



Heat Stress Differentially Regulates Wheat Genotypes in Respect of the Contribution of Culm Reserves to Grain Yield

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ABSTRACT

Grain filling determines the grain weight, a major component of grain yield in cereals. Grain filling in wheat depends on current assimilation and culm reserves. A field experiment was conducted at the Field Lab, Department of Crop Botany, Bangladesh Agricultural University, Mymensingh during October 2013–May 2014 to study the grain filling patterns and the contributions of culm reserves to grain yield under heat stress. The experiment consisted of two factors—wheat cultivars (10 cultivars) and heat treatments (control and heat stress). Heat stress was imposed by late sowing (Dec 20); the seeds were sown in normal time (Nov 15) for control. The tillers were sampled once a week during grain filling period to determine the changes in dry weights of different parts, viz., leaves, culm with sheath, spikes, and grains; and to examine the contribution of culm reserves to grain yield. The result in this experiment revealed that the grain yield was reduced by 3–49% due to the stress. The reduction in grain yield was attributable mainly to lighter grain weight due to the stress. Heat stress drastically reduced the grain filling duration by 25–40%. However, the stress increased the grain filling rate by 6–60%. The stress induced early leaf senescence indicated as the decline in SPAD readings. The result indicates less contribution of current assimilation to grain yield under the stress. However, the duration of stay green of leaves varied with the cultivars. The amount of reserves remobilized to grain varied among the cultivars ranging from 0.52 to 1.2 g spike⁻¹ in control and from 0.44 to 0.97 g spike⁻¹ in stressed plants. The stressed wheat plants exhibited lower accumulation of reserves in culm but they showed almost its complete remobilization to the grain. The contribution of culm reserves to grain yield varied from 33 to 67%, and 36 to 61% in control and in stressed plants, respectively. In conclusion, culm reserves is the important attributes in grain yield in Bangladeshi wheat cultivars but the contribution remains almost unaffected due the post-anthesis heat stress.

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Introduction

Wheat (*Triticum aestivum* L.) is the second most important cereal crop in Bangladesh after rice. The annual production of wheat in Bangladesh is about 1.1 million metric tons with the average yield of 3.13 metric tons ha⁻¹ (BBS, 2019); much lower than the world average. The lower yield in Bangladesh is usually blamed on heat stress especially during grain filling period (Hossain *et al.*, 2009a, 2011a, 2013). In addition, the temperature in Bangladesh is increasing (Poulton and Rawson, 2011) and will likely affect the wheat production more adversely in future. Therefore, it needs to explore the tolerant genotypes that will ensure higher grain yield under high temperature especially during grain filling. The grain yield in wheat depends on grain number per unit area and individual grain weight. The

grain number is mainly determined during the period immediately previous to anthesis and the individual grain weight is defined during the grain filling period (from anthesis to physiological maturity). The grain filling starts with the division of endosperm cells followed by the increase in cell volume through the accumulation of assimilates. The cell division defines the final number of endosperm cells per grain and thereby the potential grain weight. The assimilate for grain filling comes from current assimilation (and subsequent direct translocation to grains) and storage (reserve) pools in vegetative plant parts, especially in the culms (Singh and Jenner, 1984). Water-soluble carbohydrates (WSCs) are considered as the main culm reserves, which may accumulate prior to anthesis and during the initial period of grain filling; and subsequently, they remobilize to

