Desalination and Water Treatment
www.deswater.com

doi: 10.5004/dwt.2020.25294

188 (2020) 406–414
June

Water limited stress at jointing stage on fresh waxy maize yield and its interactions with plant density under field conditions

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Received 28 June 2019; Accepted 19 December 2019

ABSTRACT

Background Limited research on waxy maize yield and commercial value in response to water-limited (WL) stress and its interactions with plant density (PD) in the field. Methods: in this study, we examined the effects on two water treatments the water-limited group, and the well-watered (WW) group at one location (Fangshan, China) for fresh waxy maize hybrid (JKN 2000), and three plant densities (3.75, 5.25, and 6.75 plants m^{-2}) in 2017 and 2018 using a block design split randomly in the field. Results: fresh waxy maize ear yield, grain yield, and yield components were affected for all treatments after WL stress lasted more than 9 d at the jointing stage. Compared with the WW treatment, WL treatment significantly decreased the fresh ear yield by 4.95%, due to decreasing ear length in waxy maize. In contrast, fresh grain yield significantly reduced by 3.75%, largely because of decreasing kernel weight and numbers per ear. The optimal PD of fresh ear yield was 6.75 plants m^{-2}. Conclusions: across all plant densities, WW treatment significantly increased the ear length distribution percentage by 19.19%, which effectively expand the commercial value of fresh ears of waxy maize. We concluded that waxy maize yield and commercial value of single-ear could be enhanced by the application of WW treatment at the jointing stage under field conditions.

Keywords: Waxy maize; Yield components; Water limited stress; Plant height and ear height; Ear length

1. Introduction

Waxy maize (*Zea mays* L. Sinensis Kulesh) was first reported in China in 1909 and is mainly used in food production in Asia [44]. Because of its specific characteristics, including a starch composition of almost 100% amylopectin, and economic value, waxy maize is becoming an important source of maize for fresh consumption, food industries, feedstuff in the world [1,2]. With the continuous improvement of economic and social development and living standards, people's food consumption habits have turned to the direction of nutrition and health [3,4]. Therefore, fresh waxy maize has become an important way for farmers to increase their income and agricultural efficiency [2,5]. In China, the annual processing capacity of fresh waxy maize ears (such as quick-freezing) has reached 10 billion ears, making the planting and production area of waxy maize the first in the world, which would contribute to broad prospects for commercial value in the processing industry of waxy maize ears [6]. As one of the major producing areas of crops, the north China

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plain (NCP, 'winter wheat' continuously followed by 'summer maize') is becoming an important production base of fresh waxy maize.

The current commercial maize (*Zea mays* L.) hybrids are superior to older hybrids because maximum grain yield per area is achieved primarily in high-density populations under field conditions [7,8]. Furthermore, maize yield is often associated with interseasonal variation in optimum plant density (PD) followed by instability and yield loss, particularly for rainfed maize under the diverse agro-ecosystems induced by ongoing climate change [9–11]. In recent years, some scholars reported high PD is needed to obtain a high yield in maize [12,13]. Under water-limited (WL) stress or drought-prone conditions, the use of density-neutral hybrids optimizes the resource-use efficiency by adjusting properly the seeding rates, PD or other cultivation technique measures, which changing the development growth phases in maize to address climate change, for example, declining rainfall [11,12]. Further, since crowded plants compete for resources like nutrient, incident radiation and water, the yield per plant is possibly decreased [7,11,13]. Therefore, assessing the yield effects of climatic variables in specific growth phases may provide a better understanding of how WL stress and irrigation impact waxy maize yield under climate change [14–16]. Although previous studies have described changes in maize yield and other agronomic traits its interactions with PD in the field [12,17–19], however, there is still little information on fresh waxy ear yield under field conditions and specifically for its commercial value.

During the past two decades, although progress has been made towards an overall increase in maize, its yield and plant sensitivity to WL stress have increased, especially erratic rainfall patterns on a global scale [20–22]. Water limited stress and often results in 20%–50% reductions in maize yield each year in China [23]. During the last decade, climate change in the NCP has been associated with a mean reduction in precipitation by 2.9 mm y^{-1} [24]. Further, precipitation across NCP is mainly concentrated in June to August, WL stress is more likely to happen during the Jointing Stage (V6-9, from Apr. to May). Previous studies have reported that declining and low precipitation has led to WL stress during different growth phases in maize, which has severely affected its agronomic traits and results in marked yielding reductions [20,23,25–28]. In recent years, several scholars have studied the effects of WL stress on waxy maize, which focused on grain yield or quality during the pollinating time or later period [29–31]. Nevertheless, waxy maize growth and development are affected differently by the weather in different growth phases. Therefore, assessing the yield effects of climatic variables at the jointing stage may provide a better understanding of how WL stress and irrigation impact waxy maize yield under climate change [32,33].

