
Relationship of Culm Anatomy and Lodging Resistance in Rice (*Oryza sativa* L.) Genotypes under Direct-Seeded System

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Lodging is prevalent in rice given its inherent weak culm morphology and is further stress by strong winds and heavy rains brought by typhoons that regularly routes the Philippines. Therefore, improving the screening and selection efficiency for lodging resistance is crucial in elevating and maintaining yield increase. Lodging-tolerant experiment on 12 newly developed direct-seeded rice lines, 26 NSIC released varieties and six local lodging checks were conducted to identify rice genotypes with high push resistance through culm strength and anatomy. Anatomy of the 5th internode was assessed through culm sectioning at full heading stage. Measurement of sclerenchyma containing parts and estimation of lignin content (LC) were used to predict lodging resistance while push resistance or culm strength exerted by the stem was measured using handy force gauge meter. High %LC (23-24%) were observed in seven (NSIC Rc396, Rc356, Rc238, PR43425-25-2-1-1-B, Rc308, Rc302 and Rc354) out of 44 (16%) genotypes which also outclassed NSIC Rc240 (16.29% LC), resistant check variety. High push-resistance in Kilogram Force (kgf) were recorded in fifteen (26%) out of 44 genotypes, whereas PR43426-13-2-3-2-B-B (1.08 kgf), NSIC Rc396 (1.06 kgf), PR39142-10-3-2-1-1-B (1.05 kgf) and PR45299-14-3-2-B (1.01 kgf) were comparable to NSIC Rc240 (1.02 kgf). Low (2-9) number of Median Vascular Bundles (MEVB) were observed in most genotypes and high MEVB were recorded for NSIC Rc396, Rc300, Rc214 (MEVB = 9) and PR40432-17-3-1-2-B-B (MEVB = 8), significantly higher than Rc240 (MEVB = 6). Significant medium correlation (0.58) was computed for %LC to NMEVB which showed that improvement of lodging resistance is a result of increased lignin and MEVB in the stem, thus breeding objectives should be towards the selection of rice genotypes with high culm strength coupled with high lignin and increased number of median vascular bundles.

Keywords: rice lodging, direct-seeded rice, culm strength, lignin, median vascular bundles

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Introduction

Lodging is the permanent displacement of rice plant from its upright position (Van Delden *et al.*, 2010) caused by the interaction of the plant and environmental forces *viz.* high rainfall intensities, frequent strong winds, and typhoon. In the Philippines, the mean annual rainfall varies from 965 to 4,064 millimeters and in six-year period of 2010 – 2015, 46 typhoons, 41 tropical storms and 19 tropical depressions have entered the country with wind speed ranging from 61 kilometers per hour (kph) to 120 kph (PAGASA, 2016). Wind speed during a typhoon is considerably stronger than the rate of wind speed required for a plant to lodge. Hitaka (1968) observed that rice plants bend to about 45 ° at wind speeds of 25 – 29 kph and nearly 90 ° at wind speeds of 43 – 50 kph. Furthermore, the breaking of culms started at 25 kph and almost all culms were broken at 54 – 57 kph.

Lodging usually occurs during grain filling period wherein the upper part of rice is heavy. Almost all parameters for grain yield and grain quality including ratio of grain length to grain width, gelatinization temperature and gel consistency are significantly lowered as influenced by lodging. Lodging one day earlier at the grain-filling stage could cause yield loss from 2.66 to 2.71%, 1.8 to 2.6% decrease in seed-setting rate, 0.26 to 0.32g reduction of 1000-grain weight, 0.097 to 0.155% decline of milled rice rate, as well as 0.13 to 0.27% increase of chalky grain rate, 0.021 to 0.024% rise of protein content, and subsequently lower the eating quality (Lang *et al.*, 2012).

Lodging lowers the market price of rough rice and milled rice. It was observed to have a greater impact on the whole grain (head rice) milling yield than the total grain milling yield compared to a non-lodged crop, although reductions in both were significant. These milling yield reductions were estimated to reduce rough rice market price by \$0.0075 to \$0.0119 per kg in the USA (Salassi *et al.*, 2013) and about ₱0.60 centavo per kg milled rice or ₱30.00 price reduction per 50 kg cavan in the Philippines.

Rice lodging is a common problem in direct seeded planting system, resulting to reduced grain yield, quality and ultimately low market price of palay. Moreover, majority of published studies and reference books related to rice lodging is under the transplanted culture, wherein there is less risk of lodging as other countries rarely experienced unfavorable weather conditions compared to the Philippine scenario. Hence, establishing screening protocols for lodging resistance based on previous and current studies undertaken internationally will be construed improperly as we do not share and satisfy genotype, environment and its interaction. Despite of these constraints, little attention has been given on the establishment of screening protocols for lodging

resistance and in turn hinders complete varietal information to plant breeders and farmers.

