



Full Length Article

Agronomic and Physiological Evaluation of Wheat Cultivars under Deficit Irrigation Condition

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Abstract

Improving crop productivity under drought conditions contributes largely to the sustainable agriculture globally. In this study, the agronomic traits and physiological processes related to osmolyte accumulation and reactive oxygen species (ROS) homeostasis during late growth stage in wheat under drought stress were studied. Three cultivars *viz.*, Shimai 22 (drought tolerant), Zhongxinmai 99 (median drought-tolerant, control), and Shi 4185 (drought sensitive) sharing contrasting drought tolerance were grown under normal irrigation (NI: with irrigations prior to sowing, and at jointing and flowering stages) and deficit irrigation (DI, with irrigations prior to sowing and at jointing) conditions. Data regarding yields, osmolyte (*i.e.*, proline and soluble sugar) contents, and antioxidant enzyme activities of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), and malondialdehyde (MDA) contents were recorded. Under deficit irrigation, the cultivars displayed modified agronomic and physiological traits. Among cultivars, Shimai 22 showed best agronomic traits (6.47 to 7.23% higher yield than control), osmolyte contents and AE activities (10.12 to 22.18% higher than control), and least MDA accumulation (12.30 to 17.06% lower than control). In contrast, Shi 4185 cultivar performed worst regarding above said traits. The transcripts of the genes in ^Δ1-Pyrroline-5-carboxylate synthetase (P5CS) family that regulates proline biosynthesis and those in AE families that modulate ROS homeostasis were evaluated. Results revealed that the P5CS genes *TaP5CS2* and *TaP5CS5* and the AE ones *TaSOD3*, *TaCAT2* and *TaCAT5* were modified on transcripts across the cultivars under DI condition, showing to be significant upregulated compared with NI. These results suggested the essential roles of osmolyte accumulation and AE proteins in improving the drought tolerance of wheat during late growth stages. In addition, this study suggested that the elevated transcription efficiencies of distinct P5CS and AE family genes under water deprivation contribute to the enhanced drought tolerance in drought-tolerant cultivars. © 2021 Friends Science Publishers

Keywords: Antioxidant enzymes; Agronomic traits; Drought tolerance; Osmolytes; Wheat

Introduction

Drought stress exerts drastic negative effects on growth and the productivity of cereal crops (Wu *et al.* 2004; Sheffield 2014; Lesk *et al.* 2016). Given the climate change and anthropogenic influences (AghaKouchak *et al.* 2015), the drought risk has been raised and led to the yield loss of cereal species in past two decades (Li *et al.* 2009; Zhao and Running 2010; Dai 2013). In North China, the large-scale cultivation of winter wheat (*Triticum aestivum* L.), a crop constituting the major cropping system (*i.e.*, winter wheat/summer maize across whole year), contributes greatly to the regional food safety and the production development. However, much more water resource has been consumed by planting winter wheat due to elevated yields of winter wheat

together with the low rainfall amount during growth cycle (started from early of October to maturity of mid-June) (Lobell *et al.* 2011; Ray *et al.* 2015; Ghahramani and Moore 2016). The intensified consumption of water storage initiated by enhanced crop productivity combined with low precipitation has been becoming the limiting factor for the sustainable agriculture (Barnabas *et al.* 2008; Praba *et al.* 2009; Lobell *et al.* 2011). Therefore, developing water-saving management for the winter wheat production has acted as an effective strategy to promote the productivity of this species in a long term.

Crop plants have evolved a suite of strategies to cope with the negative effects of drought, including accumulation of osmolytes in plants once challenged with osmotic stress conditions (Anjum *et al.* 2017; Tanveer *et al.* 2019). Several

