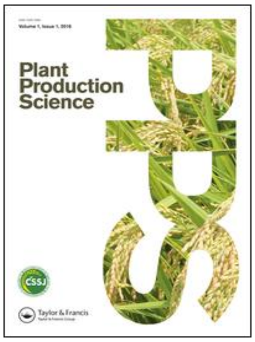

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Growth and yield responses of upland NERICAs to variable water management under field conditions

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ABSTRACT

This study aimed to investigate the possible causes for inconsistent performances of upland New Rice for Africa (NERICA) varieties in uplands and lowlands, while identifying important determinants in grain yield under deficient soil moisture. We compared the growth and yield of NERICA 1 and NERICA 5 to those of Yumenohatamochi, a Japanese upland variety, and Hinohikari, a Japanese lowland variety, subjected to different water management regimes (continually flooded, supplementary irrigation, and non-irrigation). Under conditions of deficient soil moisture, panicle number per square meter, spikelet number per panicle, and 1000-grain weight of NERICAs decreased, whereas the panicle number of the Japanese varieties experienced little change. In contrast, the grain filling ratio was unaffected by water management, irrespective of variety. The primary source of yield reduction under low soil water conditions was a decrease in spikelet number per panicle, and water stress intensity was the primary factor for the degree of this reduction. Variation in the abortion of secondary rachis-branches caused differences between NERICAs in their spikelet number response to soil moisture deficiency. The inconsistency in NERICA performance across uplands vs. lowlands can be partially attributed to variation in yield response to low soil water conditions. Moreover, water stress intensity and the presence of a water gradient along the vertical soil profile may combine to affect the fluctuation in NERICA performance under upland conditions.

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CLASSIFICATION
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1. Introduction

Rice consumption is increasing dramatically in sub-Saharan Africa due to population growth and changes in eating habits, especially among urban areas (Balasubramanian et al., 2007). However, despite a 3.6-fold increase in rice production from 1971 to 2010 (FAOSTAT, 2015), only approximately 40% of the total demand is currently being met (Fujiie et al., 2010; Saito et al., 2010). Part of the problem is that efforts to increase rice production in sub-Saharan Africa have focused mainly on expanding cultivation areas (Africa Rice Center, 2007). To maximize production, rice yield per unit area must also be improved, accomplishable through the establishment of cultivation techniques and the development of high-yield varieties suitable to sub-Saharan environmental conditions. Against such a background, the Africa Rice Center (Africa Rice), formerly known as the West Africa Rice Development Association, developed New Rice for Africa (NERICA) through the hybridization of *Oryza sativa* and *Oryza glaberrima* (Jones, Dingkuhn et al., 1997; Jones, Mande, et al., 1997). The variety was intended to be suitable for the rain-fed upland conditions of sub-Saharan Africa (Jones, Dingkuhn et al., 1997), combining the high yield of *O. sativa* and the stress tolerance of *O. glaberrima*, which is resistant to drought, low fertility, weeds, and various diseases (Diagne et al., 2010; Jones, Dingkuhn et al., 1997; Jones, Mande, et al., 1997; Kaneda, 2007a). The first NERICA varieties, NERICA 1 to NERICA 7, were released in 2000 (Kaneda, 2007a; Manneh & Ndjiondjop, 2008). Since then, NERICAs have been promoted in many sub-Saharan countries, and are expected to increase rice production there (Diagne et al., 2010; Kaneda, 2007b).

Upland NERICAs are also occasionally cultivated in lowlands and wetlands to further increase yield (Fujiie et al., 2010), suggesting adaptability to a wide range of agro-ecosystems. However, various studies have reported inconsistent NERICA growth and yield under various soil water conditions. For instance, NERICA yield under paddy

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conditions in Uganda exceeded yield under upland conditions unless rainfall supplied sufficient water (Matsumoto et al., 2014). In contrast, Matsunami et al. (2009) indicated that adequate rainfall resulted in better NERICA performance under upland conditions than under paddy conditions. Additionally, Fujii et al. (2004) demonstrated that NERICAs have higher drought tolerance than that of other lowland and upland varieties, but a study evaluating deep-rooting ability found no evidence of this advantage in NERICA varieties (Sakagami & Tsunematsu, 2003). To clarify these inconsistencies and identify the major determinants of productivity under low soil moisture in the field, we compared the growth and yield responses of upland NERICAs with Japanese upland and lowland varieties across differing water availability.

2. Materials and methods

2.1. *Experimental design and cultural practices*

Experiments were conducted at a field in the Education and Research Center for Subtropical Field Science (FSC), Faculty of Agriculture, Kochi University, Japan (33°55′ N, 133°68′ E) during 2011 and 2012. The experiment used four rice varieties: NERICA 1 (N1, upland rice, non-glutinous), NERICA 5 (N5, upland rice, non-glutinous), Yumenohatamochi (YMH, Japanese upland rice, glutinous), and Hinohikari (HH, Japanese lowland rice, non-glutinous). Of the Japanese varieties, YHM is well known as drought-tolerant (Nemoto et al., 1998), whereas HH is a popular and typical variety in southwestern Japan, including the Kochi prefecture (where the field experiments were performed).

