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GRAIN FILLING AND CONTRIBUTION OF CULM RESERVES TO GRAIN YIELD IN RICE

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Abstract

To study the grain filling and contribution of culm water soluble carbohydrates (WSCs) on yield, three rice cultivars - Lucky *dhan* (traditional), BRRI *dhan*29 (modern) and SL-8H (hybrid) were used as experimental materials. The grain yield was highest in SL-8H followed by BRRI *dhan*29 and the lowest in Lucky *dhan*. The maximum and residual amounts of culm WSCs in Lucky *dhan*, SL-8H, and BRRI *dhan*29 were 33, 21 and 8 mg/culm; and 12, 6 and 4 mg/culm, respectively. The amount of remobilized culm WSCs in grain and the remobilization efficiency in Lucky *dhan*, SL-8H, and BRRI *dhan*29 were 21, 15, and 4 mg/culm; and 63, 73, and 52%, respectively. The grain filling duration was higher in Lucky *dhan* and SL-8H than in BRRI *dhan*29. Grain filling rate was highest in SL-8H followed by BRRI *dhan*29 and lowest in Lucky *dhan*. The higher grain yield in SL-8H was attributable to the higher grain filling rate with longer grain filling duration. The remobilized culm WSCs had little impact on the variation of grain yield among the rice cultivars.

Introduction

Rice (*Oryza sativa* L.) is the staple food of ca. 160 million people of Bangladesh. It provides 35-60% of dietary calories to more than 3 billion people of the world (Fageria 2007). Rice is the agricultural commodity with the fourth-highest worldwide production, after sugarcane, mixed grasses and legumes and maize (FAOSTAT 2013). Total rice production in Bangladesh was ca. 10.6 million tons in the year 1971; in contrast the present production is ca. 33.9 million tons (BBS 2014). This increased rice production has been possible largely due to the adoption of modern rice cultivars on around 80% of the rice land which contributes about 90% of the country's total rice production (BRRI 2013).

The grain yield in rice can be described as the product of 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) (Fischer 1985). Grain weight is the product of rate and duration of grain filling (Yang *et al*. 2008). The grain filling starts with the division of endosperm cells followed by the increase in cell volume through the accumulation of assimilate (Singh and Jenner 1984). 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 developing grains (Ehdaie *et al*. 2006a, b, 2008, Bingham *et al*. 2009). Most of the culm WSCs are remobilized to the grains when current assimilation is restricted leading to senescence (Tahir and Nakata 2005). Hence, the grain filling depends on two major sources of carbon, namely current photosynthesis in leaves and to some extent in inflorescence, and mobilization of stored WSCs from culm to growing grains. When the current photosynthesis is depressed by stresses like drought (Ehdaie *et al*. 2008), high temperature

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(Tahir and Nakata 2005), and foliar diseases (Serrago *et al*. 2011) grain filling becomes more dependent on mobilized WSCs, and thereby WSCs act as buffers to have a steady rate of grain filling under the post-anthesis stresses by accelerating the remobilization of culm WSCs to grains. The amount of accumulated and mobilized culm reserves is estimated either by monitoring the changes in culm dry weight (Ehdaie *et al*. 2006a) or directly by measuring culm WSCs content during the grain-filling period (Ehdaie *et al*. 2006b). Post-anthesis changes in dry weight and WSCs content of the main culm of a diverse set of wheat cultivars indicated that estimation of the amount of culm reserves, accumulated and mobilized, was dependent on genotype, experimental conditions and the method of measuring reserves (Ehdaie *et al*. 2006a, b). Information on the grain filling in rice is very scanty (Yang *et al*. 2008); hitherto, there is no published report on grain filling physiology of Bangladeshi rice cultivars. Therefore, the present study was undertaken to study the grain filling and contribution of culm reserves to grain yield in Bangladeshi rice cultivars.

Materials and Methods

The experiment was conducted at the Field Laboratory, Department of Crop Botany, Bangladesh Agricultural University, Mymensingh (24°75' N latitude and 90°50' E longitude) during December, 2012 - May, 2013. The cultivars of rice used for the study were Lucky *dhan* (traditional), BRRI *dhan*29 (modern) and SL-8H (hybrid). The experiment was laid out as single factor experiment in RCBD with 3 treatments and 3 replications. Healthy rice seedlings of 35 days old were transplanted on 21 December, 2012 at the spacing of 20 cm × 15 cm. The standard rice cultivation procedure was followed as described by BRRI (2013).

