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Full Length Article

Gas Exchange Traits, Growth and Yield Attributes in Winter Wheat under Waterlogging Stress during Anthesis

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Abstract

Waterlogging has received considerable attention because of its negative effect on the production of winter wheat. In order to improve waterlogging tolerance, two-year field experiment was conducted to study the responses of winter wheat to waterlogging stress during the anthesis phase. Wheat plants were grown in lysimeters and exposed to five treatments, including no waterlogging stress (control), maintaining the groundwater depth at 200 mm and 400 mm each below ground level for 3 and 5 days during the anthesis phase. The results showed that the photosynthesis rate decreased by 3.8–13.4% after five days of waterlogging stress compared to the control. The photosynthesis rate gradually increased after waterlogging stress ceased, the growth traits including plant height, root and shoot mass including root/shoot ratio were significantly reduced for the groundwater depth of 200 mm for 5 days compared to the control ($P \leq 0.05$). Grain yield decreased by 3.8 and 6.0% for the groundwater depth of 400 mm for 3 and 5 days treatments, respectively. While waterlogging of groundwater depth of 200 mm and 400 mm for 3 days treatments also reduced grain yield by 10.2 and 13.1%, respectively. The reduction in number of panicles and spikelets was the cause for the decline in final grain yield and yield had a significant negative correlation with waterlogging stress. The findings of this study also showed that in terms of alleviating the negative effect of waterlogging, the treatment groundwater depth of 400 mm for 3 days should be adopted as a water management strategy to a maintain a high grain yield for winter wheat. © 2020 Friends Science Publishers

Keywords: Groundwater; Waterlogging duration; Biomass; Photosynthesis; *Triticum aestivum* L.; Anthesis stage

Introduction

Waterlogging is an abiotic stress and characterized by the saturation of root zone soil by water, ultimately resulting in anoxia or oxygen deprivation (Sairam *et al.* 2009; Xu *et al.* 2016). It has increasingly become one of the major constraints to crop growth and production, resulting in severe economic losses (Shabala 2011; Zeng *et al.* 2013). Waterlogging is often encountered over vast regions of the world due to excessive rainfall, lack of soil drainage, and irregular topography (Xu *et al.* 2014, 2016). It has been estimated that nearly 10% of global irrigated land has suffered from waterlogging, causing a yield loss between 40 and 80% for grains (Zeng *et al.* 2013; Zheng *et al.* 2017). Therefore, it is necessary to identify suitable agricultural management strategies to alleviate the negative impact of waterlogging on crop growth, yield and ultimately total production.

The exploration of crop tolerance towards waterlogging stress is a potential strategy, especially where the current agricultural drainage infrastructure is poor, particularly in rural areas (Setter and Waters 2003; Shao *et al.* 2013). The tolerance of crops towards waterlogging stress is related to the crop genotype and the growth stage when waterlogging occurs, the duration of waterlogging, and the depth of the groundwater (Xu *et al.* 2015; Pampana *et al.* 2016; Ghobadi *et al.* 2017). As one of the most widely cultivated crops, winter wheat (*Triticum aestivum* L.) is highly sensitive to waterlogging during the reproductive phase, especially during booting, heading, flowering and filling stages (de San Celedonio *et al.* 2014; Marti *et al.* 2015; de San Celedonio *et al.* 2017). However, studies about the duration of waterlogging stress for winter wheat have shown different results in terms of the impact on grain yield. Some studies have shown that short-term waterlogging, even for one or two days, can reduce grain yield (Melhuish *et al.* 1991; Malik *et al.* 2002), while Meyer and Barrs (1988) reported no adverse effects on yield after four days of waterlogging. In areas of shallow groundwater tables, the impact of waterlogging can be severe due to oxygen deprivation in the root zone (Malik *et al.* 2001). Multiple studies have identified the trend of winter wheat growth and grain yield under waterlogging stress by examining different duration or groundwater depth throughout the whole growth period (de San Celedonio *et al.* 2014; Pampana *et al.* 2016; Ghobadi *et al.* 2017). However, few studies have examined the individual and interactive effects of duration and groundwater depth of waterlogging during one growth stage, particularly during anthesis.

When plants are exposed to waterlogged conditions, the stomatal resistance of leaves increases, which affects several physiological and biochemical processes (Malik *et al.* 2001; Shao *et al.* 2013). Some researchers have reported that waterlogging decreased the stomatal conductance, resulting in a reduction in the transpiration and photosynthetic rates of winter wheat (Zhang *et al.* 2008; de San Celedonio *et al.* 2014). However, waterlogged plants generally have shown a potential to recover from waterlogging stress (Pang *et al.* 2004; de San Celedonio *et al.* 2017). The dynamics of these physiological traits during the waterlogging and subsequent recovery period have rarely been studied. It is, therefore, essential to understand the mechanisms of winter wheat waterlogging tolerance during anthesis in order to maintain crop production.

