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Yield Responses of Upland Rice Varieties to Low N Conditions in Central Kenya

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Abstract

Growth, yield, and yield components of five upland rice varieties (MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109) were evaluated under four different soil N conditions (0, 26, 52, and 78 kg N/ha) to identify the factors contributing to their adaptability to low soil-fertility. The results showed that MWUR 1, MWUR 4, and NERICA 4 had greater adaptability to low N conditions. Specifically, MWUR 1 showed the highest adaptability to low soil fertility. The greater low soil-fertility adaptability of these varieties was attributed to their ability to maintain dry matter production. Furthermore, their greater dry matter production under low N conditions could be attributed to the increased root length, which allowed improved soil nutrient absorption. Our findings suggest that rice grain yield was mainly restricted by sink size, particularly panicle number per plant under low N conditions. The higher grain yield of MWUR 1 under low N conditions could be attributed to greater tillering ability. Thus, MWUR 1 could be a good candidate for cultivation under nutrient-poor soil conditions.

Keywords: upland rice, yield response, low soil fertility

1. Introduction

Rice is the third most important cereal in Kenya, after maize and wheat (Ministry of Agriculture [MoA], 2009). The national rice consumption is estimated at 550 000 mt, compared to an annual production of about 150 000 mt (KNBS, 2016). Thus, the domestic production meets only 26.8% of demand, with the deficit being met through imports valued at over 90 million U.S. dollars. Rice consumption is increasing at an annual rate of 12%, attributed to increasing population and change in eating habits (Seck et al., 2012). Therefore, production must increase to ensure self-sufficiency (MoALF, 2012, Onyango, 2014). In 2017, Kenya imports over 634,000 tonnes of rice annually (FAOSTAT, 2019).

Rice farming in Kenya offers great potential for food security and incomes to subsistence farmers. More than 80% of all rice produced in Kenya is cultivated under the irrigated lowland ecosystem while the proportion of rainfed production is negligible (MoA, 2009). In contrast, the potential area for upland rice production is about 1 million ha, compared to only 540 000 ha for irrigated lowland ecosystem (MoA, 2009; Rosemary et al., 2010). Despite the huge area that has potential for rainfed rice production, only 449 ha is currently being utilized (Saito et al., 2015). Thus, many potential areas remain unexploited (Diagne et al., 2013).

In Kenya, potential yield under the rainfed upland conditions is estimated to be 7 t/ha (MoA, 2009), whereas actual mean yield is around 1.0-1.3 t/ha (Kimani et al., 2011; Diagne et al., 2013). Under rainfed ecologies in Kenya, similar to many other African countries, rice is mainly grown by small-scale farmers as a staple food and a commercial crop (Kimani et al., 2011). The recommended rate of N application for the upland rice cultivation in the country is 50 kg N/ha (MoA, 2009). However, a survey on levels of fertilizer input among farmers in the central region of Kenya showed that farmers either applied levels lower than the recommended rate or did not apply the fertilizer at all (Kimani et al., 2011). The low rates of fertilizer application by smallholders is mainly due to the high costs of chemical fertilizers in Africa (Otsuka & Kalirajan, 2006). Thus, the low productivity of upland rice can be attributed to low soil fertility, which is one of the major constraints to rice production (Gupta & O'Toole, 1986; Maclean et al., 2013).

Introduction of low soil-fertility adaptable varieties is one of the strategies implemented to address the challenge of low productivity under deficient soil fertility conditions. The MWUR 1 and MWUR 4 that have been bred in Kenya are expected to adapt to the low N conditions of the upland ecosystem (Sikuku et al., 2016a). However, the factors contributing the adaptability of these varieties to low soil-fertility have not been clarified.

In this study, we aimed to identify the factors contributing the adaptability of the improved upland varieties such as MWUR 1 and MWUR 4 to low soil-fertility. We compared their growth and yield with other upland varieties under different N application levels, under supplemental irrigation precluding drought stress.

2. Materials and Methods

2.1 Experimental Site

Experiments were conducted in an upland field at the Kenya Agricultural and Livestock Research Organization (KALRO) research farm, located in Mwea, Kenya (0°37′S lat, 37°20′E long). In Kenya, upland rice is cultivated two rainy; long rainy season from March and short rainy season from September. Thus, seeds were sown in February 2015 and August 2016 in our study. The soil of the experimental field was Nitisol. Soil chemical properties of top soil (0-20 cm) were determined at KALRO National Agricultural Research Laboratory. Soil pH and solution were determined using a glass calomel electrode system as described by Crockford and Nowell (1956) while organic matter was determined by wet oxidation chromic acid digestion method adopted from Walkey and Black (1934). The soil N was determined by the micro-kjedahl method (AOAC, 1995). The soil K, Ca, Mg, and Na was extracted with a 1M NH_4OAc pH 7 solution and analyzed with a flame photometer. The soil Mg was determined with an atomic absorption spectrophotometer (Ogunwale & Undo, 1978). The exchangeable acidity (H^+ and Al^{3+}) were measured from 0.1M HCl extractant by titrating with 0.1 M NaOH (Mclean, 1965). The micronutrients Cu, Zn, and Fe were extracted with 0.1 M HCl (Ogunwale & Undo, 1978) and read on a Perkins Klimer atomic absorption spectrophotometer.

