Biomass Production and Lodging Resistance in 'Leaf Star', a New Long-Culm Rice Forage Cultivar

Taiichiro Ookawa¹, Kenichi Yasuda¹, Hiroshi Kato², Makoto Sakai³, Maina Seto¹, Kaoruko Sunaga¹, Takashi Motobayashi¹, Seisyu Tojo¹ and Tadashi Hirasawa¹

(¹Graduate School of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan;

²National Institute of Crop Science, Tsukuba 305-8518, Japan;

³National Agricultural Research Center for Kyushu Okinawa Region, Fukuoka 833-0041, Japan)

Abstract: Biomass production and lodging resistance in the new long-culm forage cultivar 'Leaf Star', developed using a precise evaluation method for lodging resistance, were evaluated by comparing these properties with those of its parents and recently improved forage rice cultivars. Leaf Star had a higher biomass production of above-ground parts than its parents, and its straw yield was 13 t ha¹. The bending moment of the basal internode at breaking in Leaf Star was three times higher than that in Koshihikari, owing to a large section modulus and a high bending stress. Biomass production of above-ground parts of Leaf Star did not differ significantly from that of other forage cultivars. However, Leaf Star had the highest straw yield of all forage cultivars. Leaf Star accumulated a large amount of starch in straw. Bending moment of the basal internode was the highest among forage cultivars owing to a large section modulus. These results show that the traits related to lodging resistance such as culm thickness and culm stiffness could be introduced into long-culm cultivars by using the precise evaluation method for the traits related to lodging resistance. The results also show that Leaf Star has a large biomass and high quality, which are suitable properties for feed and biofuel production.

Key words: Biomass production, Culm stiffness, Culm thickness, Forage rice cultivar, Leaf Star, Lodging resistance, Long-culm cultivar.

Rice cultivation on abandoned cultivated land for multiple uses such as feed and processed food has been promoted in Japan, because it improves the country's self-sufficiency of feed and contributes to the rural economy and the security of food supply. New rice cultivars for whole crop silage use have been released by the Ministry of Agriculture, Forestry and Fisheries (MAFF), Japan (Sakai et al., 2003).

Rice straw is one of the most potent sources of lignocellulosic biomass for second-generation bioenergy in Japan and other Asian countries. The utilization of rice straw biomass could also improve energy self-sufficiency in rural communities and contribute to the creation of a recycling-oriented society. New cultivars have the potential to increase biomass production and crop yield.

In the past, semi-dwarf type rice cultivars with short and erect leaves have been improved by using semi-dwarf genes such as *sd1*. These improved cultivars have been widely cultivated for high yields in Asia, because their lower plant length and weight confer high lodging resistance, and they have good light-intercepting characteristics and a high

harvest index (Peng et al., 2000). The maximum recorded grain yield of indica semi-dwarf rice cultivars is about 10 t ha⁻¹ in Japan (Xu et al., 1997; San-oh et al., 2004) and the tropical irrigated lowlands of Asia (Peng et al., 2000; Yang et al., 2007). However, this yield has changed little over recent years (Peng et al., 1999; Yang et al., 2007). Short-culm cultivars have a lower potential for biomass production than long-culm cultivars (Takeda et al., 1983; Kuroda et al., 1989), and semi-dwarf genes suppress rice plant growth (Hirotsu et al., 2008).

One way of breeding rice cultivars with a high biomass and yield might be to utilize the potential of long-culm rice for high biomass production. Recently improved cultivars with greater plant height have increased biomass production in Japan, the Philippines and China (Peng et al., 2000; Yang et al., 2007). Long-culm rices have particular characteristics that favor high biomass production. Notably, long-culm rices have a lower leaf area density (LAD) than short-culm rices because of their greater height. A low LAD is associated with a high gas diffusion efficiency inside stands, which provides a strong

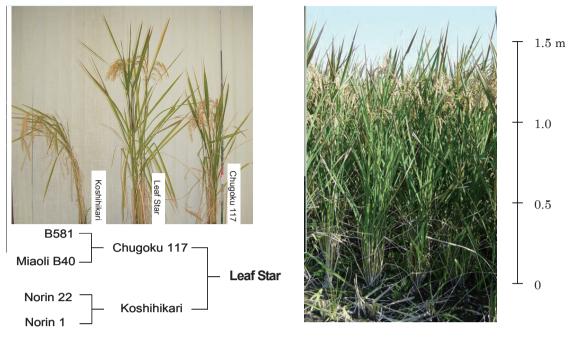


Fig. 1. Plant appearance of Leaf Star and its parents, and the pedigree chart of Leaf Star.

