

Organic Acids Exuded From Roots Increase the Available Potassium Content in the Rhizosphere Soil: A Rhizobag Experiment in *Nicotiana tabacum*

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Abstract. Organic acid secretion from higher plant roots into the rhizosphere soil plays an important role in nutrient acquisition and metal detoxification; however, their precise functions and the related mechanisms in abiotic stress tolerance remain poorly understood. Tobacco is an important crop plant, so thoroughly elucidating these factors in tobacco is of high priority. In the present study, the activation effect on soil potassium (K), contents of exuded organic acids, and physiological changes in the roots of various tobacco varieties under both normal K supply and K-deficiency stress were investigated. Our results showed that one high-K variety (ND202) exhibited a significantly higher total content of organic acids in the root exudates and the highest available K content in the rhizosphere soil, compared with two common ones (K326 and NC89). Moreover, the high-K tobacco variety was less affected in terms of root vigor under K-deficiency stress, and displayed greater increases in the activities of the stress-resistant enzymes consisting of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT). Taken together, these results provide evidence that tobacco roots exude large amounts of organic acids to increase the available K content in the rhizosphere soil and improve the utilization rate of soil K.

Potassium (K) is one of the major elements absorbed by plants and plays a critical role in plant growth, development, and physiological metabolism. Tobacco is known to be a K-favoring crop. Potassium is not only a crucial nutrient for tobacco, it also improves the flammability of tobacco leaves and so decreases the amount of tar produced during burning (Guo et al., 2002; Luo et al., 2000). Using larger amounts of K fertilizers and promoting the availability of K can increase K content in tobacco leaves (Wang et al., 2014); however, in addition to increasing costs, the extensive use of fertilizers can destroy soil structures, decrease the amount

of organic matter in the soil, and aggravate environmental pollution (Furoc-Paelmo et al., 2012). Therefore, an alternative to chemical K fertilizer is necessary for the sustainable development of agriculture.

One possible alternative could be to fully exploit the reservoir of K in the soil. Soil has rich reserves of K, among which only 1% to 2% can be directly absorbed by plants (Zhang et al., 2014); however, the acidification and dissolution of soil K are prevented in calcareous soil due to the high pH and calcium content (Yang and Peng, 2006). It may be more economically viable to transform the fixed slow-release K into readily available K that can be absorbed by plants. It is hypothesized that malate release results in the building up of malate levels in the rhizosphere soil, where it increases the available K content (Shi et al., 2011). Cluster roots are characterized to release organic acid anions at a high level, and citrate is demonstrated to be the predominant acid released by cluster roots of tobacco under a K-deficient condition (Wu et al., 2013). Collectively, tobacco

roots will exude greater amounts of substances and thereby increase the available K content in the rhizosphere soil, which is a response of tobacco plants to improve their absorption and utilization of soil K.

Recent studies on root exudates have mainly focused on species such as rice (Hao et al., 2010), maize (Ling et al., 2011), watermelon (Wu et al., 2008), and cucumber (Chen et al., 2011; Zhang et al., 2013). The previously identified components of root exudates include sugars, enzymes, amino acids, organic acids, phenolic acids, sterols, nucleotides, flavonoids, growth factors, and other substances (Sison et al., 2010). The root exudates have a significant influence on soil properties, the microbial community, and soil functions (Haichar et al., 2014). The exudation of organic acids, such as oxalate, citrate, malate, oxalate, succinate, and fumarate, by plant roots constitutes a response mechanism under different stress situations, which may be caused mainly by a nutritional deficiency (Carvalhais et al., 2011; Hoffland et al., 2006; Lipton et al., 1987; Mohan et al., 2015), the presence of a toxic element, or a lack of nutrition (Ae et al., 1990; Chiang et al., 2006; Gandner et al., 1983; Hoffland et al., 1989; Zeng et al., 2008).

