RESEARCH ARTICLE

Stem lodging parameters of main culm and primary tiller of upland rice cultivars as affected by nitrogen fertilizer rates

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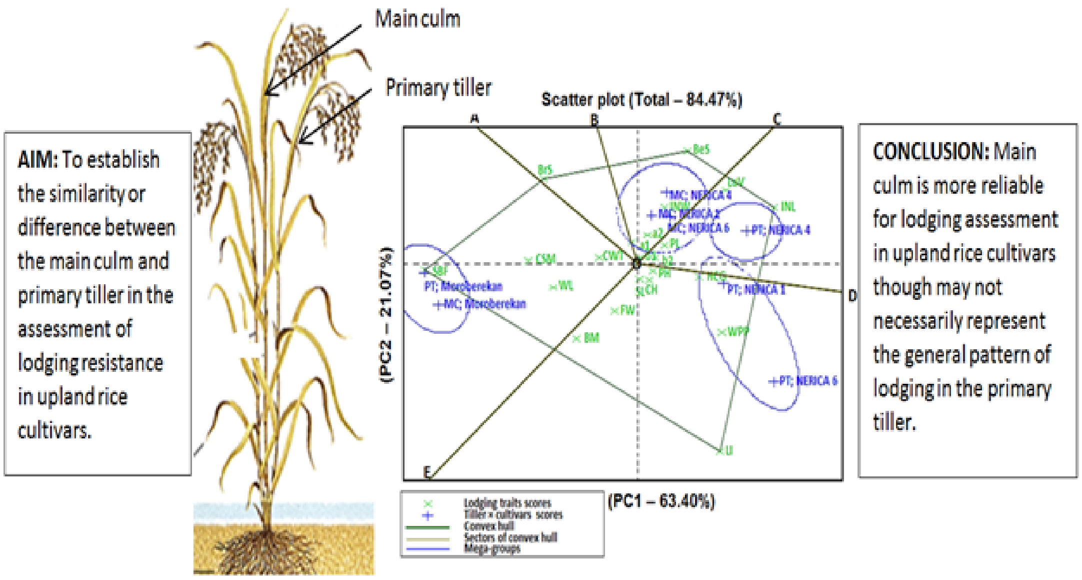

Highlights

- Stem lodging parameters varied among tillers and is cultivar dependent.
- Index of lodging is influenced mainly by weight related lodging traits.
- Moroberekan is an ideal cultivar for testing stem strength in upland rice.
- Moderate application of nitrogen fertilizer do not affect lodging index of tillers.
- Main culm is more reliable for assessment of lodging than the primary tiller.

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Stem lodging parameters of main culm and primary tiller of upland rice cultivars as affected by nitrogen fertilizer rates

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Abstract: Lodging resistance (LR) assessment is usually carried out using the main culm (MC) which can be mixed-up with the primary tiller (PT), both of which can vary in morphology. Four rice cultivars namely: NERICAs 1, 4, 6 and Moroberekan were established under three rates (0, 60, 120 kg ha^{-1}) of nitrogen fertilizer. At 20 days after heading of each of the MC and PT, the culms were harvested for LR assessment. Higher nitrogen fertilizer rates increased the outer minor diameter, stem breaking force and stem length from breaking point to panicle top of both the MC and PT. Lodging traits (LTs) varied among the rice cultivars but the rice cultivars responded similarly to application of nitrogen fertilizer in the MC unlike the inconsistencies observed in the PT. The LTs were higher in MC and with lower lodging index than in the PT. The LTs of MC and PT of Moroberekan were similar unlike differences observed between the two tillers among the NERICAs. The MC remains reliable for the assessment of LR but does not represent the general pattern of lodging in the PT of upland rice cultivars. Consistency in tiller selection is required for an unbiased assessment of lodging among upland rice cultivars.

Keywords: Lodging index; main culm; NERICAs; nitrogen fertilizer; primary tiller.

INTRODUCTION

Lodging is a major problem in achieving high yields in many crops, especially in cereals, due to the hollow nature of the stem (Berry and Spink, 2012). Lodging, which describes bending to the prostrate appearance of the stem, can result in an 80% loss in crop yield if not properly managed (Foulkes *et al.,* 2011; Muhammad *et al.,* 2020). Lodging develops either as a result of the inability of the root to anchor plants to its substratum (Manzur *et al.,* 2014) or the possession of a weak stem that cannot withstand the weight of a panicle (Plaza-Wüthrich *et al.,* 2016). Variations in basal and aerial stem diameter combined with increased fruit weight instigated by increased nitrogen fertilizer rates have also been reported to contribute to lodging (Olagunju *et al.,* 2019). Culm lodging traits such as increased primary panicle weight, culm height, plant height, height at the center of gravity, culm wall thickness, internode diameter, internode weight, and internode length and lumen volume are some of the traits associated with lodging that has been used to assess lodging resistance in cereals (Zhang *et al.,* 2016b; Olagunju *et al*., 2021). Assessment of lodging using these traits is usually limited to the main culm as a good representative of tillers on rice plants, whereas there is an increased possibility of selection of a primary tiller in place of the main culm, which may affect the reliability of the overall assessment. Investigation of the similarity or otherwise of culm lodging traits of primary tiller in expressing resistance to lodging as the main culm, which could guide the selection of tillers for lodging resistance assessment, requires adequate attention.

Tillers are formed in cereals from non-elongated internodes at the base of the stem in acropetal succession (Yoshida, 1981; Mohapatra *et al.,* 2011). The main culm is usually higher in vigour than the tillers and it usually bears the heaviest panicle weight though the panicle on the primary tiller can also compete well with the main culm in some cultivars. Previous studies have reported the variations in panicle weight of the main culm and the primary tiller and their contribution to total grain yield (Duy *et al.,* 2004; Wang *et al.,* 2017; Huang *et al.,* 2020). However, there is a scarcity of information on differences in lodging traits of the main culm and the primary tiller that terminate in the panicle and their contribution to lodging in upland rice. The number of vascular bundles decreases from the primary to tertiary tillers of rice cultivars and could limit the amount of assimilates transported to late-emerging tillers (Mohapatra *et al*., 2011). A slight variation in vigour and panicle weight of tillers can result in differing responses in lodging resistant traits. Among the culm lodging traits influencing lodging resistance in upland rice, panicle weight plays a pivotal role in demanding increased strength of the culm walls to sustain the vertical form. This can differently influence the culm lodging traits between the main culm and the primary tiller.

One of the management practices influencing panicle weight in cereals is the application of nitrogen fertilizer to stimulate increase in grain yield of rice through an increase in the number and weight of filled spikelets (Yi *et al.,* 2019). Nitrogen also significantly affects tillering in

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upland rice and can modify the growth form of tillers due to its regulatory role in tiller bud growth (Wang *et al.,* 2016; Wang *et al*., 2017). Upland rice responds well to nitrogen fertilizer by increasing vegetative organs and producing higher panicle weight. Increased nitrogen fertilizer rates can predispose upland rice to lodging, attributed to reduced structural carbohydrates combined with assimilating loading from the stem into the grains especially when nitrogen is applied at very high rates (Wang *et al.,* 2015; Zhang *et al.,* 2016b). Past studies on the effect of nitrogen fertilizers on lodging traits had reported increased culm wall thickness, culm diameter with reduced internode length and breaking strength at high fertilizer rates (Zhang *et al.,* 2016b). The ability of a cultivar to balance the heavy weight of the panicle with sturdiness of the basal part for improved lodging resistance is a way to achieve high yield in lodging prone areas under nitrogen fertilizer application (Ma *et al*., 2004; Nomura *et al*., 2019). However, balancing the panicle weight with a sturdy basal stem can vary between the main culm and the primary tiller.

