Expression analysis and physiological response of sunTIP7 aquaporin gene to different water regimes in sunflower

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Abstract
The response of a plant to drought stress is positively related to physiological traits and gene expression. Various recent studies suggest that membrane channel proteins, named aquaporin (AQPs), by affecting stomatal conductance behavior could be involved in plant responses to stress conditions. The sunTIP7 gene is a member of AQPs protein that is included in different environmental stress such as drought stress. In this study in order to investigate the sunTIP7 gene expression and its relation with relative water content (RWC), stomatal conductance, shoot fresh and dry weight, root area, chlorophyll index (SPAD) and electrolyte leakage (EL), six selected sunflower (Helianthus annuus L.) inbred lines were planted in a greenhouse under normal irrigation and water deficit conditions. The water deficit treatments were applied during 4th leaflet to flowering stage. Drought conditions reduced crop growth and physiological traits. The highest stomatal conductance was found in the C138 line under both conditions. Sunflower lines had different fold change expression of sunTIP7 gene under drought stress. The expression of the sunTIP7 gene was the lowest in C138, and this downregulation may explain its highest stomatal conductance. However, there was not any clear relationship between physiological traits and expression of sunTIP7 gene in all six sunflower inbred lines. These results suggest that drought tolerance in sunflower is a complex trait and there is no simple molecular explanation for drought tolerance in sunflower lines.

Keywords: Aquaporin; Drought stress; Stomatal conductance; Sunflower; sunTIP7.

Introduction
Regardless of the comparatively high water permeability of cell membranes, the plants contain the appointed channels of water that can help and regulate water passage. Some water-selective-channels proteins, that are called aquaporins (AQPs), relative to the major intrinsic protein (MIP) family, are present in all kingdoms. In plants, MIPs are sorted into several subfamilies: small basic intrinsic proteins (SIPs), tonoplast intrinsic proteins (TIPs), nodulin-like intrinsic proteins (NIPs) (Johanson et al. 2001; Zardoya and Villalba 2001; Forrest and Bhave 2008), GlypF-like intrinsic proteins (GIPs) (Gustavsson et al. 2005), x intrinsic proteins (XIPs) (Venkatesh et al. 2015) and hybrid intrinsic proteins (HIPs) (Danielson and Johanson 2008). AQPs play a critical role in supporting plants to retain water balance and homeostasis under water stress status (Johansson et al. 2000; Galmés et al. 2007). Two classes of AQPs, the PIPs and the TIPs, have been most considered in water relations of shoots and roots. TIPs subfamily is used in turgor homeostasis and cell elongation with intermediating the
transport of small molecules and water across the vacuolar membrane (Sarda et al. 1999). TIPs also are involved in response to drought and salt stress in different plants. For example, rTIP1 in rice (Liu et al. 1994), sunTIP20 in sunflower (Sarda et al. 1999) and BobTIP26 in cauliflower (Barrieu et al. 1999) showed overexpression in drought stress.

Expression of AQPs in guard cells of stomata have been reported in various species, such as tobacco (NtAQP1), Arabidopsis thaliana (AtPIP1;2), spinach (SoPIP1;1), barley (HvPIP1;6), broad bean (VfPIP1), maize (ZmPIP1;2; ZmPIP2;1/2;2) and the sunflower tonoplast intrinsic proteins SunTIP7 and SunTIP20 (Huang et al. 2002; Leonhardt et al. 2004; Fraysse et al. 2005; Wei et al. 2007; Hachez et al. 2008). According to Sarda et al. (1997), SunTIP20 expression did not show a significant effect on the stomatal movement, but SunTIP7 mRNA accumulated during stomatal closure. They indicated that SunTIP genes are differentially regulated in the same cell. Another TIP family expression was found by in situ hybridization in guard cells of mature organs and seedlings of Picea abies (Oliviussion et al. 2001).

However, there is little direct evidence for the functional effects of AQPs in stomatal movement. For example, RNA interference-mediated decreases in the expression of the water and CO2 diffusion facilitator NtAQP1 (PIP1-like) has lower stomatal conductance in contrast to wild-type tobacco plants (Uehlein et al. 2008).

