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Gene expression pattern of K transporter *GhHAK5* gene of potassium efficient and in-efficient cotton cultivars based on morphological physiognomies as affected by potassium nutrition and reduced irrigation

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Abstract

Background Under K deficiency the uptake and distribution pattern in plant cells is mediated through different transport proteins and channels which were controlled by specific gene family. Therefore, a hydroponic experiment was conducted under control condition for testing the gene expression pattern of the K transporter under adequate and low K supply levels. After that, a 2-year field experiment was conducted to evaluate five selected cotton cultivars (four K-efficient cultivars, viz., CIM-554, CYTO-124, FH-142, IUB-2013, and one K non-efficient, BH-212) screened from the initial hydroponics culture experiment and two levels of potassium (0 K_2O kg·ha^{-1} and 50 K_2O kg·ha^{-1}) were tested under reduced irrigation (50% available water content; 50 AWC) and normal irrigation conditions (100% available water content; 100 AWC).

Result Results revealed that the transcript levels of *GhHAK5aD* in roots were significantly higher in K^+ efficient cultivars than that in K^+ non-efficient cultivars. The *GhHAK5aD* expression upon K^+ deficiency was higher in roots but lower in shoots, indicating that *GhHAK5aD* could have a role in K^+ uptake in roots, instead of transport of K^+ from root to shoot. Similarly, under field conditions the cultivar FH-142 showed an increase of 22.3%, 4.9%, 2.4%, and 1.4% as compared with BH-212, IUB-2013, CYTO-124, and CIM-554, respectively, in seed cotton yield (SCY) with K application under reduced irrigation conditions. With applied K, the FH-142 showed an increase in net photosynthetic rate by 57.3% as compared with the rest of the cultivars under reduced irrigation over K control. However, the overall performance indicators of K-efficient cultivars like FH-142, CYTO-124, CIM-554, and IUB-2013 were better than BH-212 (K in-efficient) under reduced irrigation conditions with applied K at 50 kg·ha^{-1}. Fiber quality trait improved significantly with K application under water deficit. The increase in micronaire was 3.6%, 4.7%, 7.8%, 3.4%, and 6.7% in BH-212, IUB-2013, CIM-554, CYTO-124, and FH-142, respectively, with K application at 50 kg·ha^{-1} over without K application under reduced irrigation conditions during the cotton growing season. Similarly, the cultivars FH-142 increased by 12% with K application under reduced irrigation as compared with other cultivars. The performance of K-efficient cultivars under reduced irrigation conditions was 30% better in SCY and quality traits with the application of K at 50 kg·ha^{-1} as compared with K-non-efficient cultivars. Similarly, water use efficiency (WUE) (40.1%)

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and potassium use efficiency (KUE) (20.2%) were also noted higher in case of FH-142 as compared with other cultivar with K application under reduced conditions.

Conclusion Higher expression of *GhHAK5aD* gene was observed in K-efficient cultivars as compared with K-non-efficient cultivars in roots indicates that *GhHAK5aD* may be contributing to genotypic differences for K^+ efficiency in cotton. K-efficient cotton cultivars can be used for the low-K environments and can also be recommended for general cultivars.

Keywords Cotton, K-efficient cultivars, Drought, Potassium use efficiency, WUE

Background

Pakistan stands the 5th largest cotton generating country among the world's cotton producing. Cotton has been declared the lifeline of the Pakistan's economy due to its 0.6% contribution to GDP and engaging 50% industrial labor force (Ahmad et al. 2021). The situation is getting worse due to the scarcity of canal water and abrupt changes in climatic conditions in Pakistan. Unfortunately, cotton production is declining from 14 million bales in 2014–2015 to 7.0 million bales in 2020–2021 (Government of Pakistan 2020–2021) in Pakistan, owing to several biotic and abiotic factors including insect pests attacks low-quality seeds, reduction in the planting area, rising temperatures, decreasing water availability, which lead to drought stress and imbalance or low use of nutrient application. Water availability in Pakistan has been on the decline, for instance, total water availability has been reduced from 103.5 million acre-feet in 2011–2012 to 96.3 million acre-feet in 2020–2021 (Government of Pakistan 2020–2021). Changing climate scenarios have been further deteriorating the situation, and water availability is projected to decrease further, while the temperature is expected to rise. Such instances have already been wreaking havoc in some parts, including those of cotton growing areas in Pakistan which have been facing drought (Ali et al. 2018).

Potassium (K) is one of the dynamic nutrients for the plant kingdom. It constitutes about 10% of the total plant biomass (Azeem et al. 2021), and is involved in various physiological and morphological processes including water relations, enzyme activation, and quality of produce. K element and irrigation water are the two major yield-limiting factors in cotton production. However, the additional use of chemical fertilizer can produce and sustain high crop yields but also increased input costs and deteriorate the environment in many ways like eutrophication, soil acidification, and air pollution (Chen and Liao 2017), and the recovery of these chemicals through plants is low in many soils. The development of such crop plants can efficiently utilize soil nutrients and can improve agricultural yields on a sustainable basis, while reducing input costs and harmful environmental effects.

Plants take up K from the soil through root epidermal and cortical cells and then transported to shoot via xylem. Under K deficiency the uptake and distribution pattern in plant cells is mediated through different transport proteins and channels. The transport protein can be classified into two main categories as high-affinity transporters which are active at low concentrations of external K and low-affinity channels which are active at higher contents of more than 0.3 $mmol{\cdot}L^{-1}$ external K (Wang et al. 2013). The K^+ concentrations that plant roots encounter in the soil are relatively low, varying from only 0.1 to 5.0 $mmol{\cdot}L^{-1}$. Therefore, most plants are subjected to low K^+ stress during certain growth periods. The first K^+ transporter with a role in nutrient uptake was the *Shaker*-like, voltage-gated, and K^+-selective channel AKT1 (Hirsch et al. 1998). Plant voltage-gated K^+ channels are divided into three sub-families regarding their response to the membrane potential (Dreyer and Uozumi 2011): (1) Inward-rectifying channels that in *Arabidopsis* include AKT1, AKT6, KAT1, and KAT2; they open at hyperpolarized membrane potentials allowing the uptake of K^+. (2) Outward-rectifying channels that mediate the K^+ release because they open at depolarized membrane potentials; this group is composed of SKOR and GORK channels. (3) Weakly rectifying channels that can mediate both K^+ uptake and release and whose *Arabidopsis* representative is AKT2 (Jeanguenin et al. 2011). AtAKT1 and AtHAK5 are two major transporters that contribute to K^+ uptake in roots.

In plants, K transporters have been revealed to control the K^+ uptake by roots. K transporter (KT)/high-affinity K transporter (HAK)/K uptake permease (KUP) is the largest K^+ transporter family in plants, which were initially identified in *Arabidopsis* and barley. The *AtAKT1* and *AtHAK5* are considered to play an important role that contribute to K^+ uptake in roots (Grabov 2007; Wang and Wu 2013). In *Arabidopsis*, the *AtHAK5* gene is expressed in roots and induced upon K^+ starvation (Ahn et al. 2004). However, little is known about this KT/HAK/KUP family in cotton. Recently, it was found that *GhHAK5aD* is a major *GhHAK5* gene involved in low K^+ stress (-K) in cotton. *GhHAK5*, which is a homolog of *AtHAK5*, was mainly expressed in roots and this expression was high upon K^+ deficiency (Wang et al. 2019).

To endure low K stress, plants utilize adaptation mechanisms such as altering root architecture to explore more soil volume, increasing carboxylate exudation including phosphatases, and the release of nucleases and different organic acids. Plants use these strategies to extract more K from exchangeable pools in the soil (Hassan et al. 2011). Zhang et al. (2007) also reported that improved plant growth under low K availability in efficient cultivars is attributed to the enlarged root system, efficient physiological processes, and transport mechanisms. The selection and development of cultivars with the potential to grow better under low K conditions can improve cotton yield and reduce input cost (Baiyin et al. 2021).

Drought stress is the key factor among abiotic stresses that severely affects plant growth by reducing vegetative development, leaf area, photosynthetic rate, transpiration rate, and decreasing cell water potential and turgor pressure, which ultimately leads to the prevention of metabolic processes (Farooq et al. 2009). Cotton plants are also affected by the extended scarcity of water and resulting in the loss of quantity as well as quality (Zahid et al. 2021). Likewise, the physiological impacts of drought on cotton crop include increased formation of reactive oxygen species, decrease in carbon dioxide intake rate attributed to stomatal closure, and down-regulation of non-cyclic transportation (Ullah et al. 2017).

Multiple approaches have been employed in the amelioration of drought stress in cotton crop among which; the use of drought tolerant crop varieties, improved seeds, water conservation techniques as well as application of different nutrients / elements have been adopted. Many cotton-growers, particularly those in Pakistan, have been using agrochemicals or inputs carelessly. Considering these circumstances it has been observed that careful application of K may have a significant role in the drought tolerance of crop plants (Kant et al. 2002). For instance, K helps plants to sustain the drought stress through its role in cell elongation, cell membrane stability, aquaporins, water uptake, osmotic adjustment, and stomatal regulation (Wang et al. 2013). A variety of crops have shown to recover or cope with the effects of drought stress when applied with K (Aksu and Altay 2020; Anokye et al. 2021; Bahrami-Rad and Hajiboland 2017; Wei et al. 2013) including cotton (Zahoor et al. 2017; Shahzad et al. 2019; Zhao et al. 2019). K application in drought-affected cotton leads to osmotic adjustment, solute accumulation, lowering of osmotic potential, increase in water intake, and maintenance of turgor pressure (Zhao et al. 2019).

