ELSEVIER

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr



Supplemental irrigation at tasseling optimizes water and nitrogen distribution for high-yield production in spring maize



Zhen Gao, Xiao-Gui Liang, Shan Lin, Xue Zhao, Li Zhang, Li-Li Zhou, Si Shen, Shun-Li Zhou*

College of Agronomy & Biotechnology, China Agricultural University, Beijing 100193, China

ARTICLE INFO

Keywords:
Spring maize
Yield
Supplemental irrigation
Water
Nitrogen
Source-sink relations

ABSTRACT

The penalty of spring maize yield is often observed due to annual and seasonal fluctuations of precipitation. To achieve a high and stable maize yield, supplemental irrigation is necessary for spring maize. In this study, a 3year field experiment was conducted during the 2014-2016 growing seasons. A single supplemental irrigation was applied at V6 (I_{V6}), V12 (I_{V12}), tasseling (I_T) and 15 days after silking (I_{S15}), respectively. The water and nitrogen consumption percentages at pre- and post-silking, source-sink relations and yield responses to various irrigation strategies were investigated. The post-silking water consumption percentage with the late irrigation treatments (I_T and I_{S15}) increased by 18.7–40.1% compared with those of I_{V6} and I_{V12} . However, there were no significant differences among the treatments in the nitrogen consumption percentages, and the main variation came from year type. The nitrogen contents in the vegetative parts at silking in I_{V6} and I_{V12} were 10.1–48.9% greater compared to I_T and I_{S15} , i.e., more nitrogen was used before silking compared with I_T and I_{S15} . Supplemental irrigation at tasseling significantly accelerated kernel sink establishment and optimized the relation between source and sink, which improved post-silking biomass production and resulted in high yield and a high harvest index. Regression analysis demonstrated that, to some extent, greater water (20-50%) or nitrogen (40-60%) consumption percentages, higher post-silking biomass production and higher yield could be achieved. Overall, supplemental irrigation at tasseling could optimize water and nitrogen distribution for kernel growth and development and improve the sink capacity to achieve high yield and resource use efficiency.

1. Introduction

The conventional double cropping system of winter wheat and summer maize rotation in the North China Plain (NCP) plays a vital role in supplying grain to China (Li et al., 2005). However, this main system consumes between 800 and 850 mm of water annually, which significantly exceeds the amount of local rainfall (Liu et al., 2002; Sun et al., 2010). Reducing irrigation, especially in winter wheat, is used to increase water use efficiency (WUE) and maintain yield (Li et al., 2005, 2010; Wang et al., 2016). Nevertheless, groundwater overdraft problems are still serious under the optimized irrigation regimes, raising the concerns of both the public and the government (Sun et al., 2015). Spring maize can probably serve as an important cropping pattern due to sufficient temperature and light resources and high WUE and yield potential in the NCP.

However, the annual and seasonal fluctuations of precipitation frequently lead to drought stress in spring maize at each growth stage (http://data.cma.cn/, Fig. 1). Water deficiencies at the different growth stages have diverse effects on maize growth due to sensitivity differ-

ences to drought (Cakir, 2004). In general, maize appears to be relatively tolerant to water deficiencies imposed during the vegetative and ripening periods (Claassen and Shaw, 1970; Doorenbos and Kassam, 1979; Hall et al., 1981; Grant et al., 1989), while around flowering, moisture stress results in embryo abortion (Setter et al., 2001; Zinselmeier et al., 1999) and significantly reduces grain yield (Cakir, 2004). To avoid water stress during critical growth stages, supplemental irrigation could be an appropriate choice in order to avoid a high yield penalty and increase WUE when water resources are restricted or the cost is excessive (Iqbal et al., 2014). Igbadun et al. (2007) suggested that good yields could be obtained with regular irrigation at the flowering growth stage, even if irrigation is limited during the vegetative and grain-filling stages. Li and Sun (2016) also showed that an application of a single irrigation can increase maize yield in both black soil and aeolian sandy soil, and supplemental irrigation in late June to early July (around silking) was recommended for maximizing maize yield and WUE in aeolian soil (10.73 Mg ha⁻¹ and $27.94 \text{ kg ha}^{-1} \text{ mm}^{-1}$) and in black soil (11.20 Mg ha⁻¹ and 27.70 kg ha⁻¹ mm⁻¹) with the lowest yield risk.

E-mail address: zhoushl@cau.edu.cn (S.-L. Zhou).

^{*} Corresponding author.

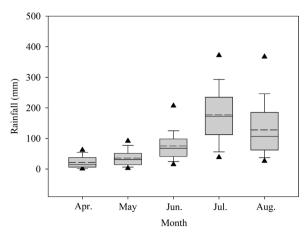


Fig. 1. Average monthly precipitation during spring maize growing seasons in Wuqiao over 1986–2016. The box plots show the 5, 25, 50, 75 and 95 percentiles. The dotted lines and solid lines in the box plots indicate the mean and medium, respectively. The triangles indicate the minimum and maximum.

It is well known that post-silking assimilation contributes approximately 90% to maize yield (Simmons and Jones, 1985; Swank et al., 1982), in consequence, taking necessary steps to guarantee maize production after silking plays an important role in obtaining high grain yield. In addition, water and nitrogen are the most limiting factors for grain yield of maize (Moser et al., 2006), and finite water and nitrogen should be allocated to the filling stage for matter production after silking. Previous studies have examined the effects of irrigation at tasseling on WUE and maize yield (Igbadun et al., 2007; Li and Sun, 2016). However, how supplemental irrigation regulates water and nitrogen temporal distribution and the relations between yield and water/nitrogen consumption percentage at pre- and post-silking are still unclear. In addition, the effects of supplemental irrigation on sourcesink changes remains to be further investigated. In this study, we hypothesized that (1) supplemental irrigation at tasseling could increase post-silking water and nitrogen consumption percentages to optimize water and nitrogen temporal distribution and that (2) irrigation at flowering would stimulate kernel sink creation and promote biomass production after silking, resulting in a high harvest index, yield and water and nitrogen use efficiency. We also had the objective to establish a simple and practical irrigation strategy for spring maize production in the NCP.

2. Materials and methods

2.1. Experimental site

The present experiment was conducted in 2014, 2015 and 2016 at Wuqiao Experimental Station of China Agricultural University (Hebei Province, China, 116.3° E, 37.4° N, altitude 20 m). The soil in the field was light loam with 11.8% clay, 78.1% silt and 10.1% sand. In the 2 m soil profile, average bulk density was 1.51 g cm $^{-3}$, average field capacity was 27.6% (g g $^{-1}$), and wilting point was 8.6% (g g $^{-1}$). The upper 40-cm soil profile contained 1.17% total organic matter, 0.95 g kg $^{-1}$ total N, 104.4 mg kg $^{-1}$ available potassium and 29.2 mg kg $^{-1}$ available phosphorus. Soil physical and chemical properties were measured at the beginning of the field experiment.

