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Rate and duration of grain filling of aerobic rice HD297 and their influence on grain yield under different growing conditions

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ABSTRACT: Aerobic rice is grown in non-puddled soil, and it typically shows low yield, harvest index, and percentage of filled grains (PFG). In lowland rice, PFG is closely related to the grain filling patterns of superior and inferior grains. A synchronous pattern leads to high PFG. Since no studies have been done on the grain filling of aerobic rice, its effects on yield are unknown. Two field experiments were conducted simultaneously to investigate the grain filling and yield formation of aerobic rice HD297 at two contrasting sites in northern China with and without nitrogen urea (150 kg/ha) as fertilizer. Nitrogen urea (fertilizer-N) significantly improved the yield of HD297 at a low soil fertility site, but not so at a high soil fertility site. Among yield components, the number of productive tillers and PFG contributed most to the yield. Fertilizer-N and high fertility improved total dry matter and tillering, but significantly decreased PFG. Grain weight of superior grains showed a typical 'S' curve with faster filling rate, while that of inferior grains continuously increased during the filling stage with low rates. The filling pattern of HD297 was asynchronous, and was not significantly affected by the fertilizer-N or the site. Fertilizer-N had little effect on the non-structural carbohydrates (NSCs) accumulation or contribution to grain. Post-anthesis, the NSC contribution was only around 70%, suggesting an insufficient carbohydrate supply to the spikelets during the filling stage. The yield of HD297 could be increased by delaying N-dressing for longer photosynthesis, increasing plant density for more superior grains, or improving the variety for the ideal filling pattern.

KEYWORDS: inferior grain, nitrogen, non-structural carbohydrate, percentage of filled grains, superior grain

INTRODUCTION

Aerobic rice is a newly developed rice variety grown in non-puddled soil[1]. Compared to lowland rice, this system saves about 50% of irrigation water but results in significantly lower grain yield[2,3]. The reported aerobic yields in China and the Philippines range from 1600 to 6100 kg/ha[2–5] showing a severe yield limitation. Even under the best management practices for aerobic rice, its harvest index is still lower than expected, resulting in low grain yield even with total shoot biomass of more than 10 000 kg/ha[2,6,7]. The low harvest index of aerobic rice in field experiments in China has been found to correlate with a low percentage of filled grains[6]. An analysis of over 139 upland rice varieties identified the percentage of filled grains as the most important factor affecting grain yield[8]. Crop yield was determined primarily by the numbers of harvest kernels per unit of land area[9], which was related to the total amount of spikelets per unit land area and the percentage of grain filling. A significant negative correlation between the number of spikelets per unit land area and the percentage of filled grains suggests that the percentage of filled grain directly affects the filled grain number and thus the final grain yield when the total number of spikelets is sufficient[7].

The percentage of filled grains depends on the grain filling rate and grain filling duration of superior and inferior grains, which may be fast synchronous, slow synchronous, or asynchronous[10]. Rice grains at the apical primary branches of the panicle are classified as 'superior', while those at the proximal secondary branches are classified as 'inferior'[11]. Fast synchronous grain filling usually results in high yields, while slow synchronous or asynchronous grain filling usually results in relatively low yields. Equations to simulate grain filling procedure of different crops (lowland rice, wheat, etc.), such as Richard's equation[12] and 'the beta growth function'[13], can estimate grain filling rate and duration precisely. Hence, we suppose that the HD297 grain-filling pattern was either slow synchronous or asynchronous, resulting in poor grain filling and low grain yield of this variety.

Growing conditions can also influence the percentage of filled grains. In lowland rice, for example, drought stress during late panicle development sharply decreases the percentage of filled grains[14]. Reducing the irrigation (and hence increasing drought stress) decreases the percentage of filled grains in aerobic rice[6]. Nitrogen can increase rice grain yield by increasing the total dry matter production, the number of panicles, and the panicle length of lowland rice[15]. Nitrogen supply to spikelets has no direct effect on kernel number per unit land area, and it improves the supply of assimilates to the grain even in N-limited crops[16]. Usually, a relatively large proportion of fertilizer-N is applied to the rice at early vegetative growth to promote tillering, and this contributes significantly to final grain yield[17]. In lowland rice, top dressing of fertilizer-N at heading has been shown to reduce the percentage of filled grains under sufficient water supply[18]. Further studies, however, have shown that top dressing of N at heading helped the plants to maintain a high photosynthesis rate, with a subsequent significant increase of grain-filling rate, grain-filling duration, and higher percentage of filled grains, compared with basal application or top dressing of N at tillering[19]. Our results for aerobic rice in northern China show that dry matter accumulation before anthesis increases with fertilizer-N application as compared to zero N input, while both dry matter accumulation at grain-filling stage, and the percentage of filled grains decreases[7]. Thus our nitrogen management (basal fertilizer plus top dressing at tillering and panicle initiation) might have little effect on the grain filling and might relate to low percentage of grain filling. Thus the relationships between nitrogen or soil fertility and grain filling need further analysis.