The present study therefore explored appropriate water management strategies to improve the waterlogging tolerance of winter wheat during the anthesis phase. The objectives of this study were to evaluate the impacts of waterlogging stress during the anthesis phase on the growth and physiological traits of winter wheat and establish their quantitative relationship under waterlogging stress.

Materials and Methods

Experimental details

The experiments were carried out in concrete lysimeters at the water saving park at Hohai University in Nanjing, P.R. China (31°57′ N, 118°50′ E, 144 m a.s.l) in 2008–2009 (2009 season) and 2009–2010 (2010 season) growing season of winter wheat. The long-term annual precipitation in the area is 1,051 mm, and pan evaporation is 900 mm, based on the climate data from 1951 to 2009. The rainfall, relative humidity and average temperature during the winter wheat growing period, as measured by an automated weather station, are presented in Fig. 1. There were 15 lysimeter test-pits with 2.5 m lengths, 2.0 m widths, and 2.0 m depths with planting areas of approximately 5 m^2. The lysimeters were built of concrete and sealed with waterproof material, and a mobile rainout shelter was installed on the ground. The lysimeters contained loamy clay soil, with a mean dry density of 1.46 g cm^{-3} and 1.45 g cm^{-3}, field water capacity of 26.47 and 27.31%, and soil organic matter of 2.41 and 2.32% for 0–30 cm soil layer in 2009 and 2010 seasons, respectively. The groundwater level of the lysimeters was adjusted by using a float valve that controlled the solenoid valve for each treatment. An irrigation system was equipped to supply irrigation for each lysimeter through pipelines, and the water amount was recorded using a flow gauge.

Winter wheat (*Triticum aestivum* L. 'Yangmai 14') was hand sown evenly with a 240 seeds/m^2 seeding rate on November 12, 2008 and November 20, 2009. Ten days prior to sowing, a compound fertilizer ($N:P_2O_5:K_2O$ = 15:10:15) was broadcasted uniformly to all lysimeters as basal fertilizer at a rate of 400 kg·ha^{-1}. The winter wheat crops were irrigated when the soil water content of each treatment reached 50% of field capacity.

Experimental design

The experiments were arranged in a complete randomized block design with three replicates. Wheat plants not exposed to waterlogging stress were considered as the control, waterlogged stress was developed by keep groundwater depth to 600 mm below ground during the tillering phase; at 800 mm below ground during the jointing–booting phase; and at 1,000 mm below ground during the heading, anthesis, and milky phase. Plants during the anthesis phase were subjected to waterlogging stress with the groundwater depth of 200 and 400 mm below ground level each for 3 days, respectively. Other treatments were exposed to 5 days of waterlogging stress with the groundwater depth of 200 and 400 mm below ground level respectively. All waterlogging treatments were imposed on April 23, 2009 and April 29, 2010. Within two days after the end of each treatment, the groundwater level was adjusted to match the control treatment.

Observations and measurement

Plant height and leaf area of ten randomly tagged plants in each lysimeter were monitored every ten days. The leaf area was measured with Li-3100C (Li-Cor, Lincoln, NE, USA). The rate of photosynthesis (P_N), stomatal conductance (g_s) and transpiration (E) of the second or third fully expanded leaf of each individual plant were measured one day prior to waterlogging, one day before beginning drainage, three and ten days after waterlogging withdrawal, using a Li-6400XT (Li-Cor, Lincoln, NE, USA) during full sun/daylight between 9:00 to 11:00 a.m.

One day before harvest, ten randomly selected plants from each lysimeter were excavated using a flat shovel. The plants were separated into four parts (root, stem, leaf and spike) and oven dried at 70°C to a constant weight for the measurement of dry biomass. The root/shoot ratio was calculated as total root dry biomass divided by above ground dry biomass, which included the dry biomass of stem, leaf and spike.

At the end of growing seasons, wheat crop in each lysimeter were harvested manually to determine yield and yield components. The number of spikes and grains per spike were counted, and the fulfilled grains ratio was calculated as the number of fulfilled grains divided by all grains which included hollow and shrunken grains. The grains of wheat were air dried for one week prior to grain yield and the thousand kernel weight was adjusted to 13% moisture content.

Analysis of waterlogging stress sensitivity

The plants that were waterlogged when the groundwater depth is less than 500 mm below the soil surface. The sum of excess water that accumulates each day in the primary root zone of the top 500 mm soil layer (SEW) was calculated with the following equation:

$$SEW = \sum_{i=1}^{m}(500 - h_i) \qquad (1)$$

where *SEW* is the sum of excess water (mm); h_i is the groundwater depth of the *ith* day (mm); *i* is the waterlogging day; *m* is the total number of days of waterlogging stress.

