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Polyamines mediate the effect of post-anthesis soil drying on starch granule size distribution in wheat kernels

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ABSTRACT

Polyamines (PAs) are important endogenous plant growth regulators responding to environmental stress and mediating many physiological processes including grain filling in cereals. This study investigated whether PAs mediate the effect of post-anthesis soil drying on starch granule size distribution, starch content, and weight of superior and inferior kernels of wheat (*Triticum aestivum* L.). Two wheat cultivars were grown in pots. Three treatments, well-watered (WW), moderate soil drying (MD) and severe soil drying (SD), were imposed from 9 days post-anthesis until maturity. PA levels in kernels and small, medium and large granules were measured. The results showed that superior kernels had much higher free spermidine (Spd) and free spermine (Spm) concentrations, larger volumes of medium starch granules, and smaller-sized large granules than did inferior kernels under all the treatments. Compared to WW, MD significantly increased the concentrations of free Spd and free Spm, activities of soluble starch synthase and granule-bound starch synthase, volume of medium granules, and starch content and kernel weight of inferior kernels, and decreased the size of large granules. SD produced the opposite effect. Application of Spd or Spm to spikes produced effects similar to those of MD, and application of an inhibitor of Spd and Spm synthesis produced effects similar to those of SD. These results suggest that PAs mediate the effect of post-anthesis soil drying on starch biosynthesis in wheat kernels by regulating key enzymes in starch synthesis and that elevated PA levels under MD increase the volume of medium granules and kernel weight of inferior kernels.

1. Introduction

Starch in the endosperm of wheat (*Triticum aestivum* L.) is a major form of carbon reserves and accounts for 65–75% of the final dry weight of a kernel [1–3]. Starch exists as discrete semi-crystalline granules with various sizes, shapes, and size distributions [4,5]. Wheat starch granules can normally be divided into two types, large A-type granules (diameter >9.9 μm) and small B-type granules (diameter <9.9 μm) [6–9]. However, small C-type granules have also been observed [10].

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In our previous study [11], the thresholds for separating wheat granules into small, medium, and large sizes were <5 μm, 5–50 μm, and >50 μm, respectively. This separation method was new and clearer than previous methods. The starch granule size distribution of wheat is an important character that can affect starch chemical composition, and consequently, influence kernel quality [12–14]. However, knowledge about the relationship between starch granule size distribution and kernel weight in wheat is very limited.

The physicochemical properties of starch and the granule size distribution in wheat are both genetically and environmentally controlled [9,15–17]. Environmental factors exert a greater effect on starch components and properties than does cultivar variation [16]. Dai [15] reported that the contents of A-, B-, and C-type starch granules in wheat were affected by soil water, genotype, and soil water × genotype interaction. Rainfed cultivation reduced the granules with diameters >9.8 μm and increased the granules with diameters of 2.0–9.8 μm and <9.8 μm compared to an irrigated treatment [18]. This finding indicates that the starch granule size distribution in a wheat kernel may vary with soil moisture. However, little is known about how post-anthesis soil drying affects starch granule size distribution.

Polyamines (PAs), including spermidine (Spd), spermine (Spm), and putrescine (Put), are considered endogenous plant growth regulators or intracellular messengers responding to environmental stress and mediating many physiological processes including grain filling of cereals [19–23]. In maize (*Zea mays* L.), PAs have been observed to be present at much higher levels in normal kernels than in aborting kernels, and that higher ratios of Spd or Spm to ethylene are closely associated with higher kernel set and kernel weight [24,25]. Similar results have been observed in rice and wheat [26–29]. Application of Spd or Spm accelerated kernel filling of wheat [29,30]. Application of Spd increased the contents of amylose, amylopectin and total starch, and a higher Spd content increased the formation of B-type starch granules in wheat kernels under severe water deficit [31]. It is not known, however, whether PAs could mediate the effect of post-anthesis soil drying on starch granule size distribution, starch content, and kernel weight.