However, as mentioned above, K application has not taken an important position in Pakistan, where 43% of Pakistani soils are already deficient in K. Now it has continuously decreased day by day due to over use of tube well irrigation. Despite high K requirements, K use in cotton production is very limited in Pakistan (Hassan et al. 2008). Moreover, modern cultivars are more sensitive to environmental stresses compared with obsolete ones (Oosterhuis and Snider 2011), which further deteriorate the circumstances of the non-alignment of cultivars with environmental and soil conditions. For instance, limited studies have been conducted on most commercial cultivars cultivated, especially, in Pakistan to identify their performance under drought stress conditions, as well as their response to the application of K, and the majority of the studies have mainly been focused on the seedling stage. Sufficient K in cotton not only increases water potential and stomatal function in cotton but also increase water use efficiency (WUE) which assists to sustain plant function during water limiting conditions (Pervez et al. 2004). Therefore, yield is a good indicator with the application of K fertilizers and the use of K efficient cultivars that provides adaptability to plants under water-limited conditions (Ahmad et al. 2013). The addition and application of K under water stress conditions improved the lint yield and quality of seed cotton as compared with no water stress conditions. K provides a charge to balance the ion flux which is required for the movement of other ions across the plasma membranes. Due to K flux the transport of sugars, amino acids, and nitrate is carried out (Marschner 1995). Therefore, accumulation of K inside the guard cell reduces the water potential within cell along with an anion and provides the osmotic potential for water uptake (Schroeder et al. 2001). Similarly, cotton fiber is the necessary raw material for textile industry. Past studies showed that K deficiency could reduce fiber quality traits, because K is required for boll formation and in the synthesis of epidermal cells and cellulose (Yang et al. 2016). At maturity more than 94% of the fiber dry weight is cellulose. Therefore, K has a significant role in the amelioration of drought stress as well as sustaining the water relations within the plant, however, it has not received much attention from the farming community, and its incautious use has affected cotton production and quality in Pakistan.

One of the reasons for limited or no use of K fertilizers is its higher prices compared with N and P fertilizers in Pakistan. It is becoming very essential to cultivate those cultivars that can withstand the stresses of different nutrient scarcities as well as the shortage of irrigation water. This step moves carefully to low nutrient input agriculture. Therefore, a significant gap was identified in farmers' understanding of the application of K fertilizers, particularly, in cotton together with the lacking information about drought tolerant cultivars of cotton in the region.

Materials and methods

Plant material and growth conditions of hydroponic experiment

Five pre-selected cotton cultivars (three K-efficient cultivars, viz., CIM-554, CYTO-124, FH-142, and one K non-efficient, BH-212) were used in this study. Cotton seeds were first surface-sterilized with 70% ethanol for 30 s and 2% sodium hypochlorite (v/v) for 30 min. The seeds were then immersed in water in the dark for 2 days at 30°C to induce germination. The condition in the climate chamber was as follows: day/night temperature, 30°C /22°C; photoperiod, 12-h-light/12-h-dark; 70% relative humidity, and light intensity of 200 $\mu mol\cdot m^{-2}\cdot s^{-1}$. The modified half-strength Hoagland's solution was supplied twice a week (Hoagland and Aron 1950) (Table 1).

Testing procedure for gene expression patterns by quantitative real-time PCR (qRT-PCR)

Total RNA was extracted from the cotton roots and shoots using a Qiagen Plant RNeasy Kit according to the manufacturer's instructions. cDNA was synthesized from 1μg of total RNA using the iScript cDNA Synthesis Kit (BIO-RAD Laboratories, Inc., Hercules, CA, Cat. No#170-8890) according to the instructions in the user manual. Primers used for quantitative real-time PCR (qRT-PCR) analysis were as follows: 5′-CCAGAGCTC CAATATTCTAGC-3′ (forward) and 5′-GGGTGGTGC TGCTGATAT-3′ (reverse) for *GhHAK5aD*; 5′-GCC TTGGACTATGAGCAGGA-3′ (forward) and 5′-AAG AGATGGCTGGAAGAGGA-3′ (reverse) for *GhActin9*. qRT-PCR was performed using SYBR Green Master Mix (Applied Biosystems; www.lifetechnologies.com) in a StepOnePlus (Life Technologies, Carlsbad, CA, USA). The second method was used to calculate the relative gene expression levels (Livak et al. 2001) and the cotton *Actin9* gene was used as an internal control to normalize the target gene expression.

Table 1 Composition of Hoagland's solution

Sr. No	Salts	Stock /($g\cdot L^{-1}$)	stock solution /($mL\cdot L^{-1}$)
Macronutrients			
1	$NH_4H_2PO_4$	115	0.5
2	KCl	74.5	According to treatments
3	$Ca(NO_3)_2\cdot 4H_2O$	236	2.5
4	$MgSO_4\cdot 7H_2O$	246	1.0
Micronutrients			
1	H_3BO_3	2.86	1.0
2	$MnCl_2\cdot 4H_2O$	1.81	1.0
3	$ZnSO_4\cdot 7H_2O$	0.22	1.0
4	$CuSO_4\cdot 5H_2O$	0.08	1.0
5	$H_2MoO_4\cdot H_2O$	0.02	1.0
6	Fe-EDTA	37.33	1.0

Field experimental layout with treatments

A 2-year field trial was conducted during cotton growing seasons in 2018 and 2019 at Central Cotton Research Institute (CCRI), Multan, Pakistan (30°12N, 71°28E). The soil characteristics before sowing and after harvesting are given in Table 2. A total of 46 diverse cotton cultivars were initially screened for potassium uptake efficiency in sand culture experiment at deficient (0.26 $mmol\cdot L^{-1}$) and adequate (3.33 $mmol\cdot L^{-1}$) K levels. Amongst low, medium, and high K use efficiency cotton cultivars were reconfirmed in the hydroponics culture study (Akhtar et al. 2022a, b). The cultivars showing consistency in K-uptake were further evaluated for their performance in drought tolerance characteristics under field condition.

Five pre-selected cotton cultivars (four K-efficient cultivars, viz., CIM-554, CYTO-124, FH-142, IUB-2013, and one K non-efficient, BH-212) screened from the initial hydroponics culture experiment were tested under reduced irrigation (50% available water content; 50 AWC) and normal irrigation conditions (100% available water content; 100 AWC) with two levels of potassium (0 K_2O $kg\cdot ha^{-1}$ and 50 K_2O $kg\cdot ha^{-1}$). The field was cultivated to a depth of 30 cm and raised beds were prepared having dimensions of 0.2 m high, 3 m wide, and 4 m long. The plots were demarcated,

Table 2 The soil properties of experimental site before and after harvest of cotton growing seasons 2018 and 2019 at 30 cm depth

	Texture Class	Soil pH	EC /($dS\cdot m^{-1}$)	Organic matter /%	NO_3-N / ($mg\cdot kg^{-1}$)	$NaHCO_3$-P / ($mg\cdot kg^{-1}$)	NH_4OAC–K / ($mg\cdot kg^{-1}$)	Bulk density
Cotton growing season 2018								
Before sowing	Silt loam	8.13	2.12	0.92	5.52	10.2	105	1.41
After harvesting	Silt loam	8.09	2.09	0.94	5.42	9.60	103	1.39
Cotton growing season 2019								
Before sowing	Silt loam	8.15	2.13	0.95	5.43	10.0	108	1.42
After harvesting	Silt loam	8.11	2.10	0.97	5.40	9.80	101	1.38

and treatments were assigned based on a randomized complete block design (RCBD) split-split plot arrangement, irrigation in the main plot, potassium in the sub-plot, and cultivars in the sub-sub plot with four replications. The soil samples were collected from each plots for physio-chemical characteristics before and after sowing (Table 2). The recommended dose of nitrogen (150 kg·ha^{-1}) and phosphorus (60 kg·ha^{-1}), whereas, potassium was applied according to the treatment plan. The phosphorus and potassium were applied at the time of sowing and nitrogen was applied in three split doses. The cotton seeds were sown by dibbling method and thinning was done after 15 days of sowing to maintain the plant to plant and row to row distance of 25 cm × 75 cm. Weeds were controlled by manual hoeing and by using weedicides. The insect pests were controlled by using recommended pesticides. Soil moisture contents were regularly measured by using a moisture meter (TDR-200; Spectrum Technologies Inc., Aurora, IL, USA) to take account of the volumetric soil water content which served as the basis of irrigation. The full quantity of irrigation was applied in normal irrigation plots, while in the reduced irrigation plot, only half the amount of water (50%) was applied. The irrigation was measured with the help of Cut-throat Flume. The cut-off irrigation was applied in the second week of September during both growing seasons.

Experimental data collection

Seed cotton yield and gas exchange parameters

The bolls were picked from randomly selected five plants (one square meter) from each plot, then, an average of all replications was recorded. The seed cotton was picked from the entire plots and the yield was converted into kg·ha^{-1}. The bolls were air-dried to obtain the constant weight, then, the weight of the individual boll was measured using a digital balance. The portable photosynthesis system CL-340 (CID-USA) were used for gas exchange parameters. The forth young leaf from the top of five plants were selected randomly from each treatments. These measurements were made during the day time after full sunshine between 10 AM to 12 PM. The reading was taken at 60 days after planting (DAP). Following traits were computed as reported by Ahmed et al. (2013); Net photosynthesis (PN = μmol (CO_2)·m^{-2}·s^{-1}), Transpiration rate (E = mmol (H_2O)·m^{-2}·s^{-1}), Stomatal conductance (gs = mmol (CO_2)·m^{-2}·s^{-1}).

Potassium use efficiency and water use efficiency

Potassium use efficiency (KUE) were calculated from the formula as suggested by Akhtar et al. (2022a, b).

$$\text{KUE}\ (\text{g}\cdot\text{mg}^{-1}) = \text{Seed cotton yield/Leaf K concentration}$$

The actual cumulative crop evapotranspiration (CCET) was estimated by multiplying the potential evapotranspiration (PET) with the appropriate value of the crop coefficient, which usually corresponds closely to the green crop cover as suggested by Doorenboss and Pruitt (1977).

Daily Penman's PET was calculated using the standard program of "CROPWAT". The water-use-efficiency (WUE) was calculated using the following formula:

$$\text{WUE}\ (\text{kg}\cdot\text{ha}^{-1}\cdot\text{mm}^{-1}) = (\text{Seed cotton yield})/\text{CCET} \times 100$$

where, CCET is the cumulative crop evapotranspiration.

Fiber quality parameters

Picking of cotton was done on maturity and ginned with a small-scale ginning machine. The samples were tested for fiber characteristics on High Volume Instruments (HVI-900A).

Statistical analysis

The data about cotton traits were analyzed with a linear model using the "lm" package in R (R Core Team 2021). The treatment means were compared by using the least significant difference (LSD) test at a significance level of $P < 0.05$ for hydroponic study. A separate analysis was done for the years 2018 and 2019 for field study. The mean separation of the cultivars within the irrigation levels and within the potassium levels was done at $P < 0.05$ using least square mean and adjusted Tukey Multiple Test comparison procedures using the "means" package in R (Lenth 2020).