The New Rice for Africa (NERICA) is among the commonly cultivated rice bred purposely for high yield and tolerance to drought and pest attack and the ensuing harsh environmental condition that crops are exposed to in the tropics (Dingkuhn *et al.,* 1998; Balasubramanian *et al.,* 2007; Ndjiondjop *et al*. 2018). The cultivars obtained from the cross between *Oryza sativa* and *Oryza glaberrima*, are known to have between moderate to tall height with high yield (Africa Rice Center, 2008). Until recently, the mechanical basis of lodging resistance in first-generation NERICA cultivars was not elucidated. Past studies on the first-generation NERICAs, *i.e.* NERICAs 1 to 8, had established good resistance of these rice cultivars to lodging based on visual scoring (Africa Rice Center, 2008). A recent study, however, conducted on the rice cultivars established significant differences in lodging resistance based on culm lodging traits under silicon application (Olagunju *et al.,* 2021). The NERICAs 1, 4 and 6 were among the few cultivars selected for having higher resistance to lodging among the cultivars in addition to Moroberekan, a well-known cultivar for its massive root system and sturdy stem. Adequate knowledge of the mechanical basis of lodging has been suggested in order to further understand lodging resistance in rice cultivars, as this can aid in achieving a milestone in reducing lodging during plant breeding programs (Crook and Ennos, 1994; Oladokun and Ennos, 2006). The mechanical basis of lodging is influenced by nitrogen fertilizer application which is yet to be established in these selected cultivars.

Studies that investigated the effect of nitrogen fertilizers on the yield of rice cultivars are many (Zhang *et al*., 2014b; Khan *et al.,* 2017; Zhang *et al.,* 2017), but scanty literature exists on the similarities or otherwise of the mechanical basis of lodging of main culm and primary tiller in differentiating lodging resistance among rice cultivars under rates of nitrogen fertilizer. Furthermore, it is important to establish the effect of nitrogen fertilizers on the culm lodging traits of the rice cultivars. We, therefore, hypothesized that the culm lodging traits contributing to lodging exhibit similar lodging resistance among rice tillers and that response of these lodging traits to nitrogen fertilizer application are the same in the main culm and primary tiller. Specifically, we ask the following questions (i) do culm lodging traits of the main culm and primary tiller confer similarities in lodging resistance among rice cultivars? (ii) Do the main culm and primary tiller of upland rice cultivars respond similarly to increase nitrogen fertilizer rates? (iii) In which of these culms do the culm lodging traits better express lodging resistance among the rice cultivars under varying nitrogen fertilizer rates?

MATERIALS AND METHODS

Experimental site

The experiment was conducted in an open field pot experiment within the Teaching and Research Farm of College of Agricultural Sciences, Olabisi Onabanjo University, Ayetoro Ogun State of Nigeria. The area was characterized by an erratic rainfall pattern with an average annual rainfall of 1200 mm. The temperature ranged between 22–23 °C in the morning to 32-33 °C in the afternoon and relative humidity from 55% to 80%. The soil texture was loamy sand based on analyses conducted before and after the experiment. The pH of the soil was moderately acidic (5.15). Exchangeable bases (Ca, Mg, Na and K), Effective Cation Exchange Capacity (ECEC), base saturation, total nitrogen, organic carbon and available P were also measured before and after the experiment (Table 1). Nutrient analyses of the soil before the experiment revealed a moderate soil fertility level which lowered after the experiment.

Soil sample collection, preparation and analyses

The soil used in the experiment was scooped to a depth of 0 - 15 cm from the Teaching and Research Farm. The soil collected was homogenized to obtain uniform soil samples across pots. A sub-sample of the soil was air-dried and sieved with a 2 mm sieve before being taken to the laboratory for analysis. A similar procedure was carried out on soil samples collected on a treatment basis after the experiment. In the laboratory, the pH of the soil was determined in a 1:2 soil water ratio with a glass electrode meter (McLean 1982) (Table 1). The hydrometer method was used to determine the particle size distribution of soil samples (Gee and Bauder 1986). calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na) were extracted using the ammonium acetate method (Thomas 1982). Following extraction of exchangeable bases, Ca and Mg were determined with Atomic Absorption Spectrophotometer (AAS), Buck Scientific 210 VGP model Norwalk, California, while K and Na were read on a flame photometer. The titration method was used in determining the exchangeable acidity (Anderson and Ingram, 1993). The summation of exchangeable bases and exchangeable acidity was used in estimating the ECEC (Anderson and Ingram, 1993). The fraction of the exchangeable bases and ECEC expressed in percentage was used in calculating the base saturation. Total nitrogen was determined by the Kjeldahl method (Bremner, 1996). Organic carbon was determined by the wet oxidation method as described by

Walkley-Black (Nelson and Sommer, 1996), while the Bray-1 method was used in determining the available phosphorus (Bray and Kurtz, 1945)

Experimental design

The experiment was a factorial combination of four upland rice cultivars, namely NERICAs 1, 4, 6 and Moroberekan; and three rates of nitrogen fertilizer: 0, 60, and 120 kg ha^{-1}, with three replicates in a Complete Randomized Design. A uniform number of seeds of each rice cultivar was first nursed in a pot containing 5 kg of loamy sand soil for 21 days. At 14 days after sowing (DAS), the seedlings were supplied with 3 g of 20N-10P-10K inorganic fertilizer in preparation for transplanting. At 21 DAS, seedlings were transplanted into pots containing 10 kg soil that had already been homogenized manually before potting to ensure uniformity in nutrient distribution within the soil. Seedlings were transplanted at one seedling per pot, after which the soils were watered to full field capacity. Pots receiving the 60 and 120 kg ha^{-1} of nitrogen fertilizer treatment were all supplied with 20N-10P-10K at 60 kg ha^{-1}N, 30 kg ha^{-1}P and 30 kg ha^{-1} K equivalent of 1.35 g of the fertilizer per pot. The remaining nitrogen dose (60 kg ha^{-1}N) for pots receiving 120 kg ha^{-1} was supplied using urea at an equivalent rate of 0.58 g per pot at the maximum tillering stage. At the seedling stage, the pots were watered every other day, which increased to every day at the maximum tillering stage. Between the maximum tillering and maturity when panicles were initiated and fully formed, the watering of pots was done in the morning and evening.