The soil was found to have a pH of 5.78, 0.19% total N, 1.8% total organic carbon, 285 mg/kg phosphorus, 2.7 me % calcium, 0.11 me % magnesium, 18.3 ppm iron and 0.97 me % potassium. Based on these results, N was categorized to be at low level. Weather data during the growth period was recorded at a weather station (Watchdog, model 2900ET, Spectrum Technologies, Inc. Plainfield, Illinois, USA) located on the research farm.

2.2 Experimental Design

The experiments comprised of four N application rates and five rice varieties in a randomized complete block design, replicated three times. The four N application rates were 0, 26, 52, and 78 kg N/ha. Fertilizer was applied in two equal splits, namely, at tillering stage and at panicle initiation stage, using calcium ammonium nitrate (CAN, 26%N). In addition, zinc (a micro-nutrient), was blanket applied as zinc sulfate, at a rate of 25 kg $ZnSO_4$/ha in all plots. Five rice varieties MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109 were used for the two years. NERICAs are rice varieties that were developed by the Africa Rice Centre to improve yield under upland conditions in sub-Saharan Africa (Jones et al., 1997a, 1997b). The MWUR 1 and MWUR 4 were developed in Mwea, Kenya, by crossing Dourado Precose and CT16317-CA-4-M, and NERICA 1 and WAB880-1-38-20-17-P1-HB, respectively.

On 2 Feb 2015 and 10 Aug 2016, seeds were directly sown in a 2.0 m × 1.5 m plot with a 20 cm × 20 cm spacing. In each hill, 4-5 seeds were sown into individual holes made using a wooden stick. At the early seedling stage, thinning and gap filling were carried out, leaving only one seedling per hill. The first fertilization was performed on 3 Mar. 2015 and 6 Sept. 2016, and the topdressing was on 24 Mar. 2015 and 4 Oct. 2016, respectively. All plants were harvested on 1 Jun. 2015 and 1 Dec. 2016, respectively. Weed control was done by hand, while diseases and pests were controlled by spraying agricultural chemicals to avoid crop damage. Supplemental irrigation was done whenever necessary to avoid severe water stress during the growth period.

2.3 Measurements and Statistical Analyses

In both seasons, data on various traits was measured as described below. Tiller number, plant length, and SPAD value (SPAD-502 plus; Konica Minolta Inc. Tokyo, Japan) were periodically measured in three plants for each experimental plot. SPAD value is indicator of chlorophyll concentration. At maturity stage, data on plant length culm length, panicle length, and number of panicles per plant was collected from the same plants. These plants were then harvested for yield and yield components analysis as follows: For each of the harvested plants, panicles were separated from straw and hand-threshed. Filled and unfilled spikelets were then separated and counted and filled grain ratio calculated by dividing the number of filled spikelets with the total number of spikelets. Grain moisture content (%) of filled grains was measured using a grain moisture tester (Ricer *f5*, Kett Electric Laboratory, Tokyo, Japan) and was used to adjust 1000-grain weight and paddy yield to 14% moisture content. The straw, from each of the data plants, was oven-dried at 70 °C for 72 h and weighed to determine dry weight. In addition, root samples from each of the data plants were extracted from the 0-20 cm soil layer using a stainless cylinder with a diameter and height of 15 cm and 40 cm, respectively. The collected roots were then washed, oven-dried at 70 °C for 72 h and weighed to determine their dry weight. However, total root length was measured before the roots were oven-dried. This was done by cutting the whole root system into 1-cm segments which were then spread in a thin film of water on a transparent plastic tray with minimum overlapping. Digital images were taken using an EPSON scanner (ES700, Seiko Epson Corporation, Japan). The digital images were then analyzed using WinRHIZO version 2013 (Regent Instruments Inc., Quebec, Canada) to determine the total root length. Specific root length (SRL; root length per unit root dry weight) was calculated to evaluate how the allocated dry matter was used to form the root system in rice. The mean separation was done by the least significant difference (LSD) test using Statistical Analysis System (version 9.0) (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1 Climatic Conditions

Total rainfall during the growing period in 2015 was higher than that in 2016 (Table 1). Mean, maximum and minimum temperatures during growth period were slightly higher in 2015 than those in 2016. Mean, maximum and minimum temperatures in during 2015 and 2016 were, 22.2, 29.0, and 16.9 °C, and 21.2, 27.4, and 16.5 °C, respectively.

