multiplying the length and width of fully expanded leaf, and the total leaf area was obtained by adding the area of each leaf (Hou *et al.*, 2021).

Roots

After the roots were protectively rinsed and cleaned, V700 image scanner (EPSON Co., Nagano, Japan) was used to scan the root system. The data were processed by the WinRHIZO root analysis software (professional version).

Biomass

At the end of the experiment, fresh weight (g) of each plant organ was measured using a balance (0.001 g). Then the root, stem, and leaves were separately packed into envelopes and placed in an oven at 105°C for 15 min to remove moisture. Dry weight of leaves, stem and root was determined after drying at 80°C until a constant weight was reached.

Statistical analysis

Mean values and standard deviation of gas exchange parameters, growth parameters, biomass and root system were calculated, and analysis of variance (ANOVA) was performed by SPSS 18.0. The least significant difference test (LSD) was used to determine significance at $P < 0.05$.

Results

Gas exchange parameters

On the 17th day of transplanting, different treatments had different effects on gas exchange parameters of cucumber as shown in Figure 2. Compared with CK, Pn of LN, HN, LK, HK, LNLK, LNHK, HNLK and HNHK treatments decreased by 22.04%, 10.40%, 16.63%, 2.51%, 38.28%, 33.80%, 27.08% and 6.06%, respectively. Gs and