The dissociation of mineral K from soil by organic acids is mainly achieved by organic complexes consisting of organic ligands that are capable of chelation of metal ions, which can accelerate the decomposition of minerals. The role of protons from organic acids lies in the dissolution of insoluble minerals and lattice substitution for K. Different types of organic acids exhibit varying capacities to decompose and release K from soil minerals (Cui et al., 2002; Melo et al., 2005). Research on the activation of mineral elements by tobacco root exudates has primarily focused on the effect of small molecule organic acids on K conversion in various types of soil and K-rich minerals (Cong et al., 2009; Jiang et al., 2012; Zörb et al., 2014). Tobacco plants grown under normal conditions are capable of activating soil phosphorus (P) and K minerals, showing minor differences among various varieties. Under P and K stress, tobacco root exudates show an improved capacity to activate soil minerals, and the differences among various varieties are increased. Moreover, there are differences among tobacco root exudates regarding nutrient use efficiency in the rhizosphere soil (Zhou et al., 2005). Research on tobacco root exudates has generally focused on their effects on tobacco seed germination, plant growth, and enzyme activities (Yu et al., 2014); however, little information is available on the types and contents of tobacco root exudates.

In the present study, we have separated the functional groups of organic acids into hydrogen ions and organic ligands to examine the chemical mechanism of soil K activation by major organic acids in root exudates. In addition, the types and total contents of organic acids in tobacco root exudates were determined, and the capacity

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of the root exudates to activate slowly available K in rhizosphere soil was compared among various varieties of tobacco. Furthermore, physiological changes in the roots were analyzed to identify the cause of the differences in the utilization rates of soil K among various tobacco varieties. This study will facilitate us to deeply understand the functions of organic acids in root exudates in the process of activating and using soil K, and further explain the differences among various varieties, so as to provide theoretical basis for K nutrition and metabolism in plants, and breeding of high-K varieties.

Materials and Methods

Experimental design. Field trials were carried out in 2016 and 2017 at the scientific and educational park of Henan Agricultural University, respectively. The park is located in Zhengzhou in Henan Province, China, which is situated in the southern part of the North China Plain. The region exhibits a continental monsoon climate, within the North Temperate Zone. The average annual temperature is 14.2 °C, the average annual rainfall is 640.9 mm, and the ≥ 0 °C average annual cumulative temperature is 5178.8 °C. The clay soil in the experimental field contained (0–20 cm depth) 9.96 g·kg⁻¹ organic matter, 0.95 g·kg⁻¹ total nitrogen, 34.12 mg·kg⁻¹ available phosphorus, 79.91 mg·kg⁻¹ available K, and 73.54 mg·kg⁻¹ available nitrogen.

The tobacco (*Nicotiana tabacum* L.) variety ND202 was used in this study. ND202 is a variety with high-K content more than 2.5% in leaves, which was bred by the College of Tobacco Science of Henan Agricultural University. Two common ones, including NC89 and K326, which are the main tobacco varieties with K content of $\approx 1.5\%$ in northern China, were also chosen in our experiment. Two treatments were set according to the rate of K application: K₁ (normal K supply) – N 0.13 g·kg⁻¹, P₂O₅ 0.13 g·kg⁻¹, and K₂O 0.39 g·kg⁻¹; and K₂ (K-deficiency stress) – N 0.13 g·kg⁻¹, P₂O₅ 0.13 g·kg⁻¹, and K₂O 0 g·kg⁻¹. Tobacco seedlings showing uniform growth (six to seven true leaves) were transplanted to plastic pots containing 10 kg of soil. Fertilization was performed three times, at transplantation, and 1 and 2 weeks after transplantation, at a dose N:P₂O₅:K₂O ratio of 2:1:1. Other practices conformed to standard tobacco field management specification. The plants were cultivated using the rhizobag method. The rhizobags consisted of 300-mesh nylon screen and were 15 cm long, 15 cm wide, and 20 cm high. Each bag was filled with 500 g of soil. The experiment adopted a randomized block design with a total of six treatment combinations and 50 pots per

treatment. After 30 d of incubation, tobacco roots of three varieties with good growth consistency were collected entirely under two K application treatments, which were used for the determination of root vigor and stress-resistant enzyme activities. Measurements were replicated six times with three plants per treatment. The soil inside of rhizobags was removed from the nylon screen, dried in the air, and then used for K analysis and root exudate collection.

