PLANT SIGNALING & BEHAVIOR
https://doi.org/10.1080/15592324.2020.1839710

Taylor & Francis
Taylor & Francis Group

Check for updates

RESEARCH PAPER

Differentiate responses of tetraploid and hexaploid wheat (*Triticum aestivum* L.) to moderate and severe drought stress: a cue of wheat domestication

Yanwen Gui[a], Mohamed S Sheteiwy[b], Shuangguo Zhu[a], Li Zhu[a], Asfa Batool[a], Tingting Jia[c], and Youcai Xiong[a]

[a]State Key Laboratory of Grassland Agro-ecosystems, Institute of Arid Agroecology, School of Life Sciences, Lanzhou University, Lanzhou, China; [b]Department of Agronomy, Faculty of Agriculture, Mansoura University, Mansoura, Egypt; [c]Department of Bioengineering, School of Chemical and Biological Engineering, Lanzhou Jiaotong University, Lanzhou, China

ABSTRACT

Differentiate mechanism of wheat species in response to contrasting drought stress gradients implies a cue of its long-term domestication. In the present study, three water regimes including well-watered control (WW, 80% field water capacity (FC)), moderate drought stress (MS, 50% FC,) and severe drought stress (SS, 30% FC) were designed to reveal different responses of eight wheat species (four tetraploid and four hexaploid) representing different breeding decades and genetic origins to drought stresses. The data indicated that 50% FC and 30% FC fell into the soil moisture threshold range of non-hydraulic and hydraulic root signal occurrence, respectively. In general, grain yield, grain number/spike weight per plant, aboveground biomass, harvest index (HI) and water use efficiency (WUE) were significantly higher in hexaploid species than those of tetraploid species under drought stress ($P < .05$). Particularly, non-hydraulic root signal was triggered and continuously operated under 50% FC, while hydraulic root signal was observed under 30% FC, respectively. Under 80% FC, the allometric exponent (α) of $M_{aboveground}$ vs M_{root} decreased from tetraploid to hexaploid (both were of <1), indicating that during the domestication, the hexaploid species allocated less biomass to root system. For the relationship of M_{ear} vs $M_{vegetative}$, the α value was significantly greater in the hexaploid species, showing that hexaploid wheat distributed more biomass to ear than tetraploid to improve yield. Under 50% FC, this trend was enhanced. However, under 30% FC, there was no significant difference in the α value between two species. Additionally, correlation analyses on yield formation affirmed the above results. Therefore, drought tolerance tended to be enhanced in hexaploid species under the pressure of artificial selection than that of tetraploid species. When drought stress exceeded a certain threshold, both species would be negatively seriously affected and followed a similar mechanism for better survival.

ARTICLE HISTORY
Received 8 September 2020
Revised 13 October 2020
Accepted 14 October 2020

KEYWORDS
Drought stress; yield; biomass allocation; water use efficiency; ploidy levels; wheat

Introduction

Drought stress can induce significant changes in higher plant at the morphological, biochemical, physiological, and molecular levels.[1–4] The changes would cause substantial negative effects on plant growth, photosynthesis, respiration and organ development, and ultimately reduce crop yield.[1,5–10] When soil water is gradually depleted, some functions of plants are inhibited. Hence, plants endure or avoid water deficit through some unique physiological and ecological mechanisms to maintain biochemical and metabolic reactions in the different tissues of the plants.[11] Physiologically, higher plant has evolved to have different mechanisms for adapting to drought, including strengthening roots, adjusting growth rates, changing plant structure and using water more efficiently, particularly in wheat (*Triticum aestivum* L.).[12] Wheat is widely planted as an important cereal crop and staple food source globally.[13] Currently, two major wheat species, hexaploid bread wheat (*Triticum aestivum*; 2 n = 6x = 42) and tetraploid durum wheat (*Triticum durum*; 2 n = 4x = 28), are commercially important.[13] Wheat crop is highly susceptible to drought stress, specifically at the flowering and grain filling stages, which negatively affect crop growth and yield.[13,14] Many factors can affect plants' responses to drought stress such as plant genotype, growth stage, stress level and variation when exposed to the stress.[15] Among the strategies of drought adaptation, drought tolerance is a complicated trait which is controlled by polygenes, differentiate gene expressions and various environmental factors.[2,7,13] To some extent, different species, subspecies, and cultivars of crops show a variation in drought tolerance under same conditions.[7] Previous efforts have been made to understand drought tolerance via the physiological, breeding, and genetic approaches.[1] Stomatal closure and relative water content (RWC) are considered to be the main physiological responses of plant to drought stress.[2] Moreover, RWC is always used to reflect the metabolic activity of plant tissues and dehydration tolerance.[1] The stomatal conductance decreased under moderate drought stress, but the shoot water status is held constant,[16] which is the first response of plant defense against drought.[17,18] Under severe drought stress, plants have to further reduce stomatal conductance to limit transpiration loss, and the shoot water status also reduce, which adversely affects plant growth and nutrient uptake, and ultimately lead to decreased reduction of yield.[19,20]

CONTACT Youcai Xiong xiongyc@lzu.edu.cn State Key Laboratory of Grassland Agro-ecosystems, Institute of Arid Agroecology, School of Life Sciences, Lanzhou University, Lanzhou 730000, China

The regulation of biomass allocation ratio and WUE in plant organs is one of the basic response mechanisms to drought stress. Plant growth and WUE are influenced not only by the distribution of biomass to different organs of plant but also by the physiological, ecological and morphological characteristics of these organs.[21] Therefore, WUE depends on the balance between these two effects. Although plant traits that increase WUE may conflict with growth-promoting traits, there is potential to improve WUE without necessarily reducing biomass production.[22] As an important indicator of plants' ability to obtain assimilates, biomass plays a vital role in plant morphological construction and organs development.[23] The biomass allocation ratio of plant organs is related to their habitats, and usually adjusted according to the conditions of the habitats, and thus can increase plant tolerance to the drought stress. WUE as an important physiological and ecological parameter, and frequently used to characterize the quality of assimilates produced by plants per unit water consumption,[24] which can precisely reflect the water consumption capacity of plants. Patterns of distribution that affect growth and WUE are closely associated with water status,[25] and distribution of root biomass is usually increased under drought conditions.[26] Higher biomass allocation to the roots can increase the capability of plant to absorb water and nutrients. Although the allocation of more biomass to the root system has negative effects on the allocation to the reproductive organs and leaves, this response may be is a kind of plant adaptive approach under adverse condition.[27]

Yield components such as spike number, grain number, grain weight, and thousand kernel weight (TKW) have been used by plant breeders to assess wheat responses to drought stress.[1] The yield components of wheat have a positive correlation with wheat grain yield. As such, if one or more of these components increase, yield potential definitely could be improved.[28–31] Additionally, genotype, agronomic practices, and environmental conditions are also the major factors that can interact to determine the crop yield.[32] Genetic improvement can increase grain yield, wheat from diploid wild species domestication to the present hexaploid agricultural cultivars, the yield has been greatly increased.[33,34] Higher grain yield of wheat was recently achieved by cultivating the modern varieties such as hexaploid species which is mainly due to their higher harvest index comparing to the traditional varieties. Moreover, the hexaploid species grow faster, have earlier flowering time, and lower leaf area index, radiation can be effectively captured.[35] Underwater deficit condition, the wheat yield and its components are differentially affected. In this regard, the grain weight is affected by moderate drought stress, while the spikelet and grain number are significantly reduced by severe drought stress.[36] Therefore, the changes in biomass allocation strategies and WUE in wheat under water stress condition are important physiological and ecological indexes for drought stress resistance which should be taken into the consideration during wheat breeding.

Drought stress as a main environmental constraint is polygenetically controlled and frequently results in the reduction of wheat growth and yield.[37,38] The study of wheat plant traits in response to drought stress is crucial for its genetic improvement to ensure high yield in water-deficit conditions. Therefore, the present study was performed in an attempt to determine the yield formation, biomass allocation and different adaptive mechanisms of tetraploid and hexaploid species of wheat in response to drought stress. This study was also performed to evaluate the effects of wheat species (tetraploid and hexaploid) on wheat yield and its attributes under drought. The allometric relationships and biomass allocation patterns of related functional components were also analyzed to predict their influence on potential drought comparatives mechanisms in both wheat species and to provide a further theoretical support for future plant breeding of wheat varieties with high yield and drought tolerance.

