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Stem Characteristic Associated with Lodging Resistance of Rice Changes with Varied Alternating Drought and Flooding Stress

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Abstract: A two-year field experiment was executed to investigate the impact of different controlled irrigation and drainage regimes on the morphological and mechanical traits related to the lodging resistance of rice in Jiangsu province, China. Three irrigation regimes were comprised of conventional flooding practices (CK), controlled irrigation and drainage mode I (CID-1), and controlled irrigation and drainage mode II (CID-2). Results indicated that there was no significant difference in the heights of rice plants under the three irrigation regimes, but the average diameter of CK treatment was 21% higher than that of CID-2 in the 2013 season. Similarly, the value of the section modulus of CK was significantly higher than that of CID-2 ($p < 0.05$). On the contrary, the length of basal internodes of CK and CID-1 was significantly lower than that of CID-2 in 2013 ($p < 0.05$). For both seasons, the safety factor against stem breakage (SFs) of CID-2 always had the lowest value under different irrigation regimes, which might be related to the significantly lower values of bending strength of culm at breaking (S) and the bending stress (BS) as well as lower ash content and cellulose content in CID-2 compared with CK and CID-1. Collectively, properly increasing the depth of water levels after heavy rain under the current water-saving mode (CID-1) would not increase the risk of lodging for rice plants, whereas if the water depth after heavy rain was kept higher than 20 cm (CID-2), the SFs would be significantly lower than that of CK, and the rice plants would be much more likely to undergo lodging.

Keywords: controlled irrigation and drainage; rice; lodging resistance; flooding stress

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1. Introduction

Lodging is a common problem in the production of cereal crops. In the lodged rice crop community, the self-shading of leaves in the canopy and the damage of vascular bundles by breaking or bending the stem could result in the reduction of photosynthetic ability and disturb the translocation of carbon and nutrients to the rice grains [1]. Lodging has detrimental effects on both productivity and grain quality [2]. As suggested by Setter et al. [3], every 2% of lodging could cause a decrease of 1% in grain yield, and severe lodging could decrease rice yield by up to 50%.

It has long been recognized that the lodging resistance of the rice plant could be determined by two main factors, the plant's mass moment and the physical strength of the lower part [4,5]; the mass moment is directly determined by the plant height and the panicle weight, whereas the physical strength was not only related to the morphological characteristics of the culm, but also the chemical composition [1,6,7]. Previous research indicated that the introduction of the *sd*-1 gene could reduce plant height and consequently improve resistance to lodging [8]. Moreover, crop management such as the application of fertilizer and growth regulators could also influence the height of the culms and the stem bending strength, thereby affecting the lodging resistance of cereals [9,10]. In addition to the factors mentioned above, irrigation strategies in the paddy field could also be one of the most important attributes in connection with lodging resistance [11–13]. Das et al. [14] indicated that flooding stress in paddy fields could enhance plant ethylene production, stimulate the elongation of the stem to relieve the flooding stress, and consequently increase the tendency towards lodging. Moreover, it was found that with the increase in irrigation depth, the lodging resistance of rice plants would be decreased [13]. On the other hand, drought effects in lowland rice caused by the 'water-saving technique' could reduce plant heights as well as decrease panicle weights [15,16] and consequently decrease the plant's mass moment and the possibility of lodging [17]. Besides the plant's mass moment, the physical strength of the rice plant, which was closely related to lodging resistance, could also be influenced by irrigation regimes [11,12]. The physical strength of rice plants was closely related to the morphological traits of internodes, such as culm diameter, culm wall thickness, and dry matter weight of basal internodes [9,18]. With the increase in culm diameter and culm wall thickness, the physical strength of the rice plant tended to be increased [19,20]. The morphological traits of inter-nodes could be influenced by irrigation regimes. As indicated by Guo et al. [11], rice plants under the treatment of water-saving irrigation had significantly higher internode wall thickness compared with traditional flooding irrigation (CK). Thus, the physical strength of rice plants might be affected by irrigation regimes through changes in culm diameter and culm wall thickness. However, there was limited direct evidence to confirm this in field experiments, especially for different CID irrigation regimes [11,12].

Rice is an intensive water-consuming crop. Freshwater consumed by paddy fields accounts for approximately 50% of all diverted freshwater in China [21]. Meanwhile, because of the greater demand for rapid urban and industrial development and the decreasing availability of freshwater resources due to pollution (chemical, salts, and silt), freshwater resources for irrigated rice production are becoming increasingly scarce [22–24]. To mitigate the competition between the increasing demand for food and the scarcity of water resources, 'water-saving techniques' for paddy fields have been introduced in China for decades [25,26]. Alternate wetting and drying irrigation (AWD), one of the water-saving strategies, characterized by alternate wetting and drying, allowing the soil to dry out to a certain extent before re-applying irrigation water, could reduce the required irrigation and consequently lead to the improvement of water use efficiency [27,28]. Even though positive effects were obtained from the AWD practices, the usage of rainfall has been reported to be constrained in this practice due to the low upper limit of the ponding layer [29]. Taking into consideration the high mean annual precipitation (approximately 1000 mm per year) and the coincidence of the irrigation season and the summer wet season in southern China, the utilization of rainwater for irrigation is, therefore, a prerequisite for sustainable paddy rice production in this area [30]. To take advantage of AWD as well as the rainwater, a novel irrigation strategy, controlled irrigation and drainage (CID), which captured more rainfall and maintained a higher depth of water than AWD during days of heavy rain, has been introduced recently [31,32]. In this irrigation mode, the maximum water-catching depth after heavy rain approaches the maximum water depth that the rice plant could endure under flooding stress. Consequently, rice plants would be alternatively under drought and flooding stress under CID [29,31,32]. Although many studies have investigated the agronomic performance of rice under different irrigation treatment [15,33–35], research about the lodging resistance of rice plants under water saving treatment, especially for CID, is still limited [11,36].