Table 1. Average daily air temperature (°C) and total rainfall (mm) during the growing period in 2015 and 2016

Year	Rainfall (mm)	Temperature (°C)		
		Mean	Max.	Min.
2015	412.4	22.2	29.0	16.9
2016	196.2	21.2	27.4	16.5

3.2 Plant Growth Performance

The results obtained in 2015 are mainly presented in this paper because the growth performance of the varieties under the different N application showed almost the same trend in 2015 and 2016. The differences in tiller number among varieties were small under 0 N, while the largest differences in tiller number among varieties was observed at 52 kg N/ha fertilization (Figure 1). MWUR 1 had the highest number of tillers among the five varieties at 0, 52, and 78 kg N/ha fertilization. On the other hand, MWUR 4 had the lowest number of tillers among the five varieties at 26, 52, and 78 kg N/ha fertilization. Regardless of the varieties, SPAD value did not differ much between the treatments (Figure 2). Irrespective of N rates, MWUR 4 and NERICA 4 tended to have higher SPAD values than NERICA 10 and IRAT109, with some exceptions.

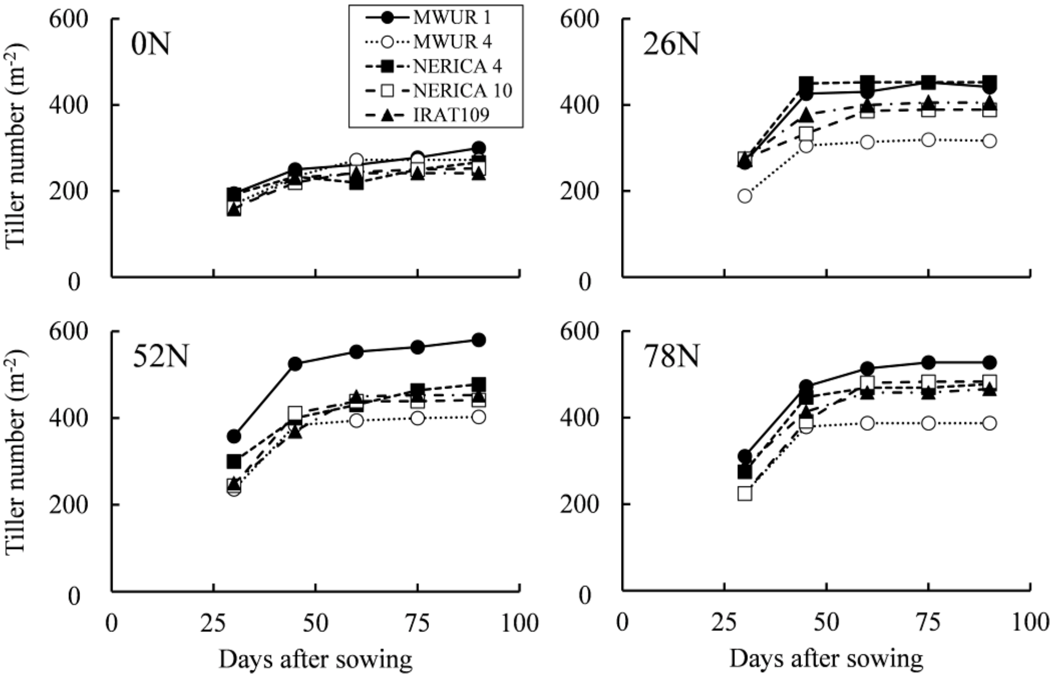

Figure 1. Changes in tiller number per square meter from transplanting to full heading in MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109 under four different N levels in 2015

