Gene Expression of Wheat (*Triticum aestivum*) Aquaporins under PEG-Induced Dehydration

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ABSTRACT

Plant aquaporin genes regulate water movement through cellular membranes and determine the plant water relationship and plant adaptation to different environmental stresses. The expression of three PIP genes and one TIP gene was studied in response to PEG-induced dehydration in four Egyptian commercial wheat varieties. Semiquantitative estimation of RNA level via cDNA synthesis and PCR was used. Results showed that variations among the four studied genes in wheat varieties under normal condition and in the presence of PEG. Under normal conditions, Misr1 exhibited the highest level of PIP1 expression, Sids1 exhibited the highest level of PIP2 and PIP3 expression, and Gemmiza7 exhibited the highest expression of TIP1. Under dehydration induced by PEG, all three PIP genes (PIP1, PIP2, PIP3) showed various levels of transcription downregulation. PIP1 gave the highest level of downregulation in all varieties. Sids1 showed the highest response to PEG-induced dehydration because under normal conditions it exhibited high PIP expression and low TIP expression, whereas under dehydration condition it showed high downregulation of PIP genes and high upregulation of the TIP gene. This would be related to its high adaptation to dehydration. Results of this study will enhance our understanding of plant aquaporin expression profile and utilizing this in improvement of plant tolerance to dehydration.

Key words: Wheat, aquaporins, gene expression, dehydration, PCR.

INTRODUCTION

Water regulates various plant biological processes including plant growth and development through its movement across membranes which are regulated by a group of membrane channel proteins (aquaporins). Aquaporins are a subgroup of the major intrinsic protein (MIP) family. Aquaporins are channel proteins present in all living organisms (Agre et al., 1998) forming membrane pores with six membrane-spanning domains and cytoplasmic N- and C- termini. One main structure feature of aquaporins is that they have two conserved NPA motifs usually located in the middle of the pore (Murata et al., 2000). Aquaporins transfer water bidirectionally across the membrane (Hub et al., 2008; Wang and Tajkhorshid, 2007). Two main types of aquaporins are well characterized. On type transfers water while the other transports various molecules, such as urea, glycerol, carbon dioxide, and ammonia (Maurel et al., 2008), even though, both types of aquaporins control the passive transport through biological membranes in all forms of life (Heller et al., 1980).

Plant aquaporins are distributed under five groups. The plasma membrane intrinsic proteins (PIP) which contain two subgroups (PIP1 PIP2) and the tonoplast intrinsic proteins (TIP). They are localized in the plasma and tonoplast membranes respectively. The nodulin26-like intrinsic proteins (NIPs) which is a homologue of GmNod26. It is found in prebacteroid membrane of nitrogen fixing nodules in soybean. The small basic intrinsic proteins (SIPs) that are mostly present in the endoplasmic reticulum, and the X intrinsic proteins (XIPs) (Chaumont et al., 2001; Sakurai et al., 2005; Danielson and Johanson, 2008). The main function of plant aquaporins is to regulate water movement between the plant and its environment and inside the plant as well. They are responsible for about 95% of the water transfer through the plasma membranes (Henzler and Steudle, 2004). They generally can regulate water movement across membranes in three major strategies that are their expression level, their trafficking after synthesis in the ER, and the regulation of opening and closing the aquaporin channel.

Genome studies showed variations in abundance of aquaporin genes in different plant genomes. Zhang et al (2013) reported 66 GmMIPs in the soybean genome that represented the five subfamilies which contain aquaporins, glyceroporins, aquaglyceroporins to regulate its water relations (Zhang et al 2013). In cotton (*G. hirsutum*), the aquaporin family was found to include 71 aquaporin genes that consist of 28 PIPs, 23 TIPs, 12 NIPs, 7 SIPs, and 1 XIPs (Park et al, 2010). Tomato genome (*Solanum lycopersicum*) was reported to have 47 aquaporin genes that were distributed in the five subfamilies; PIPs, TIPs, NIPs, SIPs and XIPs (Reuscher et al 2013).

