Differential responses of maize yield to drought at vegetative and reproductive stages

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ABSTRACT

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Determining the effects of progressive drought (PD) on dry matter production, partitioning, and grain yield of maize will help in designing a suitable strategy for water management. Though influences of drought on maize growth and development have been investigated extensively, few of them focused on the effects of different duration and occurrence stage of PD on yield formation of maize. Six variations of PD, in the form of withholding irrigation for varying lengths of time from jointing or tasselling, were tested in the field, using a mobile rain shelter, in terms of their effects on aboveground biomass accumulation, partitioning, and grain yield in 2015–2016. The results showed that grain yield was significantly reduced by PD during either vegetative or reproductive stage, and the reduction in grain yield from reproductive PD (41.6–46.6%) was greater than that from vegetative PD (18.6–26.2%). The decrease in grain yield was largely caused by the decrease in kernels per ear ($r^2 = 0.88$, P < 0.001). This research implied that guaranteeing water supply for maize during reproductive stage is crucially important to avoid the reduction in kernels per ear and grain yield.

Keywords: drought stress; corn; kernels per ear; yield component; *Zea mays* L.

Maize (*Zea mays* L.) is one of main crops in northeastern China (NEC), accounting for more than 36% of the area sown to crops in NEC and for more than 30% of China's maize production (Liu et al. 2013). Although maize yield can be affected by many environmental factors, drought is considered as the mostly important one in this region (Yin et al. 2016). Yin et al. (2016) reported that the increase in the duration of drought is mainly occurred in the western region of NEC, in which progressive drought (PD) during the crucial stages (from the end of vegetative to ear formation) in the maize-growing season was observed in 2014 and 2015, and maize yield decreased significantly

(Fang et al. 2018). Moreover, both frequency and intensity of drought was projected to increase by 2050 (Zhao and Luo 2007), which will significantly affect the production of maize in NEC.

Drought is known to affect morphology, photosynthesis, and dry matter (DM) accumulation as well as grain yield and the nutritional composition of maize (Çakir 2004, Soler et al. 2007, Hao et al. 2016, Gheysari et al. 2017). It is widely recognized that maize is sensitive to drought throughout the growing season, especially during its reproductive stages (Denmead and Shaw 1960, Grant et al. 1989, Çakir 2004, Saseendran et al. 2014). Denmead and Shaw (1960) noted that drought stress during the

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Table 1. Soil parameters of 0–50 cm of the study site

Danamakan	Soil layer (cm)					
Parameter	0-10	10-20	20-30	30-40	40-50	
Soil bulk density (g/cm ³)	1.55	1.65	1.61	1.66	1.68	
Soil field capacity (gravimetric, %)	21.1	21.5	21.7	22.3	22.6	
Wilting coefficient (gravimetric, %)	6.0	6.0	6.4	6.1	6.5	

vegetative stage of maize production reduced grain yield by 25%, drought stress during silking reduced grain yield by 50%. Ge et al. (2012) reported that maize development and grain yield are affected not only by the severity of drought stress but also by the stage of development at which the plant is exposed to that stress. Mild and severe drought stress treatments reduced final grain yield by 63% and 85%, respectively, and by 13% and 26%, respectively in two years' experiment of Earl and Davis (2003) setting three irrigation treatments (control, mild water stress, severe water stress). Ge et al. (2012) studied the effects of drought on summer maize throughout the grow cycle by setting the soil water to 75% field water capacity (FC), 55% FC medium stress, and 35% FC high stress. While during the actual experiment, soil water content was difficult to control for a long time since the inhomogeneous irrigation and infiltration problems, which result in the reduced final grain yield of the same treatment exiting large differences. Though influences of drought on maize growth and development have been investigated extensively, few of them focused on the effects of different duration and occurrence stage of PD on yield formation of maize. Therefore, the objectives of this study are to (1) examine the effects of PD at the vegetative and the reproductive stage of maize on biomass accumulation and partitioning; (2) analyse the response of yield and yield components to PD at two development stages.