kinds of cellular metabolites, such as proline, soluble sugars, and a subset of small molecules, are over-accumulated through enhanced biosynthesis metabolism upon osmotic stressors, which regulate the plant adaptation to adverse environments (Anjum *et al.* 2017). Thus far, it has been recorded that osmolyte amounts are associated with improved physiological processes in the drought-challenged plants, due to their positive roles in regulating cellular osmotic potential and photosynthetic function (Farooq *et al.* 2009). Additionally, exogenous application of osmoprotectants enhances the yield traits of crop plants given improved regulation of the osmotic potential that confers plants drought resistance (Ashraf and Foolad 2007). For example, external glycine betaine has endowed plants enhanced drought tolerance, which is largely ascribed to the improvement of leaf stomatal conductance, photosynthetic function, and proline biosynthesis metabolism (Ma *et al.* 2007; Hussain *et al.* 2008). Exogenous application of spermidine, a kind of osmolytes frequently induced under osmotic stress, alleviates the adverse effects of drought on the growth and development behaviors of cereal plants (Kubis 2003). Moreover, transgene analysis on the genes encoding rate-limiting enzymes involving osmolyte biosynthesis, such as proline, has validated the function of distinct genes in improving plant drought tolerance. These drought tolerant-associated genes enhance the capacities of cell vigor and improve the drought response-associated physiological processes (Gubis *et al.* 2007). These findings together suggested the essential roles of osmolytes in plant drought responses.

Cellular oxidative condition in abiotic stress-challenged plants is present at the subsequent stage following stress progression. Under drought stress, plants over accumulate reactive oxygen species (ROS), such as superoxide radicals ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2) (Hussain *et al.* 2018). The ROS initiated exert negative roles to plant cells given the damage of cellular macro-molecules, such as lipids, proteins, and nucleic acids (Gill and Tuteja 2010). On the other hand, plants have evolved effective strategies to alleviate the negative effects of ROS under osmotic stresses. Among them, the antioxidant enzyme (AE) system is activated and plays essential roles in scavenging ROS, contributing to plant stress tolerance *via* alleviation of cellular oxidative stress condition (Sunkar *et al.* 2006). Superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), the critical enzymes effecting on antioxidant enzyme (AE) system, sustain relatively cellular ROS homeostasis under abiotic stresses (Signorelli *et al.* 2013). Moreover, distinct genes in AE families are modified on transcripts abundance upon osmotic stress (Karinne *et al.* 2015). Over expression of a suite of AE genes, such as SOD ones, endowed plants drought tolerance *via* improving cellular ROS homeostasis as well as alleviating the extent of plant oxidative stress (Wang *et al.* 2005; Karinne *et al.* 2015). These results together provided novel insights in breeding drought tolerant cultivars using the improved ROS homeostasis system.

Many efforts have been performed to evaluate behaviors of agronomic trait, physiological processes and yield formation capacity in cereal crops under varied water supply conditions (Kanbar 2013; Signorelli *et al.* 2013; Li *et al.* 2015; Li 2016). However, the behaviors of osmolyte accumulation, cellular ROS homeostasis, and the associated molecular processes during late stage in drought-challenged plants of winter wheat are needed to be further defined. In this study, we used wheat cultivars sharing contrasting drought response to investigate osmolyte- and ROS-associated parameters as well as related gene expression patterns under deficit irrigation. The results provide insights into understanding of the drought-associated physiological and molecular processes in wheat plants and benefit breeding of wheat cultivars cultivated under the water-saving conditions.

Materials and Methods

Experimental details and treatments

Experimental material: The field experiments were conducted at Liujiashuang village, Gaocheng City, China, during the 2017–2018 and 2018–2019 growth seasons. Meteorological factors at spring growth stage during the two growth seasons are shown in Table 1. The climate for experiments is specified with temperate continental monsoon, with rainfall amounts to be concentrated at summer season. The surface soil layer for experiments was loamy and contained organic matter 19.22 g kg^{-1} , available nitrogen 63.86 mg kg^{-1} , available phosphorus (Olsen-P) 21.44 mg kg^{-1} , and exchangeable potassium $121.75 \text{ mg kg}^{-1}$ (determined based on conventional assay for soil sample). The soil texture was alluvial type with soil pH 7.73.

