การค้นหาลักษณะทางสัณฐานวิทยา-กายวิภาคที่เกี่ยวข้องกับการหักล้มของลำต้นและการสูญเสียผลผลิตภายใต้การเก็บเกี่ยวล่าช้าในข้าวลูกผสม (*Oryza sativa* L.)

Determination of Morpho-Anatomical Characteristics Related to Stem Lodging and Yield Loss Under Delayed Harvesting in Hybrid Rice (*Oryza sativa* L.)

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Abstract: Delayed harvest drastically affects grain yield owing to plant lodging, which is difficult to perform on time with the mechanical harvester. In addition, hybrid rice is prone to lodging due to the hybrid plants' height. Therefore, this study focused on the relationship among morpho-anatomical traits, grain yield, and lodging through eighty-seven lines of F_1 hybrids, both late harvested and on-time harvested. The range of lodging score (3.5–7.0) of F_1 in late harvesting was higher than that of lodging score (1.0–4.0) in on-time harvesting. In addition, the average grain yield in late harvest decreased dramatically when compared with on-time harvest (68 g/plant in on-time and 6 g/plant in late harvest). In terms of environmental factors, it was found that the frequency of rainfall and wind speed during the harvesting period were the main causes of rice plant lodging. The path coefficient analysis revealed that grain yield had a negative direct effect on lodging and plant height had a positive direct effect on lodging in both conditions. Moreover, basal stem diameter was the most negative directly affected by lodging, followed by the top tissue area, basal parenchyma tissue and basal vascular bundle area. In addition, top stem diameter was the positive directly affected by lodging. It can be concluded that reducing plant height and increasing the culm diameter and culm wall thickness of the hybrid rice

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tend to improve the breeding program for reduced grain loss in hybrid rice, especially in an unsuitable environment. In addition, on-time harvesting must be a concern for rice production.

Keywords: rice, lodging, hybrid, morphology, anatomy, agronomic, yield, delayed harvest

บทคัดย่อ: ปัญหาการหักล้มของต้นข้าวในระยะเก็บเกี่ยวส่งผลกระทบอย่างมากต่อผลผลิต โดยเฉพาะอย่างยิ่งเมื่อมีการเก็บเกี่ยวข้าวล่าช้าเนื่องจากต้นข้าวแสดงอาการหักล้มง่ายและถือเป็นหนึ่งในสาเหตุหลักที่พบเจอเสมอ แม้มีการนำรถเกี่ยวข้าวเข้ามาช่วยในกระบวนการเก็บเกี่ยว เนื่องจากเป็นเรื่องยากต่อการบริหารจัดการการเก็บเกี่ยวในระยะอายุของข้าวที่เหมาะสม โดยเฉพาะอย่างยิ่งในกรณีข้าวลูกผสมซึ่งมีแนวโน้มที่จะหักล้มง่ายเนื่องจากความสูงของต้นข้าวลูกผสม ดังนั้นงานวิจัยนี้จึงมีวัตถุประสงค์เพื่อศึกษาความสัมพันธ์ระหว่างลักษณะทางสัณฐานวิทยา-กายวิภาค และผลผลิตข้าวกับการหักล้มของข้าวในสายพันธุ์ข้าวลูกผสม F_1 จำนวน 87 สายพันธุ์ที่ปลูกภายใต้สภาวะการเก็บเกี่ยวแบบล่าช้าและการเก็บเกี่ยวตรงเวลา พบค่าคะแนนการหักล้มของลูกผสม F_1 ภายใต้สภาวะเก็บเกี่ยวล่าช้า (3.5-7.0) มีค่าสูงกว่าค่าคะแนนการหักล้มภายใต้สภาวะเก็บเกี่ยวตรงเวลา (1.0-4.0) และพบผลผลิตเฉลี่ยจากการเก็บเกี่ยวล่าช้าลดลงอย่างมากเมื่อเทียบกับการเก็บเกี่ยวตรงเวลา (68 กรัมต่อต้น ในการเก็บเกี่ยวตรงเวลา และ 6 กรัมต่อต้น ในการเก็บเกี่ยวล่าช้า) ในด้านปัจจัยสภาพแวดล้อมพบว่า ความถี่ของฝนและความเร็วลมในช่วงการเก็บเกี่ยวเป็นสาเหตุหลักที่ทำให้ต้นข้าวมีการหักล้ม จากการวิเคราะห์ค่าสัมประสิทธิ์เส้นทางพบว่าผลผลิตข้าวได้รับความเสียหายโดยตรงจากการหักล้ม และพบความสูงของต้นมีผลโดยตรงต่อกับการหักล้มของข้าวภายใต้ทั้งสองสภาวะ นอกจากนี้ยังพบว่าเส้นผ่านศูนย์กลางของฐานลำต้นมีผลโดยตรงต่อการหักล้มมากที่สุด รองลงมาคือพื้นที่เนื้อเยื่อด้านบน เนื้อเยื่อพาเรนไคมาที่ลำต้นส่วนล่าง และพื้นที่วาสคิวลาบัลเดนที่ลำต้นส่วนล่าง โดยพบเพิ่มเติมเส้นผ่านศูนย์กลางลำต้นส่วนบนยังส่งผลกระทบเชิงบวกโดยตรงจากการหักล้ม สรุปได้ว่าการลดความสูงของต้น การเพิ่มขนาดเส้นผ่านศูนย์กลางลำต้นและความหนาของผนังลำต้นในข้าวลูกผสมมีแนวโน้มที่จะสามารถลดการสูญเสียผลผลิตในข้าวลูกผสมโดยเฉพาะอย่างยิ่งในสภาพแวดล้อมที่ไม่เหมาะสม และสามารถนำมาปรับใช้ในโปรแกรมการปรับปรุงพันธุ์ข้าวได้ อย่างไรก็ตามการเก็บเกี่ยวข้าวในเวลาที่เหมาะสมยังเป็นสิ่งที่ต้องคำนึงเพื่อลดการสูญเสียผลผลิต

คำสำคัญ: ข้าว, การหักล้ม, ลูกผสม, ลักษณะทางสัณฐานวิทยา, ลักษณะทางกายวิภาค, ลักษณะทางการเกษตร, ผลผลิต, เก็บเกี่ยวล่าช้า

Introduction

Rice is currently the staple meal for nearly half of the world's population (Costa de Oliveira *et al*., 2020), and demand for rice is expected to increase until at least 2035 (Pan *et al*., 2019). Thus, to ensure the safety of rice production, paddy rice losses should be avoided in each process of rice production with limited land resources (Wang *et al*., 2021).

Harvesting is one of the activities in the production process of the value chain of rice production. Rice harvesting must be carried out at an appropriate time. However, as impacted by weather, manpower, or agricultural machinery dispatching, rice is difficult to harvest on the optimal harvest date (Dumitru *et al*., 2020). Delayed harvest causes a significant reduction in the recoverable quantity and quality of rice (Chandegara *et al*., 1999). Once the harvesting is delayed, it will inevitably lead to a decline in rice production and constrain resource utilization and environmental sustainability

(Hossain *et al*., 2009). Baktiar *et al*. (2013) and Kandil *et al*. (2010) reported that rice harvesting at 30 to 35 days after flowering was found to be suitable for higher grain quality in respect of head rice, elongation (%), and amylose content.

