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Expression analysis of K^+ transporter genes associated with salinity tolerance in grape

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ABSTRACT: Molecular information of K^+ accumulation in grapes is strongly required. Under salinity condition potassium transporters are inhibited by Na^+. The aim of this study was to investigate the effects of salinity on the expression of K^+ transporter genes in grape. Based on the previous screening study on 18 grape genotypes, 'H6' and 'Gharashani' (tolerant) and 'Shirazi' and 'GhezelUzum' (sensitive) were selected. Plants were treated with 50 mM NaCl as a critical concentration that was not lethal for grapevine plants. Interestingly, the expression of *VvKUP1*, *VvKUP2* and *VvK1.1* genes highly increased in leaves of sensitive genotypes compared to tolerant ones. Also the expression of *VvKUP1* and *VvKUP2* genes were similar in the leaves of sensitive genotypes. There was a significant positive correlation ($P<0.05$) between the expression of K^+ transporters –*VvKUP1* and *VvKUP2*- and the accumulation of Na^+ in the leaves of sensitive genotypes. Roots of all genotypes showed increase in expression of *VvK1.1* under salinity. The findings highlighted a strong relationship between the accumulation of specific transcripts and the degree of stress tolerance.

KEYWORDS: Gene expression, Potassium transporters, Salt stress, Vitis

INTRODUCTION

Due to worldwide increase in soil salinity, the identification of genes conferring tolerance to abiotic stresses has been a subject of intensive studies. Recent studies have shown that gradual application of salt and drought stresses induced massive changes in grapevine gene expression (11).

Comparative gene expression analysis could be a useful approach for understanding the mechanisms of tolerance and susceptibility Roots absorb water and nutrients from the soil and are the first organ that perceives abiotic stresses like drought and salinity. Grape roots also accumulate some defense compounds (4).

Previous genetics and functional genomics studies have provided some molecular knowledge of plant salt tolerance. Some important genes encoding proteins for ion channels have been recognized That information is useful for the improvement of grape quality (6). In grapevine like other plants, K^+ is an essential macronutrient and a major osmoticum. It is often the most abundant cation in plant tissues. Potassium transporters mediate high-affinity K^+ uptake, whereas low-affinity uptake has been relegated to potassium channels (13).

Information on major molecular determinants of K^+ accumulation in grapes is strongly required (17). Efforts in this field have led to the identification of several K^+ transport systems, among which are: VvSIRK, a Shaker K^+ channel expressed in guard cells (19); and two KUP/KT/HAK-type potassium transporters expressed in the berry skin (5).

Specific transport systems have been shown to be inhibited by the presence of large amounts of ions such as Na^+. These include high affinity K^+ transporters of the KUP family. Significant alterations in transporter transcript level during

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salinity stress may point to the potential roles of these gene products and their substrates during plant salinity stress (20).

The most studied members of the KT/KUP/HAK family belong to the two largest groups, which were named I and II (2). In growing grapevine fruits (*Vitis vinifera*), the expression of *VvKUP1* and *VvKUP2* potassium transporter genes is dependent on their developmental stage. It is likely that these transporters are required for the potassium-driven cell expansion in young grape berries (5). *VvK1.1* is mainly expressed in the root cortex like its Arabidopsis AKT1 counterpart, which has been shown to be involved in K^+ uptake from the soil (10). *VvK1.1* transport activity is especially dedicated to K^+ uptake from external media (soil or apoplast) containing low K^+ concentrations.

In previous experiments, 18 grape genotypes were screened from the view point of salt tolerance parameters (14, 16). The genotypes with lower (GhezelUzum and Shirazi) and higher (H6 and Gharashani) capacity for salinity tolerance were selected for molecular analysis.

The aim of the present molecular study was to compare genes expression related to potassium transporters in the roots and leaves of tolerant and sensitive grape genotypes under salinity.

MATERIALS AND METHODS

Plant materials and growth conditions

Hardwood cuttings of four grape genotypes ['H_6 Hybrid' (*V. vinifera* cv. GharaUzum × *V. riparia* cv. Kober 5BB), 'Gharashani', 'GhezelUzum', and 'Shirazi'] were obtained from Kahriz vineyard (Agricultural Research Center, grape genotypes collection). The cuttings were disinfected with benomyle (1% w/v), and then the basal parts were soaked in Indole-3-butyric acid 0.1% (w/v) for 5-10 s. All cuttings were struck in a mist house (relative humidity 80%) with a heat-bed temperature of 20-30 ºC. After two weeks, the rooted cuttings were transferred into 2 L pots containing containing aerated Hoagland solution. The pots were protected with Aluminum foil to avoid light effects and alga proliferation.