Treatments: The plots were arranged based on a randomized split design with triplicates, with irrigation as main-plot whereas cultivar as sub-plot. The main-plot included two irrigation treatments: normal irrigation (irrigation practices conducted prior to sowing and at stages of jointing and flowering) and deficit irrigation (irrigation practices performed prior to sowing and at jointing stage). Water irrigated amount was 70 mm controlled by water amount analyzer at each time. The sub-plot included three cultivars: median drought-tolerant Zhongxinmai 11 (control), drought-tolerant Shimai 22, and drought-sensitive cultivar Shi 4185. Area of each plot was 24 m^2 ($6 \text{ m} \times 4 \text{ m}$) and seeds of each cultivar were sown on October 8 and 7 during the 2017–2018 and 2018–2019 seasons, respectively. All the plots were fertilized using amount 600 kg ha^{-1} basal complex fertilizer (N: P_2O_5 : K_2O for 20: 15: 15, Liuguo Chemical Co., Ltd., Anhui, China) together with top-dressed N 120 kg ha^{-1} at jointing stage. During two growth seasons, seeds were sown in row pattern with 15 cm distance to establish an approximately 3,750,000 seedling per hectare. Prior to sowing, the straws of last crop (*i.e.*, summer maize) were mechanically broken into pieces and mixed well with

the basal fertilizers as well top soil after ear harvest. Other cultivation techniques conducted were similar to those adopted by the local farmers.

Measurements of yields and yield components

At maturity, the spikes in 2 m² in each plot were counted to calculate the population spike numbers. The seeds in each plot were separately threshed at maturity (June 13 and 11 at 2018 and 2019, respectively) using a mini harvesting machine. After air-drying, the seeds harvested were weighed for calculation of yields. Seed weight was obtained by weighing one thousand air-dried seeds and seed numbers per spike were calculated based on total seed amounts in thirty representative spikes.

Measurements of osmolytes contents

At late growth stages (*i.e.*, stages of flowering, mid-filling, and maturity), contents of osmolytes in the tested cultivars, including proline and soluble sugar, were determined under normal and deficit irrigation conditions using the upper expanded leaves as samples. Of which, the contents of proline in various cultivar plants under different irrigation treatments were measured as described previously by Bates *et al.* (1973) whereas the contents of soluble sugar were analyzed following the procedure of Hu *et al.* (2016).

Measurements of ROS-associated traits

At late stages mentioned above, a subset of parameters associated with cellular reactive oxygen species (ROS) homeostasis, including activities of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), and contents of malondialdehyde (MDA) that reflect cellular over-oxidation degree upon stressors, were assessed under the normal and deficit irrigation treatments. Likewise, the upper leaves of the tested cultivars under various irrigation treatments were used as samples. Procedures for assessing the ROS-associated parameters mentioned above were performed to be similar to those described previously (Beauchamp and Fridovich 1971; Kar *et al.* 1976; Huang *et al.* 2013).

Assay of expression patterns of the P5CS family genes

Five genes encoding delta-1-pyrroline-5-carboxylate synthase (P5CS) proteins in *T. aestivum*, which act as the rate-limiting enzymes in proline biosynthesis metabolism, were subjected to evaluation of transcript levels in the tested cultivars under various irrigation treatments. The GenBank accession numbers of the P5CS family genes (*i.e.*, *TaP5CS1* to *TaP5CS5*) are shown in Table 2. Transcripts of the genes were detected based on qRT-PCR performed as previously described (Guo *et al.* 2013), using gene specific primers (Table 2). The upper leaves of the cultivars under normal

irrigation and deficit irrigation were used as samples. *Tatubulin*, a constitutive gene in *T. aestivum*, was used as an internal reference to normalize transcripts of the target genes (Table 2).

Assay of expression patterns of the AE family genes

To understand the putative genes in modulating AE activities in the water deprivation-treated wheat plants, a subset of genes encoding SOD and POD proteins, respectively, were subjected to evaluation of the expression levels in drought-challenged wheat cultivars. Gene information of the five genes coding for SOD proteins (*TaSOD1* to *TaSOD5*) and six for CAT proteins (*TaCAT1* to *TaCAT6*) are shown in Table 2. Transcripts of the AE genes mentioned were analyzed based on qRT-PCR performed to be similarly in evaluating the P5CS genes as aforementioned, with gene specific primers (Table 2). Likewise, *Tatubulin* was used as an internal standard to normalize the transcripts of the AE genes.

