Full Length Article

Potassium Uptake, Physiological and Molecular Responses in Different Winter Wheat Cultivars under Deficit Irrigation and Potassium Levels

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Abstract

Improving potassium (K) use efficiency (KUE) is beneficial for the sustainable production of cereal crops. In this study, the effects of K input level on its uptake and agronomic trait of the winter wheat under deficit irrigation were investigated in K deprivation responses, using two cultivars contrasting (low-K tolerant cultivar Kenong 9204 and K deprivation sensitive one Jimai 120). Under sufficient-K treatment (K180, SK), the two cultivars showed similar K contents, and K accumulation, biomass, photosynthetic parameters in upper expanded leaves, including yield components. Under deficient-K (K60, DK) condition, both cultivars showed varied behaviors of the K-associated traits, physiological parameters, growth and agronomic traits; however, better response was observed in Kenong 9204 than Jimai 120. These results suggested the essential roles of low-K tolerant cultivars under the K-saving management together with deficit irrigation. Two genes of the potassium transporter (HAK) family, *TaHAK3* and *TaHAK5*, showed expression of significantly upregulated upon K deprivation, with much more transcripts shown in the K-deprived Kenong 9204 plants than Jimai 120 ones. Transgene analysis on the HAK genes validated their positive roles in modulating the K accumulation and biomass production of plants under low-K condition. These results indicated that distinct HAK family genes are transcriptionally regulated underlying K deprivation signaling and contribute to plant K uptake and biomass production under low-K conditions. This study suggested the drastically genetic variation on K uptake and biomass production across winter wheat cultivars treated by K- and water-saving conditions, associated with transcription efficiency of the distinct HAK genes which modulate K uptake, growth and development of plants. © 2021 Friends Science Publishers

Keywords: Wheat; K input level; Plant biomass; K acquisition; Agronomic traits; Gene expression

Introduction

Potassium (K) is one of the critical inorganic nutrients for plant growth and development, playing essential roles in the regulation of various physiological processes including photosynthesis (Lupton 2008), water uptake (Zamir *et al.* 2013), inorganic nutrient accumulation (Wu *et al.* 2005), biomass production (Shen *et al.* 2014), and yield formation capacity of the cereal crops (Wani *et al.* 2014). However, K use efficiencies (KUE) of crop cultivars for K fertilizer applied are frequently low and urgent to be further elevated for the sustainable development of regional agriculture (Rengel and Damon 2008). Developing high KUE cultivars combined with K-saving cultivation in wheat has been one of the effective strategies in promoting the crop productivity around the world.

As one essential cropping pattern, the winter wheat/summer maize planting system contributes greatly to the food security in North China (Hu *et al.* 2014). Of which, the growing cycle for winter wheat lasts approximately eight months in this ecological region (*i.e.*, from early of October to mid-June next year). Due to less precipitation during the growth duration, the winter wheat plants are supplied by much more of natural water resources provided by irrigation at several growth stages, such as prior to seeds-sown, jointing, flowering, and mid-filling. However, this kind of affluent irrigation management has resulted in drastic consumption of the underground water resource, leading to the limitation in regional sustainable crop production and causing the environmental issues (Ma *et al.* 2015; Wang *et al.* 2016). Establishment of suitable water-saving cultivation system is valuable for the winter wheat production in North China and other zones with similar ecology.

A set of studies has indicated the close associations between the K availability in growth media and the plant growth, development, and the yield formation capacity of cereal crops (Lupton 2008; Wani *et al.* 2014). Thus far, the properties of K uptake and internal K translocation across plant tissues have been elucidated in *T. aestivum* species under various cultivation treatments (Wu *et al.* 2005; Erdei *et al.* 2006). A drastic variation on K acquisition and its deprivation response has been recorded among the wheat cultivars. Based on behaviors of plant K acquisition, biomass, and grain yields under K deprivation conditions, the wheat cultivars are categorized into different KUE including high, middle, and low KUE ones (Rengel and Damon 2008). The plants of high KUE cultivars generally possess enhanced capacities of K uptake, dry matter production, and yield formation under K-limited conditions with respect to the low KUE ones, due to the improvement on root development, photosynthetic function, and the related biochemical processes (Song *et al.* 2017). Moreover, distinct molecular processes associated with K uptake and internal K remobilization across plant tissues in response to external K levels have also been investigated (Erdei *et al.* 2006). Further elucidation of the mechanisms impacting on KUE under K deprivation can promote high KUE cultivar breeding of winter wheat, which benefit the crop cultivation under the K-saving and limited-water management.