Salinity treatments

Two-month plants were treated with 50 mM NaCl (threshold salinity was determined for the genotypes). According to the screening study, 50 mM salt was sufficient to reduce water potentials, but did not kill the grapevine plants when exposed for several days. Leaf and root tissues were collected at different time points (0, 24 hours and 14 days), frozen in liquid nitrogen immediately and stored at -80 °C until RNA isolation

RNA isolation, cDNA synthesis and RT-PCR

Total RNA was extracted from root tissues using Louime *et al.* (12) method with a small modification. The RNA concentration was determined by Biophotometer (Eppendorf, Germany). The integrity of RNA was checked on agarose gel. First-strand cDNA was synthesized from total RNA using a first strand cDNA synthesis Kit (Fermentas) according to the manufacturer's instructions. The cycling protocol for 20 µl reaction mix was 5 min at 65 °C, followed by 60 min at 42 °C, and 5 min at 70 °C to terminate the reaction. Second strand cDNA synthesis was made up with PCR Master Kit (Cinnagen Co.). PCR conditions were as following protocol: initial denaturation at 95 °C for 3 min, followed by 28-30 cycles at 95 °C for 30 s, 60-64 °C for 30 s and 72 °C for 20 s and final extension at 72 °C for 5 min. The *VvEF1* gene (Elongation Factor 1) was used as internal reference. Forward and reverse primers sequences are shown in Table 1.

The products of RT-PCR were separated on 1.5% agarose gel which contained Ethidium Bromide (0.5 µg/ml) and were visualized using Gel Logic 212 pro Imaging System (Carestream, USA).

The experiment was repeated three times. The intensity of the RT-PCR bands was measured using Image J software 1.43.

Table1. Primers used in RT-PCR experiment

Genes	Sequence (5'→3')	T_m (°C)
VvKUP1	TGAGCTTTGAAACATGGGAAGACT	66.8
	TTCTTGTTACCAAGCCTTCCGG	67.9
VvKUP2	ATGCTTCCTGCCATTTCCACATA	68
	GGTTGGCATGGTTTATATCGTCTG	66.9
VvK1.1	TTGTTGAAACGTGGTCTGGA	64.2
	GCCCTGCCCCATAATCTAGT	63.9
VvEF1-α	TCTGCCTTCTTCCTTGGGTA	53.46
	GCACCTCGATCAAAAGAGGA	53.2

Statistical analysis

Statistical analyses were done using SPSS software (Version 14.0). Error bars on graphs were SEM. Normality of the data was tested by Kolmogorov-Smirnov method. One-way analysis of variance with post-hoc tests and two-way analysis of variance (General Linear Model) with Tukey's multiple range tests ($P<0.05$) were used to determine differences between the means.

RESULTS

Salinity effects on the expression of potassium transporter genes in grape genotypes

Figure 1 showed the profile of K^+ transporter genes (*VvKUP1*, *VvKUP2* and *VvK1.1*) in the leaves and roots of tolerant ('H6' and 'Gharashani') and sensitive ('Shirazi' and 'GhezelUzum') grape genotypes (*Vitis* L.) at different time points treated by 50 mM NaCl.

Salinity effects on the expression of VvKUP1 gene

VvKUP1 gene belongs to a potassium transporter. The expression of *VvKUP1* gene first (after 24 hours of treatment) increased and then (after 14 days of salinity) decreased in the leaves of tolerant genotypes, but we observed accumulation in sensitive genotypes under salinity (Figure 2).

The increase in 'Shirazi' genotype was higher compared to 'GhezelUzum'. The roots of sensitive genotypes showed no significant change ($P<0.05$) under salinity compared to control, whereas *VvKUP1* transcripts down regulated in roots of 'Gharashani'. The roots of 'H6' genotype showed first decrease and then increase in gene transcripts under salinity. However, the roots of H6 genotype showed no significant difference ($P<0.05$) between control and 14-day salinity treatment. GLM analysis showed that the difference in the expression of *VvKUP1* was not significant ($P<0.05$) between 'H6' and 'Shirazi' genotypes in leaves. Also the difference between 24-hour and 14-day treatments was not significant. But in roots, the difference in *VvKUP1* transcripts was significant ($P<0.05$) among genotypes and also among salinity treatments.