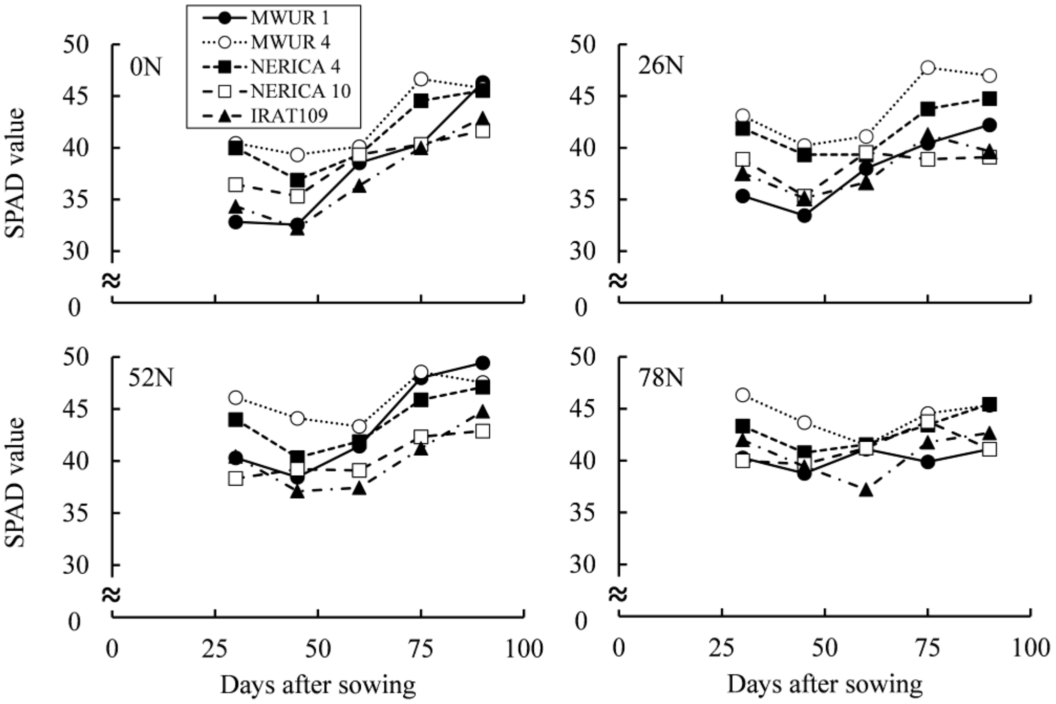

Figure 2. Changes in SPAD values from transplanting to full heading in MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109 under four different N levels in 2015

Plant and culm lengths and total dry weight tended to increase with increasing N rates (Table 2). Irrespective of N rates, MWUR 1 had the highest plant and culm length. Moreover, MWUR 1 had a significantly higher plant and culm lengths than those of IRAT109 regardless of N level. MWUR 1, MWUR 4, and NERICA 4 had comparable plant and culm lengths at 0, 26, and 78 kg N/ha fertilizer conditions. However, at 52 kg N/ha application the two traits were significantly higher in MWUR 1 than in MWUR 4 and NERICA 4. Regardless of N levels, MWUR 1, MWUR 4 and NERICA 4 did not differ significantly in panicle length, except for MWUR 4 under 78 kg N/ha. Panicle length of IRAT109 tended to be shorter than that of MWUR 1, MWUR 4 and NERICA 4, with some exceptions. Root dry weight peaked under 52 kg N/ha fertilization for all varieties except that of NERICA 10, which tended to increase with increasing N fertilizer rates. However, there were no varietal differences in root dry weight across treatments. On the other hand, total root length was directly dependent on the amount of N applied and was the lowest under 0 kg N/ha and highest under 78 kg N/ha conditions, except for MWUR 1 (Figure 3). The MWUR 1 and IRAT109 showed greater root length than the other three varieties under 0 kg N/ha and 26 kg N/ha fertilization, except for NERICA 4 under 26 kg N/ha. Under 52 kg N/ha and 78 kg N/ha conditions, MWUR 4 and NERICA 4 had the greatest root length among five varieties. For MWUR 1, SRL—the ratio of root length to root dry weight—tended to increase as the amount of N fertilizer decreased. On the contrary, SRL for NERICA 4, NERICA 10, and IRAT109 was greatest under 72 kg N/ha. At 0, 26, and 52 N/ha, MWUR 1 had the highest total dry weight (Table 2). Moreover, MWUR 1, MWRU 4, and NERICA 4 had comparable total dry weight at 0, 26, and 52 kg N/ha fertilizer conditions.

Table 2. Plant length, culm length, panicle length, root weight, and total dry weight in MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109 at maturity under four different N levels

Treatment	Variety	Plant length (cm)	Culm length (cm)	Panicle length (cm)	Root weight (g per plant)	Total dry weight (g per plant)
0N	MWUR 1	79.7 a	59.9 a	19.9 a	2.67 a	34.1 a
	MWUR 4	72.8 ab	53.7 ab	20.6 a	2.60 a	30.9 ab
	NERICA 4	71.7 ab	51.8 ab	19.9 a	2.44 a	32.0 a
	NERICA 10	62.6 bc	45.4 bc	17.1 b	2.56 a	20.7 bc
	IRAT109	54.0 c	37.1 c	16.9 b	2.40 a	19.6 c
	Mean	68.2	49.6	18.9	2.53	27.5
	CV	14.6	17.5	9.2	4.4	24.7
26N	MWUR 1	85.8 a	66.8 a	19.0 ab	2.84 a	59.2 a
	MWUR 4	78.0 ab	58.3 ab	19.7 ab	2.79 a	43.7 ab
	NERICA 4	86.0 a	65.1 a	20.9 a	2.70 a	51.0 ab
	NERICA 10	72.3 ab	52.3 ab	20.0 ab	2.96 a	36.5 b
	IRAT109	62.4 bc	45.2 b	17.2 b	2.79 a	34.0 b
	Mean	76.9	57.5	19.4	2.82	44.9
	CV	12.9	15.6	7.2	3.4	23.2
52N	MWUR 1	103.7 a	83.4 a	21.4 ab	3.12 a	78.3 a
	MWUR 4	93.0 b	71.3 b	21.8 a	3.16 a	63.3 ab
	NERICA 4	91.2 b	68.4 bc	22.8 a	3.21 a	60.0 b
	NERICA 10	81.0 c	61.3 c	19.7 b	3.15 a	61.0 b
	IRAT109	67.5 d	50.4 d	17.1 c	3.34 a	40.2 c
	Mean	87.3	67.0	20.6	3.20	60.6
	CV	15.7	18.3	10.9	2.7	22.4
78N	MWUR 1	96.9 a	77.7 a	19.3 b	3.00 a	71.9 ab
	MWUR 4	90.8 ab	68.3 ab	22.5 a	3.11 a	85.9 a
	NERICA 4	94.0 ab	72.8 ab	21.1 ab	2.95 a	77.2 ab
	NERICA 10	80.7 ab	61.0 b	19.7 ab	3.27 a	56.7 b
	IRAT109	75.6 b	56.9 b	18.7 b	3.06 a	55.9 b
	Mean	87.6	67.3	20.3	3.08	69.5
	CV	10.4	12.6	7.6	4.0	18.9

Note. Values followed by the same letter in a column within each treatment are not significantly different at 5%.