 ${\rm CO_2}$ supply for photosynthesizing leaves (Kuroda et al., 1989; Ookawa et al., 1991). This property of the canopy architecture in long-culm cultivars is important for maintaining a high canopy photosynthetic rate. If the disadvantage of lodging in long-culm rices could be overcome, their potential for increasing biomass yield could be realized.

To use the high biomass yield potential of long-culm rice cultivars to breed high yielding cultivars, it is important to determine the traits related to a high lodging resistance. Large varietal differences in breaking strength of the basal culm are related to lodging resistance, which is associated with basal culm thickness, culm stiffness and reinforcement by leaf sheaths (Ookawa et al., 1992). To improve lodging resistance in long-culm cultivars, we applied precise evaluation methods to select individual traits related to high lodging resistance in a cross between Koshihikari, with a small section modulus, and Chugoku 117, with a large section modulus. Because the section modulus showed a high heritability value in F₂ progenies, this trait is expected to be effective in selecting for high lodging resistance. Three plants in F2 progenies had very high breaking strength, owing to a large section modulus and a high bending stress (Ookawa and Ishihara, 1997). From F₄ progenies, collaboration breeding started with the Chugoku National Agricultural Experimental Station in Hiroshima, Japan. From F₇ progenies, two lines were developed at the National Agricultural Research Center, Tsukuba, Japan. The new long-culm line with strong culms for forage use was designated as Kanto-shi 215 by the National Institute of Crop Science in Tsukuba, and its local adaptability evaluated. In 2005, Kanto-shi 215 was

recognized as having superior lodging resistance and biomass yield, and then officially registered as 'Paddy Rice Norin 413' by the Japanese MAFF, and named 'Leaf Star' (Kato et al., 2009).

To confirm whether the traits related to lodging resistance can be introduced to long-culm cultivars, we evaluated the traits associated with lodging resistance in Leaf Star by comparing these traits with those of its parents and of recently improved forage cultivars. The beneficial properties of biomass production in Leaf Star for feed and biofuel production were also determined.

Materials and Methods

1. Plant materials and cultivation

The rice (*Oryza sativa* L.) cultivar Leaf Star and its parents 'Koshihikari' and 'Chugoku 117' were used in 2005 and 2006 (Fig. 1), and Leaf Star and other improved forage cultivars, 'Takanari', 'Kusahonami' and 'Tachisugata', were used in 2006. Field experiments were conducted on the Experimental Farm of Field Science Center, Tokyo University of Agriculture and Technology in 2005 and 2006. Because growth conditions were similar in these two years, only the cultivation methods for 2006 are described here.

Seeds were sown in nursery boxes on 27 April, 2006. Seedlings at the fourth-leaf stage were transplanted to a paddy field on Tama River alluvial soil at a rate of three plants per hill on 22 May, 2006. Planting density was 22.2 hills m², at a spacing of 15 cm×30 cm. Manure was applied at the rate of about 20 t ha¹¹ before puddling, and compound fertilizer, containing 14% each of N, P_2O_5 and K_2O , was applied as a basal dressing at a rate of 50, 50 and

50 kg each of N, P and K per ha, respectively. Topdressing was applied at a rate of N and K at 30 kg each per ha 20 d before heading and 20 kg each per ha on the day of heading. The field was kept under submerged conditions throughout the course of experiments.

The experiment was designed with three randomly arranged replicates (36 m² for each replicate).

2. Measuring total biomass production, total digestible nutrients (TDN) yield, and straw starch yield

Thirty hills were sampled from each replicate for measurements of total biomass production and straw yield at the harvest time (42 d after heading). Eight plants with the average number of ears in each replicate were selected and separated into leaves, culms plus leaf sheaths, and ears. The samples were oven dried at 80°C for 72 hr. After weighing, dried samples were powdered with a ball mill (TissueLyser, Reche) for measuring TDN and starch

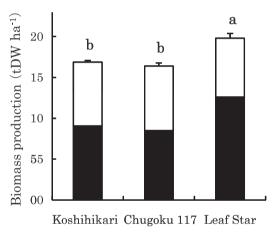


Fig. 2. Comparison of biomass production and straw yield between Leaf Star and its parents in 2005. Solid part of bars: straw dry weight; open part of bars: ear parts dry weight; vertical bars: standard deviation (n=3). Means followed by different letters are significantly different at the 5% level by Tukey's test.

contents. TDN content was determined by near infrared spectroscopic analysis, according to Amari et al. (1998). Starch content was determined with a microplate reader (PowerWave XS, Bio-tek), according to the enzymatic protocol developed for the measurement of multiple samples (Gibon et al., 2002).