Salinity effects on the expression of VvKUP2 gene

VvKUP2 gene belongs to a potassium transporter. As shown in figure 3, the expression of *VvKUP2* was similar to *VvKUP1* transcripts in the leaves of sensitive genotypes. Tolerant genotypes showed first increase and then decrease, but sensitive genotypes showed increase in both gene transcripts.

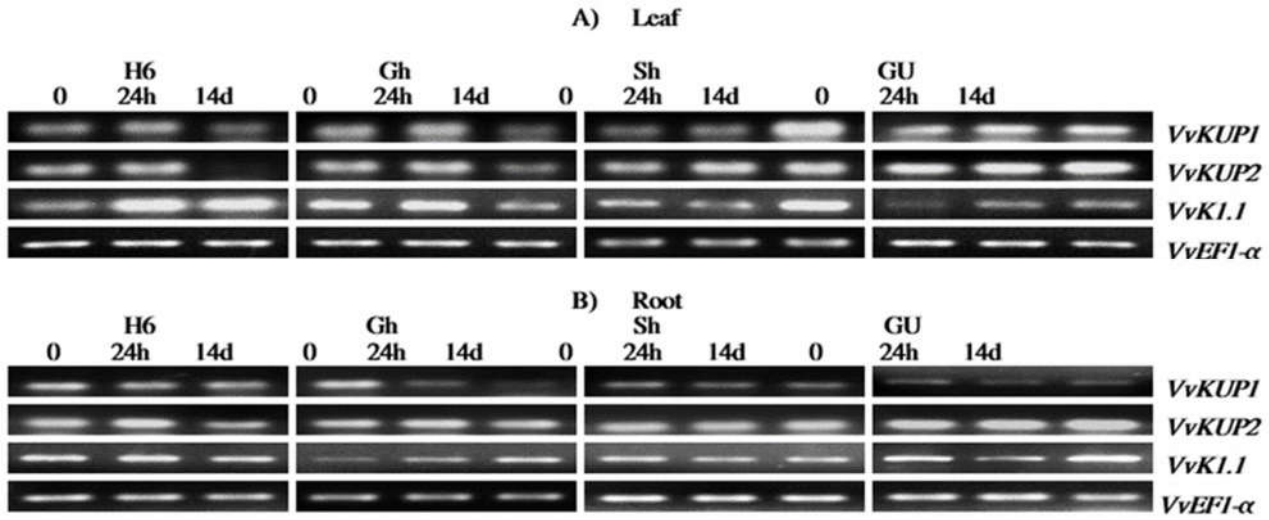

Figure 1. Expression profile of potassium transporter genes in leaves (A) and roots (B) of four grape genotypes [H_6 (*V. vinifera* cv. GharaUzum × *V. riparia* cv. Kober 5BB), Gh: Gharashani, Sh: Shirazi and GU: GhezelUzum] after 0, 24 hours and 14 days treated by 50mM NaCl.

In the roots of tolerant genotypes, we observed first increase and then decrease, but sensitive genotypes showed first decrease and then increase in the expression of *VvKUP2* gene. It means that *VvKUP2* transcripts showed inverse status in the roots of tolerant and sensitive genotypes.

After 14 days of salinity treatment, we observed accumulation in the roots of all genotypes compared to control, except for 'H6'.

However, that increase in 'Shirazi' genotype was not significant (*P<0.05*). GLM analysis showed that the difference in the expression of *VvKUP2* was not significant (*P<0.05*) in leaves of 'Shirazi' and 'Gharashani' genotypes, but the difference among time points was significant. In roots, the difference between 'Shirazi' and 'GhezelUzum' genotypes as well as the difference between 0 and 14 days salinity was not significant (*P<0.05*).