This study determines the grain-filling pattern of HD297 and analyses the reason why nitrogen or soil fertility has little effect on improving the grain filling of HD297.

Table 1 Initial soil chemical and physical properties of 0–30 cm soil depth, and perched shallow groundwater depth during growing stage of aerobic rice HD297 at the Farm and the Station.

Location	Farm	Station
Total N (g/kg)	0.98	0.74
Organic matter (g/kg)	15.3	11.7
Olsen-P (mg/kg)	52	39
Available K (mg/kg)	109	60
pH	7.9	7.8
Bulk density (g/cm^3)	1.39	1.31
Soil texture	Silt loam	Sandy loam
GWD (m)	0.2–1.0	> 2.0

MATERIALS AND METHODS

Experimental site and design

Field experiments were conducted at two contrasting sites in Beijing, North China, in 2006: (1) Shangzhuang Experimental Station (39°54′N, 116°24′E, 50 m ASL) of China Agricultural University and (2) Shangzhuang Experimental Farm located 17 km from the Station. The Station was previously cultivated with maize and has a deep groundwater table, whereas the Farm was previously cultivated with lowland rice and has a shallow groundwater table. The soil texture was silt loam at the Farm and sandy loam at the Station (Table 1). At the Farm, total soil N, soil organic matter content, and available phosphorus and potassium were higher than at the Station at a soil depth of 0–30 cm. The precipitation, sunshine hours, and active cumulative temperature ($\geqslant$ 10 °C) during the growing stage were 410 mm, 962 h and 3662 °C, respectively. The daily maximum and minimum temperatures ($T_{\max}$, $T_{\min}$) during the period from 6 days before anthesis (-6 DAA) to 18 days after anthesis (18 DAA) were relatively stable (Fig. 1).

The experiments included three fertilizer-N rates and three irrigation levels[7]. The treatments were arranged in a randomized complete block design with four replications in 6 m $\times$ 10 m plots. Due to time constraints, measurements on grain filling were only made in four treatment combinations of N by irrigation: zero N and 150 kg urea-N/ha (of which 30% was applied at sowing, 40% at the onset of tillering, and 30% at panicle initiation), and two irrigation treatments (W1, W2). The irrigation treatments were guided by the soil water potential as measured at 15–20 cm depth with a tension meter. The plots were irrigated whenever the soil water potential dropped below -20 kPa in W1, or below -60 kPa in W2. The

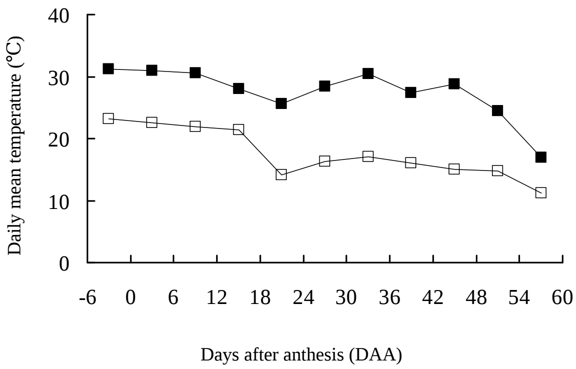

Fig. 1 Mean temperature with a six-day interval from anthesis at farm (DAA=0) and station (DAA=6) to maturity. Filled and open symbols represent $T_{\max}$ and $T_{\min}$, respectively.

aerobic rice variety HD297 was sown on 10 May at the Farm and on 11 May at the Station at the rate of 67.5 kg seed/ha in rows spaced 30 cm apart. At sowing, 24.4 kg/ha P [$Ca(H_2PO_4)_2 \cdot H_2O$], 46.5 kg/ha K (K_2SO_4), 22.5 kg/ha Fe ($FeSO_4$), and 15 kg/ha Zn ($ZnSO_4$) were applied. Rice seeds were coated with 'CAU-URSSC-upland rice special seed coating', provided by the Department of Plant Breeding at China Agricultural University, Beijing. The crop was optimally protected against pests, diseases, and weeds by use of pesticides (3% Furadan granules developed by FMC Corporation), herbicides (CAU-URSH_1 28% emulsion, upland rice special herbicide, provided by the Department of Plant Breeding at China Agricultural University, Beijing), and hand weeding. The crops were harvested on 11 October at the Farm and 13 October at the Station.

