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RESEARCH ARTICLE

Ethylene and Spermidine in Wheat Grains in Relation to Starch Content and Granule Size Distribution Under Water Deficit

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Abstract

Two wheat cultivars (*Triticum aestivum* L.) were used to evaluate the effects of post-anthesis severe water deficit (SD) on starch content and granule size distribution and their relations with ethylene and spermidine (Spd). Comparison to the well-watered (WW) treatment, SD led to lower Spd and higher 1-aminocylopropane-1-carboxylic acid (ACC) concentrations and ethylene evolution rate (EER) in grains at the critical stage of forming starch granules. Application of Spd or aminoethoxyvinylglycine (AVG) significantly reduced ACC concentration and EER and increased Spd concentration, while ethephon or methylglyoxal-bis (MGBG) had an opposite impact. The volume and surface area distribution of starch granules showed a bimodal curve, while the number distribution exhibited a unimodal curve. SD caused a marked drop in grain weight, grain number and starch content, also led to a significant reduction in the proportion (both by volume and by surface area) of B-type starch granules (<10 μm), with an increase in those of A-type starch granules (>10 μm). Application of Spd or AVG increased the proportion (both by volume and by surface area) of B-type starch granules under SD. Correlation analysis suggested that ethylene and Spd showed an antagonism relation in the formation of B-type granules. These results suggested that it would be good for the formation of B-type starch granules to have the physiological traits of higher Spd and lower ACC concentrations and ethylene emission under SD.

Key words: ethylene evolution rate, 1-aminocylopropane-1-carboxylic acid, spermidine, severe water deficit, wheat (*Triticum aestivum* L.)

INTRODUCTION

Starch, as well known, accounting for 65-70% of the final grain weight, is a major component of grain yield (Hurkman *et al*. 2003). The starch granules, as the main existent form of starch in grains, play significant roles in affecting the processing quality of wheat (Park *et al*. 2004). As previous reports, the starch granules present bimodal size distribution, which can be divided into the large A-granules and the small B-granules by a boundary diameter of 10 μm (Vincent *et al*. 2008; Li *et al*. 2010; Zhang *et al*. 2010). The very small C-granules had also been illustrated in previous studies (Bechtel *et al*. 1990; Bechtel and Wilson 2003), and debated to be classified as B-granules due to the difficulty in plotting the boundary between them. The variation of physical and chemical properties of A- and B-granules can lead to the difference of starch functionality (Tester *et al*. 2004). An increase

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in the A-granule content decreased farinograph water absorption and improved pasta quality (Soh *et al*. 2006). The pasting properties of flour have a close relation with the distribution of starch granules, the B-granules have a higher peak viscosity than A-granules (Peterson and Fulcher 2001). The distribution of starch granules varied with grain developmental stage (Bechtel *et al*. 1990). The A-granules begin forming at 4-5 days post-anthesis (DPA) and continue to form until reaching a maximum diameter at about 19 DPA, while the B-starch granules begin forming at about 12-14 DPA and continue to enlarge until 21 DPA (Bechtel *et al*. 1990; Hurkman *et al*. 2003).

Unfavorable environmental factors, such as extreme temperatures, drought and nutrient deficiency, can affect grain development and starch accumulation also having effects on starch content and granule size distribution. Panozzo and Eagles (1998) reported that environmental factors variation was greater than cultivar variation for starch components and properties. Low light reduced the starch content and induced significant changes in distribution of starch granule size in grains (Li *et al*. 2010). High temperature from anthesis to maturity reduced the duration of starch accumulation and induced significant changes in distribution of starch granule size in wheat (Zhao *et al*. 2008). Ni *et al*. (2011) reported that P fertilization resulted in a significant increase in the proportion (both by volume and by surface area) of B-granules (<9.9 μm). Zhang *et al*. (2010) conclude that post-anthesis water deficit reduced the B-granules volume percent and surface area percent. However, the mechanism by which these stress induced the changes in starch accumulation and granule size distribution remains unclear. As responding signals to environmental stimulus, ethylene and spermidine (Spd) play important roles in many physiological processes, such as cell division, fruit set and growth, senescence and so on (Davies *et al*. 1995; Papadakis and Roubelakis-Angelakis 2005; Alcazar *et al*. 2006). An overproduction of ethylene caused by drought closely related to the grain weight reduction in wheat and rice (Beltrano *et al*. 1999; Yang *et al*. 2004). However, a series of reports suggested that the water deficit decreases, rather than increases, ethylene production rates (Morgan and Drew 1997), depend on the severity and duration of soil-drying (Yang *et al*. 2006). Application of ethylene inhibitors increase grain weight (Yang *et al*. 2006) and improve dry matter partitioning and grain filling of basal rice kernels (Naik and Mohapatra 2000), whereas application of ethephon, an ethylene-releasing agent, had an opposite impact. Higher levels of Spd was observed to be closely associated with higher kernel set and better seed development in maize and a greater grain filling rate in rice (Yang *et al*. 2008; Feng *et al*. 2011), which was verified by exogenous Spd (Wang *et al*. 2012). Wang *et al*. (2012) concluded that the variations of Spd concentration and ethylene emission, induced by the exogenous chemicals or soil moisture conditions, play key roles in grain filling by regulating the key enzymes involved in the sucrose-to-starch conversation. Reports also indicated that Spd levels under stress varied with the plant species, some might increase, while others decrease their endogenous Spd levels (Liu *et al*. 2007). The study on the variations of ethylene and Spd under severe water deficit (SD), and their relations to granule size distribution, however, are scanty.

The previous results indicated that starch content and granule size distribution were obviously affected by harsh environmental factors. Ethylene and Spd, as responding signals, may be involved in the process of regulating starch accumulation and granule size distribution. However, little is known about how Spd and ethylene are involved in these processes under SD conditions. The main research objective of this study was to elucidate the effects of SD on starch content and granule size distribution and their relations with ethylene and Spd. The chemical substances were also used to verify the roles of the two regulators.

RESULTS

Ethylene evolution rate (EER), Spd and 1-aminocylopropane-1-carboxylic acid (ACC) concentrations in grains

EER and ACC concentrations were high initially at the early grain-filling stage and sharply declined till 21 DPA (Table 1). SD significantly increased the EER and ACC concentration in grains. Application of methylglyoxal-bis (guanylhydrazone) (MGBG) or ethephon increased, while Spd or amino-ethoxyvinylglycine (AVG) decreased the EER and ACC concentration. Compared with the well-watered (WW) treatment, SD significantly