

Eco-Physiological Study of Root Lodging Tolerance in Direct-Seeded Rice Cultivars

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Abstract

To investigate the morphological and physiological characteristics relating to root lodging tolerance in direct-seeded rice plant, anchoring ability, root growth and its distribution to soil layers were compared among root lodging-susceptible Japanese varieties, tolerant USA varieties and Korean semi-dwarf indica varieties. Pushing resistance, i. e. the maximum resistance of plant to horizontal pushing and inclination of shoot to 45° toward the vertical direction, was higher in tolerant USA varieties and Korean semi-dwarf indica varieties than in susceptible Japanese varieties. Tolerant varieties developed a larger amount of roots at full heading stage than susceptible Japanese varieties, due to the higher rate of dry matter allocated to roots in USA varieties and higher crop growth rate in Korean semi-dwarf indica varieties. Also, tolerant varieties developed a larger amount of roots in deeper soil layers than susceptible varieties. The pushing resistance was remarkably reduced when root elongation to the subsoil layers was prevented by laying an unwoven cloth between the topsoil and subsoil layers. The higher soil strength and bulk density in the subsoil layers was attributed to the higher efficiency of a unit root weight in the subsoil layers for anchoring compared with that in the topsoil layers. The above results indicate that root growth, especially root development in the subsoil layers, contributes significantly to the anchoring ability and lodging tolerance in direct-seeded rice plant.

Discipline: Crop production

Additional key words: anchoring, dry matter allocation, pushing resistance, soil bulk density, varietal difference

Introduction

In direct seeding rice (*Oryza sativa* L.) cultivation under submerged paddy field conditions, root lodging is frequently observed and considered to be one of the serious problems, since seeds are sown on the surface or to the shallower layers of soil and plants grow with less physical support of soil. Genetical and cultivation improvements of root lodging tolerance are required to stabilize the productivity of direct seeding cultivation^{1,22,23}, especially in the case of seeds broadcasted on submerged field. In maize (*Zea mays* L.), varietal difference in root lodging tolerance was examined based on vertical pulling resistance measurement and a significant genotypic effect was reported^{2-4,6,11}. Pinthus^{12,13} studied the relationships between the root lodging tolerance and root morphological characteristics based on a comparison among several wheat (*Triticum aestivum* L.) varieties. In rice plant, a few researchers have pub-

lished data related to root lodging. Among them, Miyasaka^{8,9} reported the presence of varietal differences in the resistance of crown root to pulling and its relation to some morphological characteristics. Also, Haga et al.⁷ estimated the anchoring ability by the chain hanging method and reported significant differences among rice varieties. However, the relationships between these characteristics and root lodging tolerance among varieties have not been well examined, and the mechanism of root lodging tolerance in rice plant remains unclear. This information is obviously essential for the breeding of suitable varieties for direct seeding cultivation. The objectives of this paper were to compare the root lodging tolerance quantitatively among Japanese varieties, which were bred under transplanting cultivation, with USA varieties selected under direct sowing cultivation and several other varieties, and to determine the morphological and physiological characteristics required for root lodging tolerance, with emphasis placed on root morphology and growth.

Varietal difference in root lodging tolerance

Fig. 1 shows a comparison of the lodging degree during the ripening stage between the Japanese variety Nipponbare and USA variety M-302 sown to submerged field at seeding rates of 100, 250 and 400 seeds per m^2 . Japanese variety Nipponbare lodged completely within 2 weeks after heading on the highest density plot (400 seeds per m^2), and the yield of the plants on this plot was reduced significantly to $220 \text{ kg}/m^2$ (Fig. 1). In this case, the type of lodging was considered to be root lodging because of the lack of damage in the stem part. On the other hand, USA variety M-302 was tolerant to root lodging; lodging degree of M-302 was less than 2.0 at harvesting stage on the highest density plot (Fig. 1). Since the culm length of M-302 was similar to that

