Terminal drought and seed priming improves drought tolerance in wheat

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Abstract Plants retain the preceding abiotic stress memory that may aid in attainment of tolerance to subsequent stresses. This study was conducted to evaluate the influence of terminal drought memory (drought priming) and seed priming in improving drought tolerance in wheat (*Triticum aestivum* L.). During first growing season, wheat was planted in field under optimal (well-watered) and drought stress imposed at reproductive stage (BBCH growth stage 49) until maturity (BBCH growth stage 83). Seeds collected from both sources were subjected to hydropriming or osmopriming (with 1.5% CaCl₂ solution); while, dry seed was taken as control. Treated and control seeds, from both sources, were sown in soil filled pots. After the completion of seedling emergence, pots were maintained at 50% water holding capacity (drought) or 100% water holding capacity (well-watered). Drought stress suppressed the plant growth (2–44%), perturbed water relations (1–18%) and reduced yield (192%); however, osmolytes accumulation (3–14%) and malondialdehyde contents (26–29%) were increased under drought. The crop raised

from the seeds collected from terminal drought stressed plants had better growth (5–63%), improved osmolyte accumulation (13–45%), and lower lipid peroxidation (3%) than the progeny of well-watered crop. Seed priming significantly improved the crop performance under drought stress as compared to control. However, osmopriming was more effective than hydropriming in this regard as it improved leaf area (9–43%), tissue water status (2–47%), osmolytes accumulation (6–48%) and grain yield (14–79%). In conclusion, terminal drought induced modifications in seed composition and seed priming improved *transgenerational* drought tolerance through improvement in tissue water status and osmolytes accumulation, and decrease in lipid peroxidation.

Keywords Drought · Plant stress memory · Seed priming · Transgenerational stress tolerance

Introduction

Drought stress is one of the major abiotic stresses, limiting the crop productivity worldwide. It adversely affects the plant growth and development by disturbing many physiological and biochemical processes. Drought disrupts the cell division and elongation, and affects the tissue water status, nutrients uptake and translocation, photosynthesis and assimilate translocation (Farooq et al. 2009). It induces alterations in photosynthetic pigments and constituents (Farooq et al. 2009), reduces enzymes activities (Fu and Huang 2001) and causes over-production of reactive oxygen species (ROS) (Farooq et al. 2009). Drought stress causes substantial reduction in crop yield through decrease in seed set owing to reduction in sink capacity and dry matter accumulation. For instance, seeds harvested from

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barley plants developed under drought stress had less grain weight and grain yield as compared to grains harvested from well-watered plants (Samarah 2005).

Drought tolerance is the ability of plants to survive and grow well with limited water supply (Passioura and Angus 2010). In response to drought, plants evolve stress tolerance mechanisms at morphological, physiological and molecular level (Farooq et al. 2009). Plants close stomata, change the leaf number and size and alter root architecture to avoid water loss and enhance water uptake under drought stress (Turner et al. 2001). Furthermore, osmotic adjustment, through accumulation of osmolytes, helps plants survive and have better growth, yield formation under drought (Farooq et al. 2009). Plants also enhance the activity of enzymatic and non-enzymatic antioxidants to protect the cellular membranes and macromolecules from damaging effect of the drought-induced oxidative stress (Gill and Tuteja 2010).

When stress progresses during grain filling stage, tolerance to dehydration may let the plants retain their metabolic activity for a few additional days, and therefore persist the translocation of formerly manufactured reserves for grain filling (Weng et al. 1982). In case of drought stress, a large assemblage of genes code for hydrophilic late embryogenesis abundant (LEA) proteins and other stress proteins, such as dehydrins, help in drought tolerance by sustaining adequate water potential (Blackman et al. 1995). These LEA and other stress proteins and osmoprotectants accumulate in vegetative tissues and seeds during periodic drought stress; hence plants are acclimatized to harsh drought conditions (Farooq et al. 2009). These substances improve the crop performance under drought and are stored in seed, which can increase the crop yield exposed to drought in succeeding years (Walter et al. 2013; Tabassum et al. 2017; Farooq et al. 2018). Thus, subjecting the crop to a stress at grain development stage may aid in the acquirement of drought stress tolerance (Farooq et al. 2018) due to accumulation of stress proteins and some compatible solutes in the seed. This also helps reducing the subsequent stress hazards to the plants even in next generation (Walter et al. 2011; Farooq et al. 2018).

