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RESEARCH ARTICLE

Linking grain yield and lodging resistance with growth patterns in rice

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Abstract
Improving grain yield and lodging resistance are two important targets for improving rice production. The aim of this study was to link grain yield and lodging resistance with growth patterns in rice. A nitrogen (N) fertilization experiment was conducted in 2020 and 2021, which consisted of two N rates (150 and 225 kg ha^{-1}) and three N split-application ratios among the basal, early tillering, and panicle initiation stages (6:3:1, 5:3:2, and 4:3:3). The results demonstrated that increasing the N rate from 150 to 225 kg ha^{-1} did not affect grain yield but increased the plant lodging index by 16%. This increase in the plant lodging index was attributable to a higher plant fresh weight resulting from improved post-heading growth and a lower plant lodging load, which was partially due to a higher leaf area index. Altering the N split-application ratio from 6:3:1 to 4:3:3 increased grain yield by 4% but did not affect the plant lodging index in rice. The increase in grain yield was due to improved post-heading growth mainly resulting from increased radiation use efficiency during the post-heading period, which was partially attributable to increased specific leaf weight. An improvement in pre-heading growth in 2021 did not affect grain yield but increased the plant lodging load and decreased the plant lodging index by 36% compared to 2020. The improvement in pre-heading growth was due to a higher intercepted solar radiation resulting from higher leaf area index and incident solar radiation during the pre-heading period. The results of this study indicate that improving pre-heading growth can maintain grain yield and increase lodging resistance, while improving post-heading growth by increasing canopy radiation use efficiency (but not the leaf area index) can increase grain yield and maintain lodging resistance.

Keywords: Growth patterns; Grain yield; Hybrid rice; Lodging resistance

Introduction

Rice is one of the most important food crops in the world and provides more than 20% of daily caloric intake for over 3.5 billion people (Seck *et al.*, 2012). Global rice production increased from 216 million tons in 1961 to 755 million tons in 2019 (FAO, 2021) and must increase to 800 million tons by 2025 to meet the food demands of a growing global population (Swaminathan, 2007). This increase in global rice production depends on higher grain yields since urban expansion will result in a loss of global croplands. This is especially true in Asia (d'Amour *et al.*, 2017), which produces and consumes more than 90% of the world's rice (Bandumula, 2018).

Grain yield is determined by biomass production and translocation and can be expressed as the product of translocation of pre-heading biomass to grains (BTpre) and post-heading biomass production (BPpost) in rice (Yang *et al.*, 2008). However, there have been arguments regarding the

critical factor between BTpre and BPpost responsible for producing higher rice yields. Miah *et al.* (1996) determined the characteristics of biomass production and translocation in high-yielding semidwarf indica and japonica-indica hybrid rice varieties by comparing them with japonica rice varieties. They found that high-yielding semidwarf indica and japonica-indica rice varieties had higher BTpre. Zhai *et al.* (2002) and Huang *et al.* (2015a) compared biomass production and grain yield between super and ordinary hybrid rice varieties and found that super hybrid rice varieties produced higher grain yields due to higher BPpost. In addition, it has been well documented that the effects of BTpre and BTpost on rice grain yield vary with the growth environment and management practices (Huang *et al.*, 2019; 2021; Yin *et al.*, 2020).

Biomass production and translocation can influence other plant traits in addition to grain yield, including lodging resistance, which has been received significant attention because lodging constrains current rice production by causing grain yield and quality losses, difficulties during mechanical harvest, and increases in production cost (Zhu *et al.*, 2016). In particular, a high BTpre may result in a low storage of pre-heading biomass in straw (BSpre) and consequently decrease straw stiffness and plant lodging resistance (Huang *et al.*, 2015b).

Biomass production and translocation are interrelated and closely associated with growth patterns in rice. Increasing BPpost (or improving post-heading growth) can decrease BTpre, while improving pre-heading growth can increase BTpre (Huang *et al.*, 2019; 2021). Therefore, we hypothesized that grain yield and lodging resistance in rice could be regulated by altering its growth patterns. While this hypothesis would be useful for developing targeted strategies for increasing grain yield and/or lodging resistance in rice, little information is available to test this hypothesis.