3. Measuring lodging resistance traits

The main culm was sampled from hills showing average growth, and the bending load at breaking was measured at a distance of 4 cm from the supporting point by the method of Ookawa and Ishihara (1992), using a universal testing machine (Tensilon RTM-25, Orientec). The degree of lodging, the lodging index, the bending moment at breaking with leaf sheaths, the degree of reinforcement by leaf sheath covering, the section modulus and the bending stress were calculated by the formula of Ookawa and Ishihara (1992). The Klason lignin was assayed according to Ookawa and Ishihara (1992) and Ookawa et al. (1993). The composition of lignin monomer was assayed by the DFRC method (Lu and Ralph, 1997).

Results

1. Comparisons with parents

(1) Properties of biomass production

Biomass production of above-ground parts of Leaf Star was 1.2 times greater than that of its parents at the harvest time in 2005 (Fig. 2). Leaf Star straw yield was 1.4 times greater than that of its parents, while ear weight was slightly lower. The above-ground parts of Leaf Star had a higher straw dry weight percentage than that of the parents.

(2) Properties of lodging resistance traits

The length of the culm and the fifth internode in Leaf Star were greater than those in Chugoku 117. The length of the fifth internode in Leaf Star did not differ significantly from that in Koshihikari in either years. The degree of lodging in Koshihikari was 3.7–4.7 at 20 d after heading in both years, but those in Leaf Star and Chugoku

Table 1. Comparisons of degree of lodging, culm length and length of the 5th internode between Leaf Star and its parents in 2005 and 2006.

	Heading	Degree of lodging		Length of the 5th	Culm length	
	date	20DAH	40DAH	internode (mm)	(cm)	
2005						
Koshihikari	11 Aug.	4.7 a	5.0 a	78.7 a	107.8 a	
Chugoku 117	18 Aug.	0 b	1.3 b	56.7 b	86.9 b	
Leaf Star	31 Aug.	0 b	$0.7\mathrm{b}$	75.4 a	107.3 a	
2006						
Koshihikari	9 Aug.	3.7 a	5.0 a	62.5 a	97.6 b	
Chugoku 117	17 Aug.	0 b	$0.7\mathrm{b}$	56.0 b	82.6 c	
Leaf Star	30 Aug.	0 b	0.3 b	65.4 a	106.9 a	

Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3). DAH, days after heading.

	Lodging index		MLS (g cm)	RLS (%)	Green leaf sheath (No.)	
2005						
Koshihikari	1.82 a	1992 с	1079 с	12.9 с	$4.0\mathrm{b}$	
Chugoku 117	1.35 b	2762 b	2041 b	21.4 a	5.8 a	
Leaf Star	1.08 c	3721 a	3462 a	17.5 b	5.3 a	
2006						
Koshihikari	1.23 a	1858 с	1525 с	24.2 b	4.4 b	
Chugoku 117	1.11 ab	2783 b	2519 b	26.7 a	5.9 a	
Leaf Star	1.03 b	3808 a	3767 a	23.8 b	5.8 a	

Table 2. Comparisons of lodging index and characteristics related to breaking type lodging resistance at 20 d after heading between Leaf Star and its parents in 2005 and 2006.

Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3). WP, bending moment of whole plant added to that of the basal (5th) internode; MLS, bending moment of the basal internode with leaf sheaths at breaking; RLS, degree of reinforcement by leaf sheath covering.

Table 3. Comparisons of bending moment of the 5th internode at breaking (M), section modulus and bending stress at 20 d after heading between Leaf Star and its parents in 2005 and 2006.

	M (g cm)	Section modulus (mm³)	Bending stress (g mm ⁻²)
2005			
Koshihikari	939 с	7.2 b	1333 a
Chugoku 117	$1606\mathrm{b}$	22.9 a	703 b
Leaf Star	2857 a	19.5 a	1475 a
2006			
Koshihikari	1156 с	8.4 b	1380 a
Chugoku 117	$1846\mathrm{b}$	22.1 a	844 b
Leaf Star	2872 a	21.5 a	1371 a

Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3).

117 was 0 in both years at 20 d after heading (Table 1). Considerable lodging, breaking and bending was observed in Koshihikari, after typhoon No. 11 struck on 26 August. Although Leaf Star was exposed to typhoon Nos. 14 and 17 on 6 September and 25 September, respectively, it did not lodge until harvest, nor did Chugoku 117.

In Koshihikari, the lodging index was the highest among cultivars in both years. The bending moment by whole plant added to the basal internode (WP) was higher in Leaf Star than in its parents, as was the bending moment at breaking with leaf sheaths (MLS). As a result, Leaf Star had a lower lodging index than its parents (Table 2).

