

Studies on Lodging in Rice Plants

II. Morphological characteristics of the stem at the breaking position

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Abstract : In order to clarify the reason why breaking occurs at the special breaking position (BP) within the broken internode, morphological characteristics of BP were compared with those of other areas within the same internode.

In the broken internode of lodging-susceptible cultivars, hardness of the internode (IN) and dry matter accumulation was lowest at BP. It seems that the two apparent tendencies are partly due to the increase in the flattening of internode of the area by tight wrapping of the leaf sheath, the decrease in both the thickness and the supplementary strengthening efficiency of the leaf sheath in this area. All these aspects together indicate that BP is the weakest area of the internode which results from the shortcomings of both the internode and the leaf sheath in the area. These results illustrate the reason why BP has the lowest breaking strength in this area which leads to breakage.

Key words : Dry matter, Flattening of internode, Hardness of internode, Special breaking position, Supplementary strengthening efficiency of leaf sheath, Thickness of leaf sheath, Width of internode.

イネの倒伏に関する研究 第2報 挫折位置における茎の形態的特性 : 王善本・星川清親 (東北大学農学部)

要旨 : 前報では、下位節間における挫折が節間の特定位置で起こることを明らかにした。本報では、挫折がなぜこの特定位置で起こるのかについて、節間を異なる部位に分けて、各部位の形態的形質を比較検討した。倒伏に弱い品種の下位節間では、節間(葉鞘つき)が最下部の部位で最も太く、挫折の起こる特定位置に向かって葉鞘が薄くなるとともに、節間が急に細くなった。またこの位置では葉鞘の補強作用が急に低くなった。挫折の特定位置における節間自身の乾物重が各部位の中で最も小さかった。これらはこの位置の節間自身の硬度が最も低いことと関連し、特定位置の節間自身が最も弱いことを意味した。さらにこの弱さに加え、葉鞘の巻き付けなどによって特定位置の扁平率が急に高くなった。

このように、挫折の特定位置において、節間が急に細く、節間自身の乾物重と硬度が最も低く、そして扁平率が急に高くなること；また葉鞘が急に薄く、その補強作用が急に低くなること、つまり特定位置における節間自身と葉鞘との状況がともに劣っていることの総合的結果として、この位置で挫折が最も起こりやすいことになっていることが解明された。

キーワード : 乾物重, 挫折の特定位置, 節間の硬度, 節間の太さ, 節間の扁平率, 葉鞘の厚さ, 葉鞘の補強率。

Basic anatomical, morphological and physiological investigations on culm characters of cereal crops have been conducted to understand fully the causes that lead to the occurrence of lodging^{1,6,7,8,10,12}). These studies on lodging, however, regarded the broken internode as a whole. Little attention has been paid to the specific breaking position in the broken internode, i.e., which part of the internode tends to break easily, and what characteristics are responsible for the existence of the breaking position, and so on.

In the previous paper²), it was shown that breakage in a broken internode takes place at a limited position in the internode. This observation brings about the fundamental problem

as to what causes such a phenomenon. It is the purpose of this paper to clarify the morphological characteristics of the breaking position from a series of comparisons among multiple morphological characters of the internode.

Materials and Methods

In the present experiments, plants of cv. Akihikari (lodging-resistant) and Koshihikari and Sasanishiki (lodging-susceptible) were grown in the paddy field under ordinary cultural conditions in 1987. Plants of the three cultivars were transplanted to the paddy field on May 8 with a planting space of 15×30 cm (two plants per hill). Lodging occurred at late ripening stage in plants in the inner portion of the field in both Koshihikari and Sasanishiki. Lodged plants were sampled soon after lodg-

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ing occurred together with unlodged plants in the border of the same field. Sampled plants were randomly taken from the paddy field by hills, then were separated into individual stems including main stems and tillers. Twenty stems for a single sample were used for morphological measurements.

In 1989, fertilizer treatments were conducted in the paddy fields with cv. Sasanishiki. The amount of nitrogen fertilizer application at active tillering stage and panicle initiation stage was 6 kg per 10 a, which was regarded as a heavy manuring treatment, with their control at the level of 1 kg applied at the two stages. Basal dressing was 4 kg per 10 a in the two heavy manuring treatments and the control. Lodging occurred in plants under the two heavy manuring treatments at late ripening stage but no lodging was observed on the control. Both lodged and unlodged plants were sampled for morphological measurements.