The objectives of the present study aims at (1) quantify the effect of WL stress at jointing stage on fresh ear yield, ear height, plant height, yield constituents and yield of fresh grain; and (2) investigate the effect of Water limited stress and PD on ear length distribution percentage (%) in waxy maize; and (3) explore the optimal management strategies for addressing WL stress with further improvements in the commercial value of fresh ear yield under field conditions.

2. Materials and methods

2.1. Experimental design

Field trials were conducted in 2017 and 2018 at Fangshan, Beijing (39.68°N, 116.05°E, Elev. 37.1 m). The weather data recorded during the maize growing season at the 2 y are revealed in Table 1. The fertility of soil within the layer from the surface down to 20 cm depth and the type of soil at the experimental location are shown in Table 2. At Fangshan, the 0–20 cm soil layer contains 14.78 g kg^{-1} organic matter, 0.89 g kg^{-1} total nitrogen (N), 25.91 mg kg^{-1} available phosphorus (P), and 102.1 mg kg^{-1} available potassium (K), and has a pH of 7.1.

As experimental crop plants, we selected the commonly cultivated hybrid waxy maize cultivar, Jingnuo, China 2000 (JKN 2000, semi-compact tall plant). The plant densities used were 6.75, 3.75, and 5.25 (farmer's traditional practice plants per square meter. The maize was hand sown using plastic film mulching at Fangshan, Beijing on 10 April 2017, and 12 April 2018, respectively. In all experiments of this study, the row spacing and the depth of sowing were set as 60 and 5 cm respectively.

The effects of two water treatments were examined under field conditions, the WL group was set up at waxy maize jointing stage [34], with water limited stress duration 9 d from 22 May to 30 May in 2017, and 11 d from 23 May to 2 June in 2018 respectively (Table 1). Plants were maintained at about 55%–65% field water capacity (FWC) of soil water content in the WL group. For the control, each plot of the well-watered (WW) group was irrigated with 60 mm of water on 28 May 2017 and 29 May 2018 respectively, in which the average moisture content of the soil was maintained at about 75%–85% FWC of soil water content (Table 3).

The experiments were conducted according to a block design split randomly in triplicate. PD acted as the principal block and WL and WW application acted as sub-blocks which were split randomly into principal blocks. In a single plot with a width of 4.8 m and length of 10 m there were eight maize rows. Fertilizer application at the experimental location in each plot followed a high yield practice, with a base fertilizer of 105 kg N ha^{-1}, 26 kg P_2O_5 ha^{-1}, 120 kg K_2O ha^{-1} applied before sowing and a further 95 kg (N) ha^{-1} applied as a top dressing at the tassel stage (VT). Each plot was irrigated with 60 mm of water immediately after sowing (Table 2). We follow the guidelines from local farmers in the other aspects

Table 1
Weather data of experimental locations in maize growing season at Fangshan

Monthly	Precipitation (mm)		Temperature (°C)	
	2017	2018	2017	2018
4-Apr.	20.6	41.9	16.8	15.1
5-May	20.4	11.8	22.6	21.6
6-Jun.	134.2	25.2	24.7	26.4
7-July	91.0	311.3	26.9	27.7
Total[a]	266.2	390.2	22.8	22.7

Note: [a]Air temperatures are monthly mean, while precipitation is monthly sums in maize growing season.

Table 2
Soil type, original fertility in the top 0–20 cm soil layer, and fertilization application of each plot at the experimental site

Soil type	PH	Original fertility				Irrigation				
		Organic matter	Total N	Available P	Available K	Before sowing			Vasseling stage	
		(g kg^{-1})	(g kg^{-1})	(mg kg^{-1})	(mg kg^{-1})	kg N ha^{-1}	kg P_2O_5 ha^{-1}	kg K_2O ha^{-1}	kg N ha^{-1}	mm (date)
Cinnamon soil	7.1	14.78	0.89	25.91	102.1	105	26	120	95	60 (April 16)

Table 3
Water treatments under field conditions in 2017 and 2018

Cultivar	Year	Treatment			
		Group divided	Test measures	Test times	FWC
JKN 2000	2017	WL	WL stress duration for 9 d at jointing stage (V8)	From 22 May to 30 May	55%–65%
		WW	Irrigated with 60 mm of water	28 May	75%–85%
	2018	WL	WL stress duration for 11 d at jointing stage (V8)	from 23 May to 2 June	55%–65%
		WW	Irrigated with 60 mm of water	29 May	75%–85%

Note: FWC of soil water content, which measured at every 10 cm in 0–20 cm soil layer by drying and weighing and at every 20 cm in 20–80 cm soil layer by the neutron scattering technique (CPN-503, USA) every 3 d during the growing period of waxy maize in water treatment times.

of agronomy. The maize was harvested on 10 July 2017 and 12 July 2018 at Fangshan, Beijing.