MLS can be subdivided into the bending moment at breaking without leaf sheath (M) and the degree of reinforcement of leaf sheath covering (RLS). Therefore, these factors were analyzed. RLS in Leaf Star was slightly

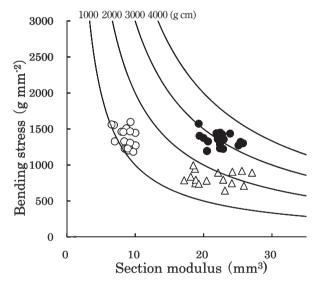


Fig. 3. Relationship between section modulus and bending stress in Leaf Star and its parents at 20 d after heading in 2006.
○, Koshihikari; △, Chugoku 117; ●, Leaf Star. Curved lines indicate the bending moments of the 5th internode at breaking.

lower than that in Chugoku 117 in both years. It was higher than in Koshihikari in 2005, but did not differ significantly in 2006. The number of green leaf sheaths in Leaf Star, and in Chugoku 117, was greater than in Koshihikari (Table 2). In both years, M was much higher in Leaf Star than in its parents (Table 3).

M can be subdivided into the section modulus and the bending stress. Therefore, these factors were analyzed to determine the reasons for the difference in M (Table 3). The section modulus in Leaf Star and Chugoku 117 was larger than that in Koshihikari, while the bending stress in Leaf Star and Koshihikari was higher than in Chugoku 117 (Fig. 3, Table 3).

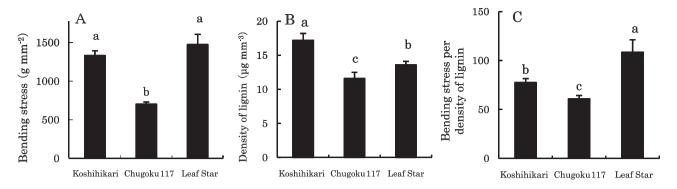


Fig. 4. Comparisons of bending stress (A), density of lignin (B) and bending stress per density of lignin (C) in the 5th internode at 20 d after heading between Leaf Star and its parents in 2006. Vertical bars represent standard deviation (n=3). Means followed by different letters are significantly different at the 5% level by Tukey's test.

Table 4. Comparison of lignin monomer composition in the 5th internode at 20 d after heading between Leaf Star and its parents in 2006.

Cultivar	H-lignin (mM g lignin ⁻¹)	G-lignin (mM g lignin ⁻¹)	S-lignin (mM g lignin ⁻¹)	S/G
Koshihikari	0.335 a	3.351 a	0.178 с	0.053 b
Chugoku 117	0.323 a	3.247 a	$0.228\mathrm{b}$	$0.070\mathrm{b}$
Leaf Star	$0.278\mathrm{b}$	$3.145 \mathrm{b}$	0.357 a	0.114 a

Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3).

To find the reasons for the differences in bending stress of the basal internode between Leaf Star and its parents, we examined the lignin density and composition. Lignin density in Leaf Star was higher than that in Chugoku 117, and lower than that in Koshihikari. Leaf Star had a higher bending stress per lignin density, and had a higher bending stress, than Koshihikari, in spite of the lignin low density (Fig. 4). The G-lignin monomer was a major component in Leaf Star and its parents. In Leaf Star, the S-lignin monomer content was 2-fold higher than that in its parents, while the H- and G-lignin monomer contents were lower than those in its parents. As a result, the S/G ratio in Leaf Star was much higher than that in its parents (Table 4).

To determine the bending type of lodging resistance, we measured the flexural rigidity (FR) with leaf sheaths of individual internodes was compared among cultivars. Leaf Star had higher flexural rigidities from the uppermost internode to the lowest internode than its parents (Fig. 5).

2. Comparisons with other forage rice cultivars

(1) Properties of biomass production and feed quality

Total biomass production and traits related to feed quality (i.e., TDN yield of above-ground parts and starch yield of straw) of Leaf Star were compared with those of the other forage rice cultivars (Table 5). There were no significant differences in biomass production of above-ground parts and total TDN yield among cultivars. Leaf

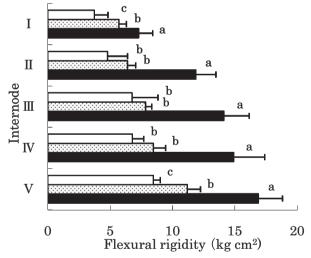


Fig. 5. Comparison of flexural rigidity with leaf sheaths of the individual internode at 20 d after heading between Leaf Star and its parents in 2005. Open bars, Koshihikari; dotted bars, Chugoku 117; solid bars, Leaf Star. Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3).

Star straw yield was 13 t ha⁻¹, the highest among the cultivars. Grain yield of Takanari was the highest of all cultivars, while that in Leaf Star was the lowest. Leaf Star accumulated a large amount of starch in straw, while starch yields in the other three cultivars were especially low at the harvest time.