The min–max normalization method was employed for dimensionless elements to eliminate interannual variability in crop growth. The calculation formula for the normalized value of a member of the set of observed values of $X\{x_1,x_2,\ldots,x_n\}$ as given:

$$z_j = \frac{x_j - min\{X\}}{max\{X\} - min\{X\}} \qquad (2)$$

where z_j and x_j are the *j*th normalized and original values in $\{X\}$, respectively, and min $\{X\}$ and max $\{X\}$ are the minimum and maximum values of *X* given its range, respectively.

Statistical analysis

ANOVA was conducted to determine the effect of waterlogging on winter wheat. Differences between means were distinguished through the least significant difference (LSD) test at the 0.05 confidence level. The quantitative relationships for crop growth, physiological traits, and grain yield with waterlogging stress were calculated through linear regression. Relative values that are standardized for each season were used to eliminate the influence of climate during different growing seasons.

Results

Physiological parameters

Waterlogging stress drastically reduced the photosynthesis rate of winter wheat in both seasons (Fig. 2). The photosynthesis rate of groundwater depth of 200 mm and 400 mm for 3 days treatments decreased by 11 and 5% in 2009 and by 13 and 11% in 2010, respectively, after three days of waterlogging, compared to the control treatment. For both seasons, the largest reduction of P_N was measured for groundwater depth of 200 mm for 5 days, whereas the smallest reduction was obtained for groundwater depth of 400 mm for 3 days treatment. The P_N of all waterlogging treatments gradually increased with the relief of the waterlogging stress. Seven days after the waterlogging was ended, the P_N for groundwater depth of 400 mm for 3 days treatment reached 19.37 μmol m^{-2} s^{-1} in 2009, and 20.71 μmol m^{-2} s^{-1} in 2010, decreasing by 5% in 2009 and 4% in 2010 compared to the control.

The transpiration rate (*E*) for winter wheat sharply decreased with waterlogging stress three and five days after the beginning of waterlogging, but no observable change of the *E* was realized for the control (Fig. 3). Compared to the control, the *E* decreased by 24 and 11% for groundwater depth of 200 mm and 400 mm for 5 days treatments in 2009 and by 43 and 24% in 2010, respectively. From the end of waterlogging, the *E* started to increase gradually, and was higher for groundwater depth of 200 mm for 3 days, groundwater depth of 400 mm for 3 days and groundwater depth of 400 mm for 5 days treatments than the control after seven days of recovery for the 2009 season.

The fluctuation of stomatal conductance (*gs*) during the waterlogging period was similar to P_N and *E* (Fig. 4). The *gs* decreased with the waterlogging stress and increased after termination of stress. When waterlogging stress was imposed for five days, the *gs* for groundwater depth of 200 mm for 5 days treatment was greatly affected with a 44 and 40% reduction for the 2009 and 2010 seasons, respectively, when compared to the control. The increase in the duration of waterlogging stress was directly proportional to the decrease of *gs*. The *gs* for groundwater depth of 200 mm and 400 mm for 5 days treatments were similar and lower than groundwater depth of 200 mm and 400 mm for 3 days treatments when waterlogging ended. After seven days of recovery, the *gs* for groundwater depth of 400 mm for 3 days treatment gradually increased from 0.23 to 0.35 mmol m^{-2} s^{-1} in 2009 and from 0.23 to 0.40 mmol m^{-2} s^{-1} in 2010.

Growth traits

The waterlogging stress duration, groundwater depth and their interactions had no significant effect on the plant height in either season ($P \leq 0.05$, Table 1). The highest plant height was obtained for the control treatment, whereas the lowest plant height was noted for groundwater depth of 200 mm for 5 days treatment. The leaf area index, root biomass and root/shoot ratio were significantly influenced by groundwater depth for both seasons ($P \leq 0.05$). Compare to the control, waterlogging increased leaf area index by 22.0 and 34.5% for groundwater depth of 200 mm and 400 mm for 3 days in 2009 and by 18.5 and 27.8% in 2010, respectively. The largest root biomass was recorded for the control for both seasons, whereas the smallest root biomass was observed for groundwater depth of 200 mm for 5 days treatment in 2009 and for groundwater depth of 200 mm for 3 days treatment in 2010. For both seasons, the largest root/shoot ratio value was obtained under the control treatment. The shoot biomass and