Currently, two conventional local screening techniques are used in determining resistance to lodging, culm lodging resistance and culm strength. Culm lodging resistance relies on the observers' rate of lodged-plant on a plant community during hard dough stage to maturity. Whereas, culm strength is determined before harvesting by inducing unmeasured manual force to representative plants, resistant plants remain upright, which indicates stiffness and resilience. Both techniques are fast and easy but lack comprehension of the applied force required bending a rice plant and its corresponding resistive force.

In recent years, breeding institutions concentrated on the generation of rice types with high yield lacking traits resistance to lodging. Yield proportion to increase fertilization increases straw to grain ratio and high water usage. In return, increase susceptibility of the variety to lodging may occur. The concept of ideotype breeding would increase the probability of selecting high value genotypes in the population with biological capacity to fight lodging. Morphological traits embedded in the lodging resistant genotypes can function well against environments favorable for lodging. The breeding of ideal plant morphology of rice is considered as a practical way of combating lodging.

Materials and methods

Rice Genetic Materials and Field Experiment

Treatments (44) were carefully selected from Philippine rice gene pool and accession (Table 1). Twelve Direct Seeded Rice Advanced Lines (DSRAL) were derived from a single crossed of distinct rice genotypes (Traditional, Korean variety, IRRI germplasm, PhilRice cultivars) developed purposely for direct wet-seeded rice environment and suspected to possess a lodging-tolerant genes. Plus, twenty-six NSIC rice varieties from three rice ecosystems: irrigated lowland (IL), saline and upland, were added in the list of test genotypes to widen the population for screening. Maturity factor was classified into early (20) and medium early (6) group. Six popular lodging checks were used to represents the three modes of resistance. The resistant checks (2) NSIC Rc240 is an IL released variety with an average yield of 5.8 tons per hectare (dsr) whereas PSB Rc14 is a rainfed lowland variety and commonly known as rio-grande. Intermediate checks (2), NSIC Rc298 is the first variety for direct seeding while NSIC Rc160 is an IL variety with good grain and eating quality. The susceptible checks (2), NSIC Rc170 and PSB Rc4 are both IL variety and early maturing. The experiment was carried out at Philippine Rice Research Institute Central Experiment Station (15°40'15" N, 120°53'37" E, 99.9m

altitude) during the rice-growing season from middle of January to early May in 2017. The field was plain level having a tropical monsoon (type 1) climate. The soil texture is classified as maligaya clay loam, in irrigated lowland having good soil drainage, with acceptable soil salinity (<160ppm) and good soil pH () at a depth of . The average temperature and rainfall for the period of January to May 2017 were 26.87 °C and 2.09 mm.

Table 1. List of entries (PhilRice lines, NSIC rice varieties and local lodging checks) during the 2017 dry season lodging-resistant trial.

Trt. No.	Variety Name / Line Designation	Trt. No.	Variety Name
1	PR39142-10-3-2-1-1-B	23	NSIC Rc238 (IL)
2	PR39149-33-1-3-3-1-B	24	NSIC Rc290 (Sal)
3	PR39628-17-2-1-1-B	25	NSIC Rc300 (IL)
4	PR40334-61-1-1-B	26	NSIC Rc302 (IL)
5	PR40432-10-1-1-1-B-B	27	NSIC Rc308 (IL)
6	PR40432-14-2-1-B	28	NSIC Rc324 (Sal)
7	PR40432-17-3-1-2-B-B	29	NSIC Rc352 (IL)
8	PR43405-10-2-3-3-B	30	NSIC Rc354 (IL)
9	PR43425-25-2-1-1-1-B	31	NSIC Rc356 (IL)
10	PR43426-13-2-3-2-B-B	32	NSIC Rc358 (IL)
11	PR43433-21-2-1-1-1-B	33	NSIC Rc360 (IL)
12	PR45299-14-3-2-B	34	NSIC Rc390 (Sal)
13	NSIC Rc11 (U)	35	NSIC Rc392 (IL)
14	NSIC Rc25 (U)	36	NSIC Rc396 (IL)
15	NSIC Rc29 (U)	37	NSIC Rc402 (IL)
16	NSIC Rc194 (Sub)	38	PSB Rc82 (IL)
17	NSIC Rc214 (IL)	39	NSIC Rc160 (I)
18	NSIC Rc216 (IL)	40	NSIC Rc170 (S)
19	NSIC Rc218 SR (IL)	41	NSIC Rc240 (R)
20	NSIC Rc222 (IL)	42	NSIC Rc298 (I)
21	NSIC Rc224 (IL)	43	PSB Rc4 (S)
22	NSIC Rc226 (IL)	44	PSB Rc14 (R)

* (PR) – PhilRice Advanced Lines; (U) – Upland; (Sub) – Submergence; (IL) – Irrigated Lowland; (Sal) – Saline; (R) – Resistant Check; (I) – Intermediate Check; (S) – Susceptible Check

Experimental Design and Field Layout

The field experiment was arranged in a randomized complete block design with three replications. Treatments were laid out in serpentine order from left to right direction, whereas plot label is placed at the corner most hill per entry to facilitate systematic observation. The experimental area was equal to 1,133 m² including pathway (50cm) and border rows (0.25cm). The area is divided into three blocks where each block is 44m length and 8.25m wide.