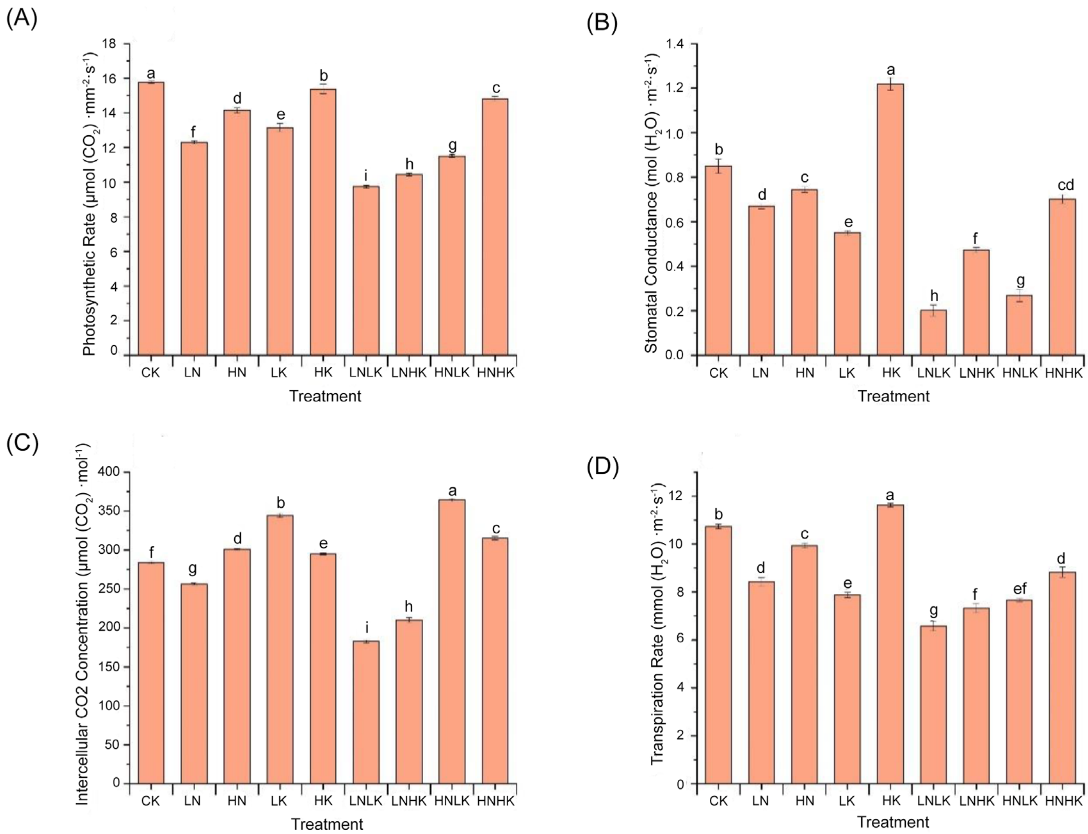

Figure 2. Effect of different treatments on the gas exchange parameters of cucumber in greenhouse. (A) Photosynthetic rate (Pn); (B) stomatal conductance (Gs); (C) intercellular CO2 concentration (Ci) and (D) transpiration rate (Tr). Different superscript lowercase alphabets indicate statistically significant differences in the gas exchange parameters of cucumber under different treatments at $P < 0.05$.

Tr of all treatments decreased by at least 12% and 7%, respectively, except for HK treatment, where Gs and Tr increased by 43.45% and 8.34%, respectively. In comparison with CK, Ci with LN, LNLK and LNHK treatments decreased by 9.69%, 35.63% and 25.98%, respectively, while Ci with HN, LK, HK, HNLK and HNHK treatments increased by 6.04%, 21.36%, 3.99%, 28.39% and 11.05%, respectively.

Growth parameters

The effects of different treatments on growth parameters of cucumber in greenhouse are shown in Table 2. As observed in the table, the effects of different treatments on leaf length and leaf width were consistent. Compared with CK, leaf length, leaf width, plant height and stem diameter of cucumber plant decreased significantly with LN, LK, HK, LNLK, LNHK and HNLK treatments, while growth parameters increased by at least 5% with HN treatment. HNHK treatment increased the length and width of leaf as well as stem diameter of cucumber whereas the plant height was reduced by 10.71%.

Changes in the biomass of cucumber plants in response to NK stress

The effects of N and K^+ on the biomass of cucumber plants are shown in Figure 3. Compared with CK, the fresh weight and dry weight of leaves decreased with all treatments except increase with HN treatment. Compared with CK, the fresh and dry weight of stem decreased with HN, LK, HNLK and HNHK treatments but increased with HK treatment. LN, LNLK and LNHK treatments decreased the fresh weight but increased the dry weight of stem compared with CK. Compared with CK, both fresh and dry weight of roots decreased with HN, LNLK, LNHK, HNLK and HNHK treatments but increased with LN and HK treatments. Compared with CK, LK treatment reduced the fresh weight but increased the dry weight of root.

Growth of cucumber root in response to NK stress

The effects of different treatments on cucumber roots are shown in Table 3. Compared with CK, total length,

Table 2. Effects of different treatments on the growth parameters of cucumber.

Treatment	Leaf area (cm^2)	Plant height (cm)	Stem Diameter (mm)
CK	2603.71 ± 117.47^c	106.8 ± 4.0^b	9.04 ± 0.27^b
LN	1439.54 ± 60.21^g	74.6 ± 2.6^e	5.91 ± 0.28^e
HN	2977.68 ± 74.86^a	112.6 ± 3.0^a	9.58 ± 0.44^a
LK	1590.58 ± 53.33^f	77.0 ± 1.2^e	7.75 ± 0.19^c
HK	2303.49 ± 95.08^d	98.7 ± 1.8^c	8.67 ± 0.19^b
LNLK	1277.51 ± 98.77^h	66.5 ± 3.3^f	5.72 ± 0.33^e
LNHK	1676.17 ± 130.32^f	83.0 ± 4.5^d	6.84 ± 0.28^d
HNLK	2061.52 ± 68.72^e	83.8 ± 4.5^d	7.54 ± 0.29^c
HNHK	2826.56 ± 148.05^b	95.4 ± 3.6^c	9.70 ± 0.53^a

Note: Different superscript lowercase alphabets indicate statistically significant differences in the growth parameters of cucumber under different treatments at $P < 0.05$.

surface area, average diameter and total volume decreased significantly with HK treatment but total tips of root increased by 4.69%. Compared with CK, LN and LK treatments increased the surface area, total length, total volume and total tips but reduced the average diameter of root. The total length and total volume with HN treatment decreased by 11.61% and 21.77%, respectively, while the total tips increased by 14.31%. Under combined stress, only the average diameter of root increased by 39.96% with LNHK treatment whereas root growth was inhibited with all other treatments. As manifested in Table 3, LNLK treatment had a great inhibitory effect on root growth, but the total length, surface area, average diameter, volume and total tips of roots decreased by 62.08%, 71.22%, 52.24%, 83.05% and 39.88%, respectively.