Seed priming is controlled hydration of seed carried out to a level where germination related metabolic activities begin but radical protrusion does not take place (Farooq et al. 2006). It is an easy and cost-effective technique to overcome adverse effects of abiotic stresses (Ibrahim 2016; Wojtyla et al. 2016). Seed priming can improve the tolerance of plants against abiotic stresses through enhanced and advanced germination, improved mechanisms of protection against oxidative stress and retained memory of previous stress (Chen and Arora 2013). For priming, seeds are soaked in low water potential solutions. A variety of

inorganic salts, plant growth regulators and organic solutes are used as priming agents (Farooq et al. 2006, Afzal et al. 2008). However, seed priming with calcium salts has been more effective and economical in improving stress tolerance in plants (Jafar et al. 2012; Tabassum et al. 2017) because calcium acts as secondary messenger in signaling pathways (White and Broadley 2003) and enhances osmolytes accumulation and antioxidant activity under stressed conditions (Farooq et al. 2017a).

Although drought stress suppressed the growth and yield of crops, however, the plants formerly exposed to one type of stress (stress priming/hardening) may develop tolerance/protection to another kind of stress through enhanced production of secondary metabolites (Tabassum et al. 2017; Farooq et al. 2018). These secondary metabolites may translocate and accumulate in seed, and may develop tolerance to another kind of stress by retaining the plant stress memory even in next generation. Furthermore, seed priming induces stress tolerance in plants by improving the defense mechanisms and retained priming memory. In recent studies, we found that transgenerational drought memory helps improve the tolerance against salt stress in wheat (Tabassum et al. 2017) and drought stress in chickpea (Farooq et al. 2018). However, information is lacking regarding the performance of wheat exposed to terminal drought during preceding season and seed priming to drought stress. This study was, therefore, conducted to investigate the effect of terminal drought stress followed by seed priming on attainment of transgenerational drought tolerance in common wheat.

Methods

Phase 1

Wheat (*Triticum aestivum* L.) cultivar Punjab-2011 was planted on November 11, 2012 at the Agronomic Research Area, University of Agriculture Faisalabad (latitude 31°N, longitude 73°E and altitude 184.4 masl), Pakistan. Terminal drought stress was imposed at reproductive stage (BBCH growth stage 49) until maturity (BBCH growth stage 83) in one set of experimental units, while the other continued to grow under well-watered conditions. The experimental soil was sandy loam having saturation percentage (27%), organic matter (0.92%), pH (7.6), electrical conductivity (1.01 dS m^{-1}), total soluble salts (10.1 mmol L^{-1}), exchangeable sodium (9.7 mmol L^{-1}), sodium absorption ratio ($5.05 (\text{mmol}_c \text{ L}^{-1})^{1/2}$), total nitrogen (0.06%), available phosphorous (5.00 ppm), exchangeable potassium (166.00 ppm), chloride ion (7.34 mmol L^{-1}), bicarbonate ion (6.48 mmol L^{-1}) and Ca + Mg ions (7.36 mmol L^{-1}).

The experiment was conducted in paired plot design with four replications. Fertilizers were applied at 100 kg ha⁻¹ N, 90 kg ha⁻¹ P and 75 kg ha⁻¹ K using urea (46% N), di-ammonium phosphate (18% N, 46% P₂O₅) and sulfate of potash (50% K₂O), respectively. Whole of the P, K and one third of the N were applied as basal dose. Remaining N was applied in two equal splits at tillering and leaf boot stages. At reproductive stage, no irrigation was applied to drought stressed crop while irrigation was applied to well-watered crop. The crop was harvested on 24th of April, 2013 at harvest maturity and seeds were collected from both sources and stored for use during second phase of the experiment.

