Full Length Article

Exogenous Glucose and Sucrose Application Effects on Differentiation and Degradation of Spikelets of Large Panicle Hybrid *Japonica* Rice

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Abstract

In order to understand the regulatory role of soluble sugar on the differentiation and degradation of the spikelet and shape the technology to cultivate large panicles for industrialized production, the large panicle hybrid japonica rice variety Yongyou 1540 was used. The crop was sprayed with exogenous glucose (167, 333, 500 and 667 mM) and sucrose (87, 175, 263, 351 mM) solutions at the beginning of panicle differentiation. The differentiation and degradation of spikelets and branches after treatment were investigated. Results showed that increasing exogenous soluble sugar concentration gradually decreased the total nitrogen content of plants, and increased the non-structural carbohydrate (NSC) content and its accumulation including C/N ratio of organs. In contrast, leaf and spike NSC accumulation initially increased and then declined. Compared to the control, the number of differentiation events, extant branches and the number of degraded primary branches and their spikelets were not significantly different, while for secondary branches and their spikelets were significantly different. In general, a higher concentration of exogenous soluble sugars produced more secondary, extant and differentiated branches, yet some of the highest sugar concentrations caused a reduction. There was a quadratic correlation between the number and differentiation of total branches and spikelets and the C/N ratio of plants at 15 days before and at heading stage. The results suggest that increasing the concentration of NSC at early stages of spike differentiation through appropriate cultivation measures can effectively promote branch and spikelet differentiation, reduce degradation and increase the number of grains and rate of seed set to achieve high yield. © 2020 Friends Science Publishers

Keywords: Soluble sugar; Large panicle hybrid *Japonica*; Branch and glumous flowers; Differentiation and degradation; Carbon and nitrogen metabolism

Introduction

Since the widespread introduction of super rice varieties, some large-ear type rice varieties are often used for high-yield or super-high-yield rice production due to multiple advantages, such as producing more glumous flowers, large storage capacity and high yield potential. Although, the yield record per plant has been broken, the total yield in large-scale production has failed to improve significantly, indicating that some of these varieties have shortcomings, such as involuntary degradation of secondary glumous flowers, and pollen sterility or infertility. These problems lead to more substantial variations in the number of surviving spikelets, grain number and rate of seed set. Therefore, yield and quality are not very stable, and their potential is not fully attained (Cheng *et al.* 2007; Wu *et al.* 2007; Yang and Zhang 2010; Dong *et al.* 2015; Hu *et al.* 2016). Studies have confirmed that the differentiation and

degradation of spikelets are not only controlled by genetics, but also by environmental ecology and cultivation conditions (Dong *et al.* 2015; Tian *et al.* 2016). The spikelets differentiation and degradation rate was affected by sowing date. For example, it was found that the spikelets differentiation decreased, the degradation rate increased, and the total spikelets were decreased accompanied by the delay of sowing date (the data was unpublished), especially large panicle rice, spikelet differentiation and degradation are quite different under different environmental conditions. Even for the same rice plant, on the secondary branches, the spikelet differentiation and degradation are very unstable, with large variation in spikelet numbers (Kovi *et al.* 2011; Dong *et al.* 2015; Zhang *et al.* 2016). Researchers have also found the NSC content and C/N ratio in the vegetative organs before heading is closely related to spikelet differentiation and degradation. At 15 days before heading, higher NSC content is beneficial to spikelet differentiation

