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Physiological Mechanism of Photosynthetic, Nutrient, and Yield Responses of Peanut Cultivars with Different Tolerances under Low K Stress

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Abstract: Potassium is one of the most important elements for crop growth and development. However, potassium deficiencies are common in the cultivated land of oil crops in the world, which limits the increase in their yields. The photosynthesis, fluorescence, and physiological indexes of peanut plants were affected by low K stress to varying degrees, and finally the yield decreased. However, the effect of low K stress on the photosynthetic physiological mechanism of peanut plants remains unclear. In this study, in order to explore the response mechanism of peanuts to low K stress, NH18 (tolerance to low K) and HY20 (intolerance to low K) were used to explore the effects of different peanut varieties under low K stress on the dry matter accumulation, protective enzyme activities, osmotic regulatory substance accumulation capacity, fluorescence characteristics, nutrient content, grain quality, and yield. The results of the 2-year experiment showed that under the stress of low K, the content of malondialdehyde in peanut leaves increased and the activities of NH18 superoxide dismutase (SOD) and peroxidase (POD) in the low-K-tolerant variety were higher than those in the low-K-intolerant variety HY20. The decrease in osmotic regulation caused by low K was compensated for by an increase in the soluble protein content. As a result, the chlorophyll content decreased significantly, F0 increased under dark adaptation, and Fm, Fv, and Fv/Fm decreased. The photosynthetic and fluorescence physiology of low-K-tolerant NH18 was less affected by low K stress. Furthermore, under low K stress, the dry matter accumulation of NH18 was reduced less, so that the final yield was less affected by low K stress than that of HY20. Under low K stress, the potassium content in the roots, stems, leaves, and fruit needles decreased significantly, and the decreasing range of stems and leaves gradually increased with the growth period, while that of the pod gradually decreased with the growth period. Under low K stress, the sodium content in the root system significantly increased and was significantly higher than that in the stem, leaf, pod, and fruit needle, indicating that the peanut plants actively absorbed more Na^+ to replace the K^+ function. This study clarified the mechanism of photosynthesis and the physiology of peanut plants under low K stress, which is of great significance for the breeding and cultivation of peanut resistance.

Keywords: peanut; low K; fluorescent

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1. Introduction

Worldwide, the main oil varieties are soybeans, rapeseed, peanuts, cottonseed, and sunflower seeds, and the combined production of these five oil varieties accounts for about 90% of the world's total oil production, with other oil crops producing relatively little [1]. Peanuts, as one of the important oil crops, account for about 8% of the total edible oilseed production in the world and about 30% of the total edible oilseed production in China [2], which is of great significance for ensuring vegetable production. At present, the peanut planting area of China is second only to India, accounting for 19% of the global peanut planting area [3], and the total national peanut production accounts for about 40%

of the global peanut production, ranking as the top peanut producer in the world for 27 consecutive years [4]. The northeast has become the fourth largest peanut-producing area in China [5]. The soil quality is generally low in China, and potassium-deficient and extremely potassium-deficient land accounts for 12.16% of the total [6]. Xie [7] found that the potassium deficiency of the soil surface is serious (available potassium <100 mg/kg), and that the potassium deficiency area accounts for 23.6% in the northeast, 36.4% in the north, 21.8% in the northwest, 47.1% in the southwest, 52.9% in the east, 65.2% in the central region, and 85.8% in the south of China. A serious potassium deficiency in the soil restricts the growth and development of peanuts and threatens the safety of vegetable oil production.

Potassium is one of the three essential nutrients for plant growth and development, and it plays an important role in regulating enzyme activity, membrane potential, and cellular homeostasis and ensuring stable protein synthesis [8]. Potassium is the most abundant cation in plants, accounting for 2−10% of the total dry matter of plants [9]. Potassium is the activator of many enzymes and it plays an important role in protein synthesis, enzyme activation, substance transport, osmotic regulation, and stress resistance [10,11]. Numerous studies have shown that potassium can promote chloroplast development, improve photosynthesis, and delay senescence in crops [12]. Mengel [13] found that potassium deficiency in plants does not lead to immediate obvious symptoms, but rather to a state of hidden starvation, with an initial decrease in growth rate followed by yellowing and necrosis in later stages. Because potassium is easily moved from older to younger leaves in the plant, the early signs of potassium deficiency are mottled or chlorinated areas at the tips or edges of the oldest leaves. As potassium deficiency progresses, the entire leaf will turn yellow, resulting in decreased chlorophyll content. Jadav [14] used marble sand without potassium as the culture medium for cultivating peanuts by pouring in a nutrient solution. At 30 days after sowing, the edges of the peanut leaves without a potassium application began to yellow, and after 60 days, the symptoms of potassium deficiency were obvious; the leaves became yellow and withered, and this gradually spread to the middle. The potassium concentration of the leaves was lower than 40 mM.

According to previous studies, the decrease in leaf photosynthesis caused by potassium deficiency could be divided into stomatal limitation, mesophyll conductance limitation, and biochemical limitation. Stomatal limitation refers to the obstruction of water and gas in and out of the stomata due to reduced stomatal opening, mainly due to an insufficient CO_2 supply, which affects the photosynthesis of plant leaves. Xu [15] concluded that whether the reduction in the net photosynthetic rate (Pn) is caused by stomatal restriction mainly depends on the direction of change of the intercellular CO_2 concentration (Ci) and stomatal limitation (Ls). If the Ci decreases and the Ls increases, the decrease in stomatal limitation is the main factor, and conversely, an increase in the Ci and a decrease in the Ls indicates that a non-stomatal factor is the main reason. Berghuijs [16] found that mesophyll conductance is a limitation, which reflects the resistance to CO_2 diffusion in the mesophyll. CO_2 was dissolved in the water of the cell wall after entering the leaf through the stomata and existed in the form of CO_2 or HCO_3^-, and further expanded to the plasma membrane, cytosol, chloroplast envelope, and chloroplast matrix through the cell wall, where enzymatic CO_2 fixation was carried out. Biochemical limitation refers to the complex physiological and biochemical processes that CO_2 needs to undergo in order to be fixed and assimilated into carbohydrates. These processes are affected by enzyme activity, ATP and NADPH supply, and oxygen free radical metabolism. Zhao found that [17] K^+ is involved in these processes, so the effect of potassium deficiency on these processes and the reduction in photosynthesis was attributed to biochemical limitation. Potassium deficiency in cotton results in decreased stomatal conductance, increased mesophyll resistance, decreased ribulose 1, 5-bisphosphate carboxylase/oxygenase (Rubisco) activity, and ultimately a reduced total photosynthetic rate of the plant.

Combined with previous studies, it was found that there have been few studies on photosynthesis and the physiology of peanut plants under low potassium stress. Therefore,

in this study, our main objectives were to (1) reveal the photosynthetic and fluorescence characteristics of tolerant peanut varieties under low K stress, (2) clarify the mechanism by which leaf antioxidant oxidase activity regulates reactive oxygen species (ROS) to maintain normal physiological activities under low K stress, and (3) determine the reaction mechanism of plant nutrient uptake and utilization, substance-coordinated distribution, and yield under low K stress. The deficiency of soil potassium, the lack of potassium ore, and the import of potassium fertilizer cause great pressure to crop planting and production in China, and the deficiency of soil potassium in some main peanut-producing areas seriously affects the yield and quality improvement of peanut plants. Therefore, it is of great significance to clarify the physiological mechanism of peanut stress under low K stress for peanut tolerance breeding and cultivation.

2. Materials and Methods

2.1. Materials

Two representative peanut varieties screened in our previous study, NH18 (tolerance to low K) and HY20 (intolerance to low K), were used in this study (Table 1).

Table 1. The sources of peanuts that were tested.

Cultivars	Abbreviation	Source	Ecological
Nonghua18	NH18	Shenyang Agricultural University	Pearl bean type
Huayu20	HY20	Shandong Peanut Research Institute	Pearl bean type

2.2. Experimental Design and Treatments

This experiment was carried out in 2020 and 2021 at the Northeast Observation and Experimental Station of Crop Physiology, Ecology and Tillage, Ministry of Agriculture, Shenyang Agricultural University (41°82′ N, 123°56′ E). A low K treatment and a high K treatment were set up in this study. No potassium fertilizer was applied in the long-term positioning of the low K field. The soil nutrient content is shown in Table 2. Under different K treatments, the application amount of nitrogen fertilizer and phosphate fertilizer remained the same: urea (N:46%), 135 kg·hm^{-2}; superphosphate (P_2O_5:12%), 600 kg·hm^{-2}; and potassium sulfate (K_2O:50%), 119.94 kg·hm^{-2}. After mixing, the fertilizers were applied evenly into the ridge once before sowing. A total of 6 plots were set up, 3 of which received a high K treatment and 3 of which received a low K treatment. The ridge length was 3.75 m, the ridge spacing was 0.5 m, and the plant spacing was 13 cm. There were 8 rows in total, with 4 rows for each variety, and the plot area was 15 m^2. The single ridge and small double row staggered planting method was adopted, and the planting density was 300,000 plants/ha. Each treatment was repeated three times. For the sampling of the pegging stage (S1), podding stage (S2), pod setting stage (S3), and mature period (S4), the processing of each organ was performed by assessing the accumulation of dry matter and nutrient content. In the S2 phase measurements, the function of the main stem leaf chlorophyll fluorescence parameters and leaf sampling were used to measure physiological indexes such as the chlorophyll content and the antioxidant enzyme activity. The field management was the same as conventional field management.

Table 2. Soil nutrient content.