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developing grains (Takahashi *et al.*, 1993, Hossain *et al.*, 2009b, 2010, 2011b). Heat stress induces early leaf senescence (Reynolds *et al.*, 2001) which reduces or restricts the current assimilation (Tahir and Nakata, 2005). Under such condition, due to the lack of source grain filling largely depends on the culm reserves remobilized to grains. Furthermore, heat stress accelerates the remobilization of culm WSCs to grains (Tahir and Nakata, 2005). Therefore, culm WSCs can act as a buffer to maintain a steady rate of grain filling under heat stress. Thus, potential accumulation of WSCs in culm and its subsequent remobilization to grains might be a key determinant for sound grain filling under heat stress during grain filling period. The genotypes having higher ability to accumulate more WSCs in culms with higher efficiency of its remobilization would be more tolerant to heat stress especially during grain filling period. Though wheat crops in almost all regions of Bangladesh experience such stress almost every year, the research on wheat in respect to the tolerance of Bangladeshi wheat genotypes to heat stress is very limited (Hossain *et al.*, 2009a, 2011a, 2013). However, there is no information about the accumulation and remobilization of culm reserves to grains in Bangladeshi wheat genotypes under heat stress. Therefore, a research was undertaken to (i) study the grain filling pattern of Bangladeshi wheat cultivars under heat stress during grain filling, and (ii) evaluate the wheat cultivars in respect of the contribution of culm reserves under the heat stress.

Materials and Methods

A field experiment was conducted at the Field Lab, Department of Crop Botany, Bangladesh Agricultural University, Mymensingh during October 2013–May 2014. Ten wheat cultivars (Akbar, BARI Gom18, BARI Gom19, BARI Gom20, BARI Gom21, BARI Gom22, BARI Gom23, BARI Gom24, BARI Gom25, and BARI Gom26) were grown under heat treatments in the field in a two-factorial randomized complete block design (RCBD) with three replications. The seeds of wheat genotypes were collected from Regional Wheat Research Centre, BARI, Gazipur; and were sown on Nov 15, and Dec 20, 2013 for control and heat stress treatment, respectively. The wheat crops were grown following the standard cultivation techniques (Mandal *et al.*, 2011).

Ten plants (tillers) were sampled once a week during grain filling period. Grain filling period was defined as the duration from anthesis to physiological maturity. The date of anthesis was determined when the anthers extruded in 50% of the spikes in the field and the date of physiological maturity was the day when the grain attained its maximum weight. Leaf greenness was measured with a chlorophyll meter (SPAD-502; Konica

Minolta Sensing Inc., Osaka, Japan) at each sampling dates. The plants were separated into culm with sheath, leaves, and spike; oven dried and weighed. The grains were separated from spike, counted and weighed to determine the individual grain weight and grain growth patterns. The culms with leaf sheaths were milled for the measurement of water-soluble carbohydrates (WSCs) using the anthrone method (Yemm and Willis, 1954) as described in Hossain *et al.*, 2012. Contribution of culm reserves were calculated based on the remobilized reserves from culm dry matter (DM) at milk ripe and at maturity. The data on yield and its attributes of the cultivars were collected and analyzed with Microsoft excel.

Results

Yield and yield components

Table 1 shows the grain yield, biomass yield, harvest index, and yield components of ten wheat cultivars as affected by heat stress during grain filling period. The heat stress had significant effect ($P < 0.01$) on grain yield. The stress imposed the reduction in grain yield by 3–49%. The grain yield varied from 353 to 535 g m^{-2} with the mean of 452.3 g m^{-2} under control while it varied from 257 to 428 g m^{-2} with the mean of 342.3 g m^{-2} under heat stress. The order of the cultivars in respect of grain yield under control condition was as follows: BARI Gom24 (535 g m^{-2}) > BARI Gom26 (509 g m^{-2}) > BARI Gom19 (500 g m^{-2}) > BARI Gom23 (493 g m^{-2}) > BARI Gom18 (487 g m^{-2}) > BARI Gom21 (448 g m^{-2}) > Akbar (421 g m^{-2}) > BARI Gom20 (391 g m^{-2}) > BARI Gom22 (372 g m^{-2}) > BARI Gom25 (353 g m^{-2}). However, the order for grain yield under stress condition was as follows: BARI Gom23 (428 g m^{-2}) > BARI Gom18 (378 g m^{-2}) > BARI Gom20 (367 g m^{-2}) > BARI Gom22 (364 g m^{-2}) > Akbar (354 g m^{-2}) > BARI Gom26 (343 g m^{-2}) > BARI Gom25 (342 g m^{-2}) > BARI Gom24 (318 g m^{-2}) > BARI Gom21 (274 g m^{-2}) > BARI Gom19 (257 g m^{-2}). Likewise, the biomass yield showed significant differences ($P < 0.05$) among the cultivars and also between the stress treatments. It ranged from 755 to 1151 and from 717 to 917 g m^{-2} under control and stress treatment, respectively. Also, harvest index (HI) significantly ($P < 0.01$) varied with the cultivars and also with the heat stress. It ranged from 39.6 to 52.8% and from 27.4 to 50.3% under control and stress treatment respectively.

