Factors Responsible for Decreasing Sturdiness of the Lower Part in Lodging of Rice (Oryza sativa L.)

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Abstract: Here, we propose new improvement targets capable of decreasing loss of the sturdiness of the lower part in the rice plant (Oryza sativa L.), thereby improving lodging resistance. In nine rice cultivars with various plant lengths, we analyzed the factors responsible for sturdiness of the lower part and, thus, for resistance to lodging. The ratio of lodging resistance to sturdiness of the lower part (RLS) was calculated. The difference in pushing resistance between the lower part and the whole plant varied among cultivars. Among the morphological traits, plant length and the weight of the upper part of plant were not correlated with RLS, but the difference between plant length and length from the ground to the ear (DPE), as well as the weight of the lower stem, were positively correlated with RLS. DPE and the weight of the lower stem were not significantly correlated with ear weight. These results suggest that improvements in DPE and in the weight of the lower stem could be primary targets for improving RLS, thus increasing lodging resistance, without affecting yield.

Key words: Lodging, Pushing resistance, Rice.

Lodging of crops is an important problem in agriculture. Leaf shading and constriction of conducting tissues caused by lodging decrease both photosynthesis and photoassimilation, causing poor grain filling and reduced yield. Lodging has been shown to reduce yield, the quality of grain, and the efficiency of mechanical harvesting (Weber and Fehr, 1966; Kono, 1995). Lodging causes the loss of as much as 22% of potential yield in soybean [Glycine max (L.) Merr.; Noor and Caviness, 1980] and 21% in barley (Hordeum vulgare L.; Briggs, 1990), and a loss of 26 kg ha−1 in rice (Oryza sativa L.; Duwayri et al., 2000).

In crops, lodging is caused by a loss of balance within the body of the plant (Mulder, 1954). The lower part of the plant supports the heavier upper part, including the ear, leaves, and upper stem. The proportionality between the sturdiness of the lower part and the weight of the upper part determines the vulnerability of a given cultivar to lodging.

In various breeding programs, reducing plant height has been the main target in efforts to decrease the effects of the upper part of the plant on the lower part, thereby improving resistance to lodging. In the “green revolution”, semi-dwarf lines were introduced to reduce lodging in rice and wheat (Triticum aestivum L.) cultivars with heavy ears (Keller et al., 1999; Khush, 1999). However, plant height is not necessarily the most important factor in determining lodging resistance (Ookawa and Ishihara, 1992; Easson et al., 1993): susceptibility to lodging differs among cultivars with similar plant heights (Ookawa and Ishihara, 1992; Easson et al., 1993). In addition, there is an optimum plant height for maximum photosynthetic capacity within a vegetation canopy (Flintham et al., 1997), and reducing plant height below this level may reduce crop yields.

Many authors have reported relationships between lodging resistance and other traits. Among morphological traits, stem diameter and weight have been directly correlated with lodging resistance and the breaking strength of the stem (Atkins, 1938; Zuber et al., 1999). Pushing resistance, an index of lodging resistance, is positively correlated with culm thickness and the weight of root in deep soil (Terashima et al., 1994; Won et al., 1998). In addition, the cellulose, lignin, and silicon contents of the stem influence its mechanical strength (Idris et al., 1975; Kokubo et al., 1989; Jones et al., 2001; Ma et al., 2002; Tanaka et al., 2003). However, the relationships between the sturdiness of the lower part of the plant and various morphological traits, including the chemical components of the stem, have not been reported. Recently, our research group identified a quantitative trait locus responsible for pushing resistance of the lower part of the rice plant (tentatively named prl5; Kashiwagi and Ishimaru, 2004). The prl5 locus was...
responsible for increased pushing resistance of the lower part by changing the morphological traits and chemical composition of the lower stem, thereby improving lodging resistance. These results suggested that improving the sturdiness of the lower part would effectively increase lodging resistance, and that the traits that contribute to the sturdiness of the lower part could be a more suitable target for improvement efforts than plant height.

It is not clear whether improving the sturdiness of the lower part by introducing the *prt5* locus into modern rice cultivars would evenly increase the lodging resistance of these cultivars. To maximize the potential sturdiness of the lower part and its impact on lodging resistance, we analyzed the factors that could potentially reduce the potential sturdiness of the lower part in nine rice cultivars with different plant lengths (95 to 175 cm).