Treatment	Available Potassium (mg/kg)	Available Phosphorus (mg/kg)	Available Nitrogen (mg/kg)	Organic Matter (g/kg)	pH
HK	147.3	16.3	96.3	12.3	7.2
LK	57.0	17.1	94.2	11.6	7.3

2.3. Determination Items and Methods

The content of chlorophyll A, chlorophyll B, and carotenoids in the inverted three leaves of healthy and consistent plants was measured by 95% ethanol extraction.

2.3.1. Determination of Chlorophyll Content

Photosynthetic pigments (chlorophyll (Chl) a and b, and total Chl) were estimated by following the methods of Naeem [18,19]. Fresh leaves were homogenized using ethanol (95%, v/v) and the absorbance of the supernatant was read at 665 and 649 nm with a UV/visible spectrophotometer (Lambda 365, PerkinElmer, Waltham, MA, USA); the results were expressed as mg g^{-1}(leaf fresh mass, FM). Related parameters were calculated by using the following formulas:

$$\text{Chl a}\left[\text{mg}\cdot\text{g}^{-1}(\text{FM})\right] = \frac{(13.95\,\Delta 665 - 6.88\,\Delta 649)\times\ \text{V}}{1000\times\ \text{W}}$$

$$\text{Chl b}\left[\text{mg}\cdot\text{g}^{-1}(\text{FM})\right] = \frac{(24.96\,\Delta 649 - 7.32\,\Delta 665)\times\ \text{V}}{1000\times\ \text{W}}$$

where Δ665 and Δ649 are the absorbances at 665 and 649 nm, respectively, V is the total volume of the extract (10 mL), and W is the leaf fresh mass (0.1 g).

2.3.2. Determination of Carotenoid Content

The carotenoid content was determined by referring to the chlorophyll content determination method. Fresh leaves were homogenized using ethanol (95%, v/v) and the absorbance of the supernatant was read at 470 nm with a UV/visible spectrophotometer (Lambda 365, PerkinElmer, Waltham, MA, USA); the results were expressed as mg·g^{-1} (leaf fresh mass, FM). Related parameters were calculated by using the following formulas:

$$\text{Carotenoids}\left[\text{mg}\cdot\text{g}^{-1}(\text{FM})\right] = \frac{[(1000\,\Delta 470 - 2.05\,\text{Chl a}\ - 114.8\,\text{Chl b})/245]\times\ \text{V}}{1000\times\ \text{W}}$$

where Δ470 is the absorbance at 470 nm, V is the total volume of the extract (10 mL), and W is the leaf fresh mass (0.1 g).

2.3.3. Determination of Dry Matter Accumulation

The plants were divided into roots, stems, leaves, fruits and needles by organs, put into cow leather bags, and placed in an air-blowing drying oven at 105 °C for 30 min. The samples were then dried at 80 °C until reaching a constant weight and the dry matter of each organ was weighed. The samples were crushed and screened for the determination of plant nutrient content in the later stages.

2.3.4. Determination of Antioxidant Enzyme Activity

Determination of SOD Activity

The method of Yan [20] was referred to and some changes were made. A total of 0.5 g of peanut leaves were accurately weighed into a pre-cooling mortar, 2.5 mL of 0.05 mol/L (pH of 7.8) phosphoric acid buffer solution was added with a pipetting gun, and a small amount of quartz stone was added. The mixture was ground in an ice bath to homogenate it, and then it was transferred to a centrifugal tube and adjusted to a constant volume of 5 mL with a buffer solution. The supernatant was centrifuged at a speed of 10,000 r/min at 4 °C for 20 min to obtain the crude enzyme solution.

The reaction system was 3 mL, including 0.05 mol/L (pH of 7.8) phosphoric acid buffer solution, 0.3 mL of a 130 mmol/L Met solution, 0.3 mL of a 750 umol/L NBT solution, 0.25 mL of ultra-pure water, 0.3 mL of a 20 umol/L riboflavin solution, and 0.05 mL of an enzyme solution added into each glass jar. A buffer solution was used instead of an enzyme solution to set 4 HK treatments; 2 were wrapped with aluminum foil paper to completely block light as a blank to set the instrument to zero, and the other 2 HK

treatments were placed together with the sample at 25 °C under a 40,001× fluorescent lamp for 15 min. Each treatment was evenly illuminated. After the irradiation reaction, a LAMBDA 365 UV/visible spectrophotometer (PerkinElmer Inc., Waltham, MA, USA) was used to measure the absorbance of each reaction system at a 560 nm wavelength and calculate the SOD according to the following formula:

$$\text{SOD activity} = \frac{(A_{ck} - A_s) \times V_T}{A_{ck} \times 0.5 \times W \times V_S}$$

In the formula, the total SOD activity is expressed in units of enzyme per gram fresh weight, and the specific activity unit is expressed in units of enzyme/mg protein. The formula includes the absorbance of A_{ck}, the absorbance of the A_S sample, the total volume of the V_T enzyme solution (mL), and the amount of enzyme solution when V_s was determined (mL); W is the sample fresh weight (g).

Determination of POD Activity

The method of Tang was referred to and some changes were made. A total of 0.5 g of peanut leaves were weighed and placed in a pre-cooling mortar, 2.5 mL of 0.1 mol/L (pH of 6.0) phosphoric acid buffer solution was added with a pipetting gun, and a small amount of quartz stone was added at the same time. The mixture was then ground in an ice bath to homogenate it, and then it was transferred to a centrifugal tube. The buffer volume was kept at 5 mL and the solution was centrifuged at 4 °C at 4000 r/min for 15 min. The crude enzyme solution was obtained by absorbing the supernatant.

To prepare the reaction solution, 56 µL of guaiacol solution was added to 100 mL of 0.1 mol/L (pH of 6.0) phosphoric acid buffer solution, the solution was stirred and mixed, and then 38 µL of 30% hydrogen peroxide was added and the solution was mixed again.

A total of 3 mL of the reaction solution and 50 µL of extraction buffer were added to the colorimetric cup as a blank zero; the other samples were in accordance with the amount of 3 mL of reaction solution and 50 µL of enzyme solution into the colorimetric cup. The solutions were mixed immediately into the spectrophotometer and the change at Δ470 within 3 min was measured. The instrument was set to automatically record a reading every 30 s. The POD activity was calculated with the following formula with a 0.01 change (increase) in absorbance per minute as one enzyme activity unit:

$$\text{POD activity} = \frac{(\Delta 470 \times V_T)}{W \times V_S \times 0.001 \times t}$$

In the formula, Δ470 represents the change in absorbance before and after the reaction, V_T represents the total volume of the extraction enzyme solution (mL), V_s represents the amount of the determination enzyme solution (mL), W represents the sample weight (g), and t represents the reaction time (min).

2.3.5. Determination of Osmotic Regulatory Substances

Determination of MDA Content

The MDA content was determined by referring to the method of Wu [21]; The method of crude enzyme extract is the same as that of SOD enzyme extract. A 2 mL centrifuge tube was selected and numbered. 0.3 mL crude enzyme extract and 0.5 mL 0.5% thiobarbituric acid (TBA) solution were added to the centrifuge tube, shaken well and placed in a boiling water bath for 15 min. After cooling, the absorption values at 532 nm and 600 nm were determined by centrifugation (8000 rpm, 10 min).The calculation formula of the MDA content is as follows:

$$\text{MDA content } (\text{nmol}\cdot\text{g}^{-1}) = \frac{(\Delta_{532} - \Delta_{600}) \times \text{T} \times \text{V/Va}}{1.55 \times 10^{-1} \times \text{W}}$$

In the formula, T is total volume of reaction liquid (ml); V is total volume of extract (ml); Va is amount of extract used for determination, W is fresh weight of sample (g).

Determination of Soluble Protein Content

The methods of Wang [22] were referred to. An amount of 0.5 g of peanut leaves was weighed into a mortar, 5 mL of distilled water and a small amount of quartz sand were added, and then the mixture was ground in an ice bath into a homogenate mixture. The mixture was transferred to a centrifugal tube and centrifuged at a low temperature of 4 °C at a speed of 4000 r/min for 10 min, 0.1 mL of supernatant was sucked, and 5 mL of Coomassie brilliant blue reagent was added. The solution was mixed well and allowed to stand for 2 min; then, the absorbance was measured at the wavelength of 595 nm. The blank HK was distilled water and the protein content was calculated through a standard curve. The standard curve was formulated with bovine serum protein. The calculation formula is as follows:

$$\text{Soluble protein content } (\mu g/g) = \frac{C \times V}{W}$$

In the formula, sample C corresponds to the protein concentration on the standard curve (μg/mL), V is the total volume of the extraction solution (mL), and W is the fresh weight of the sample (g).

2.3.6. Determination of Chlorophyll Fluorescence Imaging

The functional leaves of the main stem were taken, treated with wet black cloth for shading, and brought back to the laboratory for fluorescence imaging using a a Chl fluorescence imaging system (FluorCam FC800, Photon Systems Instruments, Brno, Czechia). The initial fluorescence (F0), maximum fluorescence (Fm), variable fluorescence (Fv) and maximum photochemical efficiency (Fv/Fm) of PSII under dark adaptation conditions were determined.

2.3.7. Determination of Plant Nutrients

H_2SO_4-H_2O_2 digestion was used for plant digestion. An amount of 0.3 g of a crushed plant sample was accurately weighed (accurate to 0.0001) and put into a 250 mL eliminate boiling tube, 5 mL of concentrated H_2SO_4 was added, and the mixture was shaken well and allowed to stand for 1 h. The solution was placed into a dissolving furnace (FOSS Company, Copenhagen, Denmark) and the temperature was set at 380 °C. After dissolving for 1 h, the sample turned brown and black. At this time, it was taken out and cooled for a bit, then dropped in H_2O_2 to continue dissolving.