The number of spikes per square meter exhibited significant differences ($P < 0.01$) among the cultivars and also between the stress treatments with the range of 265–478, and 260–454 under control and the stress, respectively. The number of grains per spike also exhibited significant differences ($P < 0.01$) among the cultivars also between the stress with the range of 18.8–35.3, and 16.3–36.5 under control and the stress,

respectively. Seemingly, the thousand grain weight varied significantly ($P < 0.01$) with the cultivars and also with the stress treatment. It varied from 34.9 to 52.2 g with the mean of 42.6 g and from 32.6 to 44.9 g with the mean of 37.2 g under control and stressed condition, respectively. The order of the cultivars in grain weight under control was as follows: BARI Gom 24 (52.2 g) > BARI Gom23 (48.2 g) > BARI Gom21 (45.2 g) > BARI Gom18 (44.3 g) > BARI Gom19 (44.1 g) > BARI Gom26 (43.1 g) > Akbar (40.5 g) > BARI Gom22 (37.3 g) > BARI Gom20 (36.1 g) > BARI Gom25 (34.9 g). The order of the cultivars under the heat stress was as follows: BARI Gom 23 (44.9 g) > BARI Gom18 (41.9 g) > BARI Gom21 (40.1 g) > BARI Gom26 (39.1 g) > Akbar (36.7 g) > BARI Gom20 (35.4 g) > BARI Gom19 (33.9 g) > BARI Gom24 (33.5 g) > BARI Gom22 (33.4 g) > BARI Gom25 (32.6 g).

Grain growth

The grain growth measured with the changes in grain dry weight during the grain filling period is shown in Fig. 1. The grain dry weight increased slowly during initial days of grain filling followed by a rapid increase until physiological maturity (PM) in almost all cultivars. However, the increasing patterns varied with the cultivars and also with the heat treatments. The stressed wheat plants exhibited sharper grain growth from the early phase of grain filling with earlier cessation of grain growth resulting in lighter grain weight at maturity compared to control. The cultivars with higher grain yield

(e.g. BARI Gom24, BARI Gom23, BARI Gom19 etc.) showed comparatively sharper trends compared to the cultivars with lower grain yield (e.g. BARI Gom20). BARI Gom23, BARI Gom18, and BARI Gom21 possessed sharper grain growth under stress condition compared to other cultivars. In addition, there was variation in the cessation of grain growth among the cultivars.

Phenological characters:

Table 2 represents the phenological characters like days to anthesis, days to physiological maturity and grain filling duration; and average grain filling rate of ten wheat cultivars under control and heat stress. The grain filling period (GFP) significantly varied ($P > 0.001$) with the cultivars and the stress treatments. It ranged from 41.0 to 56.0 days (d) with the mean of 48.4 d under control. Heat stress drastically reduced the grain filling duration. GFD ranged from 27.3 to 33.0 d with the mean of 29.8 d under the heat stress. Wheat cultivar, Akbar possessed longest grain filling period (56 d) and BARI Gom23 possessed shortest period (40.7 d) under normal sowing while BARI Gom20 possessed longest grain filling period (33 d) and BARI Gom24 possessed shortest period (27.3 d) under heat stress. The days to anthesis showed significant ($P > 0.001$) differences among the cultivars and also between the heat treatments. It ranged from 59 to 73 d and from 66 to 70 d under control and stress condition, respectively.