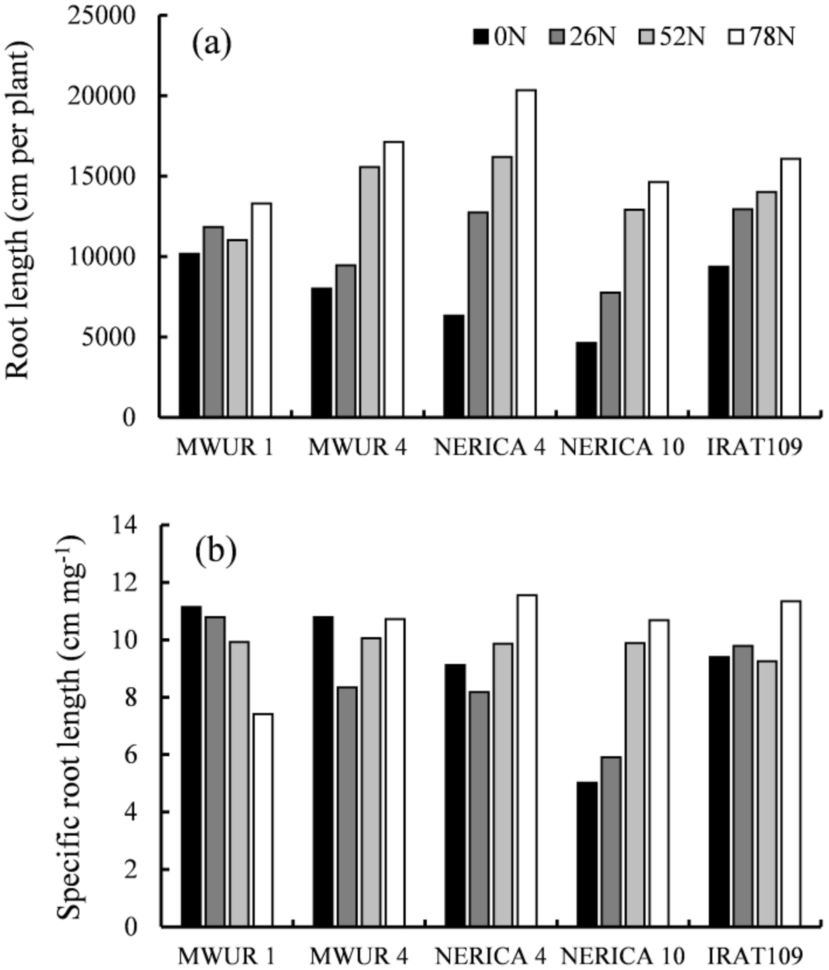

Figure 3. Root length per plant (a) and specific root length (b) in MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109 under four different N levels in 2016

3.3 Yield and Yield Components

Panicle number per plant was the highest under 78 kg N/ha for all varieties except for NERICA 10 in 2015, and NERICA 4 in 2016 (Table 3). Under 0 kg N/ha and 26 kg N/ha, MWUR 1 tended to have the highest panicle number in both years. Irrespective of N rates, MWUR 1 and IRAT109 had lower spikelet numbers per panicle than other three varieties, with some exceptions in 2015. Among the five varieties, IRAT109 tended to have the lowest filled grain ratio irrespective of the N rates in both years, while no clear difference was observed among other four varieties. Compared to other three varieties, MWUR 1 and IRAT109 had higher 1000-grain weights irrespective of N rates. There was significant effect on grain yield due to nitrogen levels in both long and short rain seasons, however there was no significant effect due to interaction between rice variety and nitrogen level during the two seasons (Table 4). Regardless of variety, grain yield increased with increasing N rates in both years (Table 3). Under 0 kg N/ha and 26 kg N/ha, grain yield of MWUR 1, MWUR 4, and NERICA 4 tended to be higher than that of NERICA 10 and IRAT109. Under 52 kg N/ha and 78 kg N/ha in both years, there was no significant difference in grain yield among the varieties, except for IRAT109 under 52 kg N/ha in 2015.