Block is comprised of 44 plots and was separated further in two columns. Plot dimension is 2m x 4m, which is 8m². Furrows were made using a pull-type 20 pins wooden-rake and every single plot has eight 4-linear meter furrows with 0.25m distance between furrows

Seed Preparation and Direct Seeding

The seeds were prepared cleanly and judiciously to prevent varietal mixture and poor quality. Fifty grams of seeds per treatment were placed on properly labeled polypropylene bags. Polypropylene bags were then pricked to promote better aeration and water diffusion. Seeds were oven dried at 50 °C temperature for 72 hours and rested at room temperature for 24 hours. After the seeds were reinvigorated it was saturated on a clean drum of water for another 24 hours. The seeds were then removed from its container and allowed to dissipate for ten minutes. The saturated seeds are laid in the incubation chamber for 24 hours after. Seed germination and temperature was regularly checked every 12 hours to assure the seeds were in the level of optimum growth condition. The pre-germinated seeds were immediately direct seeded in the field after the 24 hours' incubation. The seeds were checked first of % germination before direct seeding. Each entry was seeded on eight 4-linear meter furrows and then 5 days later seedling emergence were monitored and recorded. The observed vacant plots and missing hills were replanted at 14 days after sowing (DAS). Plot naming system containing the nature of crop establishment and identification number was followed for easy treatment identification

Determination of the Pushing Resistance of the Culm

Culm strength was determined by measuring the pushing resistance of the stem using a handy force-gauge meter HF50-100061. Twenty days after full heading, the force-gauge meter was perpendicularly set to the plant 20cm above soil surface according to the method reported by Kashiwagi and Ishimaru (2004). A wood board measuring 0.40m length x 0.40m height x 0.05m wide was served as guideboard in data collection. Push-resistance of ten representative plants were measured until the test plant had inclined a vertical 45 ° angle. Furthermore, the sturdiness of the basal stem and root anchorage was represented by the value (in kilogram force) measured by the force-gauge meter.

Determination of the Anatomical Traits of the Culm

Anatomical structures and lignin contents of the stem were observed using an Olympus CS-41 light microscope (SNU-CTR30-2 T2 8F09171) and photographed by Olympus DS72 (12.8MP) digital camera. Biological stain solution was made by diluting 1% Safranin-O in 30% EOH (Johansen, 1940).

Collection, preparation and staining of stem samples

Vigorous primary tillers were collected at 10 days after 100% flowering from 7am to 9am. The samples were sterilized, dissected carefully and placed in a clean pitcher of water. The 5th internode was cross-sectioned by hand at approximately 20 µm thick. Four cross-sectioned samples were made and placed on a clean microscope slide. Freshly made hand samples were then stained with 0.2ml (1% Safranin-O; 30% EOH) solution and allowed to air-dry for 45 minutes at room temperature. After air drying, the stained hand sections were immediately examined under the microscope.

Examination under Olympus CS-41 microscope (SNU-CTR30-2 T2 8F09171)

Stained cross-section of the 5th internode was mounted on the microscope stage and viewed under low (LPO4x) and high (HPO10x) power objectives. For every set of magnification, clear 12.8MP jpeg image was captured (Olympus DS72) and stored. At LPO4x, 5 selected anatomical structures were identified, namely: The Abaxial (ABVB), Median (MEVB) and Adaxial Vascular Bundles (ADVB), Thickness of Sclerenchymatous Cells (TSC) and Culm Wall Thickness (CWT). These 5 anatomical structures were further evaluated under HPO10x.

Measurement of the 5 anatomical structures using Olympus DP2-BSW application software

Stored LPO4x and HPO10x jpeg images was viewed on a computer using the Olympus DP2-BSW application software. The software was used to determine the number and area of ABVB, MEVB and ADVB using LPO4x images while HPO10x images were used to measure the TSC and CWT.

Determination of the lignin content (%LC)

Lignin contents of the 5th internode were indirectly measured using an image color summarizer v.0.76 (Martin Krzywinski | mkweb.bcgsc.ca). First, clear copies of LPO4x jpeg images were edited and converted to PNG format. Second, the PNG images were processed and pixels of colors were grouped by k-means clustering. Finally, the clustered colors were divided into five major groups with corresponding percent number of pixels.

Statistical Analysis of the Data

Quantitative data sets were reviewed and arranged according to the General Linear Model (GLM) procedure of Statistical Analysis System (SASv.7.3) software. Analysis of variance (ANOVA) for each independent variable was produced using SASv7.3. Rice genotypes were group significantly using Duncan's Multiple Range Test (DMRT). Rice characteristics with significant ANOVA of at least 0.05 probability levels were used to compare test genotypes on every lodging check by Dunnett's t-tests. Relationship of several rice descriptors were determined by Pearson correlation coefficient test.