Sunflower is one of the most important sources of plant oil in the word that mainly is grown in warm to moderate semi-arid climatic areas. However, water deficit stress is a limiting factor in sunflower performance (Blanchet et al. 1981) and has significant impact on grain yield and composition of fatty acids (Alberio et al. 2016). Water deficit stress also stimulates many plant responses such as relative water content (RWC) and stomatal conductance (Ghobadi et al. 2013) and the expression of drought stress-inducible genes (Lim et al. 2012). In this study, considering the role of AQPs in plant response to water stress, we focused on some physiological traits and expression of sunTIP7 gene under drought stress and regular irrigation in six inbred lines of sunflower.

Materials and Methods

Plant materials and water stress treatments

The sunflower inbred lines in this experiment were provided by Seed and Plant Improvement Institute (SPII), Karaj, Iran. The seeds were planted in 3.5 L pots filled with 50% sand and 50% field soil. The inbred lines and irrigation levels formed a complete factorial experiment. The pots were arranged in a randomized complete block design with four replications in a greenhouse of University of Zanjan, Iran. After determining the field capacity (FC) of the soil, 50% FC was considered as drought stress and 90% FC as the normal irrigation treatments. Drought stress was applied from the 4-leaf to flowering stages.

Measurements of morpho-physiological traits

All traits were measured at the flowering stage. Stomatal conductance was measured by leaf porometer (Nunes Instruments Co., India) as mM m⁻² s⁻¹ (Poormohammad Kiani et al. 2007).

RWC was determined based on the following formula:
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\[
RWC = \left( \frac{FW - DW}{TW - DW} \right) \times 100
\]

where, FW is fresh weight, TW is turgid weight after 24 h of rehydration at 4 °C in a dark room by placing the petioles in a container with distilled water, and DW is dry weight after drying up for 24 h at 80 °C (Poormohammad Kiani *et al.* 2007). Shoot fresh weight was measured just after harvesting, and shoot dry weight was determined after drying the plants in oven at 72 °C for 72 h. To measure the electrolyte leakage (EL), leaves were washed with the sterilized distilled water to remove surface contamination of leaves (Blum and Ebercon 1981). Leaf segments, containing 2 gr were placed in the vials with 10 ml of deionized water and incubated at 25 °C on a rotary shaker with 100 rpm. Then, the electrical conductivity of the solution (\(L_t\)) was measured after 24 h. Samples were then dried at 100 °C for one hour and the last conductivity reading (\(L_o\)) was gathered upon equilibration at 25 °C. The EL was finally calculated as \((L_t/L_o) \times 100\) (Lutts *et al.* 1996). Chlorophyll index (SPAD) was assessed by using a portable chlorophyll meter (CCM-200, Opti-Sciences, England). For this purpose, measurements were made at upper, middle and lower points of each leaf (three leaves per plant). For the measurement of root area, the pots washed with water. The roots were separated from the soil and stained with black color, and then the root area was determined by the scanner (Mardani *et al.* 2012).

**RNA extraction and gene expression analysis**

To analyze the *sunTIP7* gene expression, leaf samples were harvested at the flowering stage and immediately frozen in the liquid nitrogen. Total RNA was extracted from each individual plant leaves by the GeneAll solution and the genomic DNA was removed by DNase I treatment. Reverse transcription reactions were performed using DNA-free RNA with cDNA Synthesis Kit (Pishgam, Iran) following the manufacturer’s instructions. Real time PCR was performed in Rotor Gene Q using the real time SYBR Green MasterMix (Pishgam, Iran), following the manufacturer’s instructions. Primers were designed by the primer3 site ([http://primer3.ut.ee/](http://primer3.ut.ee/)) and OligoAnalyzer ([https://eu.idtdna.com/](https://eu.idtdna.com/)). For normalization of gene expression, we used two housekeeping genes, 18s rRNA and actin. The results showed that the expression stability of the two reference genes was similar. The reference gene was 18s rRNA (Table 1).