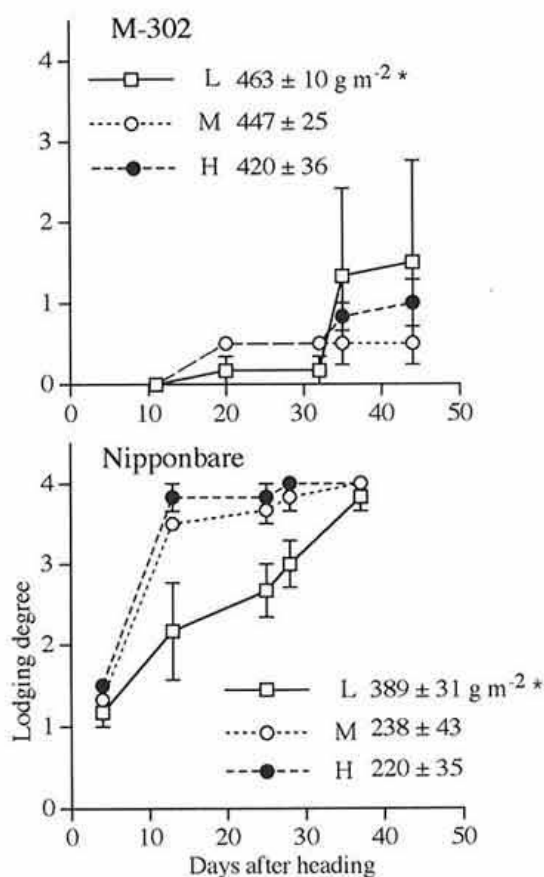


Fig. 1. Varietal difference in root lodging under direct sowing cultivation

L: Seeding rate 100 plant m^{-2} .

M: Seeding rate 250 plant m^{-2} .

H: Seeding rate 400 plant m^{-2} .

* Yield: Average \pm standard error.

Error bars in figures indicate standard error.

of Nipponbare, the above difference in the lodging degree may have been caused by the higher anchoring ability of M-302 than Nipponbare. Varietal difference in root lodging tolerance was also detected when other varieties including Japanese, USA and Korean varieties were compared. Although older USA varieties with longer culm length than 1 m lodged earlier because of their larger plant height, modern USA varieties were mostly tolerant to root lodging¹⁶. Semi-dwarf and long ear type indica varieties bred in Korea (Korean indica varieties) also did not lodge throughout the ripening stage¹⁶. These varietal differences in root lodging tolerance were also reported by Haga et al.⁷ and Takita and Kushibuchi¹⁴. Therefore, it was concluded that there was a significant difference in the root lodging tolerance among varieties, and that the Japanese varieties bred under transplanting method were prone to root lodging compared with USA varieties selected under direct sowing cultivation.

Varietal difference in pushing resistance

Pushing resistance, which is defined as the maximum resistance of plant to horizontal pushing and inclination of shoot to 45° toward the vertical direction and reflects the anchoring ability of the plant²¹, was compared among root lodging-tolerant and susceptible varieties under several cultivation conditions. The cultivation factors, such as difference in sowing depth¹⁶, water management¹⁵, planting density¹⁸ and soil physical properties^{19,20} affected the pushing resistance. For example, pushing resistance of rice plants grown under continuously flooded conditions was lower than that of plants grown with intermittent irrigation¹⁵, and the resistance of the plants grown under high density conditions was also lower than that of the plants grown at a lower density¹⁸. However, varietal difference in pushing resistance was significant in all the cultivation treatment plots, and the USA varieties and Korean indica varieties, which were root lodging-tolerant, showed apparently a higher pushing resistance than the root lodging-susceptible Japanese varieties (Fig. 2). Fig. 3 shows the relationships between the pushing resistance and root lodging degree. Although varieties with a longer culm tended to be prone to root lodging, there were significant negative correlations between the pushing resistance and root lodging degree compared with varieties with similar culm length. Additionally, multiple regression analysis of the lodging degree with the pushing resistance and the torque of the top