Data analysis

The yields, yield components, osmolytes contents, AE activities, MDA contents, and the transcripts of the P5CS and AE family genes were derived from randomized split design with three replications. Averages, standard errors, and significant test analysis were statistically conducted based on two-way ANOVA using COSTAT computer software (COHORT, Monterey, California).

Results

Yield and yield components

The three wheat cultivars examined displayed improved grain yield and yield components (*i.e.*, population spike numbers, spike seed numbers, and grain weight) under the normal irrigation condition relative to those shown under deficit irrigation treatment (Table 3). Among the tested cultivars, although they showed different yield components under normal irrigation, their yields were comparable with each other. Under DI, the yields of drought-tolerant cultivar Shimai 22 were shown to be the highest (6.47 to 7.23% higher than control), followed by Zhongxinmai 11 (control), and the drought-sensitive cultivar Shi 4185 the lowest (9.41 to 12.35% lower than control), which were closely associated with the variation on population spike amounts across the cultivars (Table 3).

The osmolytes contents

At the growth stages of flowering, mid-filling, and maturity, the proline and soluble sugar contents in the tested cultivars were shown to be consistent with the yields obtained under normal and deficit irrigation. The three cultivars were

similar on contents of proline and soluble sugar under normal irrigation whereas elevated on above osmolyte amounts under deficit irrigation (Fig. 1A–B). In addition, the osmolyte contents were highest in Shimai 22 and lowest in Shi 4185 at various stages assessed under the deficit irrigation conditions (Fig. 1A–B).

The expression patterns of the P5CS family genes

Five genes in the P5CS family (*i.e.*, *TaP5CS1* to *TaP5CS5*) were subjected to expression pattern assessment in the cultivars treated with normal and deficit irrigation conditions. Among the genes examined, two of them, namely, *TaP5CS2* and *TaP5CS5*, displayed modified transcripts in the cultivars upon altered irrigation treatments, showing significantly upregulated expression levels under deficit irrigation with respect to normal irrigation at various stages (Fig. 2). Additionally, the expression induction extent of the genes under deficit irrigation was the highest in Shimai 22, followed by Zhongxinmai 11, and the lowest in Shi 4185 (Fig. 2). The expression patterns of these two P5CS genes under deficit irrigation were in agreement with the proline contents shown in the tested cultivars.

The ROS-associated parameters

Under normal irrigation condition, the three cultivars exhibited higher SOD and CAT activities, and less MDA contents compared with those shown under deficit irrigation. Additionally, they were comparable on the POD activities under normal irrigation and deficit at various stages (Fig. 3A–D). Under DI, the AE activities of SOD and CAT and the contents of MDA were significantly varied across the tested cultivars. Shimai 22 showed highest SOD and CAT activities whereas lowest MDA contents, followed by Zhongxinmai 11, and Shi 4185 the lowest on above AE activities and the highest on MDA accumulation (Fig. 3A–D).

The expression patterns of the AE family genes

The expression patterns of a subset of AE family genes (*TaSOD1* to *TaSOD5* and *TaCAT1* to *TaCAT6*) were investigated using leaves of the tested wheat cultivars under NI and DI as samples. In contrast to the genes that were unchanged on transcripts across cultivar and irrigation treatments, *TaSOD3*, *TaCAT2*, and *TaCAT5* displayed significantly modified expression levels in the tested cultivars under DI relative to NI. They all exhibited induced transcripts under deficit irrigation compared with normal irrigation, with more transcripts detected in Shimai 22 and less ones in Shi 4185 (Fig. 4A–B).