**Statistical analysis**

Analysis of variance was performed for the measured data and means were compared by Duncan’s multiple range test. Furthermore, Pearson’s correlation coefficients among traits were calculated using the SPSS software. The expression fold change of the *sunTIP7* gene was analyzed by the \(2^{-\Delta\Delta Ct}\) method (Livak and Schmittgen 2001). Because the relative expression data in the real-time PCR analysis was based on a small sample size and data were not normally distributed, test of significance for the relative expression of the *sunTIP7* gene was carried out by applying the bootstrap resampling method with 1,000 resamples using the REST software (Pfaffl *et al.* 2002).
Results and Discussion

The higher resistance to water-deficit stress conditions can be achieved by altering some traits that help plants to cope with the drought stress effectively (Skoric 2009). In this study, analysis of variance and comparison of means showed significant differences among the lines for the physiological traits and the sunTIP7 gene expression in both water regimes. Drought stress reduced stomatal conductance, RWC, shoot fresh weight, shoot dry weight, root area, SPAD and increased EL in all inbred lines, but the amount of change between lines was different (Tables 2 and Table 3). Because the sunTIP7 gene is expressed in sunflower guard cells, we focused on the stomatal conductance in the sunflower inbred lines. C138 showed significantly higher stomatal conductance than other lines under both conditions. Although C138 had higher RWC and shoot dry weight than other lines in both conditions, it was not significantly different from C111 and C148 for RWC under drought stress and from A19 and R217 for shoot dry weight under normal irrigation (Tables 2 and 3). Moreover, this inbred line demonstrated smaller changes of stomatal conductance (16.92%) from normal irrigation to drought stress conditions compared with other lines (Tables 2 and 3). Although drought tolerant plants were often known by low stomatal conductance in drought stress condition, because they attempt to loose less water caused by transpiration (Poormohammad Kiani et al. 2007); however, Blum et al. (1981) have indicated that genotypes which have ability to retain more water without closing their stomata, are suitable for arid regions. Regarding these results, the genotypes such as C138 can be considered as drought-tolerant, because, despite the high stomatal conductance, its relative water content was higher than other inbred lines. The high RWC in C138 means that it has the ability to preserve more water under drought stress. The plant's root system is essential for optimizing water uptake and has an important role in drought stress, because root traits such as root length, root biomass and lateral root density determine the plant efficiency in water absorption from the soil (Rauf 2008). Reports showed that sunflower roots were affected by water shortage (Pekcan et al. 2016). Our results revealed that the root area is dramatically affected by drought stress. C138 showed significantly higher root area than other inbred lines under drought conditions (Table 3). The studies have indicated that genotypes with the extensive root systems access more water and maintain stomatal conductance under stress conditions (Wasson et al. 2012). Therefore, high stomatal conductance and RWC in C138 may be due to its higher root area.

Table 1. Oligonucleotides used for the real time PCR analysis.

<table>
<thead>
<tr>
<th>Primer</th>
<th>Sequence</th>
<th>Gene ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>18s_H.a</td>
<td>F: TACCGTCCTAGTCTCAACCAT</td>
<td>AF107577.1</td>
</tr>
<tr>
<td>18s_H.a</td>
<td>R: TCAGCCTTGCGACCATAC</td>
<td>AF107577.1</td>
</tr>
<tr>
<td>Actin_H.a</td>
<td>F: CCCCCTTCTTTACTGAGGCA</td>
<td>AF28264.1</td>
</tr>
<tr>
<td>Actin_H.a</td>
<td>R: TCCAGAATCCAGCACAATACC</td>
<td>AF28264.1</td>
</tr>
<tr>
<td>SunTIP7</td>
<td>F: CAACCTCTGGCTCAACCCTT</td>
<td>x95950.1</td>
</tr>
<tr>
<td>SunTIP7</td>
<td>R: GTAAACAGTGAACCATTGCGA</td>
<td>x95950.1</td>
</tr>
</tbody>
</table>
Table 2. Mean values for growth and physiological traits in inbred lines of sunflower under normal irrigation.