2.2. Measurements

At harvest, a 24 m^2 area inside the interior two rows of a single plot was collected by hands to determine fresh ear and grain yields. Ear density, as the number of ears per unit ground area, ear weight, and ear size length for all plants in the sampling area of each plot was measured at the time of harvest. Kernel number per ear and thousand-kernel weight were measured using 10 randomly selected ears from the sampling area in each plot.

Commercial ears of its length distribution percentage were calculated as Eq. (1) as follows: percentage of commercial ears = ears of specific length/all ears (1). Where specific length is divided into different levels: superfine, the ear length greater than or equal to 20 cm; first, the ear length ranged from 18 to 20 cm; second, the ear length ranged from 16 to 18 cm; and ear length less than or equal to 16 cm are classified as the others. And all ears are the number of the ear in each plot.

At the dough stage (R3, milk) on 8 July 2017 and 9 July 2018 at Fangshan, Beijing five plants from each plot with at least 0.6 m distant from the spot of harvesting samples were collected to measure the characteristics in the morphology of ear and plant height.

2.3. Statistical analysis

Treatment effects on fresh ear yield, fresh grain yield, yield components, and morphological traits (ear and plant height) were analyzed using analysis of variance, in the general linear model procedure of SPSS 21 (Chicago, IL, USA). The unchanged factors in this model included plant density, year as well as water treatment, including all interactions. Replicate was considered a random factor. The means of data were compared using Duncan's multiple range test at $P < 0.05$. The figures were drawn using Origin 8.6.

3. Results

3.1. Fresh ear yield

Water treatment and PD significantly affected fresh ear yield across 2 y (Table 4). There was no interaction between water treatment and plant density. WL stress significantly decreased the fresh ear yield by 4.95% across all plant densities and years (Table 5). The highest yield of JKN 2000 was obtained by WW application at an optimal PD of 6.75 plants m^{-2} across the 2 y, indicating a significant interaction by management (e.g. WW application and plant density). However, there were no significant interactions among the year, water treatment, and PD (Table 4).

Water treatment significantly interacted with the year, indicating that the water treatment (WL stress) effect was influenced by climate factors, for example, rainfall. The average fresh ear yield of JKN 2000 across all plant densities in 2017 (14.64 ton ha^{-1}) was higher than that in 2018 (14.16 ton ha^{-1}) (Table 5). Fresh ear yield was higher in 2017 than 2018 across all plant densities due to high rainfall, that the total rainfall over the first three monthly sums during maize growing season in 2017 was 175.2 mm which was 96.3 mm higher than 2018.

3.2. Fresh grain yield

Fresh grain yield differed significantly with year, water treatment, and PD ($P < 0.01$) (Table 4). The average fresh grain

Table 4
Results of ANOVA analysis for the effects of Year (Y), PD, and water treatments (WW and WL) on fresh ear yield, fresh grain yield, yield components, morphological traits, and ear length distribution percentage in waxy maize

Year	Effect	*df*	Fresh ear yield	Fresh grain yield	Ear density	Thousand kernels weight	Kernel numbers per ear	Plant height	Ear height	Ear length distribution percentage		
2017	WS	1	16.71**	20.99**	3.46ns	4.13*	47.55**	35.97**	37.4**	Superfine	First	Second
	PD	2	87.46**	9.32*	163.89**	8.91**	27.68**	6.87*	18.95**			
	WS * PD	2	0.98ns	0.61ns	0.14ns	0.24ns	0.08ns	0.76ns	0.87ns			
2018	WS	1	27.61**	11.22*	2.71ns	35.62**	47.41**	21.28**	13.01*	52.98**	8.01*	9.72*
	PD	2	21.42**	15.21**	96.98**	6.21*	26.69**	9.64**	11.15**	9.78**	111.49**	10.45**
	WS * PD	2	0.22ns	1.11ns	0.03ns	0.56ns	0.11ns	0.21ns	1.18ns	1.87ns	0.02ns	1.25ns
2 Y	Year	1	4.42*	7.77*	2.97ns	17.75**	4.96*	1.51*	7.97**			
	WS	1	41.42**	24.89**	6.11*	21.17**	95.56**	56.32**	31.71**			
	PD	2	74.26**	22.67**	250.46**	5.65*	52.75**	17.52**	21.58**			
	rep	2	2.46ns	1.46ns	1.73ns	0.39ns	0.09ns	2.17ns	0.19ns			
	Year * WS	1	4.81*	0.63ns	0.03ns	1.09ns	6.77ns	0.05ns	0.12ns			
	WS * PD	2	0.56ns	0.67ns	0.11ns	0.42ns	0.04ns	0.15ns	1.72ns			
	Year * PD	2	1.79ns	3.87*	0.12ns	10.77**	5.36*	1.05ns	0.81ns			
	Year * WS * PD	2	0.27ns	1.24ns	0.02ns	0.21ns	0.19ns	0.71ns	0.25ns			