Mechanized harvesting is needed due to rice production's enormous planting area. The current harvest of rice products in Thailand differs from the past when manual labor was primarily used. Combine harvesters have become increasingly popular due to their efficiency; they work rapidly and can shorten the harvesting process, resulting in an increase in demand among farmers. However, weather conditions, workforce availability, and harvester scheduling remain hurdles to timely rice harvesting (Teasdale *et al*., 2004). Therefore, delays in harvesting caused plants to lodge, grains to fall from the panicle, and diseases to infect the grains, resulting in lower productivity and quality.

Thailand is among the world's major rice producers and exporters. About half of the total annual rice produced in Thailand comes from the Chao Phraya river basin, both in wet and dry seasons (Stuart *et al*., 2018). The dry season, is the planting season with the most lodging problems, resulting in a significant loss of rice yield. Since the dry season, rice harvest occurs during the start of the rainy season, between May and June. During that time, the southwest monsoon winds become stronger. This results in strong winds and heavy rains, causing tall rice plants with weak root systems to lodge. Rice lodging during physiological maturity causes the panicle of rice to make contact with the ground, resulting in high seed moisture content, humidity, and the seeds germinating or plants collapsing, causing difficulties for harvest operations such as increased demand for grain drying, decreased harvesting efficiency, or increased production costs (Jatuporn, 1997; Islam *et al*., 2007).

In the natural environments, lodging occurs when the upper part of the plant, especially when the panicle increases in weight and during heavy rains coupled with strong winds, becomes more susceptible to lodging (Shrestha *et al*., 2020; Zhao *et al*., 2019). Lodging is classified into two types: stem lodging and root lodging. Stem lodging is associated with the buckling of a stem on the ground caused by wind force, whereas root lodging is termed when root fails to maintain strong soil contact or has poor anchorage in a soil (Berry *et al*., 2003). Generally, lodging is intimately related to plant morphological traits and stem physical strength (Shah *et al*., 2019). The plant height and the height of the center of gravity were the major morphological variables influencing lodging resistance (Islam *et al*., 2007). However, the relationship between plant height and lodging risk is not yet fully understood (Wu *et al*., 2022).

Hybrid rice had a yield advantage of about 15% over the best pure line cultivars in farmers' fields (Yuan et al., 1994). Recently, hybrid rice varieties have been commercialized in India, Vietnam, the Philippines, and Bangladesh (Virmani, 2003) but not in Thailand. However, Virmani (2003) reported that lodging occurred frequently in farmers' fields where hybrid rice was grown because the hybrid plants were too high. Therefore, this study focused on the correlation between morpho-anatomical traits, grain yield, and lodging through hybrid rice lines during late harvesting compared with on-time harvesting. We aimed to quantify the key morphological and anatomical traits associated with lodging resistance, particularly stem lodging, when harvesting is delayed.

The genotypic variation in lodging resistance and other traits among hybrid lines was also determined. Understanding these characteristics can help inform future breeding programs to develop more resilient and high-yielding rice varieties. Additionally, the results of this research may provide valuable insights for breeders looking to optimize the harvest timing and minimize losses due to lodging, which will benefit farmers even further.

Materials and methods

Plant materials and experimental field management

The eighty-seven lines of F1 hybrid rice from National Center for Genetic Engineering and Biotechnology (BIOTEC), Thailand were used in this study (Table supplement 1). The experiment was conducted in the research field at Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom, Thailand (14°02'69.6"N, 99°97'46.9"E, 10 m above sea level) in two seasons: wet season (WS) and dry season (DS). In WS, hybrid plants were grown from May until September 2020 (WS2020), and the harvest time was conducted 30 days after flowering reached 100%. This is classified as on-time harvested during the rice-growing season. On the other hand, DS was started from February to July 2021 (DS2021), and the harvest time was conducted on 60 days after days to 100% flowering. This is classified as late-harvested during the dry season.

Field experiments were arranged in a randomized block design with three replications, both in wet and dry seasons. Each hybrid line was planted in 2 rows (4 m/row) with a spacing of 25x50 cm, and the transplanting method under flooded conditions was applied. In addition, the experimental plots for two seasons were conducted in the same field. The rice plants were seeded in a field nursery. After 15 days, each seedling plant was transplanted into the experimental plot. The fertilizer was applied 15 days after planting at a rate of 75 kg/ha of N, 37.5 kg/ha of P_2O_5, and 37.5 kg/ha of K_2O. The second split of fertilizer was applied at the booting stage (65 days after planting) at a rate of 37.5 kg/ha of N. The water management was conducted in flooded conditions by maintaining a water depth of 10 cm above the soil surface, and the water levels were not allowed to be more than 5 cm above the soil from 15 days after transplanting to 14 days before harvest. Other management practices were performed in accordance with conventional high-yield cultivation approaches following Thai rice department. The weather data, including air temperature, relative humidity, amount of rainfall, and wind speed, were measured every 3 hours per day with a microclimate weather station (WatchDog 2000 Series Micro Stations, Spectrum Technologies, Inc., USA).

Phylogenetic analysis based on whole genome sequencing (WGS)

A phylogenetic analysis was conducted to establish the genetic information of the parent lines required to produce F_1 progenies. The gDNA from the leaves was isolated according to the DNeasy Plant Mini Kit (Qiagen) protocol. The DNA quantity was tested with a NanoDrop 8000, and the concentration exceeded 50 ng/µl. The DNA was then sequenced on an Illumina HiSeq X by Novogene AIT, Singapore. The Bowtie 2 program was subsequently used to align the nucleotides (Langmead and Salzberg, 2012), and the GATK program was used to analyze the single-nucleotide polymorphisms (SNPs) in each sample (McKenna *et al.*, 2010). Finally, the nucleotide sequences from the parent lines were utilized to generate a phylogenetic tree via the MEGA X program.

Assessment of agronomic and morphological traits

Agronomic data were collected over two seasons, including plant height (cm), days to 100% flowering, panicle length (cm), effective tillers per plant, filled grains per panicle, unfilled grains per panicle, 1000-grain weight (g), and grain yield per plant (g). Each plot was sampling five plants as the survey unit. Plant height, days to 100% flowering, and effective tillers per plant were measured at the end of the vegetative stage, while the other traits were measured at the maturity stage. In addition, the grain yield moisture was adjusted to 14% and then extrapolated to units of g/plant. The morphological traits, including culm diameter and culm wall thickness, were also measured after removing the leaf sheath.

Lodging scores were evaluated after 100% flowering. Lodging severity was scored visually as a percentage of plants that lodged at maturity, as described by IRRI (2014). These were assessed on a 1–9 scale, where 1 was totally upright and 9 was totally lodged.

Observation of the anatomical of the culm

The anatomical traits were collected on WS compared between resistance and susceptibility to lodging. The primary culm was cut one day after 100% flowering from the top 10 lines of lodging susceptibility and 10 lines of lodging resistance. The top and basal stem were collected at 5 cm and 3 cm below the neck panicle and basal ground, respectively. The samples were fixed in FAA solution (Formaldehyde Alcohol Acetic Acid, 70%:5%:5%+30% water). The samples were cross-sectioned by hand using sharp razor blades. The biological stain solution was made with 0.05% Toluidine blue-O. The cross-sectioned samples were placed on a slide, stained with a 70% ethanol solution, and allowed to air-dry at room temperature. The stained cross-section was observed on the microscope (Leica, model ICC50 HD). Top vascular bundle number (TVBN), basal vascular bundle number (BVBN), top vascular bundle area (TVBA), basal vascular bundle area (BVBA), top tissues diameter (TTD), basal tissues diameter (BTD), top tissues area (TTA), basal tissues area (BTA), top parenchyma tissues (TPT), and basal parenchyma tissues (BPT) were measured using the GNU Image Manipulation Program (GIMP 2.10.22), as base values of pixels were calibrated and calculated.