<table>
<thead>
<tr>
<th>Inbred line</th>
<th>Stomatal conductance</th>
<th>Relative water content</th>
<th>Shoot fresh weight</th>
<th>Shoot dry weight</th>
<th>Root area</th>
<th>SPAD</th>
<th>Electrolyte leakage</th>
</tr>
</thead>
<tbody>
<tr>
<td>A19</td>
<td>210.50±2.64</td>
<td>71.42±1.01</td>
<td>123.16±1.40</td>
<td>14.14±1.33</td>
<td>221.97±3.57</td>
<td>29.57±1.09</td>
<td>46.46±0.55</td>
</tr>
<tr>
<td>C111</td>
<td>173.00±7.74</td>
<td>77.25±1.03</td>
<td>110.91±1.91</td>
<td>9.86±1.81</td>
<td>184.68±8.35</td>
<td>18.95±1.03</td>
<td>41.86±0.92</td>
</tr>
<tr>
<td>C123</td>
<td>189.90±3.69</td>
<td>71.08±0.49</td>
<td>126.35±1.65</td>
<td>10.17±0.81</td>
<td>212.33±2.97</td>
<td>19.10±1.97</td>
<td>44.39±1.15</td>
</tr>
<tr>
<td>C138</td>
<td>263.00±3.36</td>
<td>85.30±1.07</td>
<td>123.12±2.27</td>
<td>14.77±1.23</td>
<td>240.94±9.11</td>
<td>20.05±0.78</td>
<td>38.08±1.54</td>
</tr>
<tr>
<td>C148</td>
<td>176.25±6.34</td>
<td>69.61±0.90</td>
<td>117.51±0.91</td>
<td>9.84±1.53</td>
<td>185.73±8.78</td>
<td>21.15±1.13</td>
<td>41.11±1.61</td>
</tr>
<tr>
<td>R217</td>
<td>222.00±3.16</td>
<td>70.84±0.30</td>
<td>122.19±3.37</td>
<td>13.07±0.85</td>
<td>204.22±6.91</td>
<td>21.32±0.90</td>
<td>48.21±1.37</td>
</tr>
</tbody>
</table>

Values are the mean of four measurements per line and ± indicates the standard error. Values followed by different letters indicate significant difference at the 0.05 probability level using Duncan’s multiple range test.

Table 3. Mean values for growth and physiological traits in inbred lines of sunflower under drought stress.

<table>
<thead>
<tr>
<th>Inbred line</th>
<th>Stomatal conductance</th>
<th>Relative water content</th>
<th>Shoot fresh weight</th>
<th>Shoot dry weight</th>
<th>Root area</th>
<th>SPAD</th>
<th>Electrolyte leakage</th>
</tr>
</thead>
<tbody>
<tr>
<td>A19</td>
<td>154.25±1.70</td>
<td>57.57±1.91</td>
<td>89.72±2.07</td>
<td>7.48±0.98</td>
<td>166.58±8.61</td>
<td>15.24±0.41</td>
<td>65.23±0.79</td>
</tr>
<tr>
<td>C111</td>
<td>124.33±3.21</td>
<td>61.65±1.12</td>
<td>105.40±0.65</td>
<td>5.09±1.10</td>
<td>128.30±3.07</td>
<td>12.70±1.25</td>
<td>56.96±0.41</td>
</tr>
<tr>
<td>C123</td>
<td>134.00±4.16</td>
<td>56.83±0.98</td>
<td>78.39±2.68</td>
<td>6.19±1.56</td>
<td>153.80±6.39</td>
<td>10.10±0.74</td>
<td>62.47±1.31</td>
</tr>
<tr>
<td>C138</td>
<td>218.50±2.64</td>
<td>62.10±0.56</td>
<td>99.09±3.22</td>
<td>9.55±0.93</td>
<td>185.56±9.53</td>
<td>14.27±0.89</td>
<td>52.84±1.75</td>
</tr>
<tr>
<td>C148</td>
<td>113.75±3.50</td>
<td>61.07±1.61</td>
<td>64.89±3.75</td>
<td>6.25±0.77</td>
<td>132.83±5.40</td>
<td>11.51±0.56</td>
<td>56.23±1.61</td>
</tr>
<tr>
<td>R217</td>
<td>162.00±5.47</td>
<td>56.13±0.90</td>
<td>96.05±4.26</td>
<td>6.21±1.21</td>
<td>144.60±8.23</td>
<td>14.55±0.82</td>
<td>59.12±3.16</td>
</tr>
</tbody>
</table>

Values are the mean of four measurements per line and ± indicates the standard error. Values followed by different letters indicate significant difference at the 0.05 probability level using Duncan’s multiple range test.

because this trait had positive correlation with stomatal conductance and RWC in the sunflower lines (Table 4).