Although the investigations related to K uptake and internal remobilization of plants have been conducted in winter wheat (Wu *et al.* 2005; Erdei *et al.* 2006), detailed processes associated with K accumulation, agronomic trait, and the corresponding molecular biology under water- and K-saving cultivation system are still needed to be further characterized. In this study, two winter wheat cultivars including Kenong 9204, a high KUE cultivar and Jimai 120, K deprivation sensitive, were selected to characterize the K uptake traits, physiological and agronomic traits, and the related molecular processes under different K levels combined by deficit irrigation. These results provide insights into the genetic variation on K-associated and agronomic traits of plants in wheat cultivars, which benefit elite cultivar breeding and resource-saving cultivation of winter wheat aimed at sustainable crop production.

Materials and Methods

Experimental design

The experiments were conducted at Liujiazhuang village, Gaocheng City, China, during the 2016–2017 and 2017–2018 growth seasons. The climate in the experimental region is specified by the temperate continental monsoon with concentrated precipitation at the summer season. Meteorological factors at spring growth stage during the two growth seasons are shown in Table 1. The surface soil layer (0–25 cm) in experimental plots was loamy and contained following nutrients: organic mater 18.25 g/kg, available N

82.46 mg/kg, available P 16.57 (Olsen-P) mg/kg, and exchangeable K 120.40 mg/kg. The soil texture was typified by an alluvial soil type generally shown in the North China plain, with pH 7.82. Plots were arranged by a randomized split design with triplicates, with K input level as main plot whereas cultivar as sub-plot. The main plot contained two K levels: sufficient-K 180 kg/ha KO$_2$ (K180, SK) and deficient-K 60 kg/ha KO$_2$ (K60, DK). The sub-plot contained two cultivars: Kenong 9204, low-K tolerant cultivar and Jimai 120, K deprivation sensitive. Seeds of the tested cultivars were sown in plots (35 m^2 with 7 m in length and 5 m in width each) on October 8 and 7 during the 2016–2017 and 2017–2018 seasons, respectively. For the K input, SK was established by using basal complex fertilizer (N: P$_2$O$_5$: K$_2$O for 15: 15: 15) with amount 600 kg/ha together with basal K$_2$O of 90 kg/ha (KCl as K source) and top dressed 135 N kg/ha (urea as N source) at jointing stage. The DK level was set up using the complex fertilizer and amount was top dressed for N nutrition mentioned above. During the two seasons, the seeds were sown in rows with 15 cm distance to establish an about 3,750 thousand-seedling population per hectare. Before seeds-sown, the straws of summer maize were mechanically broken into pieces after harvest and mixed well with the basal fertilizers. To manage deficit irrigation, two irrigations, one prior to seeds-sown and another at jointing stage with water amount of 67.5 mm each controlled by a water calculator, were conducted for all of treatments. Other cultivation techniques were like the conventional ones used by local farmers.

Measurements of yields and yield components

At maturity, the spikes in two square meters were counted in each plot to calculate the population spike numbers. The spike grains were threshed from each plot using a mini harvest machine at maturity (June 13 and 11 at 2017 and 2018, respectively) to calculate the yields after seed air drying. The grain weights were obtained by weighing one thousand air-dried grains. The spike kernel numbers were obtained by counting the seeds in thirty representative spikes.

Plant biomass and the K-associated traits

At stages of jointing, flowering, mid-filling, and maturity, twenty representative plants in each plot were sampled to measure biomass, K concentrations, and the K accumulative amounts. Among these, plant biomass was obtained based on the oven-dried samples; K concentrations in the samples were measured using the methods (Guo *et al.* 2011). The K accumulative amounts in plants were calculated by multiplying the biomass and the K concentrations.

Measurements of photosynthetic traits

During the two growth seasons, photosynthetic parameters

Table 1: Meteorological factors at spring growth stage during the 2016–2017 and 2017–2018 seasons

Year	10 d	Average temperature (°C)			Precipitation (mm)			Total sunshine (hour)			Solar radiation (W/m^2)		
		April	May	June	April	May	June	April	May	June	April	May	June
2017	First	10.23	21.23	24.22	1.22	1.56	13.22	78.23	86.83	84.63	202.23	233.02	250.38
	Second	13.23	24.80	27.23	0.32	10.22	5.12	89.12	113.04	84.90	253.23	283.34	252.06
	Third	16.43	24.48	27.01	6.23	14.65	36.04	102.32	110.71	80.42	231.21	266.28	224.18
2018	First	8.92	20.30	26.52	2.23	8.60	23.84	80.12	87.88	86.13	213.08	242.03	232.33
	Second	14.23	22.02	26.58	1.03	22.63	25.12	68.23	45.73	82.83	239.23	250.16	239.41
	Third	17.03	23.61	30.11	10.22	40.56	2.23	90.48	111.42	85.82	261.22	274.42	231.00