Sampling and measurement for lodging traits

At 20 days after heading of each main culm and primary tiller, both stems were cut from the soil level with the leaf and leaf sheaths intact. The primary tiller was harvested 7 days after harvesting the main culm in all cultivars, while harvesting the main culm and the primary tiller was delayed correspondingly by two weeks in the late maturing Moroberekan. Data were collected from the harvested culms immediately after harvesting of each main culm and primary tiller. The culms were taken to the laboratory for assessing the lodging resistance traits. The leaves and the leaf sheaths were first carefully removed to expose the inner skeleton of the culm while at the same time preventing the breakage of the culm during leaf sheaths removal. The height of the plant was determined by measurement from the base of the culm to the panicle top. Culm height was measured from the culm base to the neck of the panicle (Yoshida 1981). The culm skeleton was thereafter placed on a pivot/fulcrum until it reached an equilibrium to determine the height at center of gravity (HCG) (van Delden *et al.,* 2010). The culm was later cut into different segments at the nodes and the panicle neck. Panicle weight was determined by placing the panicle on a sensitive weighing machine (Model BY-B, 0.00g). Panicle length was also measured with a ruler from the panicle neck to the top of the panicle.

The second internode from the base of the culm was identified and further morphological analyses were conducted. Internode length, the distance between the two terminal ends of the internode, was measured using a meter ruler on a centimeter scale. Due to the oval nature of the culm, the internode diameter readings consisting of the minor diameter (the smaller diameter, a_1) and the major diameter (bigger diameter, b_1) were obtained by using a leaf thickness gauge (Model YH-1, Top Instrument, China). Internode weight was determined by placing the second internode on the sensitive weighing machine (0.00 g). To determine the stem breaking force (SBF), the internode segment was placed on two supports, separated at 4 cm, of a plant culm strength tester (Model TYD-1,Top Instrument, China), where a force was applied at the middle point of the internode until it breaks (Zhang *et al.,* 2014a). The maximum force applied, which gave the stem breaking force (SBF), was then recorded. The culm wall thickness was determined by cutting out a thin section of the culm walls along the length of the internode and placing it under the leaf thickness gauge. Lumen diameter, the diameter of the hollow space within the culm, which was also of two types viz inner minor (a_2) and inner major diameter (b_2) of the lumen, was determined using the following formula for the minor and major diameter.

$$\text{Lumen diameter (mm)} = \text{internode diameter (mm)} - 2 * \text{ culm wall thickness (mm)}$$

The lumen volume was determined using the formula;

$$Lumen\ volume\ (mm^3) = \pi\ a_2 b_2 \mathrm{h}$$

where a_2, b_2, and h are minor and major diameters of the lumen and length of the internode, respectively. The cross-section modulus, which measures the inherent stiffness and robustness of the stem, was computed as

$$Cross - section\ modulus\ (mm^3) = \left\{\frac{(a_1^3 * b_1 - a_2^3 * b_2)}{a_1}\right\} * \frac{\pi}{32}$$

(Zhang *et al.,* 2014a).

The stem length (SL) and fresh weight (FW) of the stem from the breaking point, the middle portion of the internode where a force was applied to determine the stem breaking force, to the top of the panicle were determined with measuring ruler and by weighing on the weighing machine, respectively. Bending moment (BM), which measures the physical strength of the rice culm, was computed as

$$Bending\ moment\ (g\ cm) = \text{Stem length from breaking point to panicle top (SL, cm)} * \text{Fresh weight from breaking point to panicle top (FW, g)}$$

Breaking strength was determined using the formula;

$$Breaking\ strength\ (g\ cm) = \frac{\text{Stem breaking force (N)} * \text{distance between the two fulcra, L (cm)}}{4 * 0.00981}$$

(Zhang *et al.,* 2016a).

Bending stress, which measures the stem rigidity as determined by cellulose and lignin content, was obtained as

$$Bending\ stress\ (g\ mm^{-2}) = \frac{\text{Breaking strenght (g cm)}}{\text{Cross} - \text{section modulus } (mm^3))}$$

The weight per unit length (W L^{-1}), which measures stem plumpness, was computed as

$$Weight\ per\ unit\ length\ (g\ cm^{-1}) = \frac{\text{weight of internode (g)}}{\text{Length of internode (cm)}}$$

Lodging index (LI), which measures the susceptibility of the rice cultivars to permanent displacement from their vertical position, was thereafter computed as

$$Lodging\ index = \frac{\text{Bending moment (g cm)}}{\text{Breaking strength (g cm)}}$$

This was achieved after converting the unit of breaking strength (N cm) to 'g cm' using a unit conversion of 1g = 0.00981N, in order to have a uniform unit.

Data analysis

Data collected on culm lodging traits of the main culm and primary tiller were subjected to Analysis of Variance separately. Significant treatment means were separated in descending order using Fisher's protected Least Significance Difference (LSD). Pearson's product moment correlation analysis was conducted between the culm lodging traits and lodging index for each main culm and primary tiller. Principal component analysis (PCA) of treatments × traits bi-plot was conducted in one analysis across the main culm and primary tiller. The statistical package used for the analyses was Genstat 15th edition (Payne *et al.,* 2009).

RESULTS

The result of analyses conducted on the soil before and after the experiment is presented in Table 1. The concentrations of exchangeable bases; Ca, Mg, Na and K, in the soil before the experiment were moderate (4.39, 1.01, 0.36, and 0.39 cmol kg^{-1}, respectively), except for the low concentration of Ca observed. The exchangeable bases became low in the soil after the experiment. The base saturation (98.09%), organic carbon (21.8 g kg^{-1}) and available phosphorus (26.29 mg kg^{-1}) in the soil were higher before the experiment and remained high after the experiment except for available phosphorus that was reduced to moderate level (13.32–14.99 mg kg^{-1}). The total N of the soil was within the critical limit of 0.15 -0.25 g kg^{-1} before and after the experiment when a higher rate (120 kg ha^{-1}) of 20N-10P-10K fertilizer was applied to the soil. At lower fertilizer rates, the total N of the soil became low (0.14 g kg^{-1}).

Nitrogen fertilizer rates significantly increased the outer minor diameter (a1), stem breaking force, cross-section modulus and stem length from breaking point to panicle top of the main culm and primary tillers of the rice

Table 1: Physico-chemical properties of the soil used in the study before and after the experiment.