MATERIAL AND METHODS

Site description. The experiment was conducted in the maize-growing season of 2015 and 2016 at the Jinzhou Agricultural Ecosystem Research Station (41°49'N, 121°12'E; 17 m a.s.l.) in southwestern NEC. The climate of the region is continental monsoon with four distinct seasons. The annual long-term (1981–2010) mean temperature is 9.9°C and mean annual precipitation is 568 mm. About

60% of precipitation is received between July and September. The soil is the typical cambisol soil with pH 6.3. The organic carbon content is 8.83 g/kg, and nitrogen, phosphorus, and potassium contents are 1.04, 0.50 and 22.62 g/kg (Cai et al. 2017). The soil bulk density, soil field capacity, and wilting coefficient of the soil moisture for each soil layer to a depth of 50 cm were presented in Table 1. Rainfed agriculture is the primary production system.

Experiment design and field management. The experiment was carried out in a set-up that made it possible to control the level of soil moisture through a mobile rain shelter (Figure 1). The experiment consisted of five plots, each with three replications, thus giving a total of 15 plots. The size of each plot was 15 m^2 (3.0 m \times 5.0 m), and each plot was surrounded by a 0.15 m thick concrete wall, raised 0.1 m above the soil surface and sunk 1.9 m into the ground to prevent lateral movement of water. A permanent rainproof shelter, with automatic control, excluded natural rainfall when required (when it rained). Irrigation was carried out with an overhead sprinkler system (Figure 2), and the amount of irrigation was monitored using a rain gauge. All the plots received natural rainfall



Figure 1. 3 m \times 5 m plots with maize and movable shelter shielding maize from natural rainfall



Figure 2. The overhead sprinkler system for irrigation

before the 3-leaf stage. After that stage, the control or check plots (CK) received the irrigation every 7 days, whereas irrigation was skipped in the other plots as required by the schedule for the treatments (Table 2). Total amount of irrigation was decided based on the water requirements, calculated according to the method described by Allen et al. (1998). Using the long-term data on precipitation and the mean dates of each growth stage, total irrigation was apportioned as follows: 20% from the 3-leaf stage to jointing, 24% from jointing to tasselling, 43% from tasselling to the milk stage, and 13% from the milk stage to maturity. The experiment comprised five treatments in 2015 (CK, and T1-T4) but only three in 2016 (CK, T2, and T5). See Table 2 for a brief description of each treatment.

A same maize cultivar (Danyu 406, the most commonly grown cultivar in the region) was used

in this research. Sowing and harvesting dates were 30 April and 23 September in 2015, and 23 May and 25 September in 2016, respectively. Approximately 2 weeks after emergence, the seedlings were thinned to maintain the population at 4.48 plants/m². A compound fertilizer (28% N, 5% P, and 10% K) was applied at the time of sowing at a rate of 750 kg/ha.

Sampling and measurements. Aboveground biomass (total, leaf, stem, and grain, as applicable) was measured every 14 days in 2015 and every 7 days in 2016, starting 34 days after sowing in 2015 and 31 days in 2016. Five plants from each treatment were cut at the ground level and separated into the stem, leaves, and grain (after silking). All the samples were oven-dried at 105°C for 30 min, and weighed after drying at 70°C to constant weight. The dry matter in each treatment was the average of five samples. The partition coefficient (PC) of each organ was calculated by dividing the total above-ground DM by the dry weight of the respective organ. At the end of the growing season, all plants (above-ground parts) in each treatment plot were harvested by hand and air-dried before recording the grain yield. Yield components, including grain weight per plant and the number of kernels per ear, were measured in 20 plants selected at random from each treatment. The ear length and ear diameter were also measured. The average weight of eight lots of 100 grains each was taken as the 100-grain weight. The harvested ears were shelled and the moisture content of grains was determined. By using moisture content of grains, grain yield was converted to that for a moisture content of 0%.

Table 2. Induced progressive drought at different development stages of maize

Year	Treatment	Description	Starting date	Ending date	Total irrigation (mm)*
2015	CK	no water stress: irrigation every 7 days from 3-leaf stage onwards	_	_	304
	T1	irrigation withheld for 20 days from jointing	18 June	7 July	284
	T2	irrigation withheld for 27 days from jointing	18 June	14 July	264
	Т3	irrigation withheld for 20 days from tasselling	9 July	28 July	258
	T4	irrigation withheld for 27 days from tasselling	9 July	8 August	233
2016	СК	no water stress: irrigation every 7 days from 3-leaf stage onwards	_	_	280
	T2	irrigation withheld for 27 days from jointing	1 July	27 July	207
	T5	irrigation withheld for 40 days from tasselling	16 July	24 August	154