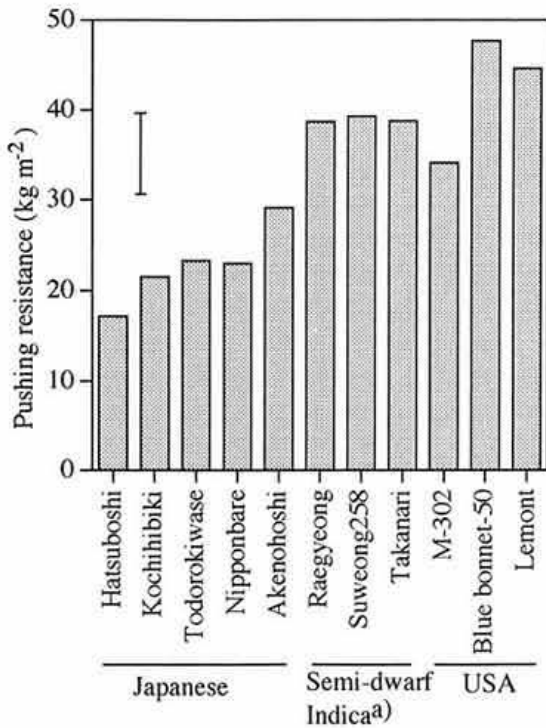


Fig. 2. Difference in pushing resistance among cultivars. Bar in the figure indicates l.s.d. ($\alpha=0.05$). a): Raeyeong and Sweong 258 are long ear type semi-dwarf indica varieties bred in Korea, and Takanari similar ones improved in Japan. Parent lines of Takanari are Korean semi-dwarf indica.

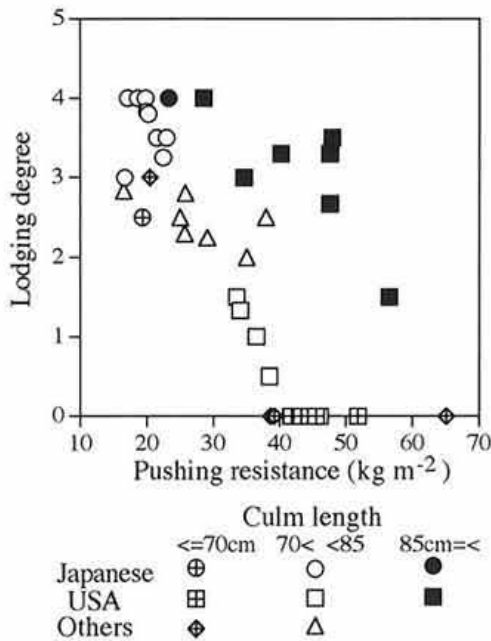


Fig. 3. Relationship between pushing resistance and lodging degree

Table 1. Multiple regression analysis of lodging degree

Independent	b ^{a)}	R ^{b)}
Pushing resistance (kg × 10 cm)	-0.77**	0.81**
Torque of top part ^{c)} (kg × cm)	0.30*	

a): Standard partial regression coefficient.

b): Multiple correlation coefficient.

c): Torque of top part was calculated by the following equation: Culm length × Total fresh weight of above-ground parts at 3 weeks after heading.

part (culm length × total fresh weight of aboveground parts at 3 weeks after heading) as independent variable, indicated that the contribution of the pushing resistance to the lodging degree was more significantly negative than that of the torque of the top part (Table 1). The above results suggest that the anchoring ability estimated by the pushing resistance was significantly related to the degree of root lodging tolerance in each variety.