### Materials and Methods

1. **Plant materials**

   We selected nine cultivars divided into three groups according to plant length: short (about 100 cm), medium-length (about 120 cm), and tall (140 cm and taller). Nipponbare and Kasalath are used commonly in genetic research (Lin et al., 1998). Calrose76 is the semi-dwarf cultivar, originating as a single gene mutant from an American cultivar, Calrose (Kikuchi and Futsuhara, 1997). IR8, the first high-yielding modern rice cultivar for the irrigated tropical lowland and New plant type, IR65598-112-2, (NPT hereafter) has large panicles, few unproductive tillers and lodging resistance, were developed by the International Rice Research Institute (Peng et al., 1999). Koshihikari is a popular Japanese cultivar, and is widely cultivated in Japan. Ai-jiao-nan-te is an indica cultivar widely used in southern and central China in the 1960 and 1970’s (Xiong et al., 1997) and Canabongbong is the tallest Pilipino cultivar of the 9 cultivars in this study. The short cultivars were Calrose76, IR8, and Nipponbare, whose plant lengths were 108.2 (± 0.5), 99.0 (± 0.6), and 101.7 (± 1.6) cm, respectively. Calrose76 and IR8 were semi-dwarf lines with *sd-l*. The medium-length cultivars were Calrose, Koshihikari, and NPT, whose plant lengths were 118.5 (± 2.8), 115.0 (± 0.5), and 121.4 (± 1.8) cm, respectively. The tall cultivars were Ai-jiao-nan-te, Canabongbong, and Kasalath, whose plant lengths were 146.1 (± 1.1), 174.6 (± 1.3), and 163.5 (± 1.8) cm, respectively. Seeds of these cultivars were sown in a greenhouse in May 2003, then the seedlings were transplanted into a paddy field in Tsukuba, Japan (latitude 38° N) in early June. N, P2O5, and K2O fertilizers were applied to the soil at a rate of 4 g m⁻² each just before transplanting.

2. **Pushing resistance**

   The pushing resistances of the whole plant and of the lower part were measured at the full-ripe stage with a prostrate tester (Daiki Rika Kogyou Co., Tokyo, Japan) according to the method reported by Kashiwagi and Ishimaru (2004). The prostrate tester was set perpendicular to the plants at a height of 20 cm above the soil surface, and the overall pushing resistance was measured until the plants had inclined to an angle of 45° to the vertical; this value represented the lodging resistance of the whole plant. The sturdiness of the lower part was represented by the pushing resistance measured after removing the upper parts of the plant at a height of 40 cm. The ratio of lodging resistance to sturdiness of the lower part (% abbreviated to RLS) equals the pushing resistance of the whole plant divided by that of the lower part with the top removed at a height of 40 cm.

3. **Analysis of morphological traits**

   We measured the following morphological traits of the upper part of the stem at the full-ripe stage: plant length, length from the ground to the ear, weight of the upper part (ear, leaf, and stem above 40 cm from the ground per plant), number of stems, stem and leaf weights in the upper part, ear weight, and ear weight per stem. The difference between plant length and length from the ground to the ear was abbreviated as DPE. The moments of the weight of the upper part of the plant and that per stem were calculated as: (weight of upper part) × (plant length) and (weight of upper part per stem) × (plant length), respectively. The moments of ear weight and ear weight per stem were calculated as: (ear weight) × (length from the ground to the ear) and (ear weight per stem) × (length from the ground to the ear), respectively. We also measured the following morphological traits at the full-ripe stage: crown width, stem number, ear weight, weight of stem below 40 cm (the lower stem), and density of lower stem. We measured the dry weight of the lower stem by oven-drying at 80°C for 3 d. The density of the lower stem was calculated as: dry weight/[π × (stem diameter/2)² × stem length (40 cm)].