Expression of plant aquaporins differs greatly under different environmental conditions in different plant species. Under drought conditions, PIP aquaporin were found to be downregulated to prevent water loss.

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Strawberry *(Fragaria vesca L.)* genome was found to have ten PIP genes. Under drought stress, four PIP genes were downregulated in roots and leaves. This led to the suggestion that transcription of PIP aquaporins is altered in response to low water availability (Surbanovski et al, 2013). In another study, drought stress induced by 250 mM mannitol changed the expression of most PIP genes in the aerial part of *Arabidopsis* (Jang et al., 2004). Different responses of aquaporin expression to water stress were observed in upland (drought-resistant) and lowland (drought-sensitive) rice (Lian et al., 2006). Therefore, it was suggested that different cultivars of the same species may respond differently to water stress by changing their aquaporin gene expression. Drought resistance is a limiting factor of wheat breeding production which is the most important food crop for the world. Several wheat aquaporin sequences have been deposited in the nucleotide database. The expression of wheat aquaporins has not been studied under stress conditions. Therefore, in this study, expression of four wheat aquaporin genes was investigated under dehydration condition.

MATERIALS AND METHODS

Induction of dehydration

Wheat seeds of seven varieties (Misr1, Giza168, Sakha94, Sids1, Gemmiza7, and Shandawel1) were germinated in 0.5% water agar containing 10% polyethylene glycol (PEG-6000) for 10 days (Table 1) (Guo et al, 2013; Elsiddig et al, 2013). Four varieties (Misr1, Giza168, Sids1, Gemmiza7) only were able to grow in the presence of PEG so that they were used in this study. The same varieties were grown in water agar without PEG. Ten-day old shoots were collected, lyophilized under vacuum at -60ºC, ground to fine powder, and used for RNA isolation.

Primer design

The nucleotide database at the National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov) was searched for wheat (*Triticum aestivum*) aquaporins cDNA sequences. Total of 29 accessions were obtained. Most of them are partial sequences, therefore 3 full length PIPs and 1 long partial TIP cDNAs were chosen for primer design. A pair of specific primers (forward and reverse) was designed on their respective wheat aquaporin cDNAs (Table 2) using primer3 plus software (http://biotools.umassmed.edu/cgibin/primer3plus/primer3plus.cgi). Information of these primers is summarized in Table 2.

RNA isolation

Total RNA was isolated from 10 day old shoots grown in the presence or absence of 10% PEG. Ten mg of ground tissue was transferred into microfuge tube and one ml of QIAzol was added and mixed (QIAGEN Inc., Valencia, CA).

Table 1. Egyptian wheat (*Triticum aestivum*) varieties used in this study

NO	Variety	Status	Characteristics
1	Misr1	New	High tillers, resistant to rusts (stem rust in particular), 13.9%Protein, yield is 25 Ardab⁄Fed.
2	Giza168	Commercial	Resistant to three rusts, heat and drought tolerant, 12%protein, 21 Ardab⁄Fed.
3	Sids 1	Commercial, (Upper Egypt)	Resistant to yellow but susceptible to leaf rust, heat tolerant, salinity tolerant, 13.2% protein, 19 Ardab⁄Fed.
4	Gemmiza 7	Commercial	Resistant to yellow and stem rust, 12.9% protein, 20 Ardab⁄Fed.

Table 2. Primer sequence used in this study, accession number, and the expected PCR product of wheat (*Triticum aestivum*) aquaporins

Primer	Sequence, 5'→3'	Product, bp	Gene	Accession
WPIP1F	ctacatgattgcgcagtgcc	591	PIP1	AF139814.1
WPIP1R	gccgaactgaactgtcgaga			
WPIP2F	gctcctactacgtgcggtac	591	PIP1	AF139815.1
WPIP2R	acgtacgaatggacggtcac			
WPIP3F	cttcgtgctcgtctactgca	593	PIP1	AF139816.1
WPIP3R	actaaccacctgatcagcgc			
WTIP11F	cgcttgcttttggtgttgga	605	TIP1-1	EU177566.1
WTIP11R	tggagaagcggaggaggaag			
ActinF	tgccaagaacagctcctcag	480	Actin	AY145451.1
ActinR	gaagcacttcctgtggacga			
PolyT	ttttttttttttttttttttt	-	-	-

