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Full Length Research Paper

Grain filling rate is limited by insufficient sugar supply in the large-grain wheat cultivar

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Wheat grain yield can be limited by source, sink or by both. Inconsistency of the previous results reflects the interactions between genotypes and environments. In north China where the hot, dry wind was frequent during grain filling, new winter wheat cultivars with large grains suffer from loss of grain weight quite often because the grain filling rate (GFR) is low. In the present study, the carbohydrate assimilation and utilization was investigated to possible role of carbon assimilation and utilization in limiting grain filling rate by comparing two winter wheat cultivars, a large-grain cultivar Jing9428 (slow GFR), and a small-grain cultivar CAU3291 (fast GFR). It was shown that there was no significant difference in net photosynthetic rate and leaf area index during grain filling between the two cultivars. However, soluble sugar concentration in stems of Jing9428 decreased much more sharply than CAU3291 when the linear grain growth phase began suggesting an insufficient supply of photosynthates for grain filling. In grains, the ratio of starch to sucrose, glucose and fructose content of Jing9428 was significantly lower than CAU3291. It was suggested that insufficient photosynthate supply rather than weak sink strength was the main reason limiting grain filling rate of the large-grain type wheat cultivars in north China.

Key words: Winter wheat, grain filling, source-sink relationship, carbohydrate.

INTRODUCTION

Wheat grain yield can be limited by source (the supply of assimilates) or sink (the capacity of the grains to accumu-late assimilates), or both (Evans et al., 1975). The results of different studies by manipulating source-sink relation-ships during grain filling through removing leaves or grains, and shading have shown inconsistent conclusions (Winzeler et al., 1989; Jedel and Hunt, 1990; Savin and Slafer, 1991; Slafer and Savin, 1994; Cruz-Aguado et al., 1999). For example, Cruz-Aguado et al. (1999) reported that wheat growth in the tropics is more source limited than in temperate areas. While in Australia, Slafer and Savin (1994) suggested that during post- anthesis period, grain yield of wheat is either sink-limited or co-limited by both source and sink but never source-limited. This in-consistency reflects the genotype and environment interactions in the availability of assimilate for grain growth (Ma et al., 1990).

In winter wheat growing region of North China, two envi-ronmental factors limit wheat yield. The short spring sea-son limits grain number per spike. The frequent hot dry wind during grain filling stage limits grain weight. There-fore, traditional wheat cultivars usually have many spike number, but few grains per spike and small grains. Com-paring with cultivars bred in 1970's, new cultivars bred in 1990's have the same spike number per hectare, a little more grains per spike, but significant larger grain weight (about 36 mg/grain versus 45 mg/grain). Grain weight has been a most important factor in increasing yield potential (Liu and Meng, 1994). To increase wheat yield further (more than 6 ton/ha), some cultivars with even larger grains (more than 48 mg/grain) has been developed in late 1990's. However, grain weight potential of such cultivars was not always realized due to their low grain fill rate (GFR). Grain filling is quite often interrupted under unfavorable weather conditions during grain filling stage. According to source/sink theory, grain filling rate can be limited by source or sink, including sink size (grain number per hectare) and sink strength (example, enzyme activity, phloem unloading, hormone control etc.) (Farrar, 1993). By using two wheat cultivars with different grain size and grain filling rate, this study aims to elucidate the possible role of photosynthate supply and utilization in limiting grain filling

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

Cultivars	Grain yield (g/m^2)	Spike number per m^2	Kernel number per spike	Grain weight (mg/grain)
CAU3291	516	527	29.1	35.6
Jing9428	467	443	28.8	43.1
T-Test	NS	NS	NS	*

*: significant at 0.05 levels.
NS: not significant.

rate in winter wheat in northern China.

MATERIALS AND METHODS

Field site and experimental set-up

The study was conducted during the 2002 and 2003 growing seasons at the experimental station of the China agricultural University, Beijing. The soil was characterized by high fertility with organic matter of 2.32%, Nitrate-N of 10.8 mg/kg, Olsen-P of 18.6 mg/kg, Ammonium acetate-K (NH_4OAC-K) of 149 mg/kg and pH of 7.6. With the intensive management, 112.5 kg N/ha was applied as granular urea at seeding and 112.5 kg N/ha at stem jointing stage. Phosphorus was applied as diammonium phosphate (DAP) at the rate of 180 kg/ha (P_2O_5) at seeding. Irrigation was conducted when needed.

