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Basal internode elongation of rice as affected by light intensity and leaf area

Xuhua Zhong[*], *Kaiming Liang, Bilin Peng, Ka Tian, Xiaojuan Li, Nongrong Huang, Yanzhuo Liu, Junfeng Pan*

Rice Research Institute of Guangdong Academy of Agricultural Sciences, Guangzhou 510640, Guangdong, China
Guangdong Key Laboratory of New Technology for Rice Breeding, Guangzhou 510640, Guangdong, China

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ABSTRACT

Short basal internodes are important for lodging resistance of rice (*Oryza sativa* L.). Several canopy indices affect the elongation of basal internodes, but uncertainty as to the key factors determining elongation of basal internodes persists. The objectives of this study were (1) to identify key factors affecting the elongation of basal internodes and (2) to establish a quantitative relationship between basal internode length and canopy indices. An inbred rice cultivar, Yinjingruanzhan, was grown in two split-plot field experiments with three N rates (0, 75, and 150 kg N ha^{-1} in early season and 0, 90, and 180 kg N ha^{-1} in late season) as main plots, three seedling densities (16.7, 75.0, and 187.5 seedlings m^{-2}) as subplots, and three replications in the 2015 early and late seasons in Guangzhou, China. Light intensity at base of canopy (L_b), light quality as determined from red/far-red light ratio (R/FR), light transmission ratio (LTR), leaf area index (LAI), leaf N concentration (NLV) and final length of second internode (counted from soil surface upward) (FIL) were recorded. Higher N rate and seedling density resulted in significantly longer FIL. FIL was negatively correlated with L_b, LTR, and R/FR ($P < 0.01$) and positively correlated with LAI ($P < 0.01$), but not correlated with NLV ($P > 0.05$). Stepwise linear regression analysis showed that FIL was strongly associated with L_b and LAI ($R^2 = 0.82$). Heavy N application to pot-grown rice at the beginning of first internode elongation did not change FIL. We conclude that FIL is determined mainly by L_b and LAI at jointing stage. NLV has no direct effect on the elongation of basal internodes. N application indirectly affects FIL by changing LAI and light conditions in the rice canopy. Reducing LAI and improving canopy light transmission at jointing stage can shorten the basal internodes and increase the lodging resistance of rice.

Abbreviations: FIL, final length of second internode; LAI, leaf area index; L_b, light intensity at base of canopy; L_0, natural light intensity; LTR, light transmission ratio; NLV, leaf N concentration; R/FR, light quality determined from red/far red light ratio

[*] *Corresponding author at: Rice Research Institute of Guangdong Academy of Agricultural Sciences, Guangzhou 510640, Guangdong, China.*
E-mail address: xzhong8@163.com. (X. Zhong).

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1. Introduction

Lodging is a major problem in rice production, especially in coastal areas where typhoons occur. Lodging can reduce yield by 20%–30% and even as much as 80% [1]. Lodging also reduces grain quality and mechanical harvesting efficiency [2,3]. The length of basal internodes is a plant morphological trait affecting the lodging resistance of crops [4–8]. Overuse of N fertilizer and high seedling density result in excessive elongation of basal internodes. Crop management techniques can be used to control internode length and reduce lodging [9].

Rice plants generally have 4–7 elongated internodes [6]. Among them, the two or three basal internodes, especially the second (counted from the soil surface upwards), have the greatest influence on lodging resistance. Plants with shorter basal internodes have stronger lodging resistance. In a study [10] using recombinant inbred rice lines, the length of the first and second basal internodes was significantly correlated with lodging resistance. Similar results were found with F_2 [11] and backcross [12] populations. Yang et al. [13] reported that the length of basal internodes of a hybrid rice (Jinyou 527) increased with N rate and seedling density and that lodging resistance was significantly correlated with internode length. Similar results were observed in winter wheat [14]. In addition to internode length, other stem characteristics such as stem diameter, culm wall thickness and internode plumpness also have marked effects on lodging resistance [11,15].

The internode elongation process and the final internode length are determined by a combination of factors. Light intensity, light quality, N fertilization, water, and endogenous hormones can influence internode elongation. However, uncertainty as to the key factors determining internode elongation remains, and a quantitative relationship between the elongation of basal internodes and canopy indices has not been established. Gao et al. [4] reported that lodging usually occurred in a rice canopy with light transmission ratio lower than 10%. Shading during the jointing stage promoted elongation of basal internodes. Internode length was 36% greater under shading than in full light [5]. In addition to light intensity, light quality in the basal part of the canopy is changed under shaded conditions. Morgan and Smith [16] reported that shading reduced the red/far red light ratio (R/FR) and consequently promoted internode elongation. Guo et al. [17] found that increasing red light intensity reduced rice plant height and increased stem diameter, in turn increasing lodging resistance. The reduction of red light under cloudy conditions can promote internode elongation and result in a thinner stem [18].