Measurements

At heading, about 100 panicles that headed on the same day were tagged in each plot. Five to ten tagged panicles from each plot were sampled at 3-day intervals from anthesis to six days after anthesis (DAA) and at 6-day intervals from 6 DAA to maturity. The grains on the sampled panicles were separated into three groups: grains on the apical position of the primary branch were labelled as superior grains, those on the low secondary branch as inferior grains[20], and the remaining in the middle were not sampled. All grains were hulled and oven-dried at 80 °C to a constant weight.

Total above-ground biomass was sampled at flowering from two rows of 0.5 m and at maturity from two rows of 1.0 m. Samples were dried at 105 °C for 15 min and then at 80 °C to a constant weight. Subsamples were taken for measuring non-structural carbohydrate, according to the method of Yoshida et al[21]. An area of 9 m^2 was harvested to determine grain yield (14% water content). The number of productive tillers, percentage of filled grains, and thousand-grain weight were also measured.

Calculation and analysis

Path-coefficient analysis was used to compare the contribution of each yield component to the grain yield[22,23]. Path-coefficient analysis is a standardized partial-regression coefficient analysis to evaluate the direct influence of one factor upon another, in which the interrelationship between concerned factors can be evaluated quantitatively[22].

Richards' equation is a commonly used growth function with which general rate parameters are deduced in a simple manner[24]. Following Zhu et al and Yang et al[12,25], we used Richards' equation to describe the grain-filling process:

$$W = A/(1 + B\mathrm{e}^{-kt})^{1/N},$$

where W is the grain dry weight at time t, A is the final grain dry weight at harvest (GW); t is the time after flowering; B, k, and N are coefficients determined by the regression with only mathematical meaning, which were used to calculate the secondary parameters of grain-filling process as follows. The active grain-filling duration (GFD, days) was defined as the days when W was from 5% (t_1) to 90% (t_2) of A. The maximum and average grain-filling rates during this period ($\mathrm{GFR}_{\max}$, $\mathrm{GFR}_{\mathrm{av}}$) were then calculated between t_1 and t_2. The time to reach the maximum grain-filling rate was $t_{\max}$. The amount of non-structural carbohydrate translocation from straw to grain (NSCT, kg/ha) $=$ NSC at anthesis $-$ $\mathrm{NSC}_{\mathrm{straw}}$ at harvest. NSC at grain filling (kg/ha) $= (\mathrm{NSC}_{\mathrm{straw}} + \mathrm{NSC}_{\mathrm{grain}}) -$ NSC at anthesis. The contribution of pre-anthesis NSC to grain is $C_{\mathrm{pre}} = \mathrm{NSCT}/\mathrm{NSC}_{\mathrm{grain}}$. The contribution of post-anthesis NSC to grain is $C_{\mathrm{post}} =$ NSC at grain filling$/\mathrm{NSC}_{\mathrm{grain}}$.

Data were analysed by the GLM (General Linear Model) procedure of the STATISTICAL ANALYSIS SYSTEM (SAS, version 8.0).

RESULTS AND DISCUSSION

Due to an unexpected heavy rainfall in the experimental year, the difference of total water input between water treatments was 100–120 mm, which account for about 10–15% of the total water input. As the statistical analysis showed no treatment effect of irrigation, and no interactions between irrigation and N,

Table 2 Grain yield, productive tillers, number of spikelets per panicle, number of spikelets per ha, the percentage of filled grains (PFG) and thousand-grain weight (TGW) of aerobic rice HD297 at the Farm and the Station as influenced by two nitrogen regimes.