Morphological measurements were conducted mainly on lower internodes since they are responsive to lodging as shown in the previous paper²⁾. A single internode was divided into five areas from its lower nodal level to the upper nodal level. These areas, as shown in Fig. 1, are defined respectively as A, B, C, D and E area, where area A and E are symmetrical areas at least 0.5 cm from the nearest node, and area B and D are also symmetrically determined by a distance of 10 to 30% of the full internode length to their nodal levels, and area C is designated as the middle area of the internode. It is apparent that area B is the special breaking area of the internode according to results as shown in the previous paper²⁾.

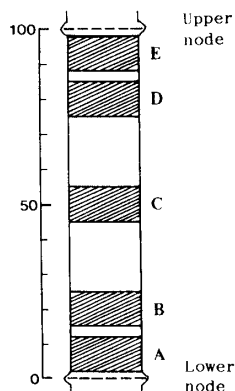


Fig. 1. Schematic diagram showing different areas of an internode.

Morphological measurements on the different areas of the internode were conducted focussing on the following characters:

1. Width of internode

Width of internode in each area was measured with a dial caliper at the major and the minor axis directions of the cross section of the internode respectively. This measurement was conducted on the internode with the leaf sheath which is regarded briefly as "IN + LS", and the internode without the leaf sheath as "IN". Width of each area was calculated as the square root of the major and the minor axes.

2. Flattening of internode

Flattening of internode in each area was calculated according to the formula employed in the previous paper²⁾:

$$\text{Flattening } (\%) = [1 - (\text{The minor axis} / \text{The major axis})] \times 100.$$

3. Thickness of leaf sheath

Thickness was studied in this study as one of the morphological characteristics of the leaf sheath since it was suggested earlier that the thickness of leaf sheath is concerned with the lodging resistance of the internode⁵⁾.

Because the width of each area was measured at the major and the minor axes directions with and without the leaf sheath, thickness of leaf sheath in each area was subsequently calculated based on the difference between the two cases as shown below:

$$\text{Thickness of leaf sheath} = \text{"IN + LS"} - \text{"IN"}.$$

(the major or the minor axis direction)

The average thickness of the leaf sheath in each area was given as the average of the values obtained at the major and the minor axis directions.

4. Hardness and supplementary strengthening efficiency of the leaf sheath

Hardness of each area, which indicates the breaking strength of the area, was measured with a hardness tester at the minor axis direction because breaking occurs at this direction. Hardness was measured with and without the leaf sheath.

Supplementary strengthening efficiency (SSE) of the leaf sheath, a criterion intended for the evaluation of the contribution of leaf sheath to the breaking strength of the internode, was calculated based on the difference of hardness when measured with and without

the leaf sheath as show below :

$$\text{SSE } (\%) = [1 - (\text{Hardness of IN} / \text{Hardness of IN+LS})] \times 100.$$

It can be seen from this formula that the bigger the value of SSE, the higher is the contribution by the leaf sheath to the breaking strength of the internode.

5. Dry matter of internode

Internode was cut off by a certain length (normally less than 1 cm) from each area with leaf sheath attached and dried to constant weight. Dry matter of each area was calculated both with and without the leaf sheath as dry matter per unit length.

Analysis of the data was performed with LSD method, and comparisons among different areas of an internode were conducted.

Results and Discussion

1. Width of internode at the breaking position

For internode IV, there is a tendency of gradual reduction from area A to E in the width of the internode with the leaf sheath. On the other hand, area A tends to have the lowest width compared to that of other areas when leaf sheath is removed (Table 1).

Cultivars that have different lodging resistance also vary in the magnitude of the difference among the width of internode in these areas. In Akihikari which is lodging-resistant, area A and B had approximately the same width in the case of "IN+LS". There was a significant difference, on the other hand, in the width between area A and B in the case of "IN+LS" both in Koshihikari and Sasanishiki

which are lodging-susceptible. This reduction was mainly due to the significant decrease in the thickness of the leaf sheath, because the width in "IN" of this area increased significantly than that of area A.