Soil parameters	Before the experiment	After the experiment			Extractant/Methods
		At 0 N kg ha^{-1}	At 60 N kg ha^{-1}	At 120 N kg ha^{-1}	
pH	5.15	5.38	5.58	5.53	Soil water ratio 1:2
Sand (g kg^{-1})	852.0	845.3	845.3	825.3	Hydrometer method
Silt (g kg^{-1})	94.0	94.0	100.7	114.0	Hydrometer method
Clay (g kg^{-1})	54.0	60.7	54.0	60.7	Hydrometer method
Texture	Loamy sand	Loamy sand	Loamy sand	Loamy sand	Soil textural triangle
Ca (cmol kg^{-1})	4.39	4.22	4.48	4.23	Ammonium acetate
Mg (cmol kg^{-1})	1.01	0.87	0.98	0.94	Ammonium acetate
K (cmol kg^{-1})	0.39	0.11	0.09	0.07	Ammonium acetate
Na (cmol kg^{-1})	0.36	0.21	0.25	0.22	Ammonium acetate
Al+H (cmol kg^{-1})	0.12	0.1	0.1	0.1	Potassium chloride / acid-base titrimetric method
ECEC (cmol kg^{-1})	6.27	5.51	5.90	5.56	Ammonium chloride/ volumetric method
Base Saturation (%)	98.09	98.12	98.29	98.20	Estimation method
Total N (g kg^{-1})	1.8	1.4	1.4	1.7	Semi-micro-Kjeldahl
Organic Carbon (g kg^{-1})	21.8	18.5	19.7	18.5	Potassium dichromate
Av_P (mg kg^{-1})	26.29	14.92	13.32	14.99	Bray No. 1

cultivars (Tables 2 and 3). Increased panicle length (PL, 26.53 cm) and plant height (PH, 100.75 cm) were observed with increased nitrogen fertilizer rates to 120 kg N ha^{-1}only in the main culm. In contrast, the outer major diameter (b1, 6.14 mm), inner minor diameter (a2, 3.57 mm), culm wall thickness (CWT, 0.93 mm) and breaking strength (5064 g cm) were significantly increased by nitrogen fertilizer in the primary tiller. Internode length was significantly reduced in the primary tiller than in the main culm by nitrogen fertilizer rates. The lodging index was not affected by nitrogen fertilizer rates in the main culm and primary tiller.

Among the cultivars, NERICA 6 and Moroberekan were observed to have the tallest culm height and plant height in both the main culm and primary tiller. The cultivars were also observed to have the broadest outer major diameter (b1) and outer minor diameter (a1), and inner major diameter (b2) in the main culm. In contrast, Moroberekan had the widest outer major (b1, 6.41 mm) and outer minor diameter (a1, 5.62 mm) in the primary tiller (Table 2). Furthermore, NERICA 6 and Moroberekan were observed to have the longest stem length, highest fresh weight from the breaking point to the panicle top, and the highest bending moment in both the main culm and primary tiller (Table 3). In the main culm, lodging index was higher in both NERICA 6 (0.16) and Moroberekan (0.15), whereas the highest lodging index (0.23) was observed only in NERICA 6 in the primary tiller. No significant interaction between cultivars and nitrogen fertilizer rates was observed in the main culm. In the primary tiller, however, a significant interaction of nitrogen fertilizer and cultivar was observed on culm height, internode length, culm wall thickness, stem bending force, cross-section modulus, lumen volume, breaking strength and lodging index. Across all the culm lodging traits, lodging traits of the main culm were higher than that of the primary tiller.

Figures 1a-h illustrate the interaction of nitrogen fertilizer rates and cultivars on the culm lodging traits of the primary tiller of upland rice cultivars. Applying 60 and 120 kg N ha^{-1} significantly increased the culm wall thickness, stem bending force and cross-section modulus of Moroberekan (Figs. 1 c-e, respectively), while applying 120 kg N ha^{-1} was more effective in improving the culm lodging traits of NERICA 6, except for the application of 60 kg N ha^{-1} that increased the culm height (88.03 cm) and lodging index (0.31) of the cultivar. The primary tiller of NERICAs 1 and 4 was not affected by nitrogen fertilizer rates except for the application of 60 kg N ha^{-1}, which significantly increased the cross-section modulus, breaking strength of NERICA 1 and the internode length of NERICA 4. The lodging index of Moroberekan, and NERICAs 1 and 4 was not affected by nitrogen fertilizer rates.

The correlation between the lodging traits and lodging index of the main culm and primary tiller is presented in Table 4. Higher correlation coefficients were observed in the main culm than in the primary tiller. The correlation coefficients of internode weight, culm wall thickness, stem breaking force and lumen volume with lodging index were not significant in both the main culm and the primary tiller. All significant correlations of culm lodging traits with lodging index in the primary tiller were also significant in the main culm but not *vice-versa* except for breaking strength (-0.25^{ns} in the main culm and -0.55*** in the primary tiller). The bending stress recorded the highest significant inverse correlation (-0.79**) with the lodging index in the main culm, while the height at the center of gravity had the highest significant correlation (0.59**) with the lodging index in the primary tiller.

The principal components biplot of tiller × cultivars by traits interaction is illustrated in Fig. 2. The biplot captured a total of 84.47% variation in tiller × cultivars by traits interaction. The biplot grouped the tiller × cultivar interactions into four groups and five sectors (Sectors AOB, BOC, COD, DOE and AOE). The main culm and primary tiller of Moroberekan were grouped together and within sector AOE, while the main culms of the NERICAs were grouped in a separate environment and within BOC sector. However, the primary tillers of the NERICAs were separated into two groups. Primary tillers of NERICAs 1 and 6 were grouped, while the primary tiller of NERICA 4 occupied a separate group within the COD sector. In sector AOE, stem bending force maintained positive trait interaction with the main culm and primary tiller of Moroberekan and was closely associated with cross-section modulus, weight per unit length and culm wall thickness. Bending stress maintained positive trait interaction with the main culm of the NERICAs and was influenced by internode weight and outer and inner minor diameters. The lodging index of the rice cultivars, however, maintained positive trait interaction with the primary tiller of NERICAs 1 and 6 within sector DOE and was influenced mainly by bending moment, stem length and fresh weight from breaking point to panicle top, culm and plant height, height at the center of gravity and panicle weight of tillers.

The biplot captured 88.16% variation in cultivar × nitrogen fertilizer by traits interaction (Fig. 3). Five groups and six sectors were identified within the biplot. Moroberekan across the three rates of fertilizer was grouped in a separate environment, NERICA 6 across the three fertilizer rates were grouped into two separate groups, while NERICA 6 under 0 and 60 kg N ha^{-1} occupied a separate group. NERICAs 1 and 4 across the three fertilizer rates were grouped within two overlapping groups. The stem bending force was observed to maintain a positive trait interaction with Moroberekan across the three rates of fertilizer with cross-section modulus, weight per unit length, breaking strength and culm wall thickness, maintaining closer association with the lodging trait within the sector AOF.

DISCUSSION

The main culm and primary tiller of different rice cultivars exhibited differences in culm lodging traits with the main culm having higher culm lodging traits than the primary tiller. It cascaded in differences in the expression of lodging index between the main culm and primary tiller of the rice cultivars, with the main culm having a higher lodging resistance (reduced lodging index) than the primary

Table 2: Effect of nitrogen fertilizer rates on culm lodging traits of main culm and primary tiller of upland rice cultivars.