Chloroform, 0.3 ml, was added to the homogenate. The mixture was then shaken for 30 s followed by centrifugation at 4°C and 13000 rpm for 20 min. The supernatant was transferred to a new tube. One volume of isopropanol was added and mixed. Samples were centrifuged for 15 min at 4°C and 13000 rpm. RNA pellet was washed with 70% ethanol, briefly dried, and dissolved in DEPC water. The integrity of RNA was checked by agarose gel electrophoresis. RNA concentration and purity were determined at 260 nm and the OD260/280 ratio.

Synthesis of cDNA

Total RNA, 2 µg, was mixed with 0.5 ng oligodT primer in a total volume of 11 µl sterilized DEPC water. The mixture was incubated in the Multigene thermal Cycler (Labnet, USA) at 65°C for 10 min for denaturation. Then, 4 µl of 5X RT-buffer, 2 µl of 10 mM dNTPs and 100 U M-MuLV Reverse Transcriptase (SibEnzyme Ltd. AK, Novosibirsk, Russia) were added and the total volume was brought to 20 µl by DEPC water. The mixture was then re-incubated in the thermal Cycler at 37°C for 1h, then at 90°C for 10 min to inactivate the enzyme. cDNA was used as template for PCR or kept at -20°C until used.

Semi-quantitative PCR

Specific primers designed on the nucleotide sequence of wheat aquaporin accessions (Table 1) were used in PCR reactions to amplify aquaporin cDNA molecules. PCR was conducted in a final volume of 25 µl containing 1 µl cDNA, 1 µl of 10 picomol of each primer (forward and reverse), and 12.5 µl 2X PCR master mix (Promega Corporation, Madison, WI, USA). PCR was carried out using one cycle of initial denaturation at 94°C for 5 minute, followed by 35 cycles of denaturation at 94 °C for 1 minute, annealing at 55°C for 1 min, and extension at 72 °C for 1 min. This was followed by one additional cycle of final extension at 72°C for 7 min. The expression of actin mRNA was tested using specific primers (Table 1) as a reference. PCR products were separated in 2% agarose gel in TAE buffer at 50 volt for 60 minutes in the presence of ethidium bromide. PCR products were visualized under UV light and photographed. Densitometeric analysis of band intensities was determined using NIH imageJ program (http://rsb.info.nih.gov/nih-imageJ).

Estimation of expression level

Percentage of expression level was calculated using the densitometeric digital data. Under normal conditions, the expression percentage of a specific aquaporin gene of the four wheat varieties was calculated as the percentage of the highest level of expression (100%) for that gene. In the presence of PEG, expression percentage for a gene was estimated as a percentage of its corresponding expression estimate under normal condition.

RESULTS

Expression of wheat aquaporin genes was investigated under PEG-induced dehydration compared to their expression under normal condition. Specific primers designed on the wheat aquaporin cDNA sequences obtained from the nucleotide database (www.ncbi.nlm.nih.gov) were used to estimate the gene expression of 3 PIP genes (PIP1, PIP2, PIP3) and one TIP gene (TIP1) (Table 2).

Expression of wheat aquaporin PIP genes

Expression of wheat PIP1 was estimated using its specific primers. There was natural variation in PIP1 expression under normal conditions among the four wheat varieties (in the absence of PEG). Under normal conditions, Misr1 showed the highest PIP1 expression level which was considered as 100% (Table 3). Gemmiza7 showed the lowest level of expression (54%) compared to Misr1 (Table 3), whereas Giza168 and Sids1 showed close level of expression (Figure 1a,c), 86% and 88% compared to Misr1 (Table 3). PEG-induced dehydration caused a substantial downregulation of PIP1expression. The four wheat varieties showed lower expression level, but there was less variation in PIP1 expression (Figure 1a,c). Expression of PIP1 in Misr1, Giza168, Sids1, and Gemmiza7 was 26%, 25%, 21%, and 31% respectively of their expression level under normal conditions (Figure 1a, c, Table 3). Actin gene expression was estimated as a reference (Figure 1b). Gemmiza7 showed the lowest expression of PIP1 under normal conditions but it showed the least downregulation in response to PEG, while Sids1 exhibited the highest level of downregulation in response to PEG (Table 2).