Note: *F* values and significance levels (* $P < 0.05$, ** $P < 0.01$ and ^{ns} $P \geq 0.05$) are given.

Table 5
Fresh ear yield (ton ha^{-1}) of waxy maize affected by PD (plants m^{-2}), and water treatments (WW and WL) in 2017 and 2018

Year	PD	WW	WL
2017	3.75	13.66 ± 0.13 *C a*	13.29 ± 0.06 *C b*
	5.25	14.53 ± 0.12 *B a*	14.18 ± 0.12 *B a*
	6.75	15.73 ± 0.29 *A a*	15.02 ± 0.15 *A a*
		14.64 ± 0.31	14.16 ± 0.26
2018	3.75	13.91 ± 0.22 *B a*	12.82 ± 0.15 *B b*
	5.25	14.69 ± 0.35 *AB a*	13.89 ± 0.15 *A a*
	6.75	15.35 ± 0.33 *A a*	14.32 ± 0.23 *A a*
		14.65 ± 0.26	13.68 ± 0.24

Note: Same capital letters indicate no significant difference between plant densities within the same year at *a* = 0.05. Same small letters indicate no significance between water treatments (WW and WL) in the same year, PD at *a* = 0.05. The mean and standard errors are reported.

Table 6
Fresh grain yield (ton ha^{-1}) of waxy maize affected by PD (plants m^{-2}), and water treatments (WW and WL) in 2017 and 2018

Year	PD	WW	WL
2017	3.75	9.71 ± 0.09 *B a*	9.49 ± 0.12 *B b*
	5.25	10.11 ± 0.22 *A a*	9.79 ± 0.11 *A b*
	6.75	10.04 ± 0.14 *A a*	9.63 ± 0.06 *AB a*
		9.95 ± 0.18	9.64 ± 0.06
2018	3.75	9.43 ± 0.07 *B a*	8.78 ± 0.26 *B a*
	5.25	10.06 ± 0.25 *A a*	9.87 ± 0.21 *A a*
	6.75	9.92 ± 0.11 *A a*	9.45 ± 0.06 *AB b*
		9.8 ± 0.12	9.37 ± 0.19

Note: Same capital letters indicate no significant difference between plant densities within the same year at *a* = 0.05. Same small letters indicate no significance between water treatments (WW and WL) in the same year, PD at *a* = 0.05. The mean and standard errors are reported.

yield for JKN 2000 across all plant densities in 2017 (9.95-ton ha^{-1}) was higher than that in 2018 (9.80 ton ha^{-1}) (Table 6). WL stress significantly decreased fresh grain yield by 3.75% across all plant densities, and years.

Although PD showed no significant interaction with water treatment, there were significant interactions between PD and year ($P < 0.05$) (Table 4). Over 2 y, the highest yield was obtained for JKN 2000 with water limited stress at an optimal PD of 5.25 plants m^{-2}, after WW treatment, the best performing for the optimal PD increased by 3.17% in 2017 and 1.89% in 2018, indicating that the interaction effect of the year (e.g. rainfall) and managements (e.g. WW and plant density) on fresh ear yield was also significant. The analysis was made using a split block design with PD as the main plot factor and Water treatments (WW and WL) as subplot factors.

3.3. Components of yields

PL instead of water treatment exerted significant effects on ear density ($P < 0.01$). Ear density increased linearly with an increase in plant density. Water treatment showed no significant interaction with PL (Table 4).

Thousand-kernel weight was significantly affected by water treatment, PD, and year (Table 4). WL stress significantly decreased the thousand-kernel weight ($P < 0.01$) by 4.78% across all plant densities and years. There were significant interactions between PD and year ($P < 0.01$) but showed no interaction with other factors (Table 4). Thousand-kernel weight decreased linearly with an increase in PD across both water treatments and all years (Fig. 1). The interactions among water treatment, plant density, and year were no significant.