4. **Analysis of stem chemical components**

   The contents of starch, sucrose and hexoses were measured enzymatically according to the method of Ishimaru et al. (2001). Samples of the lower stems dried at 80°C for 3 d were powdered with a Wonder Blender (Osaka Chemical Co., Osaka, Japan), and 50-mg samples were re-powdered in liquid nitrogen using a mortar and pestle. The powdered samples were extracted twice with 80% (v/v) ethanol at 80°C and centrifuged at 12000 g for 5 min, then the supernatants were collected, vacuum-dried, and used for the determination of sucrose content by means of an enzymatic method (Kashiwagi and Ishimaru, 2004). To determine the starch content, we boiled the dried pellets in distilled water for 2 h, then digested...
them with amylglucosidase for 15 min at 55 °C. The resultant hexoses were determined enzymatically as described above (Kashiwagi and Ishimaru, 2004). The silicon content of stem was measured by the method of Kashiwagi and Ishimaru (2004). The relative silicon content was analyzed with an energy-dispersive X-ray-fluorescence spectrometer (Element Analyzer JSX-3201, JEOL, Tokyo, Japan); powdered 200-mg samples were formed into 13-mm-diameter tablets in a hydraulic press (Evacuable KBr Die, Shimadzu, Kyoto, Japan). The measurements were performed at 30 kV for 600 s, and were replicated three times for each sample. Silicon was analyzed at a peak of 1.739 keV; the relative content was calculated as the counts-per-second ratio by the method of Vázquez et al. (1999).

Results

1. Pushing resistances of the whole plant and the lower part, and RLS values

Fig. 1 shows the pushing resistances of the whole plant and of the lower part in the nine cultivars that were measured at the full-ripe stage. The pushing resistance of the lower part in the short cultivars, Calrose76, IR8, and Nipponbare, averaged 0.056 (±0.050), 1.166 (±0.065), and 0.753 (±0.011) N cm^{-2}, respectively. The corresponding RLS values were 60.7, 79.3, and 53.7%, respectively. The pushing resistance of the whole plant and that of the lower part differed significantly only in the Nipponbare (P < 0.001). The pushing resistance of the lower part in the medium-length cultivars, Calrose, Koshihikari and NPT, averaged 0.167 (±0.045), 0.482 (±0.084), and 1.199 (±0.059) N cm^{-2}, respectively. The corresponding RLS values were 53.3, 64.9, and 114.7%, respectively. The pushing resistance of the whole plant and the lower part differed significantly only in the Koshihikari (P < 0.05). The pushing resistance of the lower part in the tall cultivars, Aijiao-nan-te, Canabongbong, and Kasalath, averaged 0.863 (±0.091), 1.316 (±0.114), and 1.329 (±0.109) N cm^{-2}, respectively. The corresponding RLS values were 55.2, 79.9, and 90.2%, respectively. The two values of pushing resistance differed significantly only in the Aijiao-nan-te and Canabongbong (P < 0.05). There was no significant correlation between plant length and either the pushing resistance of the whole plant or the pushing resistance of the lower part (P > 0.05, data not shown).

| Table 1. Correlations between the ratio of lodging resistance to the sturdiness of the lower part (RLS) and morphological or componential traits. |
|-----------------|-----------------|
| Traits | Correlation with RLS |
|-----------------|-----------------|
| Heding date | 0.460 |
| Traits in upper part of plant | |
| Plant length | 0.274 |
| Length from the ground to the ear | 0.054 |
| DPE | 0.907*** |
| Weight of upper parts | 0.169 |
| Weight of upper parts per stem | 0.573 |
| Densit of weight of upper parts | 0.218 |
| Moment of weight of upper parts per stem | 0.533 |
| Ear weight | 0.132 |
| Ear weight per stem | 0.540 |
| Moment of ear weight | 0.132 |
| Morphological traits | |
| Crown width | 0.047 |
| Stem number | -0.039 |
| Stem diameter | 0.063 |
| Weight of lower stem | 0.726*** |
| Densit of lower stem | -0.358 |
| Chemical components of lower stem | |
| Silicon | -0.293 |
| Starch | -0.395 |
| Sucrose | -0.650 |
| Hexoses | -0.215 |

DPE: Difference between plant length and length from the ground to the ear.

***, *: significant at P = 0.001 and 0.05, respectively.

Fig. 1. Pushing resistance values of the whole plant and of the lower part in nine rice cultivars. The data represent the means of four or more independent plants in each cultivar; vertical bars indicate the standard errors. The numbers in parentheses indicate the ratio of lodging resistance to sturdiness of the lower part (%). ***, * significant at P = 0.001 and 0.05, respectively.
2. Correlation between RLS and traits of the upper part of the plant

To detect any adverse influence of the characteristics of the upper part of the plant on the sturdiness of the lower part, we compared RLS with plant length, length from the ground to the ear, DPE, weight of upper part, weight of upper part per stem, moment of the weight of upper part, moment of weight of upper part per stem, ear weight, ear weight per stem, moment of ear weight, and moment of ear weight per stem (Table 1). The weight and moment of the upper part of the plant and those of the ear were not significantly correlated with RLS, nor were plant length and length from the ground to the ear. However, DPE was significantly and positively correlated with RLS ($r = 0.907, P < 0.001$).