N fertilization is a common management practice that can alter crop growth patterns, grain yield, and lodging resistance in rice (Ibrahim *et al.*, 2013; Zhang *et al.*, 2014). In rice production, N application is generally required to improve crop growth and reach high grain yield because N is the most limited nutrient for rice growth in almost all environments (Chen and Wang 2014); however, overuse of N fertilizers and improper N split-application ratios may cause plant lodging (Pan *et al.*, 2019; Peng *et al.*, 2009). This study conducted an N fertilization experiment over 2 years to establish different crop variables and test the hypothesis presented above by linking grain yield and lodging resistance with growth patterns in rice.

Materials and Methods

Experimental details

A field experiment was performed from 2020 to 2021 in the town of Yongan (28°09′ N, 113°37′ E, 43 m asl), located in Hunan Province, China. The climate of the experimental field was moist subtropical monsoon and had 15.6 and 17.5 MJ m^{-2} of daily solar radiation and daily mean temperatures of 28.2 and 28.9°C in 2020 and 2021, respectively (Figure 1A and B). The experimental field had a clay soil texture and these chemical characteristics at a soil depth of 0–20 cm: water extraction pH = 6.20, KMnO$_4$-oxidizable organic matter = 33.3 g kg^{-1}, NaOH-hydrolyzable N = 179 mg kg^{-1}, NaHCO$_3$-extractable phosphorus (P) = 23.8 mg kg^{-1}, and NH$_4$OAc-extractable potassium (K) = 113 mg kg^{-1}.

In each year, Guiliangyou 2, a high-yielding hybrid rice variety, was grown under six N treatments: a factorial combination of two N rates and three N split-application ratios among the basal (1 day before transplanting), early tillering (7 days after transplanting), and panicle initiation stages. The N rates were moderate (150 kg N ha^{-1}, N150) and high N (225 kg N ha^{-1}, N225). The three N split-application ratios were 6:3:1 (R631), 5:3:2 (R532), and 4:3:3 (R433).

The N treatments in factorial combinations were arranged in a randomized complete block design with three replications. The plot size for each N treatment was 35 m^2. Pre-germinated seeds were sown in a seedbed on 5 May 2020 and 7 June 2021 to raise seedlings. Twenty-day-old
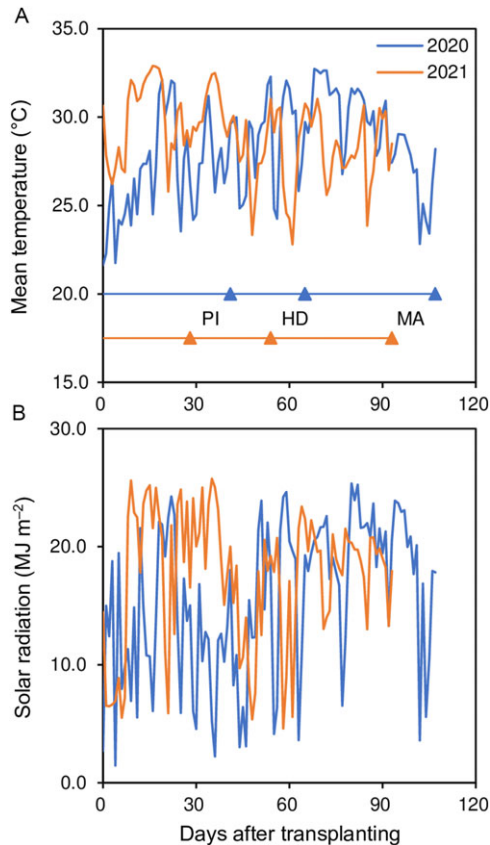
Figure 1. Daily mean temperature (A) and solar radiation (B) during the rice-growing season in 2020 and 2021. Data were obtained using an on-site automatic weather station (Vantage Pro2, Davis Instruments Corp., Hayward, CA, USA). In (A), horizontal lines show the growth process, and triangles represent the panicle initiation (PI), heading (HD), and maturity (MA) stages, respectively.

seedlings were transplanted at a hill spacing of 20 cm × 20 cm, with two seedlings in each hill. P and K fertilizers were applied at rates of 75 kg P_2O_5 ha^{-1} and 150 kg K_2O ha^{-1}, respectively. All the P fertilizers were applied at the basal stage, while half of the K fertilizer was applied at the basal stage and half at the panicle initiation stage. A floodwater depth of 5–10 cm was kept from transplanting until 7 days prior to maturity, at which point the plots were drained in preparation for harvesting. Agrochemicals were used to control pathogens, insects, and weeds.

