Variations in Carbohydrate and Protein Accumulation among Spikelets at Different Positions Within a Panicle During Rice Grain Filling

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Abstract: The accumulation dynamics of kernel components for spikelets at different positions within a rice panicle were investigated during grain filling to understand the physiological reasons for the variation of grain quality. Two rice cultivars, Yangdao 6 (indica) and Yangjing 9538 (japonica), were field-grown, and the grain filling characters and contents of starch, soluble sugar, and protein of the spikelets at different positions were studied. There were significant differences in matter accumulation among spikelets at different positions during grain filling. The early-flowering spikelets presented dominance over the late-flowering spikelets in initial time and initial rate of accumulation. At the initial and mid filling stages, the contents and the rates of starch and amylose accumulation in spikelets decreased with the flowering sequence, but soluble sugar content (SSC) exhibited the opposite trend. The difference in SSC among the spikelets of Yangjing 9538 was greater than that of Yangdao 6, but amylose content in mature spikelets showed no obvious relationship to their flowering sequence. The crude protein content (CPC) of early-flowering spikelets decreased more rapidly than that of late-flowering ones at the initial filling stage, and CPC in the spikelets on the secondary branch was higher than that on the primary branch, but CPC in early-flowering ones was lower than that in late-flowering across the whole grain filling period. Grain water content (GWC) of early-flowering spikelets decreased more rapidly than that of late-flowering spikelets on the same branch at the initial and mid filling stages, especially for the top grain on each primary branch. The results suggested that poor grain filling of late-flowering spikelets may be attributed to their low biological activity rather than carbohydrate supply limitation.

Key words: spikelet position; starch; protein; accumulation dynamic; variation; rice; grain filling

Starch and protein accounting for about 80% and 8% of grain weight, respectively, play a decisive role in the formation of rice quality (Liu et al, 2008). Studies on the differences in the accumulation dynamics of starch and protein in spikelets at different positions within a rice panicle have an important guiding role for understanding the mechanism of quality formation and improving the grain quality through breeding and cultivation approaches. Rice starch is composed of amylose and amylopectin. Previous research had shown that amylose content (AC) had a direct impact on rice cooking quality, and the ratio of amylose and amyllopectin was regarded as an important indicator for rice cooking quality, thus AC is also regarded as an effective indicator to determine rice quality at home and abroad (Umemoto et al, 1995; Lii et al, 1996; Zhou et al, 2002; Dipti et al, 2003). Protein is the second largest component, 80% of which consists in the endosperm. Accordingly, crude protein content (CPC) of brown rice is always regarded as a nutritional quality index. The formation of rice quality is dependent on physiological and biochemical metabolisms of the kernel components, and the carbon and nitrogen metabolisms are the most basic metabolic processes. Under the combined effects of genetic and environmental factors, these complex but orderly metabolic activities during grain filling give rise to a spontaneous change of the internal chemical composition and physical structure, and thus affect the ultimate quality of rice grain. The differences in carbon and nitrogen metabolisms lead to the differences of amylose and protein contents with the progress of spikelet development, respectively (Tomaki et al, 1989; Cai et al, 2004; Lu et al, 2007). Previous research indicated that the differences in synthesis and accumulation patterns of starch and protein existed not only among varieties or panicles, but also among spikelets within a panicle. Generally, the early-flowering spikelets which are regarded as superior spikelets have higher filling rate and more complete development, compared with late-flowering spikelets (referred to as inferior spikelets). The differences in matter synthesis and accumulation eventually contributed to grain quality diversity (Wang et al, 1990; Xie et al, 2001; Wang and Cheng, 2004; Lu et al, 2007). The diversity of grain quality among spikelets at different positions and its physiological mechanism had been studied (Wang and Cheng, 2004; Yang et al,
2006; Dong et al., 2007, 2008; Jin et al., 2008), however, the differences on the formation of grain quality among spikelets at different positions have not been reported yet. The purpose of this research is to examine the matter accumulation, such as starch, soluble sugar content (SSC) and CPC, and to explain the physiological mechanism of grain quality diversity of spikelets at different positions.