Kernel number per ear was also significantly affected by water treatment, PD, and year (Table 4). Across all plant densities and years, kernel number per ear significantly increased by 2.86% after WW treatment application ($P < 0.01$). Whereas this parameter was significantly increased linearly by an increase in PD ($P < 0.01$) across all years and both water treatments (Fig. 2). Interactions between water treatment and other factors were not significantly different, whereas there was a significant interaction between water treatment and years ($P < 0.01$) (Table 4).

3.4. Plant height and ear height

Water treatment, PD and year affected plant height in a statistically significant way (Table 3). PD made plant height increase remarkably (Fig. 3), across all water treatments and in both years. WL stress decreased plant height by 4.07% with statistical significance ($P < 0.01$) across the entire year and PD grades and showed no significant interaction with other factors ($P < 0.01$) (Table 2).

Ear height was also significantly affected by water treatment, plant density, and year (Table 3). WL stress significantly reduced ($P < 0.01$) ear height by 7.97% across entire year and PD grades. Also the effect of WL stress in lowing ear position less at low PD than high PD (Fig. 4).

3.5. Ear grade in size

Ear distribution percentage was significantly affected by water treatment, and PD (Table 4). There were no significant interactions between water treatment and plant density. Ear length distribution percentage was significantly shorter at high plant densities, especially in superfine grade ears (ear length greater than or equal to 20 cm) (Fig. 5). After the WW treatment application, the ear length distribution percentage ($P < 0.01$) significantly increased by 19.19% across all plant densities in 2018.

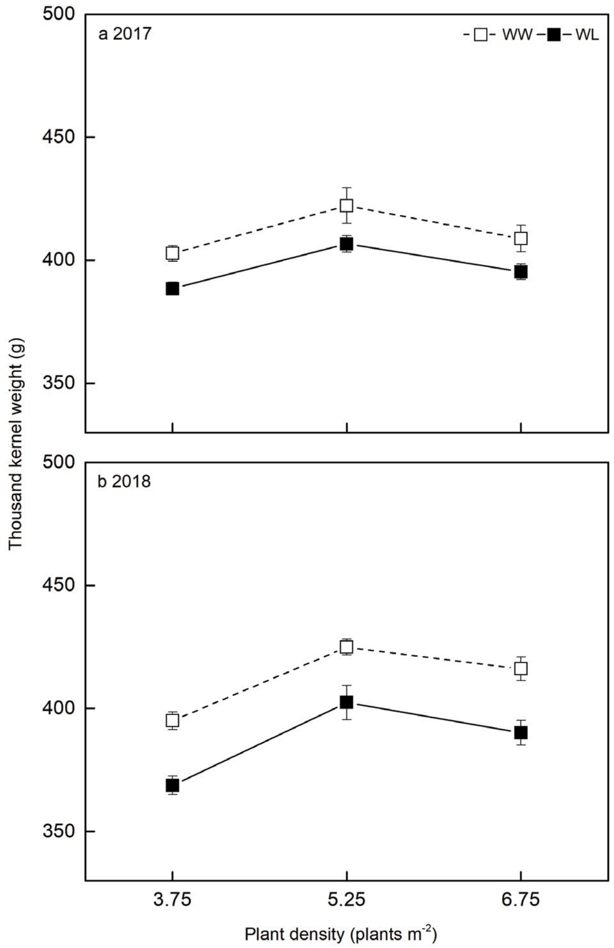

Fig. 1. Effects of water treatments (WW and WL) on the thousand kernel weight of waxy maize cultivar planted at three densities in 2017 and 2018.