Statistical analysis

The statistical analysis of agronomic, morphological, and anatomical traits was evaluated among F_1 lines by analysis of variance. The means were separated using Duncan's test at alpha levels of 0.05. If there was a significant difference among the experiments for a given parameter, then the values from all the experiments for that parameter were used to obtain the means and standard error. In addition, the path coefficient was analyzed to determine the direct effect of agronomic, morphological, and anatomical traits. The R program version 4.2.1 (R Core Team, 2022) and the package agricolae version 1.4.0 (v1.4.0; Felipe & Muhammad, 2020) were used to analyze all the data for analysis of variance and path coefficient, respectively.

Results

Phylogenetic relationships of parental lines

Based on the results obtained for the WGS analysis, a phylogenetic tree was divided into three groups. Each group contained both female-parent TGMS lines and male-parent limes. For female parents, group I contained T6-4 and T6-6, group II contained 18LMP-FS-8, 18LMP-FS-9, and 18LMP-FS-10, and group III contained 18LMP-FS-1, 18LMP-FS-2, 18LMP-FS-3, 18LMP-FS-4, 18LMP-FS-5, 18LMP-FS-6, and 18LMP-FS-12 (Figure 1). In addition, it was found that some of the F_1 lines were derived from female and male parents in the same group and among groups (Figure 1 and Table supp. 1).

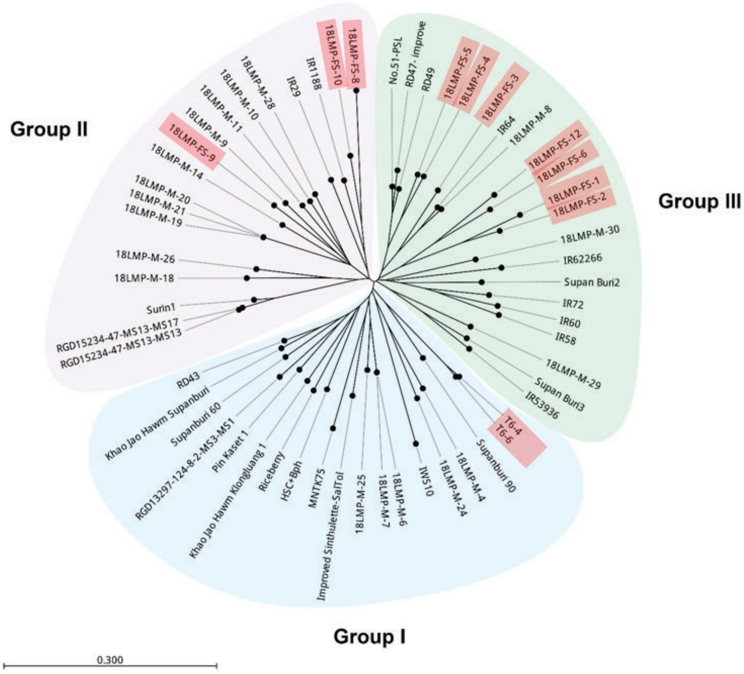

Figure 1 Phylogenetic relationships of parental lines based on whole genome sequencing (WGS). Marked brown refers to female parents.

Weather conditions

The experiment was conducted in WS 2020 and DS 2021. In WS 2020, the average temperature from May to August was 31.1°C daytime/27.1°C nighttime, while the average temperature in DS2021 from February to July was 30.3°C/26.7°C, daytime/nighttime. The average of relative humidity when compared between WS2020 (74%RH/88%RH, daytime/nighttime) and DS2021 (73%RH/87%RH, daytime/nighttime) was slightly different as the RH of WS2020 was higher than that of DS2021. However, the amount of total rainfall in WS2020 (528.7 mm) was clearly higher than that of DS2021 (246.7 mm). In addition, the rain distribution in WS2020 was more uniform than that in DS2021. The frequency of rainfall in WS2020 was greater in June (tillering stage) and August (ripening stage), while the frequency of rainfall in DS2021 started from the end of May (flowering stage) until August (late harvesting). Interestingly, the average wind speed in DS2021 (8.7 km/h and 3.7 km/h, daytime/nighttime) was greater than that of

WS2020 (4.6 km/h daytime and 2.0 km/h daytime/nighttime). Furthermore, high wind speeds in both WS2020 (27 km/h) and DS2021 (27 km/h) were reported at the end of the experiment, which coincided with both seasons' harvesting periods. However, the rice plants in DS2021 continued in the field 30 days after maturity, whereas the grain yield in WS2020 was harvested on time (Figure 2A–H).

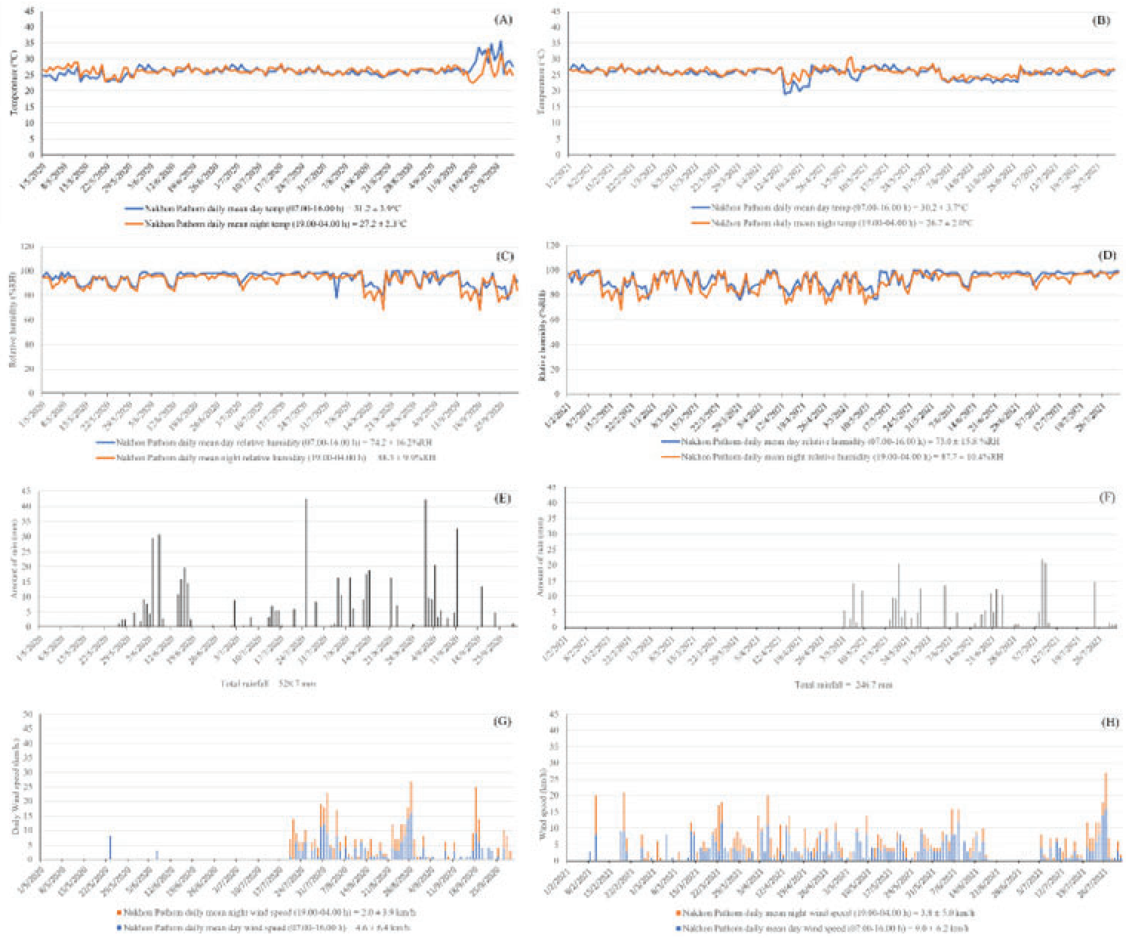

Figure 2 Weather data, including air temperature (A, B), relative humidity (C, D), amount of rainfall (E, F) and wind speed (G, H) from wet season 2020 and dry season 2021.