MATERIALS AND METHODS

Rice materials

The field study was conducted at the experimental farm of Yangzhou University, Jiangsu Province, China (32°30′N, 119°25′E) during rice growing seasons (May to October) from 2005 to 2007. Two rice genotypes, Yangjing 9538 and Yangdao 6, were grown in paddy fields. Seedlings were raised in the fields with sowing date on 10 May and transplanted on 11 June at a hill spacing of 0.2 m × 0.2 m with 2 seedlings per hill. Plot dimension was 6 m × 8 m. Each of the genotypes had four plots as repetitions in a complete randomized block design. The soil of the fields was sandy loam that contained organic matter of 20.3 g/kg and available N-P-K of 108.0, 34.2 and 66.9 mg/kg, respectively. A total of 190 kg/hm² nitrogen (420 kg/hm² as urea) were applied during the whole growth period with a ratio of 5:2:3 for basal fertilizer, tillering fertilizer and panicle fertilizer, respectively. At the same time, 60 kg/hm² P₂O₅ (445 kg/hm² as single superphosphate) and 90 kg/hm² K₂O (150 kg/hm² as KCl) were applied and incorporated before transplanting. Except drainage at the final tillering stage (11–15 July), the field was kept 1 to 2 cm water level during the whole growth period.

Sampling

Two thousand panicles that headed on the same day were chosen and tagged for each plot, and the flowering data of some panicles and the position of each spikelet in the panicle were recorded. About 250 tagged panicles from each plot were sampled at 7 d after flowing (DAF) and 10 DAF, and at a 7-day interval after 14 DAF to grain maturity. Each panicle was divided into different samples according to different parts and grain positions. Normally, Yangdao 6 had 11–12 primary branches on a panicle, and Yangjing 9538 had 9–10 primary branches. All primary branches in a panicle were averagely divided into the upper, middle and basal parts, which are of equal length. The grains were numbered as one to six on a primary branch and one to three or four on a secondary branch from the panicle top to the base. The grains of the same part and position were combined as one group, sterile and half-filled spikelets were removed and the fully-filled grains were air-dried for quality observation.

Measurement methods

AC was measured according to the Standard of the Ministry of Agriculture (Ministry of Agriculture, 1988). CPC was calculated from the nitrogen content × 5.95, while the nitrogen content was determined using the Kjeldahl method (Shanghai Plant Physiology Academy, 1985). Water content of spikelets was measured according to the method of Wang et al. (1990). Starch and soluble sugar contents were determined using the enthrone method (Cai and Yuan, 1982).

The samples of grain water content (GWC), starch, SSC, AC and grain filling rate (GFR) were selected from spikelets at middle part in a panicle, while CPC from the whole panicle.

The average data of the three years were used for analysis because of the similar trends.

RESULTS

Grain-filling rate (GFR)

The dynamics of GFR of spikelets at different positions on the primary branches was consistent with those on the secondary branches, therefore, only GFR of spikelets on the primary branches was used for illustration (Fig. 1). There were significant differences in the maximum GFR and the time reaching maximum GFR among different position spikelets and cultivars. But GFR of spikelets at the same branches decreased with the flowering sequence for the two cultivars. For example, the first and the sixth spikelets on the primary branch and the first grains on the secondary branch, which flowered earlier, got the maximum cell division rate at first, and had greater GFR and longer actively increasing period of grain weight, while those of the second grains which flowered at last were contrary. The maximum GFR of grains at different positions of Yangjing 9538 was lower than that of Yangdao 6, and the time reaching the maximum GFR was correspondingly later.