Sampling and measurements

A SunScan canopy analysis system (Delta-T Devices Ltd., Burwell, Cambridge, UK) was used to measure the percentage of solar radiation intercepted by the canopy at the panicle initiation, heading, and maturity stages. The intercepted solar radiation from transplanting to panicle initiation, from panicle initiation to heading, and from heading to maturity was calculated according to the method of Huang *et al.* (2016a).

Ten plants were sampled at the panicle initiation, heading, and maturity stages from each plot. At the panicle initiation stage, the plants were separated into leaves and stems, while at the heading stage the plants were separated into leaves, stems, and panicles. A leaf area meter (LI-3000C, Li-Cor, Lincoln, NE, USA) was used to measure the leaf area, and the leaf area index was

calculated by dividing the leaf area by the plant coverage area. All plant organs were dried in the oven at 70°C to a constant weight to obtain the biomass. Specific leaf weight was calculated by dividing leaf weight by leaf area. The panicle number of plants sampled at the maturity stage was counted, after which they were hand-threshed to determine spikelets per panicle, spikelet filling percentage, and grain weight. Filled and unfilled grains were separated by submerging them in tap water. Three subsamples of 30 g of filled spikelets and all unfilled spikelets were taken to count the number of spikelets. The filled and unfilled spikelets and straw were dried to a constant weight in a 70°C oven to determine their biomass.

BPpost, BTpre, BSpre, and crop growth rate and radiation use efficiency from transplanting to panicle initiation, from panicle initiation to heading, and from heading to maturity were calculated using the following formulae:

BPpost = biomass accumulation at maturity − biomass accumulation at heading

BTpre = dry weight of filled spikelets − BPpost

BSpre = biomass accumulation at heading − BTpre

Crop growth rate = biomass accumulation during a given growth period/duration of the corresponding growth period

Radiation use efficiency = biomass accumulation during a given growth period/intercepted solar radiation during the corresponding growth period

Eight plants were chosen 25 days after the heading stage from each plot (except for the outside rows) to determine the plant height, aboveground fresh weight, and plant lodging load (i.e., the lateral force needed to bend the whole plant from 90° to 45°). The plant lodging load was measured by a prostrate tester (DIK-7401, Daiki Rika Kogyo Co. Ltd., Tokyo, Japan) according to the method of Kashiwagi and Ishimaru (2004). The plant lodging index was calculated using the equation of Tao *et al.* (2022).

The rice grains were harvested at maturity from a 5-m^2 area in each plot and dried in the sun for 3 days. A subsample of 50 g of sundried grains was oven-dried at 70 °C to a constant weight to determine moisture content of the sundried grain. Grain yield was calculated by adjusting the grain moisture content to 14% according to the following formula:

Grain yield = sundried grain weight × (1 − moisture content of the sundried grain)/
(1 − 14%)

Statistical analysis
Statistix 8.0 (Analytical Software, Tallahassee, FL, USA) was used to perform an analysis of variance (ANOVA) on the data. The ANOVA statistical model included replication, N rate, N split-application ratio, year, and two- and three-way interactions of N rate, N split-application ratio, and year. The significance level was set at the 0.05 probability level. The means of three N split-application ratios were compared using a least significant difference test at the 0.05 probability level when the main effect of the N split-application ratio was significant.