Dry matter production and its allocation to each organ in root lodging-tolerant varieties

Root lodging-susceptible Japanese varieties Hatsuboshi, Nipponbare and tolerant USA varieties M-302, Lemont, were seeded to compare the dry matter production and its allocation to each organ. Aboveground parts and roots in the top soil were sampled at each growth stage, and the dry weight of each organ was measured after washing out the soil. Total dry matter production of the USA medium grain variety M-302 was mostly similar to that of the Japanese variety Hatsuboshi with a growth duration almost identical with that of M-302, and the USA long grain variety Lemont accumulated less dry matter than other varieties throughout the growth stages¹⁷⁾. The ratios of root dry matter to total one in the USA varieties were significantly higher than in the Japanese varieties without any difference between long and medium grain type, and root dry weight at full heading stage was also larger in the USA varieties than in the Japanese ones (Fig. 4). These characteristics of dry matter partitioning to root and vigorous root growth in the USA varieties were preserved under different cultivation conditions including difference in planting density, nitrogen fertilization rate, irrigation control and sand culture with nutrients (Terashima et al., unpublished).

Similarly, root lodging-tolerant Sweong 258 (Korean indica variety) and susceptible Kochihibiki (Japanese variety) were examined to compare the dry

matter production and its allocation. Crop growth rate of Sweong 258 was higher at the reproductive stage than that of the Japanese variety Kochihibiki, and root dry weight of Sweong 258 was also larger than that of Kochihibiki in spite of almost the same partitioning rate of dry matter to root¹⁷⁾. Therefore, it was inferred that the root lodging-tolerant varieties developed a larger amount of roots than the susceptible varieties even though there were differences in the causes among varieties, for example, a higher ratio of dry matter partition to root like in the USA varieties or higher total dry matter production as shown in the Korean indica varieties.

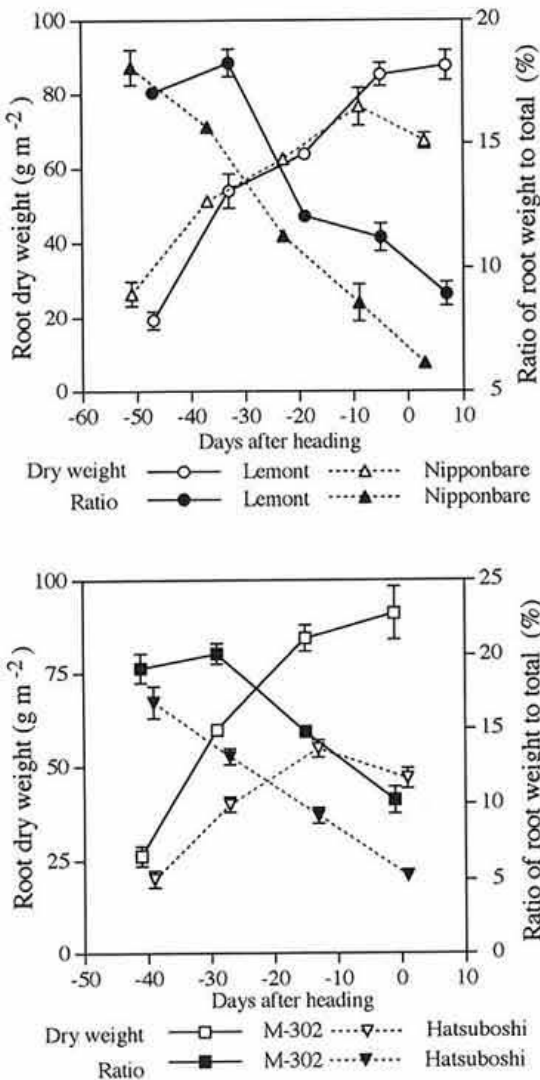


Fig. 4. Comparison of root dry weight and its ratio to total dry weight between USA varieties and Japanese varieties
Standard error is shown when it is larger than that indicated by the symbol.