	N input (kg/ha)	Grain yield (kg/ha)	Productive tillers ($\times 10^4$/ha)	Spikelets (No./panicle)	Spikelets ($\times 10^6$/ha)	PFG (%)	TGW (g)
Farm	0	4266^{aA}	244^{bA}	72^{aA}	176^{bA}	81^{aA}	29.2^{aA}
	150	4349^{aA}	306^{aA}	80^{aA}	244^{aA}	60^{bB}	27.6^{bA}
Station	0	3296^{bB}	201^{bB}	63^{aA}	127^{bB}	84^{aA}	27.5^{aB}
	150	3909^{aA}	233^{aB}	74^{aA}	172^{aB}	78^{bA}	26.1^{bB}
	N	ns	**	*	***	***	***
ANOVA	Site	***	***	*	***	***	***
	N × Site	ns	ns	ns	ns	**	ns

Data were pooled over water treatments at each site as there was no significant difference among water treatments or interaction between water and nitrogen, $n = 8$. For this table and the next, for each site, means within each column and N rate followed by the same small letters are not significantly different ($P < 0.05$). Within the same nitrogen treatment, means within each column and site followed by the same capital letters are not significantly different ($P < 0.05$).
*, **, ***, and ns represent significant at 0.05, 0.01, 0.001 levels, and not significant, respectively.

irrigation and site, or irrigation and nitrogen and site, data values were pooled over irrigation treatments at each site to evaluate N and site effects.

Grain yield and growth parameters

Grain yield ranged from 3296 to 4349 kg/ha (Table 2) which is similar to values reported for aerobic rice[2,5], but substantially lower than values for flooded lowland rice. The application of fertilizer-N significantly increased the grain yield at the Station, but not at the Farm. Grain yield at the Farm was significantly higher than at the Station with zero fertilizer-N, but not with N application of 150 kg/ha. As the soil at the Farm was more fertile than at the Station (Table 1), dry matter accumulation and tillering were both higher at the Farm than at the Station, leading to a higher proportion of unfilled grains at the Farm. This result implies that N fertilization needs to be carried out carefully to achieve a large sink size and a sufficient sink filling capacity under conditions of high soil fertility/large soil N reserves. The relative contribution of yield components to yield was productive tillers > percentage of filled grains > spikelets per panicle > thousand-grain weight, with path coefficients of 0.690 ($P < 0.01$), 0.530 ($P < 0.01$), 0.512 ($P < 0.05$), and 0.236 (not significant), respectively.

The number of spikelets per unit land area was significantly correlated with dry matter accumulation at anthesis (Fig. 2a, $r = 0.70$, $p < 0.0001$) and productive tillers (Fig. 2b, $r = 0.88$, $p < 0.0001$). Fertilizer-N increased total dry matter accumulation and tillering, which resulted in a high value of spikelets per unit of land area. However, the increase in spikelet numbers was offset by a reduction in the percentage of filled grains (Fig. 2c, $r = 0.85$, $p < 0.0001$), indicating insufficient grain filling. Moreover, the increase of tiller number and total dry matter accumulation implies that primary and secondary tiller formation had been promoted. There are reports showing that the beginning of grain filling is normally delayed for primary and secondary tillers as compared to main stems because the grains from the main stem use carbohydrates earlier and easier[26].

Grain filling

Grain-filling rates and weight accumulation are presented in Fig. 3. Grain weight accumulation of superior grains showed a typical 'S' shape with faster grain-filling rate, while the dry weight of inferior grains continuously increased during the entire filling stage with extremely low filling rates, independent of N treatment at either site. Neither fertilizer N addition nor the site affected the grain-filling pattern significantly. Hence a comparative study of HD297 under flooded and aerobic soil conditions would be needed to determine whether the different filling pattern of inferior grains with lowland rice[10,25] is mainly determined by the rice variety or by the soil water regime.

Pooled over the treatments, the average $t_{\max}$ was some 15 days longer for inferior than for superior grains (Table 3). The total duration of grain filling was 40 days longer for inferior than for superior grains. The average and maximum grain-filling rates of superior grains were about 3.8 times higher than that of inferior grains. Thus filling of inferior and