Determination of Potassium and Sodium Content

The content of potassium and sodium was determined using the flame photometer method. A Sherwood 410 flame photometer (Cambridge, UK) was used. The potassium and sodium standards were KCl and NaCl with superior purity, which were dried for 2 h at 110 °C, weighed accurately to prepare 100 ug/mL mother liquor, and then diluted into standard samples of each concentration according to the gradient. On the machine for measurement, the flow meter was checked after the reading achieved stability of the record. The concentration of the standard sample was the abscissa and the flow meter reading was the ordinate. The standard curve was drawn, then each sample was measured and the reading was recorded.

$$\text{Plant nutrient content } (mg/g) = \frac{C \times V}{1000 \times m}$$

In the formula, C is the concentration of the sample solution after conversion according to the standard curve (μg/mL); V is the constant volume after cooking (mL); and m is the weight of the sample (g).

2.3.8. Determination of Yield and Yield-Related Traits

When peanuts are ripe and harvested, a whole row of peanuts were selected in each plot, 10 plants in a row were taken, and the whole plant was placed into a yarn net bag. After air drying to a constant weight in the shade, a seed test was conducted, the number of fruit per plant was counted, and the fruit satiety per plant and fruit weight per plant were determined.

2.3.9. Statistical Analysis of Data

The data from each of the treatments with three replicates were subjected to a one-way analysis of variance (ANOVA) and least significant difference (LSD) testing at $p < 0.05$ by using SPSS 19.0 software (SPSS, Inc., Chicago, IL, USA). The Origin 2017 software (Origin Lab, Northampton, MA, USA) was used to produce the graphs. The data in graphs were presented as the mean ± standard deviation.

3. Results

3.1. Effect of Low K Stress on Dry Matter Accumulation of Peanuts at Maturity

The dry weight at the maturity stage reflects the final dry matter accumulation of peanut plants throughout their growth period. The dry matter accumulation of the HY20 and NH18 organs under low K stress in the mature stage is shown in Figure 1.The dry weight of HY20 and NH18 under low K stress was 4.0–18.1% and 2.8–15.8% lower than that under HK, respectively, with significant differences ($p < 0.05$). The stem dry weight was 23.2–25.5% and 24.1–27.1% lower than that under HK, respectively, with significant differences among the treatments ($p < 0.05$). In 2021, the leaf dry weight ratio of HY20 decreased the most (38.4%), and there was a significant difference among the treatments ($p < 0.05$). The dry pod weight was 11.0–16.9% and 6.4–22.9% lower than that under HK, respectively. Compared with the plants under HK, the total dry weight of plants was 18.0–22.0% and 15.6–23.2% lower, respectively, and there were significant differences among the treatments ($p < 0.05$). The overall dry weight of plants in 2021 was significantly higher than that in 2020, because the growing environment temperature in 2021 was higher and the plant vegetative growth was too fast, which eventually led to an increase in the dry matter weight. The pod dry weight decreased significantly in the mature stage under low K stress, indicating that low K stress would eventually lead to a reduction in peanut yield.

3.2. Effects of Low K Stress on Chlorophyll Content in Leaves

It can be seen that low K stress has an impact on chlorophyll content (Table 3). The cultivar and treatment significantly ($p < 0.05$) affected the peanut chlorophyll a content. The year, cultivar, and treatment significantly ($p < 0.05$) affected the peanut chlorophyll b and chlorophyll (a + b) content. The year, cultivar, treatment, and year × treatment significantly ($p < 0.05$) affected the peanut carotenoid content. Under low K stress, chlorophyll a of HY20 and NH18 decreased by 7.9–8.3% and 9.5–18.0% compared with the plants under HK, respectively, and NH18 was significantly different ($p < 0.05$). Compared with HK, chlorophyll b decreased by 5–6.7% and 11.4–12.9%, and NH18 was significantly different in 2020; the total chlorophyll content decreased by 10.3–10.4% and 18.4–18.8%, respectively, with significant differences. There was no significant difference in the carotenoid content between the LK and HK treatments ($p > 0.05$).

3.3. Effects of Low K Stress on the Activity of Antioxidant Enzymes in Leaves at Pod Setting Stage

The SOD activity of peanut leaves under low K stress increased as a whole compared with that of the high K treatment (Figure 2), and the SOD activity of HY20 was higher than that of NH18, indicating that the membrane lipid peroxidation of HY20 was more serious than that of NH18. The results were consistent over two years. Based on the two-year data, it can be seen from Figure 2 that the POD enzyme activity of peanut leaves under low K stress was much higher than that under the high K treatment. The POD activity of HY20

was higher than that of NH18. There were significant differences between the HK and LK SOD and POD activities of the varieties in 2020 and 2021 ($p < 0.05$).

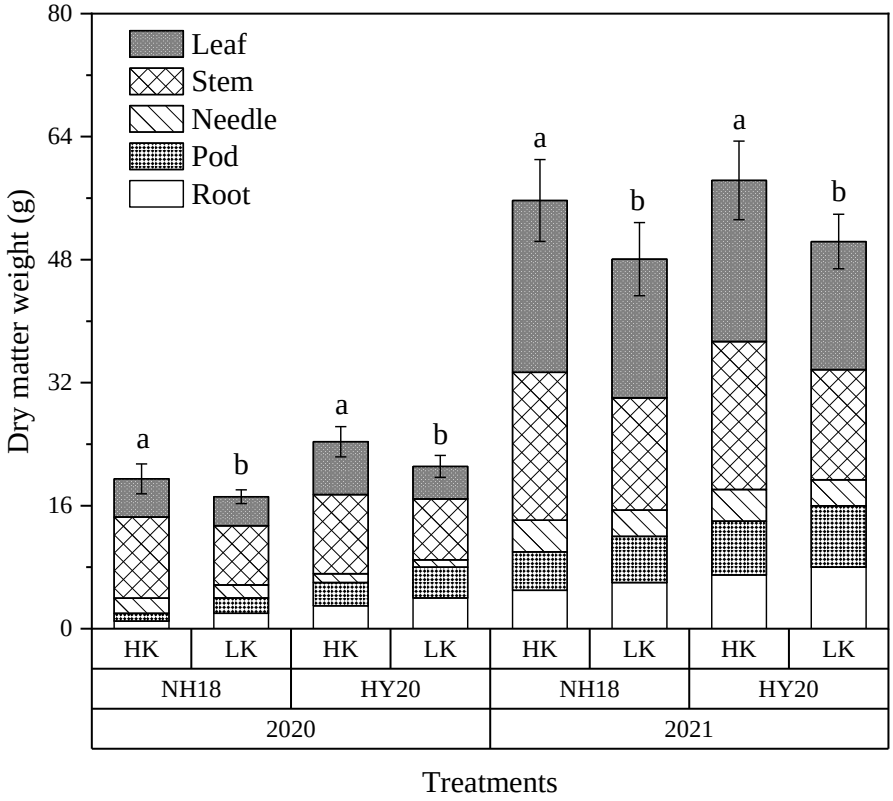


Figure 1. Effects of low K stress on dry matter accumulation of peanuts at maturity. HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

Table 3. Effects of low K stress on chlorophyll content in leaves.

Year	Cultivars	Treatments	Chlorophyll a (mg·g^{-1} (FM))	Chlorophyll b (mg·g^{-1} (FM))	Chlorophyll (a + b) (mg·g^{-1} (FM))	Carotenoids (mg·g^{-1} (FM))
2020	NH18	HK	0.95 ± 0.02 a	0.35 ± 0.02 a	1.33 ± 0.03 a	0.06 ± 0.01 a
		LK	0.78 ± 0.06 b	0.31 ± 0.01 b	1.08 ± 0.08 b	0.08 ± 0.01 a
	HY20	HK	1.11 ± 0.05 a	0.45 ± 0.01 a	1.55 ± 0.05 a	0.11 ± 0.01 a
		LK	1.02 ± 0.07 a	0.42 ± 0.02 a	1.39 ± 0.08 b	0.09 ± 0.01 a
2021	NH18	HK	1.03 ± 0.03 a	0.46 ± 0.04 a	1.41 ± 0.07 a	0.15 ± 0.0.1 a
		LK	0.86 ± 0.06 b	0.40 ± 0.07 a	1.26 ± 0.03 b	0.11 ± 0.01 a
	HY20	HK	1.14 ± 0.08 a	0.54 ± 0.05 a	1.68 ± 0.05 a	0.18 ± 0.02 a
		LK	1.05 ± 0.02 a	0.44 ± 0.08 a	1.49 ± 0.06 b	0.14 ± 0.01 a
Year			0.186	0.003	0.001	0.000
Cultivar			0.000	0.002	0.000	0.000
Treatment			0.001	0.025	0.000	0.002
Year × Cultivar			0.880	0.359	0.803	0.378
Year × Treatment			0.528	0.290	0.563	0.002
Cultivar × Treatment			0.419	0.684	0.600	0.173

HK: high K treatment; LK: low K treatment. For the table, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.4. Effects of Low K Stress on Osmotic Regulatory Substances in Leaves

3.4.1. Effects of Low K Stress on MDA Content in Leaves

Based on the two-year data, the MDA content of HY20 under low K stress significantly increased by 10.5% and 18.5% compared with that under HK, and the MDA content of NH18 significantly increased by 18.3% and 21.8% compared with that under HK (Figure 3). The results showed that low K stress could increase the level of cell membrane lipid peroxidation and accelerate senescence, which is not conducive to peanut growth and development.