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and reduced degradation, but the opposite occurs at 20 days or 25 days before heading (Dong *et al.* 2017). It is known that sugar is an important regulator of plant growth and gene expression. It is not only an energy source and a structural substance, but also has a hormone-like primary messenger effect in signal transduction (Sheen *et al.* 1999; Horacio and Martinez 2013; Lastdrager *et al.* 2014) and regulates plant growth, development, maturation and senescence. And many other processes have a regulatory role (Koch *et al.* 2000; Lastdrager *et al.* 2014). The glucose concentration is associated with mitogenic activity during the development of *Arabidopsis* cotyledons, and glucose is a developmental stimulating factor regulating the expression of cyclin *D* genes (Riou *et al.* 2000). Fructan accumulation and consumption at the pre-flowering stage can strongly influence the formtion of panicles, and therefore it is believed that the fructan metabolism has an important physiological significance (Hendrix *et al.* 1986). Within 8 days before flowering, a strong reduction in sugar concentration in the panicle occurs, and this is closely associated with the final number of spikelets produced (Wang *et al.* 1997). Therefore, spikelet development is sugar-reducing dependent, and this reduction mainly comes from hydrolysis of fructose and degradation of sucrose. These studies suggest that soluble sugar, which is an important component of NSC, is closely related to cell division in seeds or young spikes, and organ differentiation and development. Sugars are not only an energy source but also an important signal substance. However, there is little known on how NSC and its components are related to the differentiation and degradation of young rice spikelets. The mechanism underpinning this relationship is still unclear. Thus, it is still a popular topic of current research and worthy of further investigation.

In this study, the large panicle hybrid japonica rice variety Yougyou 1540 was used as the crop material, and the crop was managed using standard high-yield cultivation practices. Different concentrations of exogenous soluble sugar (glucose and sucrose) were sprayed during the panicle differentiation period, and the differentiation and degradation of the spikelets and branches were monitored. These results are expected to form the basis for further studies on the regulation mechanism of NSC on rice spikelet differentiation and development.

Materials and Methods

Experimental field and testing variety

The experiments were carried out in the Guli modern agricultural demonstration zone located in Changshu City, Jiangsu Province (31°34'53"N, 120°52'25"E) in 2016 and 2017. Soil in the experimental field is clay, and wheat has been grown and harvested there before. In 2016, the organic matter content of the soil tillage layer was 2.59% and available nitrogen, phosphorus and potassium were 127.8,

7.8 and 118.3 mg/kg, respectively. In 2017, the organic matter content of the soil tillage layer was 2.49%, and available nitrogen, phosphorus and potassium were 135.3, 8.2 and 117.9 mg/kg.

Experimental design

The heading time was recorded by counting the number of remaining leaves. During the initial heading period (25 ± 1 d before heading), from 7: 00 to 8: 00, glucose solutions (167, 333, 500 and 667 m*M*, termed as G1, G2, G3 and G4) we sprayed to the rice plants at the top of the leaves. At the same time, sucrose solutions (87, 175, 263, 351 m*M*, termed as S1, S2, S3 and S4) were also applied. The same amount of water was sprayed as a control (CK). There was no rain during the treatment period. An RX-60AM high-speed seedling transplanter was used to transplant seedlings (2 to 3 seedlings per hole) during dry conditions. Plot area was 60 m^2 (10 m × 6 m) with 3 replicates. The seeds were sown on May 15 and the seedlings were transplanted on June 15. Seedling age was 31 days with 5.3 to 5.5 leaves. The machine-inserted row spacing was 33 cm and hole-spacing was 12 cm, with 2 to 3 seedlings per hole. Seedling planting density is 64×104. The heading period began on September 2nd.

A total of 270 kg/hm^2 of pure nitrogen (N: P$_2$O$_5$:K$_2$O = 2:1:1) was applied over the entire growth period. The ratio of the nitrogen fertilizer was 4:2:2:2, comprising the following fertilizers: base, tillering, panicle and flower, respectively. Phosphate fertilizer was applied as base fertilizer once. The ratio of potassium fertilizer was base fertilizer: panicle fertilizer (flower promotion fertilizer), 5:5. Appropriate cultivation measures such as water management and pest control were carried out in accordance with their respective high-yield cultivation requirements. The experimental design in the first and second year was identical.

Measurements and methods

Determination of the differentiation and degradation of branch and spikelet

At heading stage (2/3 spikelets developed), 10 main stems were selected for measuring the differentiation and degradation of branches and spikelets. Using the Matsushima Shozo trace method (Matsushima 1966), the primary branches, the number of extant and degraded primary spikelets, secondary branches, and secondary spikelets were observed and recorded. The degraded spikelets exhibit a white-small-flower-like film trace. Some can be counted with the naked eye, but others have smaller traces, so a stereo microscope was used. The numbers of spikelets and branches per panicle were the sum of all those which degenerated or were still alive. The primary branches per spike were evenly divided into upper, middle and lower

parts (if there were 11 or 13 primary branches, then the ratio was 4:3:4 or 4:5:4). The numbers of upper, middle and lower branches and spikelets were counted. Degradation rates are: primary branch (spikelets) degradation rate (%) = the number of degraded primary branches (spikelets) / the number of differentiated primary branches (spikelets) $\times$ 100%; secondary branch (spikelets) degradation rate (%) = the number of secondary branches (spikelets) / the number of differentiated secondary branches (spikelets) $\times$ 100