Two cultivars, CAU3291 and Jing9428 were used in the study. CAU3291 is a small-grain genotype with fast grain filling rate (GFR). Jing9428 is a big-grain genotype with slow GFR. Both cultivars were bred in the same ecological area around Beijing, and released in late 1990's. Seed was sown at a rate of 225 kg/ha in rows 20 cm apart. The experimental design was a randomized complete block with 4 replications and plot size of 21.6 m^2.

Sampling

On the 3rd, 9th, 15th, 19th and 24th day after anthesis, 20 randomly chosen plants were sampled from each plot. Grains, stems (including leaf sheaths) and leaf blades of the main stems were separated, dried, weighed and ground. Grains and stems were used for the determination of carbohydrates. In the last sample, the total plant (main stem plus tillers) was used to determine the average grain number per spike.

At maturity (26th day after anthesis when 50% of the spikes become yellow), the spike number per m^2 was determined by counting the total spike number in an area of 0.2 m^2 (two 1 m-long rows) in each plot. Grain yield and the average grain weight were recorded in plants cut at ground level for a 3 m^2 area from each plot.

Determination of sucrose, glucose, fructose and soluble sugar and starch

Samples of grain and stem were extracted with 80% ethanol (50). Sucrose, glucose and fructose were analyzed by HPLC methods (Shimada LC-10A). The HPLC conditions were as follows: Waters 600 Pump, Waters 600 controller, Waters 474 Scanning Fluorescence Detector, Aminex HPX-87C Column. Soluble sugar was assayed by an anthrone method (Zhang, 1992). Starch in the residue was determined after extraction with perchloric acid (Bai and Tang, 1993).

Leaf area index (LAI) and net photosynthetic rate (Pn)

On the 0th, 14th, and 21st day after anthesis, an area of 400 cm^2 was sampled from each plot to determine the leaf area index. The leaf area was measured with a ruler (length x maximum width x 0.78) (Quarrie and Jones, 1977). On the same day, net photosyn-thetic rate of the flag leaves was measured using a portable photosynthesis system (BAU-1, a joint product of Beijing Analytical Instrument Factory and the Department of Agronomy, China Agricul-tural University). This is a closed system that measures changes in CO_2 concentration over time. Measurements were made between 9:30 to 12:00 a.m. when the photosynthetically active radiation (PAR) was 1021 $\pm$ 56 μmol m^{-2} s^{-1} and the leaf chamber tempera-ture was 27 $\pm$ 2°C. Three replicate plants were measured in each plot. Measurements were made at ambient CO_2 concentration.

Statistics

Data were analyzed by using the SAS statistics program (V6.03) (SAS Institute Inc., 1985-1987).

RESULTS

Yield and yield components

Wheat yield is determined by spike number, grain number and grain weight. CAU3291 got higher yield which was greatly contributed by its relatively more spikes per hectare, and more grains per spike (Table 1). However, its grain weight is significantly lower than that of Jing9428. The result was typical for these two cultivars when there was hot, dry weather during grain filling stage. Though the grain weight of Jing9428 was much higher than that of CAU3291, it is lower than the potential value which was reported as about 48 mg/grain in favorable weathers. Therefore the grain fill process was analyzed to clarify the reason.

Grain fill

Grain growth of wheat can be divided into three phases, (1) the initial lag phase; (2) the apparent linear phase; and (3) the maturation phase (Herzog, 1986). In the pre-sent experiment, no significant difference was found between CAU3291 and Jing9428 during the initial lag phase (Figure 1). Then, grain filling rate CAU3291 increased much quickly than that of Jing9428 in the linear phase (Figure 1). On the 19th day after anthesis, the grain of CAU3291 reached the maturation phase, while that of Jing9428 kept linearly growth. It seemed that the grain of Jing9428 stopped growth suddenly on day 24 after