Agronomic variation between WS2020 and DS2021

The combined analysis of agronomic traits revealed that every agronomic trait (excluding grain weight) differed significantly between WS2020 and DS2021. Moreover, there was significant phenotypic variation for each trait across F_1 lines, and all phenotypic values were approximately normally distributed in both WS2020 (on-time harvest) and DS2021 (delayed harvest) (Figure 3 and Table 1). However, the range of distribution in each trait compared between WS2020 and DS2021 showed differences. The range of lodging scores (3.5–7.0) in DS2021 was higher than that of lodging scores (1.0–4.0) in WS2020. On the other hand, the range of panicle length, filled grains per panicle, and grain yield in WS2020 were significantly higher than those in DS2021. However, the range of plant height, tiller per plant, and grain weight between WS2020 and DS2021 were slightly different.

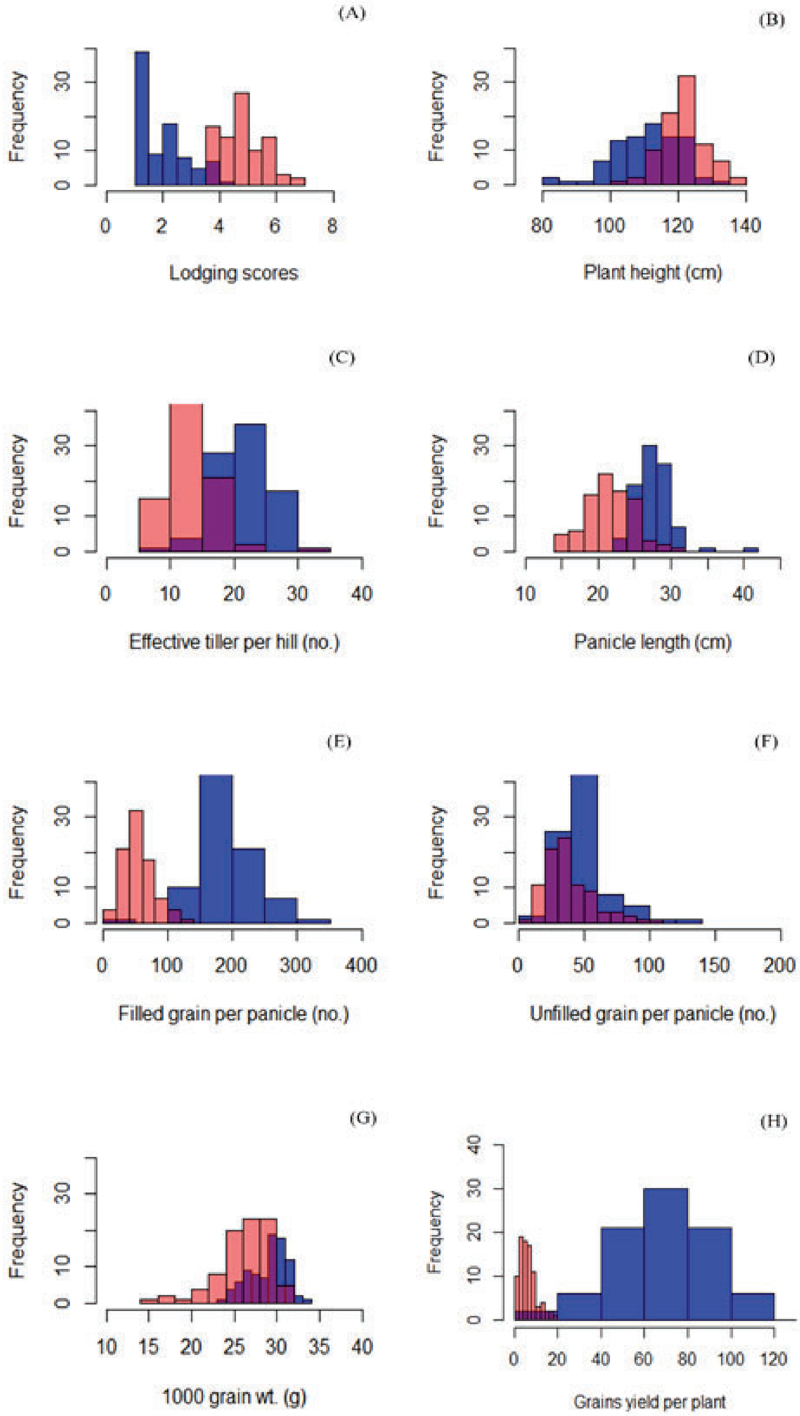

Figure 3 Lodging score and agronomic variation in F$_1$ hybrid rice (A-H) between WS2020 (bule color) and DS2021 (orange color). The dark brown color refers to the average distribution of two seasons.

Table 1 ANOVA means and ranges of agronomic traits of F_1 lines under normal condition, in WS2020 and delayed harvest condition in DS2021.

Traits	Years	F_1 lines						
		Mean +/- SD	LSD	Min	Max	CV%	*F-value*	*P-value*
LS	WS2020	1.98 ± 1.41B	1.10	1.00	4.33	40.59	1.49	**
	DS2021	4.92 ± 0.71A	0.94	3.50	7.00	20.03	4.37	*
PH	WS2020	111.40 ± 7.78B	4.35	79.62	135.00	2.91	10.47	**
	DS2021	122.09 ± 2.12A	4.66	100.00	138.00	2.83	28.31	**
PL	WS2020	27.96 ± 2.71A	8.13	22.44	42.39	24.53	2.81	ns
	DS2021	22.07 ± 0.75B	4.47	14.94	32.00	15.15	1.04	ns
ETP	WS2020	21.71 ± 7.46A	7.30	9.33	34.00	24.53	1.98	**
	DS2021	16.83 ± 4.28B	5.87	6.33	34.00	31.77	2.43	**
FGPP	WS2020	190.86 ± 66.86A	55.89	42.78	329.44	21.44	2.05	**
	DS2021	54.20 ± 25.50B	37.47	7.78	129.33	50.65	3.06	**
UGPP	WS2020	47.86 ± 26.71A	30.09	19.22	135.00	45.71	1.73	**
	DS2021	38.57 ± 18.27B	25.02	6.67	110.00	47.31	2.27	**
TGW	WS2020	28.93 ± 1.08	2.26	23.10	33.37	5.80	6.20	**
	DS2021	26.16 ± 0.06	1.96	15.57	30.75	5.44	5.07	**
GYP	WS2020	68.80 ± 4.87A	36.31	17.91	145.54	39.43	1.15	**
	DS2021	6.31 ± 3.40B	7.47	0.92	18.27	87.67	1.61	**

LS = Lodging score, PH = Plant height (cm), PL = Panicle length (cm), ETP^{-1} = Effective tiller per hill, FGPP = Filled grains per panicle, UGPP = Unfilled grains per panicle, TGW = 1000 grains weight (g), GYP = Grain yield per plant.