Ten effective tillers were sampled once a week during grain filling period for all cultivars. 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 panicle in the field and the date of physiological maturity was the day when the grain attained its maximum weight. The tillers were separated into culm with sheaths, leaves, and panicle. All the plant parts were heated for 30 min at 110°C and dried for 48 hrs at 70°C, and finally weighed after cooling. The grains were separated from the panicle and weighed. Average rate of grain filling was estimated as maximum grain weight divided by duration (Julian days), assuming that grain weight was zero at anthesis. The culms with leaf sheaths were milled for the measurement of water-soluble carbohydrates (WSCs) using the anthrone method as described below. The plants in a 1.0 m^2 (1.0 × 1.0 m) area were harvested at 80% ripening stage (maturity) for yield and yield components in all cases. The panicles were counted and the plants were dried for 48 hrs at 80°C and weighed to determine the biomass yield. All panicles were hand-threshed and dried at 14% moisture level and weighed for grain yield. One thousand grains were counted and weighed to determine 1000-grain weight. The harvest index was calculated as the grain yield divided by total dry mass. The number of grains per panicle was calculated as the grain yield divided by panicle number and 1000-grain weight.

The WSCs in culms (with leaf sheaths) were extracted and measured using anthrone method (Yemm and Willis 1954) as described in Hossain *et al*. (2011). The dried culm were chopped and milled to a rough powder. The culm powder was weighed and extracted once with 80% ethanol at 60°C for 30 min followed by 2 successive 15 min extractions with distilled water at 80°C. The extracts were combined and evaporated to dryness at 65°C. The dried carbohydrates were dissolved in 10 ml distilled water. A fraction of the extract solution (about 1 ml) was taken in a Micro-centrifuge tube (1.5 ml) and charcoal powder was added to it. After mixing the powder and extract solution with a vortex (touch mixer), the solution was centrifuged at 5000 rpm for 5 min to make a clear solution. The clear solution was diluted 5-10 times with distilled water. Diluted solution (0.10 ml) was mixed with ice-cold anthrone reagent (5.0 ml). The mixture was heated for

10 min in a boiling-water bath and subsequently cooled with ice water. The absorbance of the reacted solution for standard and samples was measured with a spectrophotometer at 620 nm. The content of WSCs in the sample was calculated as mg WSCs per gram of culm dry mass using regression equation. The amount of WSCs in culm at anthesis, milk ripe and maturity was estimated based on the dry mass of culm harvested at respective stages. The amount of remobilized culm WSCs was estimated from the difference between total culm WSCs at milk ripe/anthesis (maximum WSCs content) and residual culm WSCs at maturity as described by Ehdaie *et al*. (2006a).

All data on yield, phenological characters and average grain filling rate were subjected to single factor (cultivar) analysis of variance in RCBD. Data on other parameters were analyzed by calculating means and standard errors of means (SEM).

Results and Discussion

The rice cultivars showed significant variation in grain yield (Table 1). The hybrid cultivar, -SL-8H produced the highest grain yield (5.97 t/ha) and Lucky *dhan* produced the lowest yield (4.50 t/ha). The grain yield in rice as in other cereals was determined by the number of grains per unit area and the grain weight. The grain weight is one of the most important components for the variation of grain yield in this study as it was significantly ($p < 0.01$) varied with the cultivars. The heaviest grain was produced by SL-8H (27.2 mg/grain) followed by Lucky *dhan* (21.1 mg/grain) and the lightest by BRRI *dhan*29 (20.9 mg/grain) (Table 1).

Table 1. Grain yield, grain weight, and grain filling parameters in three rice cultivars.

Cultivar	Grain yield (t/ha)	Grain weight (mg/grain)	Grain filling duration (d)	Gain filling rate (mg/grain/d)	Remobilization efficiency of culm WSCs (%)
BRRI *dhan*29	5.63	20.9	21	0.72	52.0
Lucky *dhan*	4.50	21.1	28	0.64	63.0
SL-8H	5.97	27.2	28	0.83	73.0
Significance	*	**	**	**	*

*Significant at $p < 0.05$, **Significant at $p < 0.01$.