Results
Grain yield and yield components
The difference in grain yield was not significant between N150 and N225 (Table 1). The panicle number per m^2 was 11% higher under N225 than under N150. There was no significant difference

Table 1. Grain yield and yield components in rice grown under two N rates and three split-application ratios in 2 years

Variable	Grain yield (t ha^{-1})	Panicles m^{-2}	Spikelets panicle^{-1}	Spikelet filling (%)	Grain weight (mg)
N rate (N)[a]					
N150	9.05 a	255 b	184 a	84.4 a	25.4 a
N225	9.26 a	282 a	182 a	84.0 a	25.1 b
N split-application ratio (R)[b]					
R631	8.91 b	265 a	178 b	84.3 a	25.2 a
R532	9.31 a	260 a	189 a	84.9 a	25.2 a
R433	9.25 a	280 a	183 ab	83.4 a	25.4 a
Year (Y)					
2020	9.23 a	261 a	171 b	86.8 a	26.2 a
2021	9.09 a	275 a	196 a	81.6 b	24.4 b
Interaction					
N × R	ns	ns	ns	ns	ns
N × Y	ns	ns	ns	ns	ns
R × Y	ns	ns	ns	ns	ns
N × R × Y	ns	ns	ns	ns	ns

Data sharing the same letters within a column for each variable are not significantly different at the 0.05 probability level.
ns denotes non-significance at the 0.05 probability level.
[a]N150 and N225 are 150 and 225 kg N ha^{-1}, respectively.
[b]R631, R532, and R433 are N split-applications among the basal (1 day before transplanting), early tillering (7 days after transplanting), and panicle initiation stages at ratios of 6:3:1, 5:3:2, and 4:3:3, respectively.

in either the number of spikelets per panicle or the spikelet filling percentage between N150 and N225. Grain weight under N225 was slightly (1%) lower than that under N150.

Grain yield was approximately 4% higher under R532 and R433 than under R631, and the difference in grain yield was not significant between R532 and R433 (Table 1). There was no significant difference in panicle number per m^2 among R631, R532, and R433. Spikelet number per panicle was 6% higher under R532 than under R631, while the difference in spikelet number per panicle was not significant between either R631 and R433 or R532 and R433. Spikelet filling percentage and grain weight did not significantly differ among R631, R532, and R433.

There was no significant difference in grain yield between 2020 and 2021 (Table 1). Panicle number per m^2 did not significantly differ between 2020 and 2021. Spikelet number per m^2 was 15% higher in 2021 than in 2020. Spikelet filling percentage and grain weight were lower in 2021 than in 2020 by approximately 5 and 6%, respectively.

Lodging resistance traits

N225 had a 16% higher plant lodging index than N150, though the difference in plant height was not significant between N225 and N150 (Table 2). Plant fresh weight under N225 was 10% higher than under N150. Plant lodging load was 5% lower under N225 than under N150.

There was no significant difference in plant lodging index among R631, R532, and R433 (Table 2). Plant height was not significantly different between R631 and R532 and was slightly (2%) higher under R433 than under R631 and R532. There were no significant differences in plant fresh weight and lodging load among R631, R532, and R433.

The plant lodging index was 36% lower in 2021 than in 2020 (Table 2). Plant height, fresh weight, and lodging load were higher in 2021 than in 2020 by 2, 18, and 90%, respectively.

Biomass production and translocation

There were no significant differences in biomass accumulation at the panicle initiation and heading stages between N150 and N225, while biomass accumulation at the maturity stage was 8%

Table 2. Plant lodging index and related traits in rice grown under two N rates and three N split-application ratios in 2 years

Variable	Plant lodging index	Plant height (cm)	Plant fresh weight (g plant^{-1})	Plant lodging load (g)
N rate (N)[a]				
N150	1.94 b	123 a	204 b	647 a
N225	2.25 a	124 a	224 a	616 b
N split-application ratio (R)[b]				
R631	2.02 a	123 b	210 a	638 a
R532	2.14 a	123 b	215 a	617 a
R433	2.13 a	125 a	217 a	638 a
Year (Y)				
2020	2.75 a	122 b	196 b	435 b
2021	1.75 b	125 a	232 a	828 a
Interaction				
N × R	ns	ns	ns	ns
N × Y	ns	ns	*	ns
R × Y	ns	ns	ns	ns
N × R × Y	ns	ns	ns	ns

Data sharing the same letters within a column for each variable are not significantly different at the 0.05 probability level.
ns and * denote non-significance and significance at the 0.05 probability level, respectively.
[a]N150 and N225 are 150 and 225 kg N ha^{-1}, respectively.
[b]R631, R532, and R433 are N split-applications among the basal (1 day before transplanting), early tillering (7 days after transplanting), and panicle initiation stages at ratios of 6:3:1, 5:3:2, and 4:3:3, respectively.

higher under N225 than under N150 (Table 3). N225 had 18% higher BPpost but 21% lower BTpre than N150. The difference in BSpre was not significant between N150 and N225.