Discussion

Drought negatively affects various physiological processes associated with plant growth, development, and yield

Table 1: Meteorological factors at spring growth stage during the 2017–2018 and 2018–2019 seasons

Growth season	Factor	April	May	June
2017-2018	Average temperature (°C)	13.39	21.98	27.74
	Precipitation (mm)	23.58	71.79	51.19
	Total sunshine (hour)	238.83	245.03	254.78
	Solar radiation (W/m ²)	713.52	766.61	702.74
2018-2019	Average temperature (°C)	12.47	20.66	27.50
	Precipitation (mm)	32.26	59.31	92.33
	Total sunshine (hour)	230.05	256.73	242.36
	Solar radiation (W/m ²)	700.48	779.52	670.95

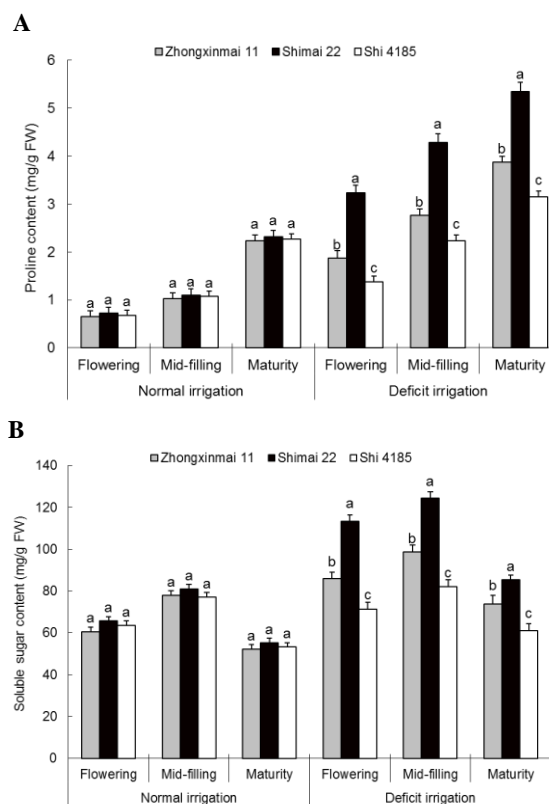


Fig. 1: Contents of proline (A) and soluble sugar (B) of the wheat cultivars under normal and deficit irrigation conditions. Means ± standard deviation with same letter differs non-significantly in wheat cultivars at each growth stage under same irrigation treatment ($P > 0.05$)

formation (Farooq *et al.* 2009). On the other hand, the plants in diverse species have also evolved a suite of effective strategies to cope with the adverse effects of the drought stressor (Duan *et al.* 2007). Among which, osmolytes that act as biochemical compounds to stabilize cellular osmotic potentials under osmotic stresses, are noticed to be increased in the osmotic-challenged plants (Wani *et al.* 2013). The increased amount of proline, sucrose, polyols, trehalose, and alanine betaine at cellular level alleviate the damages of cell stress (Duan *et al.* 2007), and enhance the adaptation of plants to a set of abiotic stresses, such as drought (Wani *et al.* 2013), high salinity (Conde *et al.* 2011), and temperature (Hayashi *et al.* 1998). In this study, the contents of proline and soluble sugar, two crucial osmolytes in plant stress

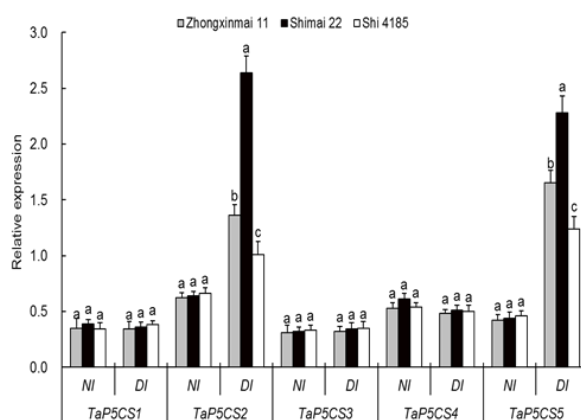
Table 2: The P5CS and AE family genes together with the PCR primers used in this study