Under CID, rice plants were not exposed to flooding stress or drought stress alone but fluctuated under drought stress and flooding stress. Even though excessive standing water during the vegetative growth stage could obviously suppress the root growth of paddy rice and stimulate the stem elongation and consequently have detrimental effects on the lodging resistance of the rice plant [37–39], the drought stress following flooding stress might have positive effects to compensate for the negative effects of lodging resistance in paddy rice [11]. In addition, the submergence withdrawal compensation effects for lodging resistance might depend on the growth stage as well as the flooding stress intensity [11,40]. If this were the case, the lodging resistance of rice plants under CID will differ with flooding stress levels. However, few studies have been dedicated to qualifying responses of rice to lodging resistance under the CID paddy field. Hence, investigating the effects of CID under different flooding stresses in rice paddies is needed.

In this study, the effects of the irrigation regimes on morphological characteristics and bending strength of culm together with the chemical concentration in culms were investigated. The objective of this study was to illustrate whether any of the effects induced by alternating flooding and drought irrigation treatment under different flooding stress levels could improve the lodging resistance of rice plants in comparison with conventional water management practices (maintaining a reasonable standing depth of water in the paddy field throughout the growing season). It is anticipated that the results obtained here will provide deeper insights into the mechanism controlling lodging resistance of rice plants induced by irrigation strategies and consequently could provide a useful dataset for the selection of irrigation strategies in field management practices in paddy fields.

2. Materials and Methods

2.1. Experimental Condition and Plant Material

A field experiment was conducted at the Key Laboratory of Efficient Irrigation-Drainage and Agricultural Soil Water Environment in Southern China, Ministry of Education (Nanjing, latitude 31°57′ N. longitude 118°50′ E, 14.4 m above sea level) from June to October in 2012 and repeated in 2013. The study area has a subtropical monsoon climate with an average air temperature of 15.3 °C and a mean annual precipitation of 1051 mm. The air temperature, relative humidity, and precipitation during the rice growing season across the 2 years (2012–2013) were measured with an automatic weather station (Hobo, Onset Computer, Bourne, MA, USA) which was 100 m away from the experimental plots. The texture of the soil was clay loam with available N of 47.4 mg/kg, available P of 10.4 mg/kg, and total K of 330.0 mg/kg. The soil had a gravimetric soil water content of 42.1% and 30.9% at saturated soil water content and field holding capacity, respectively. One high-yielding rice (*Oryza sativa* L. Nanjing 44) currently used in local production was grown in the field in this study. Seeds were sown in the seedbed on 20 April 2012 and 30 April 2013, respectively, for both seasons. Seedlings at the fifth-leaf stage were transplanted to plots using two seedlings per hill on 1 June 2012 and 15 June 2013, respectively, for both seasons. The planting density was 25 hills m^{-2}. Each plot was approximately 20 m^2 (2.5 m × 8 m), with plastic films buried to 45 cm under the ridges to prevent the lateral flow of water between the plots. Fertilizer was applied at a rate of 265-80-75 kg/hm^2 of N-P-K in this experiment, according to the local farming practices. Nitrogen fertilizer was split into three stages (at transplanting stage, at tillering stage, and at panicle initiation stage, respectively).

2.2. Treatments and Experimental Design

Three treatments, i.e., CK, CID-1, and CID-2, were used to evaluate the effects of irrigation regimes on the lodging resistance of rice plants in the 2012 and 2013 seasons. In these treatments, when ponding water depth or soil water content is reduced to the lower limit of the designed water level, irrigation water is added until the water depth in the paddy field reaches the upper limit of the designed water level. When rainfall increases water depth beyond the maximum water-catching depth, drainage occurs. For the CK treatment, the soil water content (or water depth in the paddy field) was kept between θ_s and 30 mm during the whole growing season, except in the re-greening stage and yellowing maturity stage. Drainage was implemented to the maximum water-catching depth after rainfall when the water depth was above 70 mm, 90 mm, 120 mm, 100 mm, and 60 mm during initial tillering stage, middle and late tillering stage, jointing and booting stage, heading and flowering stage, and milk and ripening stage, respectively. Detailed information on water management for CID-1 and CID-2 during growing stages in the paddy field is shown in Table 1. The field experiment had a total of 9 plots, arranged in a randomized block design with three replicates per treatment. Except for the irrigation and drainage practices, the control for insects and diseases were the same during the whole growing season.

Table 1. Soil moisture limits for irrigation at different stages of rice under different irrigation regimes (2012–2013).