Results and Discussion

Culm strength at 20 days after full heading (Handy Force-gauge HF50-100061)

Push resistance of the lower part of the plant

Resistive force exerted by the stem was measured and recorded using ten representative plants. Check varieties ranges from 0.77 to 1.01 kgf. NSIC Rc240, the resistant check can withstand an average pushing resistance of 1.01 kgf and significantly higher than Rc298 (0.83 kgf), PSB Rc14 (0.78 kgf) and Rc4 (0.77 kgf) (Table 2). Push resistance of the 26 NSIC Rice varieties ranges from 0.73 to 1.05 kgf. Eleven out of 26 NSIC Rice varieties showed significantly comparable push resistance to NSIC Rc240 (1.01 kgf) viz., NSIC Rc402 (0.91 kgf), Rc214 (0.91 kgf), Rc218 (0.91 kgf), Rc300 (0.91 kgf), Rc226 (0.92 kgf), Rc360 (0.93 kgf), Rc224 (0.93 kgf), Rc354 (0.97 kgf), Rc160 (0.97 kgf), Rc29 (1.03 kgf) and Rc396 (1.05 kgf). Push resistance of the 12 DSRAL lines ranges from 0.77 to 1.08 kgf whereas PR43405-10-2-3-3-B (0.93 kgf), PR43425-25-2-1-1-1-B (0.94 kgf), PR40432-10-1-1-1-B-B (0.97 kgf), PR45299-14-3-2-B (1.01 kgf), PR39142-10-3-2-1-1-B (1.04 kgf) and PR43426-13-2-3-2-B-B (1.08 kgf) showed comparable strength to NSIC Rc240

(1.01 kgf). There was significant difference in pushing resistance of the lower part of the plant as shown in Table 2. High resistance in the lower part was the primary target for genetic improvement of lodging resistance in rice (Keller *et al.*, 1999; Khush, 1999; Kashiwagi and Ishimaru, 2008). In rice dynamics, resistance to lodging is a direct relationship of weight of grains and strength of the stem (Mulder 1954; Ishimaru 2008). PR43426-13-2-3-2-B-B (1.08 kgf) and NSIC Rc396 (1.05 kgf) possessed a high push resistance and can be used as a new source of lodging-tolerant genes that could help improved the strength of the lower part of rice even in direct seeded condition.

Table 2. Pushing resistance in kilogram force per cm² of 12 PhilRice lines, 26 rice varieties and 6 check varieties under direct seeded condition.

Trt. No.	Variety Name / Line Designation	Pushing Resistance (kgf)	Trt. No.	Variety Name	Pushing Resistance (kgf)
1	PR39142-10-3-2-1-1-B	1.05	23	NSIC Rc238 (IL)	0.83
2	PR39149-33-1-3-3-1-B	0.86	24	NSIC Rc290 (Sal)	0.85
3	PR39628-17-2-1-1-B	0.89	25	NSIC Rc300 (IL)	0.91
4	PR40334-61-1-1-1-B	0.78	26	NSIC Rc302 (IL)	0.82
5	PR40432-10-1-1-1-1-B-B	0.98	27	NSIC Rc308 (IL)	0.81
6	PR40432-14-2-1-B	0.81	28	NSIC Rc324 (Sal)	0.83
7	PR40432-17-3-1-2-B-B	0.82	29	NSIC Rc352 (IL)	0.82
8	PR43405-10-2-3-3-B	0.93	30	NSIC Rc354 (IL)	0.98
9	PR43425-25-2-1-1-1-B	0.94	31	NSIC Rc356 (IL)	0.88
10	PR43426-13-2-3-2-B-B	1.08	32	NSIC Rc358 (IL)	0.82
11	PR43433-21-2-1-1-1-B	0.85	33	NSIC Rc360 (IL)	0.93
12	PR45299-14-3-2-B	1.01	34	NSIC Rc390 (Sal)	0.81
13	NSIC Rc11 (U)	0.86	35	NSIC Rc392 (IL)	0.85
14	NSIC Rc25 (U)	0.85	36	NSIC Rc396 (IL)	1.06
15	NSIC Rc29 (U)	1.03	37	NSIC Rc402 (IL)	0.91
16	NSIC Rc194 (Sub)	0.86	38	PSB Rc82 (IL)	0.74
17	NSIC Rc214 (IL)	0.91	39	NSIC Rc160 (I)	0.98
18	NSIC Rc216 (IL)	0.87	40	NSIC Rc170 (S)	-
19	NSIC Rc218 SR (IL)	0.91	41	NSIC Rc240 (R)	1.02
20	NSIC Rc222 (IL)	0.89	42	NSIC Rc298 (I)	0.83
21	NSIC Rc224 (IL)	0.94	43	PSB Rc4 (S)	0.77
22	NSIC Rc226 (IL)	0.92	44	PSB Rc14 (R)	0.78

* **pvalue** (<.0001); **r²** (0.61); **cv** (8.44)

Culm Anatomical Traits

Frequency and area of abaxial, median and adaxial vascular bundles

Variation in number, width and length of different vascular bundles were presented in Figure 1. The vascular bundles are found in three rows, the outer (abaxial), median and the inner (adaxial) in all rice cultivars. The ABVB are smaller, ADVB are larger while the MEVB are medium in size. ABVB are embedded in the hypodermis and have been found to push outwards forming outgrowths which are more or less oval with narrow base, rectangular, tangentially flattened or square. ADVB are embedded in the ground tissue while MEVB are near the hypodermis and form wavy circumference in the stem.