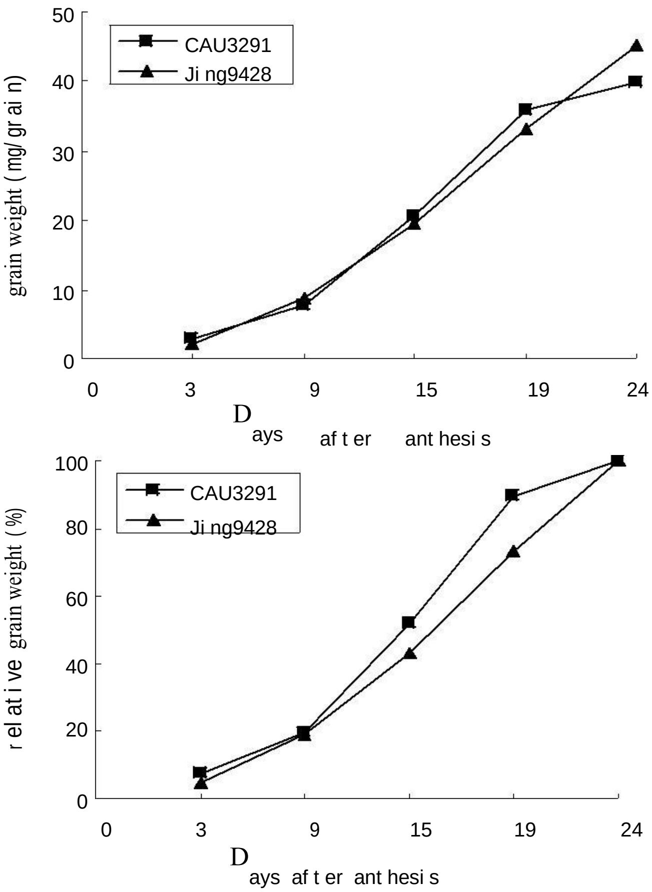

Figure 1. Grain growth process of two wheat cultivars Jing9428 and CAU3291. Upper, absolute grain weight (l.s.d. (0.05) = 1.32); lower, relative grain weight (l.s.d. (0.05) = 3.5%).

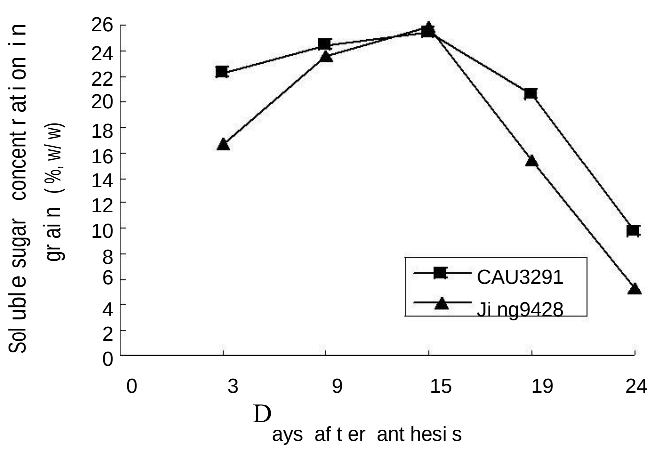

Figure 2. Soluble sugar concentration in stems and leaf sheathes of two wheat cultivars Jing9428 and CAU3291 during grain filling stage (l.s.d. (0.05) = 2.04).

Jing9428 kept linearly growth. It seemed that the grain of Jing9428 stopped growth suddenly on day 24 after anthesis without reaching the maturation phase, possibly because of the hot weather. So it was necessary to analyze the physiological limitation accounting for the grain growth pattern of Jing9428.

Carbohydrate supply and utilization

In general, factors controlling grain growth may include two aspects, one is carbohydrate supply from the current photosynthate or sugar stored in vegetative organs (mainly stems and leaf sheaths) pre- or/and post-anthesis (source), the other is carbohydrate utilization in grain (sink). Leaf area index (LAI) can be a measurement of source size. In this experiment, no difference was found in LAI of these two cultivars during grain filling stage (Table 2). The soluble sugar storage in stems and leaf sheaths of both cultivars increased to the maximum on day 15 post-anthesis then decreased with the linear growth of grains (Figure 2). However, sugar concentration in stems and leaf sheaths of Jing9428 decreased more sharply after day 15, suggesting an insufficient supply of current photosynthate for grain filling.