Table 3. Panicle number per plant, spikelet number per panicle, filled grain ratio, 1000-grain weight, and grain yield in MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109 under four different N levels in 2015 and 2016

Year	Treatment	Variety	Panicle number plant^{-1}	Spikelet number panicle^{-1}	Filled grain ratio (%)	1000-grain weight (g)	Grain yield (g m^{-2})
2015	0N	MWUR 1	8.9a	74.6bc	76.2a	30.6a	365ab
		MWUR 4	6.8a	114.5a	74.5a	26.0b	363ab
		NERICA 4	8.5a	85.0ab	81.3a	27.3ab	395a
		NERICA 10	8.4a	60.4bc	78.9a	24.9b	251bc
		IRAT109	8.6a	44.4c	57.6b	31.0a	162c
		Mean	8.2	75.8	73.7	28.0	307
		CV	10.0	35.0	12.7	10.0	31.9
	26 N	MWUR 1	15.7a	59.3a	77.8a	37.6a	658a
		MWUR 4	10.1b	87.2a	79.8a	25.9c	574a
		NERICA 4	12.6ab	101.9a	82.3a	26.3c	718a
		NERICA 10	10.7ab	108.8a	75.4a	24.3c	517a
		IRAT109	10.4ab	73.1a	55.0b	32.8b	377a
		Mean	11.9	86.1	74.1	29.4	569
		CV	19.6	23.6	14.8	19.2	23.2
	52 N	MWUR 1	16.3a	70.8b	80.7a	34.1a	855a
		MWUR 4	11.8bc	127.4a	86.0a	27.0b	846a
		NERICA 4	14.6ab	96.3ab	82.7a	26.0bc	898a
		NERICA 10	17.1a	90.8ab	80.2a	25.2c	790a
		IRAT109	10.3c	75.0b	68.6a	34.0a	440b
		Mean	14.0	92.1	79.6	29.3	766
		CV	20.7	24.4	8.3	15.1	26.2
	78 N	MWUR 1	16.4a	64.9a	88.3a	33.6a	867a
		MWUR 4	13.0a	105.2a	88.8a	24.9b	805a
		NERICA 4	18.1a	104.3a	86.1ab	26.6b	1063a
		NERICA 10	14.0a	106.6a	78.9bc	24.9b	821a
		IRAT109	15.7a	75.9a	72.3c	33.5a	683a
		Mean	15.4	91.4	82.9	28.7	848
		CV	13.0	23.8	8.6	15.6	16.3
2016	0 N	MWUR 1	6.8a	47.2b	91.8a	32.0ab	232a
		MWUR 4	6.1ab	49.7b	91.8a	31.1b	206ab
		NERICA 4	4.7ab	64.2a	92.2a	26.5c	187ab
		NERICA 10	6.1ab	65.9a	90.7a	24.4c	112b
		IRAT109	4.2b	64.6a	69.8b	34.2a	157ab
		Mean	5.6	58.3	87.3	29.6	179
		CV	19.4	15.6	11.2	13.7	25.9
	26 N	MWUR 1	10.4a	77.0a	91.9a	33.3b	578a
		MWUR 4	10.3a	78.2a	93.1a	29.5c	493ab
		NERICA 4	7.9a	91.9a	94.0a	27.1d	430ab
		NERICA 10	8.6a	97.1a	84.8a	26.1d	351b
		IRAT109	8.8a	97.6a	84.2a	35.7a	555a
		Mean	9.2	88.4	89.6	30.3	481
		CV	12.0	11.4	5.3	13.5	19.3
	52 N	MWUR 1	10.6a	74.6b	92.0a	33.6a	739a
		MWUR 4	11.8a	80.9ab	93.7a	29.5b	693a
		NERICA 4	10.8a	99.4ab	91.1a	27.0b	660a
		NERICA 10	9.6a	107.1a	90.0a	27.1b	500a
		IRAT109	10.2a	96.1ab	81.6b	35.6a	737a
		Mean	10.6	91.6	89.7	30.6	666
		CV	7.7	14.7	5.3	12.7	14.7
	78 N	MWUR 1	12.3ab	86.6b	91.4a	35.2a	824a
		MWUR 4	12.7ab	116.3a	92.0a	29.9b	1078a
		NERICA 4	10.7b	123.1a	90.6ab	27.4b	829a
		NERICA 10	13.8a	119.2a	91.5a	27.4b	1017a
		IRAT109	12.0ab	105.3ab	85.9b	35.5a	993a
		Mean	12.3	110.1	90.3	31.1	948
		CV	9.1	13.4	2.8	13.0	12.2

Note. Values followed by the same letter in a column within each treatment are not significantly different at 5%.

Table 4. ANOVA table, grain yield season 1 and 2

Season	Source of variation	DF	MS	F value	Pr > F
2015	Block	2	167.4	3.6	0.0388
	Variety	4	331.5	7.1	0.0003
	N level (N)	3	1306.8	28	<0.0001
	Variety × N	12	15.8	0.3	0.9759
2016	Block	2	102.3	2.2	0.1267
	Variety	4	41.7	0.9	0.4783
	N level (N)	3	2257.5	48.4	<0.0001
	Variety × N	12	30.3	0.7	0.7851

3.4 Relationship Between Traits

There was strong correlation between total dry weight and root weight per plant under low N rates (2015: r = 0.636*, 2016: r = 0.710*) (Figure4). The same trend was observed on root length (2015: 0.489†, 2016: r = 0.683*). There was a significant correlation between grain yield and total dry weight under low N rates (0N and 26N) (Table 5). Among yield components, grain yield was highly correlated with panicle number per plant in both years under low N rates. Positive and significant correlations were obtained between grain yield and spikelet number per panicle, and spikelet number per plant, in 2016 at low N rates; however, these relationships were not significant in 2015. No significant correlation was found between grain yield and filled grain ratio, and 1000-grain weight in both years.