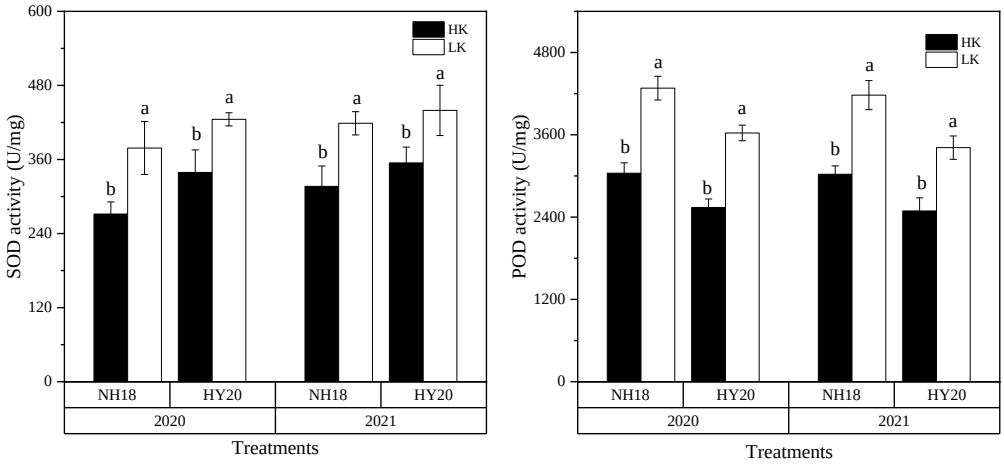


Figure 2. Effects of low K stress on antioxidant enzyme activity in leaves. HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

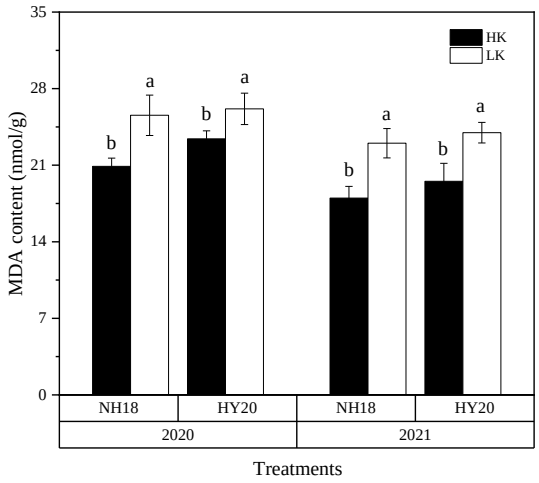


Figure 3. Effects of low K stress on MDA content in leaves. HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.4.2. Effects of Low K Stress on Soluble Protein Content in Leaves

The soluble protein content in the peanut leaves under low K stress was higher than that under the high K treatment (Figure 4). Compared with the HK treatment, the protein content for HY20 and NH18 increased by 34.1% and 25.7%, respectively, in 2020. Compared with the HK treatment in 2021, the protein content for HY20 and NH18 increased by 32.8% and 19.5%, respectively, with significant differences among treatments ($p < 0.05$). There were significant differences between HK and LK in the two years of data. The soluble protein content of HY20 was higher than that of NH18. The results showed that the decrease

in osmotic regulation caused by low K was compensated for by an increase in the soluble protein content of leaves.

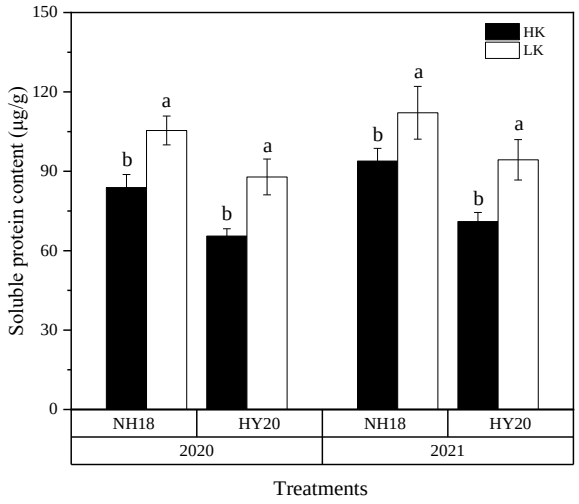


Figure 4. Effects of low K stress on soluble protein content in leaves. HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.5. Effects of Low K Stress on Fluorescence Parameters

Under low K stress, the partial red of HY20 and NH18 leaves was darker than that of leaves under HK, indicating that the F0 in these areas increases under low K stress (Figure 5A). The F0 of HY20 increased by 25.3% and 13.9% (Figure 5B), respectively, compared with NH18 under low K stress in two years, and there was a significant difference between treatments ($p < 0.05$).

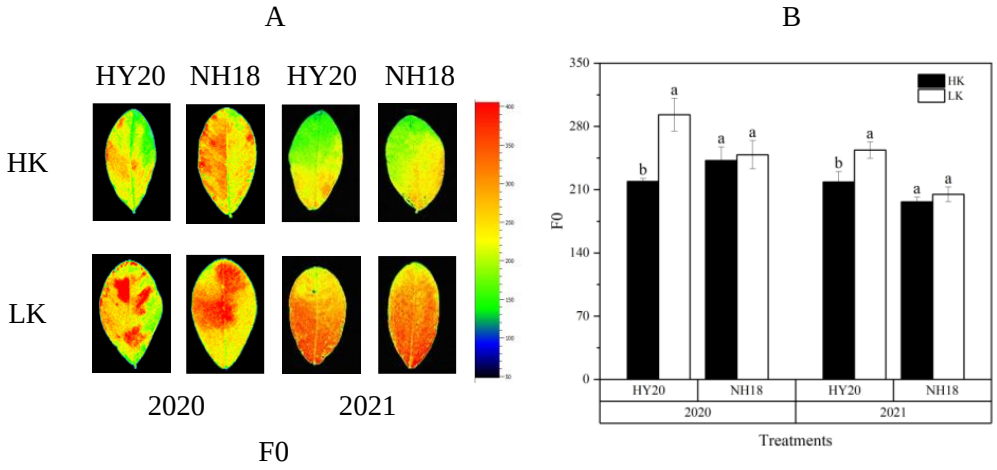


Figure 5. Chlorophyll fluorescence imaging under low K stress. Chlorophyll fluorescence imaging under low K stress-F0 (**A**); Effect of low K stress on fluorescence parameter F0 (**B**). HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

The leaves under the high K treatment had a uniform color and were redder than those under the low K treatment (Figure 6A). The Fm decreased under low K stress (Figure 6B). Local chlorosis occurred at the edge of HY20 leaves due to potassium deficiency, and the Fm was significantly lower than that in the middle of leaves, among which NH18 had a significant difference in 2020 ($p < 0.05$).

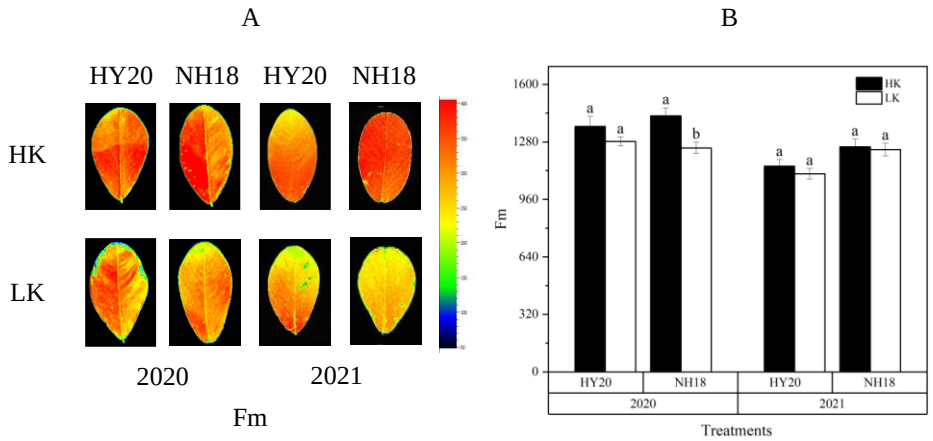


Figure 6. Chlorophyll fluorescence imaging under low K stress. Chlorophyll fluorescence imaging under low K stress-Fm (**A**); Effect of low K stress on fluorescence parameter Fm (**B**). HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

The Fv decreased under low K stress, and NH18 decreased the most in 2020, which was 15.6% (Figure 7), with significant differences among treatments ($p < 0.05$).