The cell membrane is vulnerable to abiotic stresses. Thus, there is an agreement that maintenance of stability and integrity of cell membranes under drought stress can be the main component of drought tolerance in different plants (Bajji et al. 2002). Our results indicated that EL was increased by water shortage. Ghobadi (2013) also reported that EL is increased with drought. Among the sunflower lines, C138 had the lowest EL (Tables 2 and 3). Since lower leaf EL is a criterion of membrane stability of the cell (Ghobadi et al. 2013), thus C138 line had the highest membrane stability among lines. EL had negative correlation with other traits under study (Table 4).

Since biomass positively correlates with chlorophyll content and RWC (Zaharieva et al. 2001), it seems that SPAD can be a beneficial criterion for selecting the genotypes with more tolerance to drought stress. Furthermore, SPAD value is regarded as an efficient and non-destructive method for screening of the genotypes. We also found a positive and significant correlation of SPAD with shoot fresh weight, shoot dry weight and RWC (Table 4). In this study, SPAD significantly decreased under drought stress. Among the lines, only A19 reserved a high SPAD value in both conditions; however, it was not significantly different from C138 and R217 under drought stress (Tables 2 and 3). Our results were consistent with those from other studies (Ghaffari et al. 2012).

A large variation was observed in the relative expression of the sunTIP7 gene among sunflower lines. As shown in Figure 1, the fold changes in three lines (C138, C111, C123) by using the bootstrap resampling method were significant and negative. Whereas, non-significant positive fold
changes in the expression of the sunTIP7 gene were observed in the other lines (C148, A19, R217). The highest downregulation of sunTIP7 was observed in C138. Thus, the highest stomatal conductance in this line may be explained by downregulation of the sunTIP7 gene in the guard cells. Nevertheless, the same relation was not observed in the other lines with negative fold change (C111, C123) (Figure 1). Also, in other studies, the overexpression of an Arabidopsis AQPs (PIP1b) in the transgenic tobacco (Nicotiana tabacum) plants did not have useful effects and even had a negative impact on efficiency of the plants under drought stress (Aharon et al. 2003). Downregulation of sunTIP7 was previously reported in leaves of sunflower in response to drought stress (Aguado et al. 2014). Also, investigations on the model halophytic plant Mesembryanthemum crystallinum showed a temporary and coordinated decrease in the expression of three aquaporin genes in salinity stress (Yamada et al. 1995). Some studies have reported the effect of AQPs expression on stomatal behavior and RWC; for instance, expression of Vicia faba PIP1 (VfPIP1) gene in transgenic Arabidopsis plants prevents water loss because of the induction of stomatal closure (Cui et al. 2008). This is inconsistent with our results, as we mentioned above, C138 had high stomatal conductance and RWC with low sunTIP7 expression in the drought condition. The higher RWC and stomatal conductance in C138 can be explained partly by its extensive root system. Martre et al. (2002) indicated that the PIPs play an important role in the recovery of Arabidopsis from the water-deficient condition. Some studies have reported that AQPs genes are down- or up-regulated by osmotic stress and drought stress in several plant species, such as sunflower, Arabidopsis, rice and cauliflower (Yamaguchi-Shinozaki et al. 1992; Liu et al. 1994; Barrieu et al. 1999; Sarda et al. 1999). Overexpression of a member of PIP1 subfamily in the transgenic rice improved its water status in drought condition (Lian et al. 2004). Furthermore, the AQPs expression of drought-adapted and non-adapted species was different (Lian et al. 2004). Due to AQP sensitivity to various factors, such as cell water status and temperature, plant water status and hydraulic conductance, they are responsive to the environmental variation (Moshelion et al. 2015). The different results about the role of AQPs in drought tolerance could be also explained by their complex nature (Alexandersson et al. 2005) and

Table 4. Pearson correlation coefficients between physiological and growth traits of sunflower.