Kernels on a wheat spike can be classified into superior or inferior ones based on their flowering date or locations on the spike [32,33]. Usually, superior kernels show a higher kernel filling rate and a heavier weight than inferior ones [34,35]. The difference in kernel weight between superior and inferior kernels may be attributed to many factors, such as differences in assimilate participation, hormonal levels, and starch biosynthesis ability [34,36,37]. However, no information is available on starch granule size distribution between superior and inferior kernels or whether PAs can regulate the distribution when wheat plants are subjected to post-anthesis soil drying.

The objective of this study was to test the hypothesis that PAs mediate the effect of post-anthesis soil drying on starch granule size distribution, starch content, and kernel weight by regulating the key enzymes in starch synthesis, and that PAs are involved in the difference in kernel weight between superior and inferior kernels of wheat. PA levels, starch granule size distribution, and activities in kernels of two key enzymes in starch synthesis, soluble starch synthase (SSS) and granule-bound starch synthase (GBSS), were investigated.

2. Materials and methods

2.1. Plant material and growth conditions

The experiment was conducted at a research farm of Yangzhou University, Jiangsu province, China (32°30′ N, 119°25′ E, 21 m altitude), during the wheat (*Triticum aestivum* L.) growing season (November 2013–June 2014), and was repeated during the wheat growing season in 2014–2015. Two cultivars, Yangmai 16 (YM16) and Ningmai 13 (NM13), that are currently used in local production, were grown in porcelain pots. Each pot (30 cm in height and 25 cm in diameter, 14.72 L in volume) was filled with 18 kg of sandy loam soil [Typic Fluvaquent, Entisol (U.S. taxonomy)] that contained 20.2 g kg^{-1} organic matter, 105 mg kg^{-1} alkali hydrolyzable N, 34.2 mg kg^{-1} Olsen phosphorus, and 68.0 mg kg^{-1} exchangeable potassium. Twenty seeds were sown in each pot. At the three-leaf stage, plants were thinned to 10 plants per pot (equivalent to a density of 204 plants m^{-2}). The plants were watered daily by hand to maintain the soil water content close to field capacity (soil moisture content 0.189 g g^{-1}) until 9 days post-anthesis (DPA), when soil drying treatments were initiated. YM16 and NM13 headed 153 and 154 days after sowing (DAS), respectively, and flowered during 160–166 DAS.

2.2. Soil drying treatments

The experiment was a 2 × 3 (two cultivars and three levels of soil water status) factorial design with six treatment combinations. Each treatment had 48 pots as repetitions in a randomized complete block design. From 9 DPA until maturity, three levels of soil water potential (ψ_{soil}) were imposed on the plants by control of water application. The well-watered (WW) treatment was maintained at −20 ± 5 kPa (soil moisture content 0.155 g g^{-1}), a moderately soil drying (MD) treatment was maintained at −40 ± 5 kPa (soil moisture content 0.119 g g^{-1}), and a severely soil drying (SD) treatment was maintained at −60 ± 5 kPa (soil moisture content 0.091 g g^{-1}). Soil water potential was monitored at 15-cm to 20-cm soil depth. A tension meter consisting of a 5-cm-long sensor (Soil Science Research Institute, China Academy of Sciences, Nanjing, China) was installed in each pot to monitor soil moisture. Tension meter readings were recorded every 4 h from 600 to 1800 h. When the reading dropped to the designated value, 200, 160, and 120 mL of tap water per pot were added to the WW, MD, and SD plants, respectively. The pots were placed in a field and sheltered from rain by a removable polyethylene shelter that was placed over them during rain.

2.3. Sampling

Three-hundred spikes that flowered on the same day were chosen and tagged in 30 pots of each treatment. Twenty to thirty tagged spikes from each treatment were sampled at 6, 18, and 30 DPA. All kernels from each spike were removed. Kernels on a spike were divided into two groups: superior and inferior kernels. The basal kernels in the middle spikelets (the fourth through twelfth spikelets) on a spike were taken as superior and the other kernels on the spike as inferior kernels