3. Correlation between RLS and other traits, including the chemical components of the lower stem

Table 1 shows the correlation of RLS with heading date, morphological traits (crown width, stem diameter, weight of lower stem, and density of lower stem) and the chemical components of the lower stem (silicon, starch, sucrose, and hexoses). Only the weight of the lower stem was significantly correlated with RLS ($r = 0.726, P < 0.05$).

4. Correlation between ear weight and measured parameters

To identify traits that affected yield, we examined the relationships between ear weight per plant and the morphological traits, including the chemical components of the lower stem (Table 2). The stem and leaf weight in the upper part of the plant was significantly and positively correlated with ear weight ($r = 0.883, P < 0.01$), but no other traits of the upper part of the plant were significantly correlated with yield. Of the other morphological traits, crown width and stem number were both significantly correlated with ear weight ($r = 0.726$ and $0.709$, respectively, $P < 0.05$). Of the chemical components of the lower stem, only the sucrose content significantly affected ear weight, and the correlation was negative ($r = -0.839, P < 0.01$).

**Discussion**

The difference between the pushing resistance of the lower part of the plant and the whole plant varied among cultivars (Fig. 1). The pushing resistance of the lower part represents the sturdiness of the lower part. Various characteristics of the upper part reduced the sturdiness of the lower part by about half in the Nipponbare, Calrose and Ai-jiao-nan-te. While, NPT and Kasalath showed no reduction of the sturdiness of the lower part by the characteristics of the upper part of the plant. In addition, differences in plant length had little effect on RLS (Fig. 1, Table 1). These results suggest that any observed decrease in the sturdiness of the lower part of the plant involved traits other than plant height.

We analyzed the morphological factors that were potentially responsible for decreased RLS. In the upper part of the plant, the weight and height characteristics did not negatively affect RLS, and only DPE was correlated with RLS (Table 1). Terashima et al. (1992) reported that the contribution of pushing resistance to resistance to lodging in the field was higher than the contribution of the moment of the upper part of the plant. These results suggested that the characteristics of tallness and heavier upper parts might not directly decrease the sturdiness of the lower part, but might still cause lodging in the presence of strong winds or rain. On the basis of our calculated correlations with RLS, DPE, which is closely related to length from the base of the flag leaf blade to the neck (LFN), could affect the potential sturdiness of the lower part of the plant. Shortening LFN could avoid decreasing the sturdiness of the lower part and could thereby contribute to improved lodging resistance.

We also analyzed other traits capable of compensating for the negative effects of the upper part of the plant to sturdiness of the lower part. Only the weight of the lower stem was significantly correlated with RLS (Table 1). Stem weight has been reported to be negatively correlated with the score of lodging observed in the field and positively correlated with the breaking strength of wheat straw (Atkins, 1938; Zuber et al., 1999). An increase in the weight of the lower stem might therefore contribute to increased stem stiffness and strength, and the stiffer stem might inhibit any decrease in the sturdiness of the lower part in response to the traits of the upper part of the plant.

The chemical components of the lower stem did not correlate with decreased sturdiness of the lower part.

Table 2. Correlations of ear weight per plant with heading date, traits in upper part, morphological traits and components in lower stem.

| Traits in upper part of plant | Correlation with ear weight |
|-------------------------------|----------------------------|
| Crown width                  | 0.726*                     |
| Stem number                  | 0.709*                     |
| Stem diameter                | 0.128                      |
| Weight of lower stem         | -0.141                     |
| Density of lower stem        | -0.204                     |
| Chemical components of lower stem |                      |
| Silicon                      | 0.387                      |
| Starch                       | -0.459                     |
| Sucrose                      | -0.839**                   |
| Hexoses                      | -0.529                     |

* : significant at $P = 0.01$ and 0.05, respectively.
as a function of the characteristics of the upper part of the plant (Table 1). However, the addition of silicon has been shown to increase lodging resistance (Idris et al., 1975), as greater accumulation of carbohydrates in the stem does (Sato, 1957; Takaya and Miyasaka, 1983; Yang et al., 2001). Improvement of lodging resistance in response to increased content of silicon or carbohydrates might therefore increase the sturdiness of the lower part, but not enough to compensate for the negative effects of various characteristics of the upper part of the plant.