Table 2: Information of the HAK family genes in *T. aestivum* and primers used for qRT-PCR analysis

Purpose	Accession number	Forward primer (5´-)	Reverse primer (5´-)
TaHAK1 expression	KU212875	CCTTACTTACCCAAATTGCAAA	ACTTCCCAGAGAAGCCAACCC
TaHAK2 expression	JF495466	CTCGGGGAGGATGAGCTTC	CCTTCTTCAAGATGGAGGA
TaHAK3 expression	DQ009003	GCAAGAGCTAAACACGATA	TCCTGGCAGATGATCTCTGGG
TaHAK4 expression	DQ015706	GTTTTGCAGCGCATATGGCAA	TTAAGCCTTCCATAGAGCATG
TaHAK5 expression	KR422354	CCGAGAGGAGATCGCTCTC	CCAGGACAAGAACCACCTTC
TaHAK6 expression	KU212870	GGCATTGTGTGAACTGTGCTTG	ATGCCTCGCCACCATGCATG
TaHAK7 expression	KU212871	GCCGTGGTGTGCATCACGGA	AATGGTATCGATCATGCATGG
TaHAK8 expression	KU212872	GCCGTGGTGTGCATCACGGA	AATGGTATCGATCATGCATGG
TaHAK9 expression	KU212873	ACACAAAACCTTACTTACCCAA	TGTACCCGGTGCTGAACCCC
TaHAK10 expression	KU212874	GGCGGAAGCTGCTCATGTCG	GTGGATTACCTGATAACCTCG
TaHAK11 expression	KU184266	GCTATTGCGACCACTATAACG	TTGAGCCTGCCGTAGAACATG
TaHAK12 expression	KF646596	AAAGGAGAAGGCTCAGAAACGA	GGCAGATGATCTCTGGGTGCA
TaHAK13 expression	KF646595	GGCATTCTCACCGCTCGGA	TGGCAGATGATCTCTGGGTG
Tatubulin expression	U76558	CATGCTATCCCTCGTCTCGACCT	CGCACTTCATGATGGAGTTGTAT
TaHAK3 overexpression cassette	DQ009003	TTTCCATGGGCCGGGTGAAAAGATT	TTTGGTAACCAATCTTTTCACCCGGCCCAT
TaHAK5 overexpression cassette	KR422354	TTTCCATGGCTGTCCGGCTGCAT	TTTGGTAACCATTATTCAGGACCAATC

Table 3: Grain yields and the yield components of the tested cultivars under various K input treatments

Growing season	K treatment	Cultivar	Spike number (10^4 ha^{-1})	Kernel numbers	Grain weight (g)	Yield (kg ha^{-1})
2016-2017	SK	Kenong 9204	703.45 a	32.22 a	40.23 a	7780.08 a
		Shimai 120	715.36 a	32.17 a	40.02 a	7816.39 a
	DK	Kenong 9204	655.50 b	31.06 ab	39.13 b	6789.66 b
		Shimai 120	632.14 c	30.23 b	38.28 b	6234.82 c
2017-2018	SK	Kenong 9204	690.32 a	32.83 a	42.64 a	8218.05 a
		Shimai 120	700.05 a	32.66 a	42.38 a	8230.27 a
	DK	Kenong 9204	659.42 b	31.55 ab	41.48 ab	7245.26 b
		Shimai 120	636.23 c	30.00 b	40.60 b	6485.49 c

SK, sufficient K (K180). DK, deficient K (K60). Data are shown by averages from triplicates and different lowercase letters indicate to be statistical significance between two tested cultivars across the K input treatments at each growth season

in each cultivar under different K input treatments were assessed at various growth stages (*i.e*., jointing, flowering, mid-filling, and maturity) using representative upper leaves as samples. The parameters assessed included chlorophyll contents (Chl), photosynthetic rate (Pn), stomatal conductance (gs), intercellular CO_2 concentrations (Ci), photosystem II photochemical efficiency (ΨPSII), and NPQ. Among them, the Chl was recorded by SPAD-502 analyser; Pn, gs, and Ci were measured using the photosynthesis assay system (Li-COR6200); PSII and NPQ in samples were determined as described previously (Guo *et al.* 2013).