The difference in biomass accumulation among R631, R532, and R433 was not significant at either the panicle initiation stage or the heading stage (Table 3). At the maturity stage, biomass accumulation was not significantly different between R532 and R631 or between R433 and R631, though it was 8% higher under R433 than under R631. Compared to R631 and R532, R433 had 18–21% higher BPpost but 31–38% lower BTpre. There was no significant difference in BPpost and BTpre between R631 and R532, and there was no significant difference in BSpre among R631, R532, and R433.

Biomass accumulation was higher in 2021 than in 2020 by 29, 39, and 12% at the panicle initiation, heading, and maturity stages, respectively (Table 3). BPpost was 16% lower in 2021 than in 2020, while BTpre was 158% higher in 2021 than in 2020. BSpre was 20% higher in 2021 than in 2020.

Growth patterns

The crop growth rate was not significantly different between N150 and N225 from transplanting to panicle initiation and from panicle initiation to heading, while it was 18% higher under N225 than under N150 from heading to maturity (Table 4). Intercepted solar radiation was 6, 4, and 3% higher under N225 than under N150 from transplanting to panicle initiation, from panicle initiation to heading, and from panicle initiation to maturity, respectively. The difference in radiation use efficiency was not significant between N150 and N225 from transplanting to panicle initiation and from panicle initiation to heading, while from heading to maturity N225 had 15% higher radiation use efficiency than N150. The leaf area index was 7 and 10% higher under N225 than under N150 at the panicle initiation and heading stages, respectively. There was no significant difference in specific leaf weight between N150 and N225 at either the panicle initiation or the heading stage.

There were no significant differences in crop growth rate, intercepted solar radiation, and radiation use efficiency among R631, R532, and R433 from transplanting to panicle initiation and

Table 3. Biomass accumulation, post-heading biomass production (BPpost), translocation of pre-heading biomass to grains (BTpre), and pre-heading biomass storage in straw (BSpre) in rice grown under two N rates and three split-application ratios in 2 years

| Variable | Biomass accumulation (g m^{-2})[c] | | | BPpost (g m^{-2}) | BTpre (g m^{-2}) | BSpre (g m^{-2}) |
	PI	HD	MA			
N rate (N)[a]						
N150	343 a	970 a	1608 b	638 b	222 a	748 a
N225	354 a	984 a	1737 a	753 a	175 b	809 a
N split-application ratio (R)[b]						
R631	352 a	972 a	1614 b	642 b	212 a	760 a
R532	349 a	1000 a	1663 ab	663 b	237 a	763 a
R433	345 a	959 a	1739 a	780 a	147 b	812 a
Year (Y)						
2020	305 b	819 b	1575 b	756 a	110 b	709 b
2021	392 a	1135 a	1769 a	634 b	284 a	851 a
Interaction						
N × R	ns	ns	ns	ns	ns	ns
N × Y	ns	ns	ns	ns	*	ns
R × Y	ns	ns	ns	ns	ns	ns
N × R × Y	ns	ns	ns	ns	ns	ns

Data sharing the same letters within a column for each variable are not significantly different at the 0.05 probability level.

ns and * denote non-significance and significance at the 0.05 probability level, respectively.

[a]N150 and N225 are 150 and 225 kg N ha^{-1}, respectively.

[b]R631, R532, and R433 are N split-applications among the basal (1 day before transplanting), early tillering (7 days after transplanting), and panicle initiation stages at ratios of 6:3:1, 5:3:2, and 4:3:3, respectively.

[c]PI, HD, and MA represent the panicle initiation, heading, and maturity stages, respectively.

