Varietal Differences in Cell Wall \(\beta-(1\rightarrow3),(1\rightarrow4)\)-Glucan and Nonstructural Carbohydrate in Rice Stems during the Grain Filling Stage

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Abstract: The contribution of cell wall components and nonstructural carbohydrate (NSC) to grain filling in rice (\(Oryza sativa\) L.) was clarified by investigating the differences in the dynamics of hemicellulose, sugar composition of hemicellulose, \(\beta-(1\rightarrow3),(1\rightarrow4)\)-glucan, and NSC among cultivars with different grain filling capacities. This investigation was performed using the stems of standard, high yield and low harvest index (HI) cultivars. Hemicellulose concentration in stems tended to decrease slightly during the grain filling stage. This decrease was attributed to a decrease in \(\beta-(1\rightarrow3),(1\rightarrow4)\)-glucan concentration, which was detected as a decrease in glucose composition of hemicellulose in the stems during the grain filling stage. The rate of decrease and decrease in the amount of \(\beta-(1\rightarrow3),(1\rightarrow4)\)-glucan in the stems differed among the cultivars. These were higher in high yield and high HI cultivars than in relatively low yield and low HI cultivars. Moreover, a positive correlation was observed between the rate of decrease in \(\beta-(1\rightarrow3),(1\rightarrow4)\)-glucan and NSC, indicating similarities in the dynamics of \(\beta-(1\rightarrow3),(1\rightarrow4)\)-glucan and NSC among the cultivars. When the top half of panicle was removed, \(\beta-(1\rightarrow3),(1\rightarrow4)\)-glucan and NSC concentrations in the culm and leaf sheath did not decrease during the grain filling stage. Therefore, the \(\beta-(1\rightarrow3),(1\rightarrow4)\)-glucan in stems might be one of the sources that supply substrate to panicle as well as NSC.

Key words: \(\beta-(1\rightarrow3),(1\rightarrow4)\)-Glucan, Cell Wall, Hemicellulose, Nonstructural Carbohydrate, Rice.
be responsible for the decrease in cell wall thickness (Nemoto et al., 2004). In addition, \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) decreased in stems during the grain filling stage, but not glucuronoarabinoxylan (Baba et al., 2001). Since \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) undergoes intensive synthesis and degradation in stems of rice plants (Sauter and Kende 1992; Baba et al., 2001), \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) in stems might have function as a temporary carbohydrate reservoir for grain filling. However, little is known about the varietal difference in the rate of \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) degradation.

In this study, the differences in the dynamics of hemicellulose, sugar composition of hemicellulose, \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \), and NSC among cultivars with different grain filling capacities were investigated using the stems of standard, high yield, and low harvest index (HI) cultivars. In addition, the contribution of \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) in the stems to grain filling is discussed.

**Materials and Methods**

1. **Plant materials**

Six rice (Oryza sativa L.) cultivars, Japonica standard cultivars (Koshikihari), Japonica-dominant low HI cultivars (Tachisugata and Leafstar), Japonica-dominant high yield cultivars (Momihroman), and Indica-dominant high yield cultivars (Takanari and Shanguichao), were grown in a paddy field at the NARO Institute of Crop Science in Tsukubamirai (Lat. 36º02’N, Long. 140º04’E), Ibaraki, Japan in 2009 and 2010. Three cultivars (Takanari, Momihroman, and Koshikihari) were grown in 2011. Each year, 20-day-old seedlings of rice were transplanted in mid-May. The plants were grown at a density of 222 (15 × 30 cm) hills per square meter, with one plant per hill. As a basal dressing, chemical fertilizer was applied at rates of 15 g m\(^{-2}\) (P\(_2\)O\(_5\) and K\(_2\)O) in Leafstar, Tachisugata, Momihroman, and Shanguichao and Takanari and 6 g m\(^{-2}\) (N as a controlled release fertilizer; LP40 and LP100) in Leafstar, Tachisugata, Momihroman, Shanguichao and Takanari and 6 g m\(^{-2}\) (N as a controlled release fertilizer; LP40 and LP100) in Koshikihari from 2009 to 2011. LP40 and LP100 fertilizers release 80\% of their total nitrogen content at a uniform rate up to 40 and 100 days after application, respectively, at temperatures between 20 and 30\°C. The experiment was designed as a randomized complete block design with three replications (23 m\(^2\) in 2009, 20 m\(^2\) in 2010, and 25 m\(^2\) in 2011 for each replicate). Eight hills were selected from each replicate for measurements of dry weight, hemicellulose, sugar components in hemicellulose, \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) and NSC. For panicle removal treatment in 2010, the top half of panicles of Takanari and Momihroman were removed immediately after flowering. Eight hills were selected from each replicate for measurement of \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) and NSC.