The 2011 experiments comprised three water management types: continually flooded (FL), supplementary irrigation (IR), and non-irrigation (NIR). In FL, the water table was kept around 3–5 cm above the soil surface throughout the growing period; in IR, irrigation water was applied 3–5 cm above the soil surface whenever the soil water potential (SWP) at 10 cm depth dropped below approximately −40 kPa; in NIR, plants relied solely on rainfall for water. The water amount in IR was measured with flow meters (MICROSTREAM Flowmeter, Aichi Tokei Denki Co., Ltd, Aichi, Japan) connected to the irrigation hoses. The study site received considerable rainfall, exceeding 1500 mm in the 2011 growing period, causing the SWP in NIR and IR being comparable. Therefore, in 2012, experiments comprised only FL and NIR.

We grew seedlings in accordance with FSC methods (Kokubo et al., 2012). On 13 May 2011 and 10 May 2012, pre-geminated seeds were sown in nursery boxes (30 cm × 60 cm). On 1 June 2011 and 30 May 2012, the seedlings were manually transplanted, with two seedlings per hill at 22.2 hills per square meter. Setup of the field experiment was a split-plot design with two replications, in which water management type was the main plot. The four rice varieties were randomly arranged in each plot (3.75 m × 3.75 m for each variety), which were kept flooded until water management treatments began, to ensure successful plant establishment. On 21 June 2011 and 22 June 2012 (20 and 23 days after transplanting, DAT), irrigation water was drained in IR and NIR to lower the water depth at the soil surface. Each plot received 100, 100, and 100 kg K ha^{-1} as slow-release compound fertilizer (14-14-14, NPK) before final puddling. Pest and disease control was performed when necessary in both years.

2.2. *Climatic data and SWP determinations*

In both years, we obtained climatic data (monthly mean temperature, rainfall, and solar radiation) during the growing period from the Automated Meteorological Data Acquisition System (AMeDAS) in Gomen station (Nankoku City, Kochi, Japan; 33°35′N, 133°39′E). 'Normal' climatic data were averaged from 1981 to 2010 for comparison, except for solar radiation, which was averaged from 1987 to 2010. The SWP in all treatments was measured using a tensiometer (DIK-3150, Daiki Rika Kogyo Co., Ltd., Saitama, Japan) installed at 10 cm soil depth, either daily or every two days after the onset of water management.

2.3. *Growth parameters and yield components*

Beginning from two weeks after transplanting until one week after full heading, we measured major growth parameters weekly, for five hills per plot in 2011 and 10 hills per plot in 2012. These parameters included plant length, tiller number, and leaf age on the main stem. At the full heading stage, three hills per plot were sampled: the leaf area of one hill per plot was then randomly selected and measured using an automatic leaf area meter (AAM-7, Hayashi Denko Ltd., Tokyo, Japan). The leaf area of the other two hills was computed from the specific leaf area (SLA) of the measured plants and the leaf dry weight.

At maturity, plant from 20 hills per plot were harvested and air-dried in a greenhouse for two weeks. Three average-sized hills per plot were then selected to determine yield and yield components. We counted the number of primary and secondary rachis-branches per panicle, as well as spikelet number on each rachis-branch. Next, we separated filled and unfilled grains using salt water with specific gravities of 1.06 and 1.03 for non-glutinous and glutinous varieties, respectively. We then counted and weighed the filled grains in each rachis-branch. The 1000-grain weight of rice from each variety was determined at a moisture content of 15%, measured using a grain moisture tester (SP-1D, Grain Moisture Tester, Kett Electric Laboratory, Tokyo, Japan). Finally, we calculated the yield per square meter from the yield components.