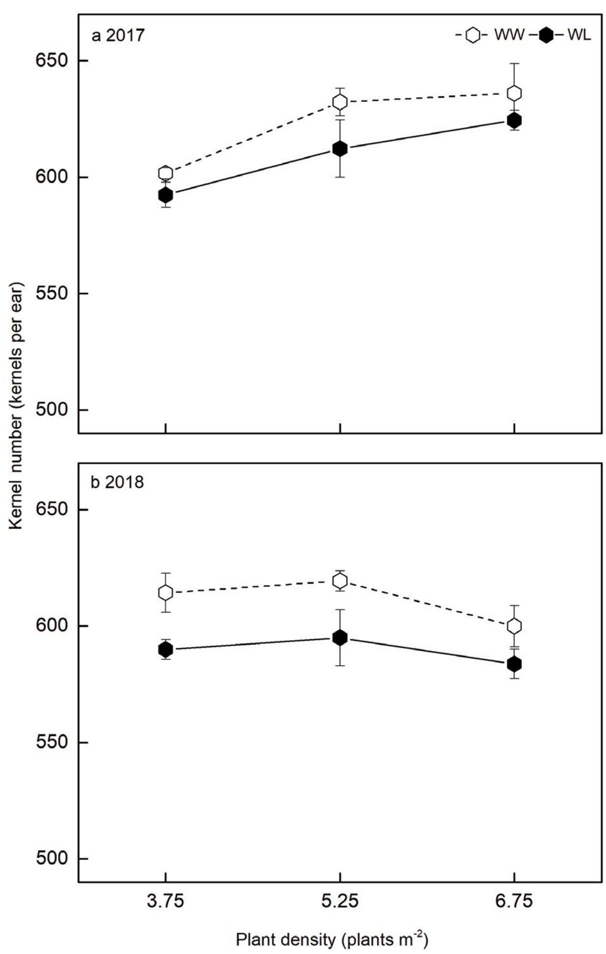

Fig. 2. Effects of water treatments (WW and WL) on the kernels per ear of waxy maize cultivar planted at three densities in 2017 and 2018.

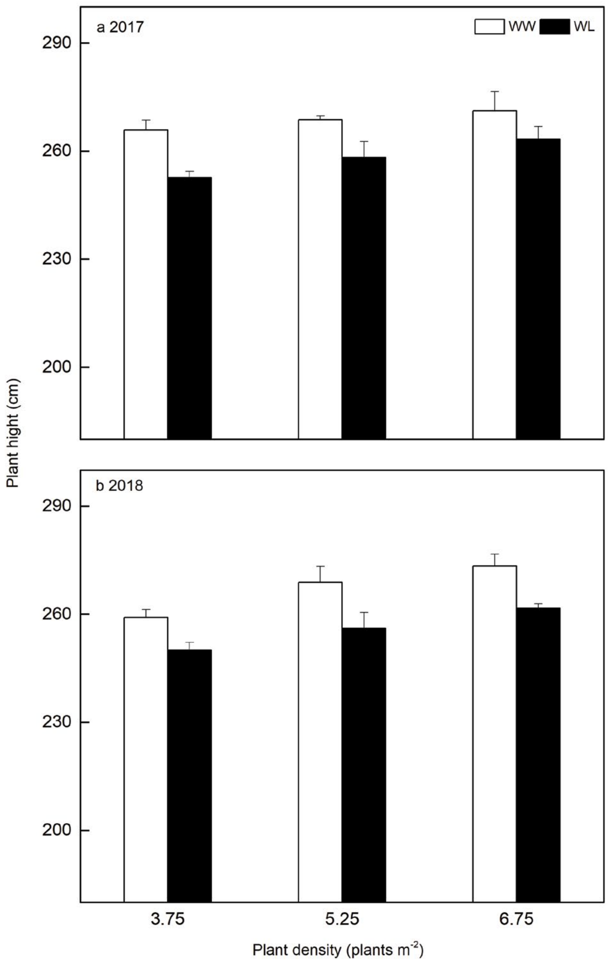

Fig. 3. Effects of plant density, and water treatments (WW and WL) on waxy maize plant height in 2017 and 2018.

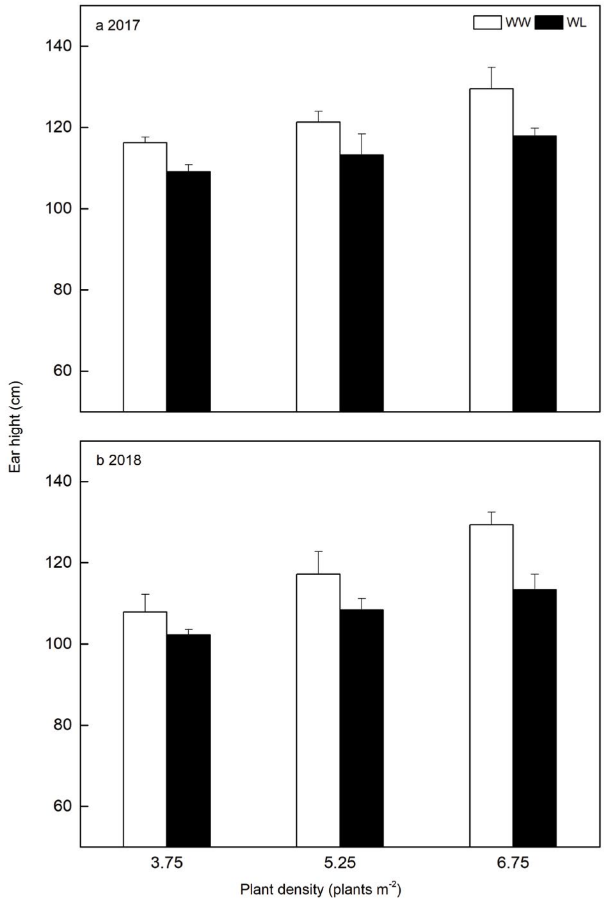

Fig. 4. Effects of plant density, and water treatments (WW and WL) on waxy maize ear height in 2017 and 2018.