^{*}Total irrigation represented the amount of irrigation during 3-leaf stage to maturity

Weighing method was used to measure gravimetric soil water content (%) to a depth of 50 cm (every 6–8 days since early June in 2015 and early July in 2016 until the end of August). The detail of the method can be referred to Song et al. (2018). We used soil relative extractable water (θ_r , equation 1) to represent the soil available water conditions.

$$\theta_r = \frac{\theta_m - \theta_{wp}}{\theta_{fr} - \theta_{wp}} \tag{1}$$

Where: θ_m – gravimetrical soil water contents (%) in 0–50 cm soil; θ_{fc} and θ_{wp} – gravimetrical soil water contents (%) at field capacity and wilting point, respectively.

The variation of 0–50 cm $\theta_{\rm r}$ during the main growing season of 2015 and 2016 was presented in Figure 3. The $\theta_{\rm r}$ of all treatments were above 0.4 during the main growing season except for the PD periods.

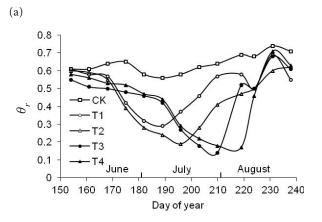
Statistical analysis. The means were separated by the least significant difference (*LSD*) test at the probability level of 0.05% using SPSS ver. 10.0 (Chicago, USA).

RESULTS AND DISCUSSION

Biomass accumulation and partitioning. Progressive drought slowed down the rate of production of DM. In 2015, the final weight of DM in T2 (irrigation withheld for 27 days from jointing) was 81% of that in the control (CK) and that in T1 (irrigation withheld for 20 days from jointing) was 87%. Accordingly, in 2016, the weight in T2 was only 66% of that in CK. In T2, the rate of DM production stagnated or even decreased, and began to increase only gradually once watering (through irrigation) was resumed (Figure 4a,b).

The total DM for T3 (irrigation withheld for 20 days from tasselling) accounted for 77% of the CK in 2015. With the increase in the degree of PD (T4, irrigation withheld for 27 days from tasselling and T5, irrigation withheld for 40 days from tasselling), the total DM were further decreased by 29% and 47%, compared to the CK. A reduction of 13-34% in biomass production in plants caused by water stress during the vegetative stage is consistent with previous reports of 28-32% (Çakir 2004). The reduction in DM from short-term water stress at the beginning of the intensive vegetative growth stage was mainly caused by the reduction in plant height and leaf size and delay in leaf tip emergence (Çakir 2004). Some results from the same experiment showed that PD effects plant growth, leaf morphological traits and photosynthetic processes at vegetative and reproductive stages and leaf function traits of the plants experienced PD cannot fully restored compared to CK (Song et al. 2018), which led to the decrease in the total biomass.

Progressive drought affected not only DM accumulation but also the partitioning of DM between leaves, the stem, and grains. The partition coefficient for leaves in CK during the growth period of maize decreased from 0.61 to 0.11 in 2015 and from 0.67 to 0.17 in 2016; the coefficient increased slightly (compared to that in CK) a few days after the point at which the water supply was withheld (Figure 5a,b) and differed greatly between T3 and T4 in 2015 at the end of growth period. The final proportion (132 days after sowing) of the DM delivered to leaves in T3 and T4 in 2015 was approximately 22%, or nearly double of that in CK (Figure 5a), whereas the difference in that



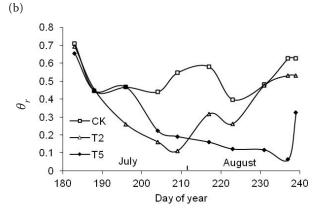


Figure 3. Variation of 0–50 cm soil relative extractable water (θ_r) during the main growing season of (a) 2015 and (b) 2016. CK – control; T1–T5 – five treatments as listed in Table 2