Discussion

Mu and Chen (2021) found that under conditions of N-deficiency, decrease of Gs and closure of stomata led to increase of Ci, which, together with decrease of electron transport rate and activity of photosynthetic enzymes caused by N-deficiency, inhibited photosynthesis. Cui *et al.* (2021) submitted that many physiological events related to photosynthesis, such as cellular ion homeostasis, phloem transport, metabolism and enzymatic activity, were affected due to K^+-deficiency. However, this was not completely consistent with the results of the present experiment. In this research, Pn of all the treatments decreased for the deficiency of N and/or K^+ on the 17th day of transplanting. Decrease in Ci with LN treatment could be due to the continuous consumption of CO_2 by photosynthesis after the stomata were closed. Under HN treatment, Gs decreased and the accumulation of CO_2 increased, leading to an increase in Ci. Decrease of Tr with LK treatment was related to the closing of stomata, and lower Gs with LK treatment than LN treatment was attributed to the key role of K^+ in regulating stomata (Sarah *et al.*, 2021). Xu *et al.* (2018) found that crops alleviated the damage caused by high concentration of K^+ to a certain extent through transpiration and ion transport. Therefore, Pn with HK treatment changed little but increase was observed in both Gs and Tr. Research conducted by Yang *et al.* (2020) showed that under K^+-deficiency condition, crops enhanced the internal transportation of K^+ in response to low K^+ stress. Thus, in order to provide more energy for K^+ transport, crops under LK treatment were to enhance respiration and produce more CO_2. In addition, stomata were closed due to low stomatal conductance under LK treatment, thereby increasing the Ci. The HK treatment promoted the opening of stomata and gas exchange so that Ci could change a little. Under LNLK treatment, continuous combined stress destroyed the regulation mechanism of stomata, resulting in a decrease in Tr. Because higher application of N increased the crop's requirement for K^+, thereby magnifying the effect of K^+-deficiency (Shah *et al.*, 2017), the Gs under HNLK treatment was decreased. Gs under HK treatment was higher, but it was relatively low under LNLK and LNHK treatments, indicating that the effect of N on crops was dominant as nutrition (Zhu *et al.*, 2020). The Gs decreased under both HNLK and HNHK treatments, which led to the continuous accumulation of CO_2. However, it is still unclear why Ci decreased with decrease of Gs with LNLK and LNHK treatments.

The growth parameters of all treatments except for HN treatment decreased significantly, and this was consistent with previous studies (Hou *et al.*, 2021; Khan *et al.*, 2021). Since, according to the description of Helena Ramirez-Solet *et al.* (2021), the expansion and growth of mesophyll cells were regulated by K^+, and N was a key element of chlorophyll and proteins required for growth and development, the growth of cucumber was inhibited when the absorption of N and K^+ was abnormal. Moreover, related research demonstrated that leaf area was determined by cell number and cell size (cell expansion). Reduction of leaf area because of K^+-deficiency decreased chloroplast density and increased distance between adjacent chloroplasts, resulting in reduced chloroplast surface area exposed to intercellular space and subsequent limitation of CO_2 transport, which ultimately reduced Pn (Hu *et al.*, 2020). As a result, under LK conditions, decrease in leaf area was more significant or observed earlier than decrease in Pn, and this could be related to the regulation of cell size by K^+. The Pn of HN treatment decreased but the growth parameters increased. Obviously, the reason was that crops were more inclined to promote greener leaves and larger leaf areas to cope with stress under high N concentrations (Chen *et al.*, 2018; Hou *et al.*, 2021).