The reagents (analytical grade) used in the experiment to study the activation of organic acids on soil available K included oxalic acid (OA), citric acid (CA), sodium oxalate (OA-Na), sodium citrate (CA-Na), and hydrochloric acid (HCl). The chemical properties of OA and CA are shown in Table 1. Three types of treatments were designed in this work: 1) acidification, with HCl; 2) complex formation, with OA-Na and CA-Na; and 3) acidification + complex formation, with OA and CA. The deionized water was used as control (CK). The concentration of each substance was set a 0.25 mol·L⁻¹. The experiment included six treatments, with three replications in each treatment. The pH value of each reagent solution is provided in Table 2. Soil from the experimental field was ground and passed through a 20-mesh screen. The soil was autoclaved three times through intermittent steaming at 120 °C and then dried at a low temperature to dryness. Soil samples (50 g) in conical flasks were weighed, followed by the addition of four types of solution until the soil water content reached 45%. The soil samples and reagents were autoclaved to eliminate microbial interference, and chloroform was added to inhibit microbial activity. The flasks were placed in a thermostat incubator at 26 °C, and the soil moisture content was kept constant. Soil available K was determined at 1, 3, 7, 18, and 25 d of incubation.

Collection of root exudates. The roots of three tobacco varieties were washed to remove the rhizosphere soil at 30 d of incubation. The plants were incubated in 500 mL deionized water, and the water was changed and collected every 24 h for 3 consecutive days. The collected root exudates were loaded onto an XAD-4 resin column and eluted three times with 300 mL of methanol. The purified samples were concentrated to dryness using a rotary evaporator at 40 °C and then adjusted to a constant volume of 20 mL with ethanol. The root exudates were stored at 4 °C for further use.

Determination of organic acids exuded by the roots. The total content of organic acids was determined through improved spectrophotometry based on the principle that the

carboxyl group reacts with the hydroxylamine group to form hydroxamic acid in the DCC system, which further develops a color on reaction with ferric ions under acidic conditions (He et al., 2011). Generation of a standard curve for organic acids: Acetic acid standard solutions with different concentrations were formulated (1×10^{-3} , 2×10^{-3} , 3×10^{-3} , 4×10^{-3} , and 5×10^{-3} mol·L⁻¹). One milliliter of the acetic acid standard solutions (using 1 mL of distilled water as a control) was added to test tubes, followed by the addition of 1 mL of a 0.08 mol·L⁻¹ hydroxylamine hydrochloride solution and 1 mL of a 0.4 mol·L⁻¹ DCC ethanol solution. The mixture was completely mixed by shaking and then heated in a 50 °C water bath for 30 min. Finally, 1 mL of a 0.7 mol·L⁻¹ FeCl₃ solution was added, and the absorbance of the reaction solution at 520 nm was measured after complete reaction. The equation for calculating the standard curve was as follows: $Y = 101.3X - 0.0157$ (correlation coefficient = 0.9996). A 2-mL aliquot of the root exudates stored at 4 °C was then added to the test tubes, and the absorbance of organic acids in the root exudates (Y₁) was measured following the same procedure. Root exudation of organic acids (g·L⁻¹) = $(Y_1 + 0.0157) \times 60 \times 0.02 / (101.3 \times 1)$.

Measurement of soil potassium content. Five grams of air-dried rhizosphere soil was passed through a 1-mm sieve. The sieved soil was added to a 100-mL flask or a large test tube, followed by the addition of 50 mL of a 1 g·mol⁻¹ NH₄OAc solution. The flask or test tube was then sealed with a rubber plug and oscillated for 30 min, after which the solution was filtered through dry, ordinary qualitative filter paper. Soil available K and slowly available K contents were determined via flame photometry (Williams and Twine, 1960).

Assay of reducing capacity and stress-resistant enzyme activities in the roots. After 30 d of incubation, the roots of various tobacco varieties were washed to remove the rhizosphere soil and then used to measure the reducing capacity and stress-resistant enzyme activities of the root system (Cui et al., 2015). The reducing capacity of the roots was analyzed using the triphenyl tetrazolium chloride method (Ryssov-Nielson, 1975). Superoxide dismutase (SOD) activity was measured via the nitro blue tetrazolium method. Peroxidase (POD) activity was measured with the guaiacol method. Catalase (CAT) activity was measured via ultraviolet absorption (Garcia-Limones et al., 2002).

Statistical analysis. For each measurement, the means from six replicates were calculated and the variance analysis was statistically analyzed using one-way analysis

Table 1. Chemical properties of the organic acids used in the experiment.

Organic acid	Structural formula	Group form	Acid dissociation constant			Stability coefficient of Al ion complex formation
			pK ₁	pK ₂	pK ₃	
Oxalic acid	HOOC-COOH	H ₂ L	1.23	4.19	—	6.16
Citric acid	HOOCCH ₂ C(OH)(COOH)CH ₂ COOH	H ₃ L	3.14	4.77	6.39	7.98

of variance with SPSS 17.0 (SPSS Inc., Chicago, IL); moreover, the differences in the means between different treatments were separated by the least significance difference test at the 0.05 *P* level.