Results

Expression profiles of *GhHAK5aD* in cotton cultivars (hydroponic study)

It has been reported that the transcript levels of *GhHAK5aD* were strongly induced upon K^+ starvation in the cotton roots (Wang et al. 2019). To explore the effect of K^+ deficiency on *GhHAK5aD* expression in the selected cotton cultivars, first, we have detected the transcript levels of *GhHAK5aD* in K-efficient cotton cultivar, CIM-554, both in root and shoot under adequate (+K) and low K (-K) conditions. When cotton seedlings were at the three-leaf stage, we transferred seedlings from adequate (+K) hydroponic solution into the low solution (-K) and grew for another 8 days. As shown in Fig. 1A, the expression patterns of *GhHAK5aD* were similar in both root and shoot, however, this effect was more pronounced in roots upon K^+ deficiency, compared with the results under normal condition. Next, we analyzed the expression patterns of *GhHAK5aD* in selected K-inefficient (BH-212 and FH-901) and K-efficient (CIM-554 and CYTO-124 and FH-142) cultivars under +K and –K conditions in both root and shoot. Under the normal condition, transcript levels of *GhHAK5aD* were similar in both K-inefficient and K-efficient cultivars (Fig. 1B). On the other hand, when we determined *GhHAK5aD* expression in low K condition, we clearly observed that transcript levels of *GhHAK5aD* were significantly greater in K-efficient cultivars than that of K-inefficient cultivars in roots (Fig. 1B). Expectedly, we did not observe the differences of *GhHAK5aD* expression pattern between K-inefficient and K-efficient cultivars under both +K and −K conditions in the shoot (Fig. 1C). This indicates that *GhHAK5a* is an important regulator of K^+ uptake in roots under K^+ deficiency in cotton.

K concentration

The data showed that K accumulation in the shoot and root of cotton cultivars was reduced at the low K (-K) levels compared with the adequate K (+K) levels. A significant variation was found for K concentration in the shoot, root, among K levels, cultivars, and K levels × cultivars interaction at $P < 0.05$ (Fig. 2D & E). The overall reduction in root K concentration was 56.3% at the low K level compared with the adequate K supply. At the low K level, the root K concentration ranged from 50.6 to 102.2 (μmol·g^{-1} DW) in cotton cultivars with a mean of 78.4 μmol·g^{-1} DW, whereas, at the adequate K level, it ranged from 97.1 – 245.2 μmol·g^{-1} DW, with a mean of 179.4 μmol·g^{-1} DW. The performance of the cultivars on the basis of K concentration, for root K concentration, the K efficient cultivars (FH-142, CIM-544, and CYTO-214) showed higer K concentration as compared with K inefficient (BH-212 and FH-901) at both K supply levels (Fig. 2D).

The K accumulation in the shoot was 19.2% greater than root at the low K level compared with the adequate K level. At the low K level, the shoot K concentration ranged from 180.2 to 255.2 μmol·g^{-1} DW in cotton cultivars with a mean value of 222.2 μmol·g^{-1} DW, whereas, at the adequate K level, it ranged from 197.0 – 343.5 μmol·g^{-1} DW, with a mean of 277.1 μmol·g^{-1} DW. The performance of the K efficient cultivars (FH-142, CIM-544, and CYTO-214) showed higher shoot K concentrations as compared with the K inefficient cultivars (BH-212 and FH-901) at both K supply levels (Fig. 2E).

Leaf area and chlorophyll content (SPAD value)

The low K supply caused a reduction in both leaf area (LA) and chlorophyll content (SPAD value) of cotton cultivars as compared with adequate K treatment (Fig. 3a & b). At the low K level, leaf area per plant ranged from 31.0 cm^2 for cultivar BH-212 to 46.2 cm^2 for FH-142, whereas, at the adequate K level, it ranged from 41.5 to 71.2 cm^2 in BH-212 and FH-142, respectively. An overall low K supply caused a 16.2% reduction in LA compared with an adequate K level. Similarly, the chlorophyll content (SPAD value) of cotton cultivars at a low K level ranged from 25.2 for cultivar BH-212 to 34.3 for FH-142 with a mean value of 30, whereas, at the adequate K level, it ranged from 35.2 to 47.3 with a mean SPAD value of 39, respectively. At the low K supply treatment, the overall reduction in the chlorophyll content of cotton cultivars was 29.0% compared with an adequate K supply level.

Leaf nitrogen, sodium, and calcium concentration

The statistical analysis revealed that nitrogen (N), sodium (Na), and calcium (Ca) concentration (%) in cotton leaves varied significantly among treatments, cultivars, and treatment × cultivar interaction (P <0.05) (Table 3). The data indicated that the N concentrations in leaves (1.94%) at a low K level decreased significantly (44.0%) compared with concentration (3.48%) at an adequate K supply level. The N concentrations ranged from 1.48% to 2.57% in cultivars BH-212 and MNH-886, with a mean concentration of 1.94% at the low K level, whereas, it ranged from 3.12% to 3.77% in BH-212 and MNH-886, with a mean value of 3.48% at the adequate K level. The comparison of cotton cultivars based on K efficiency ratio (KER) for N concentration indicated that seven cultivars including MNH-886 (68.1%), FH-142 (57.9%), CIM-554 (57.6%), CYTO-124 (56.9%), CIM-707 (56.4%), IUB-2013 (55.5%), and CIM-599 (52.6%) were more than 50% of their respective controls, whereas, the remaining two cultivars FH-901(48.4%) and BH-212 (47.5%) were ≤ 50% of the control, respectively. The Na concentration ranged from 0.09% to 0.19% in cultivars MNH-886 and BH-212, with a mean concentration of 0.13% at the low K level, whereas, it ranged from 0.06% to 0.12% in MNH-886 and BH-212, with a mean value of 0.09% at the adequate K level (Table 3). There was an 8.63% decrease in Ca concentration of the leaves at a low K supply level compared with the adequate K level in cotton cultivars. At the low K level, Ca concentration in leaves ranged between 2.10% to 2.55% in cultivars BH-212 and CIM-544, with a mean value of 2.41%, respectively. Whereas, it ranged from

(See figure on next page.)

Fig. 1 Effect of K^+ deficiency on the transcriptional expression of *GhHAK5aD* in cotton. **A** The relative expression levels of *GhHAK5aD* under adequate (+K) and K^+ low (-K) conditions in cotton cultivar CIM-554 in root and shoot. The expression levels in the root were normalized to 1. **B**, **C** K-inefficient (BH-212 and FH-901) and K-efficient (CIM-554, CYTO-124, and FH-142) cultivars at the three-leaf stage was transferred from adequate (+K) into K^+ low (-K) solutions and grown for another 8 days. Root (**B**) and Shoot (**C**) samples were collected for qRT-PCR analyses. Bars represent mean ± SD ($n = 3$ biological replicates). Statistical analysis was performed using two-way analysis of variance (ANOVA) and Tukey's post hoc test. Different letters denote significant differences ($P < 0.05$)

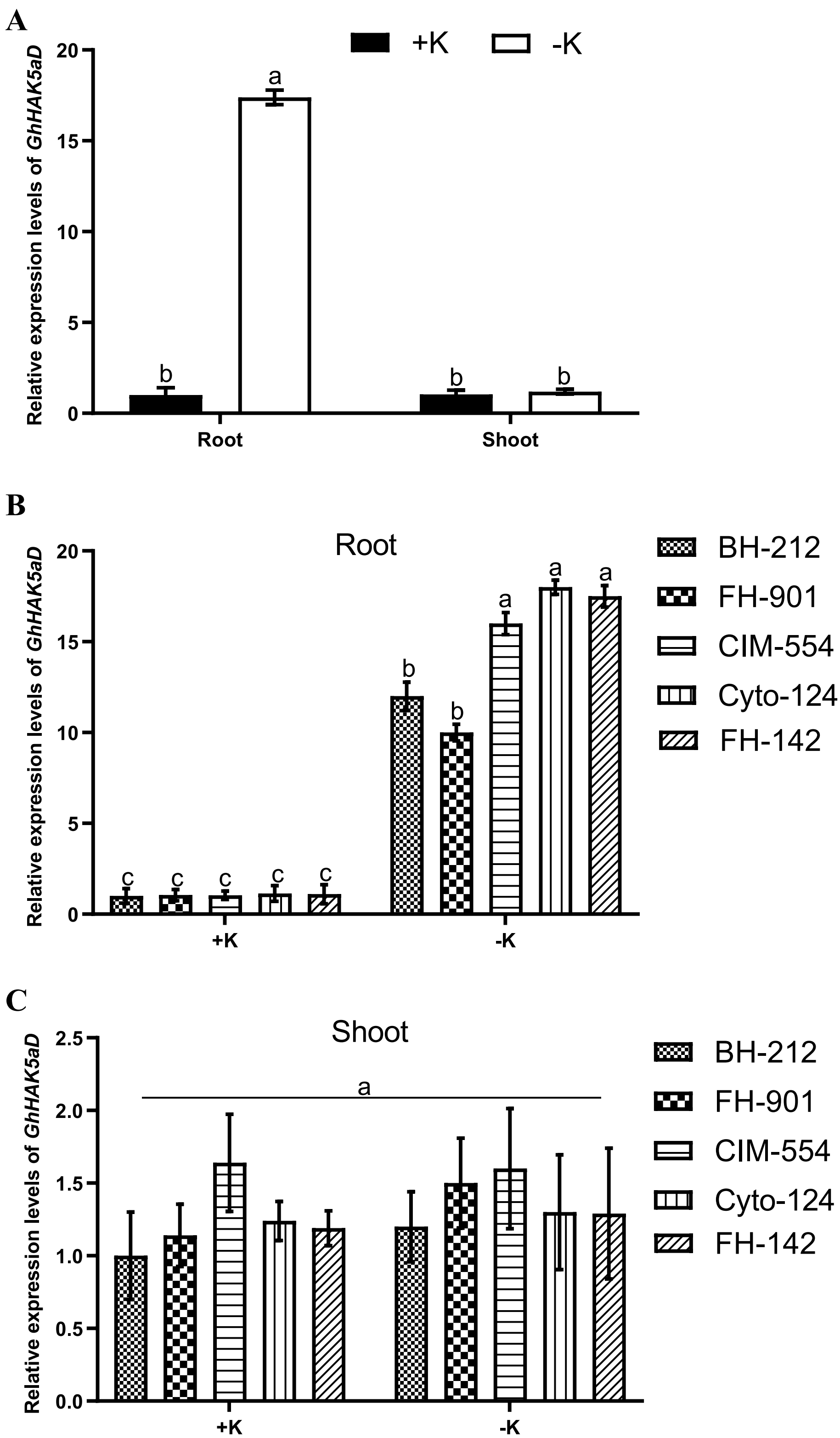

Fig. 1 (See legend on previous page.)