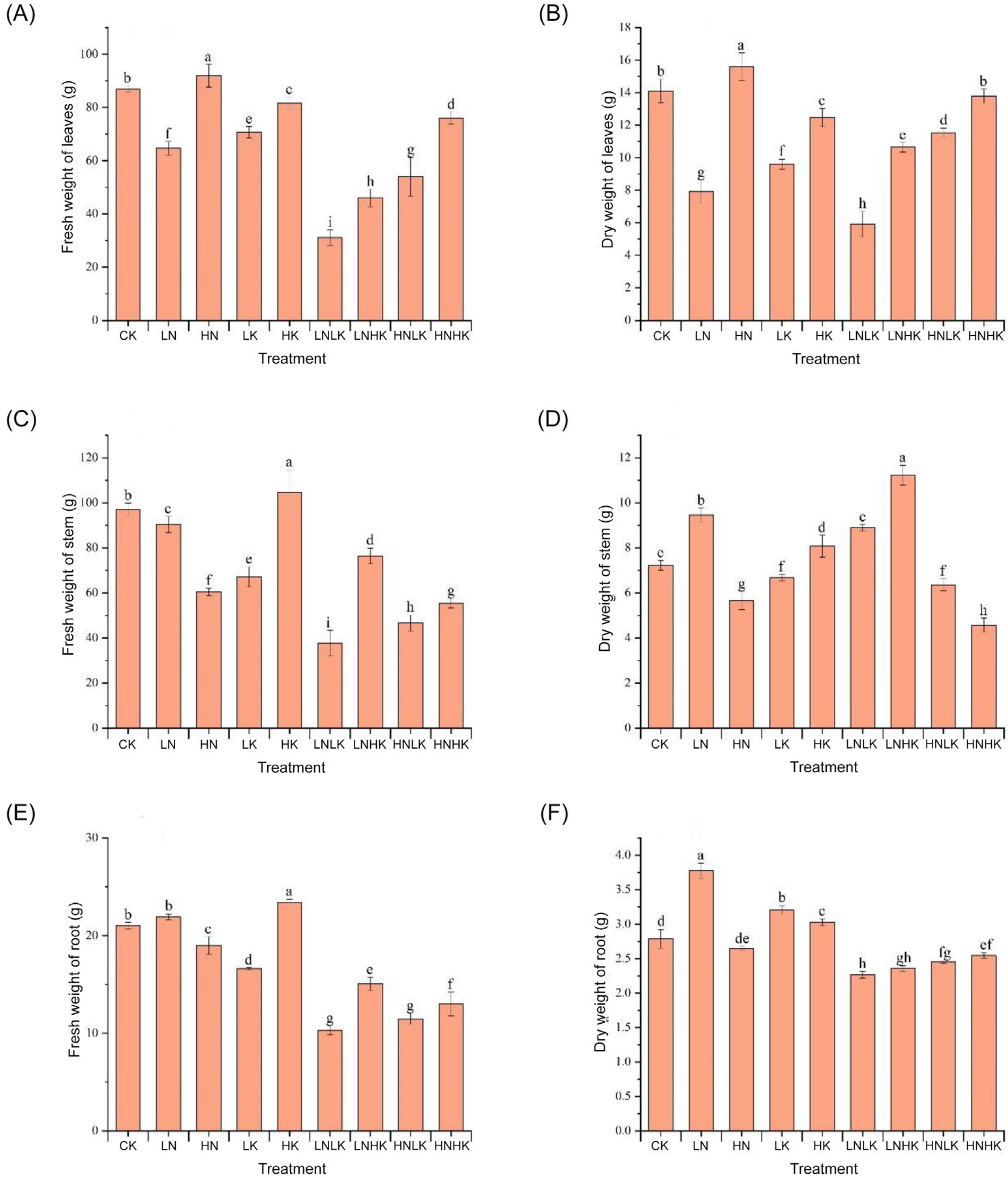

Figure 3. Effect of different treatments on the growth parameters of cucumber in greenhouse. (A) Fresh weight of leaves; (B) dry weight of leaves; (C) fresh weight of stem; (D) dry weight of stem; (E) fresh weight of root and (F) dry weight of root. Different superscript lowercase alphabets indicate statistically significant differences in the growth parameters of cucumber under different treatments at *P* < 0.05.