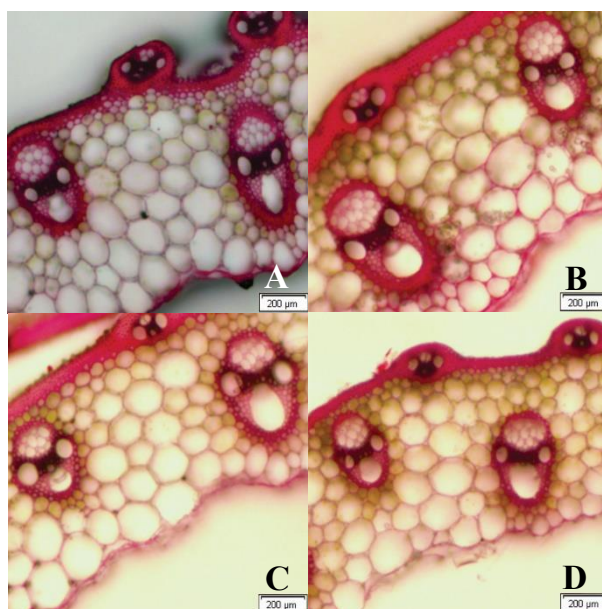


Figure 1. Stem anatomy of (a) NSIC Rc396, (b) Rc356, (c) PR43425-25-2-1-1-B and (d) Rc240 rice cultivars under HPO showing the arrangement of the different types of vascular bundles.

Number of ADVB of check varieties ranges from 11 to 15 whereas NSIC Rc240 has the highest (NADVB = 15) and NSIC Rc298 is lowest (NADVB = 11). For the 26 NSIC rice varieties, NADVB ranges from 9 to 17 viz., NSIC Rc224 has 17 number of ADVB and Rc194 is 9 ADVB. The 12 DSRAL number of ADVB ranges from 9 to 14 and PR39142-10-3-2-1-1-B is the highest (NADVB = 14). Area of ADVB ranges from $27.2 \times 10^3 \mu\text{m}^2$ to $47.0 \times 10^3 \mu\text{m}^2$. Five out of 44 rice genotypes showed significant comparison to NSIC

Rc240 ($45.0 \times 10^3 \mu\text{m}^2$) namely, NSIC Rc308 ($47.0 \times 10^3 \mu\text{m}^2$), Rc396 ($44.0 \times 10^3 \mu\text{m}^2$), Rc224 ($42.8 \times 10^3 \mu\text{m}^2$), Rc29 ($42.5 \times 10^3 \mu\text{m}^2$) and Rc302 ($42.1 \times 10^3 \mu\text{m}^2$) (Table 3).

Low (2-9) number of median vascular bundles (NMEVB) were observed in most of the rice genotypes and high NMEVB were recorded for NSIC Rc214, Rc300, Rc396 and Rc402 (MEVB = 9) and PR40432-17-3-1-2-B-B (MEVB = 8), significantly higher than Rc240 (MEVB = 6). Cell size of MEVB ranges from $18.3 \times 10^3 \mu\text{m}^2$ to $30.3 \times 10^3 \mu\text{m}^2$.

Table 3. Anatomical characteristics of the 5th internode of top 10 highest lignin genotypes and six local lodging checks under direct seeded condition

Trt No.	Variety Name / Line Designation	FREQUENCY			AREA			THICKNESS	
		AD VB	ME VB	AB VB	ADV B (μm^2)	MEVB (μm^2)	ABVB (μm^2)	(TSC (μm))	CWT (μm)
9	PR43425-25-2-1-1-1-B	11	5	22	39577.0	21025.7	4638.7	28.6	544.3
20	NSIC Rc222	15	7	23	31612.8	20465.0	6280.7	46.3	549.2
23	NSIC Rc238	14	7	21	35187.1	26960.2	7193.3	26.0	482.1
26	NSIC Rc302	14	7	23	42101.7	29449.4	8443.8	30.7	592.0
27	NSIC Rc308	11	7	22	46941.9	28319.0	6730.5	32.7	579.7
30	NSIC Rc354	12	7	19	23330.4	23330.4	7025.6	31.9	483.4
31	NSIC Rc356	10	5	16	28382.0	20053.3	4409.4	31.0	451.7
32	NSIC Rc358	11	5	24	32602.5	21046.5	4742.7	38.3	518.5
33	NSIC Rc360	14	7	25	39404.5	23864.2	7768.0	46.9	572.8
36	NSIC Rc396	13	9	24	43927.0	26145.6	5114.5	26.1	740.8
39	NSIC Rc160	11	4	21	35855.3	23895.4	8228.3	37.7	557.1
40	NSIC Rc170	-	-	-	-	-	-	-	-
41	NSIC Rc240	15	6	22	45046.7	30306.6	9169.5	26.7	479.5
42	NSIC Rc298	12	3	20	32077.8	24312.6	6158.9	38.3	492.8
43	PSB Rc4	13	7	19	32010.5	23167.4	6315.8	35.9	398.3
44	PSB Rc14	12	5	18	38024.3	27829.5	6443.2	31.8	464.6
	pvalue	<.0001	<.0001	<.0001	<.0001		<.0001	<.0001	<.0001
	r²	0.58	0.88	0.87	0.92		0.91	0.90	0.90
	cv	14.97	13.73	6.26	4.94		8.63	8.26	5.50