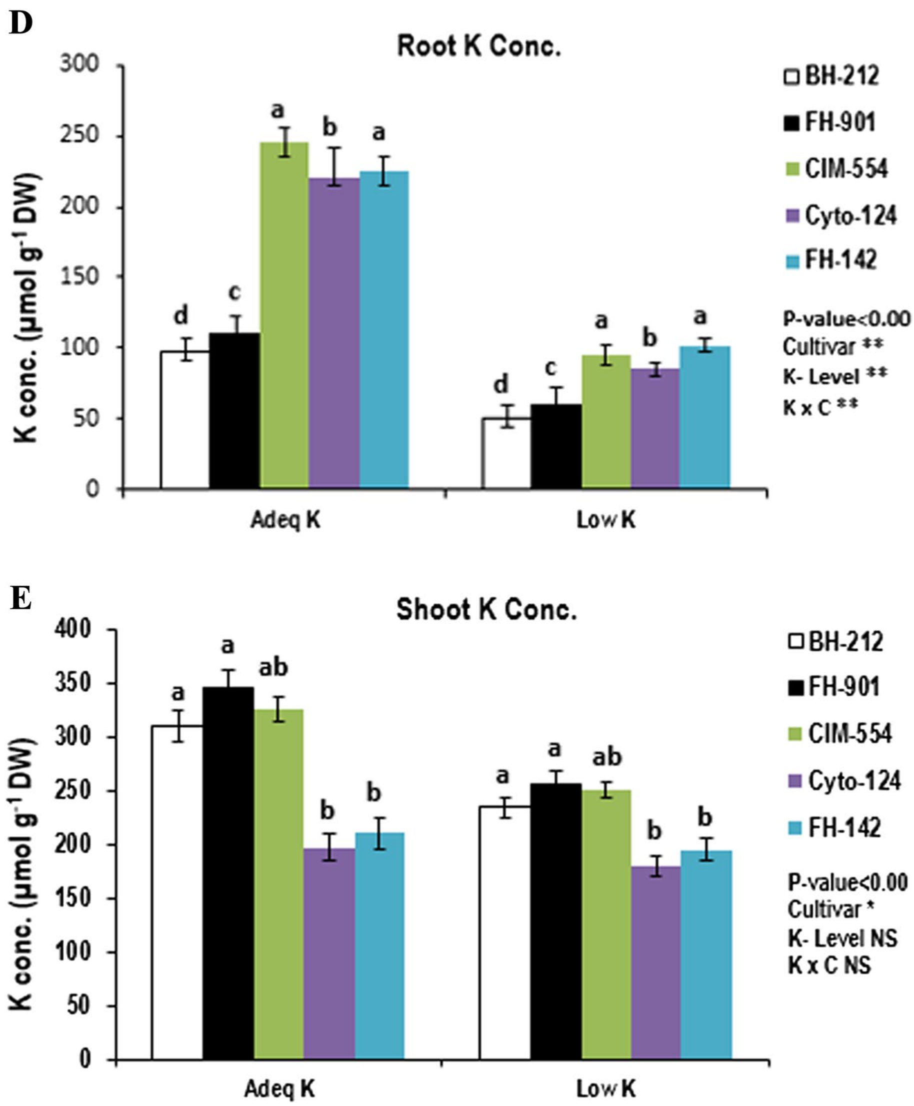

Fig. 2 Effect of K^+ deficiency on K concentration in cotton cultivars at the adequate and low K supply levels. **D** K concentration in roots. **E** K concentration in shoots. Bars represent mean ± SD ($n = 3$ replicates). Statistical analysis was performed using two-way analysis of variance (ANOVA) and Tukey's post hoc test. Different letters denote significant differences ($P < 0.05$)

2.41% to 2.75% in BH-212 and CIM-544, with a mean value of 2.62% at the adequate K level. The seven cultivars which maintained more than 90% of their KER for leaf Ca concentration at the low K supply level include CYTO-124, CIM-544, FH-142, MNH-886, CIM-707, IUB-2013, and CIM-599, respectively (Table 3).

The number of bolls per plant and boll weight (field study)

The main effect of irrigation levels, potassium levels, and cultivars on the number of bolls per plant were significant during both growing seasons in 2018 and 2019 at $P < 0.05$ (Table 4). The application of potassium in both growing seasons showed a higher number of bolls per plant as compared with no K application. The normal irrigation conditions showed a higher number of bolls per plant in both growing seasons 2018 and 2019 as compared with 50% reduced irrigation conditions. Among the cultivars, FH-142 performed better as compared with other cultivars (BH-212, IUB-2013, CIM-554, and CYTO-124). BH-212 showed the lowest response for the number of bolls per plant in both growing seasons. FH-142 registered an increase of 46.7%, 22.2%, 10.0%, and 10.0% in bolls per plant as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, in normal irrigation with and without potassium application in the 2018 growing season (Table 5).

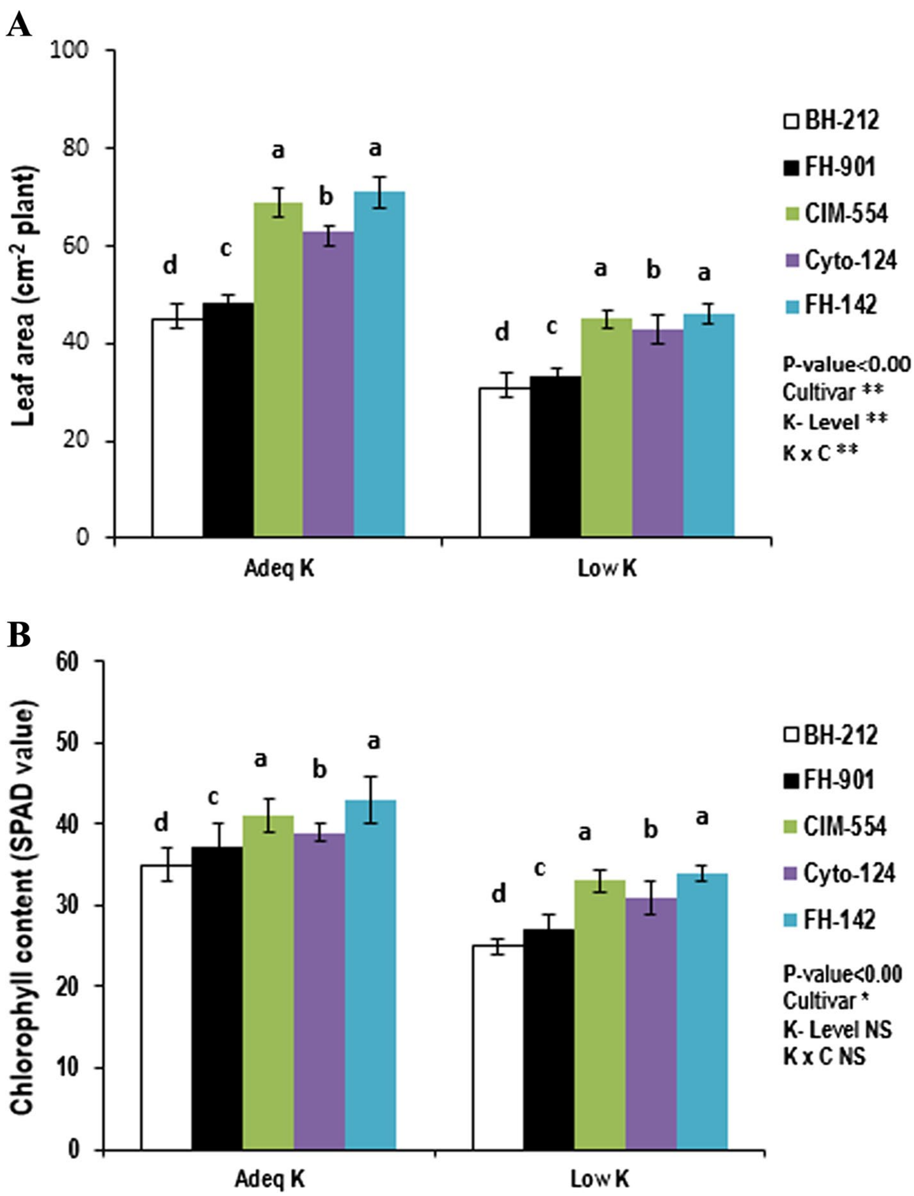

Fig. 3 Effect of K^+ deficiency on K concentration in cotton cultivars at the adequate and low K supply levels. **a** Leaf area. **b** chlorophyll content (SPAD value). Bars represent mean ± SD ($n = 3$ replicates). Statistical analysis was performed using two-way analysis of variance (ANOVA) and Tukey's post hoc test. Different letters denote significant differences ($P < 0.05$)

The main effect of irrigation levels, potassium levels, and cultivars was significant on boll weight in both growing seasons 2018 and 2019 at $P < 0.05$, except the main effect of K level in the growing season 2018. CYTO-124 exhibited an increase of 14.8%, 12.2%, and 5.1% as compared with BH-212, IUB-2013, CIM-554, and FH-142, respectively, with K application at 50 kg·ha^{-1} under normal irrigation in the growing season 2018 (Table 5).