Wheat PIP2 expression also showed natural variation among wheat varieties in the absence of PEG. Sids1 showed the highest level of expression (100%) (Table 3). Misr1, Giza168, and Gemmiza7 showed close level of expression; 89%, 79%, 83%, compared to Sids1 expression respectively (Figure 2a,c; Table 3). Also, PEG-induced dehydration caused downgegulation of PIP2. Misr1, Giza168, Sids1, and Gemmiza7 exhibited 85%, 65%, 68%, and 58% of PIP2 expression under normal conditions (Figure 2a,c; Table 3). Misr1 showed the least downregulation of PIP2, whereas Gemmiza7 exhibited the highest level of downregulation (Table 3). Actin gene expression was estimated as a reference (Figure 2b).

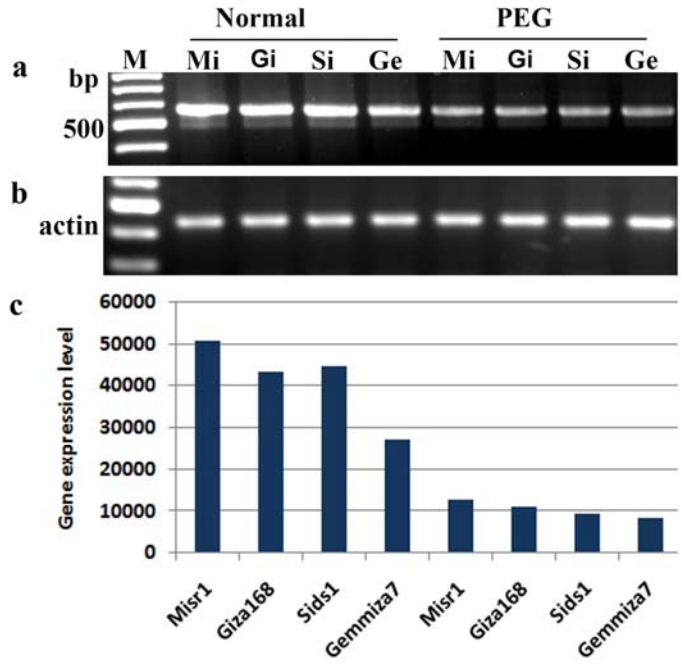

Figure 1. Wheat PIP1 expression. a. PIP1 expression; b. actin gene expression as reference. M: 100 bp ladder; Mi: Misr1; Gi: Giza168; Si: Sids1; Ge: Gemmiza7. c. Semiquantitative estimation of PIP1 expression of panel a.