Table 1. Grain yield, biomass yield, harvest index, and yield attributes in ten wheat cultivars as affected by heat stress during grain filling period.

Cultivars	Heat stress	Grain yield (g m ⁻²)	Biomass yield (g m ⁻²)	Harvest index (%)	Number of spikes m ⁻²	No. of grains spike ⁻¹	1000-seed weight (g)
Akbar	Control	421	796	47.8	441	21.3	40.5
	Stressed	354	714	49.4	298	32.7	36.7
BARI Gom18	Control	487	865	47.6	451	20.4	44.3
	Stressed	378	751	50.3	327	27.9	41.9
BARI Gom19	Control	500	1151	39.6	454	22.8	44.1
	Stressed	257	912	27.4	454	16.3	33.9
BARI Gom20	Control	391	802	42.7	446	21.3	36.1
	Stressed	367	910	40.8	331	31.4	35.4
BARI Gom21	Control	448	874	46.6	478	18.8	45.2
	Stressed	274	717	38.1	295	23.1	40.1
BARI Gom22	Control	386	770	44.1	364	25.0	37.3
	Stressed	364	781	46.9	334	32.8	33.4
BARI Gom23	Control	493	853	52.8	387	24.6	48.2
	Stressed	428	917	47.9	325	30.6	44.9
BARI Gom24	Control	535	1024	47.4	265	35.3	52.2
	Stressed	318	813	39.3	260	36.5	33.5
BARI Gom25	Control	353	755	42.5	365	25.7	34.9
	Stressed	342	772	44.3	364	28.8	32.6
BARI Gom26	Control	509	974	47.4	398	27.1	43.1
	Stressed	342	773	41.1	314	25.8	39.1
Significance (F value)	Cultivar (C)	1.72 ^{NS}	2.22*	8.76**	4.77**	7.49**	22.8**
	Stress (S)	38.8**	4.89*	10.25**	29.4**	17.8**	100.3**
	CxS	2.32*	1.16 ^{NS}	2.83*	2.24*	2.80*	9.43**

*, ** Significant at 5% and, 1% level of significance, respectively. NS: non-significant