Seed cotton yield and net photosynthetic rate

The main effect of irrigation levels, potassium levels, and cultivars on seed cotton yield in both growing seasons 2018 and 2019 was significant at $P < 0.05$ (Table 6). The interaction effect of irrigation levels × potassium rate was also significant in cotton-growing season 2018. The reduced irrigation decreased the seed cotton yield (SCY) in both growing seasons as compared with normal irrigation conditions. FH-142 showed an increase of 22.3%, 4.9%, 2.4%, and 1.4% as compared with BH-212, IUB-2013, CYTO-124, and CIM-554 with an application of K at 50 kg·ha^{-1} in normal irrigation during the growing season 2018. FH-142 produced 18.2% and 20.4% higher seed cotton yield with K application at 50 kg·ha^{-1} over no potassium

Table 3 Leaf nitrogen, sodium, and calcium concentrations of nine cotton cultivars at different K supply levels in hydroponic culture

Cultivars	N /%			Na /%			Ca /%		
	Adequate K	Low K	KER	Adequate K	Low K	KER	Adequate K	Low K	KER
MNH-886	3.77 ± 0.09	2.57 ± 0.14	68.1	0.07 ± 0.02	0.10 ± 0.01	142.9	2.67 ± 0.21	2.49 ± 0.11	93.3
Cyto-124	3.63 ± 0.12	2.07 ± 0.20	56.9	0.06 ± 0.03	0.09 ± 0.02	150.0	2.62 ± 0.18	2.52 ± 0.16	96.2
CIM-707	3.37 ± 0.18	1.90 ± 0.10	56.4	0.09 ± 0.02	0.13 ± 0.01	144.4	2.76 ± 0.12	2.54 ± 0.13	92.0
FH-142	3.57 ± 0.09	2.07 ± 0.13	57.9	0.08 ± 0.01	0.11 ± 0.03	137.5	2.70 ± 0.13	2.47 ± 0.10	91.5
BS-13	3.47 ± 0.15	1.92 ± 0.08	55.5	0.09 ± 0.04	0.13 ± 0.04	144.4	2.64 ± 0.10	2.51 ± 0.11	95.1
CIM-554	3.67 ± 0.03	2.11 ± 0.23	57.6	0.07 ± 0.01	0.10 ± 0.01	136.4	2.75 ± 0.22	2.55 ± 0.13	92.6
CIM-599	3.43 ± 0.19	1.81 ± 0.08	52.6	0.10 ± 0.03	0.15 ± 0.08	150.0	2.58 ± 0.10	2.43 ± 0.15	94.2
BH-212	3.12 ± 0.10	1.48 ± 0.05	47.5	0.12 ± 0.04	0.19 ± 0.09	158.3	2.47 ± 0.13	2.10 ± 0.13	85.0
FH-901	3.27 ± 0.09	1.58 ± 009	48.4	0.11 ± 0.02	0.17 ± 0.07	154.5	2.41 ± 0.11	2.12 ± 0.09	87.8
Mean	**3.48**	**1.94**	**55.7**	**0.09**	**0.13**	**146.5**	**2.62**	**2.41**	**92.0**
F test:									
Cultivars (C)	**0.5384****			**0.00532****			**0.1405****		
K levels (K)	**18.5136****			**0.01289****			**0.3006****		
C×K interaction	**0.0236 (NS)**			**0.00027 (NS)**			**0.0092****		
LSD – value									
Cultivars (C)	**0.2924**			**0.0264**			**0.0395**		
K levels (K)	**0.1688**			**0.0152**			**0.0228**		

NS no significant difference

**different at P<0.01

application treatment in both growing seasons, respectively (Table 6).

The main effects of irrigation levels, potassium levels, and cultivars were significant for the net photosynthetic rate. The interaction effect of water level × potassium level was also significant (Table 4). The normal irrigation with potassium application at 50 kg·ha^{-1} showed a higher response as compared with reduced irrigation with no potassium application. The net photosynthetic rate was higher in the cotton-growing season 2018 as compared with the cotton-growing season 2019. Overall, the response of the cotton cultivar FH-142 was higher on net photosynthetic rate as compared with other cultivars (BH-212, IUB-2013, CIM-554, and CYTO-124), respectively (Table 6). It improved the net photosynthetic rate by 57.4%, 17.2%, 1.8%, and 11.1% when compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, under normal irrigation with K application at 50 kg·ha^{-1}.

The main effect of irrigation levels, potassium levels, and cultivars was found significant on the stomatal conductance in both growing seasons 2018 and 2019 at $p<0.05$ (Table 4). The interaction effect of potassium levels × irrigation levels was also significant. The FH-142212 showed higher stomatal conductance in both normal irrigation and reduced irrigation under potassium application and no potassium application. The FH-142 showed an increase of 33.2, 11.8, 9.7, 2.9, and 5.9% as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, under K application at 50 kg ha^{-1} with reduced irrigation in both cotton-growing seasons (Table 6).

Transpiration rate and stomatal conductance

The main effect of irrigation levels and potassium levels was significant on the transpiration rate at $P<0.05$ (Table 4) in both growing seasons 2018 and 2019. A higher transpiration rate was observed with no potassium application as compared with K application. The reduced irrigation resulted in a decrease in transpiration rate in both potassium applied and no potassium applied plots. The mixed effect of cultivars was seen on the transpiration rate. FH-142 under normal irrigation with no potassium application showed an increase in transpiration rate by 30.0%, 5.3%, 0.4%, and 2.1% as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, in the cotton-growing season 2018 (Table 7). In the 2019 cotton growing season, CIM-554 showed an increase in transpiration rate by 27.3%, 1.8%, 1.1%, and 2.8% as compared with BH-212, IUB-2013, CYTO-124, and FH-142, respectively, under normal irrigation with no K application (Table 7).

The main effect of irrigation levels, potassium levels, and cultivars was found significant on the stomatal conductance in both growing seasons 2018 and 2019 at $P<0.05$ (Table 4). The interaction effect of potassium levels × irrigation levels was also significant. FH-142 showed higher stomatal conductance in both normal irrigation and reduced irrigation under potassium

Table 4 *P* values of main and interactive effect of irrigation levels, potassium levels, and cultivars on leaf, seed lint, fruit K concentration, and fiber traits during 2018, 2019 crop growing seasons

	Bolls per plant	Boll weight	Seed cotton yield	Micronaire	Fiber strength	Degree of reflectness	Fiber elongation	GOT	Seed index	Short fiber index
Cotton growing season (2018)										
Irrigation level (W)	0.018	0.020	< 0.001	0.010	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Potassium level (K)	< 0.001	0.050	< 0.001	0.020	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Cultivars (C)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
W × K	0.978	0.870	0.238	0.790	< 0.001	0.730	0.600	0.340	0.090	< 0.001
W × C	0.995	1.000	0.960	0.120	< 0.001	0.630	0.830	0.080	0.040	< 0.001
K × C	0.878	0.920	0.161	0.830	< 0.001	0.100	0.250	0.880	0.050	0.350
W × K × C	0.972	1.000	0.822	0.940	< 0.001	0.850	0.680	0.510	0.150	0.040
Cotton growing season (2019)										
Irrigation level (W)	< 0.001	0.020	< 0.001	0.18	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Potassium level (K)	< 0.001	0.010	< 0.001	0.20	< 0.001	< 0.001	0.02	< 0.001	< 0.001	< 0.001
Cultivars (C)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
W × K	0.184	0.740	0.318	0.86	0.63	0.76	0.66	0.28	0.11	< 0.001
W × C	0.797	0.970	0.948	0.82	0.36	0.65	0.99	0.10	0.60	< 0.001
K × C	0.773	0.790	0.089	0.98	0.10	0.13	0.96	0.69	0.58	0.04
W × K × C	0.889	0.991	0.783	1.00	0.80	0.95	1.00	0.67	0.87	0.01

The values mean ± standard deviation of four replications. The values with same letter (s) within irrigation level and potassium rate are statistically non-significant at $P < 0.05$

Table 5 Impact of reduced irrigation and potassium levels on bolls per plant and boll weight in two cotton growing seasons 2018 and 2019

Cultivars	Bolls per plant				Boll weight /(g·plant^{-1})			
	Reduced irrigation		Normal irrigation		Reduced irrigation		Normal irrigation	
	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})
Cotton growing season (2018)								
BH-212	15.0 ± 2.04a	19.0 ± 2.48a	18.0 ± 2.97a	20.0 ± 4.6a	1.98 ± 0.07a	2.04 ± 0.10a	2.12 ± 0.08a	2.16 ± 0.18a
IUB-2013	18.0 ± 2.97ab	23.0 ± 2.97ab	20.0 ± 2.2ab	24.0 ± 2.48ab	2.06 ± 0.04a	2.16 ± 0.08a	2.18 ± 0.06ab	2.21 ± 0.17ab
CIM-554	20.0 ± 2.2ab	25.0 ± 2.04ab	22.0 ± 2.48ab	28.0 ± 1.65b	2.17 ± 0.09ab	2.29 ± 0.07b	2.29 ± 0.05b	2.39 ± 0.03b
CYTO-124	22.0 ± 2.45b	27.0 ± 3.49b	24.0 ± 2.48b	30.0 ± 1.83b	2.21 ± 0.08b	2.37 ± 0.11b	2.31 ± 0.07b	2.48 ± 0.14b
FH-142	22.0 ± 2.45b	27.0 ± 3.49b	24.0 ± 5.1b	30.0 ± 2.04b	2.18 ± 0.09b	2.23 ± 0.11ab	2.29 ± 0.07b	2.36 ± 0.09ab
Cotton growing season (2019)								
BH-212	14.2 ± 2.3a	15.0 ± 1.8a	16.0 ± 2.5a	17.7 ± 2.66a	1.97 ± 0.07a	2.03 ± 0.09a	2.10 ± 0.08a	2.14 ± 0.18a
IUB-2013	15.2 ± 1.3a	18.3 ± 0.85ab	18.0 ± 1.6ab	21.0 ± 1.87ab	2.05 ± 0.04a	2.17 ± 0.09a	2.17 ± 0.06ab	2.21 ± 0.17ab
CIM-554	17.7 ± 1.8ab	18.0 ± 1.47ab	19.0 ± 2.1b	21.7 ± 1.87ab	2.16 ± 0.09ab	2.32 ± 0.07ab	2.28 ± 0.05ab	2.46 ± 0.14b
CYTO-124	16.0 ± 0.8ab	18.7 ± 1.3ab	20.0 ± 1.6b	24.0 ± 1.41b	2.20 ± 0.09b	2.43 ± 0.08b	2.32 ± 0.05ab	2.46 ± 0.14b
FH-142	19.0 ± 1.3b	20.0 ± 1.1b	20.0 ± 1.7b	25.0 ± 1.96b	2.17 ± 0.08ab	2.25 ± 0.11ab	2.35 ± 0.06b	2.37 ± 0.09ab

The values mean ± standard deviation of four replications. The values with different letter (s) within irrigation level and potassium rate are statistically significant at $P < 0.05$

Table 6 Impact of reduced irrigation and potassium level on seed cotton yield and net photosynthetic rate in two cotton growing seasons 2018 and 2019