Materials and methods

Plant material

The seeds were provided by the Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences, Beijing, China, in which eight genotypes (four tetraploid, *T. dicoccum* Schuebl. and four hexaploid, *T. aestivum* L.) were used in this study (Table 1). These genotypes were used to represent the two different periods of domestication.[39–41] The four tetraploids of *T. dicoccum* have an indehiscent ear with AABB genome. The genotypes were introduced in China about 1980s. The four hexaploid of *T. aestivum* were selected to represent the domestication of hexaploid wheat. The *T. spelta* wheat is the ancestor of hexaploid wheat, formed by chromosome hybridization between domesticated tetraploid wheat and goat grass (*A. tauschii*), has an indehiscent ear and hulled grain with AABBDD genome. While other three hexaploid wheat were modern cultispecies wheat with indehiscent ears and naked grain domesticated from *T. spelta*.

Table 1. Details and characteristics of eight genotypes (four tetraploids, *T. dicoccum* Schuebl and four hexaploid, *T. aestivum*) used in the study.

Species	Geno types	Ploidy	Genome	Ear	Domestication	Ploidy	Grain
T. durum	N002	Tetraploid	AABB	Indehiscent	Cultispecies	28(4 n)	Naked
T. turgidum	S821	Tetraploid	AABB	Indehiscent	Cultispecies	28(4 n)	Naked
T. plolonicum	K1113	Tetraploid	AABB	Indehiscent	Cultispecies	28(4 n)	Naked
T. turanicum	TR1	Tetraploid	AABB	Indehiscent	Cultispecies	28(4 n)	Naked
T. spelta	SP9	Hexaploid	AABBDD	Indehiscent	Old cultispecies	42(6 n)	Hulled
T. aestivum	J5050	Hexaploid	AABBDD	Indehiscent	Modern cultispecies	42(6 n)	Naked
T. compactum	Z1695	Hexaploid	AABBDD	Indehiscent	Modern cultispecies	42(6 n)	Naked
T. sphaerococcum	SM3	Hexaploid	AABBDD	Indehiscent	Modern cultispecies	42(6 n)	Naked

Growth conditions

Pots experiment was carried out in rainout shelter at the Yuzhong Experiment Station of Lanzhou University, Gansu Province, China (35°56′N, 104°08′E; altitude, 1620 m). This site is a representative of the semi-arid climate in northwest China, with long-term average annual rainfall of 330 mm and evaporation of 1700 mm. During the growing season of wheat (March–July), the mean temperature is 14.5°C and the relative humidity is 57%. The rainout shelter prevented from the rain-water in rainy days by closing it. The pots (300 mm diameter × 400 mm high) were filled with 13 kg mixture of silty-loam loess soil, from a nearby field site and vermiculite (soil: vermiculite = 2: 1, v/v) with a field capacity (FC, the percentage of water in the soil after the soil has been allowed to drain for 48 h following saturation) of 38%. Each pot was supplied with 2.5 L nutrient solution (containing $NH_4NO_{3:}$ 6.41 g L^{-1} and KH_2PO_4 2.74 g L^{-1}) before planting. Fifteen seeds were sown in each pot on 20 March 2015 and watered to facilitate germination. Thinning was performed after 2 weeks to maintain 12 plants per pot.

Drought treatment

For the first month after seeding, each pot was well-watered (80% FC). Thereafter, the pots were subjected to three water regimes as 1) well-watered (WW) in which pots were watered daily in the late afternoon (18:00–19:00 hours Beijing Standard Time) to 80% FC throughout the growing period to maturity, 2) moderate water stress (MS) in which the soil water content of the pots was allowed to fall down to 50% FC and maintained at 50% FC to maturity by daily weighing and watering in the late afternoon, and 3) severe water stress (SS) in which the soil water content of the pots was allowed to fall down to 30% FC and maintained at 30% FC to the maturity by daily weighing and watering in the late afternoon.

Measurements

At the elongation and flowering stages, 30 representative plants (six plants were randomly selected from each pot, and there were five replicates for each genotypes and treatment) were randomly selected and labeled for measuring the rate of leaf stomatal conductance (g_s) between 9:30 a.m. and 10:30 a.m. on fully expanded leaves using a portable Li-6400 gas exchange system (Li-Cor Inc.). The relative water content (RWC) of the leaves was measured on one fully expanded leaf in each of the five replicating pots. For RWC, fresh weight (FW) was determined immediately after cutting, placed in fresh distilled water for 12 hours, then dried and weighed to obtain the saturated weight (SW). Dry weight (DW) was measured after oven-drying at 80°C for 24 h. Then, the RWC was calculated according to the following formula:

$$\mathrm{RWC}(\%)=(\mathrm{FW}--\mathrm{DW})/(\mathrm{SW}--\mathrm{DW})\times 100$$

At the maturity stage, the predetermined 30 plants were cut off at soil level used to characterize the aboveground biomass, fertile spikelet number, and yield and yield components. For the above-ground biomass measurement, the shoots were divided into spike, leaves and stems, and then were oven-dried at 80°C for 48 h then weighed with a digital balance. When the shoots were harvested, each pot was soaked and thoroughly recovered the root from the soil by a 1.4 mm sieve and flowing water. These root samples were oven-dried at 80°C for 48 h for dry weight. For the shoots, the mean of the six individual plants was the value used as the replicate of the five replicates per genotype and treatment, while the root biomass per pot was divided by the number of plants (normally 12) to give the root biomass per plant.

Relative variables were calculated according to the following formula: harvest index (HI) = grain yield/aboveground biomass.

Statistical analyses

Treatments were arranged in completely randomized block design in a factorial experiment. In this study, there are eight genotypes, three treatments, five replications, and three harvests which equated to 360 pots. Data in Microsoft Excel were organized and analyzed by Analysis of variance (ANOVA). Linear regressions and correlation were analyzed and figures draw in Origin 8.0 (Microcal Software Inc.). Allometric relationship was determined by the standardized major axis tests and routines (SMATR) software package.[42]

Results

Stomatal conductance (g_s) and leaf relative water content (LRWC) in tetraploid and hexaploid wheat under different water regimes

At jointing and flowering stages, LRWC and g_s were measured under different water regimes. Results showed that LRWC decreased with the reducing of soil moisture during the jointing and flowering stages (Figure 1). At 50% FC, LRWC did not change significantly, while the leaf g_s was significantly decreased, indicating that there is a significant non-hydraulic root signal phenomenon (Figure 1). With the aggravation of soil drying, the leaf g_s and LRWC were significantly decreased. These results suggested that the hydraulic signal is activated to deal with the severe drought stress. Moreover, the results showed that g_s of hexaploid species was significantly higher than that of tetraploid species, indicating that hexaploid species has higher metabolic activity than tetraploid species.

Yield formation and water use efficiency under different drought stress in two genotypes of wheat

Grain yield, aboveground biomass and the harvest index were significantly higher in the hexaploid species than that of tetraploid species under the three water conditions (Table 2). Drought stress reduced the grain yield, aboveground biomass and the HI of wheat. Under moderate drought stress, the reduction of yield of tetraploid and hexaploid species was 41% and 37%, respectively, while the reduction of the aboveground biomass was 41% and 39%, respectively, and the HI was decreased by 4.7% and 3.6%, respectively. While under severe drought stress, the reduction in yield of both species was 72%