The grain weight at harvest is determined by the rate and duration of grain filling, the period between anthesis and physiological maturity period (Yang *et al*. 2008). The grain filling patterns in three cultivars are shown in the Fig. 1. The grain dry weight increased very slowly during initial days of grain filling followed by a rapid increase until physiological maturity in almost all cultivars (Hossain *et al*. 2011). The cultivar with higher grain yield i.e. SL-8H showed sharper trend of grain filling compared to the cultivars with lower grain yield (e.g. BRRI *dhan*29 and Lucky *dhan*) (Fig. 1). The rate of grain filling exhibited significant variation among the cultivars (Table 1). Hybrid, SL-8H showed maximum grain filling rate (0.83 mg/grain/d) and Lucky *dhan* showed the minimum rate (0.64 mg/grain/d). In addition, grain-filling period varied with the cultivars (Table 1). It was longer in Lucky *dhan* and SL-8H (28 days) compared to that in BRRI *dhan*29 (21 days). In this study, SL-8H showed sharp trend in grain growth with longer duration and higher rate compared to BRRI *dhan*29 and Lucky *dhan* which resulted in heavier grains in SL-8H at maturity (Fig. 1, Table 1).

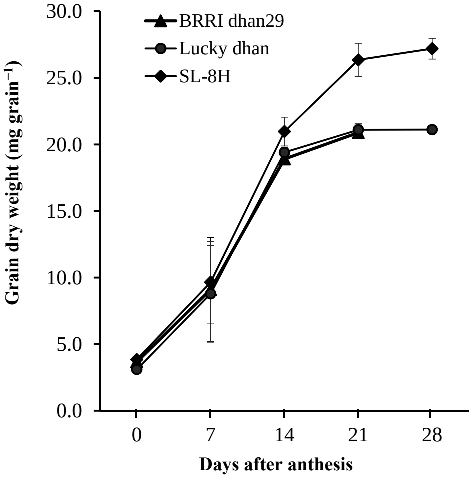

Fig. 1. Grain growth pattern in three rice cultivars showing LSD values against different days after anthesis.

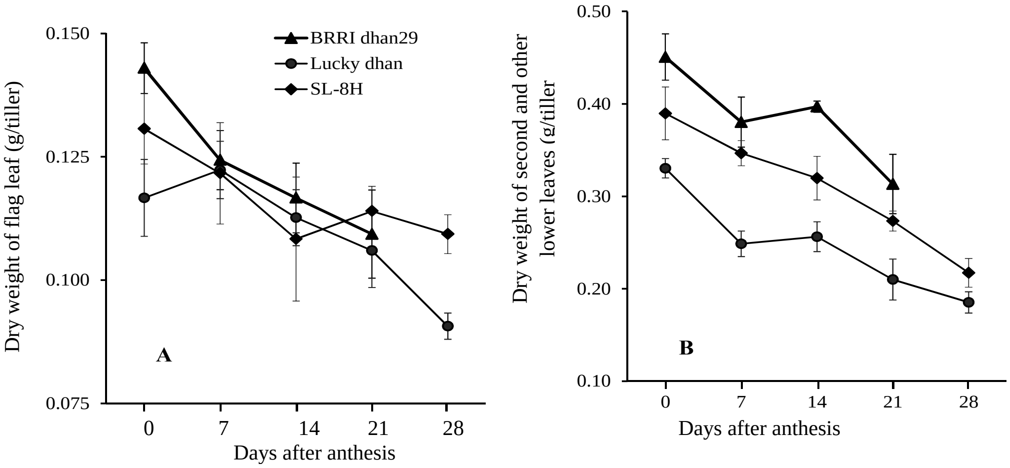

Fig. 2. Changes in dry weight of flag leaf (A), second and other lower leaves (B) during grain filling period in three rice cultivars showing LSD values against different days after anthesis.

Changes in dry weights of leaves varied with the cultivars (Fig. 2). At the anthesis, the dry weight of flag leaf was higher in BRRI *dhan*29 followed by SL-8H than in Lucky *dhan*. Flag leaf dry weights increased from anthesis until 7 days after anthesis (DAA) followed by decreasing trends in almost all cultivars. The changes in dry weights of other lower leaves showed the pattern more or less similar to that in flag leaf dry weight. The changes in total dry mass (TDM) during the grain-filling period varied with the rice cultivars (Fig. 3). The cultivars, SL-8H and Lucky *dhan* exhibited higher TDM at anthesis compared to BRRI *dhan*29. SL-8H and Lucky *dhan* showed gradual increase in TDM from anthesis until 14 DAA followed by showing more or less unchanged patterns towards the maturity. The cultivars also showed variation in changes of culm dry weight during the grain filling period (Fig. 4A). Increase in culm dry weight indicates the accumulation of culm reserves and the decrease in weight indicates the remobilization of reserves to the grain (Takahashi *et al*. 1993). Generally, culm dry weights increased from anthesis to 7 DAA followed by the decreasing trend towards maturity in SL-8H and Lucky *dhan* except in BRRI *dhan*29 which showed decreasing trend from the anthesis. Moreover, there were variations in the content of WSCs in culm at different times during grain filling (Fig. 4B). The WSCs content was higher in SL-8H and in Lucky *dhan* (Fig. 4B) compared to BRRI *dhan*29. However, SL-8H showed the maximum remobilization efficiency (73%) and BRRI *dhan*29 showed the minimum efficiency (52%) (Table 1).