Seedling density strongly influences internode elongation. It was reported that rice internode length increased with seedling density, ultimately reducing lodging resistance [5]. Leaf area index (LAI) was found to be closely associated with the length of basal internodes. Kamiji et al. [19] reported that the total length of basal internodes of rice increased with LAI at 30 days before heading. Kahlen and Stutzel [20] used LAI as one of two independent variables in predicting the final internode length of greenhouse-grown cucumber.

N fertilization also exerts a strong effect on internode elongation. Yan and Hu [21] found significantly increased length of the first and second basal internodes with increasing N application rate in all tested rice varieties. Similar results were found in hybrid rice [13] and diverse wheat varieties [14]. However, there are conflicting explanations for the manner in which N fertilization affects internode elongation. Some researchers have claimed that N application increases internode elongation by directly increasing plant N concentration. Chang et al. [22] used the term “N factor” to describe the effect of rice plant N concentration on internode elongation. As stem N concentration increased, the internodes became longer. Similar results were reported in wheat [23], castor bean [24], and soybean [25]. Other researchers, however, found that plant N concentration is not a direct cause of internode elongation. Kamiji et al. [19] found that rice plants receiving topdressed N at internode elongation stage had even shorter basal internodes when LAI was low. They postulated that the primary factor in the variation in lengths of basal internodes is light intensity in the lower part of the canopy. Duy et al. [26] found that sparse planting density and low N input at early growth stage resulted in short basal internodes and increased lodging resistance in consequence of reduced LAI and greater light transmission at jointing stage. Whether plant N concentration has a direct effect on the elongation of basal internodes remains unclear.

The present study aimed (1) to identify the key factors influencing the elongation of basal internodes, with special attention paid to leaf N concentration, and (2) to establish a quantitative relationship between basal internode length and canopy indices. The second basal internode was chosen in this study as the internode most closely associated with lodging resistance.

2. Materials and methods

2.1. Field experiment

2.1.1. Experiment design

Two field experiments were conducted during the early and late seasons of 2015 at Dafeng Experimental Station of Guangdong Academy of Agricultural Sciences (23°17′N, 113°23′E), Guangzhou, Guangdong province, China. The paddy soil of the experimental field is a lateritic red soil with pH of 5.9, 13.0 g kg^{-1} organic matter, 1.42 g kg^{-1} total N, 29 mg kg^{-1} bicarbonate-extractable P, and 174 mg kg^{-1} exchangeable K. The rice variety used was Yinjinruanzhan, an *indica* inbred with five elongated internodes. The experiment was laid out in a split-plot design with three N rates as the main plot and three seedling densities as subplots, with three replicates (Table 1).

Seeds were sown in a seedbed on March 5 in early season and July 18 in late season. Seedlings were transplanted on April 6 in early season and August 6 in late season. Heading began on June 11 in early season and September 25–29 in late season. For all treatments, N in the form of urea was applied with 40% as basal, 20% at mid-tillering (MT), 30% at panicle initiation (PI), and 10% at heading (HD). Phosphorus (as calcium superphosphate) was applied as basal at 45 kg P_2O_5 ha^{-1} for early season and 27 kg P_2O_5 ha^{-1} for late season. In both seasons, potassium (potassium chloride) was applied at

Table 1 – Treatment design of the field experiments conducted in the 2015 early and late seasons at Guangzhou, Guangdong province, China.

Treatment	N rate (kg N ha^{-1})		Hill density (cm)	Seedlings per hill	Seedlings m^{-2}
	Early season	Late season			
T1	0	0	30 × 20	1	16.7
T2	0	0	20 × 20	3	75.0
T3	0	0	13.3 × 20	5	187.5
T4	75	90	30 × 20	1	16.7
T5	75	90	20 × 20	3	75.0
T6	75	90	13.3 × 20	5	187.5
T7	150	180	30 × 20	1	16.7
T8	150	180	20 × 20	3	75.0
T9	150	180	13.3 × 20	5	187.5

135 kg K_2O ha^{-1} with 50% as basal and 50% at PI. Shallow floodwater was held in the field until 7 days before harvest. Pests, diseases, and weeds were well controlled to avoid yield loss.