2. Thickness of leaf sheath in the break-

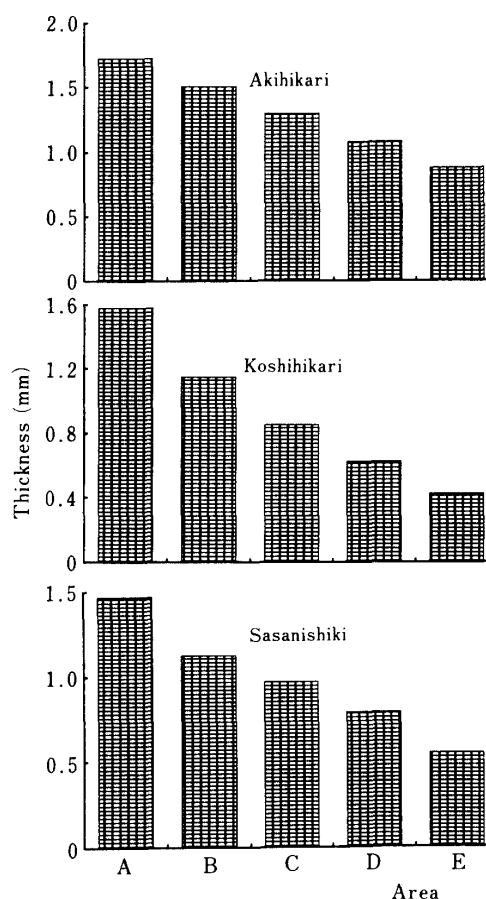


Fig. 2. The average thickness of leaf sheath in different areas of the IV internode.

Table 1. Comparison of the width (mm) of the internode among different areas of the IV internode.

Cultivar		Area				
		A	B	C	D	E
Akihikari	IN+LS ¹⁾	5.77d	5.73d	5.57c	5.34b	5.11a
	IN ²⁾	4.05a	4.27b	4.35c	4.33c	4.28b
Koshihikari	IN+LS	5.18e	5.02d	4.69c	4.38b	4.09a
	IN	3.61a	3.87d	3.83d	3.77c	3.69b
Sasanishiki	IN+LS	4.66e	4.56d	4.44c	4.17b	3.92a
	IN	3.26b	3.36c	3.32c	3.22b	3.15a

1) : internode with leaf sheath ; 2) : without leaf sheath ; Values with the same letter in a row are not significantly different at the 0.05 level.

Table 2. Comparison of the thickness (mm) of leaf sheath in the major axis (MaA) and the minor axis (MiA) directions among different areas of the IV internode.

Cultivar	Axis	Area					LSD (0.05)
		A	B	C	D	E	
Akihikari	MaA	1.80	1.58	1.41	1.15	0.97	0.25
	MiA	1.65	1.44	1.20	1.00	0.78	0.23
Koshihikari	MaA	1.68	1.26	0.93	0.71	0.47	0.27
	MiA	1.47	1.03	0.77	0.53	0.37	0.18
Sasanishiki	MaA	1.62	1.25	1.04	0.87	0.68	0.26
	MiA	1.31	1.00	0.89	0.70	0.42	0.15

ing position

The average thickness of leaf sheath in different areas of the internode tended to decrease acropetally from area A which holds the thickest leaf sheath. This tendency is common in the three cultivars Akihikari, Koshihikari and Sasanishiki as shown in Fig. 2, suggesting that the gradual reduction in the thickness of leaf sheath in different areas may be a natural adaptation of the plant to prevent lodging. From the histogenetic standpoint of the rice plant, the upper part of the internode is generally more matured and lignified than the lower part. It seems that basipetal gradual increase in the thickness of leaf sheath enables the lower part of the internode to have considerable strength against lodging.

For lodging-susceptible cultivars, however, the extent of decrease in the thickness of leaf sheath in area B was higher compared to that of lodging-resistant cultivar. Table 2 shows that in both the major and the minor axis directions, there was no significant reduction in the thickness of leaf sheath in area B in Akihikari. The thickness of leaf sheath in area B of Koshihikari and Sasanishiki, however, was significantly lower than that of area A. Another apparent observation in Table 2 is that reduction in the thickness of leaf sheath in area B was higher in the minor axis direction than that in the major axis direction in the two lodging-susceptible cultivars. These apparent trends in the reduction in the thickness of leaf sheath of area B in the two cultivars in the minor axis direction, may partly explain why breaking occurs specially at area B and at the minor axis direction of this area²⁾.