Assay of expression patterns of the potassium transporter (HAK) family genes

At stages of flowering during the two seasons, representative flag leaves of the tested cultivars were sampled under K input treatments and subjected to expression evaluation of the potassium transporter (HAK)

family genes. The genes of the HAK family examined included *TaHAK1* to *TaHAK13*. The information of the HAK family genes examined is shown in Table 2. Transcripts of the genes were determined based on qRT-PCR using gene specific primers (Table 2) performed as previously described (Guo *et al.* 2013). *Tatubulin*, a constitutive gene in *T. aestivum*, was used as the internal reference to normalize the target transcripts.

Transgene analysis on the differential HAK gene

TaHAK3 and *TaHAK5*, two differential genes shown in the K-deprived plants of the two tested cultivars, were functionally characterized for the roles in mediating plant K uptake under DK treatment. With this purpose, the open reading frames of *TaHAK3* and *TaHAK5* were amplified based on RT-PCR in sense orientation. The products were then separately integrated into the vector pCAMBIA3301 and genetically transformed into *T. aestivum* (cv. Kenong

9204) (Guo *et al.* 2013). Two T3 lines HAK3-1 and HAK3-3 with *TaHAK3* overexpression and HAK5-2 and HAK5-3 with *TaHAK5* overexpression together with wild type (WT) were subjected to DK treatment by growing the three-leaf seedlings in the modified MS solution containing low K (0.1 m*M* K₂O). Four weeks after the treatments, the K concentrations, biomass, K accumulative amounts, and photosynthetic parameters in transgenic and WT plants were assessed.

Statistical analysis

Averages, standard errors, and significant test analysis for plant biomass, K-associated traits, photosynthetic parameters, agronomic traits, and the transcripts of the HAK family genes were calculated based on S.P.S.S. 16.0 statistical software supplemented in Excel of the Windows system.

Results

The yield and its components

Two cultivars (*i.e.*, Kenong 9204 and Jimai 120) examined had similar phonological dates at each growth stage under various K input treatments (data not shown). Compared with under high K input treatment (SK), the yields and the yield components of the two cultivars were lowered under deficient-K treatment (DK) (Table 3). The Kenong 9204 showed comparable above agronomic traits with Jimai 120 under SK. However, under DK conditions, the former exhibited higher yields and much more improved population spike amounts, kernel numbers per spike, and grain weights than the latter (Table 3).

Plant biomass and the K-associated traits

The K concentrations, plant biomass, and K accumulative amounts in the tested cultivar plants were higher at various stages (*i.e.*, jointing, flowering, mid-filling, and maturity) under SK than DK (Fig. 1A–C). Likewise, compared with Jimai 120, Kenong 9204 was similar on the plant biomass and K-associated traits at each growth stage under SK and significantly improved these traits under DK (Fig. 1A–C).

Behaviors of the photosynthetic parameters

In consistent with the plant biomass upon different K levels, the plants in tested cultivars displayed improved photosynthetic parameters, including higher *Chl*, *Pn*, *gs*, PSII, and lower *Ci* and NPQ under SK than DK (Fig. 2A–F). Additionally, these traits were much more improved in Kenong 9204 plants under DK than Jimai 120 ones (Fig. 2A–F). These results suggested that the enhanced photosynthetic function shown under DK was associated with the improved K uptake which further positively
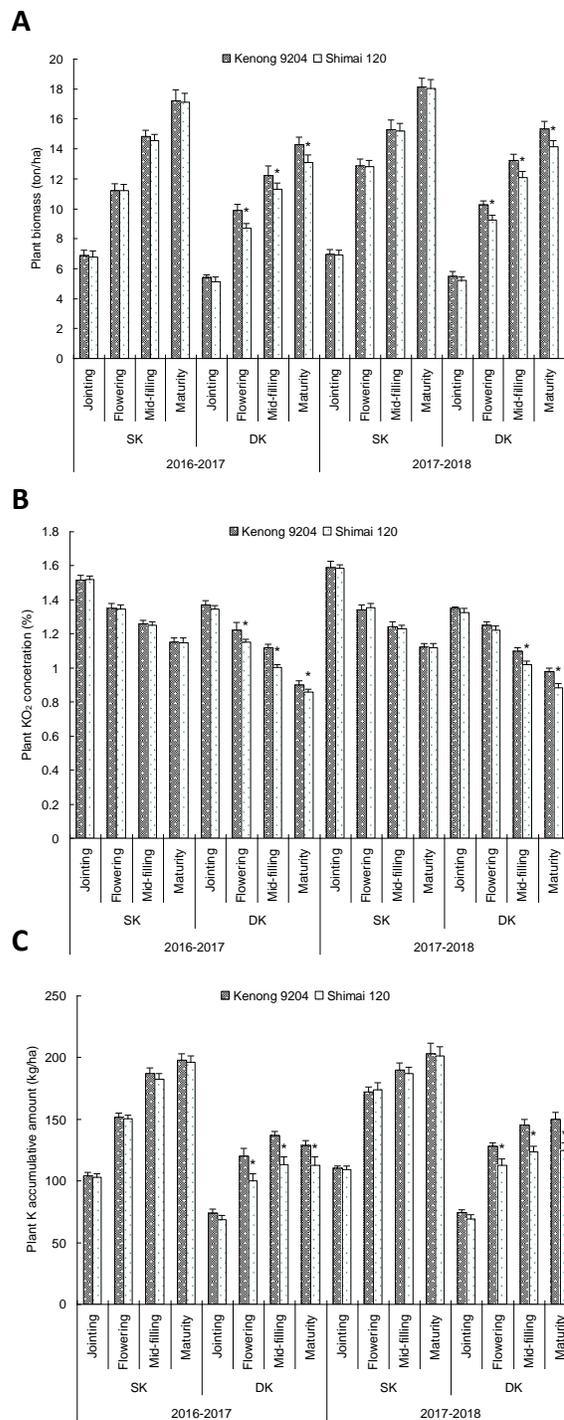
Fig. 1: Plant growth and K-associated traits at various growth stages in tested cultivars under different K input treatments
A, plant biomass; **B**, plant K concentrations; **C**, plant K accumulative amounts. SK, sufficient-K. DK, deficient-K. Data shown are averages derived from triplicate results together with standard errors. Symbol * indicates to be statistically significant between the cultivars at each assay time under same treatment, according to Student T-test at 0.05 level