In addition, vigorous growth and enhanced respiration by leaves that lead to increased accumulation of CO_2 under HN treatment was another reason for higher Ci besides decrease in stomatal conductance.

According to the research conducted by Boussadia *et al.* (2010), crops transported more carbohydrates to roots under N-deficiency conditions. Therefore, both fresh and dry weight of leaves decreased, and biomass accumulation of root increased with LN treatment. On the contrary, green leaves were larger in size, and both fresh and dry weight of root decreased under HN treatment because crops tended to retain more carbohydrates for their development. The biomass accumulation in each organ with the exception of dry weight of stem was lowest with LNLK treatment. This was because LNLK treatment destroyed growth and osmotic pressure regulation of crop and affected the absorption of water and synthesis and accumulation of carbohydrates, which was an all-round impact (Li *et al.*, 2021b; Waqas *et al.*, 2021;

Table 3. Effects of different treatments on roots of cucumber.

Treatment	Total length (cm)	Surface area (cm^2)	Average diameter (mm)	Total volume (cm^3)	Total tips
CK	1124.209 ± 65.659^{c}	292.208 ± 3.071^{c}	1.100 ± 0.069^{b}	7.531 ± 0.216^{c}	5952.362 ± 23.268^{e}
LN	1410.797 ± 42.557^{a}	375.604 ± 14.342^{a}	0.604 ± 0.027^{d,e}	16.013 ± 0.286^{a}	8729.542 ± 95.146^{a}
HN	993.670 ± 20.181^{d}	309.836 ± 3.530^{b,c}	1.211 ± 0.150^{b}	5.891 ± 0.701^{d}	6804.451 ± 29.667^{c}
LK	1234.961 ± 14.721^{b}	326.085 ± 8.045^{b}	0.634 ± 0.033^{d,e}	10.650 ± 0.715^{b}	8098.823 ± 51.629^{b}
HK	895.832 ± 27.813^{e}	232.166 ± 9.202^{d}	0.791 ± 0.039^{c}	4.490 ± 0.459^{e}	6231.920 ± 5.338^{d}
LNLK	426.356 ± 42.725^{h}	84.090 ± 15.167^{g}	0.526 ± 0.031^{e}	1.276 ± 0.128^{h}	3578.216 ± 20.632^{i}
LNHK	578.833 ± 65.654^{g}	150.251 ± 15.081^{f}	1.540 ± 0.132^{a}	2.294 ± 0.485^{g}	5024.667 ± 65.333^{h}
HNLK	734.603 ± 13.798^{f}	214.255 ± 4.059^{d}	0.695 ± 0.037^{c,d}	3.376 ± 0.265^{f}	5379.357 ± 62.539^{f}
HNHK	776.207 ± 12.541^{f}	190.984 ± 2.922^{c}	0.661 ± 0.040^{c,d,e}	2.909 ± 0.084^{f,g}	5219.681 ± 46.333^{g}

Note: Different superscript lowercase alphabets indicate statistically significant differences in the growth of cucumber roots under different treatments at $P < 0.05$.