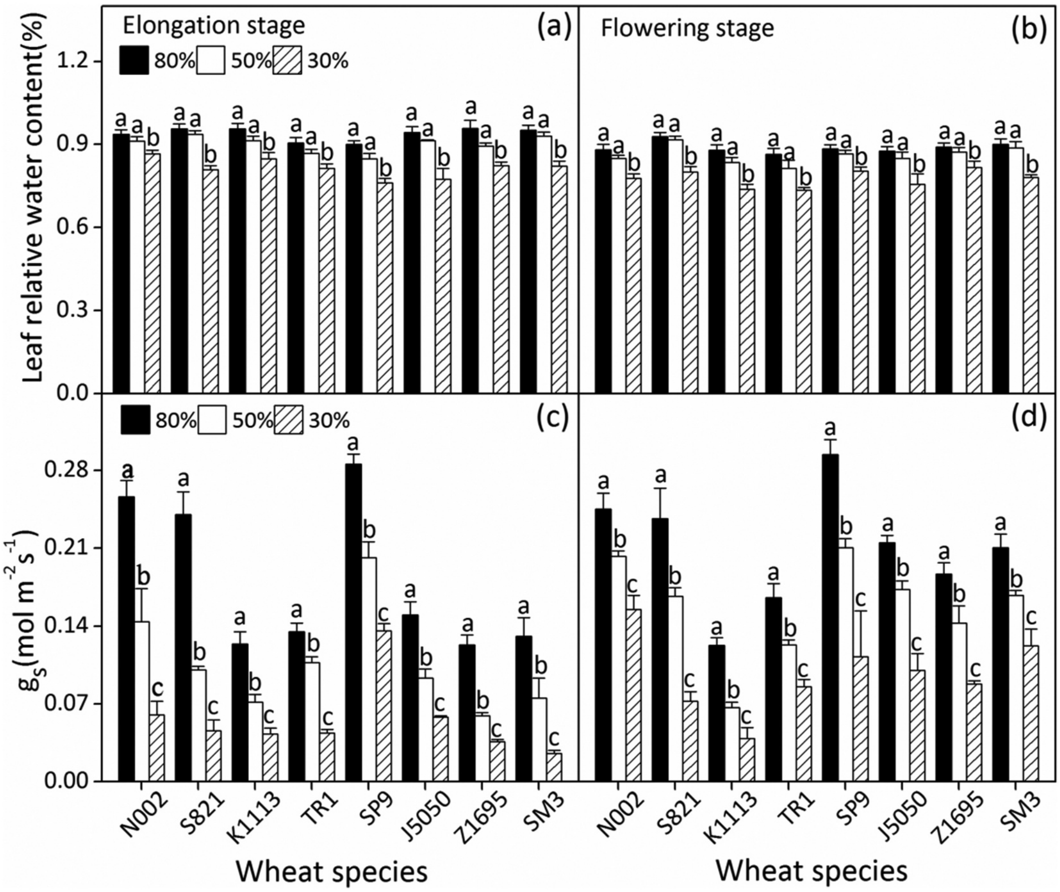

Figure 1. Leaf relative water content (%) (a and b) and leaf stomatal conductance (g_s)(c and d) in eight wheat species under three different water regimes (80% FC, 50% FC, and 30% FC).

and 72%, aboveground biomass was 65% and 66%, respectively; while HI was 26% and 26%, respectively. It could be suggested that under moderate drought stress, the decrease of grain yield, aboveground biomass and HI of hexaploid species was lower than that of tetraploid species, but there was no significant difference between them under severe drought stress.

Water use efficiency of aboveground biomass (WUE_A) and water use efficiency of grain yield (WUE_G) was significantly higher in the hexaploid species than that of tetraploid species under drought stress (Table 3). Under the drought stress, the WUE_A and WUE_G were decreased. At 50% FC, the reduction of WUE_A of tetraploid and hexaploid species was 16% and 14%, respectively, while the reduction of WUE_G was 18% and 16%, respectively. At 30% FC, the reduction of WUE_A of both ploidy was 25% and 25%, however, the reduction of WUE_G was 34% and 34% for both wheat species. The decrease of WUE_A and WUE_G of hexaploid was lower than that of tetraploid species under moderate drought stress, while there were no significant differences between them under severe drought stress. The retention rate of aboveground biomass was higher in the hexaploid species of wheat under well-watered condition (Table 3); however, drought stress decreased the retention rate of aboveground biomass and grain. Under moderate drought stress, the aboveground biomass and grain retention rate of tetraploid and hexaploid species were 59% and 61%; 59% and 62%, respectively. Under severe drought stress, the reduction of the retention rates of the aboveground biomass and grain was 35% and 34%; 27% and 28%, respectively. It could be concluded that hexaploid species had higher retention rate of aboveground biomass and grain under moderate water control comparing to tetraploid species, while there were no significant differences between them under severe drought stress.

Yield components of wheat genotypes under different drought stress

Results showed that spike weight, the number of spikelet number and grain number per plant in the hexaploid species were significantly higher than that of the tetraploid species. Drought stress reduced ear weight, spikelet number and grain number per plant, and this reduction was obvious under severe drought stress (Figure 2(a–c)). At 50% FC, the reduction of ear weight per plant of tetraploid and hexaploid species was 41% and 38%, respectively, the reduction of spikelets per plant of tetraploid and hexaploid species was 46% and 33%, respectively, and the reduction of grain number in tetraploid to hexaploid species was 42% and 39%, respectively. When water was withheld, the loss rate of ear weight per plant of both ploidy was 73% and 73%, that of spikelets per plant were 59% and 59%, and the

Table 2. Grain yield (g plant^{-1}), aboveground biomass (g plant^{-1}) and harvest index of different wheat genotypes subjected to different levels of water regimes (80% FC, 50% FC and 30% FC).

		Grain yield (g plant^{-1})			Aboveground biomass (g plant^{-1})			Harvest index		
Ploidy	Species	80%	50%	30%	80%	50%	30%	80%	50%	30%
Tetraploid	N002	2.40 ± 0.16cd	1.29 ± 0.11c	0.33 ± 0.04d	4.95 ± 0.32d	2.89 ± 0.22c	1.59 ± 0.10d	0.486 ± 0.016a	0.445 ± 0.012a	0.210 ± 0.029d
	S821	2.65 ± 0.17c	1.39 ± 0.14c	0.83 ± 0.07a	7.00 ± 0.65c	3.40 ± 0.28c	2.18 ± 0.11bc	0.396 ± 0.012b	0.383 ± 0.017b	0.383 ± 0.025a
	K1113	2.94 ± 0.23bc	1.82 ± 0.14b	0.84 ± 0.04a	7.67 ± 0.60bc	4.62 ± 0.24b	2.43 ± 0.14b	0.393 ± 0.015b	0.382 ± 0.001b	0.351 ± 0.018abc
	TR1	1.28 ± 0.16e	1.03 ± 0.12c	0.55 ± 0.05bc	3.06 ± 0.37e	2.53 ± 0.27c	1.78 ± 0.15cd	0.418 ± 0.021b	0.405 ± 0.007b	0.307 ± 0.008c
Hexaploid	SP9	3.25 ± 0.17ab	2.11 ± 0.14ab	0.93 ± 0.08a	10.60 ± 0.53a	6.48 ± 0.32a	3.19 ± 0.23a	0.367 ± 0.006c	0.356 ± 0.009c	0.321 ± 0.014bc
	J5050	1.93 ± 0.20d	1.08 ± 0.08c	0.41 ± 0.05cd	4.85 ± 0.33d	3.06 ± 0.16c	2.19 ± 0.14cd	0.397 ± 0.035b	0.383 ± 0.024c	0.225 ± 0.019d
	Z1695	3.75 ± 0.14a	2.44 ± 0.18a	0.95 ± 0.07a	8.60 ± 0.28b	5.28 ± 0.39b	2.45 ± 0.12b	0.495 ± 0.004ab	0.472 ± 0.006a	0.384 ± 0.010a
	SM3	1.91 ± 0.16d	1.19 ± 0.18c	0.73 ± 0.05b	4.73 ± 0.58d	2.81 ± 0.44c	2.03 ± 0.08d	0.482 ± 0.017b	0.466 ± 0.006ab	0.365 ± 0.013ab

Note: Means followed by different lowercase letters indicated significantly different between cultivars at $P = 0.05$.

Table 3. Water use efficiency for aboveground biomass (g kg^{-1}), and water use efficiency for grain (g kg^{-1}) of two wheat genotypes subjected to different levels of water regimes (80% FC, 50% FC and 30% FC).