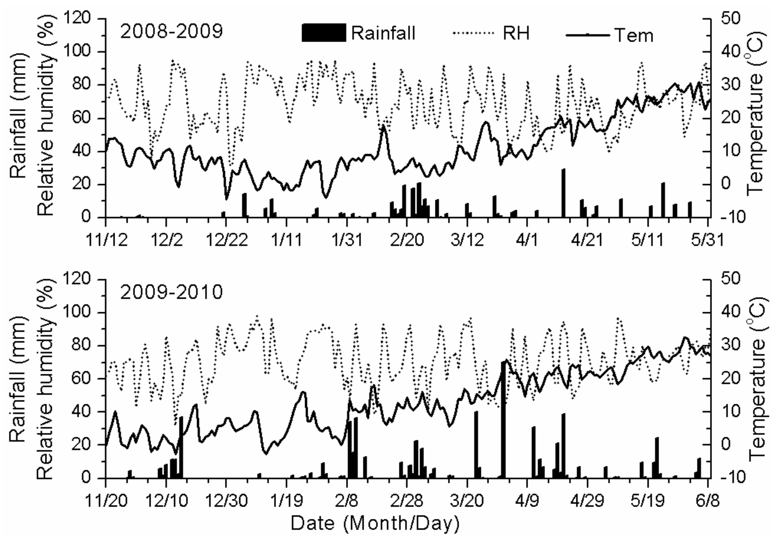

Fig. 1: Average daily air temperature, relative humidity and rainfall during the 2009 and 2010 seasons

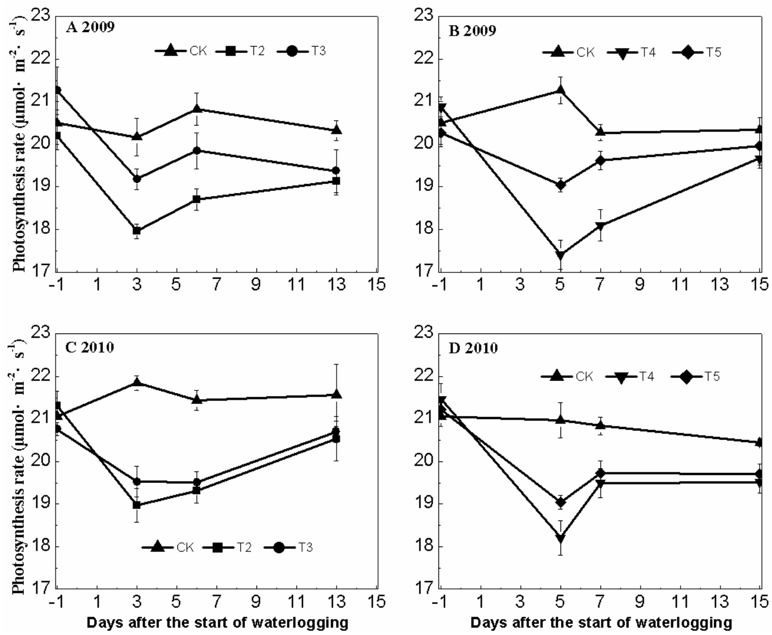

Fig. 2: Changes in the photosynthesis rate for the different waterlogging treatments during the anthesis phase for the 2009 and 2010 season. CK denotes no waterlogging; T2 and T3 denote maintaining the groundwater depth at 200 mm and 400 mm below soil surface for three days; T4 and T5 denote maintaining the groundwater depth at 200 mm and 400 mm below the soil surface for five days

total dry biomass were not significantly affected by waterlogging duration, groundwater depth and their interactions for the 2009 season ($P \leq 0.05$).

Grain yield and yield components

The waterlogging duration had no significant effect on the grain yield in either season, while the grain yield decreased with groundwater depth ($P \leq 0.05$, Table 2). For both seasons, the highest grain yield was recorded in the control treatment, followed by the groundwater depth of 400 mm for 3 days and 5 days treatments, and the lowest yield was obtained for groundwater depth of 200 mm for 5 days treatment. The spike number significantly decreased with the duration of waterlogging and groundwater depth in 2010 ($P \leq 0.05$), while the interaction between the duration and groundwater depth was significant only in 2009 ($P \leq 0.05$). The highest and lowest number of spikes was obtained for the control and groundwater depth of 200 mm for 3 days treatments in 2009, respectively, and groundwater depth of 400 mm for 3 days and 200 mm for 5 days treatments in 2010. The number of spikelets decreased significantly by