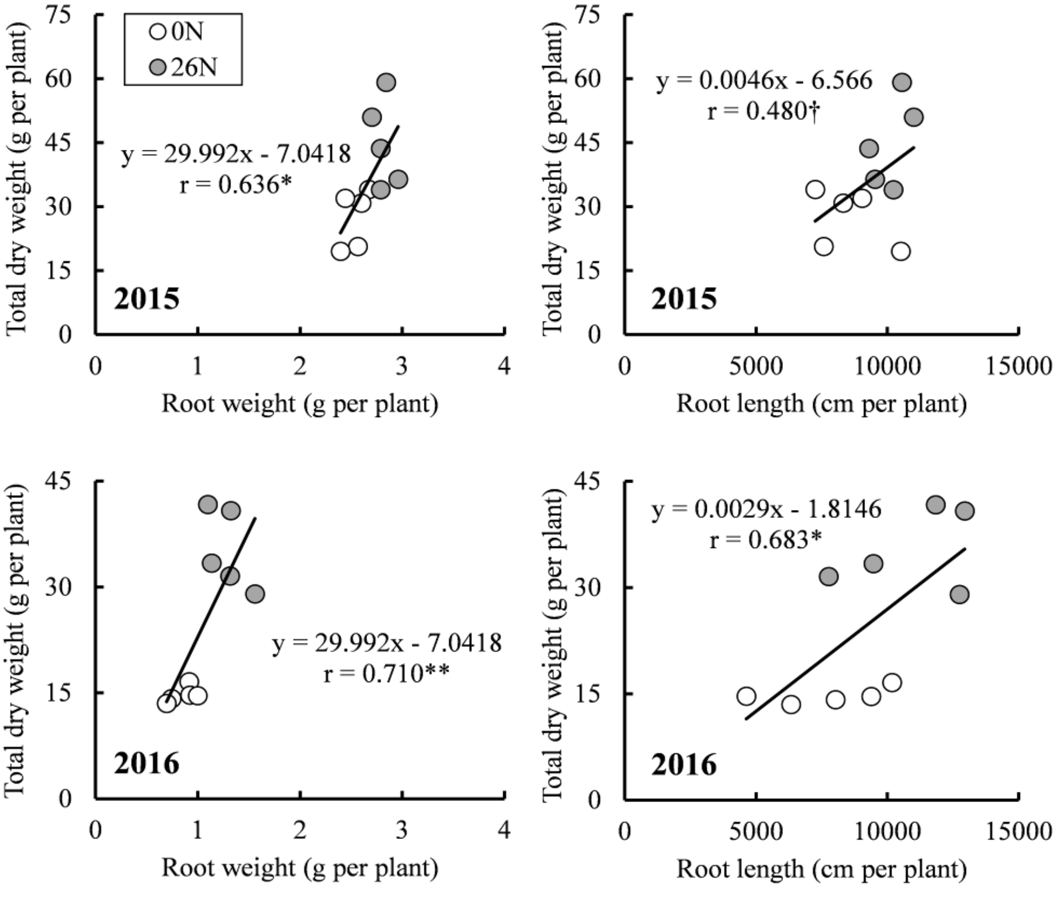

Figure 4. Relationship between total dry weight and root weight, and root length for MWUR 1, MWUR 4, NERICA 1, NERICA 4, and IRAT109 grown under low N conditions (0N and 26N) in 2015 and 2016

Note. *, ** and † indicate significant differences at $P < 0.05$, $P < 0.01$ and $P < 0.1$, respectively.

r-value indicates correlation coefficient.

Table 5. Correlation coefficients obtained from regression analyses between grain yield and total dry weight, panicle number, spikelet number per panicle, spikelet number per plant, filled grain ratio, and 1000-grain weight under low N conditions (0N and 26N) in 2015 and 2016.

Year	Total dry matter (g)	Panicle number per plant	Spikelet number per panicle	Spikelet number per plant	Filled grain ratio (%)	1000-grain weight (g)
2015	0.949 ***	0.768 **	0.449 n.s.	0.598 n.s.	0.545 n.s.	0.073 n.s.
2016	0.970 ***	0.895 ***	0.681 *	0.901 ***	0.223 n.s.	0.386 n.s.

Note. *, **, ***, and ns indicate significant differences at $P < 0.05$, $P < 0.01$, $P < 0.001$, and non-significant difference, respectively.

4. Discussion

Air temperatures in 2015 and 2016 did not differ much. Although insufficient rainfall amounts were experienced in 2015 (Table 1), the experiments were conducted with supplemental irrigation to eliminate drought stress. Therefore, we considered that the difference in rainfall during the growth period between 2015 and 2016 did not affect the results.