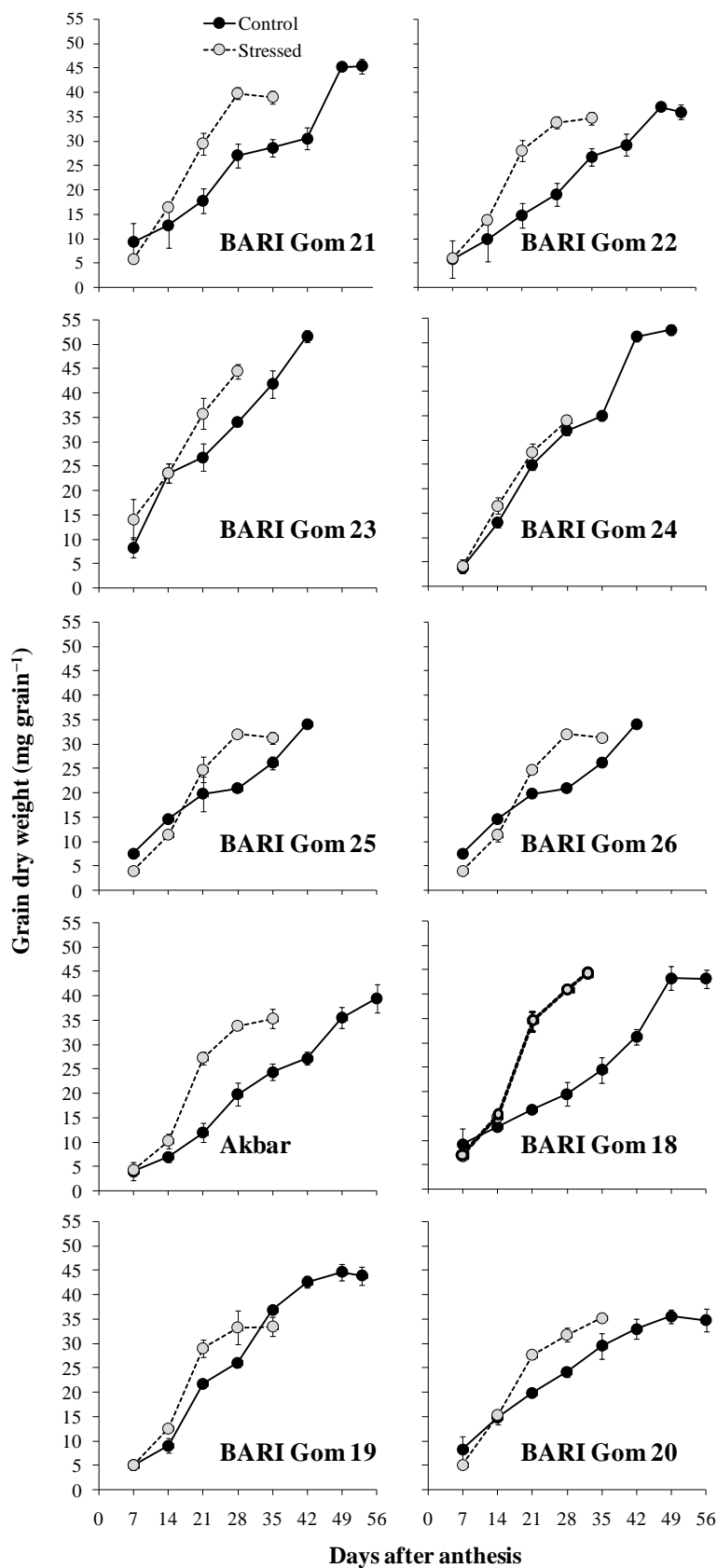


Figure 1. Grain growth patterns in ten wheat cultivars as affected by heat stress during grain filling period. The vertical bars represent SEM (n=3)

Table 2. Phenological characters, grain filling rate and maximum grain weight in ten wheat cultivars as affected by heat stress during grain filling.

Cultivars	Heat stress	Grain filling duration (d)	Days to anthesis (d)	Days to physiological maturity (d)	Grain filling rate (mg grain ⁻¹ d ⁻¹)	Maximum grain weight (mg grain ⁻¹)
Akbar	Control	56.0	62.0	118.0	0.71	39.46
	Stressed	31.7	65.7	97.3	1.11	35.17
BARI Gom18	Control	53.7	61.0	114.7	0.81	43.12
	Stressed	31.7	67.3	99.0	1.38	43.75
BARI Gom19	Control	50.3	71	121.3	0.90	43.82
	Stressed	28.3	69.3	97.7	1.29	36.51
BARI Gom20	Control	51.3	62.0	113.3	0.69	35.51
	Stressed	33.0	66.0	99.0	1.067	35.21
BARI Gom21	Control	52.0	62.0	114.0	0.90	46.73
	Stressed	31.0	66.7	97.7	1.30	40.02
BARI Gom22	Control	50.0	59.0	109.0	0.74	36.91
	Stressed	29.7	66.0	95.7	1.18	34.73
BARI Gom23	Control	41.0	73.0	114.0	1.26	51.58
	Stressed	28.3	69.7	98.0	1.57	44.39
BARI Gom24	Control	45.0	69.0	114.0	1.17	52.54
	Stressed	27.3	69.7	97.0	1.24	33.93
BARI Gom25	Control	41.0	68.0	109.0	0.83	34.07
	Stressed	29.7	66.0	95.7	1.12	32.97
BARI Gom26	Control	43.3	71.0	114.3	1.08	46.59
	Stressed	27.7	70.3	98.0	1.53	42.29
Significance (F value)	Cultivar(C)	18.65***	579.4***	7.59***	32.0***	20.97***
	Stress (S)	1356***	448.0***	1111***	287.6***	61.22***
	C×S	7.12***	177.5***	4.197***	4.46***	7.13***