		Water use efficiency for aboveground biomass (g kg^{-1})			Water use efficiency for grain (g kg^{-1})			Aboveground biomass retention rate		Grain retention rate	
Ploidy	Species	80%	50%	30%	80%	50%	30%	MD	SD	MD	SD
Tetraploid	N002	2.88 ± 0.09bc	2.31 ± 0.12cd	1.96 ± 0.14c	0.88 ± 0.04c	0.65 ± 0.05c	0.41 ± 0.06c	0.56 ± 0.07b	0.31 ± 0.01b	0.50 ± 0.06b	0.13 ± 0.02c
	S821	2.95 ± 0.18ab	2.55 ± 0.12ab	2.26 ± 0.27abc	1.20 ± 0.05a	1.04 ± 0.07a	0.89 ± 0.15a	0.47 ± 0.06b	0.30 ± 0.04b	0.48 ± 0.06b	0.30 ± 0.03b
	K1113	2.93 ± 0.12b	2.49 ± 0.11abc	2.25 ± 0.08abc	1.16 ± 0.08a	0.95 ± 0.05ab	0.78 ± 0.03ab	0.56 ± 0.02b	0.29 ± 0.03b	0.60 ± 0.02ab	0.26 ± 0.02b
	TR1	2.66 ± 0.19c	2.24 ± 0.21d	2.07 ± 0.15ab	1.03 ± 0.09ab	0.86 ± 0.07b	0.77 ± 0.05ab	0.79 ± 0.09a	0.53 ± 0.08a	0.78 ± 0.06a	0.40 ± 0.09a
Hexaploid	SP9	3.37 ± 0.14a	3.17 ± 0.10a	2.52 ± 0.24abc	1.24 ± 0.05ab	1.04 ± 0.06ab	0.85 ± 0.08ab	0.61 ± 0.01b	0.28 ± 0.02b	0.65 ± 0.03ab	0.29 ± 0.01b
	J5050	3.13 ± 0.28a	2.67 ± 0.09ab	2.63 ± 0.10a	1.14 ± 0.13ab	0.96 ± 0.07ab	0.76 ± 0.06ab	0.63 ± 0.06b	0.39 ± 0.02b	0.55 ± 0.12b	0.24 ± 0.02c
	Z1695	3.03 ± 0.04a	2.53 ± 0.15ab	2.14 ± 0.09bc	1.36 ± 0.02a	1.15 ± 0.07a	0.92 ± 0.06ab	0.61 ± 0.06b	0.30 ± 0.01b	0.66 ± 0.07ab	0.26 ± 0.01bc
	SM3	2.87 ± 0.23b	2.35 ± 0.28cd	2.07 ± 0.05c	1.16 ± 0.06ab	0.93 ± 0.11ab	0.72 ± 0.03b	0.60 ± 0.06b	0.38 ± 0.05b	0.62 ± 0.07ab	0.33 ± 0.04b

Means followed by different lowercase letters indicated significantly different between cultivars at $P = 0.05$. MD (Moderate drought), SD (Severe drought

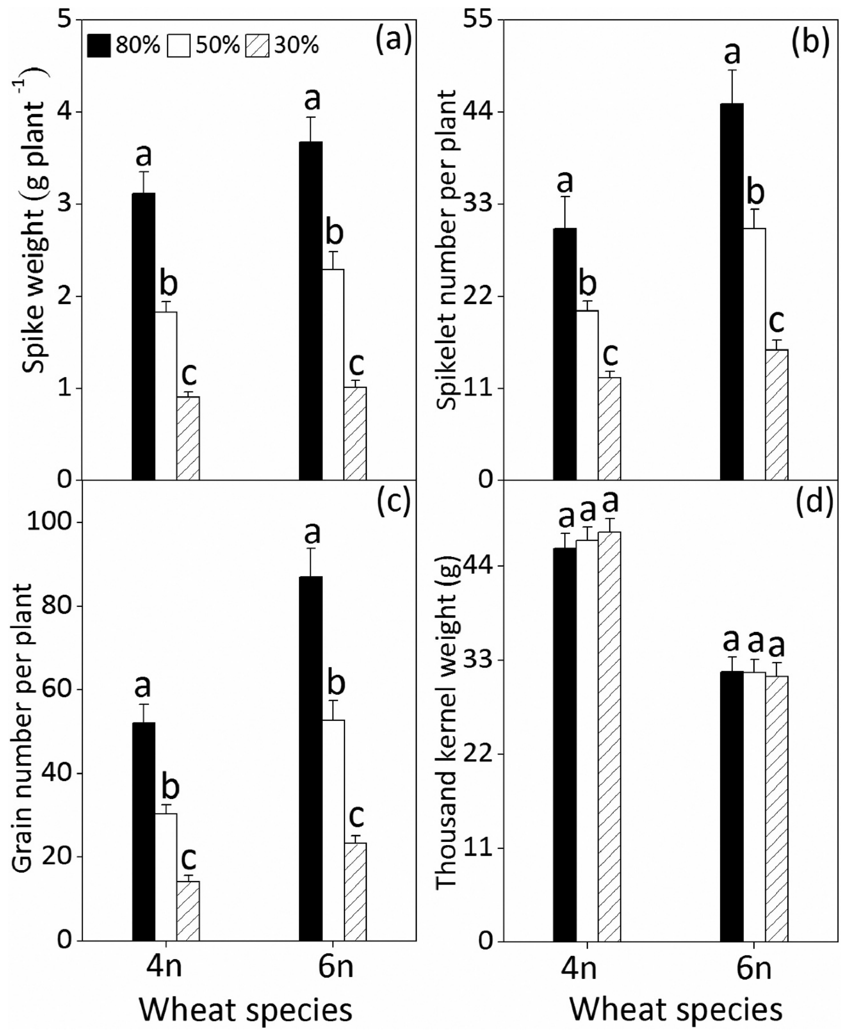

Figure 2. Spike weight per plant (a), spikelet number per plant (b), grain number per plant (c), and thousand kernel weight (d) in different species subjected to three water regimes (80% FC, 50% FC, and 30% FC).

reduction of grain number per plant of tetraploid and hexaploid was 71% and 70%, respectively. Thus, the reduction of spike weight, the number of spikelet number and grain number per plant of tetraploid species was higher than that of hexaploid under moderate drought stress, while there was no significant difference between them under severe drought stress. The TKW of tetraploid was significantly higher than that of hexaploid under the three water conditions (Figure 2(d)), and there were no significant effects of water stress on the TKW of both tetraploid and hexaploid species of wheat.

Correlation between yield and yield components of two wheat genotypes under different levels of drought stress

Correlation analysis showed spikelet number per plant, grain number per plant, spike weight per plant and aboveground biomass of tetraploid species had a significant positive correlation with grain yield (Table 4). At 80% FC and 50% FC, there was no correlation between the TKW and yield of tetraploid species, but there was a significant negatively correlated with yield at 30% FC. HI had no correlation with grain yield under 80% FC and 50% FC, while had a significant positive correlation with grain yield under 30% FC (Table 4). Under well-watered condition, grain number per plant, spike weight per plant and aboveground biomass were significantly positively correlated with spikelet number per plant, while the TKW was significantly negatively correlated with the spikelet number per plant. Under severe drought stress, the grain number per plant was positively correlated with the spikelet number per plant, while the spike weight per plant and above-ground biomass had no correlation with the spikelet number per plant (Table 4). The TKW was negatively correlated with the spikelet number per plant. Spike weight per plant and aboveground biomass were significantly positively correlated with grain number per plant, while there was a significant negative correlation between TKW and grain number per plant. The spike weight per plant and aboveground biomass had no correlation with TKW. But there was a significant positive correlation between spike weight per plant and aboveground biomass (Table 4).

For hexaploid species of wheat, grain number per plant, spike weight per plant and aboveground biomass had a significant positive correlation with grain yield (Table 4). However, there was no correlation between TKW and yield. The spikelet number per plant was positively correlated with grain yield under 80% FC and 50% FC but was not correlated with grain yield under 30% FC. At 80% FC and 50% FC, HI had

Table 4. Correlation between yield and yield components of tetraploid and hexaploid species of wheat subjected to different levels of water regimes (80% FC, 50% FC and 30% FC).