Determination of total nitrogen content and NSC content

Fifteen days before and at heading stage, two plants with identical growth and average number of tillers were selected; the ears, leaves and sheaths were separated and packed in kraft paper bags. They were first placed for 60 min in a constant temperature oven at 105°C, then dried and weighed at 80°C. Stem sheaths and leaves were crushed and sifted by a small high-speed mill for the determination of nitrogen (N) and NSC content. The total N content was determined by the Kjeldahl method, and the content of NSC (soluble sugar and starch) was determined by anthrone colorimetry.

NSC content (mg/g) = total soluble sugar content + starch content

C/N = NSC content / total N content

NSC cumulative (kg/hm^2) = dry matter weight $\times$ NSC content

Determination of yield and its constituent factors

For each plot, 50 holes of plants were selected for sampling confirmed panicles. For plants in every 3rd hole, the number empty or flat grains, 1000-grain weight, and the total weight were calculated and averaged. The number of grains per panicle, seed rate and theoretical yield and actual yield were also recorded.

Data processing

The data of differentiated, degraded and extant branches and spikelets recorded during the two years (Table 1). The exogenous sugar treatment data was basically the same for two years, and thus it took the average for subsequent analysis. Microsoft Excel 2007 and SPSS 13.0 were used for statistical analysis and plotting of the data.

Results

Effects on the formation of rice branches

Compared with the control, the differences in the number of primary differentiated branches, primary degraded branches and primary extant branches after glucose and sucrose treatment were not significant (Table 2). For secondary and total branches, the differences were significant or extremely significant. With increasing concentration, the number of differentiated secondary branches and total branches initially increased and then declined. Different concentrations of exogenous glucose and sucrose always caused a decrease in number of degraded branches, indicating that the treatment can negatively regulate panicle degradation. However, different concentrations of glucose and sucrose had different effects, in the G1 treatment, for example, significantly higher numbers of degraded branches occurred than the other treatments. And for sucrose, the effects had no obvious difference among all treatments.

The number of total extant branches total and the number of total differentiated branches had a quadratic-curve relation with the concentration of exogenous glucose and sucrose (r= 0.51**, 0.69**, 0.50**, 0.77**), indicating that an optimal concentration can promote the differentiation of stems and increase the number of branches that survive (Fig. 1). Conversely, extremely high concentrations are not favorable for the differentiation of spikelets.

Effects on the formation of spikelets in rice concentrations

Compared with the control, the number of primary differentiated spikelets, primary degraded spikelets and primary extant spikelets after treatment with different concentrations of exogenous glucose and sucrose showed no significant differences (Table 3). However, the difference between the number of differentiated, degraded and extant spikelets (secondary and total) was very significant.

The number of differentiated spikelets (secondary and total) initially increased and then decreased with increasing concentration. The number of secondary differentiated spikelets peaked when the concentration of exogenous glucose was 333 m*M*. The number of differentiated spikelets was always lower than control, except for high glucose, when it was only slightly lower. The most secondary differentiated spikelets were found at 263 m*M* sucrose treatment. At the same concentration, the number of differentiated spikelets decreased significantly, to a level slightly lower than in the control. At 333 m*M*, exogenous glucose level produced significantly higher number of total differentiated spikelets and extant spikelets than other treatments.

Correlation analysis showed (Fig. 2) that there was a quadratic curve correlation between the total extant spikelets, differentiated spikelets and the concentration of exogenous glucose and sucrose (r= 64**, 0.73**, 0.58**, 0.82**). This indicates that an optimal concentration of sugar can promote panicle differentiation, increasing the extant spikelets. However, excessive concentrations are also unfavorable to spikelet differentiation.