Treatment	T [a]		J/B	H/F	M/R
	IT	MT/LT			
CK	θ_s~30~70 [b]	θ_s~30~90	θ_s~30~120	θ_s~30~100	θ_s~30~60
CID-1	0.8θ_s~θ_s ~80	0.7θ_s~θ_s~100	0.7θ_s~θ_s~100	0.8θ_s~θ_s~150	0.8θ_s~θ_s~80
CID-2	0.8θ_s~θ_s ~100	0.7θ_s~θ_s~120	0.7θ_s~θ_s~200	0.8θ_s~θ_s~200	0.8θ_s~θ_s~80

Note: [a] T, IT, MT/LT, J/B, H/F and M/R represent tillering stage, initial tillering stage, middle and late tillering stage, jointing and booting stage, heading and flowing stage, and milky and ripening stage, respectively. In this study, tilling stage was from 14 June to 20 July in 2012 and from 28 June to 31 July in 2013. Jointing and booting stage was from 21 July to 10 August in 2012 and from 1 August to 18 August in 2013. Heading and flowing stage was from 11 August to 25 August in 2012 and from 18 August to 3 September in 2013. Milky and yellow ripening stage was from 26 August to 1 October in 2012 and from 4 September to 8 October in 2013. [b] The data in the table, for example, θs~30~70, represents the lower limit of irrigation, upper limit of irrigation, and the maximum water-catching depth after rain, respectively. θ_s means that the lower limit of irrigation is saturated soil water content for the 0–30 cm soil layer; 30 and 70 represent that the water depth for higher limit of irrigation and maximum water-catching depth after rainfall is 30 mm and 70 mm, respectively.

2.3. Shoot Morphological and Mechanical Properties

2.3.1. Shoot Morphological Properties

Since the rice plants were most likely to lodge during the mature grain stage, stem morphology and mechanical properties relating to lodging resistance were measured on 25 September 2012 and 24 September 2013, respectively. At the full ripen stage, two plants, randomly collected from the middle row of each of the replicate plots, were carefully uprooted. After covering the root and stems with a polythene bag, rice plants were immediately taken to the laboratory for morpho-physical studies. About 20 min after uprooting, both the root systems and the stem bases were kept immersed in water to maintain turgor until just before measurements were taken. Within 3 h of sampling, the morphological traits, such as plant height, centers of gravity, and culm diameters were examined per the main tiller in the laboratory. Plant height was determined by measuring the distance from the base to the tip of the panicle with a ruler. The center of gravity was determined by placing tillers across a knife blade and moving the tiller along the knife blade until the balance point was reached; the height of the center of gravity is the distance from the base of the stem to the center of gravity [41]. Plant fresh weight was measured by a top loading balance (MP1100B, Shanghai, China). Culm diameters were measured at the central part of the second internode from the plant base in two directions by an electronic vernier caliper (Shenghan 0-200, Shanghai, China). After that, the lower part of the rice culms was cut into four sections (named N_1, N_2, N_3, and N_4, respectively) from the base by a blade, and the length of each section was approximately 12 cm.

2.3.2. Physical Properties of Culms

Physical properties of the culms were measured and calculated as follows: Since stem lodging usually occurs at the IV and V internode [42], only the N_2, N_3, and N_4 of the culm counted from the base were subjected to a three-point bending test with a universal force testing device (model CMT6104, Ningbo, China) for the measurement of bending strength. The culm fragments were placed on two metal supports 100 mm apart, while a blunt rubber probe, which touched the midway of the stem, was moved down at a speed of 0.1 mm s^{-1} to bend it. A force/displacement graph was simultaneously recorded on an interfacing computer and used to calculate the mechanical properties of the stem section. The bending strength of the culm S expressed in N m is given by

$$S = \frac{F_{max}\, L}{4} \tag{1}$$

where F_{max} is the maximum force that the stem will withstand before it breaks, and L is the distance (100 mm) between the supporting points.

Cross section modulus (SM m^3) of the base oval hollow internode (N_2, N_3, and N_4) was calculated using the formula:

$$SM = \frac{\pi\left(a_1{}^3 b_1 - a_2{}^3 b_2\right)}{32 a_1} \tag{2}$$

where a_1 is the outer diameter of the minor axis in an oval cross-section, b_1 is the outer diameter of the major axis in an oval cross-section, a_2 is the inner diameter of the minor axis in an oval cross-section, and b_2 is the inner diameter of the major axis in an oval cross-section.

Bending stress of culms (BS, N m^{-2}) was calculated as follows:

$$BS = \frac{S}{SM} \tag{3}$$

where S is the bending strength of a culm, and SM is the cross-section modulus of the base oval hollow internode.

2.4. Self-Weight Mass Moment and Safety Factor

The morphological and mechanical parameters measured above were combined to calculate two further sets of parameters, i.e., the self-weight moments of individual tillers and the self-weight safety factors of the plant against stem breakage [41].

2.4.1. Self-Weight Mass Moment of the Individual Tiller

When a rice plant is leaning, the self-weight of the individual tiller will accelerate the stem to bend permanently. According to Crook and Ennos [41], the self-weight mass moment of an individual tiller (M_p) could be estimated by the inclination angle of the stem and its mass distribution using the following formula:

$$M_p = mghsin\theta \tag{4}$$

where m is the mass of individual tillers, g is the acceleration due to gravity, h is the height of the center of gravity of each tiller, and θ is the inclination angle of each stem from the vertical. In this paper, the self-weight mass moment of individual tillers was calculated assuming the inclination angle of each stem was 30° from the vertical.

2.4.2. Safety Factor against Stem Breakage

The ability of each stem to withstand the overturning moments generated by the wind and the self-weight of the individual tiller depends on the basal bending strength. The safety factor against stem breakage (SF_s) was calculated as follows:

$$SF_s = \frac{S}{M_p} \tag{5}$$

where S is the bending strength of the stem base, and M_p is the self-weight mass moment generated by a single tiller at an angle of 30° from the vertical. According to previous study, stem lodging of rice rarely occurred at internode I and II but usually occurred at internode IV [43]. Thus, in this study, the N_2 section was chosen to measure the S value and consequently to calculate the SF_s values of different treatments.