***Significant at a 0.1% level of significance

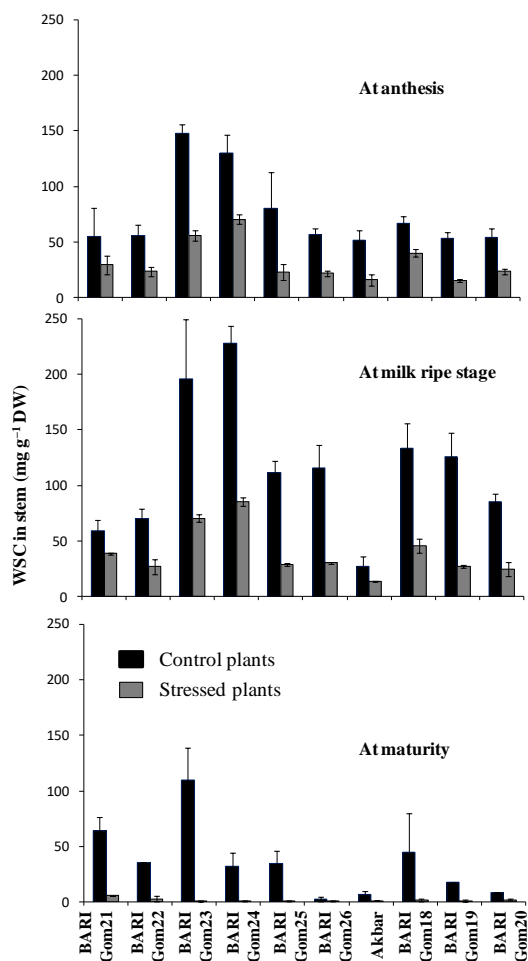


Figure 2. Water soluble carbohydrates (WSCs) in culms at anthesis, milk ripe and maturity in ten wheat cultivars as affected by heat stress during grain filling period. The vertical bars represent SEM (n=3)

The days to physiological maturity (PM) also varied significantly ($P > 0.001$) with the cultivars and with the stress treatment. It ranged from 109 to 121 d and from 96 to 99 d under control and stress condition, respectively. BARI Gom19 required the longest time (121 d) and BARI Gom22 and BARI Gom25 required the shortest time (109 d) to attain PM. The average grain filling rate exhibited significant ($P > 0.001$) variation among the cultivars. It also varied with the heat treatment. The range and mean of average grain filling rate are 0.67–1.23 and 0.88 mg grain⁻¹ day⁻¹, respectively under normal sowing. The heat stress increased the grain filling rate with the range and mean of 1.07–1.57 and 1.28 mg grain⁻¹ day⁻¹, respectively. Generally, the high yielding cultivars (e.g. BARI Gom24, BARI Gom23, BARI Gom26 etc.) showed comparatively higher grain filling rate compared to the low yielding cultivars (e.g. BARI Gom20).

Culm reserves

Figure 2 shows the changes in water-soluble carbohydrates (WSCs), the main reserves in culms, at anthesis, milk ripe and maturity of ten wheat cultivars under heat stress during grain filling period. There were large variations in the content of WSCs in culm at different times during grain filling. The increase in WSCs content in culm shows post-anthesis accumulation of culm reserves and the decrease in WSCs contents shows the remobilization of the reserves to the grains. The WSCs content at anthesis varied from 51.5 to 147.8 and from 15.7 to 70.7 mg g⁻¹ culm dry mass under control and stress environment, respectively. The WSCs content at milk ripe stage varied from 27.4 to 227.7 and from 14.1 to 85.64 mg g⁻¹ culm dry mass under control and stress environment, respectively. The highest value of WSCs content was recorded in BARI Gom24 and the lowest value in Akbar. In general, high yielding cultivars possessed higher WSCs content at milk ripe compared to low yielding cultivars. The cultivars also exhibited large variations in the residual WSCs content in culm at maturity. The residual WSCs in culm ranged from 3 to 138 mg g⁻¹ culm dry mass. The highest value was recorded in BARI Gom23 and the minimum was in BARI Gom26. Under stress environment, the remobilization was largely influenced resulting almost no residual WSCs in culm at harvest irrespective of cultivars.