High (17-27) number of abaxial vascular bundles (NABVB) were detected in the test genotypes whereas five cultivars showed significantly higher than NSIC Rc240 (NABVB = 21) viz., NSIC Rc29 (NABVB = 27) and Rc214, Rc224, Rc360 and Rc390 (NABVB = 25). Area of ABVB ranges from $3.82 \times 10^3 \mu\text{m}^2$ to $9.80 \times 10^3 \mu\text{m}^2$ and was the smallest of the three vascular bundles. NSIC Rc29 ($9.80 \times 10^3 \mu\text{m}^2$) was the largest ABVB and comparable to NSIC Rc240 ($9.17 \times 10^3 \mu\text{m}^2$).

Thickness of Sclerenchymatous Cells (TSC) and Culm Wall Thickness (CWT)

Thickness of sclerenchymatous cells and culm wall also showed distinct variations than can provide rigidity and culm strength. TSC of the 44 rice

genotypes ranges from 24.50 to 49.80 μm whereas PR39149-33-1-3-3-1-B is thickest TSC of 49.80 μm and significantly higher than Rc240 (26.70 μm). Culm wall thickness determines the diameter on which anatomical characters were embedded. CWT of 44 rice genotypes ranges from 398.28 to 741.20 μm , from which PR43433-21-2-1-1-1-B showed thickest culm wall at 741.20 μm and significantly higher than Rc240 (479.50 μm) (Table 3).

Lignin Content of the 5th internode

Lignified tissues appear pinkish brown to bright purple and was identified by the color of reactions of lignin (+) to safranin-O (-). Lignin depositions in the 5th internode are significantly different among all rice cultivars. Seven out of 44 genotypes showed significantly higher lignin than Rc240 (16.29% LC) resistant check, viz., NSIC Rc396 (24.03% LC), Rc356 (23.76% LC), Rc238 (23.64% LC), PR43425-25-2-1-1-1-B (23.39% LC), Rc308 (23.20% LC), Rc302 (23.03% LC) and Rc354 (23.02 LC) (Table 4).

Table 4. Lignin content present in the cross-section of the 5th internode of 12 PhilRice lines, 26 rice varieties and six check varieties under direct seeded condition

Trt. No.	Variety Name / Line Designation	Lignin Content (%)	Trt. No.	Variety Name	Lignin Content (%)
1	PR39142-10-3-2-1-1-B	16.95	23	NSIC Rc238 (IL)	23.64
2	PR39149-33-1-3-3-1-B	17.08	24	NSIC Rc290 (Sal)	20.83
3	PR39628-17-2-1-1-B	18.70	25	NSIC Rc300 (IL)	20.53
4	PR40334-61-1-1-B	19.76	26	NSIC Rc302 (IL)	23.03
5	PR40432-10-1-1-1-B-B	20.94	27	NSIC Rc308 (IL)	23.20
6	PR40432-14-2-1-B	19.67	28	NSIC Rc324 (Sal)	17.39
7	PR40432-17-3-1-2-B-B	21.92	29	NSIC Rc352 (IL)	19.90
8	PR43405-10-2-3-3-B	20.46	30	NSIC Rc354 (IL)	23.02
9	PR43425-25-2-1-1-1-B	23.39	31	NSIC Rc356 (IL)	23.76
10	PR43426-13-2-3-2-B-B	20.65	32	NSIC Rc358 (IL)	22.12
11	PR43433-21-2-1-1-1-B	17.35	33	NSIC Rc360 (IL)	21.45
12	PR45299-14-3-2-B	20.54	34	NSIC Rc390 (Sal)	19.94
13	NSIC Rc11 (U)	19.37	35	NSIC Rc392 (IL)	16.33
14	NSIC Rc25 (U)	20.24	36	NSIC Rc396 (IL)	24.03
15	NSIC Rc29 (U)	20.21	37	NSIC Rc402 (IL)	19.62
16	NSIC Rc194 (Sub)	16.41	38	PSB Rc82 (IL)	18.44
17	NSIC Rc214 (IL)	20.50	39	NSIC Rc160 (I)	15.87
18	NSIC Rc216 (IL)	20.15	40	NSIC Rc170 (S)	-
19	NSIC Rc218 SR (IL)	18.91	41	NSIC Rc240 (R)	16.29
20	NSIC Rc222 (IL)	22.01	42	NSIC Rc298 (I)	13.78
21	NSIC Rc224 (IL)	20.88	43	PSB Rc4 (S)	19.04
22	NSIC Rc226 (IL)	18.60	44	PSB Rc14 (R)	15.93