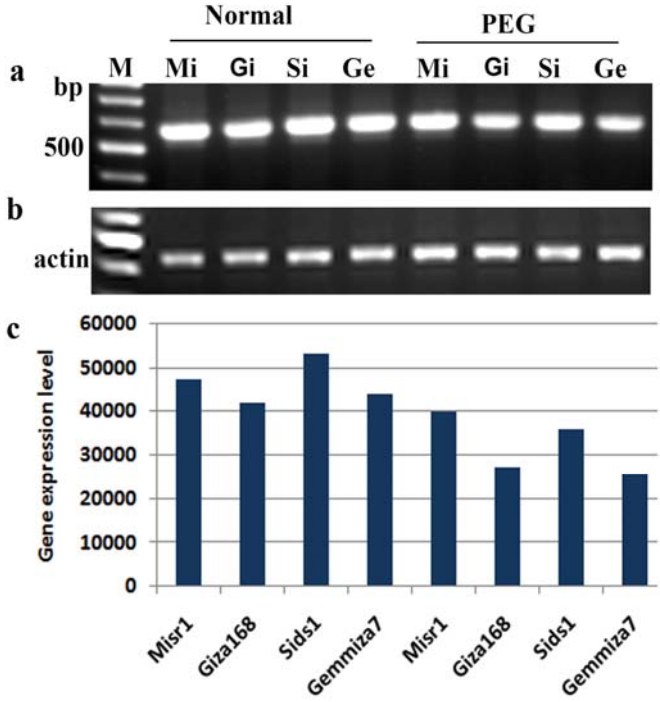

Figure 2. Wheat PIP2 expression. a. PIP2 expression; b. actin gene expression as reference. M: 100 bp ladder; Mi: Misr1; Gi: Giza168; Si: Sids1; Ge: Gemmiza7. c. Semiquantitative estimation of PIP2 expression of panel a.

Table 3. Wheat aquaporin gene expression level (%) under normal and PEG-induced dehydration.

	% Expression level							
Gene	Normal				PEG-induced dehydration			
	Mi	Gi	Si	Ge	Mi	Gi	Si	Ge
PIP1	100	86	88	54	26	25	21	31
PIP2	89	79	100	83	85	65	68	58
PIP3	80	88	100	62	47	86	57	77
TIP1	83	82	40	100	203	240	357	202

Mi: Misr1; Gi: Giza168; Si: Sids1; Ge: Gemmiza7.

Expression of PIP3 gene also exhibited variations in the presence or absence of PEG. Under normal conditions, Sids1 exhibited the highest level of expression (100%), while Misr1, Giza168, and Gemmiza7 showed 80%, 88%, and 62% of PIP3 expression in Sids1. In the presence of PEG, Misr1, Giza168, Sids1, and Gemmiza7 gave 47%, 86%, 57%, and 77% of PIP3 expression under normal condition (Figure 3a,c; Table 3). Actin gene expression was estimated as a reference (Figure 3b). Misr1 showed the highest level of downregulation, whereas Giza168 exhibited the lowest level of downregulation of PIP3 in response to PEG.

Expression of wheat aquaporin TIP1 gene

On the contrary to the three studied PIP genes above, TIP1 gene showed upregulation in response to PEG treatment. Under normal condition, Gemmiza7 showed the highest level of TIP1 gene expression (100%) and Misr1, Giza168, Sids1 gave 83%, 82%, 40% of Gemmiza7 TIP1 expression (Figure 4a, c; Table 3). In the presence of PEG, also Gemmiza7 gave the highest TIP1 expression. It showed 202% of its expression under normal condition. Misr1, Giza168, and Sids1 showed 203%, 240%, and 357% of TIP1 expression under normal condition. Gemmiza7 showed the lowest level of TIP1 upregulation, while Sids1 showed the highest level of TIP1 upregulation (Figure 4a, c; Table 3).