Discussion

Wheat cultivars used in this experiment exhibited significant variations in grain yield and yield attributes. The heat stress imposed by late sowing significantly reduced grain yield (Table 1). Grain yield in wheat is determined by 3 yield components—number of spikes per m², number of grains spike⁻¹ and 1000-grain weight.

Though all the components showed significant variations in F test, the F value indicates that grain weight is the most important components for the variations and also for reduction in grain yield (Table 1).

Grain weight is determined during the grain filling period, the period between anthesis and physiological maturity. Grain filling is the accumulation assimilates in grains during the grain filling (Austin *et al.*, 1980). The assimilates for grain filling come from current photosynthesis and stored reserves in culm (Austin *et al.*, 1980; Hossain *et al.*, 2011b). In this study, wheat cultivars producing higher grain yield (BARI Gom23, BARI Gom24, BARI Gom26, etc.) showed sharper grain growth from anthesis towards physiological maturity (Figure 1) with increased grain filling rate (Table 2) compared to low yielders (BARI Gom22, BARI Gom25, etc.) which resulted in heavier grains (Figure 1) in the high yielding cultivars. The difference in grain filling among the cultivars could be accounted for by the difference in post-anthesis carbon assimilation and culm reserves remobilized to grains (Takahashi *et al.*, 1993; Hossain *et al.*, 2009b; Islam *et al.*, 2016, 2018, Rana *et al.*, 2017, Karim *et al.*, 2018). Carbon assimilation can be monitored by the changes in total dry mass (Hossain *et al.*, 2009b). The high yielding cultivars usually exhibited greater accumulation of TDM compared to low yielding ones (data not shown). Moreover, high yielding ones had the ability to retain leaf greenness longer time after anthesis compared to low yielders (data not shown). These results indicate that high yielder usually contributed more to fill the grain through current assimilation compared to the low yielders (Takahashi *et al.*, 1993; Hossain *et al.*, 2009a).

The culm reserves play a vital role in buffering grain yield when current assimilation is restricted as senescence due to heat stress (Tahir and Nakata, 2005). The culm elongates and stores water-soluble carbohydrates (WSCs) during initial and early period of grain filling (from anthesis to milk ripe, at around 14 days after anthesis) and they are remobilized to grains during the late and final period (from milk ripe to maturity) (Takahashi *et al.*, 1993). There were wide variations in the accumulation and remobilization of culm WSCs among the cultivars studied. Usually, high yielders had the ability to accumulate more WSCs in culms with the variant degree of remobilization and contribution to grain yield. For example, the culm of BARI Gom24 contained 228 mg WSCs g⁻¹ Culm DW at milk ripe stage while it contained 48 mg WSCs g⁻¹ Culm DW at maturity contributing 180 mg WSCs g⁻¹ Culm DW for final grain weight. In contrary, Akbar contained 27 and 7 mg WSCs g⁻¹ Culm DW in its culm at milk ripe and maturity, respectively indicating only 20 mg g⁻¹ Culm DW WSCs for final grain weight. However, the accumulation and

remobilization were largely influenced by the heat stress (Fig. 2). Though the accumulation of culm reserves was greatly reduced by the stress the remobilization was highly increased. The cultivars having ability to accumulate more Culm reserves like BARI Gom 23, BARI, Gom 18, etc. exhibited better in respect of grain yield under the stress. However, further researches especially in different seasons and locations are needed to confirm the tolerance of the cultivars to heat stress in respect of culm reserves dynamics.

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Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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