* pvalue (<.0001); r^2 (0.86); cv (6.91)

The rigidity of the rice stem depends on its biochemical components, such as starch, cellulose, lignin and silicon (Kawano and Takanashi, 1961; Hozyo and Oda, 1965). Lignin is confined exclusively to vascular plants and mostly deposited in cell walls of tissues involved in mechanical support or in water conduction (principally xylem, but also sclerenchyma, phloem fibers, and periderm) (Baucher *et al.*, 2010). Lignin deposition occurs when the cell growth is completed and the cell wall undergoes secondary thickening.

NSIC Rc396 showed remarkably high lignin content (24.03% LC) in the 5th internode, averaged number of adaxial vascular bundles (13 ADVB), highest NMEVB = 9, high number of abaxial vascular bundles (24 ABVB), large area of adaxial vascular bundles ($43.9 \times 10^3 \mu\text{m}^2$ ADVB), large area of median vascular bundles ($26.1 \times 10^3 \mu\text{m}^2$ MEVB), averaged size of abaxial vascular bundles ($5.11 \times 10^3 \mu\text{m}^2$ ABVB), medium thickness of sclerenchymatous cells ($26.05 \mu\text{m}$ TSC) and large culm wall thickness ($740.80 \mu\text{m}$ CWT) (Figure 2).

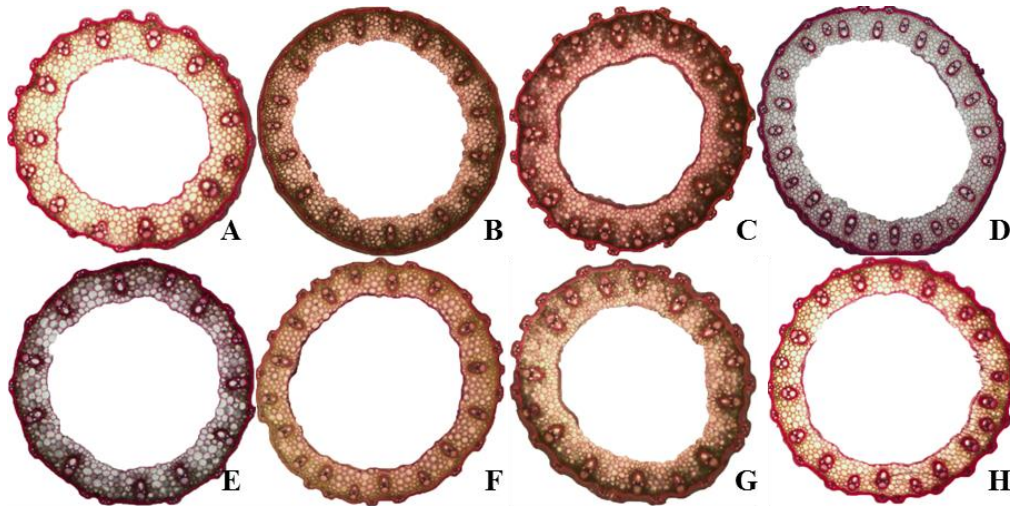


Figure 2. Stem anatomy of top seven rice genotypes (a) NSIC Rc396, (b) Rc356, (c) Rc238, (d) PR43432-25-2-1-1-1-B, (e) Rc308, (f) Rc302, (g) Rc354 and (h) NSIC Rc240, resistant check with high lignin content under LPO.

Lignin content and composition are known to vary among taxa, individuals of a population, tissues, and individual cell types within a tissue as well as to correlate with the developmental stages and the environmental conditions (Wardrop, 1976; Monties, 1985, 1991; Monties and Lapierre, 1981; Wu *et al.*, 1992; He and Terashima, 1991).

NSIC Rc240, the resistant lodging check were identified to have medium amount of lignin (16.29% LC) in the 5th internode. It has an averaged number of ADVB = 15, 6 MEVB and 21 ABVB. Large area of vascular bundles was observed ($45.0 \times 10^3 \mu\text{m}^2$ ADVB, $30.3 \times 10^3 \mu\text{m}^2$ MEVB, $9.17 \times 10^3 \mu\text{m}^2$ ABVB) and recorded. Although it has high amount and large area of vascular bundles, we observed that TSC ($26.70 \mu\text{m}$) and CWT ($479.50 \mu\text{m}$) is thin.

NSIC Rc356, the second rice genotype with high lignin (23.76% LC) has also varied anatomical characters such as average number of adaxial (10 ADVB), low number of median (5 MEVB) and 16 ABVB. Cell size of this vascular bundles was small ($28.4 \times 10^3 \mu\text{m}^2$ ADVB, $20.1 \times 10^3 \mu\text{m}^2$ MEVB, $4.41 \times 10^3 \mu\text{m}^2$ ABVB). It has $30.95 \mu\text{m}$ TSC and $451.70 \mu\text{m}$ CWT.