Root distribution to soil layers in the root lodging-tolerant varieties

To compare the root distribution to the soil layers among the USA, Japanese and Korean indica varieties, root dry weight in each soil block at different depths from the soil surface and different distances from the center of the plant was measured using a monolith sampler 5 cm thick and 25 cm deep. Root distribution of the USA varieties in the subsoil layers was larger than that of the Japanese varieties¹⁷⁾. Korean indica varieties also developed a larger amount of roots in deeper soil layers compared with the Japanese varieties¹⁷⁾. Study of the relationships between the pushing resistance and root dry matter in the soil layers revealed the presence of a significant positive correlation between the pushing resistance and root dry weight in the deeper soil layers including the subsoil (E, F and G in Fig. 5). In contrast, there was a negative correlation between the pushing resistance and root dry weight in the soil block at a depth less than 5 cm and with a distance longer than 5 cm from the center of the hill (B in Fig. 5). A similar tendency was reported by Ekanayake et al.⁵⁾ for the relationship between the pulling resistance and root distribution in deeper soil layers when drought-tolerant and susceptible rice varieties were compared.

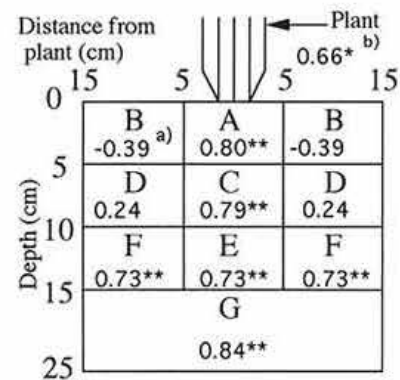


Fig. 5. Correlation coefficient between root weight in each soil block and pushing resistance
a): Relationships between root weight in each soil block and pushing resistance at full heading stage were analyzed based on measurements of 7 varieties (Nipponbare, M-302, Blue bonnet-50, Lemont, Takanari, Suweong 258, Akenohoshi) in 1989, and 4 varieties (Hatsuboshi, Nipponbare, M-302, Lemont) in 1990.
b): Correlation coefficient between total root weight in 30 × 5 × 25 cm monolith sample and pushing resistance.

Effect of root pruning on pushing resistance

To analyze the relationships between the root distribution in soil and anchoring ability, the effect of root pruning with a steel board (Fig. 6) on the pushing resistance was investigated using the USA varieties Lemont and M-302 and the Japanese variety Nipponbare. Root pruning with a steel board from the soil surface to a 5 cm depth at 4 or 5 cm distance from the center of each hill, did not affect the pushing resistance significantly (Fig. 7). There

was a remarkable reduction in the resistance when the roots were pruned by inserting the steel board to a depth of 10 or 15 cm (Fig. 7). The ratio of decrease in the pushing resistance by the root pruning treatment to the amount of roots pruned by the same treatment (k_5 , k_{10}), was estimated based on the root distribution to the respective soil layers (Fig. 6, Table 2)²⁰. The value of k_5 ($=R_5/W_{10}$), the ratio of the decrease in the pushing resistance to the dry weight of roots pruned by inserting the steel board to a 5 cm depth (W_5), was much lower than k_{10} for the roots pruned by inserting the board