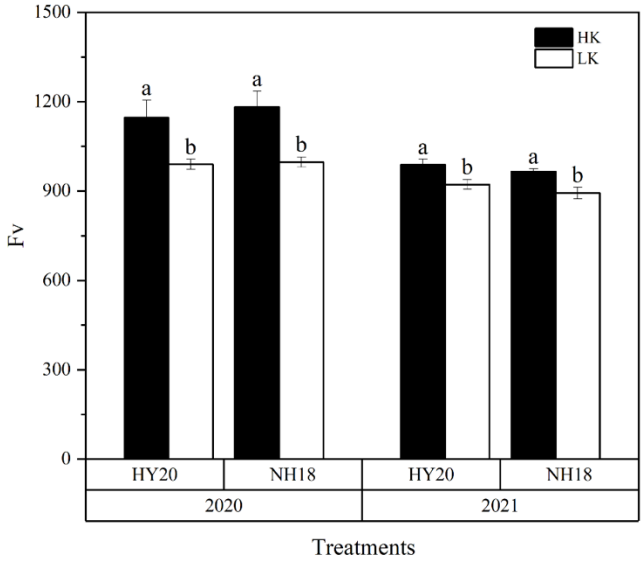


Figure 7. Effects of low K stress on fluorescence parameters of dark adaptation. HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

Fv/Fm is the maximum photochemical quantum efficiency of PSII, which is used to reflect the potential photochemical capacity of plants. Under low K stress, there were partial yellow or bluish-colored areas in the Fv/Fm fluorescence imaging effect diagram (Figure 8A). By comparing the color scale, it could be seen that the Fv/Fm value of these areas was significantly lower than that under the high K treatment. Fv/Fm decreased significantly in two years under low K stress (Figure 8B), with a significant difference between treatments ($p < 0.05$). Compared with HK, HY20 showed a more significant difference and was subjected to deeper stress. These results indicate that low K stress caused damage to the photosynthetic mechanism of leaves to a certain extent, resulting in the obstruction of electron transfer and the destruction of the structure of the photosystem, and affecting the normal progress of photosynthesis.

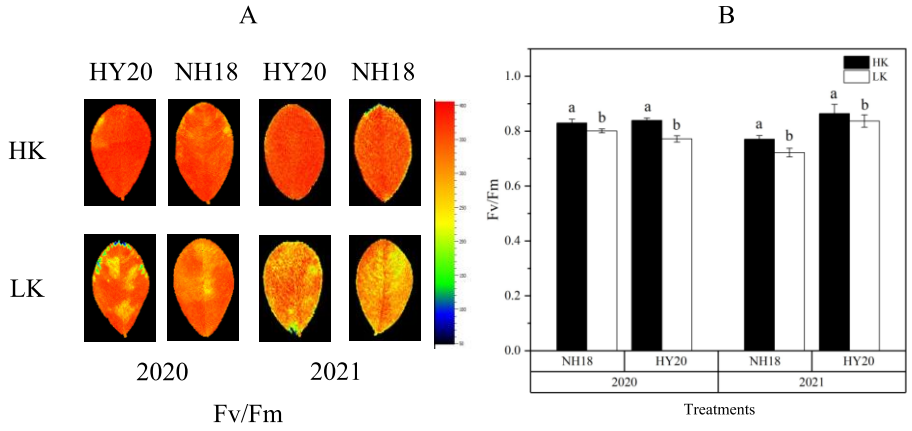


Figure 8. Chlorophyll fluorescence imaging under low K stress. Chlorophyll fluorescence imaging under low K stress-Fv/Fm (**A**); Effect of low K stress on fluorescence parameter Fv/Fm (**B**). HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.6. Effects of Low K Stress on Fluorescence Parameters under Light Adaptation

3.6.1. Effects of Low K Stress on Photochemical Quenching Coefficient

Under low K stress, the photochemical quenching coefficients of leaves were all reduced, with slightly different decreasing ranges (Figure 9). The decreasing ranges of HY20 in the two years were greater than that of NH18, at 6.57% and 6.53%, respectively, reaching a significant difference level ($p < 0.05$). The results showed that low K stress resulted in the closure of the PSII reaction center and the obstruction of photosynthetic electron transfer, which affected the photosynthetic efficiency.

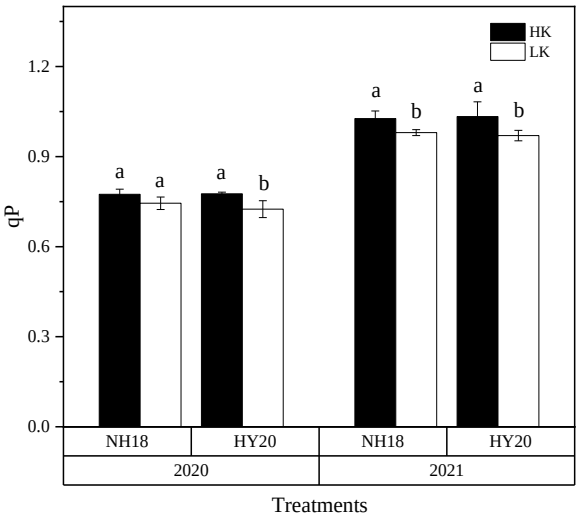


Figure 9. Effect of low K stress on photochemical quenching coefficient. HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.6.2. Effects of Low K Stress on Non-Photochemical Quenching

Under normal growth conditions, the above results confirmed that the qP decreased under low K stress, indicating that the proportion of energy used for photosynthetic electron transport decreased. The NPQ of leaves increased under low K stress (Figure 10). In 2021, the NPQ of HY20 increased by 59.2% compared with that under HK, and significant differences were reached between treatments ($p < 0.05$).

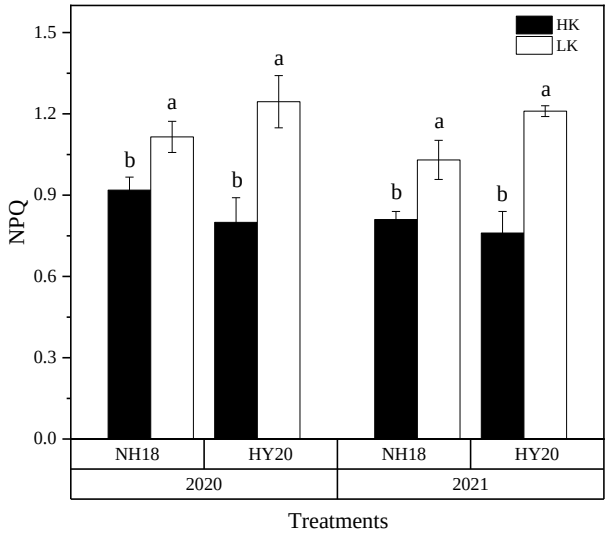


Figure 10. Effect of low K stress on non-photochemical quenching coefficient. HK: high K treatment; LK: low K treatment. For the bar chart, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.7. Effects of Low K Stress on Nutrient Content

3.7.1. Influence of Low K Stress on Potassium Content

The potassium content in each organ of the plant decreased during the whole growth period under low K stress (Figure 11). There were significant differences in the potassium content in the roots, stems, leaves, and fruit needles among different treatments, and the overall trend was the same over two years. The potassium content in all the plant organs in 2021 was lower than that in 2020, and the decrease in the potassium content was the largest in the leaves. In terms of the whole growth period, the variation range of the potassium content in the roots of the two cultivars under low K stress was 3.6 $mg \cdot g^{-1}$ to 6.2 $mg \cdot g^{-1}$, while the potassium content remained at 5.29 $mg \cdot g^{-1}$ to 13.1 $mg \cdot g^{-1}$ under the high K treatment, indicating that the potassium content in the roots was relatively stable during the whole growth period. Under low K stress, the potassium content of the stem in the S4 period decreased more than that under HK; that in HY20 was 73.5–73.8% lower than that under HK, and NH18 was 73.7–73.9% lower than that under HK. The overall trend in the leaves was the same as that of stems, and the potassium content was most affected by low K stress in the S4 period. The decrease in the potassium content in the needles was smaller than that in leaves and stems during the whole growth period under low K stress. The potassium content in the pods decreased throughout the whole growth period. In the S2 stage, the potassium content of HY20 and NH18 under low K stress was 12.6–20.2% and 10.5–13.3% lower than that under HK, respectively, and there were significant differences among the HY20 treatments ($p < 0.05$). There was no significant difference between the treatments of S3 and S4.

3.7.2. Influence of Low K Stress on Sodium Content

The results of the two-year experiment showed that the Na^+ content in all plant organs increased with the growth period on the whole, rising slowly in the early stages and faster in the late stages (Figure 12). However, the overall Na^+ content in 2021 was higher than that in 2020. The content of Na^+ in the roots was significantly higher than that in the stems, leaves, pods, and fruit needles. The effect of low K stress on the Na^+ content in the roots was also the greatest, and the content of Na^+ in the roots increased significantly under low K stress. Compared with HK, the Na^+ content in the roots of HY20 in 2020 increased by 56.0%, 56.2%, 69.8%, and 56.5% in the S1, S2, S3, and S4 stages, respectively. In 2021, the content of Na^+ in HY20 roots increased by 32.5%, 37.8%, 34.9%, and 38.3%, respectively. In 2020, the content of Na^+ in NH18 roots increased by 68.7%, 105.1%, 99.8%, and 98.4%,

respectively. In 2021, the Na^+ content in NH18 roots increased by 37.3%, 39.6%, 39.0%, and 46.0%, respectively, with significant differences among treatments ($p < 0.05$). The K^+ content in the roots significantly decreased, while the Na^+ content significantly increased, indicating that the peanut plants actively absorbed more Na^+ to replace the K^+ function. The content of Na^+ in the stem under low K stress was slightly higher than that under high K, and the difference was significant ($p < 0.05$). There was no significant difference in the Na^+ content in the leaf, pod, or fruit needle among treatments ($p > 0.05$).