*, ** and ns = represent significant differences at 0.05, 0.01 levels and no significant difference, respectively

When the lodging score was considered in WS2020, the results showed that the F_1 lines were identified as having strong resistance (score = 1) to moderate resistance (score = 4). Among these, thirty-five F_1 lines were identified as having strong resistance (Figure 4A). However, the lodging score increased dramatically in all F_1 lines in DS2021 from moderate resistance (score = 3.0) to weak resistance (score = 7.0). Furthermore, grain yield in all F_1 lines declined significantly in DS2021. The range of grain yield in WS2020 was 17.91–145.54 g/plant, while grain yield in DS2021 ranged from 0.92–18.27 g/plant. The maximum grain yield was obtained in F1 hybrid "RGD18511" (145.54 g/plant), while in DS2021, RGD18153 had the highest yield (18.27 g/plant) (Figure 4B). The parents of these F_1 lines are derived from different groups. In addition, most of the low-yielding F_1 lines came from crossbreeding between parents in the same group (Figure 1).

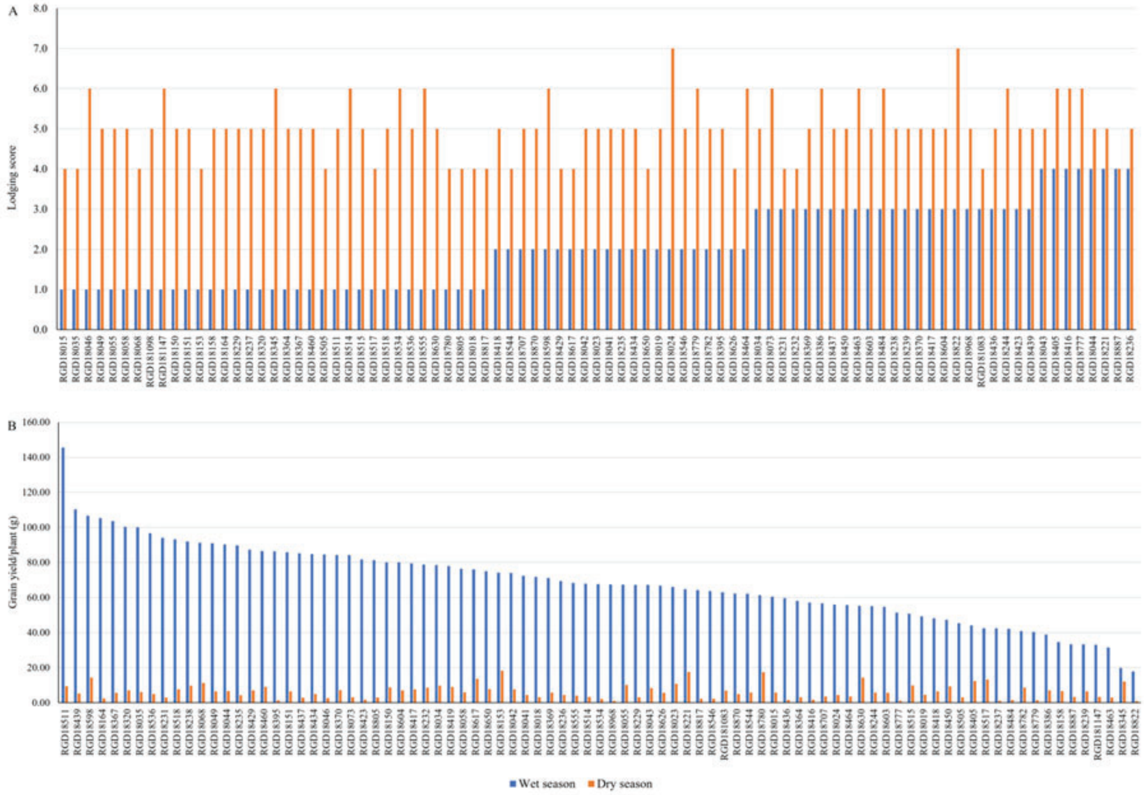

Figure 4 Lodging score (A) and grain yield /plant (B) ranking during the wet season (WS2020) and the dry season (DS2021). The WS2020 data served as the basis for the ranking direction.

The findings of seed setting followed the same pattern as grain yield. In WS2020, the average percentage of seed set was 80% and ranged from 90-61%, whereas in DS2021, the average percentage of seed set was decreased to 58% and ranged from 87%-11%. In addition, it was noticed that the mean of total spikelets on panicle in DS2021 (93 spikelets) was significantly lower than in WS2020 (239 spikelets) (data not shown).

In this study, the relationship between stem lodging and agronomic traits was investigated under both normal (WS2020) and delayed harvest (DS2021). Under normal conditions, lodging had a positive correlation with plant height (r = 0.41). In contrast, lodging had a significant negative correlation with grain yield/plant (r = -0.34). Furthermore, grain yield was strongly positively linked with plant height (r = 0.46) and tiller number (r = 0.46) (Table 2). The correlation in the delayed harvest condition showed the same results as in the normal condition. The lodging had a negative association with grain yield (r = -0.55) but a positive correlation with plant height (r = 0.37). Moreover, the grain yield was positively correlated with tiller number (r = 0.46) and filled grain/panicle (r = 0.38), respectively (Table 2).

Table 2 Correlation analysis among agronomy traits of F1 lines in WS2020 and DS202.

Traits	LS	GY	PH	PL	TN	FG	UF	SS	GW
WS2020									
LS	1.00								
GY	-0.34*	1.00							
PH	0.41*	0.46*	1.00						
PL	-0.05	0.03	0.12	1.00					
TN	-0.26	0.46*	0.25	-0.01	1.00				
FG	0.04	0.17	0.31	0.20	-0.10	1.00			
UF	0.08	0.05	0.02	0.01	-0.02	0.30	1.00		
SS	-0.05	0.06	0.18	0.14	0.02	0.39*	-0.73**	1.00	
GW	-0.09	0.11	-0.08	0.06	0.32*	-0.48*	-0.17**	-0.13	1.00
DS2021									
LS	1.00								
GY	-0.55**	1.00							
PH	0.37*	-0.07	1.00						
PL	-0.20	0.22	0.14	1.00					
TN	-0.25	0.46*	-0.24	0.25	1.00				
FG	0.04	0.38*	0.12	0.12	0.15	1.00			
UF	-0.19	-0.18	0.07	0.17	0.04	-0.03	1.00		
SS	0.14	0.37*	-0.01	-0.11	0.04	0.65**	-0.71**	1.00	
GW	-0.03	0.13	-0.18	0.04	0.12	-0.12	0.01	-0.09	1.00

*, **Significant at the 0.05 and 0.01 probability levels, respectively

LS= lodging score, GY = grain yield, PH = Plant height, PL = Panicle length, TN = Tiller number, FG = Filled grains per panicle, UF = Unfilled grains per panicle, SS = Seed set and GW = Grains weight.

Path coefficient analysis, which furnishes the cause and effect of different agronomic traits, provides a better index for selection than mere correlation coefficients. Therefore, path analysis was used to determine the direct and indirect effects contributing to lodging in both normal and delayed harvest conditions. Under normal conditions, lodging had the greatest negative impact on grain yield (-0.592), with plant height having an indirect effect (0.364). Furthermore, the plant height (0.791) showed the most positive direct influence on lodging. This finding was consistent with the path coefficient analysis in the delayed harvest scenario, in which grain yield had a negative direct influence on lodging (-0.768) and plant height had a positive direct effect on lodging (0.386) (Table 3).