affected the plant biomass production and the yield formation capacity.
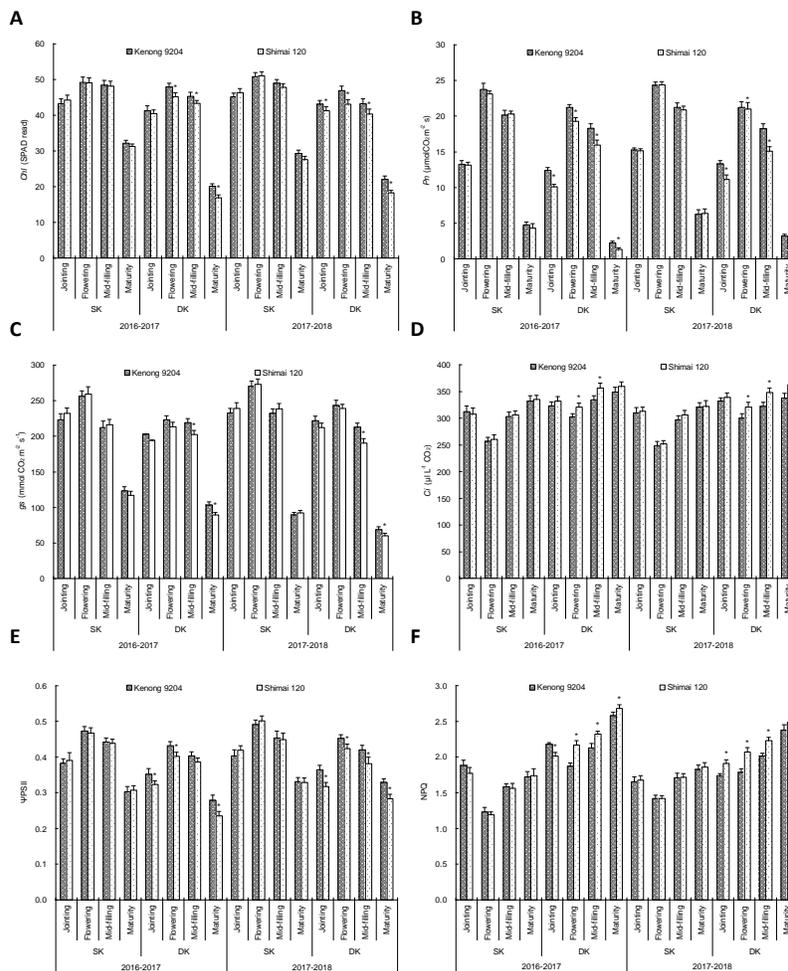
Fig. 2: Photosynthetic parameters at various growth stages in tested cultivars under different K input treatments
A, *Chl*; **B**, *Pn*; **C**, *gs*; **D**, *Ci*; **E**, ΨPSII; **F**, NPQ. SK, sufficient-K. DK, deficient-K. Data shown are averages derived from triplicate results together with standard errors. Symbol * indicates to be statistically significant between the cultivars at each assay time under same treatment, according to Student T-test at 0.05 level
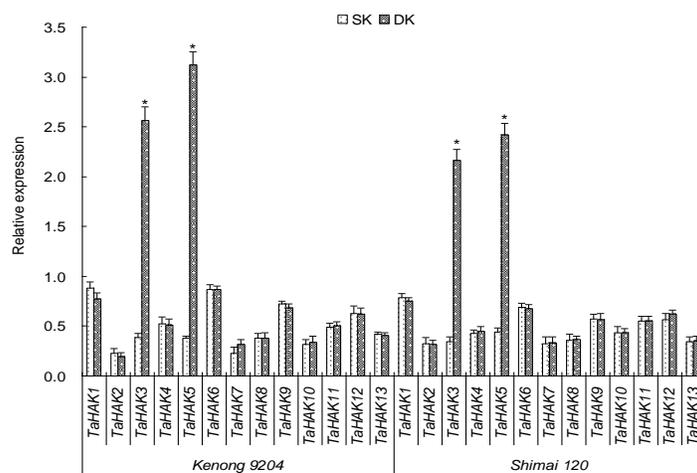
Fig. 3: Expression patterns of the potassium transporter family under different K input treatments
SK, sufficient-K. DK, deficient-K. Transcripts of the target genes were normalized by internal standard *Tatubulin*, a constitutive gene in *T. aestivum*. Data sets shown are averages derived from triplicate results together with standard errors. Symbol * indicates to be significantly different in the tested cultivars under treatments relative to control according to Student T-test at 0.05 level