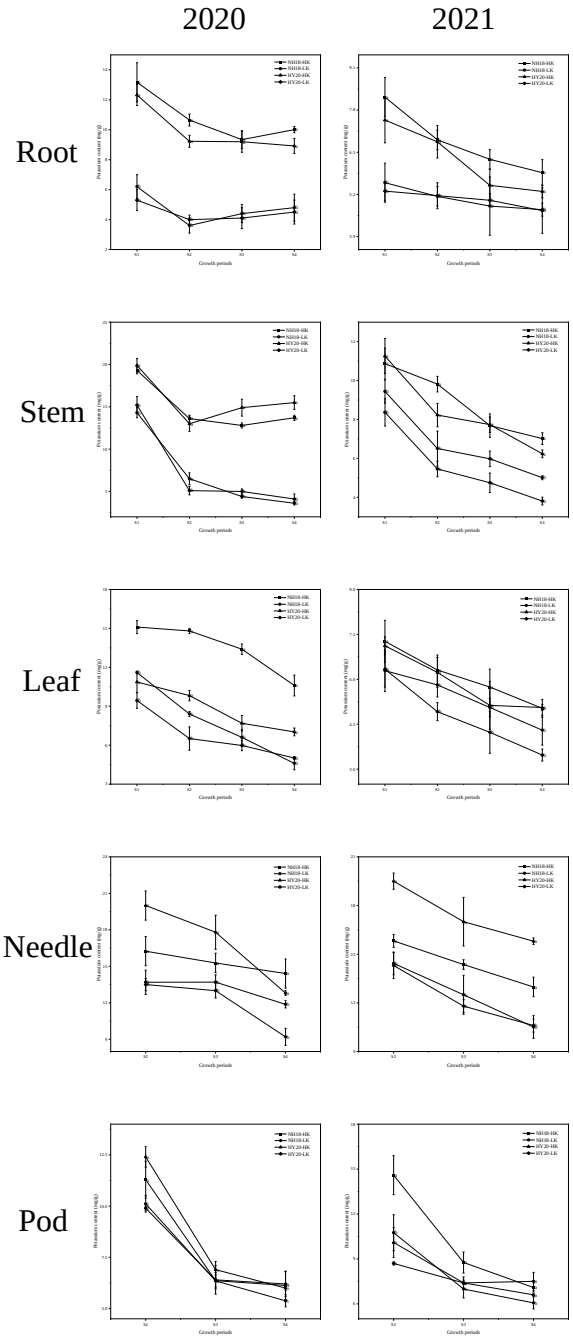


Figure 11. Changes in potassium (K) content in peanut organs under low K stress (mg/g). HK: high K treatment; LK: low K treatment. For the figure, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.8. Effects of Low K Stress on K/Na Ratio of Peanut Organs

The K/Na ratio of plants can directly reflect the relationship between potassium absorption and sodium in various organs. Based on the analysis of the two-year experimental data, the K/Na ratio of each organ of the plant showed a downward trend during the whole growth period under low K stress, and there were significant differences among all organs and treatments (Table S1). The potassium content in each organ of the plant in 2021 was lower than that in 2020, while the sodium content was higher than that in 2020, ultimately resulting in the K/Na ratio in each organ of the plant in 2021 being lower than that in 2020.

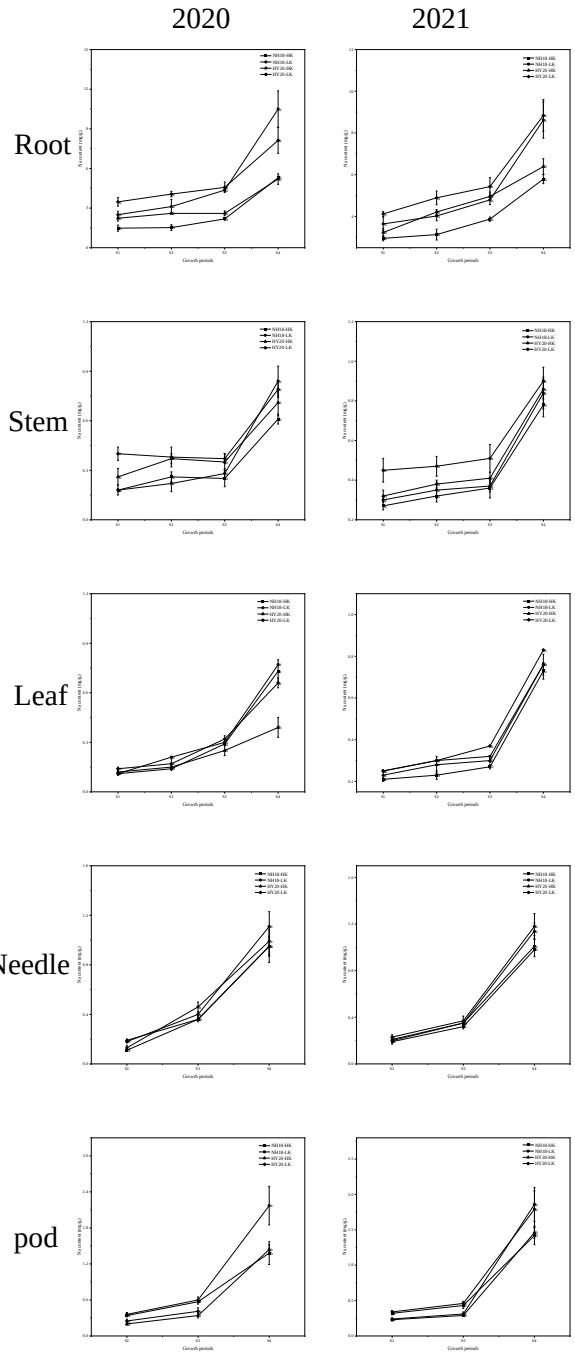


Figure 12. Changes in sodium (Na) content in peanut organs under low K stress (mg/g). HK: high K treatment; LK: low K treatment. For the figure, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

3.9. Effects of Low K Stress on Yield and Yield Components

The cultivar and treatment significantly affected ($p < 0.05$) the number of peanut pods per plant (Table 4). Only the cultivar × treatment had no significant effect on the number of full pods per plant ($p > 0.05$). The year × cultivar had no significant effect on the full pod weight ($p > 0.05$). The year, Cultivar, treatment, and cultivar × treatment significantly ($p < 0.05$) affected the peanut 100-pod weight and 100-kernel weight. The year, treatment, and year × treatment significantly ($p < 0.05$) affected the peanut yield. Low K stress significantly affected the yield traits of the peanuts. Low K stress reduced the pod number per peanut plant. Compared with the high K treatment, the number of pods in HY20 and NH18 decreased by 19.0% and 7.5%, respectively, in 2020, while NH18 showed no significant difference ($p > 0.05$). Compared with the high K treatment, HY20 and NH18 decreased by 23.6% and 20.6%, respectively, in 2021. All reached the significant difference level ($p < 0.05$). The number of full peanut pods under low K stress was also lower than that under high K stress. In 2021, the number of full pods in HY20 decreased by 25.5% compared with that under high K, and the numbers for HY20 in 2020 and 2021 both reached a significant level. The full pod mass was lower than that under the high K treatment, and there was a significant difference between the two experimental treatments compared with HK ($p < 0.05$). Compared with HK, the HY20 and NH18 treatments showed a significant difference in the 100-pod mass ($p < 0.05$), and the 100-seed mass also decreased compared with that under the high K treatment, with a significant difference between treatments ($p < 0.05$). In terms of yield, the yield per plant was reduced under low K stress, which was 19.2% and 22.9%, respectively, in 2020. In 2021, the decrease rates of the two varieties were 40.6% and 26.4%, respectively, reaching significant differences ($p < 0.05$). The yield results of the two years were consistent with the rule of yield components.

Table 4. Effects of low K stress on yield and yield-related traits.

Year	Cultivars	Treatments	Pods per Plant	Full Pods per Plant	Full Pod Weight (g)	100-Pod Weight (g)	100-Kernel Weight (g)	Yield (g per Plant)
2020	HY20	HK	30.67 ± 1.26 a	18.00 ± 0.90 a	21.45 ± 1.42 a	155.91 ± 7.62 a	63.63 ± 3.53 a	24.19 ± 0.85 a
		LK	24.83 ± 2.93 b	15.15 ± 0.69 b	16.51 ± 0.66 b	133.64 ± 3.37 b	52.06 ± 1.48 b	19.56 ± 0.86 b
	NH18	HK	22.33 ± 1.53 a	12.90 ± 0.52 a	19.68 ± 0.94 a	172.67 ± 5.51 a	70.29 ± 3.61 a	23.59 ± 1.50 a
		LK	20.67 ± 1.04 a	11.10 ± 1.13 a	15.45 ± 0.82 b	160.14 ± 5.29 b	63.24 ± 1.39 b	18.20 ± 1.51 b
2021	HY20	HK	31.55 ± 1.25 a	22.22 ± 1.31 a	37.24 ± 1.12 a	132.55 ± 4.44 a	72.73 ± 3.54 a	41.82 ± 2.12 a
		LK	24.11 ± 1.59 b	16.56 ± 1.49 b	21.47 ± 1.16 b	103.16 ± 6.18 b	60.07 ± 2.51 b	24.86 ± 1.04 b
	NH18	HK	27.44 ± 0.96 a	19.00 ± 1.25 a	30.03 ± 1.39 a	143.59 ± 5.28 a	77.60 ± 3.52 a	39.40 ± 2.55 a
		LK	21.78 ± 1.13 b	15.33 ± 1.55 b	23.08 ± 0.86 b	133.08 ± 6.33 b	72.46 ± 1.89 b	28.98 ± 1.12 b
Year			0.061	0.000	0.000	0.000	0.000	0.000
Cultivar			0.000	0.000	0.008	0.000	0.000	0.963
Treatment			0.000	0.000	0.000	0.000	0.000	0.000
Year × Cultivar			0.066	0.046	0.366	0.893	0.913	0.229
Year × Treatment			0.075	0.045	0.000	0.647	0.877	0.000
Cultivar × Treatment			0.081	0.179	0.003	0.031	0.034	0.125

HK: high K treatment; LK: low K treatment. For the table, a,b indicates a significant difference between different treatments for the same variety ($p < 0.05$).