2. **Measurement of starch, soluble sugar, hemicellulose, and \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \)**

Aboveground samples were dried at 70\°C and separated into leaves, stems (culms and leaf sheaths), and panicles. After dry weight measurement, the stem samples were powdered to produce particles approximately 5 μm in size using a milling machine (TI-100; CMT Co., Japan) before analysis. HI was calculated by dividing the panicle weight by the total aboveground weight, \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) and NSC contents were calculated on the basis of the dry weight of stems and their concentrations.

Cell wall and NSC were fractionated and analyzed using the method of Nishitani and Masuda (1979, 1982) with several modifications. A 100 mg sample of the three biological replications was used for each analysis. Soluble sugar was extracted with 80\% ethanol. Starch was hydrolyzed using α-amylase derived from porcine pancreas (Sigma Co., USA). Starch and soluble sugar concentrations in the extracts were quantified by a phenol-sulfuric acid assay. Absorbance was measured at a wavelength of 490 nm using a spectrophotometer (DU730; Beckman Coulter, USA) with glucose (Nakalai Tesque Inc., Kyoto, Japan) as the standard. The NSC concentration is the sum of soluble sugar and starch concentrations. Hemicellulose was released by adding 4 M potassium hydroxide and decomposed into monosaccharides using trifluoroacetic acid. The monosaccharides were analyzed with a high-performance liquid chromatography system (Shimadzu; Kyoto, Japan) equipped with a Corona detector (Corona CAD; ESA Biosciences Inc., Chelmsford, MA, USA). Water was used as the mobile phase at a flow rate of 1.0 mL min\(^{-1}\). \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \) was quantitated with a Mixed-Linkage Beta-Glucan assay kit (Megazyme International Ireland Ltd., Wicklow, Ireland), according to the manufacturer’s instructions. Absorbance was measured at a wavelength of 510 nm using a microplate reader (SH-9000; Corona Electric Co., Ibaraki, Japan).

The decrease in the amount of hemicellulose, sugar composition of hemicellulose, \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \), and NSC during grain filling was calculated by subtracting the minimum amount during the grain filling stage from the amount at heading [the decrease in the amount (g m\(^{-2}\)) = amount at heading (g m\(^{-2}\)) – minimum amount (g m\(^{-2}\)). The rate of decrease in hemicellulose, \( \beta-(1\rightarrow3), (1\rightarrow4)-\text{glucan} \), and NSC concentrations and sugar composition of hemicellulose was calculated by dividing the decrease in the concentration during the grain filling stage by the concentration at heading [the rate of decrease (%) = (concentration at heading – minimum concentration during the grain filling stage)/concentration at heading × 100].

3. **Statistical analysis**

Statistical analyses were performed using Kyplot software (version 5.0, Kyence, Tokyo). Duncan’s multiple range test was used to test the significance of differences in the components among cultivars (\( P < 0.05 \)).
Results

1. Plant growth

The panicle weight at maturity was higher in Takanari, Momiroman, and Shanguichao and lower in Leafstar compared with the other cultivars (Table 1). In contrast, stem weight at maturity was higher in Leafstar and Tachisugata compared with the other cultivars. HI was higher in Takanari and Shanguichao and lower in Leafstar compared with the other cultivars.

2. Hemicellulose concentration

The hemicellulose concentration in the stems tended to decrease slightly from heading to 35 days after heading (DAH) (Table 2). The rate of decrease in the hemicellulose concentration and the decrease in the amount of hemicellulose during the grain filling stage differed among the cultivars. The rate of decrease in hemicellulose concentration ranged from 2.2% to 9.7% (average, 5.5%), and the decrease in the amount of hemicellulose ranged from 2.4 g m⁻² to 17.2 g m⁻² (average, 10.0 g m⁻²). The decrease was higher in Takanari and Shanguichao but lower in Leafstar compared with the other cultivars.