Across all plant densities, the highest ear length distribution percentage (77.24%) was greater than or equal to 20 cm, which more than other grade ears (Fig. 5). However, the effect of WW treatment in superfine grade ears (5.24%, ear length distribution percentage concentrated in ear length ≥ 20 cm) lower than the first-grade ears (18.65%, for the ear length, ranging from 18 to 20 cm), and secondary (33.68%, for the ear length, ranged from 16 to 18 cm).

4. Discussion

Globally, maize is an economically important crop that is highly susceptible to WL stress [26,35]. The frequency of WL stress events increased in large parts of NCP because of the uneven distribution of rainfall and limited irrigation water resources [4,36–40]. Has reported that only one-week drought can impair maize growth (Lehoczky et al., 2009). In waxy maize of this study, as a result of extended WL stress lasted more than 9 d at the jointing stage, fresh ear yield, fresh grain yield and various other yield components decreased obviously. Compared with the WW treatment, WL treatment significantly decreased the fresh ear yield by 4.95% across the 2 y due to decreasing ear length in waxy maize. In contrast, fresh grain yield significantly reduced by 3.75% due to decreasing kernel weight and numbers per ear by WL stress. For the past few decades, in addition to the improvement of new varieties, the yield of maize is increased due to the usage of innovative cultivation techniques (e.g. reasonable irrigation time, suitable for plant density) in the field [9,10,12–13]. A study reported that suitable irrigation aims at matching water requirements for sensitive phenological stages of crops with limited water supply to avoid the occurrence of years with low yields and stabilizes yields at a level greater than under rainfed conditions [38,46]. In our experiments, the highest fresh ear yield (15.54-ton ha^{-1}) was obtained by WW treatment at an optimal PD of 6.75 plants m^{-2} over 2 y, which is probably bringing about the high commercial value of single ear for waxy maize. Further, averaged fresh grain yield were significant interactions between PD and year ($P < 0.05$) (Table 4), the best performing for the optimal PD increased by 3.17% in 2017 and 1.89% in 2018 resulted from WW treatment. The present results indicated that the yield of the waxy maize was possibly optimized through the application of WW treatment under field conditions.

The plant height of hybrid maize was slightly increased and the ear height was decreased based on an elevation in

