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Effect of non-structural carbohydrate accumulation in the stem pre-anthesis on grain filling of wheat inferior grain

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ABSTRACT

To promote the grain weight of wheat, the key is to improve the grain filling of inferior grain. The remobilization of non-structural carbohydrate (NSC) stored in reserve in the stem (sheath + culm) pre-anthesis is important for the grain filling of cereal. However, the mechanism that regulates the NSC reserve in the stem pre-anthesis on grain filling of inferior grains of wheat remains unclear. In the present study, six wheat cultivars with different grain weight were used. Additionally, different rates of nitrogen (N) fertilizer were examined. The objective of the present study was to investigate the relation between the NSC reserve in the stem pre-anthesis and grain filling of inferior grain of wheat and determine the mechanism of that relation. The results showed that the grain weight of inferior grain was significantly lower than that of superior grain, and the inferior grain was more affected by environmental factors than the superior grain. The superior grain had higher content of zeatin (Z) + zeatin riboside (ZR) and activities of synthase (SS) and ADP-glucose pyrophosphorylase (AGPP) and lower rate of ethylene (ETH) evolution than those of inferior grain. Because of these differences, the superior grain had higher sink strength and grain-filling rate and therefore had higher grain weight than that of inferior grain. With a high NSC reserve stored in the stem pre-anthesis, the Z + ZR content increased and the ETH evolution rate decreased in inferior grain significantly, which promoted the sink strength and grain-filling rate of inferior grain of wheat. Suitable nitrogen (N) fertilizer application notably increased the NSC reserve stored in the stem pre-anthesis, which promoted the sink strength and grain-filling rate of inferior grain. However, excess N fertilizer significantly decreased the NSC accumulation in the stem pre-anthesis and inhibited the sink strength and grain-filling rate of inferior grain of wheat.

1. Introduction

Wheat (*Triticum aestivum* L.) is an important crop in China. With increasing population and decreasing area of agricultural land, promoting crop production is essential in China. For wheat, the grain yield is separated into three components, and an effective approach to promote the grain yield of wheat is to increase the contributions of these components. However, the panicle number per plant has likely reached the highest level and continuing to increase the number may lead to serious problems such as lodging, premature senescence, and increased damage by diseases and insects, among others. Thus, the inevitable approach to increase the grain yield of wheat is to increase the grain weight or grain number per panicle, based on a suitable panicle number per area. Grain filling of cereals determines the grain weight, and therefore, improving grain filling is important for high grain weights and grain yields of cereals such as wheat (Chen et al., 2013; Yang and Zhang, 2010; Kato et al., 2007).

According to the grain filling characteristics, the grain of wheat is divided into two types, superior and inferior grain. Superior grain primarily consists of earlier flowering flowerets and is located at the bottom of a spikelet, and the inferior grain primarily consists of later flowering flowerets and is located at the top of a spikelet of wheat (Jiang et al., 2003). In a previous study, inferior grain had higher temporal and spatial variation than that of superior grain, and the inferior grain was more sensitive to environmental factors (Yang, 2010). The poor grain filling of inferior grain is the primary explanation for the inability of large panicle rice cultivars to reach their high yield potentials (Yang and Zhang, 2010). Thus, the key to promote wheat grain weight and grain yield is to improve the grain filling of inferior grain.

Mechanisms have been proposed to explain the poor grain filling of inferior grain. Some previous studies suggest a priority in the photosynthate supply to the superior grain, which may lead to a deficiency of

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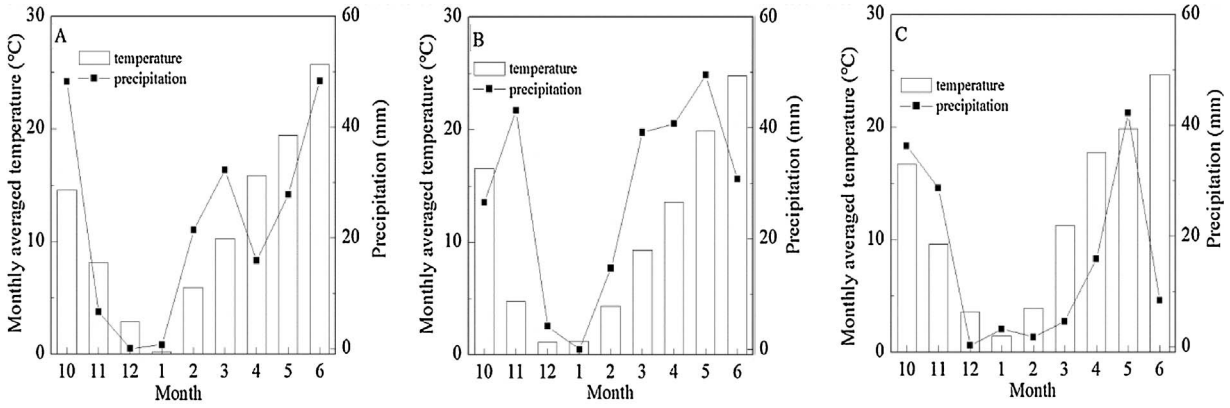

Fig. 1. The average monthly temperature and precipitation during the wheat growing seasons in experimental fields at Yangling (A. 2014–2015; B. 2015–2016) and Doukou Experimental Station (C. 2015–2016).

Table 1
Grain yield and yield components of different wheat cultivars.