In breeding, efforts to improve lodging resistance should target traits that will not affect crop yield. Ear weight, one of the more important components of yield, was significantly correlated with the stem and leaf weight in the upper part of the plant, with crown width, with stem number, and with sucrose content in the lower stem (Table 2). High-yielding lines have greater aboveground biomass than lower-yielding lines (Borrell et al., 2000; del Blanco et al., 2001; Donmez et al., 2001). The number of stems also directly affects the number of ears. Crown width involves stem number, stem diameter, and the distance among stems. In particular, changes in biomass and stem number might decrease grain yields. In the present study, the stem and leaf weight of the upper part of the plant, the crown width, and the stem number were not correlated with RLS (Table 1); thus, improving RLS by targeting smaller LFN values or heavier stems should not negatively affect the yield.

The increase in carbohydrates in the stem at maturity contributes to a higher lodging resistance (Sato, 1957; Takaya and Miyasaka, 1983; Yang et al., 2001). In rice, the main storage form of (non-structural) carbohydrates in the stem is starch, which is decomposed into glucose and resynthesized into sucrose when this carbon source is remobilized from the stem into the grains. Increasing stem carbohydrates through breeding might lead to poor grain filling and decreased yield, because it would imply less remobilization of carbohydrates from the stem into the rice grains. Sucrose content of the stem was negatively correlated with ear weight per plant in this study (Table 2). To improve lodging resistance by breeding to increase stem carbohydrates at maturity, carbohydrates other than sucrose should be targeted.

On the basis of our results and previous reports on improving lodging resistance, we developed a model for improving lodging resistance. In rice breeding, lodging resistance has been improved by reducing plant height (Fig. 2A), thereby lowering the center of gravity and reducing the effect of strong winds and rain. However, because there is an optimum plant height for maximum yield (Flintham et al., 1997), it is necessary to find a target other than plant height to increase lodging resistance. Cultivars with reduced sturdiness of the lower part are more easily lodged...
in the field, even in semi-dwarf lines (Terashima et al., 1992). The next target for improvement would therefore be the sturdiness of the lower part. To increase this sturdiness, we need to improve the morphological traits of the lower stem, its chemical composition, and the root condition. The presence of a quantitative locus for pushing resistance of the lower part, tentatively named prl5, increased the sturdiness of the lower part and thus improved lodging resistance (Fig. 2B: Kashiwagi and Ishimaru, 2004). The introduction of prl5 into modern cultivars could thus improve lodging resistance. In addition, Terashima et al. (1994) suggested that higher lodging resistance would require heavier roots and the penetration of these roots into deeper soil layers. Genetic investigation of root morphology will be very important to further improve the sturdiness of the lower part, and identification of a quantitative locus for root morphology would facilitate breeding for this component of lodging resistance.

In this study, we identified the causes of reduced sturdiness of the lower part. DPE and stem weight were significantly correlated with RLS (Table 1). A shorter LFN value or a heavier lower stem would prevent reductions in the relative sturdiness of the lower part in response to characteristics of the upper part of the plant (Fig. 2C). Lodging is determined by a precarious balance between the sturdiness of the lower part and the weight of the upper part of the plant (Mulder, 1954). Thus, reducing plant height, increasing pushing resistance, decreasing LFN, and increasing the weight of the lower stem are all important targets for improvement that could improve this balance and increase lodging resistance. A cultivar that combines all these improvements might show excellent performance (Fig. 2D).

In conclusion, we demonstrated that decreased sturdiness of the lower part in response to changes in the upper part was related to LFN and the weight of the lower stem, and that changes in these traits did not negatively affect yield. Improvements in these traits might thus increase the sturdiness of the lower part, which is directly linked to increased lodging resistance, without adversely affecting yield. Breeding to incorporate the prl5 locus in rice cultivars, combined with a shorter LFN and a heavier lower stem, should thus be considered as new targets to improve lodging resistance in rice.

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