Expression patterns of the HAK family genes upon K deprivation

A set of K transporter (KT) family genes in *T. aestivum* species, including *TaHAK1* to *TaHAK10*, were subjected to expression evaluation to address the molecular processes underlying plant K uptake under the SK and DK conditions. Among the genes examined, *TaHAK3* and *TaHAK5* were upregulated in the K-deprived cultivar plants, which was in contrast to the other HAK genes which unaltered in expression patterns in the plants under both SK and DK conditions (Fig. 3). Moreover, induced extent on these two HAK gene transcripts under DK was intensified in the Kenong 9204 plants with respect to Jimai 120 ones (Fig. 3).

Growth and K-associated traits of *TaHAK3* and *TaHAK3* transgenic lines under DK conditions

Under the SK condition, the transgenic lines were comparable on K concentrations, biomass and K accumulative amounts with the wild type (Figs. 4A–4C). Under DK treatment, however, the lines were much more improved on the plant biomass and the K-associated traits with respect to wild type (Figs. 4A–4C).

Photosynthetic parameters of *TaHAK3* and *TaHAK3* transgenic lines under DK conditions

The transgenic lines with overexpression of *TaHAK3* and *TaHAK5* were subjected to assessment of the photosynthetic parameters. Similar to the behaviors on plant biomass, the transgenic lines (HAK3-1, HAK3-3, HAK5-2, and HAK5-3) showed comparable photosynthetic parameters (*i.e.*, Pn, gs, PSII, and NPQ) under SK conditions (Figs. 5A–5D). In contrast, the lines were much more improved on photosynthetic function under DK treatment, showing higher Pn, gs, and PSII and lower NPQ values than wild type plants (Figs. 5A–5D).

