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RESEARCH ARTICLE

Effect of polyamine on seed germination of wheat under drought stress is related to changes in hormones and carbohydrates

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Abstract

Drought is a multifaceted stress condition that inhibits crop growth. Seed germination is one of the critical and sensitive stages of plants, and its process is inhibited or even entirely prevented by drought. Polyamines (PAs) are closely associated with plant resistance to drought stress and seed germination. However, little is known about the effect of PA on the seed germination of wheat under drought stress. This study investigated the involvement of PAs in regulating wheat seed germination under drought stress. Six wheat genotypes differing in drought resistance were used, and endogenous PA levels were measured during seed germination under different water treatments. In addition, external PA was used for seed soaking and the variation of hormones, total soluble sugar and starch were measured during the seed germination under different water treatments. These results indicated that the free spermidine (Spd) accumulation in seeds during the seed germination period favored wheat seed germination under drought stress; however, the free putrescine (Put) accumulation in seeds during the seed germination period may work against wheat seed germination under drought stress. In addition, seed soaking in Spd and spermine (Spm) significantly relieved the inhibition of seed germination by drought stress; however, soaking seeds in Put had no significant effect on seed germination under drought. External Spd and Spm significantly increased the endogenous indole-3-acetic acid (IAA), zeatin (Z)+zeatin riboside (ZR), abscisic acid (ABA), and gibberellins (GA) contents in seeds and accelerated the seed starch degradation and increased the concentration of soluble sugars in seeds during seed germination. This may promote wheat seed germination under drought stress. In conclusion, free Spd and Put are key factors for regulating wheat seed germination under drought stress and the effects of Spd and Put on seed germination under drought notably related to hormones and starch metabolism.

Keywords: polyamine, drought, seed germination, wheat, abscisic acid, starch

1. Introduction

Abiotic and biotic stresses occur frequently during a plant's life cycle (Munne and Muller 2013). Drought is one of the main abiotic stresses that can limit crop growth and accounts for considerable grain yield reduction in crops. Winter wheat (*Triticum aestivum* L.) is one of the most important food crops in China and the world. However, the rainy season in the main wheat-producing region of China does not coincide with the growth stages of winter wheat (Li *et al*. 2000). As

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a result, drought is a common occurrence during the winter wheat growth stage.

Seed germination is usually the most crucial phase during seedling establishment (Hubbard *et al*. 2012; Shi *et al*. 2014). However, this process is inhibited or even entirely prevented by drought (Hubbard *et al*. 2012). In the northern arid and semi-arid regions, one of the most important wheat producing regions in China, drought is one of the main factors that limits seed germination and the grain production of wheat. Hence, methods that can relieve the inhibition of the seed germination of wheat by drought are important for the wheat production of China and the world.

Polyamines (PAs) are endogenous plant growth regulators that mediate many plant physiological processes and the response to environmental stressors. The three main PAs in plants are spermidine (Spd), spermine (Spm) and putrescine (Put) (Paschalidis and Roubelakis-Angelakis 2005; Alcazar *et al*. 2006; Tomosugi *et al*. 2006; Kusano *et al*. 2007; Yang *et al*. 2008). Polyamine is involved in the seed germination of plants. The PA content increases during the first 15 d of *Ocotea catharinensis* seed germination and then decreases and stabilizes between 30 and 60 d of germination (Dias *et al*. 2009). Exogenous PAs improve the seed germination of the hot pepper (Khan *et al*. 2012). Inhibition of PA biosynthesis retards the pea germination process (Villanueva and Huang 1993). The PA levels increase during the seed development of soybeans and rice (Sen *et al*. 1981; Lin *et al*. 1984). In addition, PAs are closely associated with plant resistance to drought stress (Groppa and Benavides 2008). The manipulation of PA metabolism may enhance crop drought resistance (Capell *et al*. 2004). Farooq *et al*. (2009) found that exogenously applied PAs increase leaf water status, photosynthesis and membrane properties, which improves the drought tolerance of rice. Yamaguchi *et al*. (2007) found that an *Arabidopsis* mutant plant, which cannot produce Spm, is hypersensitive to drought and that this phenotype was cured by Spm pretreatment. Yang *et al*. (2007) suggested that the increasing of free Spd, free Spm and insoluble-conjugated Put during water stress significantly correlated with the yield maintenance ratio of rice. These studies suggested that PAs were notably related to the drought resistance and seed germination of plants.

Plant hormones play important roles in regulating seed germination. Abscisic acid (ABA) inhibited the seed germination of plants such as *Arabidopsis thaliana* (Kucera *et al*. 2005; Muller *et al*. 2006). Graeber *et al*. (2010) suggested that ABA delayed the radicle expansion, which inhibited seed germination. Gibberellins (GA) antagonized the effect of ABA on seed germination (Miransari and Smith 2014), which stimulated the synthesis and production of hydrolases, especially α-amylase, resulting in the germination of seeds (Yamaguchi 2008). Auxins and cytokinins (CTK) are also involved in the regulation of seed germination. CTKs are active during all stages of seed germination (Chiwocha *et al*. 2005; Nikolic *et al*. 2006; Riefler *et al*. 2006). MicroRNA60 inhibits auxin response factor 10 during *Arabidopsis thaliana* seed germination, which allows seed germination (Liu *et al*. 2007).

There was a significant relationship between PAs and hormones on the regulation of plant growth. PAs and ethylene share the biosynthetic precursor S-adenosyl-L-methionine (SAM), and increases in Spd and Spm biosynthesis are likely to affect the rate of ethylene synthesis (Walden *et al*. 1997; Liang and Lur 2002). Exogenous Spd and Spm significantly increased the zeatin (Z)+zeatin riboside (ZR) content in rice grains (Yang *et al*. 2008). Both PA and ABA are involved in the response of grape rootstocks to salinity (Upreti and Murti 2010).

These studies provide clear evidence that PAs significantly affect the seed germination and the drought resistance of plants. However, little is known about the effect of PAs on the seed germination of wheat under drought stress. Pieruzzi *et al*. (2011) suggested that the effect of PA on the seed germination of *Araucaria angustifolia* (*Gymnosperm*) and *Ocotea odorifera* (*Angiosperm*) was significantly related to indole-3-acetic acid (IAA) and ABA. However, it is not known whether the effect of PA on seed germination of wheat is related to these hormones.

In our previous study, we found that the seed germination of different wheat cultivars was significantly different under drought stress (Xu *et al*. 2014). In the present study, two experiments were conducted: (1) six wheat cultivars, the seed germination of which varied in drought resistance, were used, and we measured the variation of Spm, Spd and Put in seed during seed germination induced by different water treatments; and (2) external Spd, Spm and Put were used for seed soaking, and the variation of hormones, total soluble sugar and starch in seed were measured during the seed germination under different water treatments. The purpose of the present study was to investigate the effect of PA on wheat seed germination under drought stress and the relationship of PA, hormones and starch during wheat seed germination induced by drought stress.

2. Materials and methods

2.1. The first experiment

Six wheat cultivars, the seed germination of which was different in drought resistance, were used. Changhan 58, Lunxuan 988 and Xiza 5 are the drought-resistant cultivars, and Wanmai 52, Luomai 18 and Zhengmai 7698 are the non-resistant cultivars (Xu *et al*. 2014). Uniform seeds