Results

Activation of organic acids on soil available K content. The soil activation capacity varies with different types of organic acids in root exudates, and for the same type of organic acids, its activation capacity changes with the treatment time. In addition, the activation capacity of organic acids on soil K includes two aspects: acidification and complex formation. When an organic acid solution is added into soil, both reactions simultaneously exert an activation effect on soil K.

The experimental results (Table 3) show that the coexistence acidification and complex formation significantly increased the soil available K content, and this effect was greater than that of individual acidification or complex formation. In the initial stage of the experiment, the effect on soil available K depended on the soil pH, regardless of whether an organic acid, inorganic acid, or organic acid salt solution was used. Due to its strong alkalinity of the CA-Na solution, the soil available K content was even lower in this treatment compared with CK at the beginning of the reaction. With an increasing

time of incubation, the soil available K content remained higher in all of the experimental treatments compared with CK. Complex formation did not produce a significant difference from CK in the middle-late stage. The activation effect on soil K was in the following order throughout the incubation period: acidification + complex formation > acidification > complex formation ≈ CK.

As shown in Table 3, the soil treatments involving HCl, OA-Na, and CA-Na all increased the soil available K content to some extent, regardless of acidification with hydrogen ions or complex formation with organic ligands. Compared with the original value, the HCl treatment produced an average increase of 24.85%, whereas the OA-Na and CA-Na treatments resulted in 18.65% and 12.8% increases, respectively. The releasing effect of acidification with HCl was greater than that of complex formation with OA-Na or CA-Na for soil K.

Compared with the HCl treatment, the OA and CA treatments increased the soil available K content by 41.0% and 17.6% at 3 d of incubation, and by 43.8% and 11.3% at 25 d of incubation, respectively. The differences between the OA or CA treatments and the HCl treatment were highly significant during the experimental period, indicating that acidification and complex formation acted synergistically to increase the soil available K content. When solutions of the same concentration were used, OA had higher acidity but decreased organic ligand levels and a lower complex formation capacity than CA. Therefore, the activation effect of OA was significantly higher than that of CA on soil K. Soil activation by organic acids was likely dependent on the acidity of the soil solution.

Organic acid contents in root exudates and their activation on soil K among various tobacco varieties. Table 4 shows that K contents were at similar levels in the rhizosphere soil of the three varieties of tobacco,

but the content of available K that could be absorbed and used by plants shows significant differences under different treatment conditions. The contents of both slowly available K and available K were substantially higher under normal K application compared with those measured under K-deficiency stress. Under K-deficiency stress, the K content in the rhizosphere soil was highest for ND202, whereas the values were much lower for NC89 and K326. This result indicated that ND202 could maintain a relatively high absorbable and available K content in the rhizosphere soil and, thus, ensured the absorption and utilization of K during normal growth of the plants.

Figure 1 shows that under K-deficiency stress, the total content of organic acids in the root exudates remained higher than under normal K treatment for all three tobacco varieties. In both the K₁ and K₂ treatments, ND202 exhibited a higher total content of organic acids in the root exudates compared with NC89 and K326, and these differences were significant. This result indicated that ND202 could exude more organic acids than NC89 and K326 through roots. This is an important reason why the root exudates of ND202 showed a higher capacity to activate soil K and resulted in a higher available K content in the rhizosphere soil.

Comparison of root vigor among various tobacco varieties. Root vigor is an important indicator reflecting the nutrient absorption, transformation, and translocation capacities of roots (Feldman, 1984). The level of root vigor directly affects the absorption of water and nutrients, thereby influencing the assimilation, conversion, or synthesis of material. Tobacco subjected to organic acid treatment shows a significantly greater root volume, dry weight, and activity than when organic acid treatment is not performed. This finding suggests that organic acids can markedly increase the growth of the tobacco root system and thereby contribute to the root absorption of nutrients (Qian et al., 1998).

In Table 5, NC89 and K326 exhibited lower root vigor than ND202 under both the K₁ and K₂ treatments. Meanwhile, NC89 and K326 displayed greater reductions in root vigor compared with ND202 that were not subjected to K application. This result showed that ND202 was less affected than NC89 and K326 by K-deficiency stress in terms of root vigor.