Effects on carbon and nitrogen metabolism during panicle differentiation in rice

Exogenous glucose and sucrose concentrations significantly reduced the total nitrogen content of rice plants at the panicle differentiation stage (Table 4). Exogenous glucose

Table 1: Statistical table of annual differentiation and degradation of branches and spikelets of large panicle hybrid *Japonica* rice

Year	Differentiated branches	Degraded branches	Extant branches	Differentiated spikelets	Degraded spikelets	Extant spikelets
2016	132.5a	58.2a	74.3b	478.3a	147.6a	330.7b
2017	123.2ab	40.4b	82.8a	463.9b	109.2b	354.7a
F	25.32**	39.47**	19.74**	18.29**	145.26**	30.05**

** represent significance at *P* < 0.01

Table 2: Effects of different concentrations of exogenous glucose and sucrose on formation of branches

Treatment	Primary branches				Secondary branches				Total branches			
	Differentiated branches	Extant branches	Degraded branches	Degraded percentage	Differentiated branches	Extant branches	Degraded branches	Degraded percentage	Differentiated branches	Extant branches	Degraded branches	Degraded percentage
G1	20.9ab	19.3ab	1.6a	7.8bc	101.5bc	58.5c	43.0a	42.4a	122.4cd	77.8de	44.6a	36.5a
G2	22.3a	20.6a	1.6a	7.3bc	113.0a	76.3a	36.8b	32.5d	135.3a	96.9a	38.4c	28.4c
G3	21.0ab	19.1ab	1.9a	9.0b	106.0b	67.9b	38.1ab	36.0cd	127.0b	87.0 b	40.0bc	31.5bc
G4	20.9bc	19.4ab	1.5a	7.2bc	102.9bc	63.8bc	39.1ab	38.0b	123.8bc	83.1bc	40.6bc	32.8bc
S1	21.4ab	19.3ab	2.1a	5.3c	99.4c	58.6c	40.8ab	41.0ab	120.8d	77.9de	41.9abc	35.5a
S2	21.5ab	20.3a	1.3a	5.8c	107.1b	67.8b	39.4ab	36.8bc	128.6b	88.0b	40.6bc	33.1ab
S3	21.6ab	20.0a	1.6a	7.5bc	103.1bc	62.8bc	40.4ab	39.2ab	124.8bc	82.8bc	42.0abc	34.2ab
S4	21.5ab	20.0a	1.5a	7.0bc	102.1bc	61.9c	40.3ab	39.4ab	123.6bc	81.9cd	41.8abc	35.9a
CK	20.1b	17.8b	2.4a	11.8a	100.8c	57.8c	43.0a	42.7a	120.9d	75.5e	45.4a	37.5a

G1, G2, G3, G4 represent 167, 333, 500 and 667 mmol/l glucose solutions, respectively. S1, S2, S3, S4 represent 87, 175, 263, 351 mmol/l sucrose solutions, respectively. CK represents water solution. Values followed by different letters are significantly different at *P* < 0.05. The same as below

Table 3: Effects of different concentrations of exogenous glucose and sucrose on formation of spikelets

Treatment	Primary spikelets				Secondary spikelets				Total spikelets			
	Differentiated spikelets	Extant spikelets	Degraded spikelets	Degraded percentage	Differentiated spikelets	Extant spikelets	Degraded spikelets	Degraded percentage	Differentiated spikelets	Extant spikelets	Degraded spikelets	Degraded percentage
G1	120.8a	111.4a	9.4ab	7.7a	357.9b	243.5b	114.4b	32.0a	478.6b	354.9b	123.8c	25.9a
G2	129.1a	121.0a	8.1ab	6.3a	393.9a	263.6a	130.3a	34.7a	523.0a	384.6a	138.4a	27.8a
G3	120.8a	113.3a	7.5ab	6.2a	342.9c	225.5bcd	117.4b	34.2a	463.6c	338.8bc	124.9c	26.9a
G4	119.5a	111.4a	8.1ab	6.8a	344.6c	215.6d	129.0ab	37.4a	464.1c	327.0c	137.1ab	29.5a
S1	124.1a	113.5a	10.6a	8.6a	344.6c	222.4bcd	122.3b	35.4a	468.8bc	335.9bc	132.9bc	28.3a
S2	124.8a	118.5a	6.3b	5.0a	355.8b	237.6bc	118.1b	33.2a	480.5b	356.1b	124.4bc	25.9a
S3	129.6a	117.1a	12.5a	9.6a	358.4b	231.6bc	126.8b	35.4a	488.0b	348.8b	139.3a	28.5a
S4	125.0a	116.9a	8.1ab	6.5a	350.8b	229.6bcd	121.1b	34.5a	475.8b	346.5b	129.3bc	27.2a
CK	125.5a	113.6a	11.9a	9.5a	344.1c	215.1d	129.0ab	37.5a	469.6bc	328.8c	140.9a	30.0a