<table>
<thead>
<tr>
<th>Trait</th>
<th>SPAD</th>
<th>RWC</th>
<th>EL</th>
<th>Shoot FW</th>
<th>Shoot DW</th>
<th>Root area</th>
<th>Stomatal cond.</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPAD</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RWC</td>
<td>0.66**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EL</td>
<td>-0.65**</td>
<td>-0.92**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoot FW</td>
<td>0.76**</td>
<td>0.73**</td>
<td>-0.73**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoot DW</td>
<td>0.78**</td>
<td>0.79**</td>
<td>-0.72**</td>
<td>0.71**</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Root area</td>
<td>0.71**</td>
<td>0.73**</td>
<td>-0.69**</td>
<td>0.70**</td>
<td>0.80**</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Stomatal Cond.</td>
<td>0.63**</td>
<td>0.73**</td>
<td>-0.67**</td>
<td>0.72**</td>
<td>0.87**</td>
<td>0.82**</td>
<td>1</td>
</tr>
</tbody>
</table>

RWC: relative water content; EL: electrolyte leakage; Shoot FW: shoot fresh weight; Shoot DW: shoot dry weight; Stomatal cond.: stomatal conductance; **significant at the 0.01 probability level.
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Figure 1. The fold change expression of the sunTIP7 gene in leaf tissues of six inbred lines of sunflower from normal irrigation to drought stress conditions. Vertical bars represent standard errors. Significance levels were determined by a bootstrap test.

also variation among and within species.

According to Sarda et al. (1997), sunTIP7 expression in sunflower increased during stomatal closure and VfPIP1 expression in broad bean (Vicia faba) induced stomatal closure (Huang et al. 2002).

**Conclusion**

In this study, the amount of growth and physiological traits, and sunTIP7 expression in sunflower inbred lines was different at both well-watered and drought conditions. Drought stress decreased all growth traits and increased EL. Expression analysis of sunTIP7 aquaporin gene showed its down-regulation in three sunflower inbred lines C138, C111 and C123. The highest down-regulation of sunTIP7 belonged to C138, which had also the highest stomatal conductance. However, this was not true for the lines C111 and C123. Thus, down-regulation of AQPs could not play a definite role in stomatal behavior in all sunflower lines under water stress. The different results about the expression of sunTIP7 gene and its relationship with physiological traits in response to water stress can be attributed to the complex nature of AQPs patterns. The higher stomatal conductance, RWC and photosynthesis of C138 as compared to other sunflower inbred lines resulted in the highest biomass of this line, which can be partly attributed to the down-regulation of sunTIP7 in the leaves and its higher root area. Therefore, C138 is recommended as a suitable inbred line to be used in hybrid seed production programs in dry zones.

**References**


Forrest KL and Bhave M, 2008. The PIP and TIP aquaporins in wheat form a large and diverse family with unique gene structures and functionally important features. Functional and Integrative Genomics 8: 115-133.


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Expression analysis and physiological response of sunTIP7 aquaporin gene

Trezhe biyan va pasakh fiziyologiyi sun TIP7 aquaporin zarafshon. 

Shokofe tabai, rasa faton, xoje klentro qalvar.

چکیده

پاسخ گیاه به تنش خشکی با صفات فیزیولوژیکی و بیان زن رابطه مناسبی دارد. مطالعات متعدد اخیر نشان می‌دهند که پروتئین‌های کانال غشایی به نام AQPs با تأثیر بر رفتار هدایت روزنه می‌توانند در پاسخ گیاهان به شرایط تنش نقش داشته باشند. Zn7، زن TIP7 ضع خلواده می‌باشد. در منطقه بررسی بینان Zn7، تنش‌های مختلف محیطی از جمله تنش خشکی درک می‌باشد. در این مطالعه به منظور بررسی بینان زن TIP7، در شرایط آبیاری نرمال و کم آبیاری در گلخانه کشت شده‌اند. بیشترین اثرات روزنه در هر دو شرایط در بینان C138 مشاهده شد. مقدار تنظیم سطح تنش TIP7 در لاین‌های آفتابگردان در شرایط تنظیم سطح بود. کمترین سطح تنش زن در لاین C138 بینان مشاهده شد که این کاهش بیان احتمالاً با رابطه مشخصی بین بیان صفات فیزیولوژیکی و بیان تنش روزنه در لاین‌های مورد بررسی مشاهده نشد. این نتایج نشان می‌دهد که تحمل به خشکی در آفتابگردان یک صفت پیچیده است و بکر راهکار مولکولی ساده قادر به توضیح تحمل خشکی در لاین‌های ایبرد.

واژه‌های کلیدی: آفتابگردان، آکواپورین، تنش خشکی، هدایت روزنه.