•	0 ,				
	Total biomass	Total TDN	Straw	Accumulated	Grain
Cultivar	production	yield	biomass	starch in straw	yield
	(tDW ha ⁻¹)	(t ha ⁻¹)			
Takanari	19.9 a	10.3 a	8.3 c	0.2 b	9.7 a
Kusahonami	19.8 a	10.7 a	11.7 b	0.1 b	8.1 a
Tachisugata	20.1 a	10.3 a	11.1 b	0.3 b	7.1 b
Leaf Star	20.4 a	11.0 a	13.0 a	1.8 a	6.4 b

Table 5. Comparisons of total biomass production of above-ground parts, total TDN yield of above-ground parts, straw biomass, accumulated starch yield in straw and grain yield at the harvest time between Leaf Star and the other improved forage rice cultivars in 2006.

Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3). Grain yield is given at a water content of 14.5%.

Table 6. Comparisons of degree of lodging during ripening and characteristics related to breaking type lodging resistance at 20 d after heading between Leaf Star and the other improved forage rice cultivars in 2006.

Cultivar	Heading	Degree o	of lodging	Culm length	Length of the 5th	Lodging	WP	MLS	RLS
Culuvai	date	20DAH	40DAH	(cm)	internode (mm)	index	(g cmx)	(g cm)	(%)
Takanari	12 Aug.	0 b	0.7 b	80.7 b	48.9 с	0.9 a	2568 b	2720 с	33.8 bc
Kusahonami	28 Aug.	2.7 a	4.7 a	106.0 a	86.8 a	1.2 a	3578 a	$2986\mathrm{bc}$	53.2 a
Tachisugata	12 Aug.	0 b	$1.7\mathrm{b}$	109.1 a	79.4 ab	1.1 a	3605 a	3297 ab	28.3 b
Leaf Star	30 Aug.	0 b	1.3 b	112.3 a	$70.0\mathrm{b}$	1.1 a	3953 a	3464 a	18.0 с

Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3). DAH, days after heading; WP, bending moment of whole plant added to that of the basal (5th) internode; MLS, bending moment of the basal internode with leaf sheaths at breaking; RLS, degree of reinforcement by leaf sheath covering.

(2) Properties of lodging resistance traits

The properties of lodging resistance traits in Leaf Star were compared with those of the other forage rice cultivars.

Degree of lodging of the long-culm cultivar Kusahonami was intermediate at 20 d after heading and lodging was severe at the late ripening stage. However, the other long-culm cultivars, Leaf Star and Tachisugata, did not lodge until harvest, nor did the short-culm cultivar, Takanari. MLS in the long-culm cultivars was significantly higher than that in Takanari, while WP in Leaf Star and Tachisugata was higher than that in Takanari (Table 6).

M and the RLS were examined to determine reasons for the differences in MLS among cultivars (Tables 6 and 7). M in Kusahonami was the lowest of all cultivars, and Leaf Star had the highest M (Table 7). On the other hand, RLS in Leaf Star was the lowest of all cultivars. The high MLS in Leaf Star resulted from its high M (Tables 6 and 7).

To determine the reasons for the differences in M among cultivars, we examined the section modulus and bending stressn(Table 7). The section modulus in Leaf Star was the largest of all cultivars. There was no difference in the bending stress among cultivars. However, Leaf Star had relatively high bending stress, in spite of its large section modulus.

These results show that Leaf Star has high yields of straw biomass, and has particularly high culm strength owing to the culm's thickness and stiffness.

Table 7. Comparisons of bending moment of the 5th internode at breaking (M), section modulus and bending stress at 20 d after heading between Leaf Star and the other improved forage rice cultivars in 2006.

Cultivar	M (g cm)	Section modulus (mm³)	Bending stress (g mm ⁻²)
Takanari	1694 с	14.3 с	1321 a
Kusahonami	1399 с	$10.7\mathrm{d}$	1313 a
Tachisugata	2361 b	17.2 b	1421 a
Leaf Star	2842 a	20.5 a	1398 a

Means followed by different letters are significantly different at the 5% level by Tukey's test (n=3).