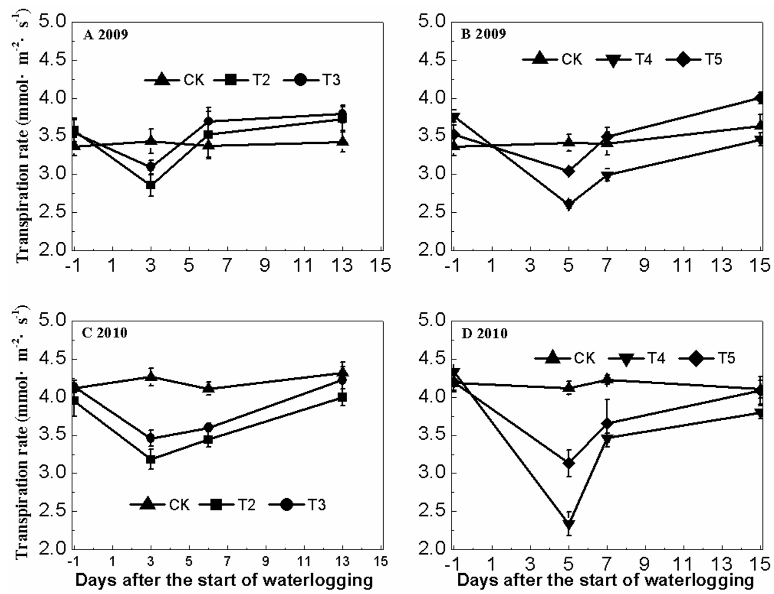

Fig. 3: Changes in the transpiration rate for the different waterlogging treatments during anthesis phase for the 2009 and 2010 season. CK denotes no waterlogging; T2 and T3 denote maintaining the groundwater depth at 200 mm and 400 mm below soil surface for three days; T4 and T5 denote maintaining the groundwater depth at 200 mm and 400 mm below the soil surface for five days

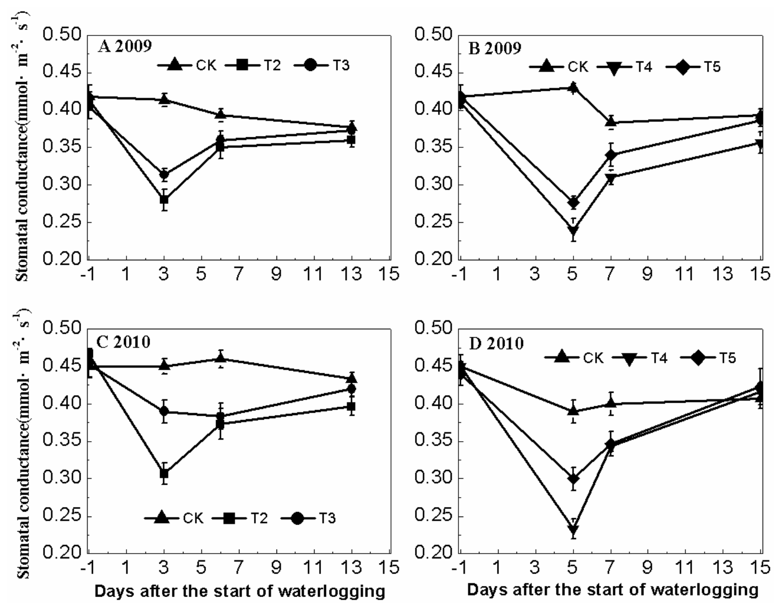

Fig. 4: Changes in the stomatal conductance for the different waterlogging treatments during anthesis phase for the 2009 and 2010 season. CK denotes no waterlogging; T2 and T3 denote maintaining the groundwater depth at 200 mm and 400 mm below soil surface for three days; T4 and T5 denote maintaining the groundwater depth at 200 mm and 400 mm below the soil surface for five days

groundwater depth for the 2010 season ($P \leq 0.05$). Compared to the control, the number of spikelets decreased by 5 and 7% for groundwater depth of 200 mm for 3 days and for 5 days in 2010, respectively. The thousand kernel weight and filled grains of winter wheat decreased with waterlogging duration, groundwater depth and their interactions, but the differences were not significant for the 2010 season ($P \leq 0.05$).

Relationship between wheat physiological parameters, growth traits, yield and waterlogging stress

The correlation analysis showed that P_N, *E* and *gs* were significantly correlated with waterlogging stress ($P \leq 0.01$; Table 3). The relationships were well fitted using a linear regression with regression coefficients of -0.92, -0.90 and -0.92, respectively. Plant height showed a significant

Table 1: Plant height, leaf area index (LAI), root biomass (RM), shoot biomass (SM), total dry biomass (TDM) and root/shoot ratio (RSR) of winter wheat at final harvest as affected by waterlogging stress during the 2009 and 2010 growing seasons