2.5. Analysis of Stem Chemical Components in Rice Culms

2.5.1. Cellulose Content and Lignin Content of Culm

After the dried samples of lower culms were powered at 15,000 rpm for 90 s in a wonder blender, the cellulose content of the powder was determined by the nitric acid ethanol method [44]. The lignin content (%) of the rice culm was determined by the method suggested by Song et al. [45].

2.5.2. N Content in Leaf Blade

Dry samples of top layer leaves (sum of the first, second, and third leaves counted from the top of the rice shoot) were finely ground to pass through a 0.15 mm sieve. N content of the sieved and ground top layer leave samples was determined using the Dumas dry combustion method.

2.5.3. Ash Content of Culms

Ash content of culms was determined after complete burning of the culm samples in a muffle furnace at 900 °C and by weighing the residue.

2.6. Gap Fraction

Photosynthetically Active Radiation (PAR) was measured above and below the canopy by a Plant Canopy Analyzer (SunScan, Delta-T Inc, Cambridge, UK) at late tillering stage (17 July), jointing stage (23 July), and milky and yellow ripening stage (15 September) in 2012 and at jointing stage (18 August), heading stage (2 September), and ripening stage (15 September) in 2013, respectively. Gap fraction (fGPAR) was defined as the ratio of the radiation below the canopy to radiation above the canopy.

2.7. Statistical Analyses

Statistical analyses were performed using SPSS 13.0 software (SPSS, Chicago, IL, USA). All data were assessed for normality and homogeneity using the Shapiro–Wilk test and Cochran's C-test, respectively. Subsequently, one-way analysis of variance (ANOVA) was performed using the general linear model univariate procedure. When significant differences were detected, the mean values of each treatment were compared using Duncan's multiple range test. In addition, a two-way analysis of variance (ANOVA) was carried out, followed by Duncan's multiple range tests to determine the effects of the irrigation, year, and position of internode on experimental parameters. Unless otherwise stated, the significance level was $p \leq 0.05$. Because the trends of trials in the two years are consistent, the results of the year 2013 are mainly reported.

3. Results

3.1. Weather Conditions

The daily average relative humidity in the 2012 season fluctuated between 46% and 84% during the rice growing season, while that for the 2013 season ranged from 47% to 88% (Figure 1). The maximum average daily temperature during the growth stage of rice was 33.0 °C in late July for 2012, while that for 2013 was 34.4 °C in early August. Compared with the 2012 season, the 2013 season had more precipitation in June and July but less precipitation in the middle of August, and the total precipitation in the 2013 season was 59 mm more than that of the 2012 season. Heavy rains (>50 mm per day) happened in the 2012 season during the jointing and booting stage, whereas that for the 2013 season was during the middle and late tillering stage (Figure 1). Thus, drainage occurred one time during the jointing and booting stage in the 2012 season, whereas one instance of drainage happened during the tillering stage in the 2013 season.