Cotton cultivars	Seed cotton yield /(kg· ha^{-1})				Net photosynthetic rate /(μmol (CO_2)·m^{-2}·s^{-1})			
	Reduced irrigation		Normal irrigation		Reduced irrigation		Normal irrigation	
	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})
Cotton growing season (2018)								
BH-212	900 ± 130a	1090 ± 140a	1300 ± 135a	1460 ± 160a	21.5 ± 2.89a	23.75 ± 2.75a	23.4 ± 2.23a	27 ± 3.92a
IUB-2013	1400 ± 160b	1700 ± 135b	1730 ± 125b	2030 ± 117b	28.25 ± 4.79b	30.75 ± 4.03b	32.12 ± 3.23b	36.25 ± 4.79b
CIM-554	1430 ± 150bc	1740 ± 130b	1780 ± 150bc	2160 ± 170b	30.50 ± 3.11b	33.5 ± 3.70b	36.38 ± 4.89ab	41.75 ± 4.87b
CYTO-124	1500 ± 145bc	1760 ± 150bc	1800 ± 135bc	2220 ± 185b	28.75 ± 4.27b	34 ± 3.56b	37.5 ± 4.05c	38.25 ± 5.12b
FH-142	1540 ± 140c	1860 ± 125c	1850 ± 126c	2300 ± 189b	29.38 ± 4.07b	34.5 ± 4.65b	36.77 ± 3.11c	42.5 ± 4.43b
Cotton growing season (2019)								
BH-212	840 ± 120a	1040 ± 130a	1260 ± 135a	1400 ± 165a	19.23 ± 4.75a	20.05 ± 3.53a	19.02 ± 4.71a	26.38 ± 3.27a
IUB-2013	1350 ± 160b	1650 ± 125b	1680 ± 110b	1980 ± 136b	25.02 ± 3.82b	25.82 ± 5.73bc	23.62 ± 1.97b	35.5 ± 2.89b
CIM-554	1370 ± 150bc	1690 ± 130bc	1720 ± 150bc	2120 ± 168b	28.75 ± 3.45b	32.88 ± 3.73c	30.75 ± 2.63b	36.92 ± 3.82b
CYTO-124	1440 ± 130bc	1720 ± 160bc	1750 ± 115bc	2120 ± 146b	25.2 ± 3.87b	29.77 ± 2.24bc	28.4 ± 2.24b	33.38 ± 3.54b
FH-142	1480 ± 140c	1800 ± 128c	1800 ± 152b	2250 ± 121b	26.45 ± 5.7b	32.42 ± 3.25c	30.5 ± 3.42b	38.05 ± 2.66b

The values mean ± standard deviation of four replications. The values with same letter (s) within irrigation level and potassium rate are statistically non-significant at $P < 0.05$

application and no potassium application. It showed an average increase of 37.4%, 9.8%, 3.8%, and 4.0% as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, under K application at 50 kg·ha^{-1} with reduced irrigation in both cotton-growing seasons (Table 7).

Fibre micronaire and strength

The main effects of water level, potassium level, and cultivars were found significant on fibre micronaire in the cotton-growing season 2018, while only main effect of cultivar was significant in the cotton-growing season 2019 at $P < 0.05$ (Fig. 4). The increase in micronaire was

Table 7 Impact of reduced irrigation and potassium level on transpiration rate and stomatal conductance in two cotton growing seasons 2018 and 2019

Cotton Cultivars	Transpiration rate /(mmol (H_2O)·m^{-2}·s^{-1})				Stomatal conductance /(mmol (CO_2)·m^{-2}·s^{-1})			
	Reduced irrigation		Normal irrigation		Reduced irrigation		Normal irrigation	
	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})	K level (0 kg·ha^{-1})	K level (50 kg·ha^{-1})
Cotton growing season (2018)								
BH-212	2.93 ± 1.0a	1.79 ± 0.87a	3.67 ± 0.82a	1.87 ± 0.54a	108.5 ± 9.73a	111.0 ± 5.07a	116.5 ± 6.91a	134.7 ± 7.72a
IUB-2013	3.81 ± 1.43b	2.02 ± 1.25a	4.53 ± 1.52a	2.14 ± 0.75a	131.6 ± 12.13b	138.7 ± 3.55b	141.8 ± 5.14ab	159.4 ± 12.27ab
CIM-554	4.02 ± 1.17b	2.18 ± 1.33a	4.75 ± 1.07a	3.41 ± 1.17a	136.5 ± 2.4b	147.3 ± 9.66b	146.7 ± 6.99b	180.7 ± 12.44b
CYTO-124	3.94 ± 1.43b	2.22 ± 0.97a	4.67 ± 1.55a	2.33 ± 1.11a	127.2 ± 3.59b	145.7 ± 9.14b	149.6 ± 3.63b	170.5 ± 6.95b
FH-142	3.95 ± 1.69b	2.25 ± 1.02a	4.77 ± 1.13a	2.26 ± 0.67a	140.9 ± 7.38b	151.8 ± 5.50b	152.4 ± 23.58b	183.4 ± 14.25b
Cotton growing season (2019)								
BH-212	2.68 ± 0.99a	1.67 ± 0.87a	3.52 ± 0.81a	2.08 ± 0.95a	103.9 ± 10.86a	107.33 ± 4.68a	114.3 ± 5.56a	130.75 ± 9.35a
IUB-2013	3.65 ± 0.68b	2.14 ± 0.9b	4.40 ± 1.51b	2.04 ± 0.36a	122.4 ± 12.67b	134.55 ± 6.56b	139.5 ± 4.91ab	153.65 ± 9.38ab
CIM-554	3.48 ± 0.43b	2.12 ± 1.36b	4.48 ± 1.29b	3.13 ± 0.83b	134.1 ± 1.49b	141.88 ± 8.25b	143.85 ± 7.47b	168.5 ± 11.1b
CYTO-124	3.50 ± 1.31b	2.10 ± 0.98b	4.43 ± 1.52b	2.20 ± 0.50a	120.3 ± 2.70ab	142.82 ± 8.94b	145.78 ± 4.72b	165.07 ± 6.14b
FH-142	3.64 ± 0.51b	2.20 ± 0.75b	4.36 ± 1.17b	2.18 ± 0.72a	134.0 ± 9.83b	148.4 ± 11.21b	149.05 ± 24.33b	171.8 ± 15.16b

The values mean ± standard deviation of four replications. The values with same letter (s) within irrigation level and potassium rate are statistically non-significant at $P < 0.05$

3.6%, 4.7%. 7.8,% 3.4%, and 6.7% in BH-212, IUB-2013, CIM-554, CYTO-124, and FH-142 with potassium application at 50 kg·ha^{-1} over no potassium application under reduced irrigation conditions during the cotton growing season 2018 (Fig. 4).

The main effect of irrigation levels, potassium levels, and cultivars were significant on the fiber strength in both cotton growing seasons 2018 and 2019, however, the interaction effects of irrigation levels, potassium levels, irrigation levels × cultivars, potassium levels × cultivars, and potassium levels × irrigation levels were significant only during the cotton growing season 2019 at $P < 0.005$ (Fig. 4). Overall, CYTO-124 showed higher values of fiber strength in both cotton growing seasons with and without the application of potassium under both irrigation levels. It showed 10.8%, 3.8%, 2.5%, and 2.1% increase in fiber strength as compared with BH-212, IUB-2013, CIM-554, and FH-142 with K application at 50 kg·ha^{-1} under reduced irrigation conditions during the cotton growing season 2019 (Fig. 4).

Fiber elongation and length

The main effects of water level, potassium level, and cultivars were significant on the fiber elongation in both cotton growing seasons 2018 and 2019 at $P < 0.05$ (Fig. 5). The reduced irrigation conditions decreased the fiber elongation as compared with the normal irrigation conditions in both cotton growing seasons 2018 and 2019. The reduced irrigation conditions with the application of K at 50 kg·ha^{-1} showed a decrease of 4.3%, 3.1%, 4.5%, 5.8%, and 5.6% in BH-212, IUB-2013, CIM-554, CYTO-124, and FH-142 as compared with the normal irrigation level during both the cotton growing season on average basis (Fig. 5). The main effects of irrigation levels, potassium levels, and cultivar was significant on the fiber length in both cotton growing seasons at $p < 0.05$ (Fig. 5). The K application showed an increase in fiber length in normal and reduced irrigation conditions in both cotton growing seasons 2018 and 2019 (Fig. 5). The K application showed an increase of 20.4%, 5.0%, 5.4%, 14.0%, and 13.5% in BH-212, IUB-2013, CIM-554, CYTO-124, and FH-142 as compared with no K application under the reduced irrigation conditions on average basis during both the cotton growing season (Fig. 5).

Ginning turnout

The main effects of irrigation levels, potassium levels, and cultivars were significant on ginning turnout in both cotton growing seasons 2018 and 2019 at $P < 0.05$ (Fig. 6). The potassium application in both cotton growing seasons under the reduced irrigation and normal irrigation conditions showed an increase in ginning turnout (GOT) in both cotton growing seasons. The potassium application showed an increase of GOT by 12.0%, 11.0%, 4.8%, 5.8%, and 6.7% in the reduced irrigation condition, while 6.1%, 5.8%, 6.5%, 5.2%, and 3.5% in the normal irrigation condition in BH-212, IUB-2013, CIM-554, CYTO-124, and FH-142, respectively, on average basis across the cotton growing seasons (Fig. 6).