Table 4. Crop growth rate, intercepted solar radiation, radiation use efficiency, leaf area index, and specific leaf weight in rice grown under two N rates and three split-application ratios in 2 years

| Variable | Crop growth rate (g m^{-2} d^{-1})[c] | | | Intercepted solar radiation (MJ m^{-2}) | | | Radiation use efficiency (g MJ^{-1}) | | | Leaf area index | | Specific leaf weight (mg cm^{-2}) | |
	TP–PI	PI–HD	HD–MA	TP–PI	PI–HD	HD–MA	TP–PI	PI–HD	HD–MA	PI	HD	PI	HD
N rate (N)[a]													
N150	10.5 a	24.9 a	15.7 b	308 b	349 b	691 b	1.11 a	1.80 a	0.92 b	4.14 b	7.07 b	36.7 a	35.8 a
N225	10.9 a	25.1 a	18.6 a	327 a	364 a	709 a	1.08 a	1.73 a	1.06 a	4.44 a	7.79 a	36.7 a	35.3 a
N split-application ratio (R)[b]													
R631	10.9 a	24.7 a	15.8 b	316 a	353 a	691 b	1.11 a	1.76 a	0.93 b	4.43 a	7.22 a	36.0 a	34.8 b
R532	10.7 a	25.9 a	16.3 b	318 a	358 a	704 b	1.10 a	1.82 a	0.94 b	4.25 a	7.74 a	36.8 a	35.6 ab
R433	10.6 a	24.4 a	19.2 a	319 a	359 a	705 a	1.08 a	1.71 a	1.11 a	4.19 a	7.32 a	37.4 a	36.2 a
Year (Y)													
2020	7.4 b	21.4 b	18.0 a	217 b	295 b	728 a	1.41 a	1.74 a	1.04 a	4.09 b	6.80 b	34.8 b	34.5 b
2021	14.0 a	28.6 a	16.3 a	418 a	418 a	671 b	0.94 b	1.78 a	0.94 a	4.49 a	8.06 a	38.6 a	36.6 a
Interaction													
N × R	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
N × Y	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
R × Y	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
N × R × Y	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Data sharing the same letters within a column for each variable are not significantly different at the 0.05 probability level.

ns and * denote non-significance and significance at the 0.05 probability level, respectively.

[a]N150 and N225 are 150 and 225 kg N ha^{-1}, respectively.

[b]R631, R532, and R433 are N split-applications among the basal (1 day before transplanting), early tillering (7 days after transplanting), and panicle initiation at ratios of 6:3:1, 5:3:2, and 4:3:3, respectively.

[c]TP–PI, PI–HD, and HD–MA are the growth periods from transplanting to panicle initiation, from panicle initiation to heading, and from heading to maturity, respectively.

from panicle initiation to heading (Table 4). Crop growth rate and radiation use efficiency from heading to maturity were not significantly different between R631 and R532, though they were higher under R433 than R631 and R532 by 18–22%. R532 and R433 had almost the same intercepted solar radiation from heading to maturity, which was slightly (2%) higher than under R631. There was no significant difference in the leaf area index among R631, R532, and R433 at the panicle initiation and heading stages. The difference in specific leaf weight was not significant among R631, R532, and R433 at the panicle initiation stage. At the heading stage, specific leaf weight was not significantly different between R532 and R631 and between R433 and R532, while it was 4% higher under R433 than under R631.

The crop growth rate was 89 and 34% higher in 2021 than in 2020 from transplanting to panicle initiation and from panicle initiation to heading, respectively, while the difference was not significant from heading to maturity (Table 4). Intercepted solar radiation was 93 and 42% higher in 2021 than in 2020 from transplanting to panicle initiation and from panicle initiation to heading, respectively, while it was 8% lower in 2021 than in 2020 from heading to maturity. Radiation use efficiency was 33% lower in 2021 than in 2020 from transplanting to panicle initiation, while the difference was not significant from panicle initiation to heading and from heading to maturity. The leaf area index was 10 and 19% higher in 2021 than in 2020 at the panicle initiation and heading stages, respectively. Specific leaf weight was higher in 2021 than in 2020 by 11 and 6% at the panicle initiation and heading stages, respectively.

Discussion

Increasing the N rate from 150 kg N ha^{-1} (moderate) to 225 kg N ha^{-1} (high) did not significantly affect grain yield in rice. This aligns with the results of previous studies assessing the same or different high-yielding rice varieties (Huang *et al.*, 2016a; 2016b; Zhang *et al.*, 2009). This suggests that high-yielding rice varieties do not necessarily need more N fertilizer to produce high grain yields.