From 1986 to 2016, during the entire spring maize growing season (April–August), the mean precipitation was 442 mm, with a range of 142–730 mm with a coefficient of variation (CV) of 33.4%. Rainfall was mainly concentrated in July and August (Fig. 1) with a CV of 49.8% and 71.5%, respectively, i.e., rainfall was extremely uneven, and water scarcity could occur at each growth stage of spring maize.

Table 1The treatments and irrigation regimes used in the present study.

Irrigation	Growth stage	Irrigation date (DAP)	Irrigation water amount (mm)
CK	_	_	-
$I_{ m V6}$	V6	41	75
I_{V12}	V12	61	75
I_{T}	Tasseling	71	75
$I_{\rm S15}$	15 DAS	87	75

DAP, days after planting; DAS, days after silking.

The data of V6 and 15 DAS in 2015 was 40 DAP and 88 DAP, respectively.

2.2. Experimental design

Zhengdan958, a commonly planted cultivar in China, was manually sown at the density of 72,000 plants ha $^{-1}$ on 22 April 2014, 20 April 2015 and 22 April 2016. Before sowing, 75 mm water was applied to guarantee germination using the surface flood method through plastic pipe. Supplemental irrigation was applied at V6 ($I_{\rm V6}$), V12 ($I_{\rm V12}$), tasseling ($I_{\rm T}$) and at 15 days after silking ($I_{\rm S15}$) (Ritchie et al., 1992) at 75 mm (Table 1) with surface flood method through plastic pipe, respectively. A flow metre was used to measure the amount of water supplied. The experimental design was a random complete block design with three replications, and the plot size was 8 m wide by 10 m long with a 2-m buffer zone between plots. In every year, fertilizer containing 72 kg N ha $^{-1}$, 105 kg P_2O_5 ha $^{-1}$ and 120 kg K_2O ha $^{-1}$ was applied before sowing. Later, 108 kg N ha $^{-1}$ of fertilizer was applied at V12. Pest, disease and weed management followed common practices. The maize was harvested on 7 September 2014, 4 September 2015 and 2 September 2016.

2.3. Sampling and measurements

2.3.1. Soil water content measurements

Soil water content measurements were taken at sowing (VS, seven days after irrigation), silking (R1, before irrigation treatment), and maturity (R6). Soil samples were collected from the 0 to 200 cm soil layer at 20-cm intervals with a soil corer. Soil gravimetric water content (g water g^{-1} dry soil) was measured by oven-drying samples at 105 °C for 48 h to a constant weight. Maize water consumption amount, i.e., evapotranspiration (ET, mm), was calculated using the soil water balance equation (James, 1988) as follows:

$$ET = P + I + \Delta SWS - R - D + CR$$

where P (mm) was the effective rainfall, I (mm) was irrigation, Δ SWS (mm) was apparent change of soil water storage in the 200-cm soil profile between sowing and silking and silking and maturity, R was runoff (considered zero because the experimental plots were surrounded with dikes), D was drainage below the 200 cm soil profile, and CR was capillary rise into the root zone. Because the groundwater table at the experimental site was 7-9 m (>4 m) below the ground surface, CR and D can be ignored (Wang et al., 2013).

2.3.2. Biomass, leaf area and nitrogen content

At silking and maturity, three representative plants were sampled per plot. A leaf was considered to have senesced when half or more of its area had yellowed. The leaf area (LA) was measured with a ruler to record length (L, from ligule to leaf tip) and width (W, the widest portion of the leaf blade) to calculate according to the formula: LA = $0.75 \times W \times L$. And leaf area index (LAI) = leaf area per plant/land area per plant (Ren et al., 2016). Next, maize was divided into the stem, leaf, grain and bract + cob to be dried at 80 °C for 48 h to a constant weight. The total N content was determined by the Kjeldahl method (Dordas and Sioulas, 2009). Dry matter and N remobilization were calculated as follows according to Cox et al. (1985) and Ruisi et al. (2016):

 $DMT (g plant^{-1}) = DMV_S - DMV_M$

NRE (%) =
$$(N_S - N_M)/N_S$$

NUtE
$$(g g^{-1}) = GY/(N_M + N_G)$$

where DMT was dry matter translocation, DMV_S was the dry matter of vegetative parts (leaf + stem) at silking, and DMV_M was the dry matter of vegetative plant parts at maturity. NRE was nitrogen translocation efficiency, N_S was the nitrogen accumulation amount of the vegetative parts at silking, N_M was the nitrogen accumulation amount of the vegetative parts at maturity, NUtE was nitrogen utilization efficiency, GY indicated grain yield and N_G was the nitrogen accumulation amount of grain.

2.3.3. Grain sink capacity

2.3.4. Grain yield

To determine yield (14% water content), nine square metres of maize (3 rows \times 5 m row length) were hand harvested per plot at maturity. All harvested areas were surrounded by at least 2 guard rows. Kernel number per ear and thousand kernels weight (TKW) were measured on 20 representative ears per plot. TKW was determined in 5 replications after drying at 70 °C to a constant weight. Water use efficiency (WUE) was calculated as follows (Howell et al., 1998):

$$WUE = GY/ET$$

where GY (t ha⁻¹) was grain yield and ET (mm) was the total seasonal crop evapotranspiration during the period of maize growth.

2.4. Data analysis

The effects of supplemental irrigation at the different stages on yield and yield components, water and nitrogen consumption amount, leaf area index and dry matter were analyzed according to the principles of analysis of variance using GLM in SPSS 17.0 (SPSS Inc., Chicago, IL, USA). Differences were judged by the least significant differences test using a 0.05 level of significance. Regression was used to evaluate the relationships between water/nitrogen consumption percentage at presilking and post-silking and yield and dry matter post-silking accumulation.

3. Results

3.1. The weather

In this experiment, the average rainfall in growing season was 405.7 mm. As shown in Fig. 2, June 2014 received greater precipitation compared to June 2015. In addition, 61 mm of rainfall at V12 resulted in omitting the irrigation treatment at this stage in 2014. Although there were more precipitation in July 2015 than July 2014, in both years, the maize experienced serious drought stress around silking because rainfall was mainly concentrated at the end of July and August (the silking stage was at the beginning of July). Fig. 2A shows that the conditions were favourable for maize before tasseling, and maize suffered mild drought stress during filling in 2014. However, dispersed rainfall ensured its validity, and abundant radiation promoted maize growth (127.6 mm pre-silking and 115.7 mm post-silking). Reversed trends of rainfall occurred in 2015 (Fig. 2B). Maize experienced severe

drought stress from V10 to the end of the lag stage of kernel development, and superfluous rainfall occurred at the late growth stage, which was unsuitable for maize growth (83.0 mm pre-silking and 308.1 mm post-silking). Given poor pollination in CK and $I_{\rm S15}$, we adopted hand pollination in CK plots and sampled plants in $I_{\rm S15}$. In 2016, there was enough precipitation (189.6 mm pre-silking and 393.2 mm post-silking) for maize during the whole growth period, and no drought stress occurred (Fig. 2C). The role of mean temperature might be unimportant because of the small variances in the three years (Fig. 2).

