



Research article

Effect of polyamines on the grain filling of wheat under drought stress

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ABSTRACT

Drought inhibits wheat grain filling. Polyamines (PAs) are closely associated with plant resistance due to drought and grain filling of cereals. However, little is known about the effect of PAs on the grain filling of wheat under drought stress. This study investigated whether and how PAs are involved in regulating wheat grain filling under drought stress. Two wheat genotypes differing in drought resistance were used, and endogenous PA levels were measured during grain filling under different water treatments. Additionally, external PAs were used, and the variation of hormone levels in grains was measured during grain filling under drought stress. The results indicated that spermidine (Spd) and spermine (Spm) relieve the inhibition caused by drought stress, and putrescine (Put) has the opposite effect. The higher activities of S-adenosylmethionine decarboxylase and Spd synthase in grains promotes the synthetic route from Put to Spd and Spm and notably increases the free Spd and Spm concentrations in grains, which promotes grain filling and drought resistance in wheat. The effect of PA on the grain filling of wheat under drought stress was closely related to the endogenous ethylene (ETH), zeatin (Z) + zeatin riboside (ZR) and abscisic acid (ABA). Spd and Spm significantly increased the Z + ZR and ABA concentrations and decreased the ETH evolution rate in grains, which promoted wheat grain filling under drought. Put significantly increased the ETH evolution rate, which led to excessive ABA accumulation in grains, subsequently aggravating the inhibition of drought on wheat grain filling. This means that the interaction of hormones, rather than the action of a single hormone, was involved in the regulation of wheat grain filling under drought.

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1. Introduction

The yield potential of wheat (*Triticum aestivum* L.) is divided into the following three major components: the panicle number per plant, the grain number per panicle, and the grain weight. Grain filling, the final stage of cereal growth, determines the grain weight (Yang and Zhang, 2006). Modern high yield crop production systems require high yield outputs, and for this reason, improved grain filling has become more important than ever (Saini and Westgate, 2000; Zahedi and Jenner, 2003).

Drought is one of the main abiotic stresses limiting crop growth and accounting for considerable grain yield reduction in crops (Jiang and Zhang, 2004). In northern China, one of the most important wheat production regions in China and world, the region's rainy season does not coincide with the growth stage for

wheat. Over 70% of its precipitation falls during the monsoon months from June to September (Li et al., 2000) and, as a result, droughts are a common occurrence during the winter wheat growth stage. In cereals such as wheat, stress caused by drought at the time of grain-filling usually shortens the grain-filling period and reduces the grain-filling rate, which leads to a reduction in grain weight and grain yield (Kobata et al., 1992; Zhang et al., 1998). Thus, how to relieve the inhibition effect of drought stress on the grain filling of wheat is important for wheat production of China.

Polyamines (PA) are organic polycations, which are low molecular weight nitrogen-containing compounds (Igarashi and Kashiwagi, 2000). They have been described as endogenous plant growth regulators or intracellular messengers that regulate plant growth, development, and responses to abiotic stresses (Alcazar et al., 2006; Kusano et al., 2007; Paschalidis and Roubelakis-Angelakis, 2005; Tomosugi et al., 2006). PAs are closely associated with plant resistance to water stress (Groppa and Benavides, 2008). Capell et al. (2004) found that the rice transgenic plant with a high expressing *Datura stramonium adc* gene produced much higher putrescine (Put, one PA) under stress and promoted spermidine

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(Spd, another PA) and spermine (Spm, another PA) synthesis, ultimately protecting the plants from drought. However, the wild-type plants were insufficient in triggering the conversion of Put into Spd and Spm, and they were sensitive for drought stress although the Put increased under drought stress. Yamaguchi et al. (2007) found that an *Arabidopsis* mutant plant, which cannot produce Spm, is hypersensitive to drought, and this phenotype was cured by Spm pretreatment. Yang et al. (2007) suggested that the increased concentrations of free Spd, free Spm, and insoluble-conjugated Put under water stress were significantly correlated with the yield maintenance ratio of rice. These observations indicate that by the manipulation of endogenous PA metabolism, an enhancement in crop drought resistance may occur. Furthermore, Farooq et al. (2009) found that exogenously applied PA increases leaf water status, photosynthesis and membrane properties, thereby improving the drought tolerance of rice. Yamaguchi et al. (2007) found that an *Arabidopsis* mutant plant, which cannot produce Spm, is hypersensitive to drought, and this phenotype was cured by Spm pretreatment. Yang et al. (2007) suggested that the increased concentrations of free Spd, free Spm, and insoluble-conjugated Put under water stress were significantly correlated with the yield maintenance ratio of rice. In addition, PA was thought to be involved in the regulation of grain development. The PA concentration of normal kernels was significantly higher than that of aborting maize kernels (*Zea mays* L.), and the PA concentration was positively correlated with the endosperm nuclei number (Liang and Lur, 2002). Yang et al. (2008) found that higher levels of Spd and Spm promote grain filling and increase the grain weight of rice (*Oryza sativa* L.); however, Put, had the opposite effect. Tan et al. (2009) suggested that low concentrations of Spd and Spm and low Spd/Put and Spm/Put ratios may be important physiological causes of the low grain filling rate and the low grain weight of inferior spikelets in super rice. These studies suggest that the PA is related to drought resistance and grain development in plants. However, the effect of PA on the regulation of wheat grain filling under drought stress and its mechanism remain unclear.