Yan *et al.*, 2021). Research conducted by Lan *et al.* (2013) and Zhu *et al.* (2020) showed that compared with K^+, N had a more significant impact on crops, and excessive K^+ affected the absorption and utilization of N. As a result, changes in the fresh weight of leaves under LNHK and HNHK treatments and the dry weight of leaves under LNHK treatment were limited, and the damage because of LNHK treatment to the accumulation of leaf matter was more serious. The decrease of fresh weight of stem with LNHK, HNLK and HNHK treatments was related to water loss caused by continuous K^+ stress destroying cell membranes (Zhang *et al.*, 2021). According to reports, the crop increased downward distribution with LN treatment (Boussadia *et al.*, 2010), but change in the the fresh weight of roots was not obvious, while the self-regulation mechanism of the crop under HK treatment significantly increased the fresh weight of stems. Shah *et al.* (2017) found that excessive application of N aggravated the damage of K^+-deficiency, and this could be the reason why both fresh and dry weights of leaves, stems and roots were significantly reduced under HNLK treatment.

Research has shown that the primary growth of roots was inhibited but growth of lateral root and root hair was promoted (Boussadia *et al.*, 2010; Fontana *et al.*, 2020; Gao *et al.*, 2015; Wang and Wu, 2013). In the present research, dry weight, surface area, length, total volume and total tips of roots increased but average diameter decreased with LK and LN treatments. Likewise, the biomass accumulation of root significantly increased with LN treatment. These were consistent with the results of previous research. Roots are the main and initial organs that sense element deficiency (Wang and Wu, 2013), and crops evolve an adaptive mechanism that uses plant hormones to regulate root morphology (Yang *et al.*, 2020). Under short-term nutritional deficiencies, crops tended to distribute more carbohydrates to roots to enhance the ability to absorb and transport nutrients. However, since increasing the contact area with the soil by promoting the growth of root hair was more conducive to the root system to obtain nutrients for the crop, growth of the root system was selective (Gao *et al.*, 2015). Under HN treatment, the total length and volume of roots decreased but the total tips increased. Based on a comprehensive analysis of results of previous studies (Boussadia *et al.*, 2010; Fontana *et al.*, 2020; Gao *et al.*, 2015; Wang and Wu, 2013) and the present research, an appropriate explanation was proposed that the number of lateral roots and root hair was significantly increased under conditions of N-sufficiency but their elongation lacked stimulation. Under LNLK treatment, both balance of cell osmotic pressure and key protein synthesis are destroyed, and root growth is inhibited. The comparison of root growth under LN, HN, LK and HK treatments with that under LNLK, LNHK, HNLK and HNHK treatments demonstrated that the combined stress caused more significant damage to crops compared to individual stress. The results were consistent with the research conducted of Wang and Wu (2013) but different from the research done by Fontana *et al.* (2020). This could be because root growth is affected by many factors, such as crop type, cultivation conditions and treatment time (Thornburg *et al.*, 2020). In addition, changes of Na^+ and Cl^-, which were used to reduce or increase N and K^+ content in experiments, were one of the factors affecting the photosynthesis, growth parameters and root development of cucumbers in greenhouse. Hence, the effect of Na^+ and Cl^- on crops should be paid more attention in the future research.

Conclusions

The comparison and analysis of greenhouse cucumber regarding growth, gas exchange parameters, dry matter distribution and root development under different treatments established the response of cucumber to N stress, K^+ stress as well as combined NK stress. Compared with control (CK), Pn, fresh and dry weight of leaves, growth parameters and root development were significantly reduced with LN, LK, HK, LNLK, LNHK and HNLK treatments (excluding HK treatment) whereas fresh and dry weight of stem and root, Gs, Tr and total tips were significantly increased with HK treatment. Likewise, fresh and dry weight of leaves, growth parameters and total tips were significantly increased with HN treatment. Compared with control, LN and LK treatments increased the surface area, length, total volume and total tips but decreased the average diameter of roots. This research demonstrated that short-term stress could promote root development. Therefore, it is possible to create artificially a state of slight stress for crops at the seedling stage, thereby promoting contact between the root system and the soil, enhancing absorption of water and fertilizer by the root system, and improving stress resistance. To sum up, the research revealed the response of crops to adversity under compound stress, and this is significant for studying crop resistance and constructing a comprehensive evaluation system for the health status of greenhouse crops.

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