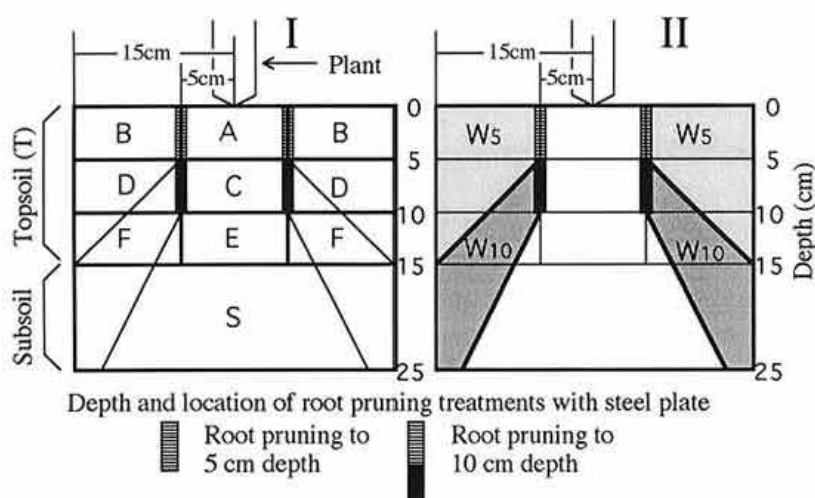


Fig. 6. Method of root pruning with steel plate, designation of each soil block in monolith sample (A-F, S), and estimation of root mass pruned when the steel plate was inserted to 5 cm depth (W_5), and from 5 to 10 cm depth (W_{10})

Table 2. Reduction of pushing resistance (R_5 , R_{10}) and its ratio (k_5 , k_{10}) to dry weight of pruned roots (W_5 , W_{10}) when a steel plate was inserted to 5 cm depth and from 5 to 10 cm depth in the field plots

Variety	T S		P	W_5	W_{10}	R_5	R_{10}	k_5	k_{10}
	(g sample ⁻¹)								
Nipponbare	1.21	0.09	1.42	0.31	0.10	0.09	0.21	0.30	1.98
M-302	1.34	0.23	1.62	0.38	0.21	0.11	0.33	0.28	1.56
Lemont	1.65	0.34	1.90	0.34	0.28	0.12	0.43	0.35	1.53

T, S: Total root dry weight in topsoil (T), and in subsoil (S) from a monolith sample (thickness: 5 cm) as shown in Fig. 6.

P: Root dry weight per hill in topsoil sampled with root sampler⁵⁾ (30 × 15 × 15 cm).

W_5 , W_{10} : Dry weight of roots pruned by inserting a steel plate to 5 cm depth (W_5) was calculated using the equation, $2 \times (P/T) \times (B + 3/4 \times D + 1/4 \times F)$, and that by inserting the same steel plate from 5 to 10 cm (W_{10}) was calculated using the equation, $2 \times (P/T) \times (1/4 \times D + 5/8 \times F + 1/6 \times S)$, where B, D, F, S indicate the root dry weight in each soil block shown in Fig. 6. (P/T) was multiplied to correct the underestimation of root dry weight in each soil block due to the smaller size of the monolith sample compared to the area occupied by one hill.

k_5 , k_{10} : k_5 and k_{10} were estimated using formula R_5/W_{10} and R_{10}/W_{10} , respectively, where R_5 indicates the reduction of the pushing resistance by root pruning by inserting a steel plate to 5 cm depth, and R_{10} indicates that by inserting a steel plate from 5 to 10 cm depth.

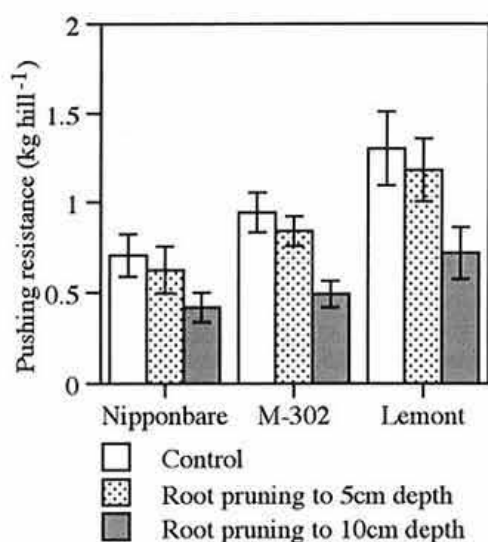


Fig. 7. Effect of root pruning on the pushing resistance
Bars in figure indicate the intervals of 95% reliability.

