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Effect of Endogenous Plant Hormones on Grain Filling under Regulated Deficit Irrigation in Wheat

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Abstract: Under regulated deficit irrigation at different stages, the changes of endogenous hormones (ABA and ZR) in developing grain were studied to identify how hormonal levels regulated the effect of water deficit on grain filling in winter wheat. Six irrigation treatments (A, B, C, D, E, F) with water deficit imposed at different development stages were set up. When water deficit was imposed at both vegetative and reproductive stages (booting or flowering) (A, B, C treatments), grain-filling rate obviously decreased and grain-filling period was shortened. On the other hand, ABA content in developing grain was obviously higher and increased faster, whereas, ZR content and the ratio of ZR to ABA in grain were much lower and increased more slowly, compared with those under the treatments (D, E, F) of no water deficit imposed at reproductive stage. With all irrigation treatments, ZR in grain reached the peak at 7 days after flowering, then declined. Among those irrigation treatments without water deficit imposed at reproductive stage, there was no significant difference in grain yield and the irrigation treatment D with water deficit conducted at both regreening and jumping stages could be suggested as a most saving and high yield irrigation way in winter wheat.

Key words: Winter wheat, water deficit, abscisic acid, zeatin riboside, yield

INTRODUCTION

In recent years, water has become a major restriction to the grain production in wheat in north and northwest of China, however, irrigation water use efficiency in those area is only about 40% (Huang, 2001; Liu, 2003). It is known that the imposition of water deficit at certain developmental stage could benefit yield in crops and the water-saving irrigation technique was called Regulated Deficit Irrigation (RDI), which was firstly proposed by Chalmers *et al.* (1981). Experiments with RDI have been successful in many crops, such as soybean (Karam *et al.*, 2005), maize (Kang *et al.*, 2000; Kar and Verma, 2005) and also in wheat (Zhang *et al.*, 1998, 2006). It has been known that plant hormones, such as Indole-3-acetic Acid (IAA), Abscisic Acid (ABA), Zeatin Riboside (ZR) and Gibberellin (GA), were closely associated with grain development (Kende and Zeevaart, 1997; Wobus and Weber, 1999; Hansen and Grossmann, 2000; Yang *et al.*, 2001). This study was therefore carried out to further understand how the hormones (ABA and ZR) regulate the grain filling under different regulated deficit irrigation conditions in winter wheat.

MATERIALS AND METHODS

The experiment was conducted under the condition of mobile rain-proof shelter during 2003-2004 at the experiment station in Qingdao Agricultural University, China. Eighteen tanks were used and the tank size was 2 m width and 2 m depth. The soil in the tank was sandy loam with 13.1 g kg^{-1} organic matter and available N-P_2O_5-K_2O at 56.47, 28.6 and 86.8 mg kg^{-1}, respectively. Before planting, organic fertilizer (60000 kg ha^{-1}), N (175 kg ha^{-1} as urea), phosphorus (135 kg ha^{-1} as single superphosphate) and potassium (150 kg ha^{-1} as KCl) were applied and incorporated. Wheat was sown at 25 cm row spacing. Each treatment had three tanks as replications in a complete randomized block design. Irrigation treatments were conducted as shown in Table 1.

Sampling and hormones analysis: one hundred panicles that headed on the same day were chosen and tagged for each plot. And ten tagged panicles from each tank were sampled every 7 days after flowering. Fresh panicles were put into liquid nitrogen immediately after sampling and stored in -80°C freezer for later analysis. Hormones (ABA and ZR) were analyzed by an Enzyme-linked Immunosorbent Assay (ELISA). And ABA and ZR extraction was as reported by King (1976). Two gram fresh samples was macerated in cold methanol overnight at 4°C, after centrifuging at 3500 g (4°C) for 5 min, the residue was re-extracted for 4 h, internal ± cis-trans ABA was used during extraction to determine the recovery. The two-time methanol supernatant was combined together and centrifuged again and the deposit was discarded. The

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Table 1: Different irrigation treatments in this experiment

Treatments	Total irrigation amount (mm)	Irrigation stages and amount (mm)						
		Winter	Regreening	Upstanding	Jointing	Booting	Flowering	Filling
A	100	50			50			
B	150	50			50		50	
C	200	50			50	50		50
D	250	50			50	50	50	50
E	300	50		50	50	50	50	50
F	350	50	50	50	50	50	50	50

methanol was evaporated under vacuum and dissolved in 0.5 M phosphate buffer (pH 8.2) prior to partitioning (3x equal volume) against ethyl acetate. The aqueous fraction was then adjusted to 2.5 and partitioned against ethyl acetate (3x equal volume), the supernatant ethyl acetate was kept. After evaporating with rotate vapor, the flask was washed with 100% methanol and the final total volume was 5 mL, then ABA extracts was measured. The mouse monoclonal antigens and antibodies against ZR, ABA and immunoglobulin G-horseradish peroxidase (Ig G-HRP) used in ELISA were produced by the Phytohormones Research Institute (China Agricultural University). The method for quantification of ZR and ABA by ELISA was described previously (Yang *et al*., 2001).