Table 4: Effects of exogenous glucose and sucrose concentrations on carbon and nitrogen metabolism during panicle differentiation in rice

Treatment	15 days before heading			Heading date		
	N content (mg/g)	NSC content (mg/g)	C/N	N content (mg/g)	NSC content (mg/g)	C/N
G1	22.5b	101.8b	4.5 bc	19.0abc	201.2b	10.5ab
G2	21.6c	105.2a	4.8 ab	18.8bc	208.5a	11.0ab
G3	20.6d	106.3b	5.1a	18.2c	209.6a	11.5a
G4	19.5e	106.8a	5.4 a	18.1c	209.1a	11.5a
S1	23.2ab	102.5ab	4.4 bc	19.4ab	198.7c	10.2bc
S2	22.9b	104.7a	4.5 bc	19.2ab	202.3b	10.5ab
S3	21.2c	104.9a	4.9 ab	18.2c	203.4b	11.1b
S4	21.0cd	105.1a	5.0a	18.0c	204.2b	11.3a
CK	23.7a	100.2b	4.2c	19.9a	195.6c	9.83c

and sucrose decreased by 11.18 and 6.86% on average at 15 days before heading, and decreased by 6.91 and 6.03% respectively, at heading date. Simultaneously, with an increase in exogenous sugar concentration, the total nitrogen content of plants decreased, in the order G1 > G2 > G3 > G4, S1 > S2 > S3 > S4. Exogenous glucose and sucrose significantly increased NSC content and C/N ratio of rice plants at the panicle differentiation stage, which contrasted with the total nitrogen content and showed that NSC content increased with increasing exogenous sugar concentration. Glucose and sucrose increased the NSC content by 4.82 and 4.11% and increased the C/N by 18.38 and 11.94% at 15 days before heading. It also increased the NSC content by 5.88 and 3.35% on average at the heading stage and the C/N by 13.81 and 10.12%.

The correlation analysis showed that the surviving and differentiation number of total branches and spikelets had a quadratic correlation with the C/N ratio of plants 15 days before heading and at heading stage (Fig. 3). Furthermore, the correlation coefficients were significant indicating that the C/N ratio of plants at panicle differentiation stage was closely related to the formation of spikelets and the appropriate C/N ratio could promote the formation of branches and spikelets.
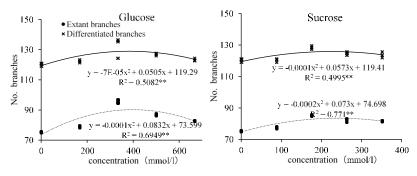
Fig. 1: Correlation between differentiation and extant number of total branches and the concentration of exogenous glucose and sucrose
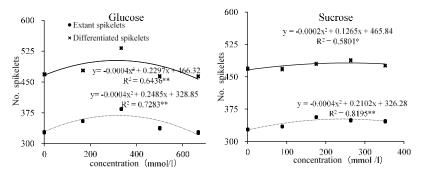

Fig. 2: Correlation between the differentiation and existing number of total spikelets and the concentration of exogenous glucose and sucrose
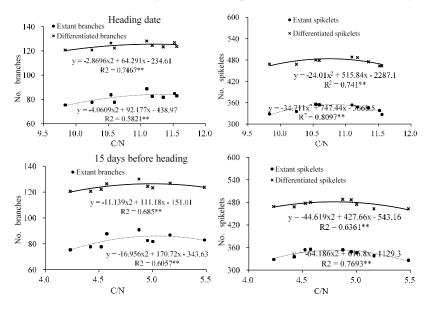