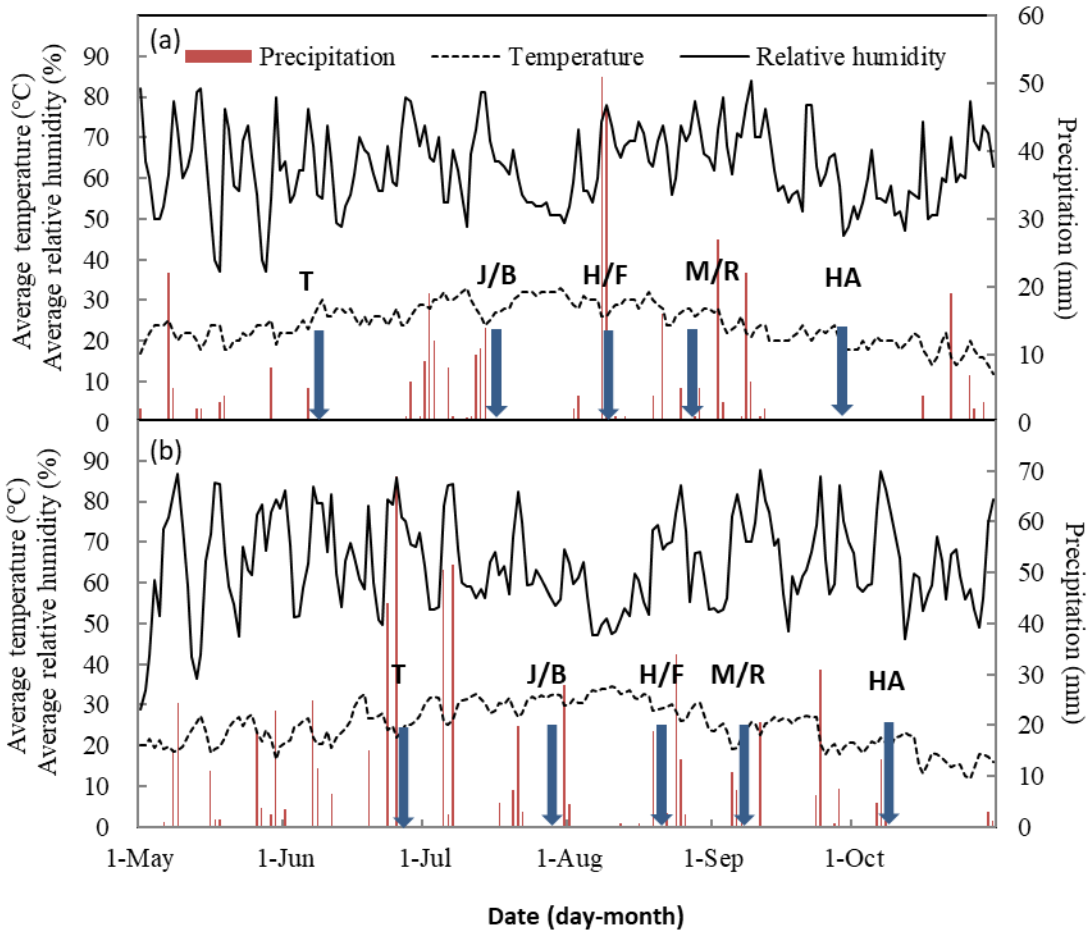

Figure 1. Average daily temperature, relative humidity, and precipitation during the rice growing season from May to October in (**a**) 2012 and (**b**) 2013. T, J/B, H/F, and M/R represent the beginning of tillering stage, jointing and booting stage, heading and flowing stage, and milky and ripening stage, respectively.

3.2. Bending Stress of Culms, Section Modulus of Culms, and the Safety Factor against Stem Breakage

There was no significant difference in the height of each tiller under different irrigation regimes (Table 2), whereas the fresh weights of the aerial part of CK had the highest value (25.6 g and 27.0 g for the 2012 and 2013 seasons, respectively) among different irrigation regimes for the two seasons, which was especially true in 2013 ($p < 0.05$, Table 2).

The results of the two-way analysis of variance (ANOVA) showed that the year had no significant effect on the height of each tiller or the fresh weights of the shoot ($p > 0.05$, Table 2). The self-weight moment of individual tillers was calculated from the weight of the aerial part, the height of the center of gravity of the tillers, and the inclination angle from the vertical for the rice plant. In this study, because the angle of inclination of each stem from the vertical was assumed to be the same (30°) and there was no significant difference in the height of gravity center of each tiller (data not shown), the differences of tiller self-weight moment under different irrigation regimes were largely determined by the weight of the aerial part of the tillers. As shown in Figure 2a, the values of the self-weight moment in CK were highest among the three irrigation regimes for both seasons, which was consistent with their heaviest aerial-part weight.

Table 2. The effects of treatments and output of two-way analysis of variance (ANOVA) for plant height, fresh weight (FW) of shoot, outer diameter (OD) of major and minor axis of internode II, and length of internode II of rice plants under different irrigation regimes during the rice-growing season of 2012 and 2013.

Year	Irrigation	Plant Height (cm)	Shoot fw (g)	Outer Diameter of the Major Axis of Internode II (mm)	Outer Diameter of the Minor Axis of Internode II (mm)	Length of Internode II (mm)
2012	CK [a]	81.3 ± 0.9 a	25.6 ± 1.2 a	5.52 ± 0.31 a	4.45 ± 0.25 a	7.80 ± 0.63 a
	CID-1	82.3 ± 1.1 a	21.9 ± 0.2 b	5.11 ± 0.25 a	4.52 ± 0.13 a	7.60 ± 0.41 a
	CID-2	80.6 ± 2.7 a	23.0 ± 1.7 ab	5.09 ± 0.21 a	4.07 ± 0.12 a	8.36 ± 0.40 a
2013	CK	81.4 ± 1.8 a	27.0 ± 0.7 a	5.69 ± 0.13 a	5.48 ± 0.12 a	6.73 ± 0.37 b
	CID-1	80.0 ± 1.9 a	21.5 ± 1.4 b	5.26 ± 0.11 a	4.87 ± 0.13 b	6.56 ± 0.32 b
	CID-2	77.8 ± 1.0 a	19.2 ± 0.9 b	4.69 ± 0.19 b	4.28 ± 0.20 c	8.83 ± 0.92 a
Irrigation		n.s.	**	*	*	*
Year		n.s.	n.s.	n.s.	n.s.	n.s.
Irrigation × Year		n.s.	n.s.	n.s.	n.s.	n.s.

Note: [a] The symbols of CK, CID-1, and CID-2 in this table denote different irrigation regimes, and detailed information on the symbols were shown in Table 1. The values in this table denote means ± SE of six replications. Means followed by the same letter in the same column during the same year do not differ significantly at the 5% level by Duncan's multiple range test. n.s., not significant. * $p < 0.05$, ** $p < 0.01$.