Cultivar	Water	Items	SN	GN	TKW	SW	AB	HI
Tetraploid	80%	GY	0.540*	0.869**	−0.279	0.977**	0.942**	−0.151
		SN		0.785**	−0.864**	0.524*	0.547*	−0.168
		GN			−0.651**	0.836**	0.803**	−0.072
		TKW				−0.244	−0.193	−0.169
		SW					0.943**	−0.250
		AB						−0.463*
	50%	GY	0.475*	0.856**	−0.160	0.985**	0.967**	0.216
		SN		0.791**	−0.818**	0.394	0.394	0.334
		GN			−0.602**	0.779**	0.820**	0.187
		TKW				−0.040	−0.139	−0.057
		SW					0.957**	0.207
		AB						−0.035
	30%	GY	0.490*	0.900**	−0.503*	0.968**	0.814**	0.877**
		SN		0.793**	−0.953**	0.374	0.433	0.393
		GN			−0.804**	0.808**	0.712**	0.808**
		TKW				−0.358	−0.378	−0.448*
		SW					0.893**	0.772**
		AB						0.448*
Hexaploid	80%	GY	0.578**	0.987**	−0.215	0.977**	0.868**	−0.016
		SN		0.556*	−0.072	0.725**	0.883**	−0.684**
		GN			−0.334	0.968**	0.856**	−0.026
		TKW				−0.249	−0.198	−0.038
		SW					0.948**	−0.201
		AB						−0.483*
	50%	GY	0.663**	0.980**	0.191	0.980**	0.888**	0.255
		SN		0.606**	0.374	0.786**	0.902**	−0.468*
		GN			0.035	0.950**	0.833**	0.343
		TKW				0.239	0.342	−0.468*
		SW					0.955**	0.085
		AB						−0.198
	30%	GY	0.420	0.978**	0.184	0.958**	0.821**	0.698**
		SN		0.451*	−0.119	0.597**	0.767**	−0.171
		GN			0.035	0.949**	0.776**	0.732**
		TKW				0.106	0.302	−0.169
		SW					0.898**	0.559*
		AB						0.180

GY (grain yield per plant), SN (spikelet number per plant), GN (grain number per plant), TKW (thousand kernel weight), SW (spike weight per plant), AB (Aboveground biomass), HI (harvest index).

no correlation with grain yield but had a significant positive correlation with grain yield at 30% FC (Table 4). Grain number per plant, spike weight per plant and aboveground biomass were significantly positively correlated with spikelet number per plant, but there was no correlation between TKW and spikelet number per plant. Spike weight per plant and aboveground biomass were significantly positively correlated with grain number per plant, while TKW had no correlation with grain number per plant (Table 4). The spike weight per plant and aboveground biomass had no correlation with the TKW also. There was a significant positive correlation between spike weight per plant and aboveground biomass.

Biomass distribution among two genotypes wheat under different drought stress

The biomass distribution among organs of tetraploid and hexaploid species was compared by the allometric growth model (aboveground biomass ($M_{aboveground}$) and root biomass (M_{root}) ; Vegetative biomass ($M_{vegetative}$) and ear biomass (M_{ear})) (Figure 3). Under 80% FC, the allometric exponent (α) between $M_{aboveground}$ and M_{root} decreased from tetraploid to hexaploid (Table 5), indicating that during the domestication, the hexaploid species allocated less biomass to the root system. Moreover, the allometric exponent (α) of tetraploid and hexaploid species were significantly lower than 1, indicating that more biomass was allocated to aboveground by tetraploid and hexaploid species. Under moderate drought stress, the allometric exponent (α) of tetraploid and hexaploid species was increased, indicating that drought stress would make wheat distribute more biomass to the root system to maintain its own growth, but the allometric exponent (α) was still lower than 1. Under severe drought stress, there was no significant difference between the allometric exponent (α) and 1 of tetraploid and hexaploid, indicating that the distribution pattern of tetraploid and hexaploid wheat had changed with the deepening of drought stress.

For the relationship between ear biomass and vegetative biomass (M_{ear} vs $M_{vegetative}$), at 80% FC, the α-value for M_{ear} vs $M_{vegetative}$ was higher in the hexaploid species, showing that hexaploid wheat distributes more biomass to ear than tetraploid to improve yield. Water restriction decreased the α-value for M_{ear} vs $M_{vegetative}$ of tetraploid and hexaploid wheat. Under severe drought stress, the α-value for M_{ear} vs $M_{vegetative}$ of tetraploid had no significant difference with 1, while the α-value for M_{ear} vs $M_{vegetative}$ of hexaploid species was still significantly higher than 1. The results showed that hexaploid species could maintain high propagation under water restriction.

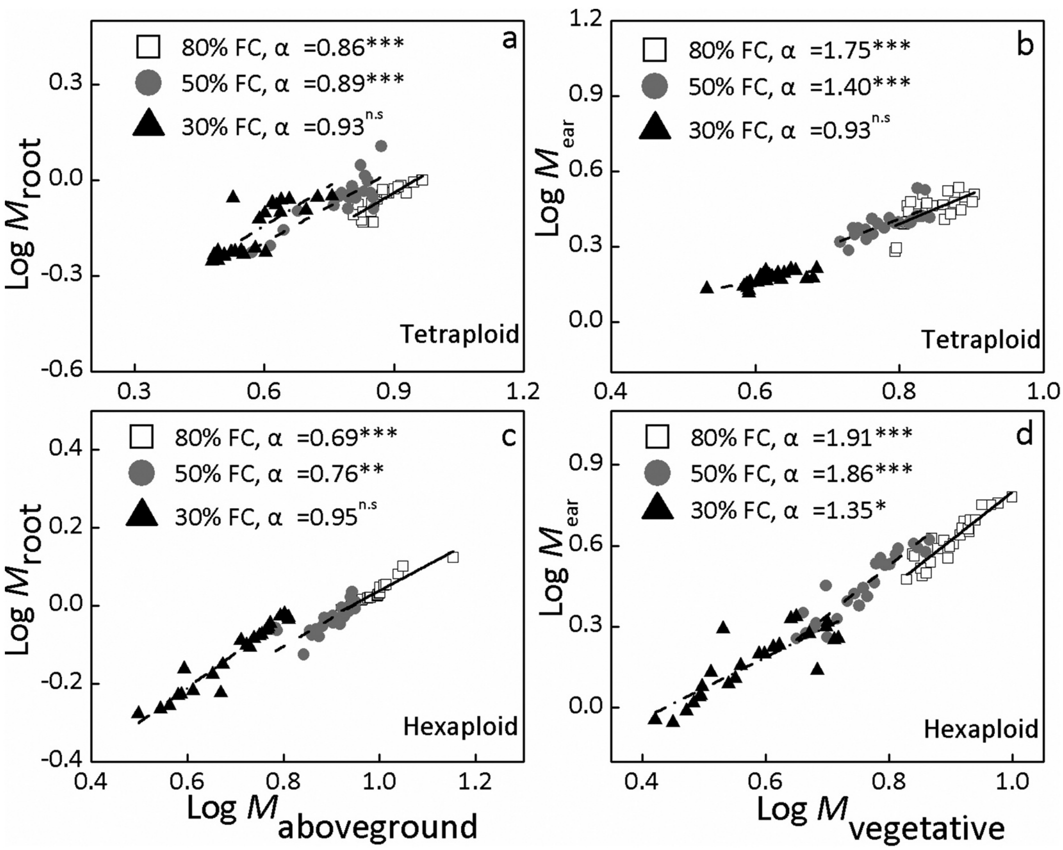

Figure 3. The allometric relationships of aboveground biomass vs root biomass ($M_{aboveground}$ vs M_{root}) (left panels) and vegetative biomass vs ear biomass ($M_{Vegetative}$vs M_{Ear}) (right panels) in tetraploid and hexaploid subjected to three different water regimes (80% FC, 50% FC, and 30% FC). α is the allometric parameter, different from 1.0 at *, *P* = .05; **, *P* = .01; ***, *P* = .001 (n.s., not significant).

Table 5. The allometric relationships between aboveground biomass and root biomass, and vegetative biomass and ear biomass in tetraploid and hexaploid of wheat species subjected to different levels of water regimes (80% FC, 50% FC and 30% FC).