3.2. Grain yield and yield components

All yield components, including ear number per m², grain number per ear and TKW, were significantly affected by irrigation treatments and year. The maximum grain yield was observed at I_T , and the highest TKW and grain number per ear were recorded at I_T in all three years. However, there was no significant difference between I_T and I_{V12} in grain yield and TKW in 2015 and 2016 (Table 2). The harvested ears had no difference in 2014 and 2016 among the treatments, but in 2015, water scarcity caused poor pollination and fertilization and consequently resulted in serious abortion. Among all the treatments in 2015, CK and IS15 were almost devastated, and harvested ears dramatically decreased compared with the other treatments. The ears number of I_{V6} was also observably reduced but was better than CK. The row number was stable and was invulnerable to irrigation stage but was slightly reduced in 2015 due to serious drought stress. The grain number per row was vulnerable to both irrigation stage and annual rainfall. Supplemental irrigation increased grain number per line, especially in a drought year. In addition, grain number per row was highest in 2014, and the maximum value was recorded at I_T for each year. TKW was also improved by irrigation in the dry years, but in 2016, TKW was almost identical. Supplemental irrigation at each stage caused a yield increase by 2.5-15.3% in 2014, 54.5-106.8% in 2015 (except I_{S15}), and 4.1–14.3% in 2016, and the maximum grain yield was observed in I_T .

3.3. Dry matter accumulation

Table 3 illustrated that supplemental irrigation at V6 and V12 could significantly increase biomass at the silking stage in all the three years. In addition, the annual growth conditions had a prominent effect on biomass production before silking. In the year with heavy rain (2016), maize achieved the highest biomass at silking. In the severe drought year (2015), vegetative growth was distinctly suppressed. Biomass production after silking was important for maize yield. In 2014, supplementary irrigation at V6, VT and at 15 days after silking improved dry matter accumulation after silking (DMAS) by 19.4%, 28.7% and 30.0%, respectively, in contrast to rain fed. In 2015, the DMAS of I_{V6} , I_{V12} , I_{T} and I_{S15} were 40.1%, 55.4%, 46.2% and 10.2% higher than the control, respectively. The highest DMAS was recorded in I_T in 2016, and there were no differences among the other treatments in that year. Dry matter translocation (DMT) was affected by both the year type and source-sink. When the sink was small and the source (LAI) was enough, DMT was frequently a negative value (2014 and 2015). To the contrary, assimilation in the vegetative organs would transfer to grain when the source was insufficient. In normal pollination conditions, irrigation at the late stages (I_T and I_{S15}) had greater harvest indexes (HI) than the treatments with irrigation at V6 and V12. Among all treatments in the three years, the highest HI was recorded in I_T .

3.4. Water and nitrogen consumption

Irrigation obviously increased the water consumption of maize (Table 4). Supplemental irrigation at V6 and V12 significantly augmented the pre-silking water consumption amount in all three years. In addition, irrigation water applied at tasseling and at 15 days after

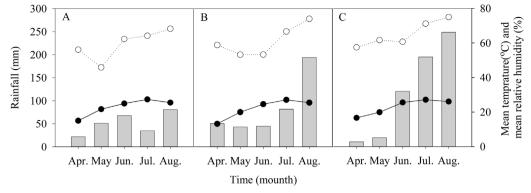


Fig. 2. Monthly precipitation (), mean air temperature () and mean relative humidity (() in the maize growth season in 2014 (A), 2015 (B) and 2016 (C).

Table 2

Effects of supplemental irrigation at the different stages on grain yield and yield components in spring maize.

Year	Irrigation	Ear no. (m ⁻²)	Row no.	Grain no. (row ⁻¹)	TKW (g)	Grain yield (t ha ⁻¹)
2014	CK	7.09a	15.8a	33.9b	278.8b	11.8c
	I_{V6}	7.09a	15.6a	32.7b	292.0ab	12.1bc
	$I_{ m V12}$	_	-	-	-	-
	I_{T}	7.10a	14.8a	36.7a	303.4a	13.6a
	$I_{\rm S15}$	7.09a	15.8a	33.9b	298.4ab	12.8b
2015	CK	4.53c	14.7a	27.2c	266.7b	4.4c
	$I_{ m V6}$	5.91b	15.1a	29.2b	279.3a	6.8b
	I_{V12}	6.81a	14.9a	29.8b	284.8a	8.8a
	I_{T}	6.87a	15.5a	32.3a	280.7a	9.1a
	$I_{\rm S15}$	3.68d	12.9b	19.7d	270.0ab	1.5d
2016	CK	6.95a	14.9a	29.1b	290.0a	9.8b
	$I_{ m V6}$	7.01a	15.7a	31.5ab	287.3a	10.8a
	I_{V12}	6.94a	15.3a	32.1a	288.0a	11.1a
	I_{T}	7.01a	15.3a	32.0a	289.4a	11.2a
	$I_{\rm S15}$	7.03a	15.2a	31.2ab	286.0a	10.2ab
ANOVA	I	***	NS	***	***	***
	Y	**	*	***	***	***
	$I \times Y$	**	NS	***	**	***

TKW, thousand kernels weight; I, irrigation treatment; Y, year type.

The 61 mm rainfall at V12 resulted in omitting the irrigation treatment at this stage in 2014. Values followed by the same letter within a column in each year are not significantly different at P < 0.05, as determined by the LSD test.

- * Significance at the 0.05 probability level.
- ** Significance at the 0.01 probability level.
- *** Significance at the 0.001 probability level.