Season	Treatment	Height (cm)	LAI (cm^2 cm^{-2})	RM (g per plant)	SM (g per plant)	TDM (g per plant)	RSR ($g \cdot g^{-1}$)
2009	No waterlogging stress	82.70 ± 1.72 a	3.13 ± 0.16 c	0.49 ± 0.03 a	6.17 ± 0.08 a	6.65 ± 0.09 a	0.079 ± 0.005 a
	Groundwater depth of 200 mm for 3 days	74.43 ± 2.49 a	3.82 ± 0.10 ab	0.34 ± 0.02 bc	5.55 ± 0.20 b	5.89 ± 0.22 b	0.061 ± 0.003 cd
	Groundwater depth of 400 mm for 3 days	75.54 ± 1.65 a	3.63 ± 0.18 b	0.42 ± 0.03 ab	5.76 ± 0.24 ab	6.18 ± 0.28 ab	0.073 ± 0.003 ab
	Groundwater depth of 200 mm for 5 days	73.90 ± 1.42 a	4.21 ± 0.12 a	0.30 ± 0.02 c	5.64 ± 0.15 b	5.94 ± 0.15 b	0.053 ± 0.004 d
	Groundwater depth of 400 mm for 5 days	78.11 ± 0.90 a	3.39 ± 0.24 bc	0.39 ± 0.02 b	5.87 ± 0.07 ab	6.26 ± 0.08 ab	0.066 ± 0.003 bc
Depth		ns	*	*	ns	ns	**
Duration		ns	ns	ns	ns	ns	ns
Interaction		ns	ns	ns	ns	ns	ns
2010	No waterlogging stress	81.17 ± 2.28 a	3.35 ± 0.24 c	0.47 ± 0.03 a	6.27 ± 0.19 a	6.75 ± 0.18 a	0.076 ± 0.006 a
	Groundwater depth of 200 mm for 3 days	74.99 ± 2.68 ab	3.97 ± 0.09 ab	0.30 ± 0.02 c	5.79 ± 0.13 a	6.08 ± 0.12 bc	0.052 ± 0.005 b
	Groundwater depth of 400 mm for 3 days	75.81 ± 1.08 ab	3.65 ± 0.14 bc	0.41 ± 0.03 a	5.86 ± 0.15 a	6.27 ± 0.18 ab	0.069 ± 0.004 a
	Groundwater depth of 200 mm for 5 days	72.76 ± 2.34 b	4.28 ± 0.11 a	0.32 ± 0.03 bc	5.27 ± 0.18 b	5.59 ± 0.16 c	0.061 ± 0.007 ab
	Groundwater depth of 400 mm for 5 days	75.94 ± 1.98 ab	3.86 ± 0.16 ab	0.40 ± 0.01 ab	5.83 ± 0.13 a	6.23 ± 0.13 b	0.068 ± 0.003 a
Depth		ns	*	**	ns	*	*
Duration		ns	ns	ns	ns	ns	ns
Interaction		ns	ns	ns	ns	ns	ns

Note: In the same column and in the same year, values followed by different letters are significantly different among treatment at the 0.05 level by LSD. ns, non-significant at 0.05 level, *, **, and *** significant at 0.05, 0.01 and 0.001 levels, respectively. Each value is the mean of three replications

Table 2: Grain yield and components of winter wheat for different waterlogging stress in 2009 and 2010 season

Season	Treatment	Spikes (# of ears m^{-2})	Spikelets (# of grains per ear)	Thousand kernel weight (g)	Filled grains (%)	Grain yield ($kg \cdot ha^{-1}$)
2009	No waterlogging stress	508.0 ± 2.7 a	32.0 ± 0.1 a	40.9 ± 0.3 a	91.7 ± 0.2 a	6093 ± 84 a
	Groundwater depth of 200 mm for 3 days	478.0 ± 2.1 c	31.0 ± 0.3 ab	39.9 ± 0.1 bc	91.0 ± 0.1 b	5378 ± 75 c
	Groundwater depth of 400 mm for 3 days	500.7 ± 2.7 ab	31.5 ± 0.2 ab	40.2 ± 0.2 ab	91.1 ± 0.3 ab	5785 ± 70 ab
	Groundwater depth of 200 mm for 5 days	483.0 ± 2.5 c	30.8 ± 0.2 b	39.2 ± 0.2 c	90.4 ± 0.2 b	5277 ± 94 c
	Groundwater depth of 400 mm for 5 days	493.3 ± 3.2 b	31.2 ± 0.5 ab	39.9 ± 0.2 b	90.9 ± 0.2 b	5590 ± 157 bc
Depth		***	ns	*	ns	**
Duration		ns	ns	ns	ns	ns
Interaction		*	ns	ns	ns	ns
2010	No waterlogging stress	431.0 ± 3.6 a	36.6 ± 0.2 a	41.7 ± 0.4 a	90.9 ± 0.1 a	5981 ± 144 a
	Groundwater depth of 200 mm for 3 days	419.3 ± 2.4 bc	34.9 ± 0.3 b	41.2 ± 0.2 a	90.5 ± 0.1 a	5462 ± 104 bc
	Groundwater depth of 400 mm for 3 days	432.3 ± 4.3 a	36.0 ± 0.2 a	41.3 ± 0.1 a	90.7 ± 0.2 a	5831 ± 115 a
	Groundwater depth of 200 mm for 5 days	410.7 ± 3.3 c	34.1 ± 0.2 c	41.1 ± 0.3 a	90.5 ± 0.1 a	5216 ± 104 c
	Groundwater depth of 400 mm for 5 days	426.3 ± 1.9 ab	35.9 ± 0.2 a	41.4 ± 0.1 a	90.9 ± 0.2 a	5753 ± 71 ab
Depth		**	***	ns	ns	**
Duration		*	ns	ns	ns	ns
Interaction		ns	ns	ns	ns	ns