Discussion

The external K levels act as one of the critical factors for crop production, regulating largely plant growth, development, and the yield formation capacity (Shen *et al.* 2014; Wani *et al.* 2014). Suitable application of potassium fertilizers can balance the environmental K nutrition and positively impact on the plant dry matter accumulation and the productivity, given the improved cellular osmotic regulation potential (Zamir *et al.* 2013), abiotic stress adaptation, and the associated physiological processes (Wu *et al.* 2005). In addition, rational management on K fertilizers enhances the water use efficiencies of plants once challenged by deficit water supplies (Wang *et al.* 2017). In this study, the K uptake and the agronomic traits in wheat cultivars were investigated under different K input treatments combined by deficit irrigation. The K concentrations, plant biomass, and
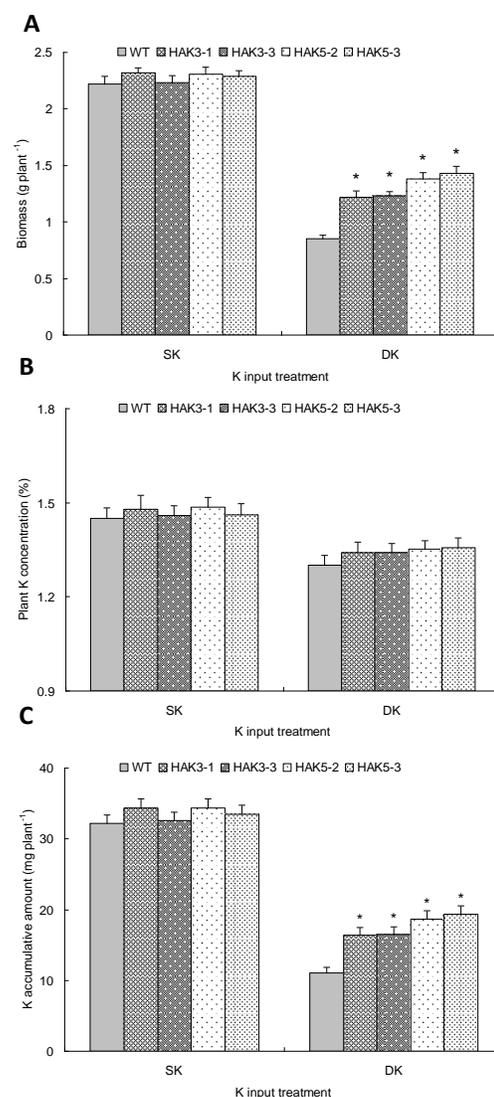
Fig. 4: Growth and K-associated traits of lines overexpressing *TaHAK3* and *TaHAK5* under different K input treatments

A, plant biomass; **B**, plant K concentrations; **C**, plant K accumulative amounts. SK, sufficient-K. DK, deficient-K. HAK3-1 and HAK3-3, two lines with overexpression of *TaHAK3*; HAK5-2 and HAK5-3, two lines with overexpression of *TaHAK5*. Data shown are averages derived from triplicate results together with standard errors. Symbol * indicates to be significantly different between transgenic lines and wild type according to Student T-test at 0.05 level

the K accumulative amounts of plants in tested cultivars were lowered at various growth stages under DK than under SK, which further affects the agronomic trait behavior of wheat cultivars. These results indicated the promotion effects of suitably supplied K nutrition on plant K uptake, which benefits the productivity of winter wheat cultivars treated by deficit irrigation.

Previous studies have suggested the genetic variation on nutrient uptake and internal translocation of inorganic nutrients among the wheat cultivars when challenged by external nutrient deprivations (Zhang *et al.* 1999; Rengel and Damon 2008). The cultivars sharing high nutrient use
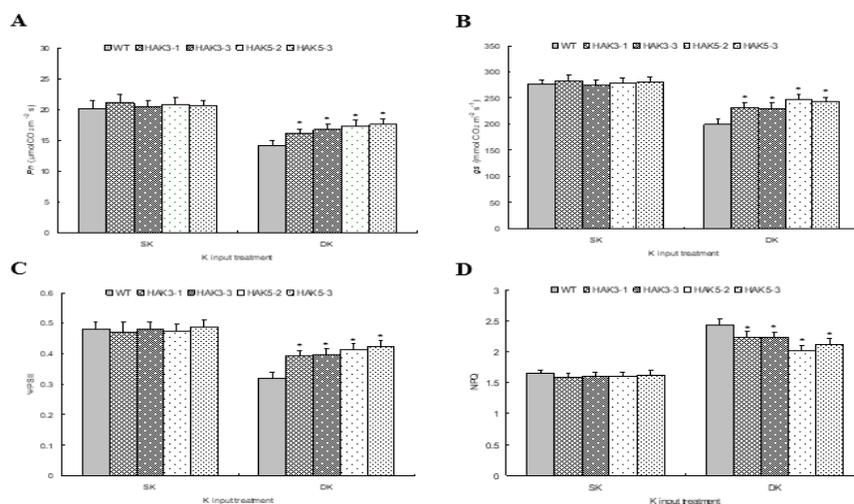
Fig. 5: Photosynthetic parameters of the lines overexpressing *TaHAK3* and *TaHAK5* under different K input treatments
A, *Pn*; **B**, *gs*; **C**, ΨPSII; **D**, NPQ. SK, sufficient-K. DK, deficient-K. HAK3-1 and HAK3-3, two lines with overexpressionof *TaHAK3*; HAK5-2 and HAK5-3, two lines with overexpression of *TaHAK5*. Data shown are averages derived from triplicate results together with standard errors. Symbol * indicates to be significantly different between transgenic lines and wild type according to Student T-test at 0.05 level

efficiency possess enhanced nutrient uptake capacity, which contributes to the improved plant biomass and grain yield production under nutrient-limiting conditions (Woodend *et al*. 1987). In this study, significant variation was found on K concentration, accumulative K amount, and agronomic traits across the tested wheat cultivars under K deprivation treatment (DK). Compared with Jimai 120, a cultivar to be K deprivation sensitive, the low-K tolerant cultivar Kenong 9204 was shown to be profoundly elevated on K concentrations, biomass, K accumulative amounts, and grain yields under DK. Therefore, it is valuable for the winter wheat cultivation by using high KUE cultivars under the K- and water-limited management, given that they possess the improved K uptake and the yield formation capacities.