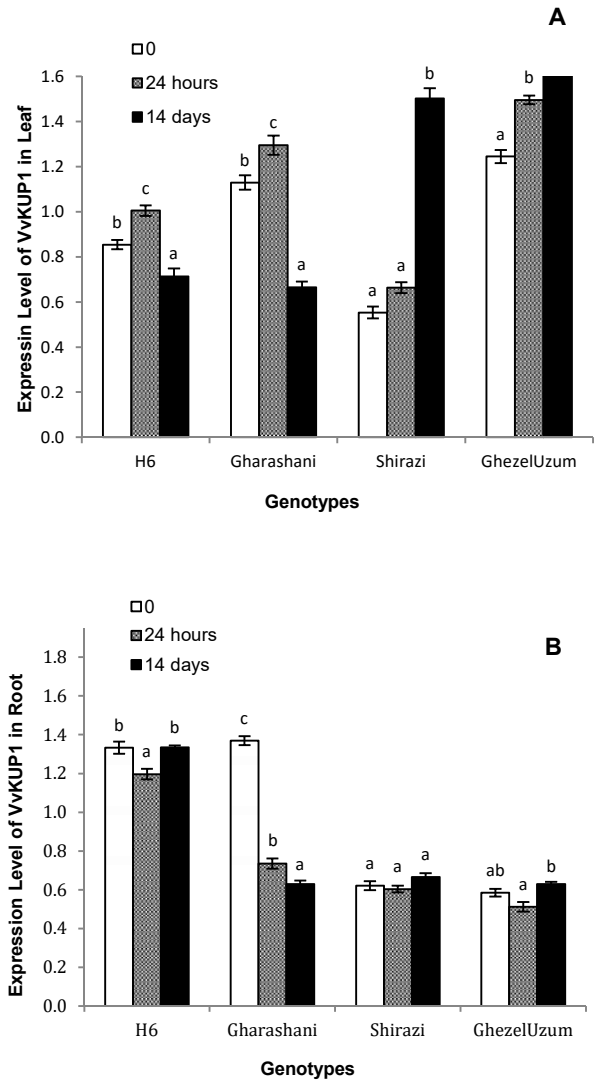

Figure 2. Expression level of *VvKUP1* gene in leaves (A) and roots (B) of four grape genotypes [H_6 (*V. vinifera* cv. GharaUzum × *V. riparia* cv. Kober 5BB), Gharashani, Shirazi, GhezelUzum] after 0, 24 hours and 14 days treated by 50 mM NaCl. Bars are the means (n=3) ± Standard Error (*P<0.05*, One Way ANOVA). Different letters above the columns indicate significant difference between the treatments according to Tukey's test.