The increased N rate significantly decreased plant lodging resistance (i.e., increase in lodging index) in rice. In this regard, it has been reported that increased N rates can weaken stem strength and lower lodging resistance in rice by altering stem morphological and anatomical traits (Zhang *et al.*, 2016). Consistently, in this study, the increased N rate significantly reduced the plant lodging load. Moreover, the decreased lodging resistance associated with an increased N rate in this study could be also due to an increase in plant fresh weight, which was primarily due to an increase in BPpost. This increase in BPpost can be explained by a higher post-heading crop growth rate due to higher leaf area index, intercepted solar radiation, and radiation use efficiency. These suggest that improving post-heading growth by increasing the N rate can decrease lodging resistance.

However, this study found that delayed N application (i.e., altering the N split-application ratio among the basal, early tillering, and panicle initiation stages from 6:3:1 to 4:3:3) improved post-heading growth mainly by increasing radiation use efficiency during the post-heading period but did not significantly decrease plant lodging resistance in rice. The increased radiation use efficiency during the post-heading period by delaying N application was partially attributable to increased specific leaf weight. In this regard, it has been documented that leaf photosynthetic rate is positively related to specific leaf weight (Liu and Li, 2016), and improving leaf photosynthetic performance can increase radiation use efficiency (Huang *et al.*, 2016a). The different effects of increased N rate and delayed N application on plant lodging resistance in rice could be because (1) the leaf area index increased by increasing the N rate but not by delaying N application, and (2) the increase in leaf area index may result in a decrease in plant lodging load by decreasing stem stiffness through reducing biomass allocation to stems and/or by elongating basal internodes through altering canopy light transmission (Duy *et al.*, 2004; Zhong *et al.*, 2020). This indicates that improving post-heading growth by increasing canopy radiation use efficiency (but not leaf area

index) does not decrease lodging resistance in rice. In addition, in this study, the improvement in post-heading growth due to delayed N application increased grain yield. This result is in agreement with the results of Zhai *et al.* (2002) and Huang *et al.* (2015a). Altogether, improving post-heading growth by increasing canopy radiation use efficiency (but not leaf area index) can increase grain yield and maintain lodging resistance in rice.

This study also demonstrated that lodging resistance was significantly higher in 2021 than in 2020. The higher lodging resistance in 2021 compared to 2020 was primarily due to the higher plant lodging load resulting from higher BSpre. BSpre can be increased by improving pre-heading growth and/or by decreasing BTpre. In this study, the higher BSpre in 2021 was due to improved pre-heading growth resulting from a higher leaf area index and intercepted solar radiation during the pre-heading period. The higher leaf area index in 2021 can be explained by a higher temperature during the pre-heading period (Figure 1A), while the higher intercepted solar radiation in 2021 was due to higher incident solar radiation and higher leaf area index (Figure 1B and Table 4). The higher temperature and incident solar radiation in 2021 than in 2020 were mainly attributable to delayed sowing. Moreover, this study showed that the improved pre-heading growth did not increase grain yield in 2021 compared to 2020, because it was compensated for by a decrease in post-heading growth. This is consistent with the results of Huang et al. (2019; 2021). Altogether, improving pre-heading growth can maintain grain yield and increase lodging resistance in rice.

The findings of this study have implications for the proper management of rice varieties with high or low lodging resistance. It is suggested to choose the management practices for improving pre-heading growth (e.g., delayed sowing in 2021 in this study) for rice varieties with low lodging resistance to increase lodging resistance while maintaining grain yields and to choose the management practices for improving post-heading growth (e.g., delayed N application by altering the N split-application ratio among the basal, early tillering, and panicle initiation stages from 6:3:1 to 4:3:3 in this study) for rice varieties with high lodging resistance to increase grain yields while maintaining lodging resistance. However, further investigations with more rice varieties are warranted to test this suggestion.

Conclusions

This study links grain yield and lodging resistance with growth patterns in a high-yielding hybrid rice variety Guiliangyou 2 and demonstrates that improving pre-heading growth can maintain grain yield and increase lodging resistance, while improving post-heading growth by increasing canopy radiation use efficiency (but not the leaf area index) can increase grain yield and maintain lodging resistance.

Conflicts of Interest. The authors declare none.

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