	Species	N	Treat-ments	(95%CI)	(95%CI)	*P*-value	R^2
$M_{aboveground}$ vs M_{root}	Tetraploid	24	80%FC	0.86***(0.80,0.92)	−0.81(−0.86,-0.76)	0.00	0.57
		24	50%FC	0.89**(0.84,0.95)	−0.77(−0.81,-0.72)	0.00	0.70
		24	30%FC	0.93^{ns}(0.85,1.02)	−0.71(−0.75,-0.66)	0.00	0.74
	Hexaploid	24	80%FC	0.69***(0.60,0.79)	−0.65(−0.75,-0.56)	0.00	0.81
		24	50%FC	0.76**(0.63,0.91)	−0.71(−0.84,-0.59)	0.00	0.84
		24	30%FC	0.95^{ns}(0.84,1.07)	−0.79(−0.87,-0.71)	0.00	0.93
$M_{vegetative}$ vs M_{ear}	Tetraploid	24	80%FC	1.75***(1.64,1.88)	−1.03(−1.13,-0.93)	0.00	0.42
		24	50%FC	1.40***(1.27,1.54)	−0.72(−0.82,0.62)	0.00	0.56
		24	30%FC	0.93^{ns}(0.84,1.05)	−0.41(−0.47,-0.35)	0.00	0.51
	Hexaploid	24	80%FC	1.91***(1.79,2.04)	−1.10(−1.21,-0.98)	0.00	0.86
		24	50%FC	1.86***(1.73,2.00)	−0.96(−1.06,-0.86)	0.00	0.86
		24	30%FC	1.35*(1.05,1.74)	−0.62(−0.83,-0.41)	0.00	0.68

α is the allometric exponent, β is the allometric coefficient. Significant differences between α and 1 are indicated: *, *P* = 0.05; **, *P* = 0.01; ***, *P* = 0.001; CI, confidence interval; N, number of observations; ns, no significant difference (*P* > 0.05)

Discussion

During the growth process, wheat is influenced by the interaction of genetic, environmental and agronomic factors. After a long period of domestication, the growth, yield and biomass distribution of wheat were significantly changed by both natural and artificial selection.[21,43] Water plays a pivotal role in nutrient availability and other physiological processes, and a major environmental factor affecting crop growth and yield.[44] In this study, although the number of genotypes of two species is still relatively small, which cannot fully represent the two species of wheat; however, the experimental data can explain somewhat the physiological response of wheat to different levels of drought stress. The present study showed that wheat had different responses to different levels of drought stress. Under moderate drought stress, wheat responds to drought in the form of non-hydraulic signals, while under severe drought stress, wheat triggers hydraulic signals in response to a deeper drought.[27]

In the present study, the wheat species had a significant effect on the yield and yield components of wheat. The results showed that grain yield, grain number and spike weight per plant, aboveground biomass and HI of the hexaploid species were significantly higher than that of the tetraploid species, and these findings are consistent with those obtained by Wang.[26] Wheat grain yield formation and grain number are genetically controlled but also affected by the environment.[45] It is well known that the level of the drought stresses resulted into a variation in the crop yield. Several studies showed that the number of spikelets and grains in wheat was strongly associated with the yield, and these components sharply decreased under drought stress.[46–48] When plants are subjected to water stress, transpiration loss is reduced by closing stomatal pores, which leads to insufficient photosynthesis, reduces crop growth, biomass accumulation and yield.[49,50] Moreover, previous reports showed that wheat yield was decreased with increasing the drought stress,[51] and different species and varieties have different responses to drought.[52] As such, in the present study, the grain yield, grain numbers, spikelet numbers, aboveground biomass and HI of wheat were decreased under drought stress. The reduction of these parameters of the tetraploid species was greater than that of the hexaploid species under moderate drought stress, while the reduction of both species was similar under severe drought stress. The TKW of tetraploid is larger than that of hexaploid, but grain yield of tetraploid is less than that of hexaploid. Drought stress had no significant effect on TKW of tetraploid and hexaploid species of wheat. These results suggest that with the domestication of wheat, the grain yield can be increased with the decrease in seed size.

When plants are subjected to drought stress, they are usually adapted to environmental changes by regulating biomass distribution. In this study, biomass allocation patterns of two genotypes of wheat have changed. Allometric growth model analysis showed that the allometric exponent (α) between $M_{aboveground}$ and M_{root} was higher in the hexaploid species than tetraploid under the different water regimes, indicating that hexaploid wheat had higher aboveground biomass, which was the main substrate for yield increase. In well-watered treatment, the allometric exponent (α) of tetraploid and hexaploid species was significantly lower than 1, indicating that more biomass was allocated to aboveground by tetraploid and hexaploid. Water shortage increased the allometric exponent (α) of tetraploid and hexaploid species, showing that wheat would distribute more biomass to the root system to maintain its own growth under drought stress. Under moderate drought stress the allometric exponent (α) was still lower than 1, but there was no significant difference between the allometric exponent (α) and 1 under severe drought stress. The results showed that the distribution pattern of tetraploid and hexaploid species of wheat would be changed with the deepening of drought stress. Studies have showed that the increase of wheat yield was mainly caused by the increase of ear.[53] In relation to biomass partitioning between the ears and vegetative parts, the α-value for M_{ear} vs $M_{vegetative}$ was higher in hexaploid species than tetraploid species in 80% FC. Our results showed that hexaploid species of wheat distributed more biomass to ear than tetraploid species. Water restriction reduces the α-value for M_{ear} vs $M_{vegetative}$ of tetraploid and hexaploid species, indicating that tetraploid and hexaploid distribute more biomass to vegetative organs under water stress. Under severe drought stress, the α-value for M_{ear} vs $M_{vegetative}$ of tetraploid had no significant difference with 1, while the α-value for M_{ear} vs $M_{vegetative}$ of hexaploid was still significantly higher than 1. The results suggested that hexaploid wheat could maintain high propagation under water restriction and had stronger adaptability to drought.[41,54]

WUE can be used to measure the crop response to water restrictions. A large number of studies have showed that WUE is significantly correlated with ploidy level.[55,56] This study found that the WUE_A and WUE_G were significantly higher in the hexaploid species, indicated that WUE was optimized in the process of wheat domestication. Under the water deficit condition, the WUE_A and WUE_G was decreased, and the decrease of WUE_A and WUE_G of hexaploid species was lower than that of tetraploid species under 50% FC; however, the reduction of the two species of wheat tends to be the same under 30% FC. The retention rate of aboveground biomass and grain was higher in the hexaploid species of wheat under moderate drought stress. The retention rate of aboveground biomass and grain was decreased with the increasing of water stress. Under severe drought stress, the retention rate of aboveground biomass and grain of two wheat species were similar. These results indicated that under moderate drought stress, hexaploid wheat is more drought-tolerant than tetraploid wheat; thus, it can maintain higher productivity, but under severe drought stress, both genotypes are negatively affected and have a similar mechanism to response against drought stress.

The correlation analysis in the present study showed that grain yield is strongly correlated with grain number and spike weight (Table 4), indicating that with the increase of grain number and spike weight, wheat yield showed a significant increase trend. A previous study showed that under drought stress condition, the reduction of the grain number lead to the reduction of the yield.[57] Our study also indicated that spike weight is strongly positive correlated with grain number and spikelet number. Previous studies have shown that grain number and TKW are negatively associated,[58] however, our results suggested that there was no correlation observed in hexaploid species, but there was a significant negative correlation in tetraploid, indicating that there were different trade-offs between grain number and grain size among different ploidy wheat. In both tetraploid and hexaploid species, the HI had no correlation with grain yield under 80% FC and 50% FC, while had a significant positive correlation with grain yield under 30% FC.

The aboveground biomass is an important factor affecting wheat yield, relatively high aboveground biomass is the main substrate for high yield. Aboveground biomass had a significant positive correlation with grain yield in this study, indicating that with the increasing of aboveground biomass, wheat yield showed a significant increasing trend. The correlation analysis also showed that grain number per plant, spike weight per plant and spikelet number per plant had a significant positive correlation with aboveground biomass.

From tetraploid to hexaploid species, the aboveground biomass was significantly increased. The present study suggested that hexaploid species of wheat distributed more photosynthetic products to the reproductive organs than that of the tetraploid species of wheat.