4. Discussion

Low potassium stress can affect dry matter accumulation in plants. Tong [23] showed that K stress reduced the average and maximum dry matter accumulation rate of soybeans. The accumulation of dry matter after anthesis was reduced; the ratio of the root, leaf, and plant dry weights of K-sensitive varieties significantly decreased; there was obvious premature senescence of leaves and roots; and a premature loss of function resulted in a significant reduction in yield. This experiment shows that under low K stress, the dry weight of all organs except the fruit needles and the dry weight of pods decreased significantly at the mature stage, indicating that low K stress would eventually lead to a

reduction in the peanut yield. In the early stages of growth, the potassium content in each organ of the plant was relatively high, so the plant could maintain normal growth, while at the later stages, due to the continuous consumption of soil potassium, the peanut plants were gradually under the stress of low K, resulting in more and more significant differences between treatments.

A potassium deficiency not only affects the chloroplast structure and function and reduces photosynthetic pigment content, but it also affects the activities of key enzymes in electron transport and carbon assimilation, resulting in decreased photosynthetic capacity and the inhibition of plant growth and development [24].

The results of this study show that low K stress has different effects on the physiological and biochemical indexes of peanut plants, such as photosynthesis, fluorescence, protective enzyme activities, and osmotic regulatory substances. Chlorophyll fluorescence parameters (PSII) can reflect the absorption, transformation, transfer, and distribution of light energy in plants. When stress occurs, the reaction center will cause different degrees of damage, inhibiting photosynthetic electron transport and photosynthesis. The Fv/Fm, ΦPSII, ETR, and qP decreased and the NPQ increased significantly under potassium deficiency stress [25]. In this study, the Fv/Fm and qP of peanut leaves significantly decreased and the NPQ significantly increased under low K stress, indicating that the opening degree of the PSII reaction center decreased, resulting in the photoinhibition of the plants. The increase in NPQ indicates that the photoinhibition of PSII was weakened by the increasing heat dissipation in leaves under stress. The decrease in Fv/Fm and qP in the leaves of NH18 under low K stress was higher than that of HY20, indicating that the photosynthetic apparatus of low-K-tolerant varieties suffers less photodamage under low K stress.

Photosynthesis is the basis of crop yield formation, and the organic matter that forms yield is directly or indirectly derived from photosynthate [26]. Chlorophyll is an indispensable component of photosynthesis in plants and plays an important role in the absorption, transmission, and transformation of light energy. Low K stress leads to a decrease in photosynthesis, which affects the transport and distribution of photosynthates. When calcium signal transduction was inhibited under low potassium stress, it was difficult to synthesize chlorophyll in tobacco leaves, thus affecting plant photosynthesis [27]. In this study, low K stress reduced the leaf chlorophyll content, but had little effect on the carotenoid content. A comprehensive analysis of two years of experimental data revealed that the NH18 chlorophyll content decreased more significantly. Chloroplasts are one of the main producers of reactive oxygen species. Under low K stress, oxidation occurs in chloroplasts and leads to chlorophyll degradation. In addition, Wang [28] suggested that the lack of chlorophyll content may be an adaptive mechanism of plants, which can reduce the excessive reduction in photosynthetic electron transport, thus reducing ROS production.

Decreased photosynthesis leads to the excessive reduction in the photosynthetic electron transport chain, which enhances ROS production and may cause oxidative damage to biological macromolecules such as lipids, proteins, and nucleic acids (Kanazawa [29]). Miao [30] showed that the MDA content and the SOD, POD, and CAT activities of soybean seedlings increased significantly under potassium deficiency conditions. The results of this study show that under the condition of low K stress, the activities of the SOD and POD and the MDA content of the two varieties increased, and the increase for HY20 was greater than that for NH18. These results indicate that low K stress causes membrane lipid peroxidation in peanut leaves to a certain extent, and at the same time, the enhancement of antioxidant enzyme activity improves the ROS scavenging ability, maintains the balance between ROS production and scavenging, and protects peanut plants from further damage. Soluble proteins are important osmotic regulatory substances and nutrients. Their increase and accumulation can improve the water retention capacity of cells, and they play a protective role in the life substances of cells and biofilms. In this study, the soluble protein content of NH18 and HY20 was significantly increased under low K stress, and the increase in HY20 was significantly higher than that in NH18. The comprehensive results showed that HY20 and osmoregulatory substances were affected more than NH18 under low K stress.

In addition to photosynthetic pigments and gas exchange parameters, PSII may be the target of deleterious stress effects. The results of this study show that the maximum fluorescence (Fm), variable fluorescence (Fv), and maximum photochemical efficiency (Fv/Fm) of NH18 and HY20 leaves were significantly decreased by low K stress, while the basal fluorescence (F0) was significantly increased. In addition, the decrease in the fluorescence parameters of the low-K-tolerant cultivar NH18 was lower than that of the low-K-intolerant cultivar HY20, indicating that the photosynthetic reaction centers of the tolerant cultivar were less damaged under low K stress.

Under the condition of potassium deficiency, the plant potassium content will decrease [31–33]. In this study, low K stress led to a downward trend in the potassium content in plant organs throughout the growth period, the potassium content in the leaves and roots decreased significantly, and the decrease in the stem, fruit needle, and pod was lower than that in the leaves and roots. After Wakeel [34] replaced K with Na, sugar beet plants showed the same growth trend, and this did not affect the yield and quality of the sugar beets. Liu [35] showed that sodium supplementation could improve the potassium utilization efficiency and biomass of rice under low K stress. In this study, the sodium content in roots was significantly higher than that in the stems, leaves, pods, and fruit needles, and the sodium content in the roots increased significantly under low K stress. A comprehensive analysis of the two years of data showed that the increase in the sodium content in the roots of HY20 was higher than that of NH18. Benito [36] suggested that sodium and potassium are structurally and chemically very similar elements, which explains their interchangeability in certain physiological processes. The content of K^+ in the roots decreased significantly, while the content of Na^+ increased significantly, indicating that the peanut plants actively absorbed more Na^+ to replace K^+.

There are significant differences in the tolerance to low K stress among different crops and different varieties of the same crop [37]. The growth of low-K-tolerant varieties is less affected by low K stress than that of sensitive varieties, and the decline in biomass and other traits is smaller. The experimental study showed that the decrease in the dry matter accumulation of the low-K-tolerant variety NH18 was lower than that of the low-K-intolerant variety HY20.

Yield can reflect the adaptability of crops in an adverse environment, and the higher the yield, the better the adaptability or resistance. Yan [38] found that the potassium content in the soil directly affected soybean yields, and soybeans treated without a potassium application had a lower pod number per plant, lower grain number, and lower 100-grain weight than soybeans treated with a potassium application. Zhong [39] showed that the yield of grafted watermelons was reduced by low K stress, and also showed that the weight of a single fruit was reduced. The results show that the pod number per plant, full fruit number, kernel weight, and yield of HY20 and NH18 under low K stress were significantly lower than those under high K stress, and the decrease in HY20 was greater than that in NH18, indicating that the yield and yield components of NH18 under low K stress were less affected by low K stress.

5. Conclusions

Low K stress caused a certain degree of damage to the photosynthetic apparatus of peanut leaves, and HY20 was more significantly affected. The stress affected the normal process of photosynthesis and eventually led to a reduction in biomass. Hypokalemia stress can aggravate the degree of membrane lipid peroxidation, accelerate aging, and increase the activity of protective enzymes and the osmoregulation effect of soluble proteins. The overall increase in HY20 was higher than that in NH18, which improves the resistance of peanut plants to hypokalemia stress. Low K stress significantly reduced the potassium content in all organs except the pods, and significantly affected the yield traits of peanuts. Yield components, such as the fruit number per plant and the fruit weight per hundred, significantly decreased, and finally resulted in a significant decrease in yield. Moreover, the yield of NH18 under low K stress was less effected than that of HY20. It can be seen that

low K stress seriously affected the growth and development of peanut plants. By studying the growth and development law, nutrient utilization law, and photosynthetic fluorescence characteristics of peanuts under low K stress, this study revealed the physiological and biochemical response mechanisms of peanut plants to low K stress, and provided a theoretical basis for peanut production and the cultivation of low-K-tolerant varieties.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agronomy13010185/s1, Table S1: Effects of low K stress on K/Na ratio in peanut organs.