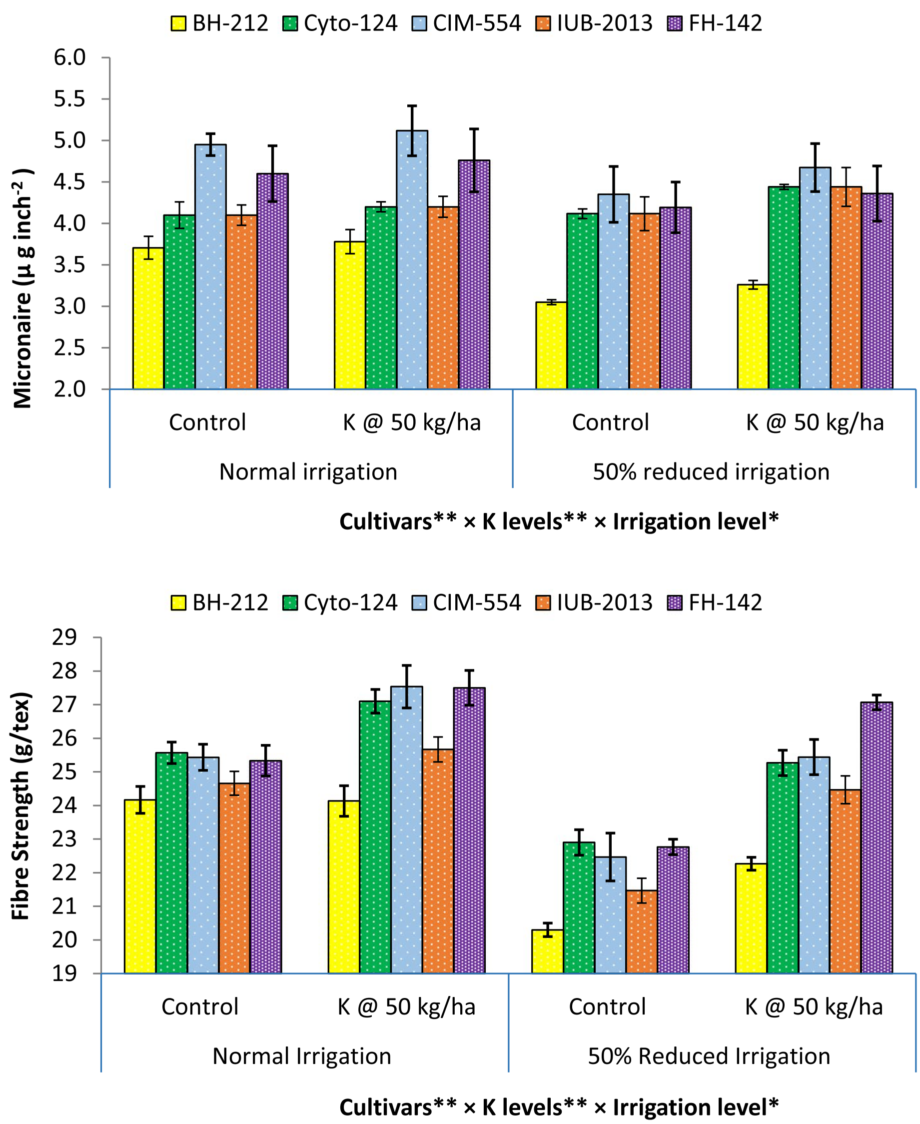

Fig. 4 The impact of irrigation and potassium levels on the micronaire and fiber strength in five cotton cultivars (Data is the average of 2 years). Error bars indicate the standard error of four replications

Potassium and water use efficiency (KUE and WUE)

The main effects of potassium levels and cultivars were significant on KUE in both growing seasons at $P < 0.05$. The interactions of irrigation levels, potassium levels, and potassium levels × cultivars on KUE were also significant during both cotton growing seasons at $P < 0.05$ (Fig. 7). The KUE among cultivars increased under normal irrigation conditions as compared with the reduced irrigation conditions with and without potassium application. FH-142 showed higher KUE over other cultivars under both irrigation levels. It showed an increase in KUE by 20.1%, 8.3%, 4.7%, and 4.1% as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, under the reduced irrigation conditions with the potassium application at 50 kg·ha^{-1} during both cotton growing seasons (Fig. 7). Whereas FH-142 showed an increase in KUE by 17.8%, 10.9%, 7.5%, and 2.7% as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, under the reduced irrigation conditions without K application during both cotton growing seasons (Fig. 7).

The main effects of potassium level and cultivars were significant on WUE in both growing seasons at $P < 0.05$. The interactions of irrigation levels, potassium levels, and potassium levels × cultivars on WUE were also significant during both cotton growing seasons at $P < 0.05$ (Fig. 7). The WUE among cultivars increased under the reduced irrigation conditions as compared with the normal irrigation conditions with and without potassium application. FH-142 showed a higher WUE over other cultivars under both irrigation levels. It showed an increase in WUE by

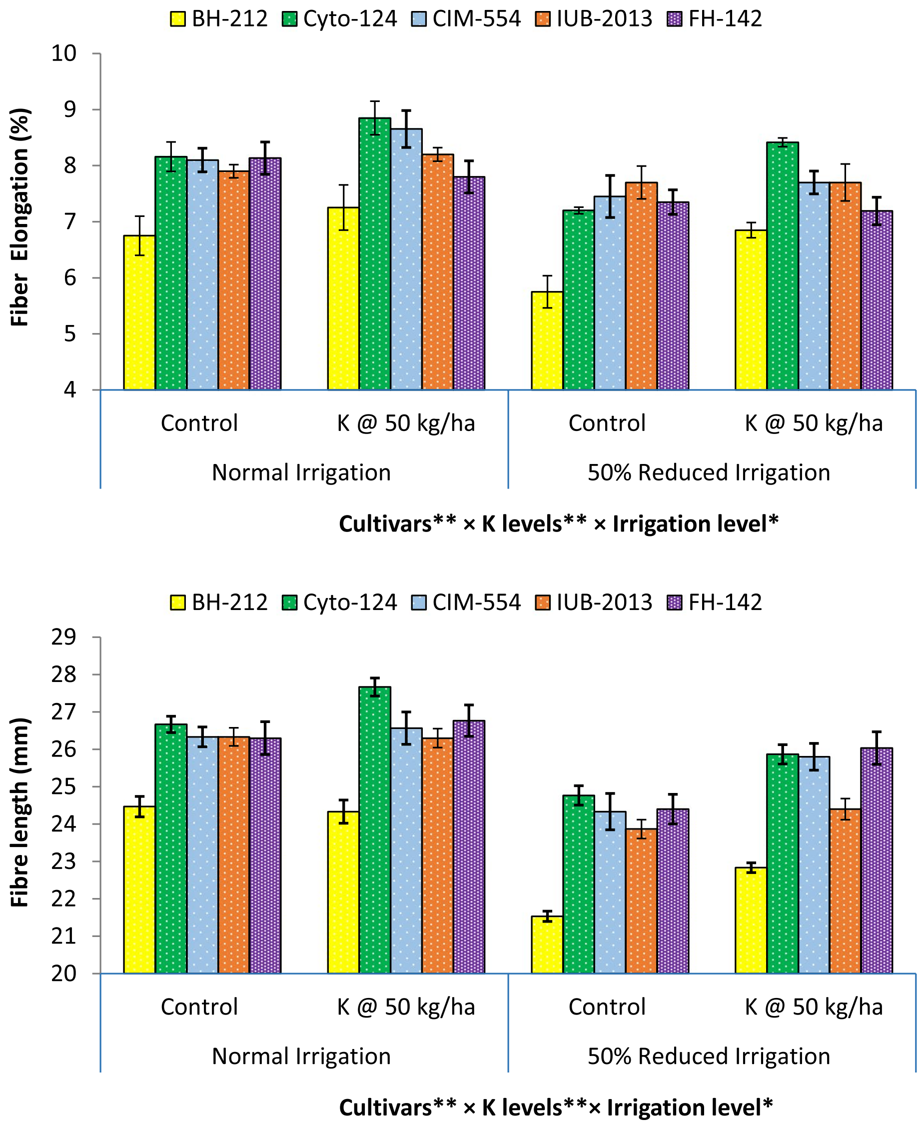

Fig. 5 The impact of irrigation and potassium levels on the fiber length and elongation in five cotton cultivars (Data is the average of 2 years). Error bars indicate the standard error of four replications

41.6%, 8.4%, 6.3%, and 5.1% as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, under the reduced irrigation conditions with K application at 50 kg·ha^{-1} during both cotton growing seasons (Fig. 7). Whereas FH-142 showed an increase in WUE by 36.5%, 12.2%, 6.3%, and 3.8% as compared with BH-212, IUB-2013, CIM-554, and CYTO-124, respectively, under normal irrigation conditions with K application during both cotton growing seasons (Fig. 7).

Discussion

HAK gene, which is remarkably induced upon K^+ deficiency in roots, has been identified in other plant species such as *AtHAK5* in Arabidopsis (Grabov 2007), *OsHAK5* in rice (Yang et al. 2014), and *ThHAK5* in *Thellungiella halophila* (Alemán et al. 2009). Therefore, in hydroponic study, we have measured the expression level of the *GhHAK5aD* gene in selected K-efficient (CIM-554, CYTO-124, and FH-142) and inefficient (BH-212 and FH-901) cultivars under +K and −K conditions in both root and shoot. In normal conditions, transcript levels of *GhHAK5aD* were similar in both K-inefficient and K-efficient cultivars. On the other hand, when we determine *GhHAK5aD* expression in K deficient condition, it was clearly observed that its transcript levels were significantly greater in K efficient cultivars than that of K inefficient cultivars in roots.

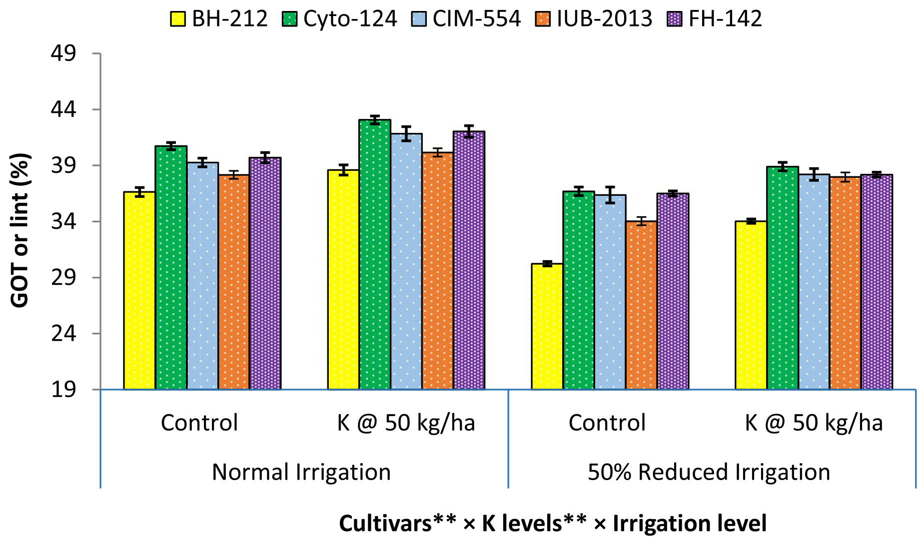

Fig. 6 The impact of irrigation and potassium levels on the lint % in five cotton cultivars during the growing season 2018–2019 (Data is the average of 2 years). Error bars indicate the standard error of four replications

Our results are supported by Wang et al. (2019) and Azeem et al. (2021).