Discussion

1. Strong culm-related properties in Leaf Star

Leaf Star did not lodge until harvest in both years (Table 1), and showed superior resistance to both breaking type (Tables 2 and 6) and bending type lodging (Fig. 5). Leaf Star had the highest M among the forage cultivars examined, owing to the largest section modulus (Table 7). The parental comparison showed that Leaf Star had a high M, owing to the large section modulus and high bending stress (Table 3; Fig. 3), overcoming the negative correlation between these factors (Ookawa and Ishihara, 1992). The section modulus of Leaf Star in this study was almost as

large as that of the corresponding selected F_2 and F_3 progenies in a previous study (Ookawa and Ishihara, 1997). Ookawa and Ishihara (1997) showed that the section modulus had a continuous distribution in F_2 progenies and a high heritability in F_2 progenies. This means that the culm thickness is a quantitative trait controlled by multiple genes, and is easy to select efficiently. The results of our study confirmed that a long-culm cultivar with a strong culm like Leaf Star could be bred by individual selection in early generations such as F_2 – F_4 . This finding suggests that superior lodging resistance can be introduced into high-yielding cultivars, not only by utilizing one recessive semi-dwarf gene but also by combining the multiple genes for strong culms located on some chromosome regions.

To breed long-culm cultivars with superior lodging resistance and high biomass by using marker-assisted selection efficiently, it is extremely important to determine what causes thick and stiff culms and to identify the quantitative trait loci (QTL) for strong culms. However, few articles have been published on the identification and characterization of QTLs for these traits (Kashiwagi and Ishimaru, 2004; Kashiwagi et al., 2008). We have been estimating some chromosome regions of QTLs for culm thickness (Ookawa et al., 2006a, b). If the QTLs for strong culms could be combined, high lodging resistance might be also introduced to the most widely cultivated cultivar, Koshihikari, which has fine and weak culms. Further studies are needed on the genetic analysis and the physiological regulation of culm thickness and culm stiffness.

In addition to culm thickness, Leaf Star has a high bending stress, an indicator of culm stiffness, in spite of the reduced lignin density (Figs. 3, 4). Reduced lignin content is known to improve feed digestibility and efficiency of saccharification in biofuel production, and to reduce lodging resistance (Zuber et al., 1977; Chen and Dixon, 2007; Li et.al., 2008). Therefore, the strong culms of Leaf Star could be an important trait for improving digestibility and energy yield of rice cultivars. It has been reported that culm stiffness is related to the main cell components such as cellulose, hemicellulose, lignin, silica, and starch, which provide the physical strength of a plant (Sato 1957; Yagi 1983; Kashiwagi and Ishimaru, 2004; Ishimaru et al., 2008; Li et al., 2008). Leaf Star contained a large amount of S-lignin monomers than its parents (Table 4), and accumulated a large amount of starch in parenchyma cells of culms and leaf sheaths (Table 5). These differences in cell components might contribute to the high mechanical strength in Leaf Star. We need to investigate the relationship between the high bending stress and the biochemical components of culm tissue.

Leaf Star has a reddish-brown pigmentation in the hull and internode. This phenotype is similar to that of its parent, Chugoku 117, and *gold hull and internode* (*gh*) mutants. The rice *gold hull and internode*2 (*gh*2) has been identified to be a lignin-deficient mutant, and encodes a cinnamyl-alcohol dehydrogenase (Zhang et al., 2006). The density of lignin in the basal internode in Leaf Star and Chugoku 117 was lower than that in Koshihikari. We need to examine the relationship between the low density of lignin and the phenotype of gold hull and internode in Leaf Star and Chugoku 117.

2. Properties of biomass production in Leaf Star

Traditional long-culm cultivars are susceptible to lodging. The depression of biomass production and yield is a consequence of reduction of light-interception due to lodging (Setter et al., 1997). Leaf Star shows a superior capacity for the biomass production of straw owing to the high lodging resistance, as compared with its parents and other forage cultivars (Fig.2; Table 5). The most notable property of canopy structure related to high biomass production in Leaf Star is a small leaf area density owing to its tall stature (Ookawa et al., 2007). In addition, Leaf Star, like Chugoku 117, has erect leaves for efficient light capture (Fig. 1). Leaf Star had a lower light extinction coefficient like the improved short-culm cultivar, Takanari, at the early ripening stage (Ookawa et al., 2007). Good light-intercepting characteristics are also important for improving the efficiency of radiation use in long-culm cultivars. We need to examine the ecophysiological factors of the high biomass production in Leaf Star and other improved cultivars, focusing on the properties of canopy structure, efficiency of CO₂ diffusion (Kuroda et al., 1989) and leaf photosynthetic rate.

Leaf Star had the greatest straw biomass of all the forage cultivars studied (Table 5). In Leaf Star, high levels of starch accumulated in culms and leaf sheaths at harvest (Table 5). Matsumura (2007) compared the non-structural carbohydrate (NSC) content of culms and leaf sheaths at harvest, using 80 genetic resources including forage rice cultivars. They found that the NSC content in Leaf Star was the highest among these genetic resources (Matsumura, 2007) and that a large amount of NSC accumulated during ripening (Matsumura, 2008). We need to examine the physiological factors of starch accumulation in straw, in terms of the capacities of source and sink and carbohydrate partitioning.