Tiller types	Sources of variation	Levels of variation	WPP (g)	PL (cm)	HCG (cm)	CH(cm)	PH (cm)	IL (cm)	b_1 (mm)	b_2 (mm)	a_1 (mm)	a_2 (mm)	INW (g)
	Nitrogen rates	0	3.30^{a}	23.73^{b}	45.45^{a}	71.22^{a}	94.96^{b}	12.02^{a}	6.04^{a}	4.36^{a}	5.24^{b}	3.57^{a}	1.83^{a}
	(N, kg ha^{-1})	60	3.96^{a}	24.46^{b}	47.85^{a}	72.07^{a}	96.53^{ab}	11.50^{a}	6.24^{a}	4.42^{a}	5.56^{ab}	3.74^{a}	1.75^{a}
		120	3.59^{a}	26.53^{a}	48.59^{a}	74.21^{a}	100.75^{a}	9.92^{a}	6.32^{a}	4.43^{a}	5.75^{a}	3.86^{a}	1.68^{a}
		LSD	*0.74*	*1.34*	*3.92*	*4.95*	*4.75*	*2.09*	*0.36*	*0.33*	*0.32*	*0.32*	*0.36*
		Significance	ns	***	ns	ns	*	ns	ns	ns	**	ns	ns
Main culm	Cultivars	NERICA 1	3.34^{a}	23.43^{c}	42.80^{c}	59.90^{c}	83.33^{c}	10.53^{ab}	5.40^{c}	3.69^{c}	4.94^{c}	3.22^{c}	1.34^{b}
	(C)	NERICA 4	3.23^{a}	24.52^{bc}	45.66^{bc}	66.29^{b}	90.81^{b}	12.72^{a}	6.02^{b}	4.33^{b}	5.32^{b}	3.64^{b}	1.75^{b}
		NERICA 6	4.22^{a}	26.46^{a}	52.51^{a}	82.74^{a}	109.20^{a}	12.59^{a}	6.59^{a}	4.76^{a}	5.80^{a}	3.97^{ab}	2.18^{a}
		Moroberekan	3.67^{a}	25.22^{ab}	48.22^{ab}	81.07^{a}	106.29^{a}	8.73^{b}	6.78^{a}	4.83^{a}	6.00^{a}	4.05^{a}	1.74^{b}
		LSD	*0.86*	*1.55*	*4.52*	*5.72*	*5.48*	*2.41*	*0.42*	*0.38*	*0.38*	*0.37*	*0.42*
		Significance	ns	***	***	***	***	***	***	***	***	***	***
	N × C		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
		Grand mean	3.62	24.91	47.30	72.50	97.41	11.14	6.20	4.40	5.52	3.72	1.75
	Nitrogen rates	0	3.88^{a}	22.93^{a}	46.08^{a}	68.74^{a}	91.67^{a}	12.37^{a}	5.47^{c}	4.01^{a}	4.64^{b}	3.18^{b}	1.36^{a}
	(N, kg ha^{-1})	60	3.90^{a}	23.32^{a}	47.81^{a}	71.85^{a}	95.17^{a}	11.74^{a}	5.84^{b}	4.16^{a}	4.91^{b}	3.22^{b}	1.35^{a}
		120	3.69^{a}	24.48^{a}	46.32^{a}	71.38^{a}	95.86^{a}	9.25^{b}	6.14^{a}	4.28^{a}	5.44^{a}	3.57^{a}	1.57^{a}
		LSD	*0.67*	*1.47*	*3.42*	*3.79*	*4.68*	*2.07*	*0.30*	*0.32*	*0.30*	*0.31*	*0.38*^{a}
		Significance	ns	ns	ns	ns	ns	**	***	ns	***	*	ns
Primary tiller	Cultivars	NERICA 1	4.38^{a}	23.66^{a}	46.29^{b}	63.50^{c}	87.16^{b}	11.84^{a}	5.51^{c}	3.88^{b}	4.80^{b}	3.18^{a}	1.26^{a}
	(C)	NERICA 4	3.22^{b}	22.21^{a}	45.62^{b}	67.78^{c}	89.99^{b}	13.80^{a}	5.50^{c}	4.09^{ab}	4.67^{b}	3.26^{a}	1.44^{a}
		NERICA 6	4.60^{a}	23.93^{a}	52.36^{a}	78.32^{a}	102.25^{a}	12.07^{a}	5.86^{b}	4.21^{ab}	4.88^{b}	3.23^{a}	1.61^{a}
		Moroberekan	3.09^{b}	24.50^{a}	42.67^{b}	73.03^{b}	97.53^{a}	6.77^{b}	6.41^{a}	4.42^{a}	5.62^{a}	3.63^{a}	1.40^{a}
		LSD	*0.77*	*1.70*	*3.95*	*4.37*	*5.40*	*2.39*	*0.35*	*0.37*	*0.34*	*0.36*	*0.44*
		Significance	***	ns	***	***	***	***	***	*	***	ns	ns
	N × C		ns	ns	ns	***	ns	***	ns	ns	ns	ns	ns
		Grand mean	3.82	23.57	46.73	70.66	94.23	11.12	5.82	4.15	4.99	3.33	1.43

*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$; ns = non-significant; means with the same letter(s) along the same column are not significantly different from one another using Fisher's Protected LSD; ns= non-significant; LSD = Least significant difference. WPP = Weight of primary panicle length; HCG = Height at center of gravity; CH = Culm height; PH = Plant height; IL= Internode length; b_1 = outer major diameter; b_2= inner major diameter; a_1= outer minor diameter; a_2= inner minor diameter; IW = Internode weight;

Table 3: Effect of nitrogen fertilizer rates on culm lodging traits of main culm and primary tiller of upland rice cultivars continued.