NS, not significant.

silking mainly improved post-silking evapotranspiration. Annual precipitation affected the maize water consumption in the different stages. The treatments of irrigation at the early stages increased the pre-silking water consumption percentage by 14.2–16.3%, 11.8–15.1% and

28.2-33.1% in 2014, 2015 and 2016, respectively. In addition, supplemental irrigation at the late stage improved the post-silking water consumption percentage by 18.9-21.6%, 31.5-40.1% and 18.7-20.0% in 2014, 2015 and 2016, respectively. A mass of soil water storage was employed due to serious drought before silking, and poor pollination and fertilization reduced the water consumption amount after silking; additionally, abundant rainfall concentrated in August (approaching maturity) resulted in less water being used after silking in 2015. In 2014 and 2016, superior water conditions led to similar pre-silking water consumption amounts; however, heavy precipitation after silking gave rise to abnormal and considerable water levels that were expended in 2016. Additionally, heavy rainfall in August reduced WUE, which might due to drainage (we had not monitored). In the drought years, supplemental irrigation significantly improved WUE, and the highest WUE was observed at I_T . In 2016, there were no differences among all treatments because of superfluous precipitation.

As shown in Table 5, spring maize with supplemental irrigation at V6 and V12 accumulated more nitrogen at silking than the control in the three years, i.e., more nitrogen was used and less nitrogen was stored in the soil under I_{V6} and I_{V12} . In 2014 and 2015, compared with the CK, supplemental irrigation increased nitrogen accumulation amount in grains, except the treatment with poor pollination (I_{S15}). In 2016, excess rain eliminated the function of irrigation and resulted in grain accumulating similar nitrogen at maturity. The relation of source and sink might play an important role in changing nitrogen remobilization efficiency (NRE). In the dry years, supplemental irrigation enhanced NRE, which resulted in less nitrogen being left in the vegetative organs. In 2014, higher NREs were obtained in $I_{\rm T}$ and $I_{\rm S15}$. In 2015, the sink capacity of $I_{\rm S15}$ was impaired, and the $I_{\rm V12}$ and $I_{\rm T}$ had greater NREs. Another phenomenon that occurred in 2016 was that even though more nitrogen transferred to the grain, the vegetative parts still retained considerable amount of nitrogen due to maize accumulating a vast amount of nitrogen pre-silking. There were no significant differences in the nitrogen consumption percentages at pre-silking/post-silking during the total growth period among the treatments in 2014 and 2015.

Table 3Dry matter accumulation (g plant⁻¹) before and after silking as affected by supplemental irrigation at the different stages.

Irrigation	2014				2015				2016					
	DMBS	DMAS	DMT	НІ	DMBS	DMAS	DMT	НІ	DMBS	DMAS	DMT	НІ		
CK	122.2b	165.1b	-12.3d	0.46b	94.7c	111.1d	-51.8d	0.15d	129.2b	169.6b	12.3c	0.47b		
$I_{ m V6}$	137.7a	185.2a	-5.3c	0.48b	120.2a	155.6b	-25.6c	0.37b	160.5a	164.9b	27.4a	0.47b		
$I_{ m V12}$	-	_	-	_	105.9b	172.7a	-7.6b	0.50a	152.4a	169.5b	20.8b	0.48ab		
I_{T}	122.2b	199.6a	8.2a	0.54a	94.7c	162.4a	3.6a	0.55a	129.2b	206.6a	4.2d	0.51a		
I_{S15}	122.2a	201.6a	1.1b	0.53a	95.7c	122.5c	-58.3d	0.30c	129.2b	180.1b	13.2c	0.52a		
Average	126.1	187.9	-2.1	0.50	102.2	144.9	-27.9	0.37	140.1	180.1	15.6	0.49		

DMBS, dry matter accumulation before silking; DMAS, dry matter accumulation after silking; DMT, dry matter translocation; HI, harvest index.

The 61 mm rainfall at V12 resulted in omitting the irrigation treatment at this stage in 2014. Values followed by the same letter within a column were not significantly different at P < 0.05, as determined by the LSD test.

Table 4
Characteristics of water consumption during the different growing periods under different irrigation strategies in spring maize.

Year	Irrigation	Water consumption amount (mm)			Water consumpti	ion percentage (%)	WUE (kg mm $^{-1}$ ha $^{-1}$)	
		VS-R1	R1-R6	TWC	VS–R1	R1-R6	-	
2014	CK	261.1b	169.1c	430.2c	60.7a	39.3b	27.4b	
	$I_{ m V6}$	300.0a	197.2b	497.2a	60.3a	39.7b	24.3c	
	$I_{ m V12}$	_	-	_	_	_	_	
	$I_{ m T}$	261.1b	203.4a	464.5b	52.8b	47.2a	29.3a	
	I_{S15}	261.1b	204.0a	465.0b	52.2b	47.8a	27.5b	
2015	CK	393.1b	119.2c	512.3b	76.7a	23.3b	8.5c	
	I_{V6}	442.6a	144.7b	587.3a	75.3a	24.7b	11.5b	
	$I_{ m V12}$	442.9a	148.4b	591.3a	74.9a	25.1b	14.8a	
	$I_{ m T}$	393.1b	208.1a	601.2a	65.4b	34.6a	15.2a	
	I_{S15}	393.1b	193.4a	586.5a	67.0b	33.0a	2.6d	
2016	CK	224.0b	366.5b	590.5b	37.9b	62.1a	16.6a	
	I_{V6}	299.5a	376.3b	675.8a	44.3a	55.7b	16.0a	
	$I_{ m V12}$	291.0a	361.0b	652.0a	44.6a	55.4b	17.0a	
	I_{T}	224.0b	445.4a	669.4a	33.5b	66.5a	16.7a	
	I_{S15}	224.0b	436.9a	660.9a	33.9b	66.1a	15.4a	
ANOVA	I	***	**	**	***	***	金金金	
	Y	***	**	**	***	***	***	
	$I \times Y$	**	*	NS	*	*	***	

VS, sowing stage; R1, silking stage; R6, mature stage; TWC, total water consumption.

The 61 mm rainfall at V12 resulted in omitting the irrigation treatment at this stage in 2014. Values followed by the same letter within a column are not significantly different at P < 0.05, as determined by the LSD test.

NS, not significant.

However, the year type had significant effects on nitrogen consumption percentage. Severe water deficit in 2015 reduced post-silking nitrogen use percentage. In addition, two unusual values appeared in I_{V6} and I_{V12} in 2016, which were considerably higher than the others due to enough rainfall before tasseling. The NUtE of the treatments with irrigation applied at the early stages was lower than the treatments occurring at the late stages. The highest NUtE was recorded in $I_{\rm T}$ in each year, and

supplemental irrigation could improve NUtE in the dry years.

3.5. Regression analysis

Regression analysis demonstrated that there was a significant quadratic relation between grain yield and water/nitrogen consumption percentage at pre- and post-silking, respectively (Fig. 3). With

Table 5

Nitrogen accumulation amount in the vegetative and reproductive parts at the silking and maturity stages in spring maize, as affected by supplemental irrigation at the different stages.