Table 3 Direct and indirect effects of agronomic traits on lodging score in WS2020 and DS2021.

Traits	Correlation with LS	Direct effect	Indirect effect							
			GY	PH	PL	TN	FG	UF	SS	GW
WS2020										
GY	-0.34*	-0.592	-	0.364	-0.003	-0.107	-0.030	0.012	0.007	0.010
PH	0.41*	0.791	-0.272	-	-0.015	-0.058	-0.055	0.006	0.020	-0.007
PL	-0.05	-0.124	-0.015	0.099	-	0.002	-0.035	0.003	0.016	0.006
TN	-0.26	-0.231	-0.275	0.198	0.001	-	0.017	-0.005	0.002	0.029
FG	0.04	-0.177	-0.099	0.246	-0.024	0.022	-	0.070	0.044	-0.043
UF	0.08	0.235	-0.029	0.019	-0.002	0.005	-0.053	-	-0.084	-0.015
SS	-0.05	0.115	-0.035	0.141	-0.017	-0.004	-0.069	-0.172	-	-0.012
GW	-0.09	0.090	-0.063	-0.061	-0.008	-0.075	0.084	-0.040	-0.015	-
DS2021										
GY	-0.55**	-0.768	-	-0.028	-0.026	0.079	0.129	0.065	-0.020	0.020
PH	0.37*	0.386	0.056	-	-0.016	-0.042	0.039	-0.025	0.001	-0.029
PL	-0.20	-0.117	-0.171	0.053	-	0.043	0.039	-0.063	0.006	0.005
TN	-0.25	0.170	-0.355	-0.094	-0.030	-	0.051	-0.013	-0.002	0.019
FG	0.05	0.331	-0.299	0.046	-0.014	0.026	-	0.011	-0.035	-0.019
UF	-0.19	-0.366	0.135	0.027	-0.020	0.006	-0.010	-	0.039	0.001
SS	0.14	-0.054	-0.281	-0.004	0.013	0.006	0.214	0.262	-	-0.014
GW	-0.03	0.156	-0.096	-0.071	-0.004	0.021	-0.041	-0.003	0.005	-

*, **Significant at the 0.05 and 0.01 probability levels, respectively

LS= lodging score, GY = grain yield, PH = Plant height, PL = Panicle length, TN = Tiller number, FG = Filled grains per panicle, UF = Unfilled grains per panicle, SS = Seed set and GW = Grains weight.

Morphology and Anatomy traits in WS2020

In WS2020, thirty-five F1 lines were identified as having high resistance to lodging, while another fifty-two F1 lines were identified as having intermediate resistance. Therefore, the lodging in WS2020 can be divided into two groups, and the statistical analysis was conducted to compare between the two groups and within the groups shown in (Table 4). The findings revealed no significant differences in morphological and anatomical features between the high and moderate resistance groups. However, some traits were significant within the group, including the top stem. Thus, the morphological and anatomical traits were not assessed again in DS2021.

Table 4 ANOVA means and ranges of morphological and anatomical root traits of F_1 lines under on time harvest in WS2020.

Traits	Lodging	F_1 lines					
		Mean +/- SD	LSD	Min	Max	F-value	P-value
Morphological							
TSD	R	2.83 ± 0.76	0.62	1.11	4.08	2.23	**
	S	2.74 ± 0.68	0.62	1.54	3.67	1.66	ns
BSD	R	5.69 ± 1.48	1.13	3.27	8.22	1.98	**
	S	5.34 ± 1.30	1.35	3.10	7.31	0.71	ns
TST	R	0.12 ± 0.03	0.02	0.07	0.18	3.65	**
	S	0.12 ± 0.02	0.03	0.08	0.17	2.47	*
BST	R	0.26 ± 0.07	0.05	0.13	0.40	2.82	**
	S	0.26 ± 0.04	0.06	0.20	0.35	0.86	ns
Anatomical							
TVBN	R	20.00 ± 3.78	3.51	11.00	31.00	4.36	**
	S	19.50 ± 3.14	3.30	13.00	26.00	3.71	**
BVBN	R	33.00 ± 2.57	0.60	24.00	40.00	3.37	*
	S	32.63 ± 2.31	2.15	28.00	39.00	5.38	**
TVBA	R	0.01 ± 0.00	2.89	0.00	0.02	1.59	**
	S	0.01 ± 0.00	2.58	0.01	0.02	3.73	*
BVBA	R	0.01 ± 0.00	3.57	0.00	0.02	1.50	*
	S	0.01 ± 0.00	2.93	0.01	0.02	1.31	ns
TTA	R	0.04 ± 0.01	1.38	0.00	0.10	1.03	ns
	S	0.03 ± 0.01	0.02	0.01	0.06	1.52	ns
BTA	R	0.04 ± 0.03	0.02	0.00	0.16	1.08	ns
	S	0.04 ± 0.02	0.01	0.01	0.09	0.69	ns
TPT	R	0.21 ± 0.16	0.21	0.11	0.18	0.93	ns
	S	0.19 ± 0.04	0.05	0.11	0.29	1.87	ns
BPT	R	0.44 ± 0.11	0.10	0.04	0.65	1.76	**
	S	0.42 ± 0.10	0.53	0.04	0.60	0.43	ns

R = Lodging resistance, S = Lodging susceptible, TSD = Top stem diameter, BSD = Basal stem diameter, TST = Top stem thickness, BST = Basal stem thickness, TVBN = Top vascular bundle number, BVBN = Basal vascular bundle number, TVBA = Top vascular bundle area, BVBA = Basal vascular bundle area, TTD = Top tissues diameter, BTD = Basal tissues diameter, TTA = Top tissues area, BTA = Basal tissues area, TPT = Top parenchyma tissues and BPT = Basal parenchyma tissues

*, ** and ns = represent significant differences at 0.05, 0.01 levels and no significant difference, respectively

The correlation analysis revealed that lodging was adversely connected with basal stem diameter (r = -0.325). Furthermore, some root morphology and anatomy traits showed strong positive correlations, such as top stem diameter with basal stem diameter (r = 0.695), basal stem thickness with basal parenchyma tissues (r = 0.569), top vascular bundle number with basal vascular bundle number (r = 0.584), top vascular bundle area with basal vascular bundle area (r = 0.852), and top tissue area with basal tissue area (r = 0.586) (Table 5).

Table 5 Correlation analysis among morphology and anatomy traits of F_1 lines in WS2020.

Traits	LS	TSD	BSD	TST	BST	TVBN	BVBN	TVBA	BVBA	TTA	BTA	TPT	BPT
LS	1.000												
TSD	0.054	1.000											
BSD	-0.058	0.695**	1.000										
TST	-0.032	-0.210	0.004	1.000									
BST	-0.089	0.083	0.152	0.453*	1.000								
TVBN	-0.100	-0.005	0.121	0.367*	0.483*	1.000							
BVBN	-0.126	0.107	0.164	0.390*	0.369*	0.584**	1.000						
TVBA	-0.151	0.006	-0.098	0.025	0.048	0.075	0.125	1.000					
BVBA	-0.184	-0.025	-0.051	0.052	0.074	0.132	0.122	0.852**	1.000				
TTA	-0.172	-0.063	-0.116	0.066	0.053	-0.042	0.004	0.210	-0.066	1.000			
BTA	-0.045	-0.098	-0.029	0.053	0.007	0.033	0.107	0.149	-0.063	0.586**	1.000		
TPT	0.182	0.054	0.047	-0.073	0.008	0.034	0.199	-0.032	-0.042	-0.129	-0.136	1.000	
BPT	-0.153	0.120	0.070	0.304*	0.569**	0.326*	0.211	0.064	0.137	-0.150	-0.275	-0.018	1.000

*, **Significant at the 0.05 and 0.01 probability levels, respectively

The path coefficient study of lodging's contribution to stem morphology and anatomical traits revealed that lodging had the greatest direct negative effect on basal stem diameter (-0.592), followed by top tissue area (-0.354), basal parenchyma tissues (-0.248), and basal vascular bundle area (-0.211). Furthermore, lodging had a direct favorable effect on top stem diameter (0.612). Thus, plant lodging is mostly influenced by the structure of the rice plant's basal stem (Table 6).