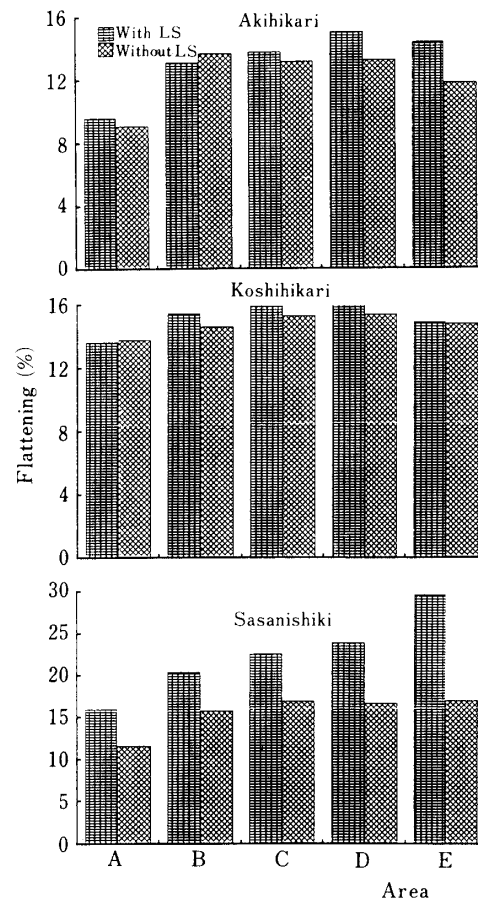


Fig. 3. Comparison of the flattening of internode among different areas of the IV internode.

3. Flattening of internode in the breaking position

The flattening of the internode tends to become higher from area B in the three cultivars (Fig. 3). This tendency appears regardless of the presence of the leaf sheath, although flattening of internode in each area is

commonly higher in IN+LS than that in IN.

Flattening of the internode was regarded to be involved in the lodging resistance of the internode²⁾. The fact that flattening became higher from area B both with and without leaf sheath may account for the reduction in the breaking strength from this area.

Flattenings of the internode at area B between lodged and unlodged plants were compared from the border plants and plants in the inner part of the same paddy field (Table 3). In Akihikari which is lodging-resistant, there was no significant increase in

flattening at area B in both with and without leaf sheath between plants of the border and the inner parts. In Koshihikari which is lodging-susceptible, however, there was a significant increase in the flattening of IN between lodged (inner plants) and unlodged plants (border plants) in the case of IN. This result suggests that the increase in the flattening of internode at the breaking position is involved in the occurrence of breaking at that position in the internode of a lodging-susceptible cultivar.

4. Hardness and supplementary stren-

Table 3. Comparison of the flattening (%) among different areas of the IV internode between border plants (BP) and inner plants (IP) of the same field.

Cultivar			Area				
			A	B	C	D	E
Akihikari	IN+LS ¹⁾	BP	9.93	11.97	12.43	13.35	13.81
		IP	12.32	13.15	13.13	14.32	13.58
			NS	NS	NS	NS	NS
	IN ²⁾	BP	6.58	11.43	12.38	11.98	11.69
		IP	9.73	12.62	13.32	13.48	12.51
			NS	NS	NS	NS	NS
Koshihikari	IN+LS	BP	12.07	12.77	13.68	14.53	14.66
		IP	15.31	16.01	16.55	19.23	19.22
			NS	NS	NS	*	*
	IN	BP	12.39	13.38	13.49	13.16	12.15
		IP	15.61	16.59	17.78	16.69	15.95
			NS	*	*	*	NS

1) : internode with leaf sheath ; 2) : without leaf sheath ; Inner Plants (IP) of cv. Koshihikari are lodged ones ; NS and * : not significant and significant at the 0.05 level, respectively.

Table 4. Comparison of the hardness (kg/cm²) and the supplementary strengthening efficiency (SSE, %) of the leaf sheath among different areas of the IV internode.

Cultivar			Area					LSD(0.05)
			A	B	C	D	E	
Akihikari	Hardness	IN+LS ¹⁾	3.41	1.92	1.63	1.44	1.89	0.49
		IN ²⁾	1.32	0.74	0.85	0.90	1.17	0.10
	SSE		61.3	61.5	47.9	37.5	38.1	6.2
Koshihikari	Hardness	IN+LS	1.83	1.19	1.02	1.08	1.46	0.14
		IN	0.64	0.48	0.59	0.71	1.04	0.05
	SSE		65.0	59.7	42.2	34.3	28.8	4.5

1) : internode with leaf sheath ; 2) : without leaf sheath.

gthening efficiency of leaf sheath in the breaking position

In evaluating the breaking strength of different areas within an internode, hardness has been used as a proper criterion by some investigators⁴). Hardness of the five areas in the IV internode was measured in Akihikari and Koshihikari. Hardness was highest in area A measured with the leaf sheath, and became lower from area B to area D, but got higher than these three areas in the uppermost area E (Table 4). When measured without the leaf sheath, however, there was an apparent tendency that hardness is lowest in area B and is highest in area E. The highest hardness in area A of IN+LS and in area E of IN may have resulted from the thickest leaf sheath in area A and the extensive maturation and lignification in area E. The lowest hardness of IN in area B may be the combined result of the poor status of the leaf sheath and the lower extent of maturation and lignification in this area. Although its width and maturation

extent was lowest among the five areas, hardness of IN in area A was higher than that in area B. This may be related to the presence of the node next to the lower end of area A.