Year	Irrigation	Silking stage		Maturity stage		NRE (%)	NUtE (g g^{-1})	
		$N_{\rm S}$ (g plant ⁻¹)	NCPE (%)	$N_{\rm M}$ (g plant ⁻¹)	$N_{\rm G}$ (g ear ⁻¹)	NCPE (%)		
2014	CK	1.79b	46.5a	1.67a	2.17b	53.5a	0.07c	35.36d
	$I_{ m V6}$	1.97a	42.4a	1.71a	2.92a	57.6a	0.13b	39.23c
	$I_{ m V12}$	-	-	-	-	-	-	-
	$I_{ m T}$	1.79b	44.9a	1.32bc	2.70a	55.1a	0.27a	48.39a
	I_{S15}	1.79b	44.2a	1.22c	2.83a	55.8a	0.31a	43.88b
2015	CK	1.61b	52.4a	2.17a	0.91c	47.6b	-0.35c	14.86d
	$I_{ m V6}$	2.01a	52.7a	1.96a	1.89a	47.3b	0.03b	27.24c
	$I_{ m V12}$	1.91a	55.2a	1.29b	1.98a	44.8b	0.32a	43.83b
	$I_{ m T}$	1.61b	53.5a	1.01b	2.01a	46.5b	0.38a	46.79a
	I_{S15}	1.61b	46.4b	2.03a	1.53b	53.6a	-0.45d	23.26c
2016	CK	1.84b	50.2b	1.22a	2.47a	49.8a	0.34b	42.64a
	$I_{ m V6}$	2.74a	70.0a	1.42a	2.48a	30.0b	0.46a	39.56a
	$I_{ m V12}$	2.64a	68.0a	1.46a	2.42a	31.1b	0.45a	39.92a
	$I_{ m T}$	1.84b	46.6b	1.38a	2.59a	53.4a	0.25c	42.99a
	I_{S15}	1.84b	48.7b	1.34a	2.45a	51.3a	0.27c	42.72a
ANOVA	I	***	***	**	***	***	***	***
	Y	***	***	**	***	***	***	***
	$I \times Y$	***	**	***	***	**	***	***

 $N_{\rm S}$, nitrogen accumulation amount in the vegetative part at silking; $N_{\rm M}$, nitrogen accumulation amount in the vegetative part at maturity; $N_{\rm G}$, nitrogen accumulation amount in grain; NCPE, nitrogen consumption percentage; NRE, nitrogen remobilization efficiency; NUtE, nitrogen utilization efficiency.

The 61 mm rainfall at V12 resulted in omitting the irrigation treatment at this stage in 2014. Values followed by the same letter within a column are not significantly different at P < 0.05, as determined by the LSD test.

^{*} Significance at the 0.05 probability level.

^{**} Significance at the 0.01 probability level.

^{***} Significance at the 0.001 probability level.

^{**} Significance at the 0.01 probability level.

^{***} Significance at the 0.001 probability level.

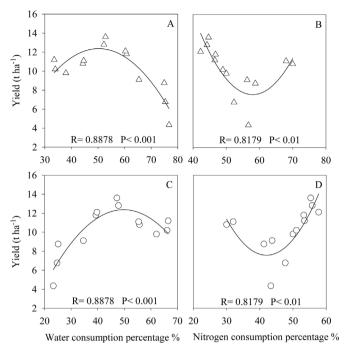


Fig. 3. Regression analysis between yield and water consumption percentage at presilking (A) and post-silking (C), and the model between yield and nitrogen accumulation percentage at pre-silking (B) and post-silking (D). Relation between A and C, B and D were completely symmetrical in one growing season.

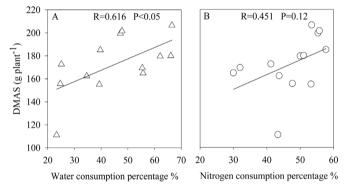


Fig. 4. Relationships of dry matter accumulation after silking (DMAS) and water consumption percentage at post-silking (A), and the relationship between DMAS and nitrogen consumption percentage at post-silking (B) in spring maize.

increasing the pre-silking water consumption percentage from 30% to 50%, the greater the pre-silking water consumption percentage, the higher the grain yield. However, yield reduced when the percentage increased from 50% (Fig. 3A). In addition, the symmetrical trend was

observed after silking (Fig. 3C). With the pre-silking nitrogen consumption percentage increasing from 40% to 60%, grain yield reduced rapidly, while nitrogen consumption percentage improved from 60% to 70%, and yield increased because of higher NRE (Fig. 3B). The entire symmetrical model was discovered after silking, i.e., spring maize yield rapidly increased rapidly with post-silking nitrogen consumption percentages from 40% (Fig. 3D). Regression analysis demonstrated that there was a significant and positive correlation between the DMAS and water consumption percentage at post-silking (Fig. 4A), whereas the correlation between the DMAS and nitrogen consumption percentage at post-silking was not significant due to the two unusual values (Table 5) we had mentioned above.

3.6. Source and sink

Higher leaf area was observed in Iv6 and Iv12, and supplemental irrigation at V6 significantly improved leaf area. Irrigation at I_{V12} also increased leaf area, but its leaf area improvement was lower than I_{V6} . Among all the leaves, the upper leaves (12th–18th) were significantly increased (Fig. 5). Fig. 6 illustrated that the LAIs of I_{V6} improved by 10.9%, 24.5% and 16.2% in 2014, 2015 and 2016, respectively, and the LAIs of I V12 were 8.4% and 6.7% higher compared with the controls in 2015 and 2016, respectively. The supplemental irrigation at tasseling and at 15 days after silking had no effects on the leaf because all of the leaves had been full developed, which were vulnerable to the annual precipitation as the control. The LAIs of the rain fed treatment before tasseling were 5.29, 4.61 and 4.90 in 2014, 2015 and 2016, respectively. In addition, the LAI in 2014 was enough for maize grain growth (DMT was negative); however, in 2016, the LAI of CK might have restricted grain filling (DMT was positive). In 2015, when the DMT was negative, LAI was not enough, and severe abortion inhibited assimilation translocation. Although the LAI of I_T and I_{S15} were low, their function durations were longer than I_{V6} and CK (as shown in Gao et al., 2016) due to favourable water and nitrogen supply conditions.