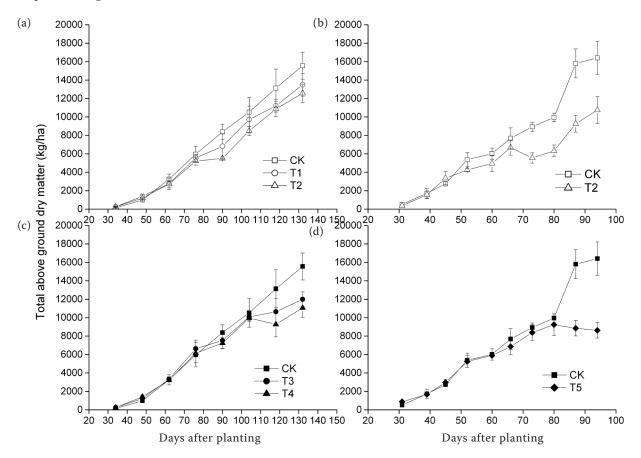


Figure 4. Total aboveground dry matter accumulation under different treatments. Top panels represent progressive drought during vegetative stage in (a) 2015 and (b) 2016; bottom panels, during reproductive stages in (c) 2015 and (d) 2016. CK – control; T1–T5 – five treatments as listed in Table 2

proportion between T5 and CK in 2016 was fairly small (Figure 5b).

The partition coefficient for the stem in CK in 2015 and 2016 showed a single peak pattern; the same pattern was seen in T1 and T2 in 2015 and in T2 in 2016, but the proportion increased slightly compared to that in CK a few days after the water supply was withheld (Figure 5c,d). The coefficient for the stem in T3 and T4 in 2015 and in T5 in 2016 at the end of the growth period was greater than that in CK. The final proportion of DM delivered to the stem was more than 50% in T3, T4, and T5, compared to only 30–35% in CK.

The partition coefficient for grain in CK in 2015 and 2016 traced an S-shaped curve. The coefficient in all the treatments (T1–T5) was smaller than that in CK by as much as 50% in T3–T5, whereas the difference between CK and T1 and T2 in 2015 and T2 in 2016 was only 10–19% amount to CK (Figure 5e,f). As reported, water stress leading to the reduction in grain yield was mostly due to a reduction in DM

allocation to grains and not as much due to lower production of DM (Oveysi et al. 2010). Currently effects of drought stress on carbon assimilation have been well considered in majority of crop growth models (Jones et al. 2003, Saseendran et al. 2014), while effects on DM partitioning were rarely considered (or considered empirically) due to an inadequate understanding of the partitioning process (Cavero et al. 2000, Li et al. 2006). Based on the functional equilibrium theory, Li et al. (2006) has developed a dynamic photosynthate partitioning model which has the unique advantage in responding to environmental factors and is applicable for the crop vegetative growing period. Our results manifested that PD during reproductive stage affected the reallocation of stem biomass and decreased the PC of grain greater than that during vegetative stage. Therefore, in simulating crop yield as affected by water stress, it should be kept in mind that the PC changes depending on both the intensity of water stress and the growth stage at which it sets in.

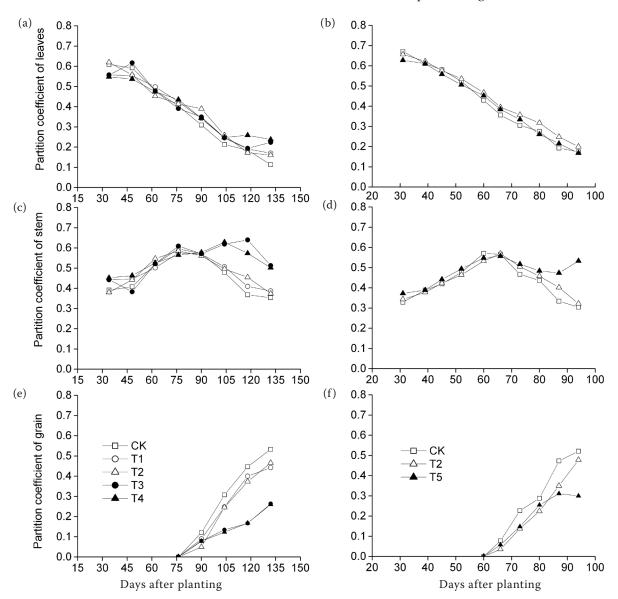


Figure 5. Differences in partition coefficients of (a, b) leaves; (c, d) the stem, and (e, f) grain under different treatments. CK – control; T1–T5 – five treatments as listed in the Table 2

Yield and yield components. Progressive drought from the jointing and tasselling stages decreased both length and diameter of the ear significantly (P < 0.05) compared to that in CK (Table 3). At harvest time in 2015, the ear length in T1 was 82.6% of that in CK, the corresponding figure for T2 being 78.9% and, in 2016, 86.5%. The extent of decrease in length in T3 and T4 in 2015 was even greater, being 69.0% and 67.1% of that in CK, respectively.