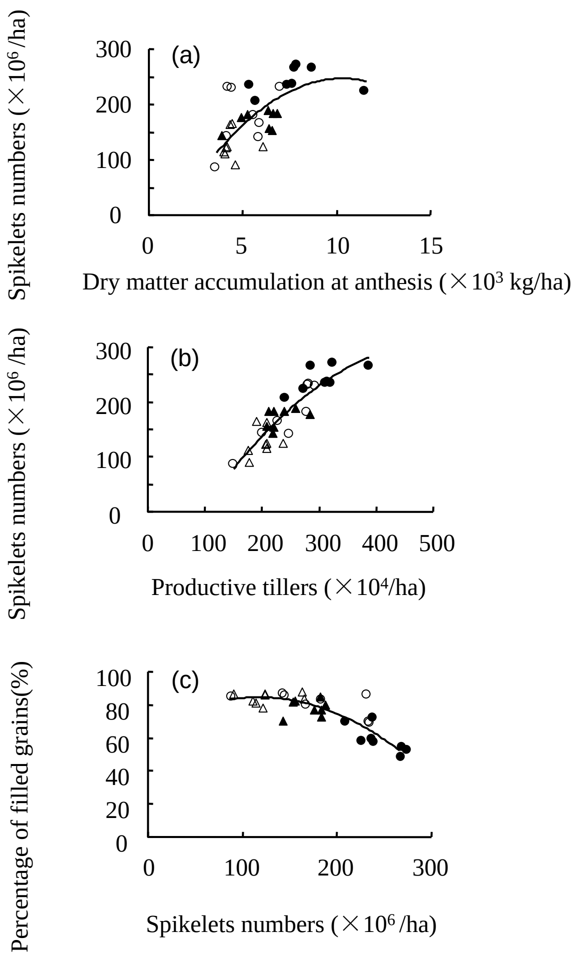

Fig. 2 (a) Spikelet numbers per hectare versus dry matter accumulation at anthesis, (b) spikelet number versus number of productive tillers, and (c) percentage of filled grains versus spikelets numbers under 0 (open symbol) and 150 kg N/ha (filled symbol) at the Farm (circle) and at the Station (triangle).

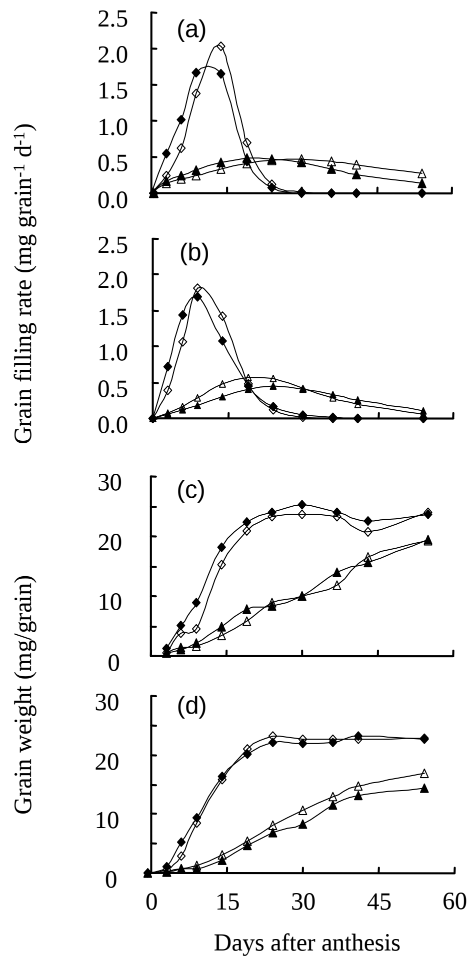

Fig. 3 (a,b) Grain filling rate and (c,d) grain weight of superior grains (diamond) and inferior grains (triangle) under zero N (open symbols) and 150 kg N/ha (filled symbols) at (a,c) the Farm and (b,d) the Station.

superior grains of HD297 was quite asynchronous, suggesting that the delay and frequent failure to fill inferior grains limit the yield. Studies with 'super rice' have also shown that asynchronous grain filling results in a lower percentage of filled grains compared to synchronous grain filling[27].

Low filling rate of inferior grains could not be attributed to temperature differences between superior and inferior grains, as the $T_{\max}$ and $T_{\min}$ during this period (-6 DAA to 18 DAA) were relatively constant (Fig. 1). Low filling rate finally led to a slow accumulation of grain weight and thus to incomplete filling of the inferior grains, resulting in a continuous increase of grain weight until harvest (Fig. 3c,d). Typically, to improve the yields through adjusting the grain-filling rate of inferior grains, nitrogen fertilizer is applied. The fertilizer-N in our experiment did not affect the filling rate or duration of inferior grains, which might partly explain the low percentage of filled grain found under N fertilization[7] (Fig. 2c). More research is needed to determine whether adapted N management, e.g., later dressings, is able to increase the grain filling of HD 297 under aerobic conditions.