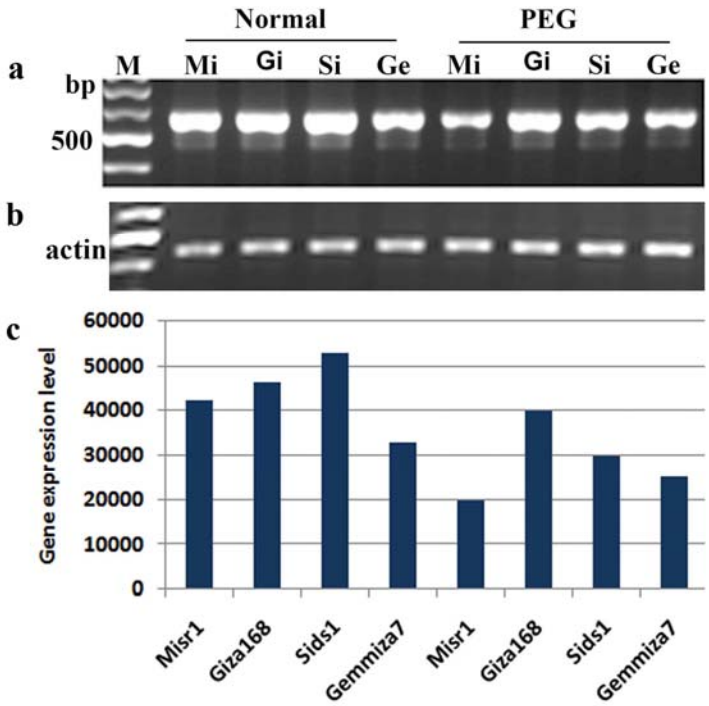

Figure 3.Wheat PIP3 expression. a. PIP3 expression; b. actin gene expression as reference. M: 100 bp ladder; Mi: Misr1; Gi: Giza168; Si: Sids1; Ge: Gemmiza7. c. Semiquantitative estimation of PIP3 expression of panel a.

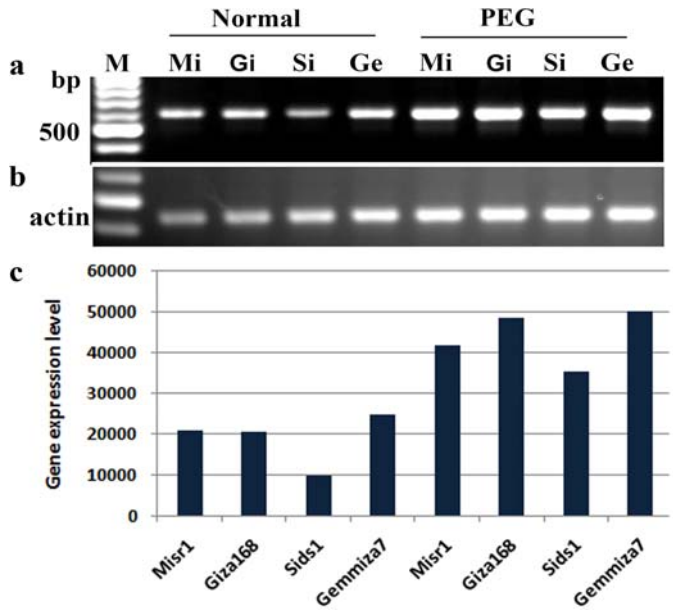

Figure 4. Wheat TIP1 expression. a. TIP1 expression; b. actin gene expression as reference. M: 100 bp ladder; Mi: Misr1; Gi: Giza168; Si: Sids1; Ge: Gemmiza7. c. Semiquantitative estimation of TIP1 expression of panel a.

DISCUSSION

Gene expression of wheat aquaporin genes (PIP1, PIP2, PIP3, TIP1) was investigated under normal condition and in the presence of PEG as dehydration inducer. The four studied genes exhibited natural variations in their expression under normal condition as well as in the presence of PEG. The three PIP genes showed various levels of downregulation (Figure 1, 2, 3), while TIP1 showed different levels of upregulation (Figure 4) in the four wheat varieties in response to PEG treatment. There were different responses for every wheat variety to PEG treatment for individual genes. Also, there were different responses of individual genes toward PEG treatment. The three PIP genes were downregulated by PEG, whereas the TIP gene was upregulated (Figure 1,2,3,4, Table 3). Results obtained from this study agree with other previous reports. Various studies were conducted on water stress–dependent expression of aquaporin genes (Maurel et al, 2002), especially the studies carried out on maize, rice, radish, and *Arabidopsis*. In these studies the expression of the whole aquaporin family was studied (Alexandersson et al, 2005; Boursiac et al, 2005; Guo et al, 2006; Jang et al, 2004; Lian et al, 2004; Maathuis et al, 2003; Suga et al, 2002; Zhu et al, 2005). General downregulation of most aquaporin transcription was reported under salt-stress in roots of *Arabidopsis* and maize (Alexandersson et al, 2005; Boursiac et al, 2005; Maathuis et al, 2003). Even though there is an overall downregulation of aquaporin gene in response to dehydration there was also specific upregulation of certain PIP transcripts in rice and *Arabidopsis* leaves (Alexandersson et al, 2005; Guo et al, 2006). For example, two upregulated transcripts in *Arabidopsis* were specifically expressed in aerial parts (Alexandersson et al, 2005). In barley (*Hordeum vulgare*) the increase in HvPIP1-6 transcripts in response to salt may indicate its role in promoting residual growth of the leaf under stress (Fricke et al, 2006). The downregulation of PIP aquaporin genes is thought to minimize water loss from plants to the dehydrated soil (Maurel et al 2008).