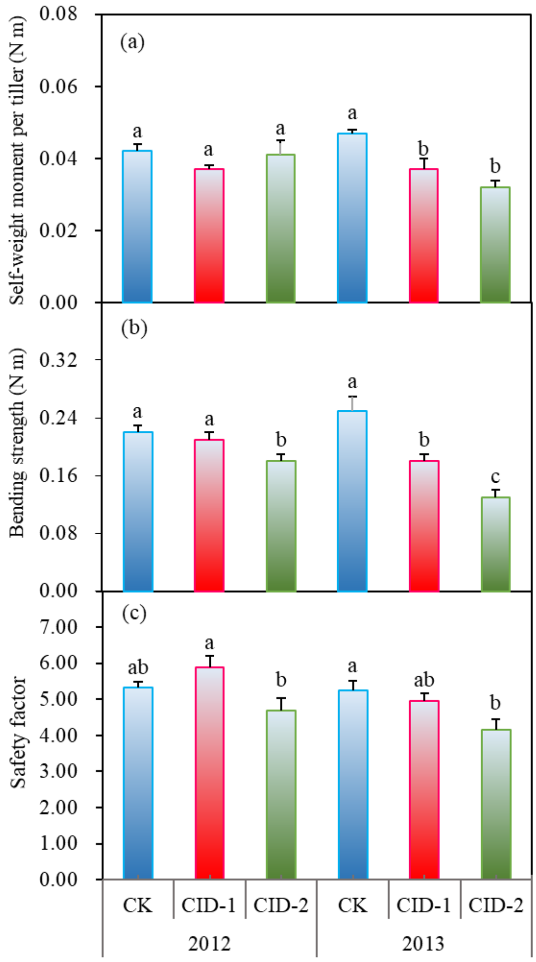

Figure 2. Effects of irrigation regimes on the (**a**) self-weight moment per tiller, (**b**) bending strength, and (**c**) safety factor of rice plants under different irrigation regimes during the rice growing season of 2012 and 2013. Data are means ± SE of six replicates. The different letters on the tops of columns for the same year indicate significant differences between treatments at 5%, according to Duncan's multiple range test.

The length and diameter of internode II under different irrigation regimes and years were illustrated in Table 2. Both the major and minor axis diameters of CID-2 (5.09 mm and 4.07 mm for the major axis and minor axis, respectively, in the 2012 season and 4.69 mm and 4.28 mm for the major and minor axis, respectively, in the 2013 season) were lower than those of CK and CID-1 in both seasons, and that was especially true for 2013 ($p < 0.05$, Table 2); the lengths of internode II in CID-2 were longer than that of CK in the 2012 and 2013 seasons by 7% and 28%, respectively, and CID-1 was in the intermediate for both seasons (Table 2). The year had no significant ($p > 0.05$) influence on the length and diameter of internode II. The bending strength (S) was one of the important parameters for the physical properties of the rice culm. In this study, the S values for N_2, N_3, and N_4 sections were shown in Table 3. For the N_2 section, the S value of CK was the highest, followed by CID-1, with the lowest value in CID-2 ($p < 0.05$, Table 3). In addition, across the irrigation regime, the S value gradually decreased from 0.192 N m in the N_2 section to 0.091 N m in the N_4 section. Similarly, as illustrated in Table 3, the section modulus (SM) values from the basal section to the following sections also showed the same trend as that of S. Across the irrigation treatment, the N_2 section had the highest value, the intermediate for N_3, and the lowest for N_4 (there were no significant differences for the SM values of the N_3 and N_4 sections). Irrigation regimes also had significant effects on the SM. Across the position of internode, CID-1 and CID-2 reduced the SM by 24.30% and 27.64%, respectively, compared to the CK treatment. The bending stress (BS) was a function of the culm cell wall component, and it could be calculated by the value of S and SM. The BS was significantly affected by the irrigation regime and interaction ($p < 0.05$, Table 3). Across the position of internode, the BS increased according to the following order: CID-2, CID-1, and CK, though the difference was tiny between CID-2 and CID-1. The values of the safety factor of the main tillers subjected to different irrigation regimes were calculated for a stem inclination from the vertical of 30°. The values of safety factor in CID-2 treatment were always the lowest in the 2012 and 2013 seasons (Figure 2c), which were consistent with the lowest values of their S values in both years.

Table 3. The output of one-way and two-way analysis of variance (ANOVA) for section modulus and bending stress under different irrigation regimes and position of internode during the rice growing season of 2013.

Irrigation	Position of Internode	Section Modulus (mm^3)	Bending Stress ($N\ mm^{-2}$)	Bending Strength at Breaking (N m)
CK	N_2	15.41 ± 1.17 a	16.55 ± 0.49 d	0.254 ± 0.016 a
	N_3	9.37 ± 1.18 bc	12.17 ± 0.91 cd	0.112 ± 0.013 cd
	N_4	7.64 ± 1.90 bc	14.36 ± 1.65 bcd	0.103 ± 0.015 cd
CID-1	N_2	10.96 ± 0.66 b	17.11 ± 0.47 bcd	0.186 ± 0.007 b
	N_3	8.26 ± 0.87 bc	13.97 ± 0.38 bcd	0.116 ± 0.015 c
	N_4	5.94 ± 1.49 c	18.87 ± 3.02 abcd	0.104 ± 0.022 cd
CID-2	N_2	10.94 ± 1.65 b	13.03 ± 1.35 abc	0.137 ± 0.012 c
	N_3	7.20 ± 0.68 bc	15.43 ± 0.55 ab	0.110 ± 0.011 cd
	N_4	5.93 ± 0.77 c	11.57 ± 0.76 a	0.067 ± 0.008 d
Irrigation		*	*	**
Position of internode		**	n.s.	**
Irrigation × Position of internode		n.s.	*	**

Note: N_2, N_3, and N_4 denote the second, third, and fourth section of rice culms counted from the base, respectively. Data are means ± SE of six replicates. Means followed by the same letter in the same column do not differ significantly at the 5% level by Duncan's multiple range test. n.s., not significant. * $p < 0.05$, ** $p < 0.01$.

3.3. Components of the Lower Culms and N Content in Flag Leaves

There were significant effects of the irrigation treatment on the chemical component concentrations of the lower part of rice culms (Table 4). For lignin concentration of the lower culms, CID-2 had the highest value, intermediate for CK, and CID-1 had the lowest values, whereas for cellulose content, the values of CK and CID-1 were almost the same, and both were significantly greater than that of CID-2 by almost 20%. In addition, there were also significant effects of irrigation regimes on ash content of the lower parts of the rice culms (Table 4). It was found that CK plants had the highest values of ash content ($p < 0.01$), followed by CID-1, with the lowest in CID-2 plants (Table 4). From Table 4, we could also see that there was no significant difference in N concentration for the top layer leaves of rice crops under different irrigation treatments ($p > 0.05$).