Phase 2

Seeds collected from well-watered as well as drought stressed wheat plants were subjected to seed priming. In hydropriming, seeds were soaking in aerated water; while, for osmopriming, seeds were soaked in aerated CaCl₂ (1.5%) solution. In both cases, soaking was done for 12 h, keeping seed to solution ratio of 1:5 (w/v). Aquarium pump was used to provide aeration. After soaking, seeds were removed, thoroughly rinsed with water and dried with forced air under shade till original weight.

The unprimed (dry seed) and primed seed were sown (15 seeds per pot) in soil filled pots (30 cm diameter and 45 cm high pots containing 15 kg soil) placed in a net house under natural conditions on 2nd week of November, 2013. The same soil was used to fill earthen pots during this phase as was used in the first phase of the experiment.

After uniformity of seedling emergence, thinning was done to keep six plants per pot, and the pots were maintained at 100% water holding capacity (well-watered) or 50% water holding capacity (drought stress). The desired levels of moisture were attained by determining the required amount of water, then weighing the pots after application of calculated amount of water and designating it as target weight. Drought was imposed by attaining the target pot weight with the application of water on every alternate day. The experiment was laid out using completely randomized design with factorial arrangement and four replications. The soil in pots was fertilized at the same rate using same sources as used for field crop to ensure adequate supply of nutrients. The crop was harvested on April 23, 2014.

Observations and measurements

Relative leaf water contents

Penultimate leaf samples from two plants per pot were collected at leaf booting stage (90 DAS) to determine the

water relation traits. Fresh leaf samples were weighed and soaked for 4 h in water to record saturated weight. Leaves were then oven dried and weighed again. Leaf relative water contents as described by Barrs and Weatherly (1962).

Mineral and biochemical analyses

Flag leaves from three plants (used for sampling for water relation traits and leaf area) were detached at leaf booting stage (90 DAS) to determine the K contents, osmolytes and lipid peroxidation. For the determination of K⁺ in leaves, the samples were dried in oven at 70 °C, soaked in di-acid mixture overnight, digested and filtered. The filtrate was fed to the flame photometer and K⁺ were determined following the method of Chapman and Pratt (1961). For determination of free leaf proline contents, fresh leaf samples were homogenized in sulfosalicylic acid and glacial acetic acid. Ninhydrin solution was added to the filtrate, incubated and cooled in ice bath, then toluene was added and vortexed. Absorbance was read at 520 nm using toluene as a blank after aspiration of chromophore containing toluene from the aqueous phase. The proline concentration was assayed according to Bates et al. (1973). For determination of glycine betaine, the fresh leaves samples were ground in distilled water and filtered. Afterwards, HCL and potassium tri-iodide was added, incubated at 4 °C for an hour, chilled water and 1, 2-di-dichloroethane were added in the cooled mixture. The mixture was vortexed and absorbance of organic layer was measured at 365 nm. The concentration of glycine betaine was determined following Grieve and Grattan (1983). Fresh leaf samples were homogenized in thiobarbituric acid (TBA) and the absorbance of supernatant was recorded at 532 and 600 nm. The MDA concentration was determined following Cakmak and Horst (1991).

Morphological and yield traits

To record data on morphological traits, three plants from each replication were selected and tagged, randomly. Plant height was measured from soil surface to tip of plants at maturity. Leaf area were measured at leaf booting stage, after detaching the leaves from one plant using digital leaf area meter (JVC TK-5310). The same leaves were dried till constant weight in an oven, and specific leaf area was recorded as ratio of leaf area to leaf weight. Number of productive tillers was counted from the remaining selected two plants. Plants were harvested and biological yield was recorded by weighing the whole plant samples. Then grains were separated from spikes and number of grains per spike was counted and weight of 100 grains was recorded using a digital weighing balance. The grains separated from spikes were weighed and averaged to record grain yield per plant.

Harvest index was calculated as the ratio of grain yield to total biological yield and was expressed in percentage.