3. Sugar composition of hemicellulose

Table 3 depicts the sugar composition of hemicellulose fractions. Hemicellulose was mainly composed of glucose, xylose, galactose and arabinose. Xylose was the dominant sugar in all cultivars where it accounted for 661 – 763 g kg⁻¹ of the total sugar content in hemicellulose. Arabinose and glucose accounted for 119 – 142 g kg⁻¹ and 59 – 182 g kg⁻¹, respectively. Galactose accounted for < 43 g kg⁻¹ in all cultivars. Only glucose showed a clear decrease during grain filling and the rate of decrease in glucose composition and the decrease in the amount of glucose composition differed among the cultivars. The rate of decrease in glucose composition ranged from 7.7% to 66.5% (average, 44.6%) and the decreased glucose composition ranged from 2.0 g m⁻² to 16.8 g m⁻² (average, 9.7 g m⁻²). The decrease was higher in Takanari and Shanguichao but lower in Leafstar compared with the other cultivars.

4. \(\beta\)-(1→3),(1→4)-glucan concentration

\(\beta\)-(1→3),(1→4)-glucan concentration in the stems decreased from heading to 35 DAH, with the exception in Leafstar stems (Fig. 1A). The rate of decrease in \(\beta\)-(1→3),(1→4)-glucan concentration and the decrease in the amount of \(\beta\)-(1→3),(1→4)-glucan differed among the cultivars. The rate of decrease in \(\beta\)-(1→3),(1→4)-glucan concentration ranged from 3.3% to 82.0% (average, 45.4%) and the decrease in the amount of \(\beta\)-(1→3),(1→4)-glucan ranged from 0.0 g m⁻² to 13.8 g m⁻² (average, 7.9 g m⁻²). The decrease was higher in Takanari and Shanguichao but lower in Leafstar compared with the other cultivars.

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Table 1. Comparison of panicle weight, stem weight and harvest index among various rice cultivars in 2009.

| Cultivar     | Panicle weight (g m⁻²) | Stem weight (g m⁻²) | Harvest index |
|--------------|------------------------|---------------------|---------------|
| Koshihikari  | 670 c                  | 611 e               | 0.46 b        |
| Leafstar     | 596 c                  | 1345 a              | 0.25 d        |
| Tachisugata  | 878 b                  | 946 b               | 0.42 c        |
| Momirroman   | 1003 a                 | 873 bc              | 0.46 b        |
| Shanguichao  | 1037 a                 | 652 de              | 0.53 a        |
| Takanari     | 1143 a                 | 780 cd              | 0.52 a        |

The panicle and stem weights were measured at maturity. Means within a column followed by the same letters do not differ significantly (P < 0.05, Duncan's multiple range test).

Table 2. Comparison of hemicellulose concentration and the decrease in hemicellulose during the grain filling stage among various rice cultivars in 2009.

| Cultivar     | Hemicellulose concentration (g kg⁻¹) | Decrease in hemicellulose (g m⁻²) |
|--------------|-------------------------------------|----------------------------------|
|              | Heading 20 DAH 35 DAH                |                                   |
| Koshihikari  | 178 175 169                           | 6.0 b                            |
| Leafstar     | 179 178 175                           | 2.4 c                            |
| Tachisugata  | 190 189 182                           | 9.0 b                            |
| Momirroman   | 196 190 188                           | 8.9 b                            |
| Shanguichao  | 179 178 165                           | 17.2 a                           |
| Takanari     | 196 180 176                           | 16.5 a                           |

The decrease in hemicellulose was calculated by subtracting the minimum amounts during grain filling stage from the amounts at heading. Means within a column followed by the same letters do not differ significantly (P < 0.05, Duncan's multiple range test).