In this study, wheat TIP1 exhibited high level of upregulation. This also is in accordance with the explanation that under water stress vacuoles will work to keep the cellular water balance by mobilization of water from or into the vacuole (Maurel et al 2008). Sids1 variety exhibited high expression level of PIP1, PIP2, PIP3, whereas it showed high response to the PEG treatment. It showed low level of PIP1, PIP2, and PIP3, while it showed the highest level of TIP1. The combination of decreasing PIP gene expression and increasing TIP gene expression give indication that Sids1 is more adaptive to dehydration than other varieties under study.

Results of this study contribute to our understanding of plant aquaporin genes which can be utilized in enhancing drought tolerance of plants via modulating their expression. This will depend on the aquaporin gene and plant species under investigation.

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الملخص العربي

تعبير جينات الأكوابورين في القمح (*Triticum aestivum*) تحت ظروف نقص الماء المستحثه بواسطة البولي إيثيلين جليكول

منى محمد الصيحي، أحمد محمد الشهاوي

جينات الأكوابورين لها دور كبير في تنظيم حركة الماء خلال الأغشية الخلوية وتحدد علاقة النبات بالماء وإستجابته للعوامل البيئية المختلفة. تم دراسة تعبير ثلاثة جينات أكوابورين المندمجة في الغشاء البلازمي (PIP)، وجين من جينات الأكوابورين المندمجة في غشاء الفجوات (TIP) إستجابة لنقص الماء المستحث بواسطة البولي إيثيلين جليكول ٦٠٠٠، وذلك بواسطة التقدير شبه الكمي لمستوي النسخ من خلال تخليق cDNA وتفاعل البلمرة المتسلسل (PCR). أظهرت النتائج إختلافات في مستوي التعبير الجيني بين الأربعة جينات المدروسة في أصناف القمح تحت الدراسة وذلك تحت الظروف الطبيعية وفي وجود البولي إيثيلين جليكول. تحت الظروف الطبيعية، أظهر الصنف مصر١ أعلي مستوي في تعبير الجين PIP1، وأظهر الصنف سدس١ أعلي مستوي في تعبير الجينات PIP2، PIP3، بينما أظهر الصنف جميزة٧ أعلي مستوي في تعبير الجين TIP1. تحت ظروف نقص الماء المستحث بواسطة البولي إيثيلين جليكول أظهرت النتائج نقص في مستوي تعبير الثلاثة جينات PIP1، PIP2، PIP3، وكان تعبير الجين PIP1 هو الأقل إنخفاضا في أصناف القمح الأربعة تحت الدراسة. أظهرت النتائج أيضا أن الصنف سدس١ أظهر أعلي إستجابة لنقص الماء، حيث أظهر أعلي مستوي تعبير لجينات PIP وأقل مستوي لجين TIP1 تحت الظروف العادية، بينما أظهر أعلي إنخفاض في تعبير جينات PIP وأعلي إرتفاع في تعبير جين TIP تحت ظروف نقص الماء. ربما يدل ذلك علي قدرة هذا الصنف العالية علي الأقلمة تحت ظروف نقص الماء. نتائج هذه الدراسة ستسهم في زيادة فهم تعبير جينات الأكوابورين النباتية وإستخدامها في تحسين تحمل النبات لظروف نقص الماء.