Table 4. Components of the lower culms and N content in leaf blade of rice plants under different irrigation regimes during the rice growing season of 2013.

Components of the Lower Culms	Treatment		
	CK	CID-1	CID-2
Cellulose (DW%)	29.6 ± 0.5 a	30.0 ± 0.4 a	25.1 ± 0.2 b
Lignin (DW%)	11.7 ± 0.1 b	9.3 ± 0.2 c	13.7 ± 0.4 a
Ash (DW%)	14.3 ± 0.1 a	11.1 ± 0.1 b	9.9 ± 0.5 c
N content in leaf blade (mg g^{-1})	11.07 ± 0.16 a	10.42 ± 0.18 a	10.75 ± 0.26 a

Note: The values in this table denote means ± SE of three replications. Means followed by the same letter in the same line do not differ significantly at the 5% level by Duncan's multiple range test.

3.4. Gap Fraction (fGPAR)

In the season of 2012, gap fraction (fGPAR) increased slightly from late tillering stage (17 July) to the jointing stage (23 July) and then decreased from jointing stage (23 July) to the milky and yellow ripening stage (15 September) for all the three irrigation regimes (Figure 3a). CID-2 showed the highest fGPAR values for the three growth stages, though there was no significant difference with varied irrigation regimes (Figure 3a). In the season of 2013, under all three irrigation regimes, fGPAR decreased from the jointing stage (18 August) to the heading stage (2 September) (Figure 3b), with lowest values in the CID-1 treatment. As shown in Figure 3b, there were significant differences for fGPAR at the heading stage (2 September) for different irrigation regimes ($p < 0.05$): CID-2 had the highest values (0.28), followed by CK (0.20), and CID-1 had the lowest values (0.18). The fGPAR of CID-2 kept a decreasing trend from the heading stage to the ripening stage, whereas CK and CID-1 increased slightly during that period.

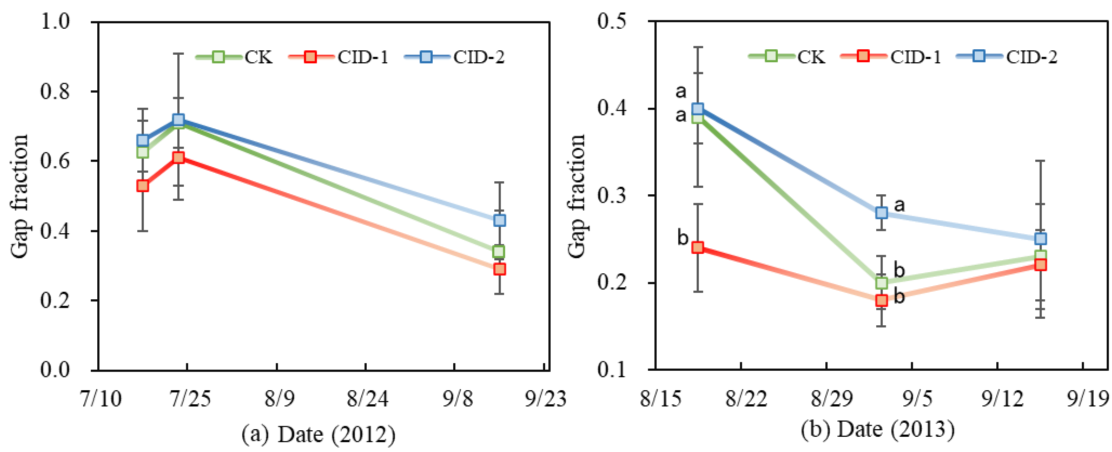

Figure 3. Effects of irrigation regimes on gap fraction (fGPAR) under different irrigation regimes during the rice growing season of (**a**) 2012 and (**b**) 2013. The date in the abscissa axis, for example 7/10, represent 10 July. Data are means ± SE of six replicates. The different letters on the tops of symbols during the same growth date indicate significant differences between treatments at 5% according to Duncan's multiple range test. The different letters were shown only when significant differences were detected.

4. Discussion

Safety factor against stem breakage (SF_s) was generally considered as an indicator to evaluate the lodging resistance of the rice plant. According to the studies by Crook and Ennos [41], with the decrease in SF_s, rice plants increase their tendency towards lodging. In this study, the lower value of SF_s for CID-2 treatment compared with CK and CID-1 treatment in both seasons (Figure 2c) might indicate that rice plants under CID-2 treatment, which kept relatively higher water levels after heavy rain than that of CK and CID-1, are much more likely to undergo lodging.