Conclusions

It was evident that wheat yield components and WUE were significantly affected by ploidy levels and drought stress gradients. Grain yield, grain number, spike weight per plant, aboveground biomass, HI and WUE were significantly greater in hexaploid species than those of tetraploid ones. Under the well-watered condition, the allometric exponent (α) of $M_{aboveground}$ vs M_{root} decreased from tetraploid to hexaploid (both were of <1), indicating that during wheat domestication, hexaploid species allocated less biomass to root system relative to tetraploid ones. For the relationship of M_{ear} vs $M_{vegetative}$, the α value turned to be significantly greater in hexaploid species, showing that hexaploid wheat distributed more biomass to ear and thus improved grain yield. In addition, non-hydraulic root signal was triggered and regularly activated under moderate drought stress, while hydraulic root signal was observed under severe drought stress, respectively. Regardless of wheat species, drought stress reduced the yield, grain number, spike weight per plant, aboveground biomass, HI, WUE, and the retention rate of aboveground biomass and grain. The hexaploid species had less damage under moderate drought stress, but the reduction of both species was same under severe drought stress. Under severe drought stress, both species were negatively affected. The α-value for M_{ear} vs $M_{vegetative}$ of tetraploid and hexaploid species was decreased under drought stress, demonstrating that the species allocated more biomass to roots under drought stress, so as to capture more nutrients and water for better growth and reproduction. In conclusion, the hexaploid species obtained by artificial selection was recorded with higher plant yield, HI, reproductive capacity and aboveground biomass, which remained unchanged under drought stress.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

Acknowledgments

The seeds were provided by the Chinese Crop Germplasm Resources Database (administered by the Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences, Beijing, China).

Funding

This work was supported by the Open Funding Project of State Key Laboratory of Grassland Agro-ecosystems (Hosted by J.L. Xiong), Overseas Master's Program of Ministry of Education (Ms2011LZDX059), Youth Science Foundation of Lanzhou Jiaotong University (1200060807), National Specialized Support Program for Outstanding Talents (2018-29-5), The Natural Science Foundation of China (31570415), the State Technology Support Programme (2015BAD22B04) and the National Specialized Support Plan for Outstanding Talents ("Ten Thousand People Plan").

References

1. Sallam A, Alqudah A, Dawood MFA, Baenziger PS, Börner A. Drought stress tolerance in wheat and barley: advances in physiology, breeding and genetics research. Int J Mol Sci. 2019;20:3137. doi:10.3390/ijms20133137.
2. Nezhadahmadi A, Prodhan ZH, Faruq G. Drought tolerance in wheat. The Scientific World J. 2013;2013:610721. doi:10.1155/2013/610721.
3. Alhaj Hamoud Y, Shaghaleh H, Sheteiwy M, Guo X, Elshaikh NA, Khan NU, Oumarou A, Rahim SF. Impact of alternative wetting and soil drying and soil clay content on the morphological and physiological traits of rice roots and their relationships to yield and nutrient use-efficiency. Agric Water Manag. 2019a;223:105706. doi:10.1016/j.agwat.2019.105706.
4. Alhaj Hamoud Y, Wang Z, Guo X, Shaghaleh H, Sheteiwy M, Chen S, Qiu R, Elbashier MMA. Effect of irrigation regimes and soil texture on the potassium utilization efficiency of Rice. Agronomy. 2019b;9:100. doi:10.3390/agronomy9020100.
5. Kasim WA, Nessem AA, Gaber A. Effect of seed priming with aqueous extracts of carrot roots, garlic cloves or ascorbic acid on the yield of *Vicia faba* grown under drought stress. Pak J Bot. 2019;51:1979–1985. doi:10.30848/PJB2019-6(41).
6. Shanker AK, Maheswari M, Yadav SK, Desai S, Bhanu D, Attal N, Venkateswarlu B. Drought stress responses in crops. Funct Integr Genomics. 2014;14:11–22. doi:10.1007/s10142-013-0356-x.
7. Budak H, Kantar M, Kurtoglu KY. Drought tolerance in modern and wild wheat. The Scientific World J. 2013;2013:548246. doi:10.1155/2013/548246.
8. Ashraf M. Stress-induced changes in wheat grain composition and quality. Crit Rev Food Sci Nutr. 2014;54:1576–1583. doi:10.1080/10408398.2011.644354.
9. Sheteiwy MS, Gong D, Gao Y, Pan R, Hu J, Guan Y. Priming with methyl jasmonate alleviates polyethylene glycol-induced osmotic stress in rice seeds by regulating the seed metabolic profile. Environ Exp Bot. 2018;53:236–248. doi:10.1016/j.envexpbot.2018.06.001.
10. Sheteiwy MS, Shao H, Qi W, Alhaj Hamoud Y, Shaghaleh H, Khan NU, Yang R, Tang B. GABA-alleviated oxidative injury induced by salinity, osmotic stress and their combination by regulating cellular and molecular signals in rice. Int J Mol Sci. 2019;20:5709. doi:10.3390/ijms20225709.
11. Liu XE, Jiang HM, Kong HY, Sun GJ, Cheng ZG, Batool A, Xiong YC, Li XG. Eco-physiolgoical role of root-sourced signal in three genotypes of spring wheat cultivars: A cue of evolution. Pak J Bot. 2014;46:1217–1224.
12. Gollan T, Passioura JB, Munns R. Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. Aust J Plant Physiol. 1986;13:459–464.
13. Kulkarni M, Soolanayakanahally R, Ogawa S, Uga Y, Selvaraj MG, Kagale S. Drought response in wheat: key genes and regulatory mechanisms controlling root system architecture and transpiration efficiency. Front Chem. 2017;5:106. doi:10.3389/fchem.2017.00106.
14. Reyer CPO, Leuzinger S, Rammig A, Wolf A, Bartholomeus RP, Bonfante A, De LF, Dury M, Gloning P, Abou JR. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. Global Change Biol. 2013;19:75–89. doi:10.1111/gcb.12023.
15. Chaves MM, Maroco JP, Pereira JS. Understanding plant responses to drought-from genes to the whole plant. Funct Plant Biol. 2003;30:239–264. doi:10.1071/FP02076.
16. Gowing DJG, Davies WJ, Jones HG. A positive root-sourced signal as an indicator of soil drying in apple, Malus x domestica Borkh. J Exp Bot. 1990;41:1535–1540. doi:10.1093/jxb/41.12.1535.