Note: In the same column and in the same year, values followed by different letters are significantly different among treatment at the 0.05 level by LSD. ns, non-significant at 0.05 level, *, **, and *** significant at 0.05, 0.01 and 0.001 levels, respectively. Each value is the mean of three replications

negative linear correlation with waterlogging stress ($P \leq 0.01$). The relationship of leaf area index with waterlogging stress was best fitted with a positive linear correlation with the slope value and determination coefficient (R^2) of 0.93 and 0.90, respectively ($P \leq 0.01$). The root biomass and biomass, total dry biomass and root/shoot ratio of winter wheat had a significant negative correlation with waterlogging stress ($P \leq 0.01$). The relationship between grain yield and waterlogging stress was well fitted using a linear regression with the regression coefficients of -0.99. Negative correlations were also found for the grain yield components, including number of panicles, number of spikelets, thousand kernel weight and the number of filled grains, with waterlogging stress ($P \leq 0.01$).

Discussion

Waterlogging stress is a limiting factor for winter wheat production (Saqib *et al.* 2004; Herzog *et al.* 2016; Li *et al.* 2016). It has been widely reported that waterlogging that occurs during the reproductive phase has more adverse effects on the growth and yield of winter wheat than during any other phase (Setter *et al.* 2009; de San Celedonio *et al.* 2014; Wu *et al.* 2015). However, the extent of the reduction in yield depends not only on the growth stage during which waterlogging occurs, but also on the severity of the waterlogging stress, especially the duration of waterlogging and groundwater depth (Herzog *et al.* 2016; de San Celedonio *et al.* 2017; Wu *et al.* 2018). This is also evident from this study, whereby the growth index and grain yield were significantly reduced for the groundwater depth of 200 mm for 3 and 5 days treatments when waterlogging stress occurred during the anthesis phase ($P \leq 0.05$).

When waterlogging occurs, oxygen will rapidly deplete surrounding the roots, resulting in the reduction of root hydraulic conductivity and an increase in stomatal resistance (Shao *et al.* 2013; Wang *et al.* 2016).

Generally, the restriction in leaf photosynthetic performance has been attributed to stomatal closure and the reduction of chlorophyll content in leaves (Bradford 1983; Yordanova *et al.* 2005). In this study, the reduction in stomatal conductance, the rate of photosynthesis and transpiration were measured during waterlogging stress period had been reported by Yordanova *et al.* (2005). It also has been reported that waterlogging stress could cause senescence and leaf yellowing, which reflects the reduction in photosynthetic activity (Shao *et al.* 2013; Wu *et al.* 2015).

Several studies have shown that it is difficult for plants to recover from stress when waterlogging occurs during the later growth phases (de San Celedonio *et al.* 2014; Wu *et al.* 2018). However, in this study, there was no significant difference in photosynthesis and transpiration rates between waterlogging treatments and the control after seven days of recovery ($P \leq 0.05$). The reason might be related to the duration of waterlogging and the groundwater depth. The waterlogging period in some studies were more than one week (Malik *et al.* 2002; Hossain *et al.* 2011; de San Celedonio *et al.* 2017), which may be beyond the tolerance capacity of wheat plants. In addition, Wu *et al.* (2018) reported that the root system of winter wheat is mainly distributed in 0–20 cm soil layer, which indicated that plants suffered from serious stress when groundwater was in a shallow condition.

Generally, plants have different mechanisms to recover from slight waterlogging stress (Setter and Waters 2003; de San Celedonio *et al.* 2014). However, short periods of waterlogging, even as little as three days, have been found to have considerable long-term impact on the growth of winter wheat (Malik *et al.* 2002). In this study, the plant height and total dry biomass of winter wheat were reduced by waterlogging during the anthesis phase (Malik *et al.* 2002; Wu *et al.* 2015). The higher leaf area index at harvest were found for groundwater depth of 200 mm and 400 mm for 3 days treatments compared to the control, which might be due to slow growth rate after waterlogging (Shao *et al.* 2013). It also has been reported that waterlogging could injure root metabolism and delay the time of maturity (Wu *et al.* 2015). In this study, the root biomass was significantly decreased for groundwater depth of 200 mm for 3 days and 5 days treatments. In fact, the root was the first organ to be affected by waterlogging, resulting in the drastic reduction of root length and root biomass (Herzog *et al.* 2016). The abiotic stresses, such as waterlogging or drought, impede plant dry matter accumulation and force redistribution in different organs and affect the root to shoot ratio (Shao *et al.* 2013; Xu *et al.* 2015; Wu *et al.* 2018). Higher root to shoot ratios are more beneficial to plants to adapt to adverse conditions (Wu *et al.* 2018). In this study, the shoot biomass was decreased for groundwater depth of 200 mm for 3 days and for 5 days treatments, but no enhanced effect on the root to shoot ratio by waterlogging was observed, perhaps because roots were not completed excavated when were dug them manually with a root shove.