2.1.2. Sampling and measurement

Leaf age was recorded every 3–4 days until 7 days before expected jointing stage and thereafter each day during internode elongation stage. The starting and ending dates for each internode elongation were determined by the leaf age according to the synchronous relationship between internode elongation and leaf age [6]. Light intensity (L_b) in each subplot was recorded every 10 min using HOBO UA-002-08 dataloggers (Onset Computer Corporation, Bourne, MA, USA) located at 10 cm height in the center of four hills. The daily mean L_b was calculated using the data between 6:30–18:30. The mean L_b for each treatment was calculated as the mean during the days of the internode elongation period. Photosynthetically active radiation (PAR) above and below the canopy was measured at six sampling points in each subplot using an AccuPAR LP-80 PAR/LAI Ceptometer (Decagon Devices, Inc., Pullman, WA, USA) and light transmission ratio (LTR) was calculated. In each subplot, 12 hills were sampled and green leaf area was measured using a LI-3100c leaf area meter (Licor, Inc., Lincoln, NE, USA) and the leaf area index (LAI) calculated. The leaf samples were oven-dried at 80 °C to constant weight, and leaf N concentration (NLV) was determined by micro-Kjeldahl digestion, distillation, and titration [27]. The length of the second basal internode (FIL) was measured at 15 days after heading. A total of 15 stems from five hills (three stems from each hill) were randomly selected for measurement in each subplot. In the early season, the red/far red ratio (R/FR) at a height of 10 cm above soil surface was recorded at 9:00, 12:00, and 15:00 using a Skye SKR116 sensor (Skye Instruments Ltd., Llandrindod Wells, Powys, UK). The mean R/FR was calculated as the mean of the five sampling points in each subplot.

The starting and ending dates of internode elongation were slightly different among treatments, and the sampling day was not necessarily consistent with the start and end of internode elongation. LTR, R/FR, LAI and NLV were accordingly measured weekly starting before and ending after the second internode elongation. Daily LTR, R/FR, LAI, and NLV were obtained by interpolation from measured values [28,29].

2.2. Pot experiment

To evaluate the effect of NLV on basal internode elongation, a pot experiment was conducted in the greenhouse during late season of 2014 at the Rice Research Institute of Guangdong Academy of Agricultural Sciences, Guangzhou. Seeds of rice cv. Yinjinruanzhan were sown in seedling trays on July 20. Sixteen-day-old seedlings were transplanted to PVC pots with 1 seedling per pot. The pots were 22 cm tall, 12 cm in diameter, and filled with 1.9 kg paddy soil. Nitrogen (50 kg N ha^{-1}), phosphorus (45 kg P_2O_5 ha^{-1} as single superphosphate), potassium (135 kg K_2O ha^{-1} as KCl) and zinc (5 kg Zn ha^{-1} as $ZnSO_4{\cdot}7H_2O$) were applied as basal on an area basis and mixed with soil two days before transplanting. The pots were sparsely arranged (50 cm apart) to eliminate possible shading effects. A 2–3 cm water layer was held in the pots during the whole season. Weeds, diseases and insects were controlled. Heading date was October 1. Leaf age was recorded every 3–4 days. At the beginning of first internode elongation, 20 pots were chosen and divided randomly into two groups with 10 pots each. Heavy N rate (150 kg N ha^{-1} on area basis, or 1.3 g urea pot^{-1}) was applied to the "+N" group, while the "–N" group received no N fertilizer. Chlorophyll content (SPAD value) of the uppermost fully expanded leaves was measured during the elongation stages of first and second basal internodes using a SPAD-502 chlorophyll meter (Minolta Company, Ltd., Osaka, Japan). Final length of the first and second basal internodes was measured at heading stage.

2.3. Data analysis

For the field experiments, the mean LTR, R/FR, LAI, and NLV during the second internode elongation were computed using the daily values from the exact starting date to the exact ending date of internode elongation. Analysis of variance (ANOVA), correlation, partial correlation, and stepwise multiple regression analysis were calculated with Statistix 8.0 (StatSoft Inc., Tulsa, OK, USA). Mean comparison among treatments was based on the least significant difference (LSD) at the 0.05 probability level. Only variables with significance $P < 0.05$ were entered into the regression model in stepwise regression analysis. For the pot experiment, SPAD and FIL differences between N treatments were tested using the *t*-test function of Microsoft Excel 2010 (Microsoft

Corporation, Redmond, WA, USA). Figures were made with SigmaPlot version 10.0 for Windows (Systat Software, Inc., San Jose, CA, USA).

3. Results

3.1. *Field experiment*

3.1.1. *Effect of N rate and seedling density on canopy indices and internode length*

As shown in Tables 2 and 3, N rate and seedling density both had significant influence on FIL. FIL increased with N rate and seedling density. Compared with T1, FIL in T9 was increased by 43% in early season and 27% in late season. Under the same N rate, FIL in higher seedling density treatments was greater than in lower seedling density treatments. Under the same seedling density, FIL was greater in higher N-rate treatments. No significant interaction effect on FIL was found between N rate and seedling density in either season. FIL was on average 41% longer in early season than in late season.

N rate and seedling density significantly affected canopy indices (Tables 2 and 3). At a given seedling density, L_b and LTR decreased while NLV and LAI increased as N rate increased. At a given N rate, LTR and NLV decreased while LAI increased as seedling density increased. L_b decreased with increasing seedling density across N rates in the late season but only with high N treatments in the early season. In early season, there were significant differences in R/FR among N and seedling density treatments. R/FR decreased as N rate and seedling density increased (Fig. 1).