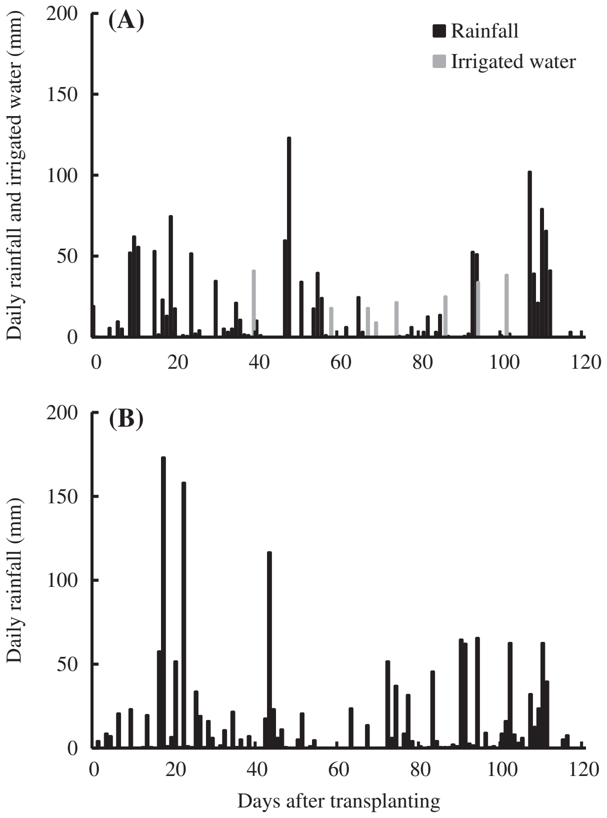

Figure 1. Daily rainfall and amount of irrigated water during the growing period in 2011 (A) and 2012 (B).

2.4. Statistical analysis

To test for differences among growth parameters and yield components in response to soil moisture variation, we performed an analysis of variance (ANOVA) using the general linear model procedure in Statistical Analysis System (version 9.0) (SAS Institute Inc., Cary, NC, USA). Water management type was the main factor and the varieties were the split-plot factor. Means of growth and yield parameters were separated using the least significant difference (LSD) test at $p < 0.05$. One-way ANOVA and one-tailed *t*-test were performed to determine the differences among the water management types within each variety in 2011 and 2012, respectively. Regression analyses were performed in Excel 2016 (Microsoft, Redmond, WA, USA) to examine the relationships among variables associated with yield and yield components.

3. Results

3.1. Climatic conditions and changes in SWP

Rainfall was evenly distributed in both growing periods (Figure 1). Rainfall events exceeding 100 mm per day were recorded twice in 2011 and thrice in 2012 (Figure 1). In the 2011 growing period, IR plots were irrigated 8 times, and the total volume of irrigation water was 339.6 L m^{-2} (Figure 1(A)).

Average monthly temperature during the growing periods of both years was slightly higher than normal (Table 1). Total rainfall during the growing period was 1584 mm in 2011 and 1374 mm in 2012, which were approximately 200 and 450 mm higher than normal total rainfall, respectively. Monthly rainfall in both years was higher than or comparable to the normal value, except during August 2011, when rainfall was extremely low. In both years, average monthly solar radiation was lower than normal, except in July and October 2012.

Under IR and NIR, we observed SWP fluctuations over the growing period, from 0 to −72 kPa in 2011 and from 0 to −85 kPa in 2012 (Figure 2). Under FL, SWP remained close to 0 kPa throughout the growing period in both years. In 2011, SWP under IR and NIR was comparable except during 62–84 DAT, when the low rainfall decreased the average SWP of NIR was 15.6 kPa lower than the average under IR (Figure 2(A)). In 2012, SWP under NIR was less than −60 kPa for 16 days during 56–71 DAT (Figure 2(B)).

3.2. Growing period

Water management did not alter the heading date of any variety (Table 2). The earliest full heading occurred at 61–63 DAT for YHM; for N5, N1, and HH, full heading occurred 3–7, 11–14, and 16–19 days later, respectively. Physiological maturity was observed first in YHM, followed by N5, N1, and HH. The grain filling periods of N1 and N5 tended to be shorter under IR and NIR than under FL, but

Table 1. Average monthly temperature (°C), rainfall (mm), and solar radiation (MJ m^{-2} d^{-1}) during the growing period (June–October) in 2011 and 2012.

	Temperature (°C)			Rainfall (mm)			Solar radiation (MJ m^{-2} d^{-1})		
Month	2011	2012	Normal value[a]	2011	2012	Normal value[a]	2011	2012	Normal value[b]
June	23.0	22.4	22.2	450.0	605.5	299.0	98.9	91.2	142.1
July	26.2	26.4	25.9	391.0	250.0	292.5	173.7	190.5	182.2
August	27.3	27.1	26.8	74.0	361.5	251.9	199.4	170.4	210.3
September	24.7	24.2	24.0	459.0	425.5	311.4	163.0	162.0	171.5

Note: Climatic data obtained from Automated Meteorological Data Acquisition system (AMeDAS) in Nissyo station (Nankoku City, Kochi, Japan; 33°32′ N, 133°40′ E). [a]The values indicate averages of monthly temperatures and rainfall from 1981 to 2010. [b]The values indicate averages of monthly solar radiation from 1987 to 2010.