Since the breaking strength of the internode is both affected by the status of the leaf sheath and of the internode itself, it is essential to evaluate the supplementary strengthening efficiency (SSE) of the leaf sheath to the breaking strength of the whole internode. Such a criterion has been employed by some investigators^{4,5,9}). A significant decrease in SSE from area B compared to that of area A was observed in the lodging-susceptible cultivar, Koshihikari, but not in the lodging-resistant cultivar, Akihikari (Table 4). This decrease in SSE may be due to the significant reduction in the thickness of leaf sheath at this area in the lodging-susceptible cultivars.

Some investigators already attempted to evaluate the supplementary strengthening efficiency of leaf sheath to the breaking strength of the internode, although they did not take into account the difference among areas in the same internode. Kato and Kato (1962) measured the extent of SSE of leaf sheath to the breaking strength of the internode in rice plants, and suggested that leaf sheath contributes 70 to 90% in the early ripening stage and 50 to 70% in the late ripening stage⁵). Yoshida (1981) also estimated that the leaf sheath of rice plants contributes to the breaking strength of the internode by 30 to 60%¹¹). In barley, Hozyo and Oda (1965) indicated that the leaf sheath efficiency for culm strength was about 10 to 70%, and was higher in the upper internodes than in the basal⁴). They also found that the hardness was not homogeneous in each area of the internode, and that the area 1 cm above the node showed the lowest hardness³). But the second area they measured was 2 cm upper from the first area, that is, 3 cm upward from the node. This position is considerably higher as compared with the breaking point obtained in the present study. In other words, they did not measure the hardness of the breaking area of the internode as identified by the present authors.

It can be concluded that significant reduction in both the thickness and SSE of leaf sheath in area B and the lowest hardness of IN in this area are responsible for the observed fact that area B is the breaking position.

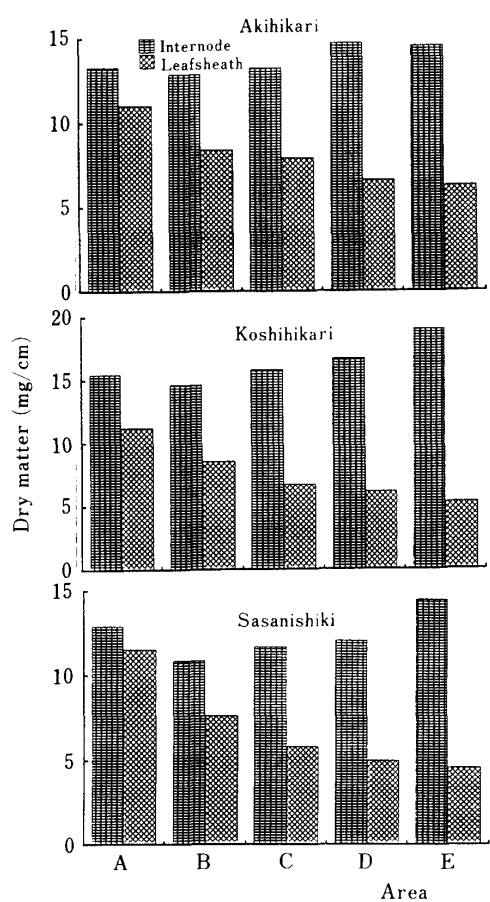


Fig. 4. Comparison of dry matter among different areas of the IV internode.

Table 5. Comparison of dry matter (mg/cm) among different areas of the IV internode between lodged and unlodged plants.

Area	Treatment 1 ¹⁾	Treatment 2 ²⁾	Control ³⁾
A	6.86 × 0.39 (106)***	8.26 × 0.94 (103)***	14.29 × 1.12 (103)
B	5.94 × 0.38 (92)***	7.13 × 0.76 (89)***	13.69 × 0.95 (99)
C	6.45 × 0.47 (100)***	8.04 × 0.70 (100)***	13.79 × 0.608 (100)
D	7.35 × 0.44 (114)***	9.21 × 0.66 (115)***	14.90 × 0.75 (108)
E	8.50 × 0.53 (132)***	9.95 × 0.72 (124)***	15.75 × 0.61 (114)

1) : topdressing at active tillering stage, plants lodged ;

2) : topdressing at panicle initiation stage, plants lodged ;

3) : plants unlodged ;

Value are shown as mean ± SE.