Statistical analysis

Experimental data were analysed statistically by Fisher's analysis of variance technique (Steel et al. 1997). For mean separation, the least significant difference (LSD) test was used at 0.05 probability level (Steel et al. 1997).

Results

Leaf area and specific leaf area were significantly reduced by drought stress when the crop was raised either from droughted or well-watered seed source; while, plant height was not affected significantly. However, under non-stressed conditions, the progeny of well-watered seed source had more leaf area and specific leaf area, while, under drought stress, the crop raised from droughted seed source performed better. Seed priming significantly improved the growth of wheat plants raised from both seed sources. Under non-stressed conditions, higher leaf area (25–29%) and specific leaf area (12–48%) of wheat plants were recorded from hydroprimed and osmoprimed seed from well-watered crop, respectively. Under drought stress, more leaf area (65%) and specific leaf area (9%) were recorded from hydroprimed seeds of terminal drought stressed crop and osmoprimed seeds from well-watered crop, respectively, as compared to unprimed control (Table 1).

Drought stress reduced the RWC and increased the accumulation of leaf K contents in wheat. However, the effect of drought stress on the plants raised from droughted seed source was significantly less adverse in terms of plant tissue water status as compared to the plants raised from well-watered seed source. Seed priming significantly improved the relative water content and accumulation of leaf K contents in progeny of both seed sources as compared to unprimed control. Under non-drought conditions, hydroprimed seeds of well-watered source had better K contents (18%), while, relative water contents (3–4%) were improved by osmopriming of seed from both seed sources, as compared to unprimed control. Under drought stress, osmoprimed seed from well-watered seed source caused maximum increase in relative water content (11%) and K contents (20%) than the unprimed control (Fig. 1).

Drought stress increased the accumulation of free leaf proline, glycine betaine contents as well as lipid peroxidation in wheat plants as compared control. On the other hand, progeny of drought stressed crop accumulated higher osmolytes but less MDA than progeny of well-watered crop under drought stress. Furthermore, seed priming

improved the production and accumulation of osmolytes while, reduced the accumulation of MDA, as compared to unprimed control. Under non-stressed conditions, osmopriming of seed from terminal drought stressed and well-watered crop increased the accumulation of free leaf proline (76%) and glycine betaine contents (35%), respectively, as compared to unprimed control. However, least MDA (24%) was produced by hydropriming of seed from water stressed seed source. Under drought stress, free leaf proline (76%) and glycine betaine (23%) were greatly improved by osmopriming of seed from terminal drought stressed and well-watered crop, respectively, as compared to unprimed control. The MDA content (23%) was decreased most by osmopriming of seed from terminal drought stressed crop (Fig. 2).

Drought stress significantly affected the biological and grain yields and yield contributing traits. Nonetheless, progeny of terminal drought stressed crop performed better under succeeding drought stress than progeny of well-watered crop. Seed priming substantially improved the yield attributes and grain yield but the effect of seed priming was more prominent from osmopriming of seed from terminal drought stressed source. Under non-stress conditions, number of grains per spike (14%), 100-grain weight (32%) and grain yield (21%) were improved by osmopriming the seed from terminal drought stressed source, while, more number of productive tillers (21%) and harvest index (10%) was observed by osmopriming the seed from well-watered crop, as compared to unprimed control. Similarly, under drought stress, osmopriming the terminal drought stressed seed caused maximum increase in number of productive tillers per plant (57%), number of grains per spike (40%), 100-grain weight (24%), grain yield (192%) and harvest index (61%) as compared to unprimed control (Tables 2, 3).