The data on yield components (Table 3) showed that PD during the vegetative and reproductive stages decreased both grain weight per plant and the number of kernels per ear significantly (P < 0.05). Water scarcity from the tasselling stage decreased

kernel set markedly. In particular, compared to the plants subjected to stress during the vegetative stage, the number of kernels per ear in all the treatments involving drought stress during the reproductive stage was much lower (by as much as 34-41%). In addition, the No. of kernels per ear showed a significant ($r^2 = 0.88$, P < 0.001) positive relationship with grain yield. So fewer kernels, and not so much lighter or poorly filled kernels, was the primary effect of water deficit on maize production. This result is consistent with that obtained by Yazar et al. (1999), who reported that the number of kernels per plant is dependent on moisture stress. Ge et al. (2012) also reported that the result of water stress

Table 3. Yield components of maize under different treatments

	Treatment	Ear length	Ear diameter	Grain weight	No. of kernels	100-kernel	Grain yield
	Treatment	(cm)		per plant (g)	per ear	weight (g)	(kg/ha)
2015	CK	21.3 ± 1.9^{a}	5.5 ± 0.2^{a}	247.0 ± 17.5^{a}	695 ± 102^{a}	38.7 ± 0.5^{a}	10 180.4
	T1	17.6 ± 1.8^{b}	$5.2\pm0.2^{\mathrm{b}}$	$185.0 \pm 10.6^{\rm b}$	673 ± 111^{ab}	35.7 ± 0.9^{b}	8288.0
	T2	$16.8 \pm 1.2^{\rm b}$	4.8 ± 0.3^{c}	180.0 ± 17.9^{b}	615 ± 49^{b}	$34.9\pm0.8^{\rm b}$	7741.4
	Т3	$14.7 \pm 1.4^{\rm c}$	4.8 ± 0.5^{c}	138.3 ± 12.1 ^c	440 ± 64^{c}	$34.8\pm1.3^{\rm b}$	5947.6
	T4	14.3 ± 2.3^{c}	4.7 ± 0.3^{c}	133.9 ± 26.4°	409 ± 65^{c}	$34.4\pm0.7^{\rm b}$	5518.8
2016	CK	20.8 ± 2.0^{a}	5.6 ± 0.3^{a}	247.9 ± 55.7 ^a	744 ± 103 ^a	35.7 ± 1.1 ^a	9795.4
	T2	$18.0\pm2.7^{\rm b}$	5.4 ± 0.5^{a}	$182.4 \pm 65.2^{\rm b}$	$595 \pm 155^{\rm b}$	31.2 ± 2.9^{b}	7231.8
	T5	17.6 ± 1.8^{b}	$4.8\pm0.5^{\rm b}$	131.3 ± 47.7°	492 ± 140^{c}	$28.1\pm4.5^{\rm b}$	5235.2

Means within columns not followed by the same letter are significantly different at P < 0.05. CK – control; T1–T5 – five treatments as listed in Table 2

was a substantial deterioration in ear formation and poor grain filling, leading to significantly fewer kernels in each ear. Water deficit at anthesis led to markedly fewer kernels due to poor receptivity of silk in maize; embryos did form but were aborted later (Zinselmeier et al. 1999), and due to delayed silking, which led to barrenness because the pollen supply was exhausted before silks appeared (Lu et al. 2011).

The extent of reduction in grain yield was different in 2015 and 2016 and was larger when PD was introduced during the reproductive stage than during the vegetative stage. Compared to those in CK, yields in 2015 in T1 were lower by 18.6% and those in T2 by 24.0%, and those in T2 in 2016, by 26.2%. As the simulated drought was extended, the reductions were even greater, being 41.6% in T3 and 45.8% in T4 in 2015 and 46.6% in T5 in 2016. When the length over which water was withheld was the same, the effect of such PD during the reproductive stage was more intense than that during the vegetative stage, which indicated that timing of water availability was critical to maize production (Benjamin et al. 2015).

In conclusion, PD during different growing stages of maize exerted different extents influence on biomass accumulation, partitioning and grain yield. Grain yield was found to be positively and significantly correlated with the kernels per ear. This implies that applying irrigation in order to increase kernels per ear during reproductive stage is an effective way to better cope with drought in maize production in Northeastern China.

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