Table 3: Relationship between photosynthesis rate, transpiration rate, stomatal conductance, plant height, leaf area index, root biomass, shoot biomass, total dry biomass, root/shoot ratio, spikes, spikelets, thousand kernel weight, filled grains, grain yield and waterlogging stress

Dependent variable	Linear regression equation	R^2 value	*P* value
Photosynthesis rate	y=-0.92 x+0.84	0.85	<0.01
Transpiration rate	y=-0.90 x+0.88	0.91	<0.01
Stomatal conductance	y=-0.92 x+0.87	0.70	<0.01
Plant height	y=-0.83 x+0.73	0.64	<0.01
Leaf area index	y=0.93 x+0.08	0.90	<0.01
Root biomass	y=-0.93 x+0.86	0.82	<0.01
Shoot biomass	y=-0.82 x+0.81	0.67	<0.01
Total dry biomass	y=-0.88 x+0.82	0.75	<0.01
Root/shoot ratio	y=-0.85 x+0.89	0.70	<0.01
Spikes	y=-0.97 x+0.96	0.80	<0.01
Spikelets	y=-0.97 x+0.91	0.87	<0.01
Thousand kernel weight	y=-0.86 x+0.80	0.75	<0.01
Filled grains	y=-0.93 x+0.88	0.67	<0.01
Grain yield	y=-0.99 x+0.92	0.89	<0.01

Restricted plant growth might have a negative effect on final yield and yield quality (Hassan *et al.* 2007; Chen and Weil 2010). The results of present study suggest that grain yield of winter wheat was reduced for the groundwater depth of 200 mm for 3 days and 5 days, and that the shallower groundwater depth aggravated this reduction. The reduction of grain yield of winter wheat was mainly attributed to a decrease in the number of spikes and spikelets under waterlogging stress (Shao *et al.* 2013; Wu *et al.* 2015). In this study, both the thousand kernel weight and filled grains were not found to decrease with the degrees of waterlogging. This result may be attributed to the reduction in the spikes and spikelet under waterlogging stress, which in turn may increase the grains weight (Wu *et al.* 2018).

Information about the relationship between winter wheat grain yield and waterlogging stress is helpful for efficient agricultural management and crop production. In the present study, a negative linear relationship was found between yield and yield components with the value for SEW, have been reported (Shao *et al.* 2010). Linear relationships were also found between the growth traits and physiological activities with SEW. These findings indicated that the critical 500 mm depth of groundwater for SEW could be considered as a reasonable assessment of waterlogging. However, there was a reduction in yield at groundwater depths of 100–300 mm rather than 500 mm (Gales *et al.* 1984; Malik *et al.* 2002; Wu *et al.* 2018). Williamson and Kriz (1970) reported that wheat yield was reduced at groundwater depths between 500 and 1200 mm. Therefore, in order to obtain a better correlation between yield and SEW, further research is needed to evaluate the critical depth of groundwater for crops in a specific region according to the cultivar, soil type, local weather conditions and other factors.

In the present study, a satisfactory grain yield was obtained for winter wheat under waterlogging stress for the groundwater depth of 200 mm and 400 mm for 5 days treatments. These management strategies will provide farmers with a beneficial option for efficient agricultural water management in grain production, especially when water and labor force are inadequate and costly. This study was limited to the effect of waterlogging stress during anthesis on growth, physiological parameters and yield of winter wheat. In this study, the effect of waterlogging was not investigated during other growth phases or the compound growth phases. Therefore, further research is needed on the effect of waterlogging stress during various growth phases to determine potential tolerance for waterlogging.

Conclusion

Waterlogging stress during the anthesis affects the physiological activities and growth of winter wheat. The transpiration and photosynthesis rates decreased with waterlogging stress and increased gradually from the end of waterlogging. The physiological activities and growth traits had negative correlations with the sum of excess water, whereas LAI has a positive correlation with waterlogging stress. Grain yield decreased linearly with the sum of excess water, mainly due to the reduction of spikes and spikelets caused by waterlogging stress.

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