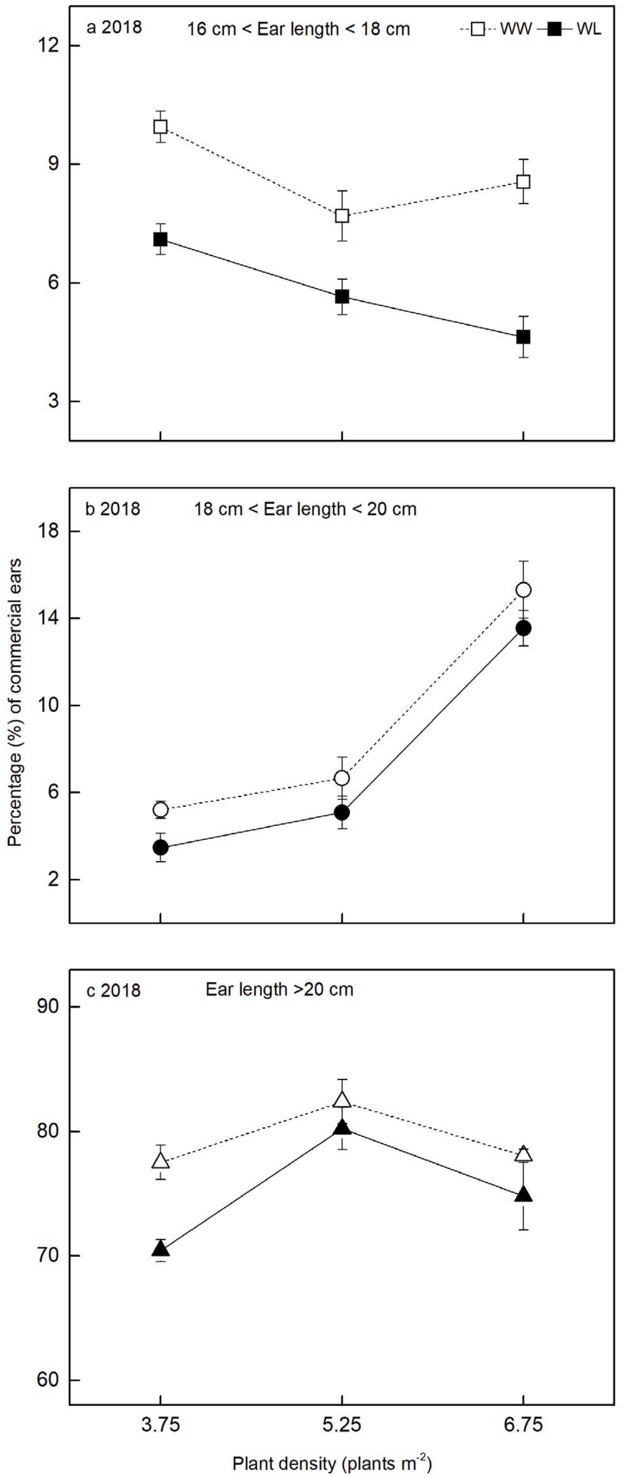

Fig. 5. Waxy maize ear length distribution percentage (%) affected by plant density, and water treatments (WW and WL) in 2018.

yield and PD [39,49]. In this experiment, WL stress decreased plant and ear height by 4.07%, and 7.97% with statistical significance. This result possibly resulted from more undesirable pollination for kernels per ear decreased because of less radiation [13,40]. In various ecological regions around the world, PD exerts an essential in maize yields [10,19,13]. The higher density of plant population leads to increased crop transpiration and decreased evaporation of soil water while optimized PD varies among the environment and receives the influence of genotype and managing measure [41–43]. Across the 2 y, WW treatment increased the fresh ear and grain yield in this study, however, WW treatment did no changed the optimal density for grain yield (5.25 plants m^{-2}) and fresh ear (6.75 plants m^{-2}), and optimized PD values were different according to discoveries in maize previously (Hernández et al., 2014; Lindsey et al., 2015). The reason largely because the degree of WL stress at the jointing stage is relatively low. Another reason is that there was only one cultivar and less environment. Accordingly, the increased frequency and severity of WL stress and more waxy maize varieties need to be more comprehensively assessed in field experiments. The findings in this study are possibly helpful to farmers in the optimization of yielding potential and PD of waxy maize under field conditions.

The ear length was negatively correlated with the number of rows ear^{-1} for the Mead and North Platte irrigated environments [31]. In the present study, ear length distribution percentage has been shown to be affected by water treatment, and PD (Table 4). Over the first three grades, across all plant densities WW treatment significantly increased the ear length distribution percentage by 19.19%. Further, its effect by 5.24% in superfine grade ears, and other grade ears more than this. Also, the optimal effect of WW in superfine grade ears increased 9.13% at 3.75 plants m^{-2}, however, its effect decreased from 5.25 to 6.75 plants m^{-2}. Nonetheless, longer ear length and its higher distribution percentage contributed to selling at a good price in a single ear for waxy maize. Thus, farmers will benefit from the high price of the single ear, result from the prospect of waxy maize industry broader and more predictable.

We concluded that WL stress lasted more than 9 d at the jointing stage in waxy maize decreased fresh ear yield, fresh grain yield by decreasing kernel weight and numbers per ear. However, the optimized PD showed no difference with fresh ear yield and fresh grain yield under field conditions. Applying WW treatment significantly increased the ear length distribution percentage, have compensatory effects offset WL stress in the field. The findings in the current study are possibly helpful to farmers in the optimization of plant yield and density associated with an extended commercial value of fresh ear yield and also help agronomists in the improvement of yielding potential under variations of climate in the future.

5. Conclusions

In general, fresh waxy maize ear yield, and grain yield were affected for all treatments after WL stress lasted more than 9 d at the jointing stage. Compared with the WW treatment, WL treatment significantly decreased the fresh ear yield by 4.95%, and fresh grain yield significantly reduced by 3.75%. WW treatment significantly increased the ear length distribution percentage by 19.19%, offset WL stress in the field, which effectively expands the commercial value of fresh ears of waxy maize.

Acknowledgements

This study was jointly supported by the Shanghai Agriculture Applied Technology Development Program of China under Grant No. G20180103, Henan Institute of Science and Technology Doctoral Research Initiation Funds under Grant No. 201010612003, and the National Natural Science Foundation of China under Grant No. 51709143.

Authors' contributions

Weiqiang Zhang and Zhichao Pei designed the study. Lina Xu and Zhichao Pei conducted fieldwork. Weiqiang Zhang and Lina Xu contributed to phenotyping and data analyses. Hongjian Zheng, Hui Wang, Pingdong Sun, Jihui Weiand Yuan Guan coordinated the study. Weiqiang Zhang and Lifeng Wu wrote the article. The final manuscript was read and approved by all authors.

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