Fig. 3: Correlation between C/N Ratio of Rice Plants and Branch and Spikelet Formation at the Panicle Differentiation Stage

Effects on NSC accumulation and distribution during panicle differentiation of rice

During panicle differentiation, more than 85% of NSCs were distributed in stem sheath, about 8% in green leaves and about 3% in panicles. Different concentrations of exogenous glucose and sucrose could increase the accumulation of NSC in different organs of plants at panicle differentiation stage. Although the accumulation of NSC in stem and sheath did not reach a significant level at 15 days before heading, it reached significant levels in other organs. The results also showed that with increasing exogenous sugar concentration, changes in NSC accumulation in stem and sheath was not obvious 15 days before heading, it increased gradually at the heading stage. Furthermore, with increasing exogenous sugar concentration, the NSC accumulation in green leaves and spike at 15 days before heading and at the heading stage initially increased and then declined.

Table 5: The correlation between NSC accumulation and spikelet formation at the panicle differentiation stage in Rice

	15 days before heading			Heading date		
	stems and leaf sheath	leaf	spike	stems and leaf sheath	leaf	spike
Differentiated branches	-0.126	0.720*	0.695*	-0.248	0.749*	0.578
Extant branches	-0.272	0.669	0.670	-0.362	0.695*	0.497
Degraded branches	-0.514	-0.510	-0.575	-0.517	-0.527	-0.249
Differentiated spikelets	-0.346	0.796*	0.752*	-0.196	0.751*	0.811**
Extant spikelets	-0.329	0.897**	0.829 **	-0.168	0.878**	0.804**
Degraded spikelets	-0.080	-0.181	-0.128	-0.091	-0.254	-0.197

*, ** represent significance at $P < 0.05$ and $P < 0.01$. The same as below

Table 6: Effects of different concentrations of exogenous glucose and sucrose on yield of rice

Treatment	Spikelets per panicle	Rate of seed set (%)	1000-grain weight (g)	Grain plumpness (%)	Theoretical yield (t/hm^2)
G1	283.9b	86.8a	21.7a	85.1a	11.6b
G2	297.7a	86.9a	21.8a	85.6a	12.3a
G3	271.0bc	87.0a	21.3a	83.9a	10.9cd
G4	261.6c	87.0a	21.9a	84.3a	10.9cd
S1	277.2b	86.5a	21.4a	84.9a	11.2bc
S2	284.9b	87.2a	21.9a	85.3a	11.8ab
S3	279.0b	85.6a	21.6a	84.6a	11.4bc
S4	268.7bc	85.5a	21.7a	83.3a	11.0c
CK	263.0c	85.9a	21.3a	85.0a	10.6d

Accumulation of NSC in stem and sheath at 15 days before heading and at heading stage was weakly correlated with differentiated, surviving and retrograded branches and spikelets (Table 5). The accumulation of NSC in green leaves and spikelets at 15 days before heading and at the heading stage was positively correlated with the differentiated and surviving spikelets (R^2= 0.80*, 0.90**, 0.75*, 0.83**, 0.75*, 0.88**, 0.81** and 0.80**, respectively). The retrograded branches and spikelets were negatively correlated with the NSC accumulation in all organs at 15 days before heading and at the heading stage, but not significantly.

Effects on yield related factors of rice

Changes caused by different concentrations of exogenous glucose and sucrose treatment on rice yield was highly significant (Table 6), both were higher than the control. However, increasing exogenous glucose and sucrose concentration, showed an initial increase in yield, followed by a decline. At a concentration of 333 m*M* glucose and 175 m*M* sucrose treatment, the yield of both exogenous sugar treatments was higher than others and rate of seed set was also high. Effects of different concentrations of exogenous glucose and sucrose per panicle were extremely significant ($F = 25.49$ **), whereas for rate of seed set, 1000-grain weight and degree of fullness, there was no significant change, indicating that field changes caused by exogenous glucose and sucrose were mainly due to changes in the number of grains per panicle.