Grain water content (GWC)

There were significant differences in the dynamics of GWC for grains at different positions, and the primary branch was taken as an example (Fig. 2). The GWC descended with grain-filling process, especially
faster at the initial and mid filling periods. The GWC in early-flowering grains of the two cultivars declined more greatly than that of the late-flowering grains at the initial and mid filling stages, and the GWC for the primary branches declined more quickly than that for the secondary branches. The GWC of the first grain on the primary branches declined the most quickly, i.e., the GWC of Yangdao 6 showed more obvious decline, which might be one of the reasons for the lighter weight of the first grain than other early-flowering grains.

**Soluble sugar content (SSC) and starch content**

The SSC of spikelets decreased with the filling process (Fig. 3). The SSC of spikelets on the primary and the secondary branches on the 10th DAF was significantly higher than those on the 21st and 35th DAF. The SSC of spikelets on the secondary branches was higher than that of the primary branches, and the SSC of Yangjing 9538 was higher than that of Yangdao 6 at the same time. There were significant differences in the SSC of spikelets at different positions of the two cultivars at the initial and mid filling stages. In general, the SSC of the late-flowering grains was higher than that of the early-flowering grains, i.e., the SSC of grains at different positions on the primary branches of the two cultivars on the 10th DAF exhibited the sequence of the second > the third > the forth > the fifth > the sixth > the first grain. The SSC of grains on the primary branches of Yangdao 6 ranged from 11.9 mg/g to 32.8 mg/g, and the maximum was higher than the minimum by about 176%, while that of Yangjing 9538 ranged from 24.6 mg/g to 122.7 mg/g, and the maximum was higher than the minimum by about 399%. The SSC of grains at different positions on the secondary branches exhibited the sequence of the forth > the second > the third > the first grain. The SSC of grains of Yangdao 6 ranged from 16.5 mg/g to 95.0 mg/g, and the maximum was higher than the minimum by about 476%, while those of Yangjing 9538 ranged from 42.5 mg/g to 210.8 mg/g, and the maximum was
higher than the minimum by 396%.

Compared with SSC, the changes of starch content exhibited an oppositely increasing trend (Fig. 4). The starch content of spikelets on the primary branches was higher than that of the secondary branches, and the starch content of Yangdao 6 was higher than that of Yangjing 9538.

The differences between starch content of spikelets at different positions at the initial and mid filling stages were more significant than those at the late filling stages, i.e., the starch content of grains at different positions on the primary branches of Yangdao 6 on the 10th and 21st DAF exhibited the sequence of the first > the sixth > the fifth > the forth > the third > the second grain. The variation of starch content at different positions on the 10th DAF was the greatest compared with those on the 21st and 35th DAF, which ranged from 566.9 mg/g to 660.2 mg/g. The starch content of Yangjing 9538 on the primary branches on the 10th and 21st DAF exhibited the sequence of the first > the sixth > the fifth > the forth > the third > the second grain, and also showed the greatest variation on the 10th DAF, which ranged from 313.6 mg/g to 374.9 mg/g. The results showed that the starch accumulation increased with the flowering sequence.

Amylose content (AC)

Fig. 5 illustrated the accumulation dynamics of AC in spikelets at different positions. The AC in spikelets on the primary and the secondary branches of the two cultivars were lower at the initial filling stage, but higher at the later filling stage, however, there were differences in accumulation rate of AC between the two cultivars. The rapidly increasing period of AC in spikelets on the primary and the secondary branches was about before the 14th DAF. For Yangdao 6, AC of the first, the fifth and the sixth grains on the primary branches peaked around the 14th DAF, and the others on the 21st DAF, then AC declined slightly and achieved a relatively low value on the 28th DAF, and later increased again. The AC in grains at different positions on the primary branches within 14 DAF exhibited the sequence of the first > the sixth > the fifth > the forth >
Fig. 4. Changes of starch content in the grains at different positions in a rice panicle.
Common lowercase letters above the bars mean no significant difference at 0.05 level for different grains at the same position within a rachis branch. The six bars from left to right represent the 1st, 2nd, 3rd, 4th, 5th and 6th grains from the top of the primary rachis branch, and the four bars from left to right represent the 1st, 2nd, 3rd and 4th grains from the top of the secondary rachis branch.