In general, the concentration of sugar and reduced sugar (glucose, fructose) in grains of Jing9428 was lower than that of CAU3291, though not significantly (Figure 3). Also, starch synthesis in grains of Jing9428 was slower than that of CAU3291 (Figure 4). The ratios of starch to sugar, glucose, and fructose content in grains indicate conversion rate of sugar to starch (Table 3). It was found that the ratios of starch to sugar, glucose, and fructose content in grains of CAU3291 were significantly lower (from the 9th day after anthesis and onward) than in Jing9428. These data suggest the insufficient supply of carbohydrates to grains of Jing9428 in comparison to CAU3291.

DISCUSSION

Slafer et al. (1994) reported that breeders have increased wheat yield potential mainly through increasing the number of grains per m^2 (sink size) rather than through increasing individual grain mass. While in east China where the climate is much favorable for wheat growth, wheat cultivars with big spike (numerous, larger grains per spike) has been successful in getting yield as high as9 ton/ha (Fu and Li, 1998). In North China, however, the grain growth of such cultivars may be limited by the short grain filling duration due to the hot, dry weather. As found in the present study, grains of Jing9428 did not reach their potential weigh because the grain filling rate was slow so that the grain fill process failed to finish in the given short maturation period (Figure 1). Thorne (1985) suggested that factors within the grains, rather than out of them, may limit grain filling. If the sink strength of Jing9428 was weak, it might have exerted a negative feedback on carbon partitioning to the grains. As a result, soluble sugar concentration in stems should have kept a high level during the rapid grain growth. We did find such

Table 2. Leaf area index (LAI) and net photosynthesis rate (Pn, mg CO_2 dm^{-2} h^{-1}) during grain filling of two wheat cultivars Pn was measured under atmosphere CO_2 concentration from 09:30 to 12:00 when the PAR was 1021 ± 56 μmol m^{-2} s^{-1}. Data are the average of three replicates with standard deviation.

	At anthesis		14 days after anthesis		21 days after anthesis	
Cultivars	**LAI**	**Pn**	**LAI**	**Pn**	**LAI**	**Pn**
CAU3291	4.4 ± 0.7	24.5 ± 3.1	4.6 ± 0.5	27.2 ± 2.7	2.5 ± 0.5	10.2 ± 2.1
Jing9428	4.1 ± 1.1	26.3 ± 2.4	4.1 ± 0.6	28.1 ± 3.1	2.8 ± 0.8	15.9 ± 3.4