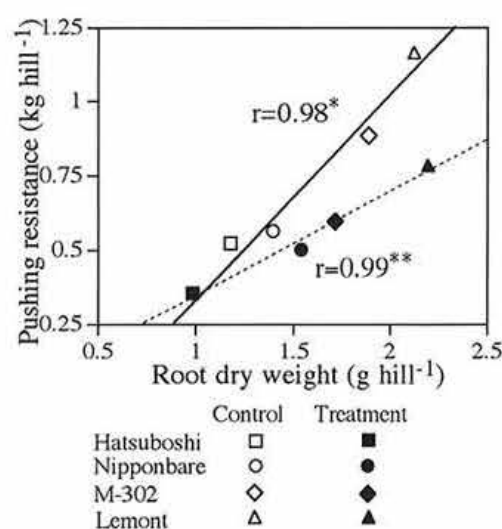


Fig. 8. Effect of unwoven cloth treatment on the relationships between root dry weight and pushing resistance

from a 5 cm depth to a 10 cm one (W_{10}) (Table 2). The above results suggest that the efficiency of anchoring was higher in the roots penetrating into deeper soil layers than shallower ones.

Effect of laying an unwoven cloth between the topsoil and subsoil on the pushing resistance

To estimate the contribution of roots in the topsoil and subsoil layers to the pushing resistance quantitatively, the effect of laying an unwoven cloth between the topsoil and subsoil on the pushing resistance was investigated²⁰⁾. The unwoven cloth was laid on the subsoil after removing the topsoil to prevent roots from elongating to the subsoil layers. Then, the topsoil was returned to the same

position on the unwoven cloth and puddled after irrigation. Both USA and Japanese varieties grown on the unwoven cloth laying treatment plot, showed a lower pushing resistance than those grown on the control plot (Fig. 8). However, the reduction of the pushing resistance by the cloth treatment was greater for the USA varieties which developed a larger amount of roots in the subsoil layers in the control plot than for the Japanese varieties (Fig. 8) (W_t and W_s in Table 3). High correlations were detected between the root dry weight and pushing resistance in both plots. However, the regression coefficient between the root weight and pushing resistance was higher in the control plot than the plot with cloth treatment (Fig. 8). These results indicate that the effect of the pushing resistance per dry weight of

Table 3. Contribution of roots in topsoil and subsoil layers to pushing resistance

Variety	W_t	W_s	k_t	k_s	R_t	R_s	R	$R_s R^{-1}$
	(g hill ⁻¹)		(g hill ⁻¹)		(kg hill ⁻¹)			
Hatsuboshi	1.07	0.10	0.34	1.57	0.37	0.16	0.53	0.30
Nipponbare	1.27	0.12	0.27	1.89	0.34	0.23	0.57	0.40
M-302	1.64	0.25	0.28	1.77	0.46	0.43	0.89	0.48
Lemont	1.73	0.39	0.29	1.71	0.50	0.66	1.17	0.56

W_t : root dry weight in topsoil, W_s : root dry weight in subsoil.

k_t : pushing resistance per unit root mass in topsoil, k_s : pushing resistance per unit root mass in subsoil.

R_t : pushing resistance contributed by roots in topsoil, R_s : pushing resistance contributed by roots in subsoil, R : pushing resistance per hill.

k_t and k_s were estimated based on data from control and porous membrane treatment plots using the equation (1), $R = R_t + R_s = k_t W_t + k_s W_s$.

root in the subsoil layers (k_s) was more pronounced than that in the topsoil layers (k_t). To quantify these data, k_t and k_s were estimated based on the equation (1) (Table 3).

$$R = R_t + R_s = k_t \times W_t + k_s \times W_s \dots\dots\dots (1)$$

R: pushing resistance, R_t : pushing resistance contributed by roots in topsoil, R_s : pushing resistance contributed by roots in subsoil, W_t : root dry weight in topsoil, W_s : root dry weight in subsoil. Results are shown in Table 3. The k_s and k_t values were similar among the examined varieties including the root lodging-tolerant and susceptible ones, and the k_s value was about 6 times higher than the k_t value in all the varieties. Contribution of roots in the subsoil to the total pushing resistance ($R_s R^{-1}$) was estimated to be 48–56% in the USA varieties even though the dry matter percentage of roots in the subsoil layers to the total was 13–18% (Table 3). The above results indicate that the root distribution to the subsoil layers is important to achieve a higher anchoring ability, and that the root distribution characteristics are significantly related to varietal differences in the root lodging tolerance.