Tiller types	Sources of variation	Levels of variation	CWT (mm)	SBF (N)	CSM (mm^3)	LuV (mm^3)	SL (cm)	FW (g)	BM (g cm)	BrS(g cm)	BeS (g mm^{-2})	W L^{-1} (g cm^{-1})	LI
Main culm	Nitrogen rates	0	0.84^{a}	17.4^{b}	12.88^{b}	1479^{a}	87.06^{b}	7.41^{a}	668^{a}	5148^{a}	4146^{a}	0.16^{a}	0.13^{a}
	(N, kg ha^{-1})	60	0.91^{a}	23.7^{a}	15.22^{ab}	1546^{a}	88.66^{ab}	8.61^{a}	788^{a}	6322^{a}	4363^{a}	0.16^{a}	0.12^{a}
		120	0.94^{a}	26.5^{a}	16.35^{a}	1353^{a}	93.07^{a}	8.62^{a}	823^{a}	6588^{a}	4089^{a}	0.17^{a}	0.13^{a}
		LSD	*0.09*	*5.46*	*2.44*	*390.2*	*4.88*	*1.20*	*149.8*	*1487.8*	*877.6*	*0.03*^{a}	*0.03*
		Significance	ns	***	*	ns	*	ns	ns	ns	ns	ns	ns
	Cultivars	NERICA 1	0.86^{a}	20.9^{b}	10.57^{b}	969^{c}	76.14^{b}	6.41^{b}	493.2^{b}	5086^{a}	4915^{a}	0.13^{c}	0.10^{b}
	(C)	NERICA 4	0.84^{a}	17.1^{b}	13.02^{b}	1573^{ab}	81.67^{b}	6.64^{b}	546.0^{b}	5477^{a}	4289^{a}	0.14^{bc}	0.10^{b}
		NERICA 6	0.92^{a}	21.2^{b}	16.76^{a}	1912^{a}	100.47^{a}	10.22^{a}	1034.4^{a}	6624^{a}	4032^{a}	0.17^{ab}	0.16^{a}
		Moroberekan	0.98^{a}	31.0^{a}	18.90^{a}	1382^{bc}	100.09^{a}	9.59^{a}	965.0^{a}	6890	3563	0.21^{a}	0.15^{a}
		LSD	*0.11*	*6.30*	*2.81*	*450.6*	*5.63*	*1.39*	*173.0*	*1717.9*	*1013.4*	*0.04*	*0.04*
		Significance	ns	***	***	***	***	***	***	ns	ns	***	***
	N × C		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	n s
		Grand mean	0.90	22.6	14.81	1459	89.59	8.22	760	6019	4199	0.16	0.13
Primary tiller	Nitrogen rates	0	0.73^{c}	13.48^{c}	8.96^{c}	1240^{a}	81.79^{b}	6.85^{a}	567^{a}	3723^{b}	4164^{a}	0.12^{a}	0.16^{a}
	(N, kg ha^{-1})	60	0.84^{b}	17.59^{b}	11.32^{b}	1208^{a}	86.83^{a}	7.48^{a}	660^{a}	4212^{ab}	3954^{a}	0.15^{a}	0.18^{a}
		120	0.93^{a}	24.53^{a}	14.61^{a}	1117^{a}	88.77^{a}	7.92^{a}	715^{a}	5064^{a}	3573^{a}	0.19^{a}	0.14^{a}
		LSD	*0.06*	*2.51*	*1.85*	*295.3*	*4.25*	*1.25*	*141.2*	*880.0*	*696.2*	*0.06*	*0.03*
		Significance	***	***	***	ns	***	ns	ns	*	ns	ns	ns
	Cultivars	NERICA 1	0.81^{b}	14.31^{b}	10.06^{bc}	1157^{ab}	78.10^{b}	7.09^{ab}	556.7^{b}	4255^{b}	4212^{ab}	0.11^{b}	0.14^{b}
	(C)	NERICA 4	0.71^{c}	11.38^{c}	8.85^{c}	1441^{a}	79.39^{b}	5.79^{b}	461.4^{b}	3924^{b}	4486^{a}	0.11^{b}	0.12^{b}
		NERICA 6	0.82^{b}	16.48^{b}	11.42^{b}	1272^{a}	93.10^{a}	8.52^{a}	806.6^{a}	3808^{b}	3499^{bc}	0.16^{ab}	0.23^{a}
		Moroberekan	1.00^{a}	31.97^{a}	16.19^{a}	883^{b}	92.59^{a}	8.26^{a}	765.2^{a}	5344^{a}	3391^{c}	0.22^{a}	0.15^{b}
		LSD	*0.07*	*2.90*	*2.13*	*341.0*	*4.91*	*1.44*	*163.0*	*1016.1*	*803.9*	*0.07*	*0.04*
		Significance	***	***	***	*	***	***	***	*	*	***	***
	N × C		***	***	*	*	ns	ns	ns	*	ns	ns	***
		Grand mean	0.84	18.53	11.63	1188	85.80	7.41	647	4333	3897	0.15	0.16

$*p < 0.05$, $**p < 0.01$, and $***p < 0.001$; ns = non-significant; means with the same letter(s) along the same column are not significantly different from one another using Fisher's Protected LSD; ns= non-significant; LSD = Least significant difference. CWT = Culm wall thickness; SBF = Stem breaking force; CSM = Cross-section modulus; LuV = Lumen volume; SL = Stem length; FW = Fresh weight; BM = Bending moment; BrS = Breaking strength; WL = Weight per unit length; BeS = Bending stress; LI = Lodging index.

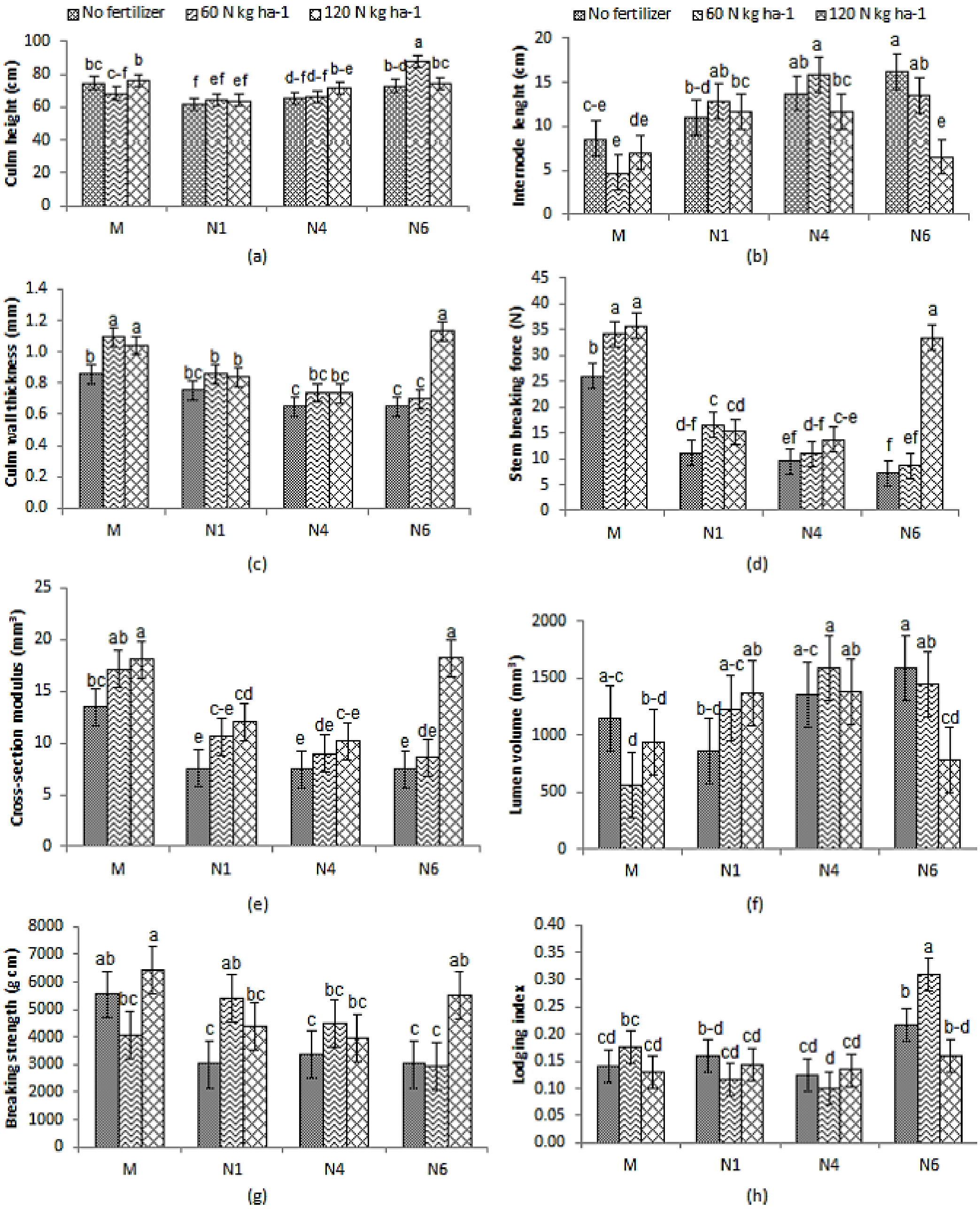

Figure 1: Interaction of nitrogen fertilizer rates and cultivar on (a) culm height (b) internode length, (c) culm wall thickness, (d) stem breaking force, (e) cross-section modulus, (f) lumen volume (g) breaking strength and (h) lodging index, of the primary tiller of rice cultivars. M = Moroberekan; N1, 4, and 6 are respectively NERICAs 1, 4 and 6.

tiller. Poor vascularization of late emerging tillers, which decreases the amount of assimilate that is transported to develop both the vegetative and the reproductive part of the tiller, could have played a role in the reduced culm lodging traits observed in the primary tiller.