Table 6 Direct and indirect effects of morphology and anatomy traits on lodging score in WS2020.

Traits	Correlation with LS	Direct effect	Indirect effect											
			TSD	BSD	TST	BST	NTVB	NBVB	TVBA	BVBA	TTA	BTA	TPT	BPT
TSD	0.054	0.612	-	-0.543	-0.001	0.012	0.000	-0.018	0.000	0.005	0.022	-0.015	0.010	-0.030
BSD	-0.325	-0.787	0.422	-	0.000	0.022	0.010	-0.027	-0.003	0.011	0.041	-0.004	0.009	-0.017
TST	-0.031	0.069	-0.013	-0.003	-	0.065	0.029	-0.064	0.001	-0.011	-0.023	0.008	-0.013	-0.075
BST	-0.088	0.144	0.050	-0.120	0.031	-	0.038	-0.061	0.001	-0.016	-0.019	0.001	0.001	-0.141
NTVB	-0.100	0.080	-0.003	-0.095	0.025	0.069	-	-0.096	0.002	-0.028	0.015	0.005	0.006	-0.081
NVBV	-0.126	-0.165	0.066	-0.129	0.027	0.053	0.046	-	0.004	-0.026	-0.001	0.016	0.036	-0.052
TVBA	-0.151	0.029	0.003	0.077	0.002	0.007	0.006	-0.021	-	-0.180	-0.074	0.022	-0.006	-0.016
BVBA	-0.185	-0.211	-0.015	0.040	0.004	0.011	0.010	-0.020	0.025	-	0.023	-0.009	-0.008	-0.034
TTA	-0.172	-0.354	-0.039	0.091	0.005	0.008	-0.003	-0.001	0.006	0.014	-	0.087	-0.023	0.037
BTA	-0.045	0.149	-0.060	0.023	0.004	0.001	0.003	-0.018	0.004	0.013	-0.207	-	-0.025	0.068
TPT	0.182	0.183	0.033	-0.037	-0.005	0.001	0.003	-0.033	-0.001	0.009	0.045	-0.020	-	0.004
BPT	-0.153	-0.248	0.074	-0.055	0.021	0.082	0.026	-0.035	0.002	-0.029	0.053	-0.041	-0.003	-

Discussion

Lodging refers to the stem-breaking type, stem-bending type, or root lodging of the plant and is one of the most concerning problems faced by farmers worldwide (Shah *et al*., 2019). In this study, lodging of the rice plants occurred dominantly near the bottom, which was mainly caused by the breaking or bending of the basal stem. Thus, the stem lodging was investigated in eighty-seven lines of F_1 hybrid rice in the wet season (on time harvested) and the dry season (late harvested).

The results showed that rice planted in the dry season with a late harvest caused severe lodging of the rice plants and a significant drop in grain yield when compared to the wet season with an on-time harvest. According to Jatuporn (1997), the dry season in Thailand has the greatest problems with plant lodging and grain production loss since rice is harvested at the beginning of the wet season, around June and July. This result is consistent with previous research, in which dry-season rice harvesting was delayed until July. Shrestha *et al*. (2020) proposed that plant lodging occurs when the upper part of the plant increases in weight due to rainfall interception during heavy rains or is unable to tolerate strong winds. In addition, De Datta (1981) found that rice plants that are exposed to strong winds after flowering are easily broken. In this study, the frequency of rainfall in the dry season was started from flowering to late harvesting (30 days after maturity stage). Furthermore, the average wind speed in the dry season was higher than in the wet season, with the maximum wind speed occurring during the harvesting period. Therefore, wind and rainfall are important environmental factors that cause lodging of rice plants (Islam *et al*., 2007; Wu *et al*., 2022).

When considering the agronomic factors that are associated with plant lodging, Wang *et al*. (2011) suggested that plant height and panicle weight are the main factors that cause rice plant lodging. In addition, Shah *et al*. (2019) and Wang *et al*. (2022) confirmed that plant height is the most important factor influencing lodging from blooming to harvest-ingstages in rice. These support the result in this study, with plant height positively correlated with lodging, and plant height was the greatest positive direct effect of lodging analyzed by the path coefficient. The mean plant height in this study was 111 and 122 cm, while Wang *et al*. (2022) suggest that lowering plant height from 95.4 to 80.5 cm can reduce plant lodging. The study also found that delayed harvesting in the dry season had a significant effect on plant lodging, and grain yield was very low compared to on-time harvesting. It suggests that although plant height is the major effect on plant l odging, the dried basal culm wall also acts as the weak point. Drying the culm after maturity can increase the severity of plant lodging (Liu *et al*., 2022). Therefore, a reduction in plant height can decrease lodging due to a lower center of gravity and a reduction in the plant's above-ground burden on the lower stem of rice (Okuno *et al*., 2014). In addition, on-time rice harvesting is also an important consideration.

In terms of morphology and anatomy of the culm, plant lodging was negatively correlated with basal stem diameter. This result can be supported by Islam *et al*. (2007) and Zhang et al. (2014), who reported that stem diameter and culm wall thickness are the primary influencing factors for plant lodging. Thus, greater culm diameter is strongly associated with the culm wall thickness, which is an integral element in improving resistance to lodging in rice (Islam *et al*. 2007). Therefore, increasing the rice plant's culm diameter and culm wall thickness tends to improve the breeding program (Kashiwagi *et al*., 2008). Moreover, semi-dwarf plants must be concerned with large culm and culm wall thickness.

However, in this study, top stem diameter was positively influenced by plant lodging. It indicates that the top of the stem has a large culm, resulting in lodging resistance in rice plants. This may indicate that the size of the culm at the top also contributes to plant lodging. However, Li *et al*. (2011) found that plant culm diameter was generally greater at the initial internode but gradually decreased in the upper direction of the plant portion.

Conclusion

The delayed harvest causes a severe problem for plant lodging and decreases grain yield. Plant height exerts a major effect on plant lodging. In addition, stem diameter and culm wall thickness are the primary influencing factors for plant lodging. Thus, the rice breeding program, particularly for hybrid types, must focus on reducing plant height while increasing culm diameter, which is highly related to culm wall thickness and can improve lodging resistance and grain yield in rice.

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Table supplement 1 List of 87 F_1 hybrid lines and crosses.