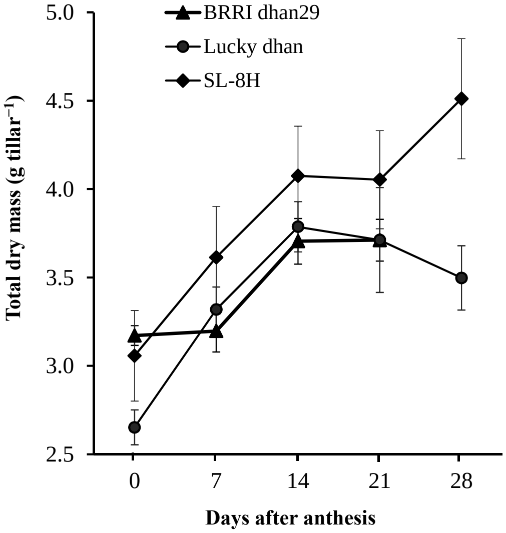

Fig. 3. Total dry mass at different days after anthesis in three rice cultivars showing LSD values against different days after anthesis.

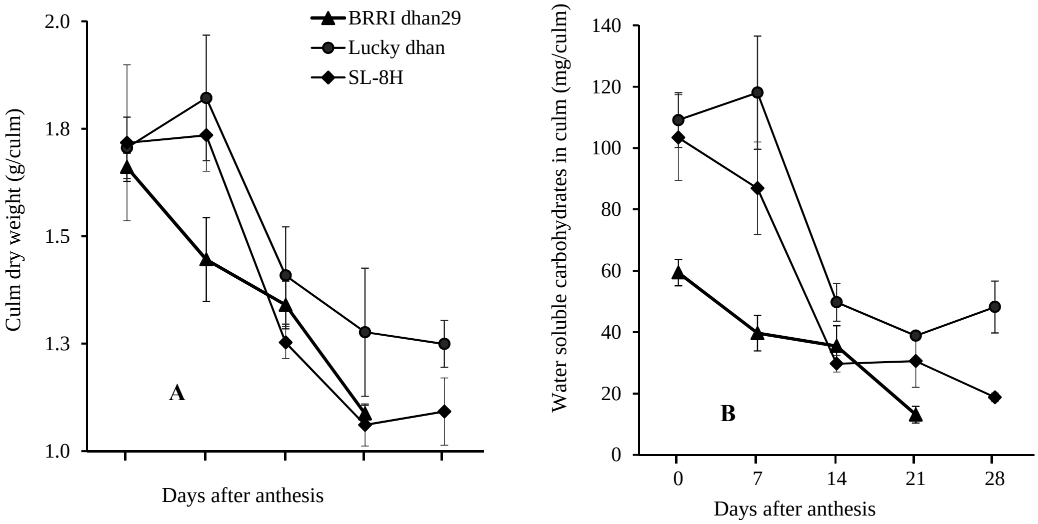

Fig. 4. Changes in culm dry mass (A) and water soluble carbohydrates in culm (B) during grain filling period in three rice cultivars showing LSD values against different days after anthesis.

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*. 2009). Carbon assimilation can be monitored by the changes in total dry mass (Hossain *et al*. 2009). The high yielding hybrid cultivar, -SL-8H exhibited greater accumulation of TDM compared to Lucky *dhan* and BRRI *dhan*29 showing higher contribution of current assimilation to grain filling (Fig. 3). The culm reserves play a vital role in buffering grain yield when current assimilation is restricted as senescence (Takahashi and Kanazawa 1996, Tahir and Nakata 2005, Ehdaie *et al*. 2006a, b, 2008). There were larger variations in the accumulation and remobilization of culm WSCs among the cultivars (Table 1). SL-8H and Lucky *dhan* had higher ability to store culm reserves compared to BRRI *dhan*29. However, SL-8H exhibited higher remobilization of culm WSCs compared to Lucky *dhan* (Table 1). The greater accumulation of culm WSCs with increased remobilization to grains might result in heavier grain and finally higher yield in hybrid rice cultivar compared to traditional and modern inbreds.

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