Fig. 5. Changes of amylose content in the grains at different positions in a rice panicle.
The lines in the figure named one to six represent the 1st, 2nd, 3rd, 4th, 5th and 6th grains from the top of each branch.
the third > the second grain, and the trend was the same as that of starch content. After the 14th DAF, AC in the sixth, the fifth, the forth and the third grains were higher than that in the first grain, and after the 35th DAF, the AC in the third and the second grains were higher than those in the fifth and the sixth grains. AC in the first grain on the secondary branches was higher than the others within 14 DAF, and it exhibited the sequence of the first > the third > the second > the forth grain. However, after the 14th DAF, AC in the second grain was basically the same as that in the third grain, but AC in the forth grain was also the lowest.

The AC in grains at different positions of Yangjing 9538 increased with the flowering sequence at the initial and mid filling stages, and was also correlated with starch content of different grains. AC in the first, the fifth and the sixth grains which flowered earlier on the primary branches increased rapidly within 14 DAF, then increased slowly, peaked on the 21st DAF and achieved a relatively low value on the 35th DAF. While AC in the second, the third and the forth grains which flowered later increased slowly at the initial stage and reached or exceeded those of the first, the fifth and the sixth grains around the 40th DAF. AC in the first grains on the secondary branches increased rapidly within 14 DAF, then increased slowly, peaked on the 21st DAF and achieved a relatively low value on the 35th DAF. While AC in the second, the third and the forth grains which flowered later increased slowly at the initial stage and reached or exceeded those of the first, the fifth and the sixth grains around the 40th DAF. AC in the first grains on the secondary branches increased rapidly within 21 DAF, while those in the second, the third and the forth grains increased rapidly within 28 DAF, and AC of the second grains continued increasing after the 28th DAF. AC of spikelets on the secondary branches exhibited the sequence of the first > the third > the second > the forth grain.

Crude protein content (CPC)

Fig. 6 illustrated the accumulation dynamics of CPC in spikelets at different positions. CPC in spikelets on the primary and the secondary branches at different parts and grains at different positions on the same branches presented the same trend. CPC was higher at the initial filling stage, while decreased rapidly within 14 DAF and reached the minimum value around the 21st DAF, and then rebounded slightly. However, it declined again around the 28th DAF for Yangdao 6 and the 35th DAF for Yangjing 9538 until grain maturity, which was not very obvious.

CPC in spikelets at different positions on the primary branches of Yangdao 6 exhibited the sequence of the lower > the middle > the upper part within a panicle at the initial filling stage. However, CPC in spikelets on the middle and lower parts decreased rapidly to the minimum value, even lower than those on the upper parts on the 14th DAF, which might be related to the rapidly growing weight of those grains. Then CPC of the lower part quickly exceeded those of the upper part, while CPC of spikelets on the middle part was lower than that on the upper part all the time, which showed that the spikelets on the lower parts have the faster rate of protein accumulation. CPC of Yangdao 6 on the secondary branches and CPC of Yangjing 9538 on the primary branches exhibited the sequence of the lower > the middle > the upper part within a panicle during the whole filling stage, and the differences of CPC among spikelets on the secondary branches were greater than those on the primary branches.