Statistical analysis: Analysis of variance was done on grain set. Comparisons between treatments were performed using one way ANOVA and Duncan test with an SAS package (SAS, 2001).

RESULTS

Grain filling and grain yield: Irrigation treatment affected grain filling rate and there was significant differences between irrigation treatments (Fig. 1). Compared with D, E, F irrigation treatments with no water deficit imposed at reproductive stage, A, B, C treatments obviously decreased grain filling rate and shortened grain filling period (Fig. 1). For all treatments, the peak of grain filling rate occurred at the same time, 14 days after flowering.

Within a certain arrange, grain yield increased with increasing irrigation amount. Among all treatments, grain yield per tank was reduced seriously under the A, B treatments, being 1.17 and 1.75 kg, respectively and the grain yield was highest (3.07 kg) with D treatment and there was no significant difference in grain yield between D, E and F treatments (Table 2). The number of ears per tank, the grain number per ear and the thousand grain weight were all significantly decreased under both A and B irrigation treatments (Table 2).

Hormonal changes in the grains: After flowering, ABA content in grain increased under all irrigation treatments

Table 2: Effect of different irrigation treatments on grain set in wheat

Treatments	Ear No. per tank	Grains No. per ear	Thousand-grain weight (g)	Grain yield (kg tank^{-1})
A	1279^{e}	24^{d}	28.80^{e}	1.17^{d}
B	1702^{d}	28^{c}	35.85^{d}	1.75^{c}
C	2114^{c}	33^{b}	37.26^{c}	2.55^{b}
D	2207^{b}	34^{a}	40.60^{a}	3.07^{a}
E	2269^{ab}	34^{a}	38.73^{b}	2.99^{a}
F	2315^{a}	34^{a}	38.29^{b}	3.01^{a}

Means followed by the same letter(s) are not different ($p<0.05$, ANOVA Duncan test)

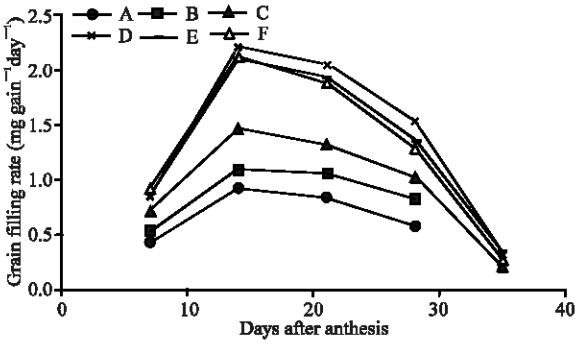

Fig. 1: Effect of irrigation treatments on grain filling rate in wheat. Values are means of three replicates

(Fig. 2), whereas ABA content in grain was much higher with irrigation treatments A and B and reached the maximum value (peak) at 21 days after flowering. There was no difference in the ABA content between other irrigation treatments and ABA reached the peak at 28 days after flowering.

ZR in grain increased at the beginning of grain filling stage and reached the highest value at 7 days after flowering (Fig. 2). After that ZR content kept stable for one more week and then decreased under D, E, F irrigation conditions. However, under A, B and C treatments, ZR content in grain started to decrease once reaching the peak.

During grain filling, the ratio of ZR to ABA in grain was decreasing (Fig. 3). However, under D, E, F irrigation conditions, the ratio of ZR to ABA was higher than one even at maturity stage. While under A, B and C irrigation conditions, the ratio of ZR to ABA was less than one after 21 days-post flowering.