Numerals in parentheses are percentages of the areas to area C.

*** : significant at the 0.001 level from the control.

5. Dry matter of internode in the breaking position

Dry matter of internode has been found to correlate with the breaking resistance of the internode¹⁰⁾. Dry matter of internode in different areas of the IV internode were measured as one of the criteria to evaluate the breaking resistance of these areas within the internode.

There was a general tendency in the three cultivars, regardless of their lodging resistance, that dry matter of leaf sheath tends to decrease gradually from area A to E. In the internode (IN), however, dry matter was lowest in area B (Fig. 4). The gradual reduction in dry matter of leaf sheath from area A to E may be related to the acropetal decrease in the average thickness of leaf sheath of each area as shown in Fig. 2.

The lowest dry matter of IN in area B as compared to other areas within the same internode, however, seems to be the result of the combined effects of the carbohydrate content and the extent of maturation and lignification in this area.

To give a more adequate evidence on the situation of dry matter in this area, comparison of dry matter in different areas of the IV internode was conducted in different treatments with cv. Sasanishiki (Table 5). Dry matter of lodged plants applied with heavy fertilizer at active tillering stage or panicle initiation stage were significantly lower than of unlodged plants in the control. This result is in accordance with that shown in Fig. 4. When comparing the extent of reduction in dry

matter of area B to area C which is the middle part of the internode, dry matter in area B is only 92% and 89% as compared to area C in lodged plants of the treatments. In plants of the control, however, area B showed approximately the same (99%) dry matter to area C. This result indicates that the extent of decrease in dry matter of area B in lodged plants is higher than that of plants in the control. It can be inferred that the significant reduction in dry matter of area B is one of the causes resulting in the breaking at this area.

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References

1. Dahnous, K., G.T. Vigue, A.G. Law, C.F. Konzak and D.G. Miller 1982. Height and yield response of selected wheat, barley, and triticale cultivars to ethephon. *Agron. J.* 74: 580—582.
2. Hoshikawa, K. and S.B. Wang 1990. Studies on lodging in rice plants. I. A general observation on lodged rice culms. *Jpn. J. Crop Sci.* 59: 809—814.
3. Hozyo, Y. and K. Oda 1965. Studies on the stiffness of culms in barley plants (*Hordeum sativum*, JESSEN). 2. The development of physical properties in culms. *Proc. Crop Sci. Soc. Japan* 33: 259—262*.

4. ——— and ——— 1985. ———. 3. The effect of leaf sheath and turgor pressure on physical properties in culms. Proc. Crop Sci. Soc. Japan 33 : 263—267*.
5. Kato, I. and Y. Kato 1962. Studies on lodging in rice varieties. II. Lodging resistance and the mechanism of leaf sheath efficiency for culm strength. Proc. Crop Sci. Soc. Japan 30 : 367**.
6. Kawahara, H. and K. Nakasatomi 1966. Studies on morphogenesis in rice plants. 1. Histological observations on the culm tissues of rice plants cultivated in the basin of the Lake Kasumigaura and the Tone River. Proc. Crop Sci. Soc. Japan 34 : 329—336*.
7. Larson, J.C. and J.W. Maranville 1977. Alterations of yield, test weight, and protein in lodged grain sorghum. Agron. J. 69 : 629—630.
8. Matsuda, T., H. Kawahara and N. Chonan 1982. Histological studies on breaking resistance of lower internodes in rice culm. I. Observation on histogenesis of elongating internodes with light and electron microscope. Jpn. J. Crop Sci. 51 : 562—569*.
9. ———, ——— and ——— 1983. ———. IV. The roles of each tissue of internode and leaf sheath in breaking resistance. Jpn. J. Crop Sci. 52 : 355—361*.
10. Seko, H. 1962. Studies on lodging in rice plants. Bull. Kyusyu Agric. Exp. Stn. 7 : 419—499*.
11. Yoshida, S. 1981. Fundamentals of Rice Crop Science. International Rice Research Institute, Manila, Philippines. 1—25.
12. Zuber, M.S. and C.O. Grogan 1961. A new technique for measuring stalk strength in corn. Crop Sci. 1 : 378—380.

* In Japanese with English summary.

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