The differences of CPC between spikelets at different positions on the primary and the secondary branches of Yangjing 9538 were greater than those of Yangdao 6 at the initial filling period, but it became less at the later period. CPC of the late-flowering spikelets on the primary and the secondary branches of Yangdao 6 were higher than those of the early-flowering spikelets, i.e., the second grain on the primary branches and the second, the third and the forth grains on the secondary branches. There were great differences on CPC of spikelets on the primary or the secondary branches of Yangjing 9538 at the initial filling stage, i.e., CPC in the second and the third grain which flowered later exhibited 7.0% and 5.8% higher than that in the first grain which flower early on the 7th DAF, respectively, but there were no differences in the first, the forth, the fifth and the sixth grains; CPC in the second, the third and the forth grains on the secondary branches were higher than those in the first grain on the 14th DAF, but the differences between spikelets on the primary and the secondary branches were narrowed after 14 DAF.

Relationship between accumulated matter contents and rice quality

The relationship between accumulated matter contents at different grain-filling stages and ultimate grain quality of rice was analyzed, and data of Yangdao 6 only are presented and listed in Table 1 because of the similar trends shown by the two cultivars. The results showed that GFR was significantly and positively correlated with the 1000-grain weight (KGW) and gel consistency (GC), but significantly and negatively correlated with the chalkiness degree (CD) and CPC at the initial filling stage, however, it was contrary at the later filling stage. The results indicated that earlier filling commence and higher filling intensity at the initial stage were beneficial to higher grain weight, gel consistency and lower chalkiness degree and CPC. At the whole filling stage, the water content of grains was significantly and negatively correlated with KGW, but significantly and positively correlated with CD and
CPC, which showed that water content of grains greatly affected the formation of CD and CPC. During the whole filling period, SSC was significantly and negatively correlated with KGW and GC but significantly and positively correlated with CD; SC and AC were significantly and positively correlated with KGW, but significantly and negatively correlated with CD and CPC; CPC was significantly and negatively correlated with KGW, but significantly and positively correlated with CD.

**Fig. 6. Changes of crude protein content in the grains at different parts in a rice panicle.**

The lines in the figure numbered one to six represent the 1st, 2nd, 3rd, 4th, 5th and 6th grains from the top of each branch.
Table 1. Coefficients of correlations for grain-filling rate (GFR), grain water content (GWC), soluble sugar content (SSC), starch content (SC), amylose content (AC) and crude protein content (CPC) during grain filling with the quality traits 1000-grain weight (KGW), head milled rice (HMR), chalkiness degree (CD), AC, gel consistency (GC) and CPC of Yangdao 6.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Filling stage</th>
<th>KGW</th>
<th>HMR</th>
<th>CD</th>
<th>AC</th>
<th>GC</th>
<th>CPC</th>
</tr>
</thead>
<tbody>
<tr>
<td>GFR</td>
<td>T1</td>
<td>0.7881**</td>
<td>0.5561</td>
<td>-0.9354**</td>
<td>-0.2008</td>
<td>0.6880*</td>
<td>-0.9372**</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>-0.6201*</td>
<td>0.0229</td>
<td>0.9363**</td>
<td>-0.1072</td>
<td>-0.1166</td>
<td>0.3727</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>-0.4986</td>
<td>-0.3678</td>
<td>0.8332**</td>
<td>0.0686</td>
<td>-0.5760</td>
<td>0.7920**</td>
</tr>
<tr>
<td>GWC</td>
<td>T1</td>
<td>-0.7907***</td>
<td>-0.4037</td>
<td>0.9591**</td>
<td>-0.1573</td>
<td>-0.5444</td>
<td>0.8392***</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>-0.8234***</td>
<td>-0.3747</td>
<td>0.9815**</td>
<td>-0.0397</td>
<td>-0.5553</td>
<td>0.9293***</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>-0.8681***</td>
<td>-0.2115</td>
<td>0.9162**</td>
<td>0.0067</td>
<td>-0.6186*</td>
<td>0.8875**</td>
</tr>
<tr>
<td>SSC</td>
<td>T1</td>
<td>-0.9214***</td>
<td>0.1544</td>
<td>0.9604**</td>
<td>-0.4976</td>
<td>-0.6606*</td>
<td>0.3531</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>-0.9624***</td>
<td>0.1309</td>
<td>0.9411**</td>
<td>-0.4451</td>
<td>-0.7820**</td>
<td>0.3722</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>-0.9053**</td>
<td>0.0233</td>
<td>0.7967**</td>
<td>-0.5053</td>
<td>-0.9557**</td>
<td>0.4713</td>
</tr>
<tr>
<td>AC</td>
<td>T1</td>
<td>0.7486**</td>
<td>-0.0419</td>
<td>-0.8388**</td>
<td>0.5542</td>
<td>0.6742*</td>
<td>-0.8934**</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>0.6629*</td>
<td>0.3212</td>
<td>-0.9229**</td>
<td>0.6030*</td>
<td>0.5571</td>
<td>-0.9263**</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>0.8190**</td>
<td>0.4504</td>
<td>-0.7870**</td>
<td>0.7419**</td>
<td>0.8205**</td>
<td>-0.7362**</td>
</tr>
<tr>
<td>SC</td>
<td>T1</td>
<td>0.7749**</td>
<td>0.0672</td>
<td>-0.9008**</td>
<td>-0.1451</td>
<td>0.6191*</td>
<td>-0.9458**</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>0.8497**</td>
<td>0.1514</td>
<td>-0.8972**</td>
<td>-0.1872</td>
<td>0.7086*</td>
<td>-0.9326**</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>0.9014**</td>
<td>0.2039</td>
<td>-0.8755**</td>
<td>-0.1961</td>
<td>0.6376*</td>
<td>-0.9094**</td>
</tr>
<tr>
<td>CPC</td>
<td>T1</td>
<td>-0.8148**</td>
<td>-0.0750</td>
<td>0.8721**</td>
<td>0.1525</td>
<td>-0.5221</td>
<td>0.9220**</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>-0.6978*</td>
<td>-0.3561</td>
<td>0.9431**</td>
<td>-0.0722</td>
<td>-0.6224*</td>
<td>0.8866**</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>-0.8798**</td>
<td>-0.1374</td>
<td>0.7802**</td>
<td>0.3014</td>
<td>-0.4835</td>
<td>0.8262**</td>
</tr>
</tbody>
</table>