Supplemental irrigation significantly stimulated kernel sink capacity as shown in Fig. 7. Particularly in 2014 and 2015, water scarcity during flowering and supplemental irrigation at tasseling effectively ensured pollination, and grain sink volume increased much faster than the other treatments in 2014. In addition, $I_{\rm S15}$ improved grain sink capacity compared with the control and $I_{\rm V6}$. There were no significant differences between CK and $I_{\rm V6}$, but jointing irrigation still increased the grain sink (Fig. 7A). In 2015, a severe drought from two weeks presilking to two weeks post-silking resulted in poor pollination and fertilization. Early irrigation ($I_{\rm V6}$ and $I_{\rm V12}$) ensured vegetative growth, but maize still suffered drought stress. Later irrigation ($I_{\rm S15}$) also did not relieve water scarcity when maize grain had almost finished endosperm cell division. The greatest grain sink volume was observed in $I_{\rm V12}$ and $I_{\rm T}$ (Fig. 7B). Abundant rainfall in 2016 prevented drought stress. Thus, no remarkable differences were discovered. While supplementary irriga-

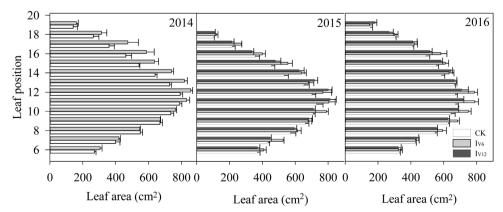


Fig. 5. Effects of supplemental irrigation at the different stages on leaf area at silking in spring maize.

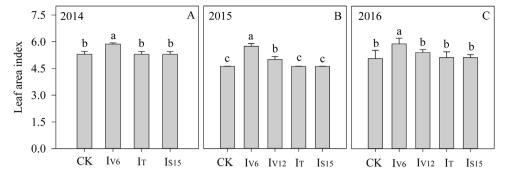


Fig. 6. Leaf area index at silking as affected by supplemental irrigation at the different stages in spring maize. Values with the same letter within a figure were not significant different at P < 0.05, as determined by the LSD test.

tion still facilitated kernel growth, supplemental irrigation at tasseling provided the best results (Fig. 7C).

4. Discussion

Supplemental irrigation at the different growth stages affected water and nitrogen distribution and changed the relations of source and sink. A single irrigation applied at tasseling could optimize the post-silking water consumption percentage and the temporal distribution of nitrogen; moreover, $I_{\rm T}$ ensured enough water and nitrogen at silking and markedly accelerated kernel sink development and relieved leaf senescence caused by water scarcity. As a result, the more water and nitrogen were distributed to the filling stage, the higher the DMAS, and the more yield and higher WUE and NUtE could be obtained.

4.1. The temporal distribution of water and nitrogen

Supplemental irrigation at V6 and V12 increased the pre-silking water consumption percentage, and a single irrigation at tasseling and at 15 days after silking improved the post-silking water consumption percentage (Table 4), especially a supplemental irrigation at tasseling, which ensured a water supply during the highly drought sensitive stage (Boyer and Westgate, 2004; Oury et al., 2016a,b) and reduced abortion. The regression analysis suggested that the higher the post-silking water consumption percentage, the higher the yield that could be achieved. However, when the post-silking percentage increased above 50%, the yield began declining. The main reasons might be abundant rainfall in the maize grain filling stage that went against grain filling (Yang et al., 2001; Yang and Zhang, 2010) or that less water was employed presilking and inhibited vegetative growth. Dry growth conditions at the vegetative stages inhibited maize growth, and maize took up less nitrogen than I_{V6} and I_{V12} (Table 5), and more nitrogen remained in the soil, which was similar with wheat reported by Myrbeck et al. (2012). Thus, taking advantage of natural drought conditions kept more nitrogen in the soil for maize growth after silking, which ensured

nitrogen availability for maintaining maize leaf function (Gao et al., 2016) and grain filling. However, the nitrogen consumption percentages at pre-silking and post-silking were not affected by supplemental irrigation, and the main differences came from year type. The main reason was that maize at I_{V6} and I_{V12} could absorb more nitrogen to maintain post-silking growth and debase NUtE. Regression analysis also demonstrated that when more nitrogen (from 40% to 60%) was assimilated after silking, the higher the yield that could be achieved (Fig. 3). However, when a majority of nitrogen was taken up presilking, high yield due to high NRE could still be achieved, but the NUtE of this pattern was low (Table 5). Therefore, we suggest that a part of nitrogen fertilizer could be applied at tasseling for maize growth. The relations between DMAS and water or nitrogen consumption percentage at post-silking were linear; there was a significant and positive correlation between DMAS and water consumption. Therefore, an appropriate water deficit at the early stages could move finite water and nitrogen into key growth stage for yield, i.e., optimizing water and nitrogen temporal distribution, which obviously increased grain yield, WUE and NUtE.

4.2. Relations between source and sink

Broadly speaking, increasing either the source or sink may increase growth (Ainsworth and Bush, 2011; Ainsworth et al., 2004; Eyles et al., 2013), suggesting that both factors can limit growth to a certain extent (White et al., 2016). Water scarcity before flowering resulted in the inhibition of vegetative organ growth, especially reducing LAI (Figs. 5 and 6). Supplemental irrigation at V6 and V12 stimulated vegetative growth, and the highest LAI was observed in I_{V6} . However, high LAI could not ensure kernel growth with drought stress at flowering because ovary development is highly drought sensitive at this stage (Boyer and Westgate, 2004) and due to carbon limitations via disruption of sucrose cleavage by cell wall invertases in developing ovaries (Boyer and McLaughlin, 2007; Ruan et al., 2012). In addition, Oury et al. (2016a) proposed that ovary abortion under water deficits was

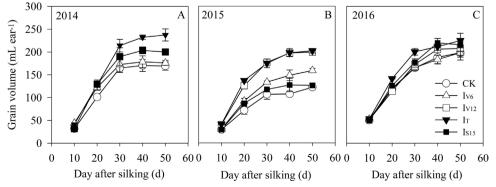


Fig. 7. Effects of supplemental irrigation at the different stages on grain volume in spring maize.

Field Crops Research 209 (2017) 120–128

caused by silk growth arrest 2-3 days after the first visible silk and that the first molecular changes associated with water scarcity in the reproductive organs occurred in the silks rather than in the ovaries. Hence, supplemental irrigation at tasseling was important in reducing ovary abortion and yield penalty. Although LAI was inhibited in I_T , more water and nitrogen were available at this sensitive stage, which could reduce ovary abortion and promote kernel sink construction. In addition, we demonstrated that late irrigation kept more chlorophyll content that helped maintain leaf function compared with the early irrigation treatments (Gao et al., 2016). Our results suggested that irrigation at tasseling enhanced the kernel sink capacity regardless of growth conditions (Fig. 7). In addition, the capacity of the kernel sink played an important role in achieving high yield (Morita et al., 2005). We also demonstrated that the application of 6-benzyladenine or Brassinolide at tasseling could facilitate endosperm cell division and establish sink capacity and enhance grain filling (Unpublished results). The water and nitrogen of I_{S15} was enough after silking, but ovary abortion was serious in the dry years. Therefore, supplemental irrigation at tasseling was of prime importance for kernel growth and development. In addition, as shown in Table 3, DMT might serve as an index for measuring source-sink relations. The negative values meant that the source supply surpassed sink capacity, and part of the assimilation stored in the stem due to kernel sink volume was inhibited. However, the vegetative growth of spring maize was suppressed by natural water deficiencies, and supplemental irrigation at tasseling accelerated kernel sink development and maintained leaf function for grain filling. The optimizing relation between source and sink significantly increased yield and improved HI. We believe that the bottleneck limiting spring maize yield was source ability and sink capacity, and tasseling management played an important role in maize production.