Gene	Accession number	Forward primer (5'-)	Reverse primer (5'-)
<i>Tatubulin</i> (internal reference)	U76558	catgcratcccrctctcgact	cgcacttcgatggagtgtat
<i>TaP5CS1</i>	AB193551	gcacgtggacctgtgggtgtg	gttttcgcggaatcctaccacg
<i>TaP5CS2</i>	KM523670	ggccgtatacatgcacgtggacct	aggtccacgtcatgtatacgg
<i>TaP5CS3</i>	KT868850	ctcttacgaggaaaggcaaa	tcattgcaaaaggaagctc
<i>TaP5CS4</i>	KT218497	caagttgataggtatttctgaa	aataaggtatctgtgcctcaa
<i>TaP5CS5</i>	AY888045	tggtactacagatgataaagt	tacttatgccaacctcagacc
<i>TaSOD1</i>	FJ890986	gacgctgatgatcttgcaagg	atcttagcctggagcccgatg
<i>TaSOD2</i>	FJ890987	ccccatgactataaaactcgt	gtcaagtctagctccacttgat
<i>TaSOD3</i>	JQ613154	caatgctgagggtgtggcggaga	tctccgccacacctcagcatt
<i>TaSOD4</i>	AF092524	accaacatctggaaggtggt	accacctccagatgttggtc
<i>TaSOD5</i>	KR069092	cagttgtggagagcgtttgt	acaaacgctctccaacaact
<i>TaSOD6</i>	TAU69536	ggtggcatgagctcagcctca	ccaggtaaaacgagaatggcgt
<i>TaCAT1</i>	D86327	gcgagaagatggtgatcga	aggagagccagatggccttg
<i>TaCAT2</i>	X94352	gcctcagctggcgtcgtac	acgctgctgacgacccccac
<i>TaCAT3</i>	GU984379	cgctcaggcaagagcattcat	atgaaatcctcttgcctgac
<i>TaCAT4</i>	HQ860268	ggagaagacgagatcaagaag	acttgagaggaagctgac
<i>TaCAT5</i>	KP892532	ccagtggtcaccgcctcgggt	acaccaactcattgttctac
<i>TaCAT6</i>	KP892533	ggcgagaagctggcgtcggg	ttcatggctacaccacagag

Table 3: Yields and yield components of tested cultivars under various irrigation treatments

Growth season	Irrigation	Cultivar	Yield (kg/ha)	Spike number (thousand/ha)	Kernel number per spike	1000-grain weight (g)
2017-2018	Normal irrigation	Zhongxinmai 11	8163.82 ± 159.67a	6888.38 ± 200.22c	32.25 ± 0.83a	42.45 ± 0.30a
		Shimai 22	8286.72 ± 147.30a	7251.56 ± 211.50b	32.10 ± 0.72a	42.03 ± 0.34a
		Shi 4185	8085.25 ± 156.82a	7480.48 ± 209.44a	31.79 ± 0.93a	39.12 ± 0.36b
	Deficit irrigation	Zhongxinmai 11	6748.62 ± 151.74b	6178.69 ± 129.95b	31.42 ± 0.88a	41.12 ± 0.32a
		Shimai 22	7236.55 ± 180.05a	6714.33 ± 121.69a	31.27 ± 0.82a	41.00 ± 0.34a
		Shi 4185	6113.86 ± 177.53c	6126.48 ± 123.50b	30.49 ± 0.94a	37.23 ± 0.36b
2018-2019	Normal irrigation	Zhongxinmai 11	8763.82 ± 212.30a	7088.35 ± 200.22c	33.25 ± 0.86a	43.22 ± 0.34a
		Shimai 22	8792.63 ± 186.26a	7435.60 ± 238.34b	32.50 ± 0.74a	42.33 ± 0.32a
		Shi 4185	8708.45 ± 200.33a	7712.13 ± 249.23a	32.79 ± 1.01a	40.34 ± 0.35b
	Deficit irrigation	Zhongxinmai 11	7243.89 ± 158.26b	6295.37 ± 120.22b	32.25 ± 0.92a	42.04 ± 0.40a
		Shimai 22	7712.72 ± 198.23a	6907.97 ± 138.36a	31.50 ± 0.78a	41.33 ± 0.58a
		Shi 4185	6349.40 ± 188.06c	6015.18 ± 149.23c	32.02 ± 1.22a	38.11 ± 0.40b

Means ± standard deviation with same letter differs non-significantly in wheat cultivars under same irrigation treatment ($P > 0.05$)