There were two main plant traits related to lodging resistance of rice. One is the plant's 'self-weight' moment, and the other is the physical strength of the culms; the former is determined by the morphological traits, such as the weight of the upper part and the plant height [17]. Moreover, of the morphological traits, plant height is one of key factors determining the lodging resistance of rice plants [1]. Previous studies indicated that flooding stress in paddy fields could stimulate stem elongation [11,38,39], whereas the drought stress caused by the 'water-saving technique' could result in lower heights compared with the reference treatment, which consisted of continuously ponding water [15]. In this study, no significant difference in plant height was detected among different irrigation regimes (Table 2), which might indicate that the reduction of plant height under drought stress could be compensated by the increase in culm length under the flooding stress following the drought stress [31,40]. Similarly, in 2013, for the values of fGPAR (which were closely related to LAI) during the heading and flowing stage, CID-2 treatment had significantly higher fGPAR values than those of CID-1 ($p < 0.05$, Figure 3b), whereas during the milky and yellow ripening stage, there was no significant difference between CID-1 and CID-2 ($p > 0.05$). This phenomenon might indicate that the compensation effects for leaf growth of CID-2, which kept higher ponding depth than CID-1, was temporarily higher than that of CID-1 during that period. The highest value of 'self-weight' moment for CK treatments among the treatments for both seasons (Figure 2a) is mainly determined by the higher values of above-ground fresh weights of CK treatments compared with the other two treatments (Table 2). Except for plant heights, the width and length of internodes immediately above the base of the shoot were also important morphological traits relating to lodging resistance of the rice plant. Shorter and thicker lower internodes increase lodging resistance [46]. Previous research reported that the length of the basal internode was closely correlated with leaf N concentration; with the decrease in leaf N concentration, the growth hormones which could promote internode elongation might be reduced and result in the reduction of internode length [47]. In this study, there was no significant difference in leaf N concentration of rice plants exposed to different irrigation conditions during the ripening stage (Table 4), so the significant difference in the length of the lowest internode might not be the result of the N content of leaves. Kamiji et al. [48] indicated that length of the lowest internode could also be affected by radiation levels at the base of the shoot; high radiation penetration around the panicle-initiation stage could shorten lower internodes. On the contrary, the highest value of fGPAR at the basal internode was accompanied by the longest basal internode for CID-2 treatment among the irrigation regimes in 2013 (Table 2 and Figure 3b), and the underlying mechanism still needs further exploration.

Bending strength (S) of lower internodes was one of the important plant traits relating to lodging resistance of rice [1,18]. Since stem lodging usually occurs at the IV and V internode [42], only the second (N_2), third (N_3), and fourth section (N_4) of the culm counted from the base were measured in this study. For the N_2 section, the S value of CK and CID-1 were significantly higher than that of CID-2 ($p < 0.05$, Table 3). S values were closely related to two parameters. One is the section modulus (SM), which is a function of culm morphological traits, such as the culm wall thickness and diameter. The other is the bending stress (BS), which is largely influenced by stem chemical components, such as silicon, starch, lignin, and cellulose content [5,6]. To illustrate the mechanism behind the low S values of CID-2 (Figure 2b and Table 3), SM values were calculated. The SM of CK was over 1.5 times larger than that of CID-1 and CID-2 (Table 3), which was the result of the large culm diameter of CK (Table 2). Similarly, for the same treatment, the significant decrease in SM from the basal section to the following sections was consistent with the dramatically decreased culm diameter and culm wall thickness from N_2 to N_4 (data not shown). Meanwhile, the BS of CK and CID-1 were higher than that of CID-2 ($p < 0.05$, Table 3), which might indicate that the compositions of the culm of CID-2 were inferior to that in the CK and CID-1 treatment with respect to lodging resistance [49]. Previous studies indicated the lower cellulose contents and higher contents of lignin could cause the culm to be brittle [13,50]. In keeping with this, the higher BS values of CK and CID-1 (Table 3) in this study might be attributed to the significantly higher level of cellulose and lower lignin content in the culms compared with CID-2 (Table 4). However, Ookawa et al. [51] indicated that the increased lignin concentration could result in the higher bending strength of the culm. Thus, the reasons for the contrasting results are still elusive and require further research. In addition to cellulose and lignin, higher silicon contents are also closely correlated with physical strength [52,53]. Ma and Yamaji [54] reported that silicon could be deposited in silicified cells in the epidermis and vascular tissues of stems, which consequently improved the rigidity and strength of cell walls, thus improving lodging resistance. Moreover, ash content has a positive, linear relationship with silicon concentration in cereal plants [55]. Even though the silicon content of the culms was not investigated in this study, we observed that the ash content was the highest in the CK culms, followed by CID-1, with the lowest in CID-2 treatments ($p < 0.05$, Table 4). The higher ash content in the CK plants might imply that the silicon concentration of CK was also higher than the other irrigation treatments and consequently contributed to the improved bending strength of the culms (Figure 2b). Collectively, irrigation regimes could not only change the morphological traits of rice plant, but also could affect the chemical concentration in the rice culms. The changes in chemical content in the basal internode could be affected by the values of fraction of canopy radiation interception or fGPAR [56,57] and translocation of carbohydrates and nutrients [58], which could be influenced by irrigation regimes [40]. Although the underlying physiological mechanism of rice for this change exposed to different irrigation regimes is not clear, alternating drought and flooding could both directly and indirectly affect the morphological traits and the strength of the culm and the resulting lodging resistance.

In conclusion, irrigation regimes could change the morphological traits as well as the chemical concentration of rice plants and consequently influence the mass moment of the aerial part of the rice plant and the breaking strength of the culms, which determines the safety factor of the rice stem. Properly increasing the depth of water levels (lower than 10 cm) after heavy rain in CID treatment under the current water-saving mode would not increase the risk of lodging for rice plants, whereas if the water depth after heavy rain was kept higher than 15 cm, the SF_s would be significantly lower than that of CK, and the rice plants would be much more likely to undergo lodging. These results will provide deeper insights into the mechanism controlling lodging resistance in rice plants induced by irrigation regimes and could help in the management of irrigation under water-saving irrigation regimes.

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