Comparison of antioxidant enzyme activity in the roots among various tobacco varieties. K-deficiency stress can result in reactive oxygen species (ROS) generation. To avoid or mitigate the damage caused by ROS, plants have developed various defense mechanisms, such as antioxidant enzymes, which are essential for maintaining the normal physiological and biochemical functions of plant cells under adverse stress (Liu et al., 2018; Qu et al., 2012). SOD reflects the ability of plants to eliminate ROS and resist the adverse situation. As one of the enzymes in the enzymatic defense system that protects against membrane lipid peroxidation, POD

Table 2. pH value of each reagent at 25 °C.

Reagent	pH
OA	1.03
CA	1.79
OA-Na	8.21
CA-Na	8.55
HCl	0.69
CK	7.12

CA = citric acid; CA-Na = sodium citrate; CK = control; HCl = hydrochloric acid; OA = oxalic acid; OA-Na = sodium oxalate.

Table 3. Soil available potassium content under different organic acid treatments (mg·kg⁻¹).

Treatment	Incubation time				
	1 d	3 d	7 d	18 d	25 d
OA	123.43 a	134.77 a	141.46 a	146.22 a	157.65 a
CA	97.21 b	115.40 b	114.24 b	120.56 b	122.03 b
OA-Na	90.68 c	91.94 c	94.09 d	97.84 c	99.53 d
CA-Na	81.08 d	91.00 cd	89.99 e	92.35 d	98.49 d
HCl	89.64 c	95.57 c	100.52 c	103.48 c	109.61 c
CK	84.66 d	86.22 d	90.81 e	94.52 d	98.36 d

Different lowercase letters in the same column indicate significant differences at *P* ≤ 0.05.

CA = citric acid; CA-Na = sodium citrate; CK = control; HCl = hydrochloric acid; OA = oxalic acid; OA-Na = sodium oxalate.

Table 4. Potassium content of different forms in the rhizosphere soil in different tobacco varieties under two K application treatments (mg·kg⁻¹).

Variety	K ₁		K ₂	
	Slowly available K	Available K	Slowly available K	Available K
ND202	703.78 c	476.1 a	684.67 c	70.45 a
NC89	837.63 b	216.74 c	773.21 b	60.41 b
K326	888.67a	316.3 b	791.62 a	59.58 b

Different lowercase letters in the same column indicate significant differences at *P* ≤ 0.05.

K₁ = normal K supply; K₂ = K-deficiency stress.

mainly plays a role in the enzymatic degradation of H_2O_2 to avoid peroxidation damage to cells. CAT is an important ROS-scavenging enzyme that catalyzes the decomposition of H_2O_2 into nontoxic O_2 and H_2O , thus preventing the accumulation of O^- and H_2O_2 . Moreover, CAT acts as a key enzyme in the scavenging of ROS in plants (Meng et al., 2017).

Table 6 indicates that under normal K treatment, SOD and POD activities were higher, whereas CAT activity was lower for K326 and NC89 plants compared with ND202. Under K-deficiency stress, SOD activity was significantly higher for K326 and NC89 compared with ND202, whereas POD activity exhibited no significant differences among the various varieties, and CAT activity was significantly higher for ND202 relative to the other two varieties. Stress-resistant enzyme activities were increased in all three varieties under K-deficiency treatment compared with normal K treatment. ND202 exhibited the greatest increase in SOD, POD, and CAT activities, showing highly significant differences from the other

two varieties. This result indicated that ND202 presented the most intense stress response under K-deficiency stress, to reduce the accumulation of ROS in its cells and enhance the stress resistance of root cells.

Discussion

There are significant differences on K uptake, utilization, and accumulation in various species and different varieties of the same species (Lu et al., 2003). The present study was conducted to interpret the differences in soil K activation and utilization by roots among various tobacco varieties under different conditions. Our results revealed that K-deficiency stress could cause higher levels of organic acid secretion in tobacco roots, which indicated stress caused by K-deficiency led to the adaptation in plants for activating slowly available K to increase K absorption (Trejo-Téllez et al., 2010). Furthermore, under both K supply conditions, the amount of organic acids and the available K content in the rhizosphere soil were higher in ND202 than in K326 and NC89. These results suggested high-K variety secreted many organic acids into the soil, thereby inducing the release of large quantities of slowly available K, accelerating its transformation into available K (Ikka et al., 2013). This finding indicated that the organic acids played an important role in transforming different K forms in the rhizosphere soil. Tobacco varieties capable of secreting higher levels of organic acids through the roots could adapt better to K-deficiency stress and absorb greater amounts of K from soil.