**Fig. 2:** Expression levels of P5CS family genes of the wheat cultivars under normal (NI) and deficit irrigation (DI) conditions. Means ± standard deviations with same letter differ non-significantly in wheat cultivars at each growth stage under same irrigation treatment ($P > 0.05$)

responses, were investigated at the seed filling stage using three contrasting drought response cultivars under various irrigation treatments. Both osmolytes display a pattern to be significantly elevated under deficit irrigation relative to those shown under normal irrigation conditions. These results were in agreement with previous findings showing

that osmolytes share a nature to be induction under water deprivation conditions in cereal crops (Conde *et al.* 2011; Wani *et al.* 2013). In addition, our results indicate a drastic variation on proline and soluble sugar accumulation across cultivar plants at late stages (*i.e.*, flowering, mid-filling, and maturity), with the pattern of Shimai 22 plants to be the

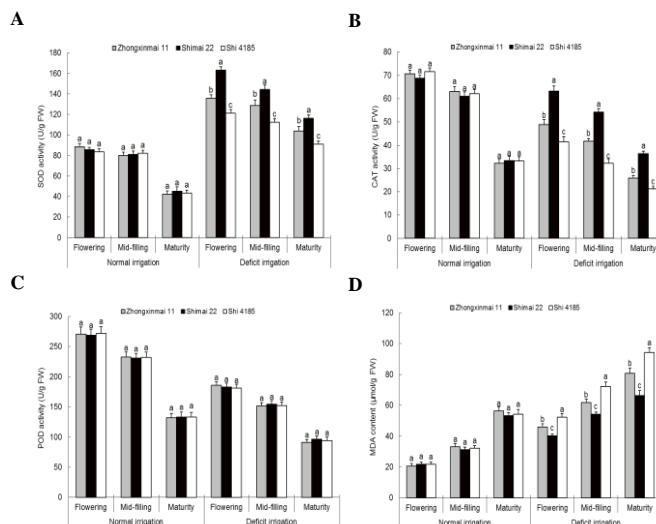


Fig. 3: Activities of SOD (A), CAT (B), POD (C) and MDA contents (D) of the wheat cultivars under normal and deficit irrigation conditions Means \pm standard deviations with same letter differ non-significantly in wheat cultivars at each growth stage under same irrigation treatment ($P > 0.05$)

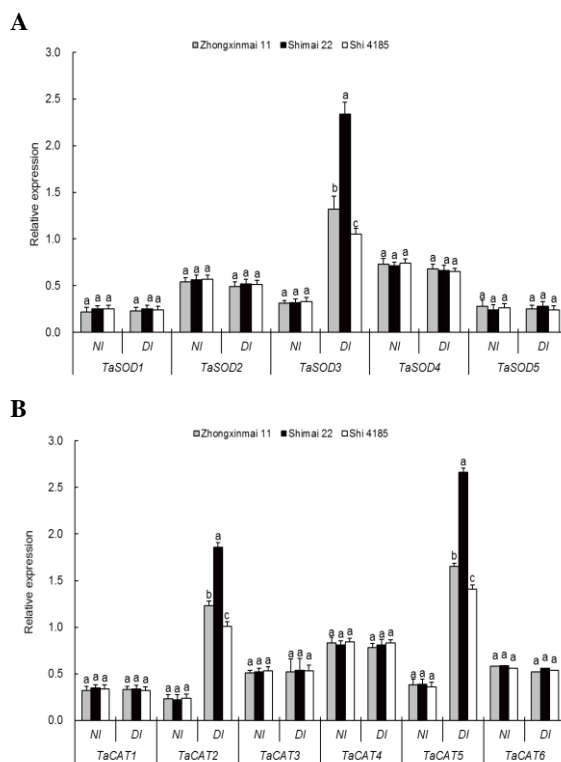


Fig. 4: Expression levels of SOD (A) and CAT (B) family genes of the wheat cultivars under normal (NI) and deficit irrigation (DI) conditions Means \pm standard deviations with same letter differ non-significantly in wheat cultivars at each growth stage under same irrigation treatment ($P > 0.05$)

highest, followed by Zhongxinmai 11 ones, and the Shi 4185 plants the lowest among the tested cultivars. Therefore, the osmolytes mentioned contribute to plant drought adaptation through positively regulating cellular osmotic-regulatory capacity under the deficit irrigation condition.