DAH: days after heading.
5. NSC concentration

The NSC concentration in the stems decreased from heading to 20 DAH and increased thereafter, with exception in Leafstar and Momiroman stems (Fig. 1B). The concentration decreased from heading to 35 DAH in Momiroman stems. The rate of decrease in NSC concentration and the decrease in the amount of NSC differed among the cultivars. The rate of decrease in NSC concentration ranged from 4.3% to 66.8% (average, 39.5%) and the decrease in the amount of NSC ranged from 17.7 g m$^{-2}$ to 122.8 g m$^{-2}$ (average, 68.6 g m$^{-2}$). The decrease was higher in Takanari and Shanguichao but lower in Leafstar compared with the other cultivars.

6. Relationship between $\beta$-(1→3),(1→4)-glucan and NSC

A positive correlation was observed between the rate of decrease in $\beta$-(1→3),(1→4)-glucan and NSC throughout the 3-year study period (Fig. 2), which indicated that there...
were similarities in the dynamics of $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and NSC among rice cultivars.

7. **Relationship between the decrease in $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and the increase in panicle weight**

   The relationship between the decrease in the amount of $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and the increase in panicle weight was analyzed to elucidate the changes in $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and panicle weight with grain filling. A positive correlation was observed between the decrease in the amount of $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and the increase in panicle weight during the 3-year study period (Fig. 3).

8. **Effect of reduced sink size on $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and NSC**

   $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and NSC concentrations in the culm and leaf sheath of Takanari and Momiroman (Intacts) decreased during the grain filling stage (Fig. 4). When the top half of panicle was removed, however, they did not decrease.

**Discussion**

   The objective of this study was to identify the differences in the dynamics of hemicellulose, sugar composition of hemicellulose, $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan, and NSC among various rice cultivars and to discuss the relationship between $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and characteristics of grain filling.

1. **Dynamics of hemicellulose, sugar composition of hemicellulose, and $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan in stems**

   Hemicellulose consists chiefly of $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan and glucuronoxarabinosylan in gramineous crops (Cosgrove, 2002). In this study, we demonstrated that the hemicellulose concentration in the stems tended to decrease slightly during the grain filling stage in five rice cultivars, except in Leafstar (Table 2). This decrease was attributed to a decrease in $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan concentration, which was detected as a decrease in glucose composition of hemicellulose in the stems during the grain filling stage (Table 3 and Fig. 1A). The rate of decrease in $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan concentration and the decrease in the amount of $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan, which is composed of glucose, varied with the cultivar. Larger decreases were observed in Takanari and Shanguichao, which exhibit high yield and high HI, compared with the other cultivars with relatively low yield and low HI (Table 1 and Fig. 1A). In contrast, xylose, arabinose, and galactose components did not decrease from heading to maturation in any cultivar (Table 3). This result suggests that $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan undergo intensive metabolic turnover during the grain filling stage in the examined cultivars, whereas glucuronoxarabinosylan does not. Similar results have been reported for Takanari (Baba et al., 2001). In addition, $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan degradation during the grain filling stage was accompanied by an increase in the expression level of $GusI$, gene, which encodes $\beta-(1\rightarrow3),(1\rightarrow4)$-glucanase capable of $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan degradation (Baba et al., 2001). The correlation between glucanase activity and $GusI$ gene expression responsible for the differences in the decrease in $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan in the stems of different cultivars requires further clarification.

2. **Dynamics of NSC in stems**

   NSC concentration in stems decreased from heading to 20 DAH in Koshihikari, Tachisugata, Shanguichao and Takanari and to 35 DAH in Momiroman (Fig. 1B). The rate of decrease in NSC concentration and the decrease in the amount of NSC differed among the cultivars and were higher in Takanari and Shanguichao with high yield and high HI than in the other cultivars with relatively low yield and low HI (Table 1 and Fig. 1B). In addition, there was a positive correlation between the decrease in the amount of NSC and increase in panicle weight (data not shown). It was clarified that the enlargement of sink size may have enhanced NSC translocation to some extent using Sasanishiki and its near isogenic lines introduced with QTLs for increasing grain number that were derived from Habataki (Ohsumi et al., 2011). The decrease in the amount of NSC was higher in high yield Takanari compared with standard Nipponbare (Xu et al., 1997).

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**Fig. 3.** Relationship between the decrease in $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan in stems of rice cultivars and the increase in panicle weight grown during the 3-year study period.