Effect of soil strength and soil bulk density on pushing resistance

To investigate the effect of the soil strength on the root lodging tolerance, pushing resistance and root dry weight were compared between a field plot drained during the growth stages and that flooded continuously. In both field plots, unwoven cloths

were laid between the topsoil and subsoil layers. Drainage of water from the field raised the soil physical strength and increased the ratio of the pushing resistance to the root dry weight (k) regardless of the varieties¹⁹⁾.

The effect of the soil bulk density on the pushing resistance was also examined for the Japanese variety Nipponbare and USA variety Lemont grown in a 1/2,000 a pot which was filled with paddy soil at different levels of bulk density. As shown in Table 4, the soil bulk density affected the pushing resistance; in the plants grown in a 1/2,000 a pot to which soil was packed at a higher bulk density, the pushing resistance increased with a higher value of k compared with the plants grown in the pot with a lower bulk density (Table 4)²⁰⁾. Nakatsuka and Ishii¹⁰⁾ reported that the soil strength in the subsoil layers was significantly higher than that in the topsoil during the rice growth period due to cultivation and puddling. Soil bulk density of the subsoil was also higher than that of the topsoil in the experimental paddy field. Therefore, it was inferred that the higher value of k_s (Table 3) could be due to a higher soil strength and soil bulk density in the subsoil layers than in the topsoil layers. Moreover, in this pot experiment, there were no varietal differences in the pushing resistance between Lemont and Nipponbare, in contrast to the presence of a significant difference between these 2 varieties under field conditions. These results indicate that the differentiation of soil into compacted subsoil and sparse topsoil in paddy fields is related to varietal differences in the pushing resistance.

Table 4. Effect of soil density on pushing resistance and contribution of a unit root mass to pushing resistance in potted plants

Variety	Soil density (kg l ⁻¹)	Dry weight		Pushing resistance (R) (kg plant ⁻¹)	k (R/W) (10 ² g g ⁻¹)
		Shoot (g plant ⁻¹)	Root (W)		
Nipponbare	1.05	113.8	14.1	1.43	1.01
	1.40	133.0	15.0	2.44	1.63
	1.58	144.2	14.2	2.68	1.90
Lemont	1.05	100.5	16.0	1.81	1.14
	1.40	116.4	16.9	2.54	1.51
	1.58	111.1	13.3	2.48	1.87
Analysis of variance (F value)					
Variety		108.7***	5.3*	2.47	0.045
Treatment		40.3***	9.8**	100.4***	93.47***

Dry weight of each organ and pushing resistance were measured 10 days after heading.
*, **, *** indicate significance with $p \leq 5\%$, $\leq 1\%$ and $\leq 0.1\%$, respectively.

Conclusion

It was concluded that the root dry weight and root distribution to deeper soil layers were the major factors affecting the root lodging tolerance, and that the genetical improvement of these characteristics is required to prevent rice plants from lodging, and to stabilize the productivity of direct sowing rice cultivation. Root lodging-tolerant varieties developed a larger amount of roots at full heading stage than the susceptible Japanese varieties, due to the higher rate of dry matter allocated to roots in the USA varieties and higher crop growth rate in the Korean semi-dwarf indica varieties. Moreover, soil physical properties including soil strength and bulk density affected significantly the anchoring by roots. Differentiation of soil physical properties between topsoil and subsoil due to cultivation and puddling¹⁰, is considered to be related to the higher contribution of roots in the subsoil to anchoring, and in turn, to the difference in anchoring ability among varieties differing in the distribution of roots in the respective soil layers.

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(Received for publication, November 7, 1996)