After that field study was conducted to evaluate the performance of five cotton cultivars (BH-212, IUB-2013, CIM-554, CYTO-124, and FH-142) under reduced irrigation and normal irrigation conditions with and without application of potassium fertilizers in 2 years of cotton-growing seasons 2018 and 2019 in arid climatic conditions. The results revealed that stress conditions badly affect the performance of all cultivars as compared with no-stress conditions. However, K application under drought conditions was found to be helpful to mitigate the stress as compared with no potassium applications. The reduced irrigation conditions without potassium application reduced the number of bolls per plant, boll weight, seed cotton yield, net photosynthetic rate, transpiration rate, stomatal conductance, as compared with potassium application in no stress conditions (Tables 5 and 6). The water shortage causes a reduction in cellular growth, leaf elongation, and floral buds which leads to low cell expansion. This low cell expansion translated into low growth of stems and roots (Nelissen et al. 2018). This might be the reason behind the reduction in seed cotton yield and its related attributes like bolls per plant and boll weight as observed by others (Wang et al. 2016; Niu et al. 2018). Drought in addition to reducing the yield attributes of cotton, also negatively affects its growth and physiology (Deeba et al. 2012; Hejnák et al. 2015; Niu et al. 2018). K application, however, showed a significant role in the amelioration of drought stress in cotton. Makhdum et al. (2007) reported that cotton cultivars showed variable responses toward the availability of potassium in the soil. The cultivars that are effective in K uptake may have a higher root surface area (Pettigrew 2008; Yang et al. 2011; Wang and Chen 2012). This can lead to more K uptake in the root-to-soil interface to maintain a wider gradient towards the roots which further improves the transportation of K to different organs, having the ability to balance the cytosolic K^+ concentration at the optimal levels (Wang and Chen 2012; Wang et al. 2014; Khan et al. 2017; Zahoor et al. 2017). Therefore, an adequate supply of K in alignment with the cultivars' requirements may lead to enhanced plant growth, yield, and yield attributes (Table 3).

An adequate supply of K in cotton is not only essential for water relations, but also for improving water use efficiency (WUE) which may help plants to survive under drought stress (Fig. 7). Pervez et al. (2004) also found that K application improved WUE in cotton, but this effect varied with cotton cultivars. According to Tsonev et al. (2011), no increase in stomatal conductance by fertilizing with K in water-stressed conditions, indicating that not all cultivars or K levels can positively impact all aspects of water relations in cotton. Under the changing climate scenarios, it is vital that more focuses are shifted towards 'more crop per drop' and to enhance the water use efficiency (Ullah et al. 2017). This study, particularly, showed that water use efficiency was strongly associated with K application (Table 8), therefore more cautious uses of potash fertilizers are encouraged and recommended. Similarly, the identification of cotton cultivars for low-K-input sustainable cotton production represents an important environment-friendly approach to genetic resource management. It would reduce the cost

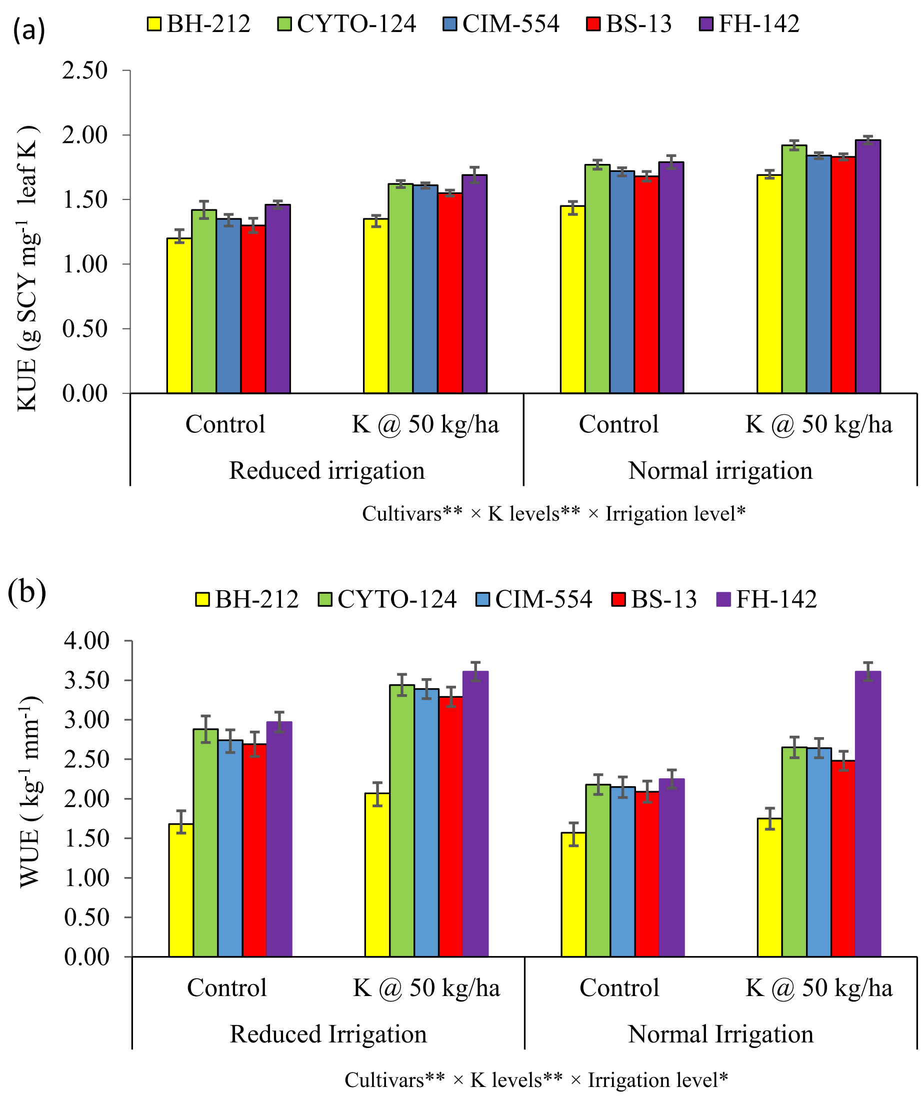

Fig. 7 The impact of irrigation and potassium levels on the potassium (**a**) and waters use efficiency (**b**) in cotton cultivars (Data is the average of 2 years). Error bars indicate the standard error of four replications

of production and K resource management in agro-ecosystems. As this study indicated that unlike the farmers of the vicinity, an adequate and cautious application of potassium can enhance cotton growth and production (Tables 6 and 7). Therefore, the identification of more nutrient-use efficient cultivars may reduce the economic as well as environmental costs of the chemical fertilizers (Baligar et al. 2001). Furthermore, an adequate supply of K increased the yield and growth parameters like shoot fresh biomass, shoot dry biomass, and cotton

Table 8 Correlation among different parameters

Parameters	WUE	KUE	Fiber length	Fiber strength	Fiber elongation	GOT
WUE	1					
KUE	0.92**	1				
Fiber length	0.87**	0.88**	1			
Fiber strength	0.88**	0.76**	0.86**	1		
Fiber elongation	0.86**	0.86**	0.88**	0.83**	1	
GOT	0.87**	0.88**	0.89**	0.87**	0.85**	1

NS no significant difference

**different at *P*<0.01

yield in the study with four cultivars conducted by Hassan et al. (2014). These findings are in line with current study where K application showed increased yield and yield contributing parameters (Table 4) (Pettigrew et al. 1996). In addition, WUE showed a positive correlation during both cotton growing seasons which indicates that higher uptake of potassium could increase the water use efficiency in cotton crop (Fig. 6).

According to Yang et al. (2011), genetic dissimilarity in K uptake was found in eight cotton cultivars under a controlled environment in a growth chamber as well as in field conditions. The K proficiency proportion (dry mass per unit of K accumulated) and K use productivity (dry mass provided per unit of K fixation) of the K efficient cultivars exceeded those of the K in-efficient cultivars by 29% and 234%, respectively. The K efficient cultivars produced 59% higher potential yield (dry weight of every regenerative organ) under field conditions, at soil K deficient level of 60 $mg \cdot kg^{-1}$. However, K deficiency symptoms appeared during flowering, boll development, and seed formation stages. The overall performance of cultivars including CYTO-124, FH-142, CIM-554, and IUB-2013 was better as compared with BH-212 based on cotton productivity under drought stress conditions with K application at 50 $kg \cdot ha^{-1}$. Under low K condition, the increase in seed cotton yield through different rates of potassium fertilizer application is well established as reported by different researchers in many crop species (Pervez et al. 2004; Yang et al. 2004; Rengel and Damon 2008; Hassan et al. 2011). In a field study, Pervez et al. 2004 described that 100 kg $(K_2O) \cdot ha^{-1}$ is appropriate for optimal seed cotton yield and related components. However, Hassan et al. (2014) reported 60 kg $(K_2O) \cdot ha^{-1}$ for optimal seed cotton yield and fiber quality traits. But, in this study, the 50 kg $(K_2O) \cdot ha^{-1}$ along with varietal selection is appropriate for improving seed cotton yield and water use efficiency at both irrigation levels (Table 7 and Fig. 6). Results indicated that CYTO-124 and CIM-554 followed by FH-142 regarding fiber quality traits performed better as compared with BH-212 under reduced irrigation condition with potassium application at 50 $kg \cdot ha^{-1}$ might be due to the increase in photosynthetic rate and cell turgor control (Hussain et al. 2021). The improvement in performance of cotton cultivars due to genetic variation among cultivars and due to K application because K is involved in many physiological and biochemical processes in plants. The protein production is mainly used for the improvement in the fiber quality traits due to K involvement in physiological reactions (Hussain et al. 2021).

It is commonly believed that plant high-affinity K^+ transporters conduct K uptake at low external K concentrations (below 0.2 $mmol \cdot L^{-1}$) (Wang et al. 2015). We did not observe *GhHAK5aD* expression pattern variation in the shoot of K-efficient and K-inefficient cultivars at both +K and −K supply levels. This indicates that *GhHAK5aD* is an important regulator of K uptake into roots under K deficiency in cotton. Therefore, it is concluded that genetic diversity existed among indigenous cotton cultivars for K acquisition and utilization. It is due to the identification of a high-affinity K transporter, *GhHAK5a* in cotton cultivars, which is important for regulation of root K uptake under K deficiency. K-efficient cotton cultivars showed comparatively less decline in growth, yield, and quality attributes under field study due to the efficient transport system in their roots. The K- efficient cultivars can be used as donors of key K acquisition traits in breeding programs to develop promising cotton varieties with enhanced yields under low K environments.

Conclusion

It is evident from the results that most of the cultivars prevalent in Punjab (Pakistan) are K-inefficient. In our studies, the K-efficient cultivars always performed better under water deficit conditions compared with K-inefficient cultivars. The K-efficient cultivars have more potential to compensate for losses in yield and quality of lint cotton caused by deficiency of water and potassium. Furthermore, balanced use of potassium is essential for better seed cotton yield and lint quality, and, to mitigate the adverse effects of drought stress on cotton crop in arid and semi-arid regions of Pakistan.

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Declarations

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