Conclusion

Leaf Star has a superior resistance to both breaking and bending type lodging, owing to a combination of culm thickness and culm stiffness. It was shown that lodging resistance could be introduced to the long-culm cultivars by using a precise evaluation method for the strong-culm traits. Leaf Star produces a large straw biomass and accumulates a large amount of starch in straw. These

properties might contribute to the improvement in feed quality and efficiency of saccharification for biofuel production.

Acknowledgments

We are grateful to Prof. Kuni Ishihara for kind suggestions. This work was supported in part by a Grant-in-Aid by the Japanese Society of Promotion of Science (Grant No. 21380013) and by a grant from the Ministry of Agriculture, Forestry and Fisheries, Japan (Genomics for Agricultural Innovation, IPG-0003).

References

- Amari, M., Masaki, S. and Abe, A. 1998. Prediction of TDN contents of hay and grass silage by near infrared reflectance spectroscopy. *Glassland Science* 44: 61-66*.
- Chen, F. and R.A. Dixon 2007. Lignin modification improves fermentable sugar yields for biofuel production. *Nature Biotech.* 25: 759-761.
- Gibon, Y., Vigeolas, H., Tiessen, A., Geigenberger, P. and Stitt, M. 2002. Sensitive and high throughput metabolite assays for inorganic pyrophosphate, ADPGlc, nucleotide phosphates, and glycolytic intermediates based on a novel enzymic cycling system. *Plant J.* 30: 221-235.
- Hirotsu, N., Kashiwagi, T., Madoka, Y. and Ishimaru, K. 2008. Time-related identification of chromosome regions affecting plant elongation in rice (*Oryza sativa* L.). *Plant Physiol. Biochem.* 46: 517-523.
- Ishimaru, K., Togawa, E., Ookawa, T., Kashiwagi, T., Madoka, Y. and Hirotsu, N. 2008. New target for rice lodging resistance and its effect in a typhoon. *Planta* 227: 601-609.
- Kashiwagi, T. and Ishimaru, K. 2004. Identification and functional analysis of a locus for improvement of lodging resistance in rice. *Plant Physiol.* 134: 676-683.
- Kashiwagi, T., Togawa, E., Hirotsu, N. and Ishimaru, K. 2008. Improvement of lodging resistance with QTLs for stem diameter in rice (*Oryza sativa* L.). Theor. *App. Genet.* 117: 749-757.
- Kato, H., Nemoto, H., Sakai, M., Ando, I., Ookawa, T., Hirabayashi, H., Ideta, O., Takeuchi, Y., Hirayama, H., Ohta, H., Sato, H., Imbe, T., Nakagawa, N., Horisue, N., Takadate, M., Tamura, K., Aoki, N., Ishihara, K., Ishii, T., Iida, S. and Maeda, H. 2009. Breeding of "Leaf Star" with high stem and leaf yield for whole crop silage rice cultivar. *Bull. Natl. Inst. Crop Sci.* 10 (In press)*.
- Kuroda, E., Ookawa, T. and Ishihara, K. 1989. Analysis on differences of dry matter production between rice cultivars with different plant height in relation to gas diffusion inside stands. *Jpn. J. Crop* Sci. 58: 374-382*.
- Li,X., Weng, J.-K. and Chapple, C. 2008. Improvement of biomass through lignin modification. *Plant J.* 54: 569-581.
- Lu, F.C. and Ralph, J. 1997. Derivatization followed reductive cleavage (DFRC method), a new method for lignin analysis: protocol for analysis of DFRC monomers. *J. Agric. Food. Chem.* 45: 2590-2592.
- Matsumura, O. 2007. Varietal characteristics about nonstructural carbohydrate accumulation in the stem of rice plant for forage use. *Jpn. J. Crop Sci.* 76 (Extra1): 50-51**.