The oxidative degree frequently intensifies at cellular level once plants are exposed to abiotic stresses. Under

drought condition, ROS in plant cells is accumulated which further lead to lipid peroxidation and injury of the plant tissues (Yue *et al.* 2011; Sun *et al.* 2012). Meanwhile, the antioxidant defense system constituting either enzymatic or non-enzymatic components is promoted in the osmotic stress-treated plants, alleviating the negative effects of oxidative stress by scavenging ROS (Farooq *et al.* 2008).

The AE proteins, such as SOD, POD and CAT that constitute the enzymatic protection system, involve the scavenging of drought-initiated ROS to sustain cellular ROS homeostasis (Anjum *et al.* 2011). In this study, the three cultivars exhibited irregular patterns on the AE activities under normal irrigation, they showed the ROS-associated parameters to be consistent with the drought tolerant capacities under the DI condition. Of which, Shimai 22, a drought-tolerant cultivar, showed highest activities of SOD and CAT, followed by Zhongxinmai 11, a median in drought-tolerant. In contrast, Shi 4185, a cultivar to be drought-sensitive, displayed the lowest activities of above AE activities. Moreover, these cultivars displayed contrast MDA contents under the water deprivation conditions. Therefore, the behavior of AE activities was also closely associated with the plant drought tolerance due to their functions in improving cellular ROS homeostasis.

Plant drought response is closely associated with the modified transcription of numerous stress defensive-associated genes (Umezawa *et al.* 2006). Results indicated that *TaP5CS2* and *TaP5CS5*, two genes in the P5CS family and *TaSOD3*, *TaCAT2*, and *TaCAT5*, three genes that encode one SOD protein and two CAT proteins, respectively, display modified transcription upon water deprivation. The transcripts of all of the genes mentioned enhanced in tested cultivars under deficit and normal irrigation conditions. Moreover, expression levels of these differential genes in tested cultivars were consistent with the behaviors on agronomic traits shown in cultivar plants, showing to be the highest in Shimai 22, followed by Zhongxinmai 11, and the lowest in Shi 4185. These results suggested that the enhanced transcription efficiency of distinct genes in P5CS and AE families positively effects plant drought tolerance in wheat plants, which is associated with the gene functions in promoting osmolyte biosynthesis and improving ROS homeostasis. In this study, though the internal relations between plant drought tolerance and osmolytes contents and cellular ROS scavenging capacity based on three wheat cultivars sharing contrasting water deprivation responses was established; however other mechanisms related to plant drought adaptation aside from above physiological traits are needed to be further addressed.

Conclusion

The drought-tolerant cultivar (*i.e.*, Shimai 22) displayed improved agronomic traits compared with the drought-sensitive cultivar (*i.e.*, Shi 4185) under deficit irrigation treatment. Shimai 22 plants showed higher osmolyte contents (*i.e.*, proline and soluble sugar), activities of antioxidant enzymes (*i.e.*, SOD and CAT), and lower MDA contents at late growth stages than Shi 4185 ones under deficit irrigation condition. Improvement of osmolyte contents and ROS-associated parameters positively regulates plant water deprivation acclimation capacity in *T. aestivum*. The genes referred to as *TaP5CS2* and *TaP5CS5*

in P5CS family and the genes *TaSOD3*, *TaCAT2*, and *TaCAT5* in AE families exhibited upregulated expression pattern upon water deprivation, with much more transcripts of these genes detected in drought tolerant cultivar. The proline accumulation was positively related to transcripts of *TaP5CS2* and *TaP5CS5* and AE activities to those of *TaDOD2*, *TaCAT3*, and *TaPOD5*. They are valuable molecular indices in the guidance in breeding the drought-tolerant cultivars of wheat.

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Author Contributions

RL, SZ and LH planned the experiments, KX interpreted the results and made the write up, LG statistically analyzed the data and made illustrations.

Conflicts of Interest

All other authors declare no conflicts of interest

Data Availability

Data presented in this study are available on fair request to the corresponding author.

Ethics Approval

Not applicable.

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