Plant roots discharge hydrogen ions and organic ligands through ion channels, which are then adsorbed on the root epidermis (Breygina et al., 2010; Dai and Chen, 2005). Organic acids in root exudates can dissolve and transform certain insoluble minerals via acidification, ligand exchange, and reduction, thus allowing nutrient release and thereby improving the bioavailability of nutrients (Guo et al., 2007). The present study demonstrated that the activation of soil organic K by organic acids was a result of acidification combined with complex formation, which was an important mechanism whereby tobacco roots improved the soil available K content under K-deficiency condition. In addition, our study confirmed that the acidification and complexation of organic acids were synergistic, and both played a vital role in improving available K content in the rhizosphere soil.

Root morphology and physiological characteristics largely determine the ability of plants to absorb K from soil (Giehl et al., 2014). In the present study, it was found that ND202 displayed a smaller reduction of root vigor but a greater increase in stress-resistant enzyme activities under K-deficiency stress. K-deficiency stress had a smaller negative impact on ND202 than on K326 and NC89, which was one of the reasons that high-K variety exhibited higher contents of exuded organic acids and activated soil available K in the rhizosphere soil (Chou and Zeng, 2010; Xue et al., 2016).

In summary, the coexistence of acidification and complex formation significantly increased the soil available K content. Furthermore, tobacco plants, which displayed relatively high root vigor and activities of stress-resistant enzymes, could maintain relatively high exudation of organic acids and activate a greater amount of slowly available K in the rhizosphere soil under K-deficiency treatment. Thus, screening of varieties with high contents of organic acids in root exudates is a possible regulatory pathway for improving K content in tobacco leaves.

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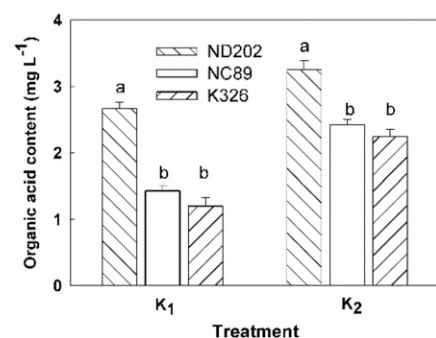


Fig. 1. Organic acid contents in different tobacco varieties under two K application treatments ($mg \cdot L^{-1}$). K_1 = normal K supply; K_2 = K-deficiency stress. Different lowercase letters in the same column indicate significant differences at $P \leq 0.05$.

Table 5. Root vigor in different tobacco varieties under two K application treatments ($mg \cdot g^{-1} \cdot h^{-1}$).

Variety	K_1	K_2	$\Delta K (K_1 - K_2)$
ND202	1.89 a	1.56 a	0.33 b
NC89	1.55 b	1.03 b	0.52 a
K326	1.51 b	1.01 b	0.50 a

Different lowercase letters in the same column indicate significant differences at $P \leq 0.05$.

K_1 = normal K supply; K_2 = K-deficiency stress.

Table 6. Stress-resistant enzymes activities in different tobacco varieties under two K application treatments.

Variety	SOD ($U \cdot g^{-1} \text{FW}$)			POD ($U \cdot g^{-1} \text{FW}$)			CAT ($U \cdot g^{-1} \text{FW}$)		
	K_1	K_2	$\Delta K (K_1 - K_2)$	K_1	K_2	$\Delta K (K_1 - K_2)$	K_1	K_2	$\Delta K (K_1 - K_2)$
ND202	223.32 c	289.16 b	65.84 a	17.92 b	26.08 a	8.17 a	3.43 a	6.80 a	3.37 a
K326	308.90 b	355.88 a	46.99 b	23.30 a	28.02 a	4.72 b	2.95 b	3.62 b	0.67 b
NC89	315.96 a	366.85 a	50.90 b	21.88 a	25.82 a	3.93 b	3.27 b	3.90 b	0.64 b

Different lowercase letters in the same column indicate significant differences at $P \leq 0.05$.

CAT = catalase; FW = fresh weight; K_1 = normal K supply; K_2 = K-deficiency stress; POD = peroxidase; SOD = superoxide dismutase.

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