Year	Cultivars	No. of panicles ($\times 10^4$ hm^{-2})	Spikelets per panicle	Grain weight (mg)	Grain yield (t hm^{-2})
2014–2015	Shuagda 1	370.02c	38.95a	57.84a	7.55ab
	Fugao 1	525.03b	37.37a	45.95b	7.91a
	Zhoumai 22	510.51b	37.58a	47.83b	7.96a
	Xiaoyan 6	615.34a	33.16b	35.85c	7.13b
	Xiaoyan 22	630.81a	36.18ab	36.34c	7.44ab
	Xinong 538	674.86a	34.56b	37.57c	7.70a
2015–2016	Shuagda 1	327.62c	40.31a	50.16a	6.95ab
	Fugao 1	493.85b	39.35a	41.24b	7.84a
	Zhoumai 22	451.46b	38.46a	42.11b	7.38a
	Xiaoyan 6	584.11a	31.67b	31.57c	6.02b
	Xiaoyan 22	601.95a	33.95b	34.61c	6.81b
	Xinong 538	612.79a	32.57b	30.15c	6.25b
F Value	Year (Y)	137.57*	0.17	57.24*	37.29*
	Cultivar (C)	619.14*	15.42*	90.070*	10.11*
	Y × C	2.792*	1.579	1.689	2.604

Values within a column and for the same year followed by different letters are significantly different at P = 0.05.

* F values significant at the P = 0.05 level.

photosynthate for the grain filling of inferior grain in rice (Murty and Murty, 1982). Kato (2004) suggest that the deficiency of sink size is the primary limitation of the grain filling of inferior grains of rice. Additionally, some studies suggest that lower activity of the enzymes that regulate the sucrose to starch conversion limits the grain filling of inferior grain, compared with the enzyme activity of superior grain (Ishimaru et al., 2005; Wang et al., 2008). However, the mechanism of the poor grain filling of inferior grain of cereals remains unclear.

Carbon and nitrogen are the primary constituent elements of wheat grain (Yu, 2003). The carbohydrates used for grain filling are supplied from two sources: current assimilation post-anthesis and remobilization of reserves stored in the stem pre-anthesis. The remobilization of non-structural carbohydrate (NSC) reserves stored in the stem (sheath + culm) pre-anthesis contributes approximately 20–30% of grain weight of wheat (Yang et al., 2004a). Horie et al. (2005) found that the reserve of NSC in the stem pre-anthesis was significantly correlated with rice growth at the early grain filling state, and Fu et al. (2011) suggested that the reserve of NSC in the stem pre-anthesis promoted the grain filling of inferior grains of rice. However, whether increasing the reserve of NSC in the stem pre-anthesis could improve the grain filling of inferior grains of wheat was unclear, and the mechanism for the regulation of reserves of NSC in the stem pre-anthesis on grain filling of inferior grains of wheat has also not been determined.

The cytokinins and ethylene (ETH) play important roles in the regulation of the grain filling of cereals. A large transient increase of zeatin (Z) and zeatin riboside (ZR) significantly promoted the endosperm cell division of grains of wheat (Morris et al., 1993). Superior grains had a higher level of ethylene (ETH) than that of inferior grains of wheat (Yang et al., 2006). Our previous study found that plastic-covered ridge and furrow planting significantly affected the Z + ZR and ETH levels in grains, which promoted the grain filling of inferior grain of wheat (Liu et al., 2013a).

Starch is the primary component of wheat grain, accounting for approximately 65–74% of grain weight. The starch of wheat grain is derived from the NSC stored in the stem, and sucrose is the primary form of stored NSC (Yang et al., 2004b). In a previous study, sucrose synthase (SS) and ADP-glucose pyrophosphorylase (AGPP) were notably involved in the regulation of the biosynthesis from sucrose to starch in wheat grain (Jiang et al., 2003). The activities of AGPP and SS in superior grains were notably higher than those in inferior grains of rice and wheat, and AGPP and SS activities were significantly correlated with grain weight of rice and wheat (Yang et al., 2001a; Jiang et al., 2003).

In these studies, the hormones and the activities of AGPP and SS in grains were all significantly correlated with the grain filling of wheat. However, the relationship between the reserve of NSC in the stem pre-anthesis and the changes in hormones and activities of AGPP and SS in grains during grain filling of wheat remains unclear, in addition to whether the effect of the reserve of NSC in the stem pre-anthesis on grain filling of inferior grains is related to the hormones and activities of AGPP and SS in grains. In the present study, six wheat cultivars that were different for grain filling and grain weight were used, and the reserve of NSC in the stem pre-anthesis and the changes in hormones and activities of AGPP and SS in grains during grain filling were measured. Additionally, different rates of nitrogen (N) were applied to the wheat cultivars, and the activities of AGPP and SS in grains during grain filling were measured. The objective of this study was to investigate the effect of the reserve of NSC in the stem pre-anthesis on grain filling of inferior grains of wheat and determine whether an effect was related to hormones and the activities of AGPP and SS in inferior grains of wheat.

2. Materials and methods

2.1. Experiment design

2.1.1. First experiment

This study was conducted from 2014 to 2016 at Northwest A & F University, Yangling, Shaanxi Province, China (34°17′ N, 108°05′ E). The organic matter content and available nitrogen (N), phosphorus (P) and potassium (K) of the 0–20 cm of topsoil in the cropland were 12.39 g kg^{-1}, 49.85 mg kg^{-1}, 24.63 mg kg^{-1} and 110.14 mg kg^{-1}, respectively.

Six winter wheat cultivars, Shuangda 1, Fugao 1, Zhoumai 22,