Discussion

The progeny of drought stressed wheat crop exhibited better performance and stress tolerance under subsequent drought stress. Seeds obtained from wheat crop exposed to drought stress at reproductive stage had some distinct modifications in seed composition to evoke stress tolerance mechanisms as compared to well-watered crop. Terminal drought stress reduced the seed moisture content, ash contents and crude fat while, increased the crude fiber, crude protein and total soluble phenolic contents as compared to control (Tabassum et al. 2017). Terminal drought stress causes alterations in source-sink relationship of plants resulting in decreased translocation and accumulation of sugars in reproductive parts which alters the composition of fatty acids and oil contents in seeds (Bellaloui

Table 1 Effect of seed priming following terminal drought on plant height, leaf area and specific leaf area of wheat under drought stress

Treatments	Plant height (cm)		Leaf area (cm ²)			
	Seeds from well-watered source		Seeds from terminal drought source		Seeds from well-watered source	
	Control	Drought	Control	Drought	Control	Drought
Unprimed	61.38 ± 3.78	46.91 ± 2.69	64.41 ± 3.34	50.54 ± 2.65	286.23 ± 4.52b	160.17 ± 3.33f
Hydropriming	64.66 ± 0.75	47.12 ± 2.18	57.53 ± 2.14	54.92 ± 1.38	370.27 ± 3.99a	217.31 ± 6.12e
Osmopriming	65.81 ± 4.54	48.83 ± 2.25	68.38 ± 0.87	59.11 ± 2.24	358.81 ± 3.40a	229.07 ± 5.87e
LSD value (<i>p</i> 0.05)	NS				15.23	
Treatments						
	Specific leaf area (cm ² g ⁻¹)		Seed from terminal drought source			
	Seeds from well-watered source		Control		Drought	
Unprimed	306.44 ± 3.93 cd		295.40 ± 4.13de		318.08 ± 2.14c	269.08 ± 7.02 fg
Hydropriming	342.97 ± 4.65de		248.21 ± 4.17 h		280.39 ± 5.08ef	251.49 ± 1.74 h
Osmopriming	452.74 ± 3.57a		292.46 ± 10.14de		337.19 ± 5.77b	258.19 ± 6.51 gh
LSD value (<i>p</i> 0.05)	15.39					

Values in the table are mean ± SE. Means sharing a letter in common don't differ significantly at $p \leq 0.05$, NS non-significant

Fig. 1 Effect of seed priming following terminal drought on **a** relative water contents and **b** leaf K content of wheat under drought stress. Each bar indicates mean of four replications $\pm$ SE. Bars sharing a letter in common don't differ significantly at $p \leq 0.05$

et al. 2013). Terminal drought stress decreases starch and sucrose in cereals, while, increases the soluble and heat shock proteins (Farooq et al. 2014; Arshad et al. 2017) which may be translocated to seeds thereby increasing seed protein content (Wehmeyer and Vierling 2000). Drought stress at post-anthesis stage increased the grain protein contents in wheat (Farooq et al. 2014). Plants accumulate phenolic compounds that act as antioxidants in response to abiotic stresses to attain stress tolerance which may also translocate to seeds (Wrobel et al. 2005; Weidner et al. 2009).

In this study, drought stress adversely affected plant growth, yield and related traits (Tables 1, 2, 3) by disturbing the water relations (Fig. 1) and causing oxidative

stress (Fig. 2). However, proline and glycine betaine contents were enhanced under drought stress; though, the increase was not much pronounced as compared to well-watered conditions (Fig. 2). This might be due to the moderate stress severity or due to sensitivity of genotype used in this study to drought stress (Farooq et al. 2017b). Moreover, Rampino et al. (2006) reported that sensitive genotypes of wheat accumulated greater proline content than resistant ones and the increase in proline accumulation was associated with drop in relative water content and relative water loss.

Progeny of water stressed crop performed better under drought stress with respect to growth and yield (Tables 1, 2, 3) by maintaining better tissue water status (Fig. 1) and

Fig. 2 Effect of seed priming following terminal drought on **a** leaf proline, **b** glycine betaine and **c** malondialdehyde contents of wheat under well-watered and drought stress. Each bar indicates mean of four replications $\pm$ SE. Bars sharing a letter in common do not differ significantly at $p \leq 0.05$

less lipid peroxidation (Fig. 2) as compared to well-watered crop. Plants exposed to drought stress get primed retaining their stress memory and reprogram their metabolic pathways (Ding et al. 2012). Hence, stress primed

plants are more tolerant to subsequent stress events through changes in their morphology, expression of stress related genes, and accumulation of stress responsive transcription factors, metabolites and heat shock proteins (Wang et al.