3.1.2. *Correlation between internode length and canopy indices*

As shown in Table 4, FIL was negatively correlated with L_b and LTR ($P < 0.01$) and was positively correlated with LAI ($P < 0.01$) in both seasons. There were no significant correlations between FIL and NLV in either season ($P > 0.05$). Correlation analysis using data pooled across the two seasons showed that FIL was significantly and negatively correlated with L_b and LTR ($P < 0.01$) and was positively correlated with LAI ($P < 0.01$). No significant correlation was found between FIL and NLV ($P > 0.05$). In early season, FIL was also negatively correlated with R/FR ($P < 0.01$) (Fig. 2-A). Thus, the internode length was closely associated with light environment and LAI but not with NLV during the elongation period.

R/FR was significantly associated with light intensity, light transmission ratio, and leaf area index (Fig. 2-B, C, D), but not with leaf N concentration (Fig. 2-E). R/FR increased as L_b and LTR increased, but decreased exponentially as LAI increased. The coefficient of determinations (R^2) of the relationships between R/FR and light intensity (Fig. 2-B), R/FR and light transmission ratio (Fig. 2-C), and R/FR and LAI (Fig. 2-D) were 0.61, 0.87, and 0.93, respectively.

3.1.3. *Stepwise regression and partial correlation analysis*

Stepwise regression analysis was performed with FIL as dependent variable and L_b, LTR, NLV, and LAI as independent variables. Only variables L_b and LAI ($P < 0.05$) entered into the regression model. The regression equation was.

$$\mathrm{FIL} = 7.23–0.0737\ L_b + 0.369\ \mathrm{LAI}. \tag{1}$$

The regression coefficients for the constant ($P < 0.0001$), L_b ($P < 0.0001$), and LAI ($P < 0.001$) were all highly significant, and the coefficient of determination (R^2) for the regression was 82% ($n = 54$).

Partial correlations analysis showed that the correlation coefficient between FIL and L_b was –0.820 when NLV and LAI were kept constant, the correlation coefficient between FIL and LAI was 0.452 when L_b and NLV were kept constant, and the correlation coefficient between FIL and NLV was –0.008 when L_b and LAI were kept constant. Thus, LAI and L_b were much more closely associated with FIL than was NLV.

Table 2 – Effects of N rate and seedling density on canopy indices during second internode elongation and the final length of the second internode in 2015 early season.

Treatment	N rate (kg N ha^{-1})	Seedling no. m^{-2}	L_b (×10^3 lm m^{-2})	LTR (%)	NLV (%)	LAI	FIL (cm)
T1	0	16.7	11.3 b	49.66 a	2.71 de	1.19 g	6.22 c
T2		75.0	14.6 a	45.17 a	2.40 f	1.68 f	6.92 c
T3		187.5	11.6 b	37.76 b	2.19 f	2.19 de	7.19 bc
T4	75	16.7	10.0 bcd	35.10 bc	3.25 b	2.06 ef	7.21 bc
T5		75.0	7.9 cde	28.50 cd	2.93 c	2.78 c	8.45 ab
T6		187.5	10.7 bc	26.95 de	2.68 e	3.34 b	7.51 bc
T7	150	16.7	7.5 de	28.29 cd	3.65 a	2.68 cd	7.41 bc
T8		75.0	7.0 ef	20.79 e	3.23 b	3.80 b	8.54 ab
T9		187.5	4.3 f	10.86 f	2.89 cd	4.76 a	8.91 a
F-value		N	19.7**	176.8**	292.9**	163.7**	10.8*
		D	ns	21.3**	62.2**	65.3**	5.3*
		N × D	5.7**	ns	ns	3.3*	ns

L_b, light intensity at the base of the canopy; LTR, light transmission ratio; NLV, leaf N concentration; LAI, leaf area index; FIL, final internode length.

Values in the table are means of three replications. Within a column, values followed by different letters are significantly different at $P < 0.05$ according to LSD test. *F*-values marked with * and ** are significant at the 0.05 and 0.01 probability levels, respectively; ns denotes that values are not significantly different at $P < 0.05$.

Table 3 – Effects of N rate and seedling density on canopy indices during second internode elongation and the final length of the second internode in 2015 late season.