Mohapatra *et al.,* (2011) observed a reduction in vascular bundles in subsequent tillers produced by rice which limited the amount of assimilate that can be transported to the primary tiller. Differences in culm lodging traits of the rice cultivars observed in both the main culm and primary tiller revealed differences in vigour and morphology of tillers on the rice cultivars. The increased culm lodging traits observed in Moroberekan among the cultivars were linked to its tall heights, robust stem and higher breaking strength. The observed increase in culm lodging traits of Moroberekan could have resulted in the grouping of the culm lodging traits of the main culm and primary tiller of the rice cultivars within the same environment in the biplot as well as grouping of the culm lodging traits of the rice cultivar across three rates of nitrogen fertilizer within the same environment. This is different to the separation of the main culm and primary tiller observed among the NERICAs. The decrease in panicle size, weight of panicle, and reduced vascular bundles which have been observed in the primary tiller of rice with and without nitrogen fertilizer by Wang *et al.,* (2016) and Wang *et al.* (2017) could therefore be said to be cultivar dependent as this appear to have limited influence on the primary tiller of Moroberekan but having a significant influence on the primary tiller of the NERICAs.

Table 4: Pearson's product moment correlation coefficients of culm morphological traits with the lodging index of the main culm and the primary tiller of upland rice across rates of nitrogen fertilizer.

Culm morphological traits	Main culm	Primary tiller
Internode length (cm)	-0.40*	-0.05^{ns}
Outer major diameter (mm)	0.39*	0.07^{ns}
Inner major diameter b_2, (mm)	0.38*	0.23^{ns}
Outer minor diameter (mm)	0.41*	-0.27^{ns}
Inner minor diameter (mm)	0.40*	-0.26^{ns}
Internode weight (g)	0.13^{ns}	0.17^{ns}
Culm wall thickness (mm)	0.14^{ns}	-0.17^{ns}
Stem bending force (N)	0.10^{ns}	-0.26^{ns}
Cross-section modulus (mm^3)	0.38*	-0.18^{ns}
Lumen volume (mm^3)	0.00^{ns}	-0.08^{ns}
Stem length (cm)	0.65***	0.50**
Fresh weight from breaking point to panicle top (cm)	0.57***	0.50**
Bending moment (g cm)	0.62***	0.53***
Breaking strength (g cm)	-0.25^{ns}	-0.55***
Bending stress (g mm^{-2})	-0.79***	-0.43**
Weight per unit length (g cm^{-1})	0.62***	0.18^{ns}
Panicle length (cm)	0.35*	0.23^{ns}
Panicle weight (g $tiller^{-1}$)	0.40*	0.48**
Height at centre of gravity (cm)	0.48**	0.59***
Culm height (cm)	0.60***	0.53***
Plant height (cm)	0.60***	0.54***

$*p < 0.05$, $**p < 0.01$, and $***p < 0.001$; ns = non-significant.

The similarity in response of lodging traits of the rice cultivars to the application of nitrogen fertilizer in the main culm and the inconsistencies in response of the lodging traits of the primary tiller to nitrogen fertilizer could have stemmed from differences in the ability of nitrogen fertilizer to elicit a similar morphological response in the primary tiller of the rice cultivars. This, combined with the inability of the rice cultivars to extend similar vigour of the main culm to the primary tiller, could have been responsible for this pattern of response to nitrogen fertilizer. The exceptional response of both the main culm and primary tiller of Moroberekan to the nitrogen fertilizer is worthy of note. In a study by Olagunju *et al.,* (2021) on culm lodging traits of first generation NERICAs, which also included Moroberekan and a locally grown Ofada cultivar, Moroberekan was identified as an exceptional cultivar with the highest culm lodging traits, vigor and sturdy stem. Olagunju *et al*. (2022) observed similar performance of Moroberekan among selected upland rice cultivars exposed to multi-growth stage water deficit and orthosilicic acid fertilizer. The increased vigour exhibited by Moroberekan even under no fertilizer re-affirms the potential of the cultivars to exhibit traits of improved lodging resistance in the main culm and the primary tiller in the absence of fertilizer. Lafarge *et al.,* (2002) observed that assimilate availability in the main culm at the time of tiller emergence is the main determinant of the fertility of the primary tiller. Nitrogen has also been implicated in modifying the growth form of tillers due to its regulatory role in tiller bud growth (Wang *et al.,* 2016; Wang *et al.,* 2017).

The non-significant differences in LI index observed across rates of nitrogen fertilizer in both the main culm and the primary tiller in this study could be attributed to the lodging resistance ability of the rice cultivars as the fertilizer rates applied are well above the rates recommended for rain-fed upland rice (Boude Bado *et al.,* 2018). Application of nitrogen fertilizer above the range adopted in this study may, however, have a different pattern on the lodging index response of the rice cultivars. A moderate application of nitrogen fertilizer has little influence on lodging but may increase the susceptibility of rice to lodging when applied

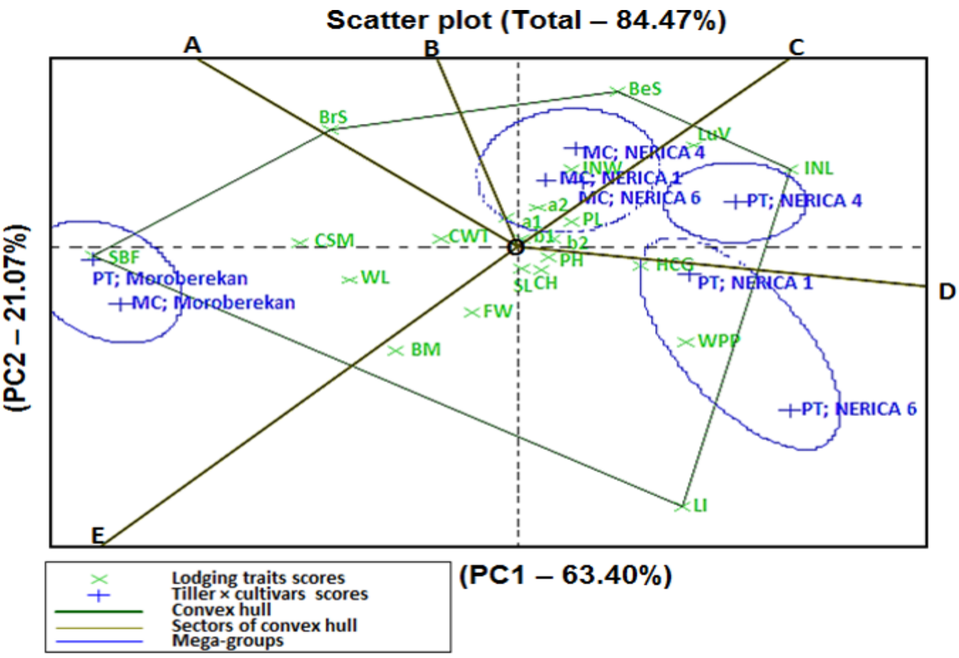

Figure 2: Principal component analysis biplot of tiller × cultivar by traits interaction of upland rice cultivars under nitrogen fertilizer rates.