Table 2 Effect of seed priming following terminal drought on number of productive tillers per pot, number of grains per spike and 100-grain weight of wheat under drought stress

Treatments	Number of productive tillers per plant		Number of grains per spike			
	Seeds from well-watered plants		Seeds from terminal drought plants		Seeds from well-watered plants	
	Control	Drought	Control	Drought	Control	Drought
Unprimed	2.15 ± 0.03c	1.40 ± 0.03g	1.80 ± 0.04e	1.60 ± 0.02f	28.00 ± 0.71b	20.00 ± 0.41d
Hydropriming	2.40 ± 0.03b	2.00 ± 0.04d	2.20 ± 0.03c	1.80 ± 0.01e	28.00 ± 0.41b	21.00 ± 0.71d
Osmopriming	2.60 ± 0.04a	1.60 ± 0.03f	2.20 ± 0.01c	2.20 ± 0.01c	32.00 ± 0.71a	20.00 ± 0.82d
LSD (<i>p</i> 0.05)	0.09				1.84	
100-grain weight (g)						
Treatments						
Seeds from well-watered plants						
Control						
Unprimed	4.41 ± 0.09f				4.86 ± 0.07de	
Hydropriming	5.74 ± 0.15ab				5.14 ± 0.03 cd	
Osmopriming	5.42 ± 0.10bc				5.82 ± 0.03a	
LSD (<i>p</i> 0.05)	0.33					
Seed from terminal drought plants						
Control						
Unprimed						4.81 ± 0.28e
Hydropriming						4.67 ± 0.11ef
Osmopriming						4.92 ± 0.08de

Values in the table are mean ± SE. Means sharing a letter in common don't differ significantly at $p \leq 0.05$

Table 3 Effect of seed priming following terminal drought on biological yield, grain yield and harvest index of wheat under drought stress

Treatments	Biological yield (g plant ⁻¹)		Grain yield (g plant ⁻¹)			
	Seeds from well-watered plants		Seed from terminal drought plants		Seeds from well-watered plants	
	Control	Drought	Control	Drought	Control	Drought
Unprimed	7.86 ± 0.34ab	3.78 ± 0.15e	7.35 ± 0.27b	4.88 ± 0.17cd	3.15 ± 0.09c	0.91 ± 0.06h
Hydropriming	8.06 ± 0.17ab	4.51 ± 0.06d	7.43 ± 0.20b	5.33 ± 0.08c	3.49 ± 0.06b	1.40 ± 0.08fg
Osmopriming	8.09 ± 0.09a	4.41 ± 0.15d	8.99 ± 0.17a	6.79 ± 0.20c	3.59 ± 0.05ab	1.20 ± 0.04g
LSD (p 0.05)	0.91				0.22	
Treatments	Harvest index (%)		Seed from terminal drought plants			
	Seeds from well-watered plants		Control		Drought	
	Control	Drought	Control	Drought	Control	Drought
Unprimed	40.33 ± 2.29abc	24.38 ± 2.45e	36.55 ± 1.04c	30.63 ± 3.05d		
Hydropriming	43.36 ± 1.41ab	31.07 ± 1.40d	43.61 ± 0.38ab	31.26 ± 0.69d		
Osmopriming	44.42 ± 1.04a	27.34 ± 1.73de	42.22 ± 0.60ab	39.34 ± 1.81bc		
LSD (p 0.05)	4.82					

Values in the table are mean ± SE. Means sharing a letter in common don't differ significantly at $p \leq 0.05$, NS non-significant

2011; Munné-Bosch et al. 2013). In this study, enhanced accumulation of proline and glycine betaine was observed in the progeny plants raised from droughted seed source under subsequent drought stress (Fig. 2). It might be due to aggregation of transcription factors for proteins and osmolytes in maternal plants due to terminal drought that aided the progeny plants later to attain the stress tolerance under drought through maintenance of better tissue water status (Fig. 1; Bruce et al. 2007). Compatible solutes accumulate inside the plant cells that act as osmoticum to retain water by lowering osmotic potential as compared to rhizosphere thereby protecting the cell membranes and macromolecules from dehydration and oxidative stress (Verslues and Juenger 2011; Fahad et al. 2017).