- Matsumura, O. 2008. Nutritional value of nonstructural carbohydrate accumulated in the stem and the leaf sheath of rice plant for forage use. *Jpn. J. Crop Sci.* 77 (Extra1): 48-49**.
- Ookawa, T. and Ishihara, K. 1992. Varietal difference of physical characteristics of the culm related to lodging resistance in paddy rice. *Jpn. J. Crop Sci.* 61: 419-425*.
- Ookawa, T. and Ishihara, K. 1993. Varietal difference of the cell wall components affecting the bending stress of the culm in relation to the lodging resistance in paddy rice. *Ipn. J. Crop Sci.* 62: 378-384*.
- Ookawa, T. and Ishihara, K. 1997. Genetic characteristics of the breaking strength of the basal culm related to lodging resistance in a cross between Koshihikari and Chugoku 117. *Jpn. J. Crop Sci.* 66: 603-609.
- Ookawa, T., Kuroda, E. and Ishihara, K. 1991. Difference of photosynthetic rates among the leaves at the equivalent positions on the main stem and its tillers in rice plants. *Jpn. J. Crop Sci.* 60: 413-420*.
- Ookawa, T., Miura, H., Kondo, M., Yano, M., Ando, T. and Hirasawa, T. 2006a. Analysis of traits affecting lodging resistance and mapping of their QTLs using the series of Habataki chromosome segment substitution in rice variety, Sasanishiki. *Jpn. J. Crop Sci.* 75 (Extra1): 182-183**.
- Ookawa, T., Mori, Y., Ebitani, T. and Hirasawa, T. 2006b. QTL analyses for the physical characteristics of the basal culm related to lodging resistance in rice, using progenies of Chugoku 117/Koshihikari//Koshihikari cross. *Jpn. J. Crop Sci.* 75 (Extra1): 208-209**.
- Ookawa, T., Todokoro, Y. and Ishihara, K. 1993. Changes in physical and chemical characteristics of culm associated with lodging resistance in paddy rice under different growth conditions under varietal difference of their changes. *Jpn. J. Crop Sci.* 62: 525-533*.
- Ookawa, T., Yasuda, K., Yoshino, T., Motobayashi, T. and Hirasawa, T. 2007. Characteristics of the biomass production and the lodging resistance of new long culm rice cultivars and lines for forage use. *Jpn. J. Crop Sci.* 76 (Extra1): 250-251**.
- Peng, S., Cassman, K.G., Virmani, S.S., Sheehy, J. and Khush, G.S. 1999. Yield potential trends of tropical rice since the release of IR8 and the challenges of increasing rice yield potential. *Crop Sci.* 39: 1552-1559.
- Peng,S., Laza, R.C., Visperas, R.M., Sanico, A.L., Cassman, K.G. and Khush, G.S. 2000. Grain yield of rice cultivars and lines developed in the Philippines since 1966. *Crop Sci.* 40: 307-314.
- Sakai, M., Iida, S., Maeda, H., Sunohara, Y., Nemoto, H. and Imbe, T. 2003. New rice varieties for whole crop silage use in Japan. *Breed.* Sci. 53: 271-275.
- San-oh,Y., Mano, Y., Ookawa, T. and Hirasawa, T. 2004. Comparison of dry matter production and associated characteristics between direct-sown and transplanted rice plants in a submerged paddy field and relationships to planting patterns. *Field Crops Res.* 87: 43-58.
- Sato, K. 1957. Studies on the starch contained in the tissues of rice plant. IV. Starch content in the culm related to lodging. *Proc. Crop Sci. Soc. Jpn.* 26: 19**.
- Setter, T., Lauyeles, E.V. and Mazaredo, A.M. 1997. Lodging reduces yield of rice by self-shading and reductions in canopy photosynthesis. *Field Crops Res.* 49: 95-106.
- Takeda, T., Oka, M. and Agata, W. 1983. Characteristics of dry matter and grain production of rice cultivars in the warmer part of Japan.

- I. Comparison of dry matter production between old and new types of rice cultivars. *Jpn. J. Crop Sci.* 52: 299-306*.
- Xu, Y.-F., Ookawa, T. and Ishihara, K. 1997. Analysis of the dry matter production process and yield formation of the high-yielding rice cultivar Takanari, from 1991 to 1994. *Jpn. J. Crop Sci.* 66: 42-50*.
- Yagi, T. 1983. Studies on breeding for culm stiffness in rice. 1.
 Varietal differences in culm stiffness and its related traits. *Jpn. J. Breed.* 33: 411-422*.
- Yang, W., Peng, S., Laza, R.C., Visperas, R.M. and Dionisio-Sese, M.L. 2007. Grain yield and yield attributes of new plant type and hybrid rice. *Crop Sci.* 47: 1393-1400.
- Zhang, K., Qian, Q., Huang, Z., Wang, Y., Li, M., Hong, L., Zeng, D., Gu, M., Chu, C. and Cheng, Z. 2006. GOLD HULL AND INTERNODE2 encodes a primarily multifunctional cinnamylalcohol dehydrogenase in rice. Plant Physiol. 140: 972-983.
- Zuber, M.S., Colbert, T.R. and Bauman, L.F. 1977. Effect of brown-midrib-3 mutant in maize (*Zea mays* L.) on stalk strength. *Z. Pflanzenzuchtung* 79: 310-314.

^{*} In Japanese with English abstract.

^{**} In Japanese.