WPP = Weight of primary panicle length; HCG = Height at center of gravity; CH = Culm height; PH = Plant height; IL= Internode length; b_1 = outer major diameter; b_2= inner major diameter; a_1= outer minor diameter; a_2= inner minor diameter; INW = Internode weight; CWT = Culm wall thickness; SBF = Stem breaking force; CSM = Cross-section modulus; LuV = Lumen volume; SL = Stem length; FW = Fresh weight; BM = Bending moment; BrS = Breaking strength; WL = Weight per unit length; BeS = Bending stress; LI = Lodging index.

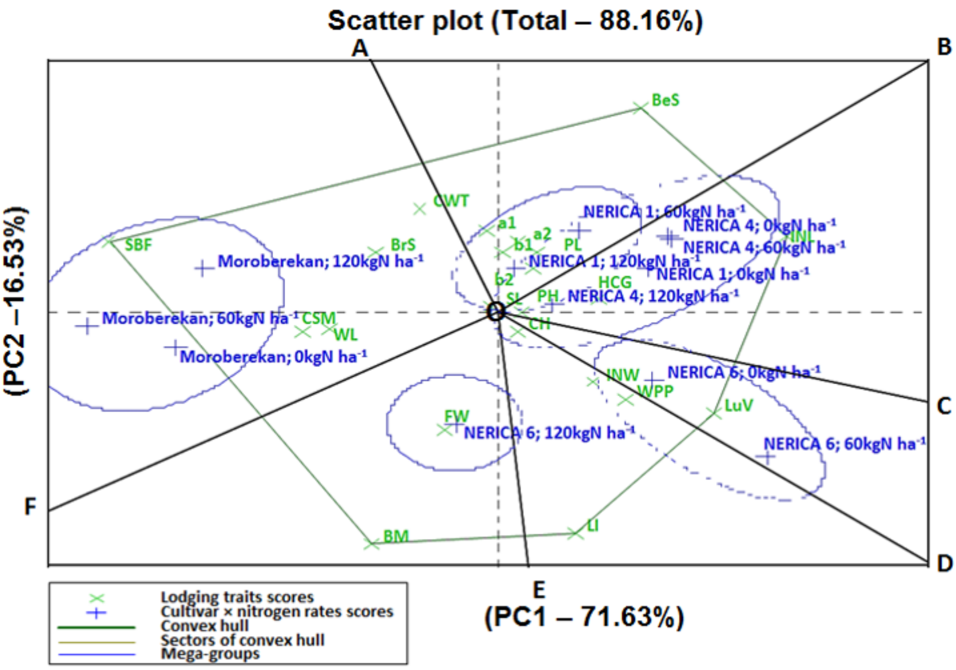

Figure 3: Principal component analysis biplot of nitrogen fertilizer rates × cultivar by traits interaction of upland rice cultivars (See Fig. 2 for the full meaning of abbreviations used in this figure).

at higher rates (Wang *et al.,* 2015). However, the reduced concentration of exchangeable bases and other elements within the soil after the experiment across rates of fertilizer applied, (except total nitrogen at 120 kg ha^{-1}) indicated the possibility that these nutrients have been taken up by the plants and the need for a higher rate of fertilizer to sustain the total nitrogen concentration of the soil towards an increase in lodging traits of the tillers.

Despite the higher lodging traits exhibited by Moroberekan, and by extension, NERICA 6 and the effectiveness of nitrogen fertilizer application at 60 and 120 kg ha^{-1} in improving the lodging traits of the cultivars in the primary tiller, the two cultivars were unable to maintain lower lodging index in both the main culm and primary tiller. NERICAs 1 and 4 were observed to have a lower lodging index, especially in the main culm among the cultivars. The lower LI exhibited was attributed to the reduced heights and weight of tillers and panicle possessed by the rice cultivars. NERICA 1 had earlier been used in the study of structural development and stability of rice (Oladokun and Ennos 2006) and has been observed as a candidate cultivar for comparing the lodging resistance among the first-generation NERICA cultivars (Olagunju *et al.,* 2021). The similarity in LI of NERICAs 1 and 4 observed implied that NERICA 4 could be a potential cultivar to be identified with NERICA 1 for selecting the most lodging-resistant cultivars under nitrogen fertilizer rates.

Bending stress contributed the highest significant and inverse correlation to lodging index among the lodging traits, especially in the main culm. Bending stress have a stronger link with NERICAs 1 and 4 than with other cultivars, as revealed in its close relationship with the two cultivars in the PCA bi-plots. A previous study on the relationship of culm lodging traits contributing to lodging resistance also revealed similar link between bending stress with NERICA 4. Bending stress is associated with culm rigidity as determined by the culm composition such as cellulose and lignin content (Zhang *et al.,* 2020). Bending stress has also been regarded as a more reliable trait for assessing the mechanical strength in the first-generation NERICAs (Olagunju *et al.,* 2021). Its close association with NERICAs 1 and 4 indicated higher mechanical strength of the culm that resulted in increased lodging resistance. The consistency in the contribution of stem length and fresh weight from breaking point to panicle top, as well as bending moment, panicle weight, height at the center of gravity, culm and plant height to lodging index across the main culm and primary tiller are indications that these traits are indispensable in lodging resistance evaluation in upland rice.

CONCLUSION

Culm lodging traits vary widely between the main culm and primary tiller of rice cultivars and do not confer similar resistance to lodging in all rice cultivars. The higher culm lodging traits in the main culm, which resulted in a reduced lodging index across cultivars compared with the higher lodging index of the primary tiller, emphasized the importance of consistency in tiller selection and the reliability of the main culm for the assessment of lodging resistance differences among rice cultivars. The higher correlation observed between the culm lodging traits of the main culm and LI and differences in the response of the cultivars to nitrogen fertilizer rates in the main culm and primary tiller, in addition, emphasized the need for this consistency. Nitrogen fertilizer can improve the lodging traits of rice cultivars in both the main culm and primary tiller. However, it has minimal effect on the lodging index of some rice cultivars when applied at moderate rates. Cultivars with reduced weight and height and LI, such as NERICAs 1 and 4, can be good varietal checks for identifying lodging-resistant cultivars under different nitrogen fertilizer rates.

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DECLARATION OF CONFLICT OF INTEREST

The manuscript is the authors own work without any breach of copyright and the authors have no conflicts of interest to declare.

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