17. Davies WJ, Tardieu F, Trejo CL. How do chemical signals work in plants that grow in drying soil? Plant Physiol. 1994;104:309–314. doi:10.1104/pp.104.2.309.
18. Xiong YC, Li FM, Zhang T, Xia C. Evolution mechanism of non-hydraulic root-to-shoot signal during the anti-drought genetic breeding of spring wheat. Environ Exp Bot. 2007;59:193–205. doi:10.1016/j.envexpbot.2005.12.003.
19. Rossini M, Fava F, Cogliati S, Meroni M, Marchesi A, Panigada C, Giardino C, Busetto L, Migliavacca M, Amaducci S, et al. Assessing canopy PRI from airborne imagery to map water stress in maize. ISPRS J Photogramm. 2013;86:168–177. doi:10.1016/j.isprsjprs.2013.10.002.
20. Zhang HH, Han M, Chávez JL, Lan YB. Improvement in estimation of soil water deficit by integrating airborne imagery data into a soil water balance model. Int J Agr Biol Eng. 2017;10:37–46.
21. Batool A, Akram NA, Cheng ZG, Lv GC, Ashraf M, Afzal M, Xiong JL, Wang JY, Xiong YC. Physiological and biochemical responses of two spring wheat genotypes to non-hydraulic root-to-shoot signalling of partial and full root-zone drought stress. Plant Physiol Biochem. 2019;139:11–20. doi:10.1016/j.plaphy.2019.03.001.
22. Dias PC, Araujo WL, Moraes GABK, Barros RS, Damatta FM. Morphological and physiological responses of two coffee progenies to soil water availability. J Plant Physiol. 2007;164:0–1647. doi:10.1016/j.jplph.2006.12.004.
23. Johnson NC, Rowland DL, Corkidi L, Allen EB. Plant winners and losers during grassland N-eutrophication differ in biomass allocation and mycorrhizas. Ecology. 2008;89:2868–2878. doi:10.1890/07-1394.1.
24. Martre P, North GB, Bobich EG, Nobel PS. Root deployment and shoot growth for two desert species in response to soil rockiness. Am J Bot. 2002;89:1933–1939. doi:10.3732/ajb.89.12.1933.
25. Ikegami M, Whigham DF, Werger MJA. Optimal biomass allocation in heterogeneous environments in a clonal plant—Spatial division of labor. Ecol Model. 2008;213:156–164. doi:10.1016/j.ecolmodel.2007.11.016.
26. Wang JY, Turner NC, Liu YX, Siddique KHM, Xiong YC. Effects of drought stress on morphological, physiological and biochemical characteristics of wheat species differing in ploidy level. Funct Plant Biol. 2017;44:219–234. doi:10.1071/FP16082.
27. Batool A, Cheng ZG, Akram NA, Lv GC, Xiong JL, Zhu Y, Ashraf M, Xiong YC. Partial and full root-zone drought stresses account for differentiate root-sourced signal and yield formation in primitive wheat. Plant Methods. 2019;15:75. doi:10.1186/s13007-019-0461-5.
28. Brancourt-Hulmel M, Doussinault G, Lecomte C, Bérard P, Buanec L, Trottet M. Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. Crop Sci. 2003;43:37–45. doi:10.2135/cropsci2003.3700.
29. Pedró A, Savin R, Slafer GA. Crop productivity as related to single-plant traits at key phenological stages in durum wheat. Field Crops Res. 2012;138:42–51. doi:10.1016/j.fcr.2012.09.016.
30. Sun YY, Wang XL, Wang N, Chen YL, Zhang SQ. Changes in the yield and associated photosynthetic traits of dry-land winter wheat (*Triticum aestivum* L.) from the 1940s to the 2010s in Shaanxi Province of China. Field Crops Res. 2014;167:1–10. doi:10.1016/j.fcr.2014.07.002.
31. Wu W, CJ L, Ma BL, Shah F, Liu Y, Liao YC. Genetic progress in wheat yield and associated traits in China since 1945 and future prospects. Euphytica. 2014;196:155–168. doi:10.1007/s10681-013-1033-9.
32. Fang QX, Ma L, Green TR, Yu Q, Wang TD, Ahuja LR. Water resources and water use efficiency in the NCP: current status and agronomic management options. Agr Water Manage. 2010;97:1102–1116. doi:10.1016/j.agwat.2010.01.008.
33. Perry MW, D'Antuono MF. Yield improvement and associated characteristics of some Australian spring wheat cultivars introduced between 1860 and 1982. Aust J Agric Res. 1989;40:457–472.
34. Siddique KHM, Belford RK, Perry MW, Tennant D. Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. Aust J Agr Res. 1989;40:473–487.
35. Siddique KHM, Tennant D, Perry MW, Belford RK. Water use and water use efficiency of old and modern wheat cultivars in a Mediterranean-type environment. Aust J Agr Res. 1990;41:431–447. doi:10.1071/AR9900431.
36. Giunta F, Motzo R, Deidda M. Effect of drought on yield and yield components of durum wheat and triticale in a Mediterranean environment. Field Crops Res. 1993;33:399–409.
37. Tricker PJ, ElHabti A, Schmidt J, Fleury D. The physiological and genetic basis of combined drought and heat tolerance in wheat. J Exp Bot. 2018;69:3195–3210. doi:10.1093/jxb/ery081.
38. Baillo EH, Kimotho RN, Zhang Z, Xu P. Transcription factors associated with abiotic and biotic stress tolerance and their potential for crops improvement. Genes (Basel). 2019;10:771. doi:10.3390/genes10100771.
39. Xiong YC, Li FM, Zhang T. Performance of wheat crops with different chromosome ploidy: root-sourced signals, drought tolerance, and yield performance. Planta. 2006;224:710–718.
40. Qin XL, Niklas KJ, Qi L, Xiong YC, Li FM. The effects of domestication on the scaling of below-vs. aboveground biomass in four selected wheat (*Triticum*; Poaceae) genotypes. Am J Bot. 2012;99:1112–1117. doi:10.3732/ajb.1100366.
41. Li PF, Cheng ZG, Ma BL, Palta JA, Kong HY, Mo F, Wang JY, Zhu Y, Lv GC, Batool A, et al. Dryland wheat domestication changed the development of aboveground architecture for a well-structured canopy. PloS One. 2014;9:e95825. doi:10.1371/journal.pone.0095825.
42. Falster DS. User's guide to SMATR: standardised major axis tests and routines ver 2.0, Copyright 2006. 2006. http://www.bio.mq.edu.au/ecology/SMATR/.
43. Lv GC, Cheng ZG, Li FM, Akram NA, Xiong YC. Comparative response to drought in primitive and modern wheat: a cue on domestication. Planta. 2019;250:629–642. doi:10.1007/s00425-019-03188-1.
44. Adu MO, Yawson DO, Armah FA, Asare PA, Frimpong KA. Meta-analysis of crop yields of full, deficit, and partial root-zone drying irrigation. Agr Water Manage. 2018;197:79–90. doi:10.1016/j.agwat.2017.11.019.
45. Wang CY, Liu W, Li QX, Ma DY, Lu HF, Feng W, Xie YY, Zhu YJ, Guo TC. Effects of different irrigation and nitrogen regimes on root growth and its correlation with above-ground plant parts in high-yielding wheat under field conditions. Field Crops Res. 2014;165:138–149. doi:10.1016/j.fcr.2014.04.011.
46. Shamsuddin AKM. Path analysis in bread-wheat. Indian J Agr Sci. 1987;57:47–49.
47. Kiliç H, Yağbasanlar T. The effect of drought stress on grain yield, yield components and some quality traits of durum wheat (*Triticum turgidum* ssp. *durum*) cultivars. Not Bot Hort Agrobot Cluj Napoca. 2010;38:164–170.
48. Bhutta MA, Munir S, Qureshi MK, Shahzad AN, Aslam K, Manzoor H, Shabir G. Correlation and path analysis of morphological parameters contributing to yield in rice (*Oryza sativa*) under drought stress. Pak J Bot. 2019;51:73–80. doi:10.30848/PJB2019-1(28).
49. Guerfel M, Beis A, Zotos T, Boujnah D, Zarrouk M, Patakas A. Differences in abscisic acid concentration in roots and leaves of two young Olive (*Olea europaea* L.) cultivars in response to water deficit. Acta Physiol Plant. 2009;31:825–831. doi:10.1007/s11738-009-0298-z.
50. Batool A, Akram NA, Lv GC, Xiong JL, Tian T, Wang JY, Cheng ZG, Yi Y, Wen J, Xiong YC. Root-to-shoot communication

and its signal cross talk in plants: A physiological and agronomic perspective. Pak J Bot. 2018;50:2059–2067.
51. Jin N, Ren W, Tao B, He L, Ren QF, Li SQ, Yu Q. Effects of water stress on water use efficiency of irrigated and rainfed wheat in the Loess Plateau, China. Sci Total Environ. 2018;642:1–11.
52. Salekdeh GH, Reynolds M, Bennett J, Boyer J. Conceptual framework for drought phenotyping during molecular breeding. Trends Plant Sci. 2009;14:488–496. doi:10.1016/j.tplants.2009.07.007.
53. Qin XL, Zhang FX, Liu C, Yu H, Cao BG, Tian SQ, Liao YC, Siddique KHM. Wheat yield improvements in China: past trends and future directions. Field Crop Res. 2015;177:117–124. doi:10.1016/j.fcr.2015.03.013.
54. Liu WX, Ma G, Wang CY, Wang JR, Lu HF, Li SS, Wei F, Xie YX, Ma DY, Kang GZ. Irrigation and nitrogen regimes promote the use of soil water and nitrate nitrogen from deep soil layers by regulating root growth in wheat. Front Plant Sci. 2018;9:32.
55. Huang ML, Deng XP, Zhao YZ, Zhou SL, Inanaga S, Yamada S, Tanaka K. Water and nutrient use efficiency in diploid, tetraploid and hexaploid wheats. J Integr Plant Biol. 2007;49:706–715. doi:10.1111/j.1744-7909.2007.00463.x.
56. Zhang SQ, Shan L, Deng XP. Change of water use efficiency and its relation with root system growth in wheat evolution. Chinese Sci Bull. 2002;47:1879–1883. doi:10.1360/02tb9411.
57. Izanloo A, Condon AG, Langridge P, Tester M, Schnurbusch T. Different mechanisms of adaptation to cyclic water stress in two South Australian bread wheat cultivars. J Exp Bot. 2008;59:3327–3346. doi:10.1093/jxb/ern199.
58. Slafer GA, Calderini DF, Miralles DJ. Yield components and compensation in wheat: opportunities for further increasing yield potential. In: Reynolds MP, Rajaram S, McNab A, editors. Increasing yield potential in wheat: breaking the barriers'. Mexico (DF): CIMMYT; 1996. p. 101–134.