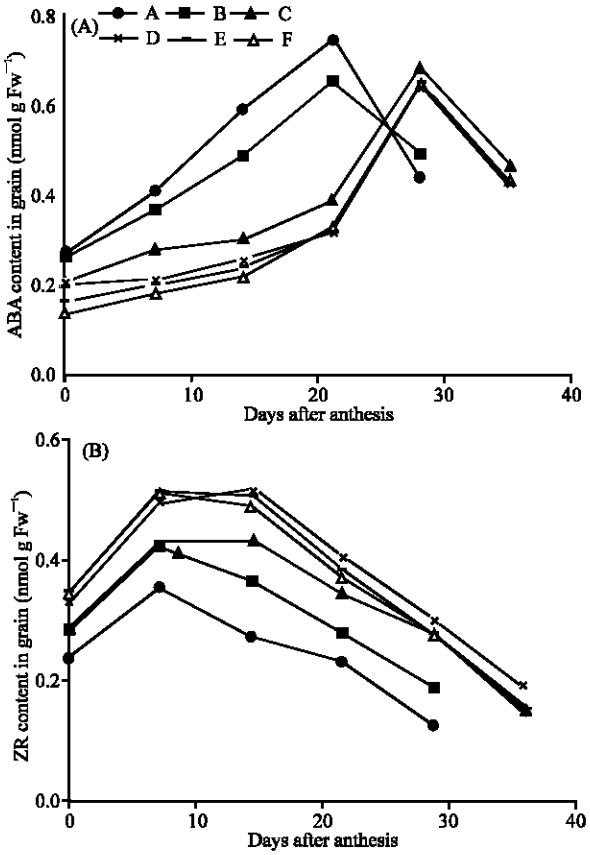

Fig. 2: Changes of ABA (A) and ZR content (B) in developing grains in wheat subjected to various irrigation treatments. Values are means of three replicates

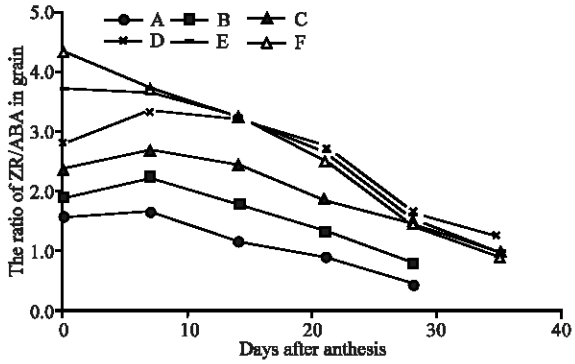

Fig. 3: Changes of the ratio of ZR to ABA in developing grains in wheat subjected to various irrigation treatments. Values are means of three replicates

DISCUSSION

Water deficit imposed during grain filling, especially at the early filling stage (A, B, C treatments), decreased grain filling rate significantly and shortened grain filling duration (Fig. 1), which is consistent with the former research (Kobata and Takami, 1983; Boonjung and Fukai, 1996; Zhang *et al*., 1998; Yang *et al*., 2000). The reduction might mainly be due to the lowered number of endosperm cells, which is directly related with the sink size per kernel, thousand grain weight (Singh and Jenner, 1982; Rahman and Yoshida, 1985; Michihiro *et al*., 1994). Present results also showed that the grain yield was not much affected when a water deficit was only conducted at vegetative stage (D, E treatments) (Fig. 1).

ABA accumulation in grain was remarkably accelerated by water deficit during grain filling (A, B, C treatments), whereas substantially decreased ZR contents in the grains (Fig. 2), so the ratio of ZR/ABA was also decreased (Fig. 3). Abscisic acid (ABA) has been reported that it could promote grain filling and enhance the remobilization of assimilates to the grains is involved in regulating grain development (Karssen, 1982; Davies, 1987; Kato and Takeda, 1993; Yang *et al*., 2000, 2001). Therefore, the maximal grain filling rate is positively correlated with the peak values of ABA (Tietz *et al*., 1981; Ackerson, 1985; Yang *et al*., 1999, 2001). However, in this research, the time of the peak of ABA occurred was obviously later than that of the maximum grain filling rate under D, E, F irrigation conditions with no water deficit at reproductive stage (Fig. 1, 2). This might be due to the longer period of grain filling under ample irrigation condition.

ZR in grain is beneficial to grain filling rate at early grain filling stage (Yang *et al*., 2003; Wang *et al*., 2006). In the current study, a marked difference in the time-course of ZR contents and the ratio of ZR/ABA between irrigation treatments with (A, B, C treatments) and without water deficit (D, E, F treatments) imposed at reproductive stage, which might explain the distinct difference in grain filling between treatments.

Therefore, it might be concluded that the altered hormonal balance (a decrease in ZR and an increase in ABA) in wheat grains regulated the grain filling rate and grain filling period under different irrigation conditions. And among all irrigation treatments, the irrigation treatment D with water deficit conducted at both regreening and jumping stages could be suggested as saving and high yield irrigation way in winter wheat.

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