4.3. Effects of year type on spring maize and irrigation strategies for spring maize in the NCP

The year type played an important role in spring maize growth and development. Enough rainfall at V12 in 2014 ensured spring maize growth before silking, and water application at flowering and dispersive precipitation during the filling stage influenced post-silking production, resulting in high GY, WUE and NUtE. In 2015, with no rainfall during V10 to 15 days after silking, both vegetative organs and kernel growth were hampered, and low GY, WUE and NUtE were obtained. Additionally, some abnormal values comparing with CK were observed in I_{S15} (Tables 2–4) because severe drought urged us to adopt artificial pollination. CK was pollinated in all the plot, however, $I_{\rm S15}$ was only pollinated in sampled plants. In 2016, excessive rainfall, especially rainfall during the filling stage went against post-silking production. In addition, heavy precipitation led to increased nitrate leaching loss (Rasmussen and Thorup-Kristensen, 2016), grain yield and WUE were limited. Therefore, establishing suitable irrigation strategies based on the year type was crucial for spring maize. As reported in previous reports (Cakir, 2004; Igbadun et al., 2007; Li and Sun, 2016), irrigation around flowering increased WUE and ensured high grain yield. Our results also demonstrated this phenomenon. In a normal dry year such as 2014, high yield and WUE could be achieved by a single irrigation applied at tasseling. However, in the worst drought year (2015), a single supplemental irrigation was inadequate for high maize yield. It is difficult to forecast annual rainfall (Fig. 1), but predicating short dated precipitation with satellite image is precise. In severe drought years such as 2015, the first irrigation could be applied at V12 if there is no rainfall within the next 2 weeks (V12-tasseling), and a second irrigation should be supplemented around flowering. In a rainy year, drought stress could be ignored, and nitrogen leaching might be the main element contributing to yield penalties. Reducing nitrogen leaching might play an important role (Rasmussen and Thorup-Kristensen, 2016), and postponing nitrogen fertilizer to tasseling may be an important management strategy (Wang et al., 2017).

5. Conclusions

In the results of a 3-year study, it was concluded that supplemental irrigation at V6 and V12 increased water consumption and the percentage and nitrogen assimilation amount at pre-silking ensured enough LAI for spring maize; however, sinks would be vulnerable in dry years. Supplemental irrigation at tasseling increased the post-silking water consumption percentage, which allocated more water and soil nitrogen for grain growth and development. At the same time, $I_{\rm T}$ optimized the relation between source and sink to effectively take advantage of water and nitrogen, resulting in enhanced post-silking biomass production. In addition, high yield, WUE, NUtE and HI were obtained by supplemental irrigation at tasseling.

Acknowledgements

This work was supported by the National Key Research and Development Program of China (2016YFD0300301), the China Agriculture Research System (CARS-02-26), the National Natural Science Foundation of China (31371558), and the Special Fund for Agro-scientific Research in the Public Interest (201203031, 201303133). In addition, we are grateful for the editor and reviewers for providing critical suggestions about revising the manuscript.

References

- Ainsworth, E.A., Bush, D.R., 2011. Carbohydrate export from the leaf: a highly regulated process and target to enhance photosynthesis and productivity. Plant Physiol. 155, 64–69.
- Ainsworth, E.A., Rogers, A., Nelson, R., Long, S.P., 2004. Testing the 'source-sink' hypothesis of down-regulation of photosynthesis in elevated [CO₂] in the field with single gene substitutions in Glycine max. Agric. For. Meteorol. 122, 85–94.
- Boyer, J.S., McLaughlin, J.E., 2007. Functional reversion to identify controlling genes in multigenic responses: analysis of floral abortion. J. Exp. Bot. 58, 267–277.
- Boyer, J.S., Westgate, M.E., 2004. Grain yields with limited water. J. Exp. Bot. 55, 2385–2394.
- Cakir, R., 2004. Effect of water stress at different development stages on vegetative and reproductive growth of corn. Field Crops Res. 89, 1–16.
- Claassen, M.M., Shaw, R.H., 1970. Water deficit effects on corn. II. Grain components. Agron. J. 62, 652–655.
- Cox, M.C., Qualset, C.O., Rains, D.W., 1985. Genetic variation for nitrogen assimilation and translocation in wheat. I. Dry matter and nitrogen accumulation. Crop Sci. 25, 430-435
- Doorenbos, J., Kassam, A.K., 1979. Yield Response to Water. Irrigation and Drainage Paper 33. FAO, United Nations, Rome, pp. 176.
- Dordas, C.A., Sioulas, C., 2009. Dry matter and nitrogen accumulation, partitioning, and retranslocation in safflower (*Carthamus tinctorius* L.) as affected by nitrogen fertilization. Field Crops Res. 110, 35–43.
- Eyles, A., Pinkard, E.A., Davies, N.W., Corkrey, R., Churchill, K., O'Grady, A.P., Sands, P., Mohammed, C., 2013. Whole-plant versus leaf-level regulation of photosynthetic responses after partial defoliation in Eucalyptus globulus saplings. J. Exp. Bot. 64, 1625–1636.
- Gao, Z., Lv, X.Y., Wang, J.H., Liang, X.G., Zhao, X., Zhou, S.L., 2016. The effects of supplemental irrigation at different stages on plant nitrogen remobilization and nitrogen utilization in spring maize. Acta Agric. Boreal. Sin. 31 (S1), 11–16.
- Grant, R.F., Jackson, B.S., Kiniry, J.R., Arkin, G.F., 1989. Water deficit timing effects on yield components of maize. Agron. J. 81, 61–65.
- Hall, A.J., Lemcoff, J.H., Trapani, N., 1981. Water stress before and during flowering in maize and its effect on yield, its components, and their determinants. Maydica 26, 19–38.
- Howell, T.A., Tolk, J.A., Arland, D.S., Evertt, R., 1998. Evapotranspiration, yield and water use efficiency of corn hybrid differing in maturity. Agron. J. 90, 3–9.
- Igbadun, H.E., Tarimo, A.K.P.R., Salim, B.A., Mahoo, H.F., 2007. Evaluation of selected crop water production functions for an irrigated maize crop. Agric. Water Manag. 94, 1–10.
- Iqbal, M.A., Shen, Y.J., Stricevic, R., Pei, H.W., Sun, H.Y., Amiri, E., Penas, A., Rio, S.D., 2014. Evaluation of the FAO AquaCrop model for winter wheat on the North China Plain under deficit irrigation from field experiment to regional yield simulation. Agric. Water Manag. 135, 61–72.
- James, L.G., 1988. Principles of Farm Irrigation System Design. John Willey and Sons, Inc., New York, pp. 453.
- Li, J.M., Inanaga, S., Li, Z.H., Eneji, A.E., 2005. Optimizing irrigation scheduling for winter wheat in the North China Plain. Agric. Water Manag. 76, 8–23.
- Li, Q.Q., Dong, B.D., Qiao, Y.Z., Liu, M.Y., Zhang, J.W., 2010. Root growth available soil water and water-use efficiency of winter wheat under different irrigation regimes applied at different growth stages in North China. Agric. Water Manag. 97, 1676–1682.
- Li, Z.Z., Sun, Z.H., 2016. Optimized single irrigation can achieve high corn yield and