*T1, T2, T3 are early (10 d after flowering), middle (21 d after flowering), late (35 d after flowering) stages of grain filling, respectively. * and **, Significant at 0.05 and 0.01 levels (n = 9), respectively.

**DISCUSSION**

**Starch and protein accumulation characteristics of grains**

Rice quality is formed mainly through the synthesis and accumulation of starch and protein (Cai et al., 2004; Liu et al., 2008). This study indicated that starch content in spikelets at different positions was consistent with the flowering sequence. The earlier the spikelets flowered, the earlier and faster the starch accumulation, the earlier the time reaching to peak value, and the higher the starch content. Starch content in spikelets on the primary branches was higher than that on the secondary branches, and the differences of starch content between spikelets at the initial filling stage were greater than those at the mid and later filling stages. CPC was higher at the initial filling stage and lower at the mid and later filling stages. CPC in late-flowering spikelets was higher than that in early-flowering spikelets, and CPC of the secondary branches higher than those of the primary branches. The differences of CPC between spikelets at different positions were similar to starch content.

The inadequate supply of assimilate was thought to be the main inhibitor for the slow and poor grain-filling of the inferior spikelets. But the research by Mohapatra et al. (1993) showed that there were no significant differences in soluble sugar, amino acids and phosphorus content between the early-flowering spikelets on the primary branches at the top part and the late-flowering spikelets on the secondary branches at the bottom part during the whole filling period. Yang et al. (1998) observed that SSC in inferior grains was twice or even more of that in superior grains in the indica-japonica hybrid rice. In this study, SSC in the late-flowering spikelets was higher than that in the early-flowering spikelets at the initial filling stage, especially in japonica rice Yangjing 9538. The results illustrate that the supply of assimilate is not the main reason causing the slow proliferation rate of the endosperm cells and poor grain filling, which is probably related with the low rate of starch synthesis and the biochemical efficiency of transformation from SSC to starch. The accumulation of starch in spikelets at different positions is consistent with the flowering sequence.