Grain yield of MWUR 1, MWUR 4, and NERICA 4 was recorded to be greater than the other varieties under lower N treatments (0 and 26 kg N/ha), whereas no varietal differences were observed in higher N treatments (52 and 75 kg N/ha). Onaga et al. (2012) and Sikuku et al. (2016a, 2016b) reported that NERICA 4 showed higher yield than other rice varieties under low N conditions in Kenya, because NERIAC 4 produce higher tiller number or panicle number under low N conditions compared with other varieties. Under 0 and 26 kg N/ha, MWUR 1 showed similar yield level to that of NERICA 4, and these varieties had higher grain yields than NERICA 10 and IRAT109 (Table 4). Compared with MWUR 1, the yield of MWUR 4 was slightly lower, but higher than NERICA 10 and IRAT109. Hence, these results suggest that MWUR varieties could be better adapted to upland rice cultivation under low N conditions in Kenya. These indicate that MWUR 1 and MWUR 4 are considered to have low soil-fertility adaptability comparable to NERICA 4.

The result of correlation analysis indicates that the greater grain yield of MWUR 1, MWUR 4, and NERICA 4 is attributed to their greater dry matter production ability under low N conditions (Tables 2 and 5). Moreover, these low soil-fertility adapted varieties had higher SPAD value than NERICA 10 and IRAT109 around 100 days after sowing (Figure 2). This suggests that these low fertility adapted varieties have an ability to maintain higher N concentration in the plant until late vegetative stage. Thus, these findings suggest that the low soil-fertility adaptability of these upland varieties could be attributed to greater N absorption.

Under low N conditions, total dry weight in upland rice was correlated with root development (Figure 4). This indicates that greater dry matter production could be attributed to the greater ability to develop root systems under low fertility conditions. Tran et al. (2014) reported that greater root development is considered to have contributed to soil nutrient uptake under low fertility conditions. In particular, SRL in MWUR 1 increased as the amount of N fertilizer decreased (Figure 3). The greater adaptability to low soil fertility in MWUR 1 might be attributed to the ability to increase root surface area by increasing thinner root production in nutrient-poor conditions.

Under low N conditions, grain yield was not significantly correlated with filled grain ratio (Table 4). This result indicates that grain yield was restricted in these conditions by sink size (spikelet number per unit area × 1000-grain weight), not by source amount. Among the sink size factors, panicle number was observed to be the highest determining factor for grain yield under low N rates in both years (Table 5). This was consistent with findings in Asia and Africa which concluded that panicle number was an important trait for higher grain yield in low fertility upland conditions (Atlin et al., 2006; Saito et al., 2007; Saito & Futakuchi, 2009). MWUR 1, which showed the highest grain yield under low N conditions, had the highest panicle number under such conditions (Table 4, Figure 1). On the contrary, IRAT109 and NERICA 10 that are less adapted to low N conditions had fewer panicle numbers. MWUR 1 showed higher tiller number than other varieties during the vegetative stage irrespective of N rate. Thus, MWUR 1's higher grain yield under low N conditions could be attributed to greater tillering ability. Sink capacity and the ability to translocate photosynthetic assimilates may have contributed to the greater low soil fertility adaptability of MWUR 1, but these were not measured in this study and require further investigation.

In our experiment, 1000-grain-weight, another determining factor for sink size, was not correlated with grain yield (Table 4). This can be explained by the fact that 1000-grain weight is determined genetically and is less affected by environmental factors (Gendua et al., 2009). Nevertheless, heavier 1000-grain weight can be an advantage for achieving higher grain yield. In our experiment, MWUR 1 and IRAT109 had heavier 1000-grain weight than other varieties in all N fertilization rates (Table 3). Also, this factor is partly related to MWUR 1's higher grain yield under low N conditions.

Between MWUR 1 and MWUR 4 under low N levels, MWUR 1 produced more panicle number than MWUR 4, whereas MWUR 4 produced more spikelet number than MWUR 1 resulting in that these differences were offset in spikelet number per unit area was same level. And, filled grain ratio showed same level between them. On the other hand, 1000-grain-weight in MWUR 4 was 10% or more lower than that MWUR 4. Thus, these results suggested that yield difference between them mainly caused by 1000-grain weight.

Our study revealed that MWUR 1, MWUR 4 and NERICA 4 have greater adaptability to low soil-fertility conditions while the MWUR 1 showed the highest adaptability to low soil-fertility. The greater adaptability of these varieties to low soil-fertility was attributed to the ability to maintain dry matter production. Furthermore, their greater dry matter production under low N conditions could be attributed to the increased root length allowing for greater efficiency of nutrient absorption. Our findings suggest that rice grain yield was mainly restricted by sink size, particularly panicle number per plant under low N conditions. Especially, MWUR 1's higher grain yield could be attributed to greater tillering ability. MWUR 1 could be a good candidate for cultivation in nutrient-poor soil conditions.

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