Treatment	N rate (kg N ha^{-1})	Seedling no. m^{-2}	L_b (×10^3 lm m^{-2})	LTR (%)	NLV (%)	LAI	FIL (cm)
T1	0	16.7	40.9 a	56.02 ab	3.03 d	1.20 e	4.72 d
T2		75.0	38.0 ab	43.28 cd	2.64 e	1.83 d	5.11 bcd
T3		187.5	34.7 bc	36.07 e	2.37 f	2.28 c	5.38 abc
T4	90	16.7	42.3 a	61.04 a	3.49 b	1.29 e	5.01 cd
T5		75.0	37.4 ab	36.60 de	2.79 e	2.23 c	5.20 bcd
T6		187.5	32.3 c	26.33 fg	3.06 d	2.79 b	5.59 abc
T7	180	16.7	37.7 ab	50.50 bc	3.74 a	1.43 e	5.21 bcd
T8		75.0	30.9 c	30.07 ef	3.19 cd	2.24 c	5.69 ab
T9		187.5	25.7 d	20.75 g	3.37 bc	3.46 a	6.00 a
F-value		N	ns	17.0^{*}	652.7^{**}	12.5^{*}	7.9^{*}
		D	25.5^{**}	151.3^{**}	41.3^{**}	251.8^{**}	8.9^{**}
		N × D	ns	3.8^{*}	3.3^{*}	9.9^{**}	ns

L_b, light intensity at the base of the canopy; LTR, light transmission ratio; NLV, leaf N concentration; LAI, leaf area index; FIL, final internode length.

Values in the table are means of three replications. Within a column, values followed by different letters are significantly different at $P < 0.05$ according to LSD test. *F*-value marked with * and ** are significant at the 0.05 and 0.01 probability levels, respectively; ns denotes that values are not significantly different at $P < 0.05$.

3.2. *Pot experiment*

There was a significant difference ($P < 0.01$) in SPAD value between the two N treatments at both the first and second internode elongation stages (Fig. 3-A). Mean SPAD values at the first internode elongation were respectively 42.0 and 29.0 for plants with and without N application, during the first internode elongation. The trend was the same for the SPAD value during the second internode elongation. However, no significant difference was found ($P > 0.05$) in final length of the first and second internodes between the two N treatments (Fig. 3-B).

4. Discussion

The elongation of basal internodes was closely correlated with light environment expressed as light intensity (L_b) and light quality (R/FR). FIL was significantly and negatively correlated with L_b, LTR and R/FR, and positively correlated with LAI (Table 4, Fig. 2-A). The finding that only L_b and LAI entered into the stepwise regression model for FIL estimation, with a coefficient of determination of 82%, indicated that L_b and LAI were the main canopy indices determining the elongation of basal internodes.

Kahlen and Stutzel [20,30] used light quantity and LAI as driving forces and developed a simplified light-based model for estimating FIL in greenhouse cucumber canopies. They found that LAI can substitute for local light quality data for estimating FIL with prediction quality even higher than the original model using R/FR as input. It is interesting that the model obtained in this study for rice, a monocotyledon, shared the same driving forces (L_b and LAI) as that for cucumber, a dicotyledon. R/FR was highly significantly and exponentially correlated with LAI in the present study (Fig. 2-D). The relationship between R/FR and LAI ($R^2 = 0.93$, Fig. 2-D)

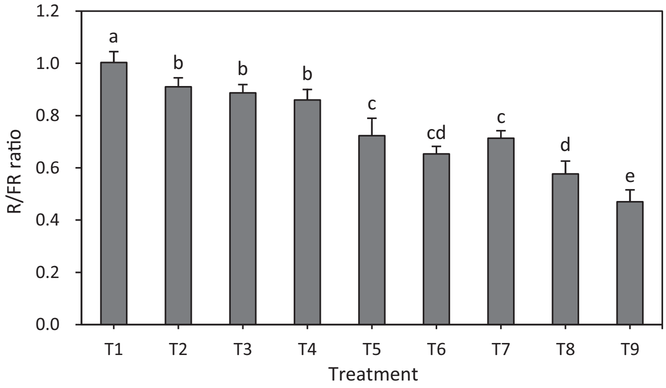

Fig. 1 – Red: far-red ratio (R/FR) at the base of canopy under different N and seedling density treatments. Vertical bars show the standard error of the mean. Different letters above bars denote significant difference at the 0.05 probability level. See Table 1 for the description of treatments.

Table 4 – Correlation coefficients between the final length of the second internode and canopy indices of rice.

Season	n	Canopy index	Correlation coefficient			
			LTR	NLV	LAI	FIL
Early season	27	L_b	0.823^{**}	-0.581^{**}	-0.752^{**}	-0.590^{**}
	27	LTR		-0.425^{*}	-0.920^{**}	-0.687^{**}
	27	NLV			0.270	0.200
	27	LAI				0.733^{**}
Late season	27	L_b	0.848^{**}	0.003	-0.835^{**}	-0.717^{**}
	27	LTR		0.221	-0.929^{**}	-0.701^{**}
	27	NLV			−0.147	0.047
	27	LAI				0.677^{**}
Across both seasons	54	L_b	0.564^{**}	0.144	-0.535^{**}	-0.877^{**}
	54	LTR		−0.009	-0.904^{**}	-0.607^{**}
	54	NLV			0.023	−0.104
	54	LAI				0.653^{**}

n, number of observations; L_b, light intensity; LTR, light transmission ratio; NLV, leaf N concentration; LAI, leaf area index; FIL, final internode length. * and ** denote significance at the 0.05 and 0.01 probability levels, respectively.

was closer than that between R/FR and light intensity (R^2 = 0.61, Fig. 2-B) and light transmission ratio (R^2 = 0.87, Fig. 2-C). It seems that LAI may play the role of light quality (R/FR) in determining the elongation of basal internodes of rice.