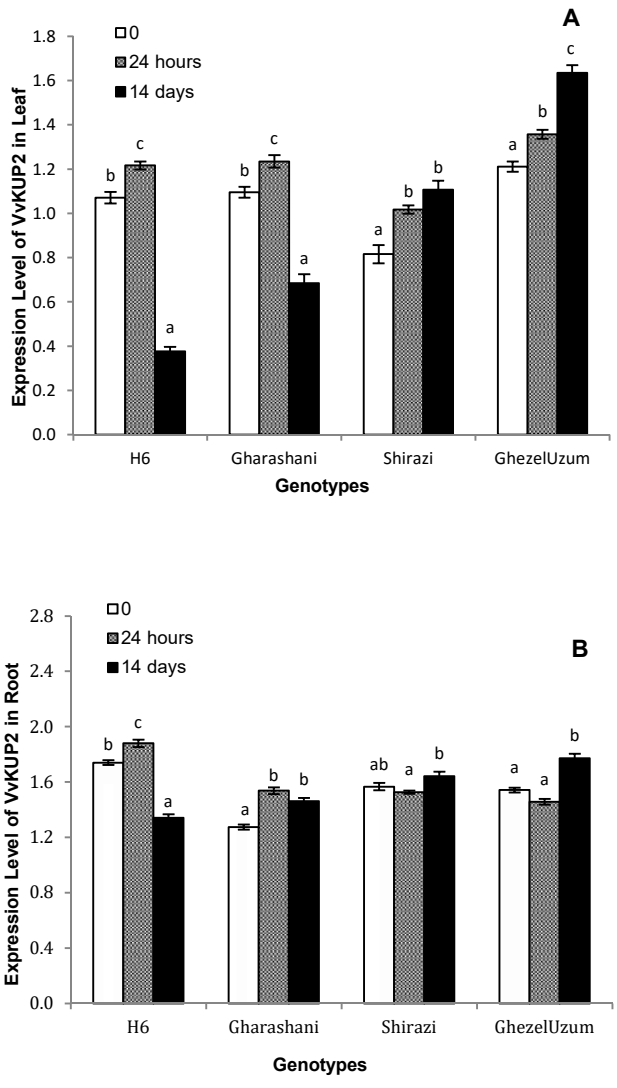

Figure 3. Expression level of *VvKUP2* gene in leaves (A) and roots (B) of four grape genotypes [H_6 (*V. vinifera* cv. GharaUzum × *V. riparia* cv. Kober 5BB), Gharashani, Shirazi, GhezelUzum] after 0, 24 hours and 14 days treated by 50 mM NaCl. Bars are the means (n=3) ± Standard Error (*P<0.05*, One Way ANOVA). Different letters above the columns indicate significant difference between the treatments according to Tukey's test.

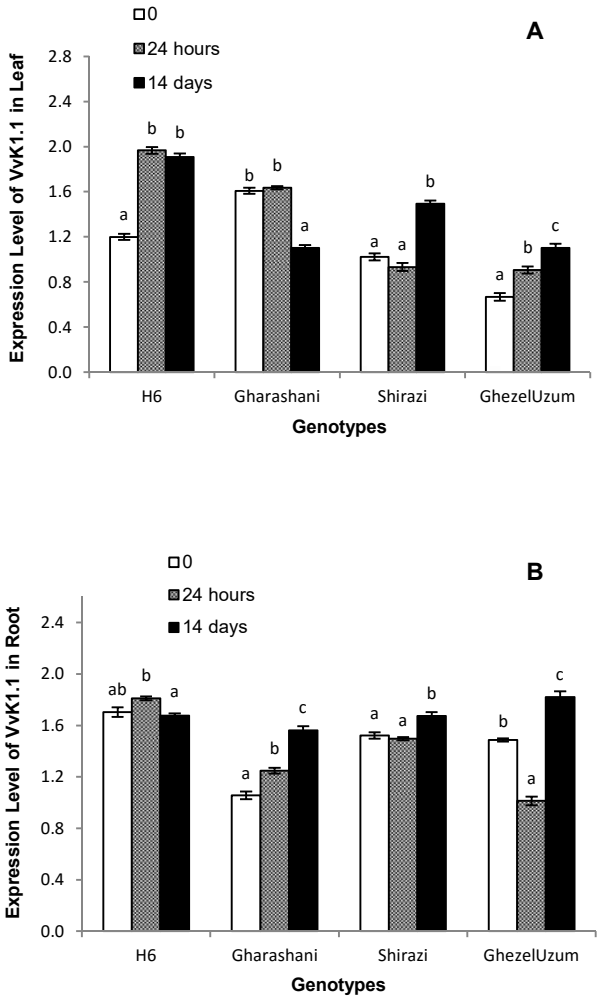

Figure 4. Expression level of *VvK1.1* gene in leaves (A) and roots (B) of four grape genotypes [H_6 (*V. vinifera* cv. GharaUzum × *V. riparia* cv. Kober 5BB), Gharashani, Shirazi, GhezelUzum] after 0, 24 hours and 14 days treated by 50 mM NaCl. Bars are the means (n=3) ± Standard Error (*P<0.05*, One Way ANOVA). Different letters above the columns indicate significant difference between the treatments according to Tukey's test.

Salinity effects on the expression of VvK1.1 gene

VvK1.1 gene belongs to a potassium channel. In long-term salinity, *VvK1.1* transcripts accumulated in the leaves of all genotypes, except for 'Gharashani' that showed decrease (Figure 4). The results showed that *VvK1.1* transcripts up regulated in the roots of all genotypes, except for H6 that showed no significant change (*P<0.05*). GLM analysis showed that the difference in the expression of *VvK1.1* in leaves and roots of all genotypes was significant (*P<0.05*). In leaves the difference between 24 hours and 14 days salinity was not significant, but in roots the difference among time points was significant (*P<0.05*).

DISCUSSION

Arabidopsis *AtKUP1* was mostly expressed in roots (8). By contrast, salinity-treated rice plants showed a reduction in HKT1 transcript level and its down regulation was because of increase in Na^+ influx during salinity (9). Under salt stress, different ion channels changed to maintain ion homeostasis. Potassium channels were induced with the increase of salt concentrations.