Discussion

The number of grains per panicle is one of the important indicators of rice yield. Especially during the promotion and implementation of super rice, the number of secondary branches, total branches, and number of grains on secondary branches were the main indicators for the number of grains per panicle (Kato and Katsura 2010). For differentiation and degradation of spikelets, studies suggest that these processes are closely related to the health of plants during differentiation and development stages, as well as carbon and nitrogen nutrition and metabolism. Meanwhile, physiological activity of young spikes is also important. From vegetative to reproductive growth of rice, a great deal of carbohydrates is needed as a carbon and energy source for the formation of young spikelets, pollen and embryo sacs. In particular, at the meiosis stage of rice pollen mother cells, carbon metabolism is beneficial to the reproductive growth of crops (Fu *et al.* 2015). Studies (Tian *et al.* 2016) show that concentration and content level are two factors that are closely associated with the differentiation and degradation of spikelets and branches. The 12 d or 4 d before heading, or during the heading stage, stem and sheath growth is high, thus, a high concentration of non-structural carbohydrate is not conducive to the differentiation and degradation of young branches and spikelets. From 16 d before heading to 8 d before heading, a higher NSC accumulation in young spikelets is necessary for the formation of large spikes. NSC is closely correlated with the number of grains. NSC, like sucrose, glucose, fructose, and fructan influence plant metabolism and yield (Yoshinagaa *et al.* 2013; Wang *et al.* 2017).

Previously plant hormones have been shown to play a regulatory role at very low concentrations, while sugars are more active when concentrations are high. In this study, the effects of exogenous sugars on the degradation of branches and spikelets at the early stage of panicle differentiation indicate that the sugar signal may induce the synthesis of NSC in plants and even at low concentrations, they can regulate the C/N ratio during the panicle differentiation

stage, facilitating the differentiation of branches and spikelets. However, when the concentration is high, the balance of C and N is disrupted, suppressing the differentiation of young spikelets and branches. To date, we have only hypotheses on how NSC (probably together with hormones) might regulate spikelet formation. Little is known about the links between sugar signaling substances (soluble sugar part of NCS) and hormones, especially the relationship between protein level and enzyme activity in the process of spikelet formation. Therefore, it is important to identify the relation between sugar and hormonal signals. Two open questions are: (1) what is the synergistic regulation of rice panicle differentiation and development and, (2) what is the signal regulation network of rice spikelet growth and development? To answer these questions, further research on signal levels is needed.

The results of this study showed that appropriate concentrations of exogenous glucose and sucrose could significantly promote rice spikelet differentiation. When the concentration was low, the interaction between exogenous sugar and hormone signaling reduced ABA content in the young panicle, promoting differentiation (Radchuk *et al*. 2010). At high concentration, spikelet numbers were lower than in the control treatment, which may also reflect a sugar-hormone interaction (Arenas *et al*. 2000; Rook *et al*. 2001). Adding exogenous sugars can reduce the number of degradations, however, it is not known if ethylene is involved (Zhou *et al*. 1998). The differentiation and development of young panicles are the result of a combination of internal and external factors, and a series of complex physiological and biochemical processes. Yet, there are still many processes that are not fully understood, such as how the external environmental conditions regulate sugar metabolism, physiology and hormones. It is suggested that the mechanism of how multiple interactions regulate young panicle formation deserves further in-depth research.

A thorough and detailed study of the internal regulatory network between the expression of soluble sugar in rice (NSC) - plant hormone – protein (Arenas *et al*. 2000) and the activity of metabolic enzymes is necessary. In particular, the differentiation and development of young panicles and the size of the sink volume by NSC should clarify the internal relationship between sugar signals and hormones and the mechanism of the formation of young panicles. An understanding of the signal regulation network of rice panicle growth and development will provide better theoretical and practical guidance for the cultivation of large panicles in production.

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understanding of the signal regulation network of Rice Panicle growth and development will provide better theoretical and practical guidance for the cultivation of large panicles in production.

Conclusion

Exogenous glucose and sucrose application at booting stage demonstrated that NSC involved in the regulation of differentiation and development of spikelets in rice. NSC is not only a kind of energy material, but also a signaling molecule. However, the mechanism of NSC regulating spikelets differentiation and degradation is not clear, which is worth further study.

Acknowledgements

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