L_b, LTR, R/FR, and LAI were closely correlated with one another (Table 4, Fig. 2-B, C, D). LTR, defined as the ratio of light intensity at the base of canopy (L_b) and that at the top of canopy (the natural light intensity, L_0), is related to LAI following the Lambert–Beer law [31]. Thus, L_b is related to LAI as follows:

$$L_b = L_0\, e^{-k\,\mathrm{LAI}}, \tag{2}$$

where k is the light extinction coefficient of the canopy.

The finding that L_b played an important role in determining the elongation of basal internodes is consistent with previous findings of Sparkes and King [32] who reported that light intensity was a dominant factor in stem lodging associated to the excessive elongation of internodes. Duy et al. [26] reported that improved light transmission reduced the length of basal internodes of rice. Ballare et al. [33] found that the stem elongation of *Sinapis alba* L. was promoted by localized shading.

Light quality, usually expressed by R/FR, can independently affect the elongation of basal internodes. In our study, a negative correlation was found between FIL and R/FR (Fig. 2-A). Ballare et al. [34] reported that when individual seedlings of *Datura ferox* and *Sinapis alba* were transferred to populations formed by plants of similar stature, they responded with an increase in stem elongation rate within three days when light intensity had not changed significantly. In soybean production, high seedling density significantly reduced the R/FR in basal part of canopy and promoted the elongation of basal internodes [35]. Park and Runkle [36] found that far-red radiation and photosynthetic photon flux density independently regulate seedling growth. It was reported that red light can inhibit the elongation of internodes by reducing the gibberellic acid (GA) levels in plants whereas far-red light has the opposite effect [37]. Morgan and Smith [16] reported that R/FR decreased with the increase of LAI. However, in our study, the relationship between R/FR and LAI could be better described by a negative exponential equation, with a coefficient of determination of 93%. Yang et al. [38] found that the response of soybean seedlings to shading by maize was influenced by the summed effects of both radiation and R/FR under relay strip intercropping systems.

Correlation, partial correlation, and stepwise regression analysis using the field experiment data showed that NLV was not directly associated with the elongation of basal internodes. In previous studies, internode length increased with N input [39,40]. Similar results were found in our study (Tables 2, 3). However, there are conflicting explanations for the manner in which N input affects internode elongation [19,22,23,26]. Our results demonstrated that NLV had no direct effect on the elongation of basal internodes. No significant correlation was found between FIL and NLV in both seasons (Table 4). The pot experiment showed that even a heavy N application at the beginning of first internode elongation did not affect FIL (Fig. 3-B). In the stepwise multiple regression analysis, only L_b and LAI and not NLV were entered into the regression equation. These results suggest that the internode length of rice was determined mainly by L_b and LAI and that NLV was not a factor directly determining internode elongation. The effect of N application on FIL was indirectly achieved by changing LAI. Kamiji et al. [19] postulated that N is not likely the direct cause for the elongation of basal internodes of rice. However, they did not provide a statistical analysis of the relationship between FIL and NLV.

Clarification of the role of fertilizer N in internode elongation is of great importance for crop management. According to the model established in this study, shorter basal internodes can be achieved by reducing LAI and increasing L_b at jointing stage, goals that can in turn be reached by reducing plant density and N input as basal and during tillering. Because higher NLV does not directly stimulate the elongation of basal internodes, more N fertilizer could be applied at or just before panicle initiation (which is synchronous with the elongation of basal internodes) to promote spikelet development without promoting basal internode elongation and reducing lodging resistance. This practice would increase the flexibility of the timing of panicle N application.

In rice production, L_b, LTR, and R/FR can be increased by agronomic measures such as reducing seedling density, manipulating the arrangement of plant hills, and/or improving fertilizer N management. These measures could ultimately reduce internode length and risk of lodging [41]. In fact, a transplanting method with wide rows and narrow within-row hill spacing has been used in high-yield cultivation since the 1970s [42]. Hu et al. [43] found that mechanical transplanting with reduced plant density improved light conditions, shortened the basal internodes, and reduced lodging risk, although they did not present a quantitative description.