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References

1. Deng, T.-H. Analysis of World oil supply and demand and trade pattern. *China Oils Fats* **2015**, *40*, 1–6.
2. Expert Committee of Market Early Warning of Ministry of Agriculture. Analysis of Supply and demand Situation of Agricultural Products in China in August. *Agric. Prod. Mark. Wkly.* **2018**, *32*, 46–53.
3. Wan, S.-B. Peanut Cultivation in China. *M. Shanghai Shanghai Sci. Technol. Press* **2003**, 610–611.
4. Liao, B.-S. Current situation and potential analysis of peanut production development. *Chin. J. Oil Crop.* **2020**, *42*, 161–166.
5. Ren, J.-Y.; Wang, J.; Ai, X.; Zhao, S.-L.; Li, R.-Y.; Jiang, C.-J.; Zhao, X.-H.; Yin, D.-M.; Yu, H.-Q. Physiological response to drought resistance of peanut seedlings under drought stress. *Chin. J. Oil Crop.* **2022**, *44*, 138–146.
6. Xu, H.-H.; Hou, G.-Y.; Li, Y.; Xiao, H.; Sun, D.; Wang, F.; Li, H. Research progress of plant potassium channel AKT1. *Biotechnology* **2018**, *28*, 1–5, 7–10.
7. Xie, J.C.; Zhou, J.-M. Progress in research on soil potassium and application of potash fertilizer in China. *Soils.* **1999**, *03*, 244–254.
8. Yang, L.-Q.; Liu, J.; Li, W.; Dai, L. Research advances in potassium lon channel AKT1 in plant. *Biotechnol. Bull.* **2019**, *35*, 94–100.
9. Huang, W.-G.; Jiang, W.-D.; Yao, Y.-B.; Song, X.; Liu, Y.; Chen, S.; Zhao, D.; Wu, G.; Yuan, H.; Ren, S.; et al. Transcriptional profiling of Flax in Response to Low Potassium Stress. *Acta Agron. Sin.* **2021**, *47*, 1070–1081.
10. Chakraborty, K.; Bhaduri, D.; Meena, H.N.; Kalariya, K. External potassium (K(+)) application improves salinity tolerance by promoting Na(+)-exclusion, K(+)-accumulation and osmotic adjustment in contrasting peanut cultivars. *Plant Physiol. Biochem.* **2016**, *103*, 143–153. [CrossRef]
11. Romheld, V.; Kirkby, E.A. Research on potassium in agriculture: Needs and prospects. *Water Air Soil Pollut.* **2010**, *335*, 155–180. [CrossRef]
12. Jiang, G.-B.; Chen, S. Effects of potassium, calcium and magnesium on crop senescence. *Sci. Agric. Sin.* **2005**, *12*, 47–48.
13. Mengel, K.; Kirkby, E.A.; Kosegarten, H.; Appel, T. Principles of Plant Nutrition. *M. Springer Neth.* **2001**, 504.
14. Jadav, J.K.; Umrania, V.V.; Rathod, K.J.; Sodha, K.H.; Gondaliya, R.P.; Anuj, S.A.; Golakiya, B.A. Effects of induced potassium deficiency in groundnut and its estimation by flame photometry. *AkiNik Publ.* **2017**, *5*, 1757–1763.
15. Xu, D.-Q. Some problems in the analysis of stomatal limitation of photosynthesis. *Plant Physiol. Commun.* **1997**, *4*, 241–244.
16. Berghuijs, H.N.; Yin, X.; Ho, Q.T.; Retta, M.A.; Verboven, P.; Nicolaï, B.M.; Struik, P.C. Localization of (photo)respiration and CO_2 re-assimilation in tomato leaves investigated with a reaction-diffusion model. *PLoS One* **2017**, *12*, 26. [CrossRef]
17. Zhao, D.; Oosterhuis, D.M.; Bednarz, C.W. Influence of Potassium Deficiency on Photosynthesis, Chlorophyll Content, and Chloroplast Ultrastructure of Cotton Plants. *Photosynthetica* **2001**, *39*, 103–109. [CrossRef]
18. Naeem, M.; Waseem, M.; Zhu, Z.; Zhang, L. Downregulation of SlGRAS15 manipulates plant architecture in tomato (Solanum lycopersicum). *Dev. Genes Evol.* **2020**, *230*, 1–12. [CrossRef]

19. Naeem, M.; Muqarab, R.; Waseem, M. The Solanum melongena COP1 delays fruit ripening and influences ethylene signaling in tomato. *J. Plant Physiol.* **2019**, *240*, 152997. [CrossRef]
20. Yan, L.; Riaz, M.; Wu, X.-W.; Wang, Y.-H.; Du, C.-Q.; Jiang, C.-C. Interaction of boron and aluminum on the physiological characteristics of rape (Brassica napus L.) seedlings. *Acta Physiol. Plantarum.* **2018**, *4*, 33. [CrossRef]
21. Wu, J.-Y.; Yu, C.-Y.; Huang, L.-L.; Gan, Y.-B. A rice transcription factor, OsMADS57, positively regulateshigh salinity tolerance in transgenic Arabidopsis thaliana and Oryza sativa plants. *Physiol. Plantarum.* **2021**, *173*, 1120–1135. [CrossRef]
22. Wang, D.; Pang, Y.-X.; Wang, W.-Q.; Wan, C.-Y.; Hou, J.-L.; Yu, F.-L.; Wang, Q.-L.; Liu, F.-B.; Zhang, X.-D. Effect of molybdenum on secondary metabolic process of glycyrrhizic acid in Glycyrrhiza uralensis Fisch. *Biochem. Syst. Ecol.* **2013**, *50*, 93–100. [CrossRef]
23. Tong, X.-N.; Tong, X.-D.; Li, X.-T.; Wang, X.-G.; Wang, N. Effects of low potassium stress on dry matter accumulation, transfer and distribution of soybean cultivars with different tolerance. *Jiangsu Agric. Sci.* **2017**, *45*, 56–59.
24. Hu, W.; Jiang, N.; Yang, J.-S.; Meng, Y.; Wang, Y.; Chen, B.; Zhao, W.; Oosterhuis, D.M.; Zhou, Z. Potassium(K) supply affects K accumulation and photosynthetic physiology in two cotton (*Gossypium hirsutum* L.) cultivars with different K sensitivities. *Field Crop. Res.* **2016**, *196*, 51–63. [CrossRef]
25. Lu, Z.-F.; Ren, T.; Lu, J.-W.; Li, X.-K.; Cong, R.-H.; Pan, Y.-H.; Li, K.-X. Main factors and mechanism leading to the decrease of photosynthetic efficiency of oilseed rape exposure to potassium deficiency. *J. Plant Nutr. Fertil.* **2016**, *22*, 122–131.
26. Xu, D. Photosynthetic rate, photosynthetic efficiency and crop yield. *Chin. J. Biol.* **1999**, *8*, 11–13.
27. Dai, X.-Y.; Xu, G.-Q.; Shi, Q.-H.; Wang, Y.-F.; Chen, P.-Y.; Zhang, T.-J.; Liu, C.; Zhang, X.-Q.; Fu, Y.-P. Effects of calcium signal inhibitors on photosynthetic characteristics and potassium uptake of tobacco seedlings under low potassium stress. *Plant Nutr. Fertil. J.* **2022**, *28*, 138–149.
28. Wang, K.-Y.; Kellomaki, S.; Zha, T. Modifications in photosynthetic pigments and chlorophyll fluorescence in 20-year-old pine trees after a four-year exposure to carbon dioxide and temperature elevation. *Photosynthetica* **2003**, *41*, 167–175. [CrossRef]
29. Kanazawa, S.; Sano, S.; Koshiba, T.; Ushimaru, T. Changes in antioxidative enzymes in cucumber cotyledons during natural senescence: Comparison with those during dark-induced senescence. *Physiol. Plant.* **2000**, *109*, 211–216. [CrossRef]
30. Miao, B.-H.; Han, X.-G.; Zhang, W.-H. The Ameliorative Effect of Silicon on soybean seedlings grown in potassium deficient Medium. *Ann. Bot.* **2010**, *105*, 967–970. [CrossRef]
31. Zheng, C.; Li, Q.-W.; Huang, Z.-R.; Ao, J.-H. Study on the difference of potassium uptake in Sugarcane varieties. *Acta Thermol. Sin.* **2011**, *32*, 2221–2225.
32. Zeng, Q.-Y.; Wu, J.-Y.; Feng, X.-M.; Zhang, N.-N.; Wu, Z.-L.; Qi, Y.-W. Differences in response of sugarcane sister lines to low potassium stress. *Chin. J. Trop. Crop.* **2021**, *42*, 739–746.
33. Liu, X.-W.; Song, Y.-L.; Li, S.-S.; Zhang, S.-H.; Yang, X.-J.; Wang, D.-W.; Zhao, Y. Effects of low potassium stress on plant element accumulation and biological traits of winter wheat. *J. Agric. Univ. Hebei* **2019**, *42*, 14–21.
34. Wakeel, A.; Steffens, D.; Schubert, D. Potassium substitution by sodium in sugar beet (*Beta vulgaris*) nutrition on K-fixing soils. *J. Plant Nutr. Soil Sci.* **2010**, *173*, 127–134. [CrossRef]
35. Liu, G.-D.; Liu, G.-y. Partial substitution of Ca and Na on K in rice genotypes. *Acta Agron. Sin.* **1996**, *3*, 313–319.
36. Benito, B.; Haro, R.; Amtmann, A.; Cuin, T.A.; Dreyer, I. The twins K^+ and Na^+ in plants. *J. Plant Physiol.* **2014**, *171*, 723–731. [CrossRef] [PubMed]
37. Xu, Y.; Yuan, Q.; Hu, H.-r.; Chen, Z.-y.; Long, Y.-h.; Du, G.-h.; Liu, F.-h. Study on tolerance difference of different hemp cultivars under low potassium stress. *Chin. Hemp Ind. Sci.* **2016**, *38*, 156–161. [CrossRef]
38. Yan, C.; Han, X.; Wang, S.; Wang, S.; Li, H.; Wang, F. Effects of potassium on dry matter accumulation, yield and quality of Soybean. *Soybean Sci.* **2008**, *01*, 113–117.
39. Zhong, Y.; Chen, C.; Nawaz, M.A.; Jiao, Y.; Zheng, Z.; Shi, X.; Xie, W.; Yu, Y.; Guo, J.; Zhu, S.; et al. Using rootstock to increase watermelon fruit yield and quality at low-K supply: A comprehensive analysis from agronomic, physiological and transcriptional perspective. *Sci. Hortic.* **2018**, *241*, 144–151. [CrossRef]

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