Plants evoke some mechanisms to combat against stress through accumulation of compatible solutes or transcription of dehydrins and LEA-genes (Lambers et al. 2008). Under stress conditions, plants increase the accumulation of osmolytes and enhance the activities of antioxidant enzymes (Niu et al. 2016; Anjum et al. 2017). In present study, less accumulation of MDA occurred in progeny of terminal drought stressed crop as compared to progeny of well-watered crop (Fig. 2). Greater accumulation of phenolics and proteins occurred in seed from terminal drought stressed crop (Tabassum et al. 2017), and proline and glycine betaine also accumulated in greater amounts in progeny of droughted crop which lead to decreased accumulation of MDA under drought stress in progeny (Fig. 2). Stress primed plants regulate the expression as well as activities of redox related genes and antioxidant defense enzymes more efficiently, and results in less lipid peroxidation (Wang et al. 2016).

This study showed that seed priming of both seed sources improved the wheat performance pertaining to growth and yield under drought stress (Tables 1, 2, 3). Seed priming improves the stress tolerance by better germination giving an early head start and accumulation of osmolytes in plants (Afzal et al. 2008; Jisha and Puthur 2014). Seed priming exposes the germinating seeds to an early stress that activates desiccation tolerance mechanisms such as ROS scavenging systems and accumulation of stress responsive proteins hence inducing cross tolerance to subsequent stresses (Chen and Arora 2013; Jisha and Puthur 2016). In present study, seed priming nullified the negative effect of drought stress on tissue water status (Fig. 1) by enhanced accumulation of proline and glycine betaine (Fig. 2) in progeny of both seed sources. It might be due to the role of Ca^{2+} as secondary messenger that enhanced the gene expression for osmolytes (White and Broadley 2003). In addition, seeds are exposed to osmotic stress during osmopriming, which activates the protective systems and expression of aquaporins thus enhancing subsequent stress tolerance (Chen et al. 2012). In this

study, the osmopriming reduced the lipid peroxidation in wheat (Fig. 2). Calcium, in osmopriming, aids in acquiring abiotic stress tolerance by regulating cell membrane rigidity and permeability, and mitigates the adverse effects of abiotic stresses by signaling anti-stress responses (Hepler 2005). Moreover, Ca^{2+} transduces anti-stress signal via Ca^{2+} -calmodulin which activates transcription factors associated with antioxidant enzymes and reduces damaging effects of ROS and lipid peroxidation (Farooq et al. 2008).

The progeny of droughted crop and osmopriming exhibited better grain yield and related traits under drought stress (Tables 2, 3). This might be due to improved tissue water status and decreased lipid peroxidation (Figs. 1, 2) which resulted in better pollen viability and assimilate translocation leading to improved grain formation and grain size under water deficit conditions (Farooq et al. 2008; Gusmao et al. 2012). Thus, the improvement in productive tillers, and grain number and weight by raising the crop from droughted seed source and osmopriming resulted in enhanced grain yield and harvest index under drought stress (Tables 2, 3). In present study, seed source and seed priming exhibited positive effects under drought stress indicating the improved drought tolerance in wheat plants (Table 3). However, it is suggested that further field studies should be performed to determine the yield responses of wheat to seed priming, after exposure to drought, under drought stress.

Conclusion

Terminal drought induced modifications in seed composition and seed priming improved transgenerational drought tolerance through improvement in tissue water status and osmolytes accumulation and decrease in lipid peroxidation. These findings may help understand the mechanism of stress hardening in crop plants.

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Compliance with ethical standards

Conflict of interest Authors declare no conflicts of interest.

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