Substituting Eq. (2) into Eq. (1), we obtain:

$$\mathrm{FIL} = 7.23–0.0737\, L_0\, e^{-k\,\mathrm{LAI}} + 0.369\,\mathrm{LAI}. \tag{3}$$

As shown in Eq. (3), FIL was determined by the natural light intensity (L_0), LAI, and light extinction coefficient (k). This equation is of great significance in crop management. According to this equation, reducing LAI at jointing stage via agronomic measures can result in shorter basal internodes. The optimal LAI could vary among locations and seasons

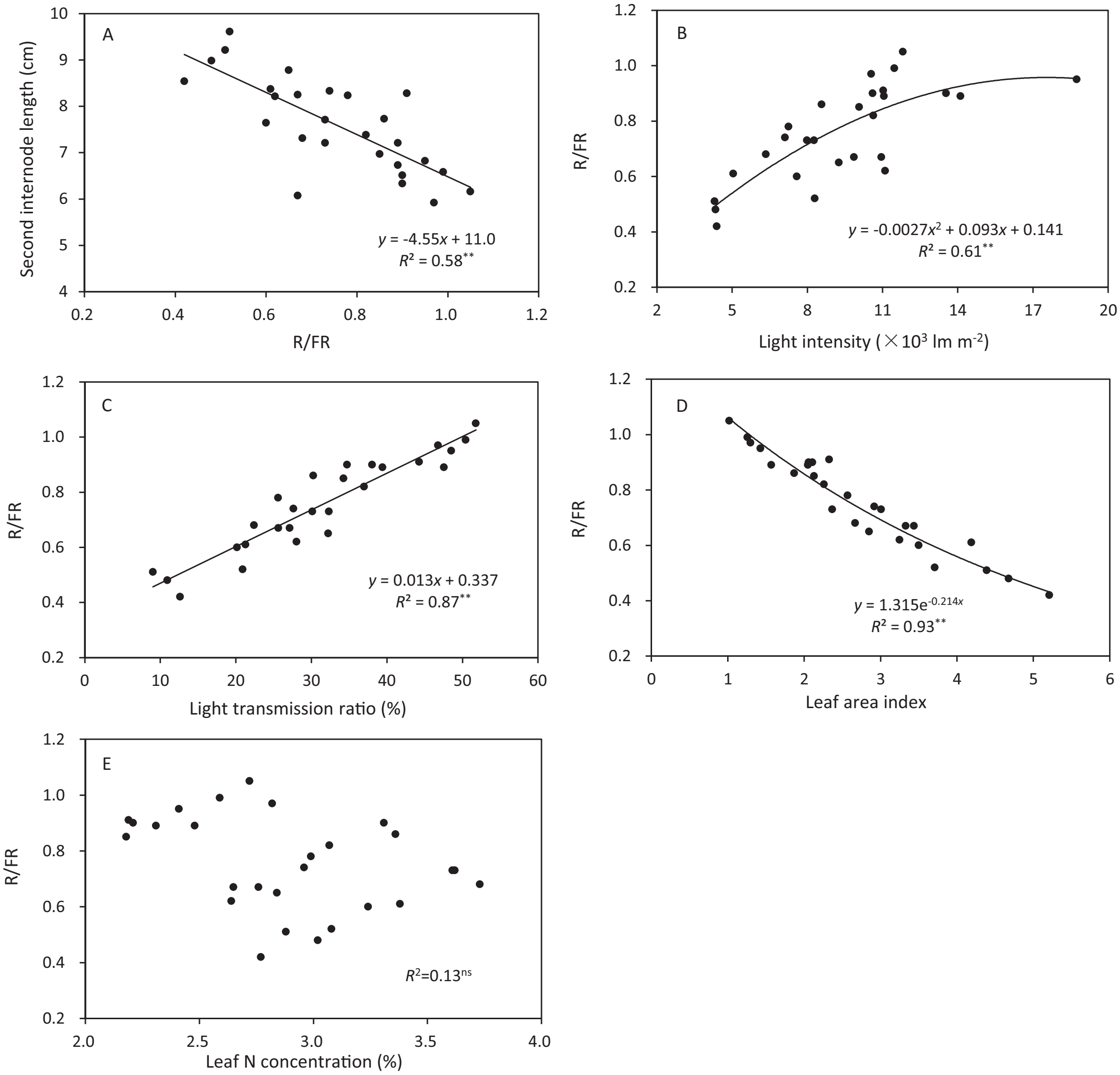

Fig. 2 – The relationship between final length of second internode and red:far-red light ratio (R/FR) (A), and between R/FR and light intensity (B), light transmission ratio (C), leaf area index (D), and leaf N concentration (E). ** denotes significance at the 0.01 probability level; ns denotes not significant at the 0.05 probability level.

because L_0 is site- and season-specific. At a given LAI, rice crops grown in locations and seasons with more favorable radiation will have shorter basal internodes and hence greater lodging resistance. Compared to the late season, radiation in the early season is generally lower, and the basal internodes are normally longer. This difference explains why lodging occurs more frequently and heavily in the early season than in the late season in rice production in southern China.