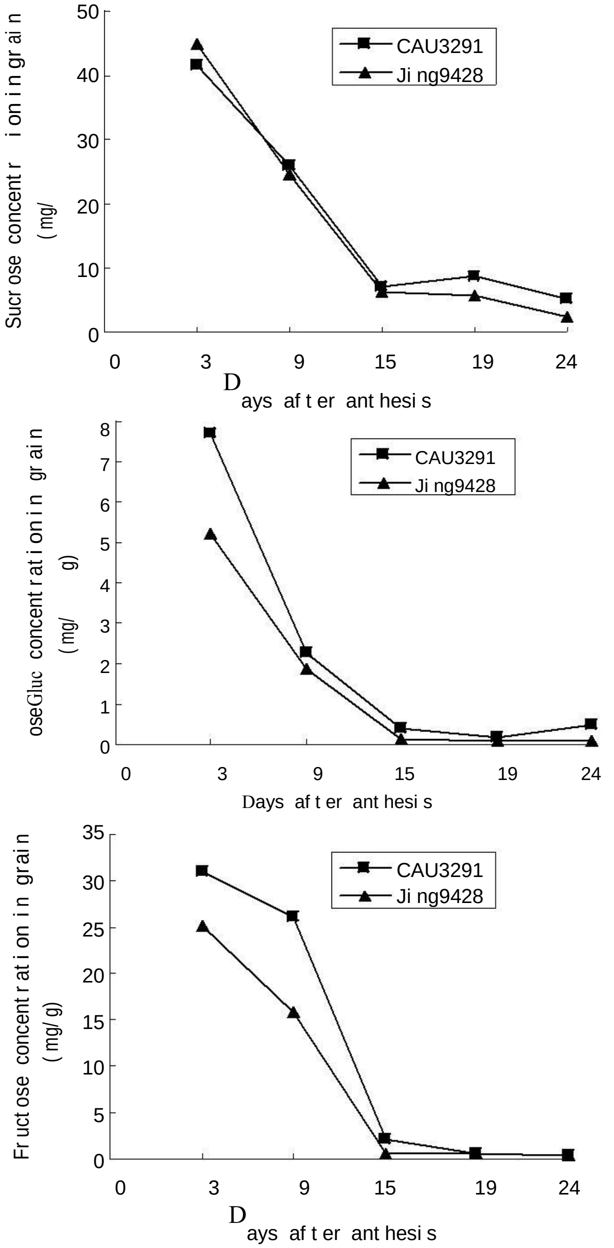

Figure 3. Sucrose (upper), Glucose (middle) and Fructose (lower) concentrations in grains of two wheat cultivars during grain filling stage (l.s.d.(0.05) is 2.07, 1.63, and 2.83 for sucrose, glucose, and Fructose, respectively).

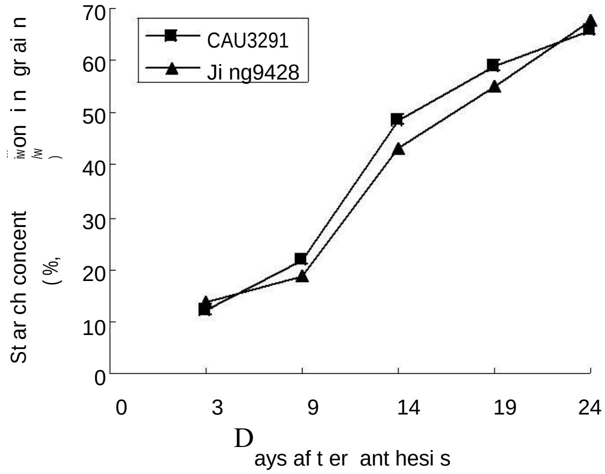

Figure 4. Starch accumulation in grains of two wheat cultivars (l.s.d.(0.05) = 2.94%).

phenomenon in the previous study in which the big-spike, stay-green cultivar LZ953 accumulated large amount of soluble sugar in stems (Mi et al., 2002). However, it seemed not the same case as in Jing9428 in which soluble sugar concentration decreased sharply during the linear grain growth phase (Figure 2). Bonnett and Incoll (1993) demonstrated in barley that there was an earlier loss of carbohydrate from the stem of plants when the incident radiation was halved and the photosynthetic input considerably reduced. Therefore, the slow grain filling rate in Jing9428 may be contributed to insufficient photosynthate supply rather than sink strength. Indeed, the LAI and Pn of leaves in Jing9428 were almost the same as in CAU3291 (Table 2), though the grain weight potential of the former was much more than that in the later (Figure 1, Table 1).

Consequently, the soluble sugar supply at the late grain filling stage was insufficient in Jing9428 in comparison to CAU3291 (Tab. 3). Blade and Baker (1991) also reported that large-seeded cultivars are more sensitive to assimilated supply.

In general, there are two ways to increase carbohydrate supply during grain filling, that is, longer leaf area duration (LAD) or higher net photosynthesis rate (Pn). Stay-green has been proven an effective trait in high-yielding corn breeding (Lee and Tollenaar, 2007; Mi et al., 2007).

Table 3. Ratio of starch to sucrose, glucose, and Fructose in grains of two wheat cultivars.

		Days after anthesis				
		3	**9**	**14**	**19**	**24**
Starch/sucrose	CAU3291	3	8	68	67	124
	Jing9428	3	8	69	95	266
	T-Test	NS	NS	NS	**	**
Starch/glucose	CAU3291	16	96	1274	3271	1339
	Jing9428	27	99	3923	5505	6765
	T-Test	NS	NS	**	**	**
Starch/Fructose	CAU3291	4	8	231	920	1526
	Jing9428	6	12	771	1059	2255
	T-Test	NS	NS	**	**	**

**: significant at 0.05 level, NS: not significant.

In wheat, high-yielding big-spike cultivars which had a longer LAD were also developed in East China where the weather is suitable for a long grain filling pe-riod (about 40 days) (Jiang and Li, 1993). In North China, however, the hot dry wind during late grain filling stage may kill the plants before the grains reach normal maturity. So, increasing Pn should be a promising way to improve such big-grain cultivars as Jing9428.

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