Improvement of photosynthetic function under abiotic stresses, such as drought, positively regulates plant biomass production and the yield potential (Liao and Wang 2002; Inoue *et al*. 2004). Previous investigations indicated the enhanced photosynthetic trait behavior in drought tolerant wheat cultivars under water deprivation condition compared with drought sensitive ones (Liu and Li 2005; Wu *et al*. 2014). In this study, photosynthetic traits, such as *Chl*, *Pn*, ΨPSII, and NPQ, obtained similar results to previous studies. Under DI condition, Kenong 9204, the drought tolerant cultivar, displayed higher *Chl*, *Pn*, and ΨPSII whereas lower NPQ in upper leaves of plants than Jimai 120, a drought sensitive one. These results suggest that the drought tolerant cultivars can sustain relatively improved photosynthetic process under water deprivation, which contributes to their enhanced yield potential in drought-challenged conditions.

The K uptake and internal K ion translocation across plant tissues are mediated by the potassium transporter (HAK)-associated proteins (Coskun *et al*. 2013). During these molecular processes, ATP initiated from respiratory cycle was used as the driving power (Ragel *et al*. 2019).

Several investigations have validated the functions of distinct HAK family members in mediating plant K taken up or the internal K remobilization processes. For example, a set of the HAK genes in plant species are K deprivation responsive at transcription level, displaying significantly upregulated transcripts in the K-deprived plants (Brauer *et al*. 2016; Cheng *et al*. 2018). The transgenic plants with overexpression of distinct HAK family genes are significantly improved on the K accumulation and the growth traits under low-K treatment (Yang *et al*. 2014; Ahmad *et al*. 2016). These findings suggest the potential roles of distinct HAK genes in regulating plant K deprivation responses. In this study, to address the molecular processes underlying improved K uptake under DK in the wheat plants, a suite of HAK family genes in *T. aestivum* (*i.e.*, *TaHAK1* to *TaHAK13*) were subjected to transcript evaluation under contrasting K input conditions. Results revealed that *TaHAK3* and *TaHAK5* are differentially expressed upon modified external K levels, showing to be upregulated in the K-deprived plants of the two wheat cultivars examined, with more transcripts abundance in the Kenong 9204 plants than that Jimai 120 ones. These results contrast with other genes unaltered on transcription in the cultivars plants between both SK and DK conditions. Based on transgene analysis, the biological roles of *TaHAK3* and *TaHAK5* in mediating plant low-K tolerance were validated; the lines with overexpression of these two HAK family genes were much improved on K concentrations, biomass, and K accumulative amounts of plants together with enhanced photosynthetic function under DK conditions. Therefore, distinct HAK members such as *TaHAK3* and *TaHAK5* act as critical regulators and exert essential roles in regulating the plant uptake of K nutrition under DK conditions (Fig. 4 and 5), which further positively impact on the physiological processes associated with photosynthesis, biomass production, and yield

formation capacity of the winter wheat cultivars. They are thus to be acted as valuable indices in evaluating behaviors of KUE and the yield potential in winter wheat cultivated under the K-saving and deficit irrigation conditions.

Conclusion

Dramatically, genetic variation on growth and K-associated traits was found in the winter wheat cultivars under K deprivation. The high KUE cultivar exhibits improved capacities to take up K, photosynthesis, plant biomass production, and agronomic traits under DK conditions. Distinct family members in the potassium transporter (HAK) family (*TaHAK3* and *TaHAK5*) display modified transcription efficiency upon K deprivation, with more transcripts in the high KUE cultivars than in the cultivars to be low-K stress sensitive. Overexpression of the differential HAK family genes leads to improved K-associated traits, photosynthetic function, plant biomass production, suggesting their essential roles in positively regulating plant K uptake under low-K treatment in winter wheat cultivars.

Acknowledgements

Author Contributions

XB, ZC, FL and SZ planned the experiments, KX interpreted the results and made the write up, YZ statistically analyzed the data and made illustrations.

Conflicts of Interest

All other authors declare no conflicts of interest

Data Availability

Data presented in this study are available on fair request to the corresponding author.

Ethics Approval

Not applicable.

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