Our observation is broadly consistent with the previous research about the general trend of AC in rice grains (Asaoka et al., 1985; Zhong and Cheng, 2003). But the differences in AC of spikelets at different positions were not obvious at the initial filling stage, while were shown at the mid and later filling stages, which is different from the conclusion by Zhong and Cheng (2003). The real cause of the difference in AC remains to be studied. Some research argued that starch properties were probably related with the activities of key enzymes controlling starch metabolism (Xie et al., 2001). Kouichi et al. (1992) pointed out that the Q-enzyme in the process of starch synthesis formed the branched carbohydrate chain by forming α-1, 6-glycosidic linkage, thus, it was the key enzyme affecting the starch composition and structure in grains.
But some scholars considered that the granule-bound starch synthase (GBSS) activities were related with the synthesis of amylase, controlling the amylose ratio (Smith et al, 1995). Q-enzyme and R-enzyme mainly affected fine structure of amylpectin though catalyzing formation and elimination of molecular chain in starch (Yang et al, 1999). We consider that the differences between spikelets at different position maybe depend on one or more physiological factors and the implicit reasons are under review.

Within a rice panicle, CPC in spikelets at the lower part was higher than those at the middle and upper parts, and CPC of the secondary branches was higher than that on the primary branches. CPC of late-flowering spikelets was higher than that of early-flowering spikelets, which is probably caused by the relatively lower starch accumulation. Generally, high CPC in rice grains will affect cooking quality, and the improvement of rice protein is mainly to increase the endogenous protein content and change its component elements. Therefore, the further mechanism is worth being studied.

Regulatory pathways for inferior grains filling

Our previous studies showed that one of the important reasons for the poor filling of the inferior grains was the low physiological activity which caused a delayed onset of grain filling (Yang et al, 1998, 1999, 2002; Xie et al, 2001). Further studies also found that there were significantly positive correlation between the grain physiological activity at the initial filling stage and sugar-spikelet ratio at the heading stage, which showed that the key approach enhancing sink (grain) strength was increasing sugar-spikelet ratio at the heading stage which could promote inferior spikelets filling. The key cultivation approaches including raising vigorous seedlings, increasing nitrogen application at later stages and enriching potassium fertilizer at heading stage are suggested, which could promote matter accumulation within 15 d before heading, increase sugar-spikelet ratio, enhance sink (spikelets) strength and ultimately promote inferior spikelets filling.

Another important reason for the poor filling of inferior grains was the low biochemical efficiency of transformation from sucrose to starch (Mohapatra et al, 1993; Yang et al, 2006; Zhang et al, 2009). There were close relations between the biochemical efficiency of sucrose transformation and the ratio of abscisic acid (ABA) to 1-aminocyclopropane-1-carboxylic (ACC) at the active grain-filling stage (Mohapatra et al, 1993; Li et al, 2000; Huang et al, 2004; Huang et al, 2005). So the improvement of ABA-ACC ratio at the active grain-filling stage is an effective regulatory approach to promote inferior grains filling. Thus, moderate soil-drying or alternate wetting and moderate-drying irrigation during grain filling are suggested in rice production to promote the ABA-ACC ratio, increase key enzyme activities and genes expression of sucrose-starch metabolism, then the transformation efficiency from sucrose to starch and eventually accelerate grain filling.

ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (Grant Nos. 30400276 and 30871480), the National Natural Science Foundation of Major International Cooperation Project (Grant No. 31061140457), the Natural Science Foundation of Jiangsu Province, China (Grant No. BK2009005), and the Scientific Research Foundation for the Talents of Jiangsu Province, China.

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