The decrease in $\beta-(1\rightarrow3),(1\rightarrow4)$-glucan was calculated by subtracting the minimum amounts during grain filling from the amounts at heading.

The increase in panicle weight was calculated by subtracting the panicle weight at heading from the panicle weight at maturity.

Symbols represent average values ($n = 3$).

* indicates a significant difference at $P < 0.01$. 

$y = 28.8x + 492.3$

$r = 0.94^*$
Then, NSC in stems is one of the sources that supply substrate to panicle in this as well as previous studies.

3. Dynamics of NSC and β-(1→3),(1→4)-glucan

While NSC concentration in stems decreased from heading to 20 DAH and re-accumulated at the late grain filling stage, β-(1→3),(1→4)-glucan concentration in the stems decreased constantly at the late grain filling stage, with exception in Leafstar and Momiroman (Fig. 1). It is possible that the decrease in β-(1→3),(1→4)-glucan in stems might result from a higher degradation rate or a lower synthesis rate, or both at the late grain filling stage. However, the physiological reasons for the decrease in β-(1→3),(1→4)-glucan in stems at the late grain filling stage remain unknown.

4. Contribution of β-(1→3),(1→4)-glucan to grain filling

We found a positive correlation between the rate of decrease in β-(1→3),(1→4)-glucan and NSC (Fig. 2). This indicates that there were similarities in the dynamics of β-(1→3),(1→4)-glucan and NSC among rice cultivars. The rate of decrease in β-(1→3),(1→4)-glucan and NSC was higher in high yield and high HI cultivars (Takanari and Shanguichao) than in relatively low yield and low HI cultivars (Table 1 and Fig. 2). In addition, when the top half of panicle removed, β-(1→3),(1→4)-glucan and NSC concentrations did not decrease during the grain filling stage in Takanari and Momiroman (Fig. 4). Wada (1993) also reported that sucrose and starch contents in stems of rice plants with a reduced sink size only decreased slightly compared with stems of control plants, which was also observed in this study. The contribution rate to panicle weight, which was calculated by dividing the decrease in the amount of β-(1→3),(1→4)-glucan during the grain filling stage by the increase in panicle weight after heading, ranging from 0.0% to 1.6% (average, 1.0%) for β-(1→3),(1→4)-glucan and from 3.5% to 13.4% (average, 9.5%) for NSC. Although the contribution rate of β-(1→3),(1→4)-glucan to grain filling was small, the positive correlations between the dynamics of β-(1→3),(1→4)-glucan and NSC (Fig 2) and β-(1→3),(1→4)-glucan and the increase in panicle weight.

Fig. 4. Changes in β-(1→3),(1→4)-glucan (A, B) and NSC (C, D) concentrations in the culm and leaf sheath of rice cultivar Takanari in 2010. Plants with panicles removed (R) and intact plants (I). Vertical bars represent standard errors (n = 3).
(Fig. 3), suggest that β-(1→3),(1→4)-glucan in stems might be one of the sources that supply substrate to panicle as well as NSC. It might be important for the improvement of grain filling to increase the carbohydrate supplied from not only NSC but also β-(1→3),(1→4)-glucan in stems. It is necessary to examine whether β-(1→3),(1→4)-glucan is actually translocated from stems to panicles.

Furthermore, in case of mechanical strength of cell walls, it has been reported that the decrease in hemicellulose could be responsible for the decrease in cell wall thickness and culm strength (Nemoto et al., 1997; Nemoto et al., 2004). The mechanical strength of stems for bending and lodging is crucial to sustain the stems. The high transport rate of NSC is one of the reasons that breaking resistance in the 4th internode becomes low and lodging might occur more easily in the field (Amano et al., 1993). Increase in the decreased amount of β-(1→3),(1→4)-glucan in stems might lead to low breaking resistance of stems and lodging in paddy fields. It might be necessary to increase other cell wall components to reduce lodging in the paddy fields. Although the cell wall β-(1→3),(1→4)-glucan is known to have several functions such as increasing the mechanical strength of stems and resistance to diseases or pests, our results suggest that β-(1→3),(1→4)-glucan might have also function as a storage carbohydrate. Thus, the function of β-(1→3),(1→4)-glucan requires further clarification.

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