No.	RGD code	F_1 (Female/Male)	Female source	Male source
1	RGD18015	T6-4 /Surin1	NSTDA[1/]	RD[2/]
2	RGD18018	T6-6 /Improved Sinthulette-SalTol	NSTDA	NSTDA
3	RGD18019	T6-6 /IR42	NSTDA	IRRI[3/]
4	RGD18023	T6-6 /RD31	NSTDA	RD
5	RGD18024	T6-6 /Phisanulok 2	NSTDA	RD
6	RGD18034	T6-6 /RGD15234-47-MS13-MS13	NSTDA	NSTDA
7	RGD18035	T6-6 /RGD15234-47-MS13-MS17	NSTDA	NSTDA
8	RGD18041	T6-4 /IR1188	NSTDA	IRRI
9	RGD18042	T6-4 /IR29	NSTDA	IRRI
10	RGD18043	T6-4 /IR58	NSTDA	IRRI
11	RGD18044	T6-4 /IR64	NSTDA	IRRI
12	RGD18046	T6-4 /Khao Jao Hawm Supanburi	NSTDA	RD
13	RGD18049	T6-4 /Supan Buri3	NSTDA	RD
14	RGD18055	T6-6 /IR49830	NSTDA	IRRI
15	RGD18058	T6-6 /IR72	NSTDA	IRRI
16	RGD18068	T6-4 /MNTK75	NSTDA	NSTDA
17	RGD18073	T6-6 /IWS10	NSTDA	NSTDA
18	RGD181083	18LMP-FS-9 /RD47- improve	LMP[4/]	NSTDA
19	RGD181147	18LMP-FS-12 /IR62266	LMP	IRRI
20	RGD18150	T6-4 /Improved Sinthulette-SalTol	NSTDA	NSTDA
21	RGD18151	T6-4 /IR53936	NSTDA	IRRI
22	RGD18153	T6-6 /IR60	NSTDA	IRRI
23	RGD18158	T6-4 /RGD13297-124-8-2-MS3-MS1	NSTDA	NSTDA
24	RGD18164	T6-6 /IR53936	NSTDA	IRRI
25	RGD18221	T6-4 /RD43	NSTDA	RD
26	RGD18229	T6-4 /Supanburi 60	NSTDA	RD
27	RGD18231	T6-4 /RD49	NSTDA	RD
28	RGD18232	T6-4 /HSC+Bph	NSTDA	NSTDA
29	RGD18235	T6-6 /Pin Kaset 1	NSTDA	KU5/
30	RGD18236	T6-6 /Supanburi 60	NSTDA	RD
31	RGD18237	T6-6 /Supanburi 90	NSTDA	RD
32	RGD18238	T6-6 /RD49	NSTDA	RD
33	RGD18239	T6-6 /HSC+Bph	NSTDA	NSTDA
34	RGD18244	T6-4 /Pin Kaset 1	NSTDA	KU
35	RGD18320	18LMP-FS-2 /Khao Jao Hawm Klongluang 1	LMP	RD
36	RGD18345	18LMP-FS-12 /IWS10	LMP	NSTDA
37	RGD18364	18LMP-FS-2 /Improved Sinthulette-SalTol	LMP	NSTDA
38	RGD18367	18LMP-FS-2 /RD31	LMP	RD
39	RGD18369	18LMP-FS-2 /Supan Buri3	LMP	RD
40	RGD18370	18LMP-FS-2 /Supanburi 90	LMP	RD

Table supplement 1 (continued)

No.	RGD code	F_1 (Female/Male)	Female source	Male source
41	RGD18386	18LMP-FS-8 /Khao Jao Hawm Klongluang 1	LMP	RD
42	RGD18395	18LMP-FS-1 /IR60	LMP	IRRI
43	RGD18405	18LMP-FS-3 /IR62266	LMP	IRRI
44	RGD18416	T6-4 /18LMP-M-7	NSTDA	LMP
45	RGD18417	T6-4 /18LMP-M-8	NSTDA	LMP
46	RGD18418	T6-4 /18LMP-M-9	NSTDA	LMP
47	RGD18419	T6-4 /18LMP-M-10	NSTDA	LMP
48	RGD18423	T6-4 /18LMP-M-14	NSTDA	LMP
49	RGD18429	T6-4 /18LMP-M-24	NSTDA	LMP
50	RGD18434	T6-6 /18LMP-M-4	NSTDA	LMP
51	RGD18436	T6-6 /18LMP-M-6	NSTDA	LMP
52	RGD18437	T6-6 /18LMP-M-7	NSTDA	LMP
53	RGD18439	T6-6 /18LMP-M-9	NSTDA	LMP
54	RGD18450	T6-6 /18LMP-M-24	NSTDA	LMP
55	RGD18460	18LMP-FS-1 /18LMP-M-25	LMP	LMP
56	RGD18463	18LMP-FS-2 /18LMP-M-8	LMP	LMP
57	RGD18464	18LMP-FS-2 /18LMP-M-11	LMP	LMP
58	RGD18484	18LMP-FS-12 /18LMP-M-6	LMP	LMP
59	RGD18505	T6-4 /18LMP-M-4	NSTDA	LMP
60	RGD18511	T6-4 /18LMP-M-30	NSTDA	LMP
61	RGD18514	T6-6 /18LMP-M-20	NSTDA	LMP
62	RGD18515	T6-6 /18LMP-M-21	NSTDA	LMP
63	RGD18517	T6-6 /18LMP-M-29	NSTDA	LMP
64	RGD18518	T6-6 /18LMP-M-30	NSTDA	LMP
65	RGD18534	18LMP-FS-2 /18LMP-M-9	LMP	LMP
66	RGD18536	18LMP-FS-2 /18LMP-M-18	LMP	LMP
67	RGD18544	18LMP-FS-2 /18LMP-M-26	LMP	LMP
68	RGD18546	18LMP-FS-2 /18LMP-M-29	LMP	LMP
69	RGD18555	18LMP-FS-3 /18LMP-M-28	LMP	LMP
70	RGD18598	18LMP-FS-1 /MNTK75	LMP	NSTDA
71	RGD18603	18LMP-FS-2 /MNTK75	LMP	NSTDA
72	RGD18604	18LMP-FS-2 /RD43	LMP	RD
73	RGD18617	18LMP-FS-1 /18LMP-M-26	LMP	LMP
74	RGD18626	18LMP-FS-3 /18LMP-M-11	LMP	LMP
75	RGD18630	18LMP-FS-3 /18LMP-M-19	LMP	LMP
76	RGD18650	18LMP-FS-5 /18LMP-M-26	LMP	LMP
77	RGD18707	18LMP-FS-4 /18LMP-M-25	LMP	LMP
78	RGD18777	18LMP-FS-2 /Supan Buri2	LMP	RD
79	RGD18779	18LMP-FS-3 /Hawm Lahn Nah	LMP	LMP
80	RGD18780	18LMP-FS-3 /IR72	LMP	IRRI

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Table supplement 1 (continued)

No.	RGD code	F_1 (Female/Male)	Female source	Male source
81	RGD18782	18LMP-FS-3 /No.51-PSL	LMP	NSTDA
82	RGD18805	18LMP-FS-5 /RD31	LMP	RD
83	RGD18817	18LMP-FS-5 /Riceberry	LMP	KU
84	RGD18822	18LMP-FS-6 /IR72	LMP	IRRI
85	RGD18870	18LMP-FS-10 /RD31	LMP	RD
86	RGD18887	18LMP-FS-12 /IR58	LMP	IRRI
87	RGD18968	18LMP-FS-2 /Pin Kaset 1	LMP	KU

[1/]NSTDA = The National Science and Technology Development Agency

[2/]RD = Rice Department, Ministry of Agriculture and Cooperatives

[3/]IRRI = International Rice Research Institute

[4/]LMP = Rajamangala University of Technology Lanna

[5/]KU = Kasetsart University