- water use efficiency in the Corn Belt of Northeast China. Eur. J. Agron. 75, 12–24. Liu, C.M., Zhang, X.Y., Zhang, Y.Q., 2002. Determination of daily evaporation and evapotranspiration of winter wheat and maize by large-scale weighing lysimeter and micro-lysimeter. Agric. For. Meteorol. 111, 109–120.
- Morita, S., Yonemaru, J., Takanashi, J., 2005. Grain growth and endosperm cell size under high night temperatures in rice (*Oryza sativa* L.). Ann. Bot. 95, 695–701.
- Moser, S.B., Feil, B., Jampatong, S., Stamp, P., 2006. Effects of pre-anthesis drought, nitrogen fertilizer rate, and variety on grain yield, yield components, and harvest index of tropical maize. Agric. Water Manag. 81, 41–58.
- Myrbeck, A., Stenberg, M., Rydberg, T., 2012. Establishment of winter wheat-strategies for reducing the risk of nitrogen leaching in a cool-temperate region. Soil Tillage Res. 120, 25–31.
- Oury, V., Caldeira, C.F., Prodhomme, D., Pichon, J.P., Gibon, Y., Tardieu, F., Turcls, O., 2016a. Change in ovary carbon status a cause or a consequence of maize ovary abortion in water deficit during flowering? Plant Physiol. 171, 997–1008.
- Oury, V., Tardieu, F., Turc, O., 2016b. Ovary apical abortion under water deficit is caused by changes in sequential development of ovaries and in silk growth rate in maize. Plant Physiol. 171, 986–996.
- Rasmussen, I.S., Thorup-Kristensen, K., 2016. Does earlier sowing of winter wheat improve root growth and N uptake? Field Crops Res. 196, 10–21.
- Ren, B.Z., Zhu, Y.L., Zhang, J.W., Dong, S.T., Liu, P., Zhao, B., 2016. Effects of spraying exogenous hormone 6-benzyladenine (6-BA) after waterlogging on grain yield and growth of summer maize. Field Crops Res. 188, 96–104.
- Ritchie, S.W., Hanway, J.J., Benson, G.O., 1992. How a Corn Plant Develops. Special Report No. 48. Iowa State Universitypp. 21.
- Ruan, Y.L., Patrick, J.W., Bouzayen, M., Osorio, S., Fernie, A.R., 2012. Molecular regulation of seed and fruit set. Trends Plant Sci. 17, 656–665.
- Ruisi, P., Saia, S., Badagliacca, G., Amato, G., Frenda, A.S., Giambalvo, D., Miceli, G.D., 2016. Long-term effects of no tillage treatment on soil N availability, N uptake, and ¹⁵N-fertilizer recovery of durum wheat differ in relation to crop sequence. Field Crops Res. 189, 51–58.

- Setter, T.L., Flannigan, B.A., Melkonian, J., 2001. Loss of kernel set due to water deficit and shade in maize. Crop Sci. 41 (5), 1530–1540.
- Simmons, S.R., Jones, R.J., 1985. Contributions of pre-silking assimilate to grain yield in maize. Crop Sci. 25, 1004–1006.
- Sun, H.Y., Shen, Y.J., Yu, Q., Flerchinger, G.N., Zhang, Y.Q., Liu, C.M., Zhang, X.Y., 2010. Effect of precipitation change on water balance and WUE of the winter wheat–summer maize rotation in the North China Plain. Agric. Water Manag. 97, 1139–1145
- Sun, H.Y., Zhang, X.Y., Wang, E.L., Chen, S.Y., Shao, L.W., 2015. Quantifying the impact of irrigation on groundwater reserve and crop production a case study in the North China Plain. Eur. J. Agron. 70, 48–56.
- Swank, J.C., Below, F.E., Lambert, R.J., Hageman, R.H., 1982. Interaction of carbon and nitrogen metabolism in the productivity of maize. Plant Physiol. 70, 1185–1190.
- Wang, B., Zhang, Y.H., Hao, B.Z., Xu, X.X., Zhao, Z.G., Wang, Z.M., Xue, Q.W., 2016. Grain yield and water use efficiency in extremely-late sown winter wheat cultivars under two irrigation regimes in the North China Plain. PLOS ONE 11, e0153695.
- Wang, J.H., Gao, Z., Qu, L.H., Lv, X.Y., Liang, X.G., Zhang, L., Zhou, S.L., 2017. Effects of postponing N-fertilizer application by drip fertigation on the characteristics of sourcesink and yield formation in summer maize. J. China Agric. Univ. 22 (in press).
- Wang, D., Yu, Z.W., White, P.J., 2013. The effect of supplemental irrigation after jointing on leaf senescence and grain filling in wheat. Field Crop Res. 151, 35–44.
- White, A.C., Rogers, A., Rees, M., Osborne, C.P., 2016. How can we make plants grow faster? A source–sink perspective on growth rate. J. Exp. Bot. 67, 31–45.
- Yang, J.C., Zhang, J.H., 2010. Crop management techniques to enhance harvest index in rice. J. Exp. Bot. 61, 3177–3189.
- Yang, J.C., Zhang, J.H., Wang, Z.Q., Zhu, Q.S., Wang, W., 2001. Hormonal changes in the grains of rice subjected to water stress during grain filling. Plant Physiol. 127, 315–323.
- Zinselmeier, C., Jeong, B.R., Boyer, J.S., 1999. Starch and the control of kernel number in maize at low water potentials. Plant Physiol. 121, 25–36.