Using Eq. (3), we can predict FIL using light intensity and LAI data as input (Table 5). We can also calculate the thresholds of FIL corresponding to a given light intensity and LAI. For example, provided that k is 0.5 and the natural light intensity is 7.5×10^4 lm m^{-2}, the LAI at jointing stage should be no greater than 1.5 in order to keep the FIL of the second basal internode no longer than 5 cm. If the FIL is to be kept below 7 cm, then the LAI at jointing should be no greater than 3.0. For a given location and season, the solar irradiation is relatively stable across years. Thus, given location, season, and rice variety, control of FIL can be simplified as control of LAI. If the LAI is greater than expected, remedial approaches, such as midseason drainage and chemical (e.g. paclobutrazol) control could be used to suppress internode elongation. A suitable LAI is also important for high yield of rice, and the parameters in Eq. (3) may be variety- and location-dependent. Further studies may identify the threshold of LAI at jointing stage at which both lower FIL and high yield can be achieved for different rice varieties and locations.

5. Conclusions

L_b and LAI are the two main factors determining the elongation of basal internodes of rice. A regression model was established to estimate FIL based on L_b and LAI. NLV is not associated with the elongation of basal internodes. N fertilization affects the elongation of basal internodes

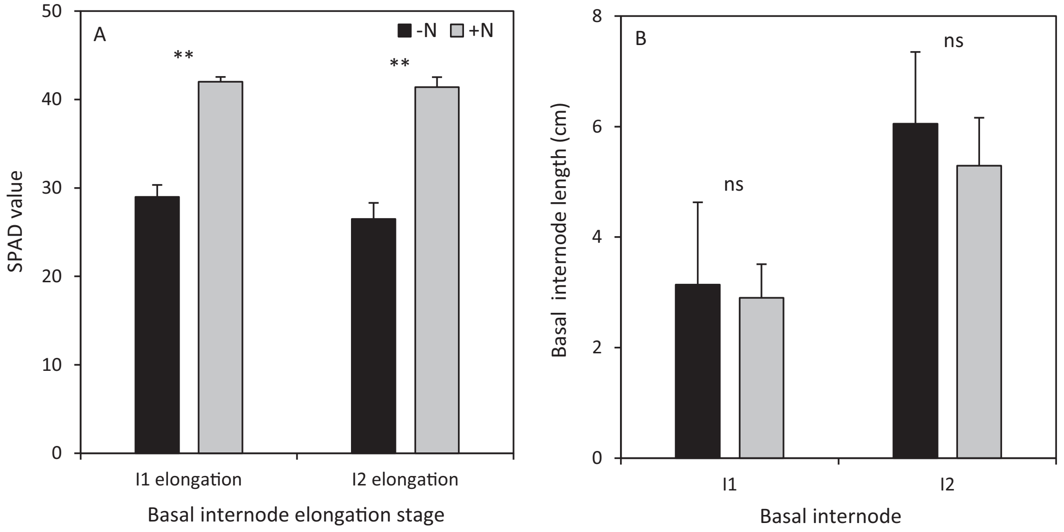

Fig. 3 – Chlorophyll content (SPAD value) of uppermost fully-expanded leaves during the elongation of first (I1) and second (I2) basal internodes (A), and the final length of first (I1) and second (I2) internodes (B) in the pot experiment. Fertilizer N was applied at the beginning of first internode elongation. ** denotes significant difference ($P < 0.01$); ns denotes not significant at $P > 0.05$ by *t*-test.

indirectly by altering L_b and LAI. Optimizing N management and plant density to manipulate LAI and light transmission at jointing stage are practical approaches to shortening the basal internodes and improving lodging resistance of rice. To our knowledge, this is the first report establishing a quantitative relationship between the elongation of basal internodes and canopy indices for rice.

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Table 5 – Calculated final length of the second internode (FIL) of rice cv. Yinjinruanzhan as a function of leaf area index (LAI) and natural light intensity (L_0, expressed in $\times 10^4$ lm m^{-2}) during the second internode elongation.

LAI	Final length of the second internode (cm)			
	$L_0 = 2.1$	$L_0 = 4.3$	$L_0 = 7.5$	$L_0 = 10.8$
1.0	6.6	5.7	4.2	2.8
1.5	7.0	6.3	5.2	4.0
2.0	7.4	6.8	5.9	5.1
2.5	7.7	7.2	6.6	5.9
3.0	8.0	7.6	7.1	6.6
3.5	8.2	8.0	7.6	7.1
4.0	8.5	8.3	8.0	7.6

The equation used is $FIL = 7.23–0.0737\ L_0\ e^{-k\ LAI} + 0.369\ LAI$, k is light extinction coefficient and $k = 0.5$.

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