Plant hormones play an important role in regulating grain development. High levels of cytokinins (CTKs) are generally found in the developing grains of cereals, peas, and beans (Dietrich et al., 1995; Michael and Seiler-Kelbitsch, 1972; Morris et al., 1993; Saha et al., 1986; Yang et al., 2000). CTKs are thought to be involved in cell division during seed development (Yang et al., 2000). In rice, superior grains have higher abscisic acid (ABA) concentrations and lower ethylene (ETH) concentrations compared with inferior grains, and the ratio of ABA/ETH is positively and significantly correlated with the grain filling rate (Yang et al., 2006). In addition, the grain filling rate is positively correlated with indole-3-acetic acid (IAA) concentration in rice grains (Xu et al., 2007). High gibberellin 1 (GA₁) and GA₁₉ levels were found in the large panicles of rice immediately before and during anthesis (Suzuki et al., 1981).

PA and ETH reportedly share the same S-adenosylmethionine biosynthetic precursor, and increasing PA biosynthesis has a notable effect on ETH synthesis rates (Liang and Lur, 2002). Exogenous PA represses ETH synthesis in oat (*Avena sativa* L.) leaves (Fuhrer et al., 1982) and rice panicles (Yang et al., 2008). In addition, exogenous ABA increased the Put concentration in chickpeas (*Cicer arietinum* L.) (Bueno and Matilla, 1992). This reduced endogenous ABA concentration led to a decrease in the PA levels in maize (Liu et al., 2005). These studies provided clear evidence that there is a close relationship between PA and hormones in the regulation of plant growth. Our previous study suggested that exogenous Spd and Spm significantly increase the endogenous zeatin (Z) + zeatin riboside (ZR), ABA, and IAA concentrations and significantly decrease the ETH concentration in wheat grains, thus affecting wheat grain filling (Liu et al., 2013). However, little is known about

the relationship between PA and hormones in the regulation of wheat grain filling under drought study.

In the present study, two winter wheat cultivars that differ in drought resistance were used. The effects of drought stress on grain filling were monitored, and changes in endogenous Spd, Spm and Put concentrations in grains and leaves were observed. The activities of the enzymes involved in PA biosynthesis, such as ornithine decarboxylase (ODC, EC 4.1.1.17), arginine decarboxylase (ADC, EC 4.1.1.19), S-adenosylmethionine decarboxylase (SAMDC, EC 4.1.1.50) and Spd synthase (EC 2.5.1.16) were measured during wheat grain filling. In addition to these observations, external Spd, Spm and Put were treated under drought stress, and the grain filling characteristics and changes in IAA, Z + ZR, ABA and ETH in the grains were measured during wheat grain filling. The objective of the present study was to investigate the effect of PA on wheat grain filling under drought stress and to determine the relationship of PA and hormones with the regulation of wheat grain filling. We also sought to determine whether the grain filling of wheat can be regulated by manipulating the PA levels under drought stress.

2. Materials and methods

2.1. Study site description

This study was conducted from 2012 to 2014 at the Crop Specimen Farm in Northwest A&F University, Shaanxi Province, north-western China. The latitude and longitude of the experimental station are 34°22'N and 108°26'E, respectively. The annual mean precipitation of the experimental station is 550 mm. The annual mean maximum and minimum air temperatures at the site are 42 °C and −19.4 °C, respectively, and the annual mean temperature is 12.9 °C. The total yearly sunshine duration is 2196 h, and the frost-free period is 220 days. The soil at the experiment farm is Eum-Orthosols (Chinese soil taxonomy), and the mean bulk density of the soil was 1.33 g cm⁻³. The readily available N, P and K quantities were 57.45 mg kg⁻¹, 17.33 mg kg⁻¹, and 118.57 mg kg⁻¹, respectively. The organic matter concentration of the 0–20 cm topsoil was 12.34 g kg⁻¹, and the pH was 7.35.

2.2. Experimental design and treatments

2.2.1. The first experiment

The experiment was performed in large waterproof sheds. The internal shed dimensions were 32 m (length) × 15 m (width) × 3 m (height). The sheds had a transparent plastic-covered roof and four open sides. Mobile sheds were used to control natural rainfall on rainy days. Each plot area was 3 m × 4 m. The plot was divided by cement barriers.

Two wheat cultivars, Changhan 343 (a drought-resistant cultivar) and Xinong 979 (a drought-susceptible cultivar), were grown. The seeds were sown on Oct 18 for the 2012–2013 growth year and on Oct 20 for 2013–2014. The sowing density was 150 kg ha⁻¹, with a row spacing of 0.20 m. Fertilizer at 150 kg ha⁻¹ urea and 150 kg ha⁻¹ diammonium orthophosphate was applied at basal levels.

The experiment was a 3 × 2 (three levels of soil moisture and two cultivars) factorial design, with 6 treatment combinations. Each of the treatments contained three plots as replicates in a complete randomized block design. From anthesis until maturity, three levels of soil moisture were imposed on the plants by controlling water application. The well-watered (WW) treatment was maintained soil water potential at −20 ± 5 kPa, the moderately soil-dried (MD) treatment was maintained soil water potential at −40 ± 5 kPa, and the severely soil-dried (SD) treatment was maintained soil water potential at −60 ± 5 kPa. Soil water potential

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