NSIC Rc238, the third rice genotype with high lignin (23.64% LC) has 14 ADVB, 7 MEVB and 21 ABVB and area of $35.2 \times 10^3 \mu\text{m}^2$ ADVB, $26.9 \times 10^3 \mu\text{m}^2$ MEVB and $7.19 \times 10^3 \mu\text{m}^2$ ABVB. Thickness of sclerenchymatous cells is $26.00 \mu\text{m}$ and culm wall thickness is $482.10 \mu\text{m}$.

PR43425-25-2-1-1-1-B, line with the highest lignin (23.39% LC) in the 5th internode has 11 ADVB, 5 MEVB and 22 ABVB with an area per vascular bundles of equal to $39.6 \times 10^3 \mu\text{m}^2$ ADVB, $21.0 \times 10^3 \mu\text{m}^2$ MEVB and $4.64 \times 10^3 \mu\text{m}^2$ ABVB. TSC = $28.60 \mu\text{m}$ and CWT = $544.25 \mu\text{m}$.

NSIC Rc308, fifth of the rice genotypes with high lignin (23.20% LC) has 11, 7 and 22 number of ADVB, MEVB and ABVB with and area of $46.9 \times 10^3 \mu\text{m}^2$ ADVB, $28.3 \times 10^3 \mu\text{m}^2$ MEVB and $6.73 \times 10^3 \mu\text{m}^2$ ABVB. It has $32.65 \mu\text{m}$ TSC and $579.65 \mu\text{m}$ CWT.

In addition, lignin plays a major role in the plant's defense. It is a constitutive physicochemical barrier against pathogens and it can be synthesized *de novo* in response to stress, such as wounding or pathogen infection (Vance *et al.*, 1980; Lewis and Yamamoto, 1990).

Correlation Analysis

Correlation is useful in determining the overall linear association between any two independent variables. Significant associations present in pushing resistance to percent lignin content and anatomical attributes present a suitable criterion for selecting lodging-resistant genotypes. Correlation analysis showed non-significant association between pushing resistance and lignin content of the 5th internode (Table 5), comparable results were obtained by (Ishimaru *et al.*, 2008). The non-significant correlation between these two most important traits in lodging may be affected by the absence of leaf sheath during lignin analysis.

Table 5. Correlation matrix of pushing resistance, % lignin content, frequency and area of ADVB, MEVB and ABVB, thickness of sclerenchymatous cells and culm wall thickness

Variables	PR	%LC	N ADVB	N MEVB	N ABVB	A ADVB	A MEVB	A ABVB	TSC	CWT
PR	1	0.102	0.291	0.143	0.419	0.349	0.241	0.361	-0.034	0.531
%LC	0.102	1	0.152	0.576	0.168	0.151	0.026	0.030	-0.054	0.140
NADVB	0.291	0.152	1	0.103	0.617	0.342	0.331	0.617	0.045	0.324
NMEVB	0.143	0.576	0.103	1	0.284	0.409	0.272	0.075	0.032	0.172
NABVB	0.419	0.168	0.617	0.284	1	0.466	0.326	0.544	0.341	0.640
AADVB	0.349	0.151	0.342	0.409	0.466	1	0.724	0.396	-0.013	0.380
AMEVB	0.241	0.026	0.331	0.272	0.326	0.724	1	0.467	-0.103	0.278
AABVB	0.361	0.030	0.617	0.075	0.544	0.396	0.467	1	-0.051	0.141
TSC	-0.034	-0.054	0.045	0.032	0.341	-0.013	-0.103	-0.051	1	0.177
CWT	0.531	0.140	0.324	0.172	0.640	0.380	0.278	0.141	0.177	1

Values in bold are different from 0 with a significance level $\alpha=0.05$

Significant positive correlation was observed for PR to NABVB (r 0.42), AADVB (r 0.39), AABVB (r 0.36) and CWT (r 0.53) similar on the findings of Zhang *et al.* (2016). High values of these anatomical traits will help increase pushing resistance under direct seeded condition. There were significant and positive correlation identified for % LC and NMEVB (r 0.58); NADVB to NABVB (r 0.62), AADVB (r 0.34), AMEVB (r 0.33) and AABVB (0.62). Highly significant and positive correlation of AADVB were analysed for AMEVB (r 0.72) therefore area of adaxial and median vascular bundles protrude the same under direct seeded system.

Conclusion

In this study, we identified the importance of pushing resistance in the lower stem and the role of adaxial, abaxial vascular bundles and culm wall thickness in the upper stem (5th internode) in improving resistance to lodging under direct-seeded system. We failed to determine the relationship of pushing resistance and lignin content; however, we recognized the need to understand the functions of leaf sheath in the stem and require further investigation as a potential key trait to consider in lodging. Preliminary investigation of the relationship of pushing resistance, lignin and culm anatomy showed structural hierarchy on increasing lodging resistance and improving screening techniques in the direct-seeded culture.

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