It was important to keep a balance between K^+ and Na^+ in the cells. Therefore, two potassium transporters from the KUP/KT/HAK family, *VvKUP1* and *VvKUP2*, were isolated from *V. vinifera* berries (7). Two evidences indicate that they were involved in potassium transport (1): First, they both shared sequence homology with other potassium transporter and second, both completed an *E. coli* mutant deficient in potassium transport (7). In grape fruits (*Vitis vinifera*), the expression of *VvKUP1* and *VvKUP2* potassium transporter genes was dependent on developmental stage.

It seems that these transporters were required for the potassium-driven cell expansion in grape. Both *VvKUP1* and *VvKUP2* were most highly expressed in reproductive tissues (berries, flowers, and seeds) in Shiraz variety (5). Since salinity stress severely impacts on K^+ homeostasis in plant, regulation of K^+ transport through cell membrane might be expected. Transcription of *KUP2*, which is mostly expressed in rapidly growing tissues and has been shown to play a role in cell expansion, is decreased in the shoots of plants treated by salinity. Its down regulation may reflect salinity-induced lack of turgor and reduction in growth. By contrast, *KUP6* and *KUP11* are both up regulated during salt stress (7). Transcript abundance of *KUP1* and *KUP4* homologues increased during K^+ starvation and salt exposure (21). We studied the expression of two potassium transporters *VvKUP1* and *VvKUP2*- under salinity conditions. As shown in Figures 2 and 3, the expression of these genes was interestingly

similar in the leaves of all genotypes. The results verified Su *et al.* (21) and Elumalai *et al.* (7) reports about up regulation of *KUP1* transcripts under salinity, because after 24 hours salinity we observed increases in expression of *VvKUP1* in all genotypes. However the results were not consistent with Elumalai *et al.* (7) report about decrease in expression of *KUP2* under salinity. We

observed increase in *VvKUP2* transcripts after 24 hours salt stress, though tolerant genotypes showed decrease after 14 days salinity It seems that because of higher Na^+ accumulation in leaves (15), sensitive genotypes needed higher expression of potassium transporters and probably Na^+ transport to the leaves through these transporters. But the tolerant genotypes didn't need the expression of these transporters, because they could control Na^+ transport to the leaves after 14 days salinity.

The expression of potassium transporters was different in roots of the genotypes. *VvKUP1* transcripts showed no significant change ($P<0.05$) compared to control, except 'Gharashani' that showed the transcripts decrease. Although the expression of *VvKUP2* increased in 'Gharashani' and 'GhezelUzum' genotypes, it didn't change significantly compared to control in 'Shirazi' and decreased in 'H6'. Considering a significant decrease ($P<0.05$) in the expression of one of potassium transporter genes in roots of tolerant genotypes, no reduction in their expression in sensitive genotypes and regarding the physiological findings (15), it could be concluded that the accumulation of these gene transcripts in sensitive genotypes was because of high Na^+ absorption via these transporters. It seems that the mechanism of gene expression in roots and shoots was different. There was a significant positive correlation ($P<0.05$) between expression of K^+ transporters –*VvKUP1* and *VvKUP2*- and accumulation of Na^+ in leaves of sensitive genotypes. Arabidopsis *AtKUP1* was mostly expressed in roots and was dependent on membrane potential (8). *KUP2* is known to regulate cell size and therefore the reduced expression of this transporter could be important for developmental and physiological responses to salt stress (7). *VvK1.1*, like other Shaker channels, was voltage dependent. The voltage dependence was independent of the external K^+ concentration, a feature classically reported in inwardly rectifying plant Shaker channels (24). Regulation of channel activity by external K^+, prevents both K^+ influx and efflux when the K^+ external concentration is decreased (22). Accumulation of AKT1 transcripts in Arabidopsis roots is not sensitive to salt stress (18). In Arabidopsis, AKT1 is mainly expressed in roots and that leads to inward K^+ channel activity involved in K^+ uptake from the soil (25). *VvK1.1* can be considered as the grapevine ortholog of Arabidopsis AKT1 because the sequence identity is high between AKT1 and *VvK1.1* (71%). In roots, the expression of *VvK1.1* in cortical cells suggests a role in K^+ uptake from the soil, as shown for the Arabidopsis AKT1 channel (10). The expression of *VvK1.1* can also be detected in phloem tissues, both in roots and in berries, indicating K^+ transport in the phloem vascular system (9). Cue'llar *et al.* (3) reported that *VvK1.1* transcript accumulation is strongly sensitive to drought stress. Whereas transcripts are accumulated in leaves and berries up to six fold, the roots