Non-structural carbohydrate accumulation and allocation in rice shoots

Carbohydrate supply is important to grain filling and increases the final grain weight. Fertilizer-N only slightly improved the accumulation of non-structural carbohydrate at different growing periods, without

Table 3 Final grain weight (GW), time to reach maximum grain filling rate ($t_{\max}$), active grain filling duration (GFD), maximum grain filling rate ($\mathrm{GFR}_{\max}$), and average grain filling rate ($\mathrm{GFR}_{\mathrm{av}}$) fitted to Richard's equation for aerobic rice HD297 under two nitrogen regimes at the Farm and the Station.

Grain Position	Site	N input (kg/ha)	GW (mg)	$t_{\max}$ (days)	GFD (days)	$\mathrm{GFR}_{\max}$ (mg grain^{-1}d^{-1})	$\mathrm{GFR}_{\mathrm{av}}$	R^2
Superior	Farm	0	23.2^{aA}	12.5^{aA}	16.3^{aA}	1.97^{aA}	1.42^{aA}	0.96
		150	24.4^{aA}	10.1^{aA}	18.9^{aA}	1.86^{aA}	1.29^{aA}	0.95
	Station	0	22.9^{aB}	9.8^{aB}	17.9^{aA}	1.85^{aA}	1.28^{aA}	0.99
		150	22.6^{aB}	8.8^{aB}	20.7^{aA}	1.61^{aB}	1.09^{aA}	0.99
	Mean		23.3	10.3	18.5	1.82	1.27	0.97
Inferior	Farm	0	22.5^{aA}	27.4^{aA}	66.2^{aA}	0.49^{aA}	0.34^{aA}	0.95
		150	22.1^{aA}	25.7^{aA}	69.0^{aA}	0.47^{aA}	0.32^{aA}	0.95
	Station	0	17.9^{aB}	22.9^{aA}	50.7^{aB}	0.52^{aA}	0.35^{aA}	0.96
		150	15.5^{bB}	23.7^{aA}	49.3^{aB}	0.46^{aA}	0.31^{aA}	0.97
	Mean		19.5	24.9	58.8	0.49	0.33	0.96

affecting grain weight (Table 3). The contribution rate of 70% at the grain-filling stage was smaller than that of other crops, such as lowland rice (81–98%)[27] or wheat (77–92%)[28]. Therefore, non-structural carbohydrate produced at the filling stage was insufficient to match the demands of the large number of spikelets per unit land area with 150 kg N/ha (Table 2). In the same experiment, we have found that about 57–89% of dry matter in the grains of HD297 was derived from post-anthesis photosynthesis[7], highlighting its importance to grain filling. A 'stay-green characteristic' of rice could potentially increase grain yield through prolonged photosynthesis during grain filling[29]. For hybrid lowland rice, delaying leaf senescence increases the percentage of filled grains[30]. In lowland rice, N top dressing at anthesis usually impairs grain filling, especially when the soil N supply is high[18]. However, top dressing at anthesis increases grain filling of large-panicle hybrid rice through delayed senescence of leaves and roots[31]. Thus one strategy to prolong leaf photosynthesis duration and increase the yield of HD297 grown in aerobic soil might be N top dressing at or after anthesis.

Further options to improve grain filling of HD297 might be (1) to increase the planting density in order to produce more panicles from main stems, thus improving the sink strength by increasing the ratio of superior to inferior grains or (2) to improve the aerobic rice varieties through breeding with a better grain-filling pattern, e.g., a fast synchronous variety.

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Table 4 Accumulation of non-structural carbohydrate (NSC, kg/ha) at anthesis, grain filling, and harvest, the amount of NSC translocation from straw to grain (NSCT, kg/ha), contribution of pre-anthesis non-structural carbohydrate to grain (C_{pre}, %), and contribution of post-anthesis non-structural carbohydrate to grain (C_{post}, %) at the Station.

N input (kg/ha)	NSC (kg/ha) Anth.	Grain f.	Maturity Straw	Grain	NSCT (kg/ha)	C_{pre} (%)	C_{post} (%)
0	1147	1295	645	1797	502	28	72
150	1330	1496	702	2124	629	30	70

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