display a decrease up to five fold in sensitive variety. Thus, drought stress in grape is probably resulted in changes in the cell membrane for K^+ transport, depending on the organ or tissue, and the balance between transporter and channel activities. ABA caused *VvK1.1* accumulation in leaves, but did not affect the accumulation level in roots. This suggests that regulation of *VvK1.1* expression in drought stress is under ABA control in leaves and independent from this hormone in roots. Also grapevine watering with 50 mM NaCl or KCl revealed no significant change in *VvK1.1* transcripts, either in roots or in leaves. Different results from salinity effects on *VvK1.1* gene were reported. Expression of *AKT1* in Arabidopsis –homolog of *VvK1.1*- was higher in roots and played a role in K^+ uptake from the soil as an inward channel (10). The results about the expression of *VvK1.1* gene in leaves under salinity were not consistent with Cue'llar *et al.* (3) report. They reported no change in expression of *VvK1.1* gene under salinity, but gene transcripts increased in leaves of our genotypes, except 'Gharashani'. The previous study showed ABA content increased with time passing under salinity (15). It verified Cue'llar *et al.* (3) report that ABA probably increased the expression of *VvK1.1* in leaves of grape genotypes under salinity. However if that opinion is true, it cannot be applied for 'Gharashani' genotype. There was a significant positive correlation ($P<0.05$) between the increase of ABA and the *VvK1.1* transcripts in our genotypes, except 'Gharashani'. The results in roots were on the contrary to Cue'llar *et al.* (3) study. They reported decrease in expression of *VvK1.1* in roots of grape under drought stress, whereas we observed increase in transcripts in roots of all genotypes after 14 days salinity, except 'H6' that showed no significant change ($P<0.05$) compared to control.

CONCLUSION

Molecular study was done in tolerant and sensitive grape genotypes by RT-PCR technique. The expression of these genes in grape showed significant difference between tolerant ('H6' and 'Gharashani') and sensitive genotypes

('Shirazi' and 'GhezelUzum'). Interestingly, the expression of *VvKUP1*, *VvKUP2* and *VvK1.1* genes highly increased in the leaves of sensitive genotypes compared to tolerant ones. The results were consistent with Su *et al.* (22) and Elumalai *et al.* (7) reports about increase in expression of potassium transporter genes under salinity. To summarize, different expression of genes in salt sensitive and tolerant grape genotypes, combined with previous studies of salt induced responses in specific cultivars (23), provide useful information for salt tolerance in grape, a crop of major economic interest that is more exposed to salt stress.

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آنالیز بیان ژن‌های ناقلین پتاسیمی مربوط به تحمل شوری در انگور

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چکیده

اطلاعات مولکولی انباشتگی K^+ در انگور مورد نیاز است، تحت شوری ناقلین پتاسیمی به‌وسیله Na^+ در انگور مهار می‌شوند. هدف این مطالعه بررسی اثرات شوری بر بیان ژن‌های ناقلین K^+ در شرایط شوری در انگور بود. بر اساس مطالعه غربالگری ما روی ۱۸ ژنوتیپ انگور"H6" و "قره‌شانی" (متحمل) و "شیرازی" و "قزل‌اوزوم" (حساس) انتخاب شدند. گیاهان با ۵۰ mM NaCl به‌عنوان یک غلظت بحرانی که برای گیاهان انگور کشنده نیست، تیمار شدند. به‌طور جالبی بیان ژن‌های *VvKUP1*، *VvKUP2* و *VvK1.1* در برگ‌های ژنوتیپ‌های حساس بیشتر از متحمل بود. همچنین بیان ژن‌های *VvKUP1* و *VvKUP2* در برگ ژنویپ‌های حساس مشابه بود. همبستگی مثبت معنی‌داری ($P<0.05$) بین بیان ناقلین K^+ و انباشتگی Na^+ در برگ‌های ژنوتیپ‌های حساس وجود داشت. یافته‌های ما یک ارتباط قوی بین انباشتگی نسخه‌های خاص و درجه تحمل به تنش نشان داد.

کلمات کلیدی: ناقلین پتاسیمی، تنش شوری ، *Viti*