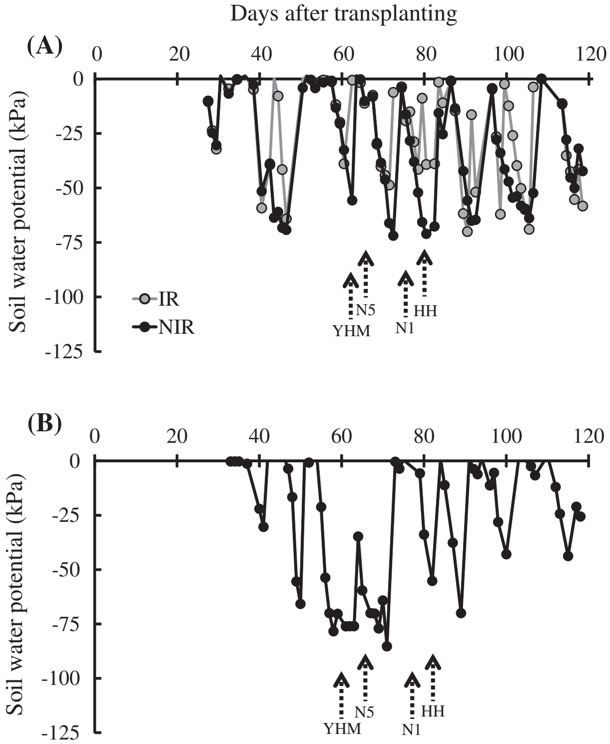

Figure 2. Changes in SWP under supplementary irrigation (IR) and non-irrigation (NIR) conditions after the onset of water management treatments in 2011 (A) and 2012 (B). Arrows indicate the timing of full heading in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under continually flooded (FL) conditions.

YHM and HH exhibited no clear differences in their grain filling periods across water management regimes.

3.3. Plant growth performance

Irrespective of water management, HH exhibited the highest final leaf number on main stem across all varieties for both years, whereas N5 exhibited the lowest number (Table 3). Within a single variety, differences in water management had no significant effect on the final leaf number on main stem except N5 in 2011.

Under all treatments in both years, plant length continually increased until one week after heading, when deficient soil moisture conditions decreased plant length in all varieties, except YHM in 2012 (data not shown). Varieties did not differ in plant length across water management regimes at the full heading stage (Table 3).

For all varieties and treatments, the number of tillers per square meter gradually increased until maximum tillering (33–48 DAT), and then decreased until plants reached maturity (data not shown). Across all treatments and both years, HH had the maximum number of tillers and of productive tillers, followed by YHM, then by the two NERICA varieties (Table 3). When examining the effect of water management on tillers and productive tillers, we observed that plants under NIR tended to have a higher maximum number of tillers than did plants under FL and IR. However, NERICAs under NIR had fewer productive tillers than NERICAs under FL. For all varieties, FL resulted in the highest productive tiller ratio, followed by IR and NIR, but regardless of treatment, N1 showed the lowest productive tiller ratio among the four varieties.

At full heading, YHM showed a conspicuously higher SLA than the other three varieties (Table 3). Water management had no obvious effect on the SLA at full heading of any variety.

3.4. Yield and yield components

In both years, HH had the largest panicle number per square meter, followed by YHM, N5, and finally N1 (Table 4). Low soil moisture conditions tended to decrease panicle number per square meter in NERICAs, except in N5 during 2012. However, water management had no clear

Table 2. Dates of full heading and physiological maturity in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three different water management regimes during 2011 and 2012: continually flooded (FL), supplementary irrigation (IR), and non-irrigation (NIR).

		2011		2012	
Variety	Treatment	Full heading	Maturity	Full heading	Maturity
N1	FL	15-Aug (75)[a]	24-Sep (115) [40][b]	12-Aug (74)	21-Sep (114) [40]
	IR	15-Aug (75)	24-Sep (115) [40]	–	–
	NIR	15-Aug (75)	22-Sep (113) [38]	13-Aug (75)	19-Sep (112) [37]
N5	FL	8-Aug (68)	14-Sep (105) [37]	4-Aug (66)	13-Sep (106) [40]
	IR	8-Aug (68)	12-Sep (103) [35]	–	–
	NIR	8-Aug (68)	9-Sep (100) [32]	6-Aug (68)	10-Sep (103) [35]
YHM	FL	1-Aug (61)	9-Sep (100) [39]	30-Jul (61)	8-Sep (101) [40]
	IR	3-Aug (63)	12-Sep (103) [40]	–	–
	NIR	3-Aug (63)	12-Sep (103) [40]	1-Aug (63)	10-Sep (103) [40]
HH	FL	20-Aug (80)	29-Sep (120) [40]	17-Aug (79)	26-Sep (119) [40]
	IR	20-Aug (80)	29-Sep (120) [40]	–	–
	NIR	20-Aug (80)	29-Sep (120) [40]	18-Aug (80)	24-Sep (117) [37]

[a] Values in parenthesis indicate days after transplanting.
[b] Values in square brackets indicate grain filling period from full heading to maturity.

Table 3. Final leaf number on main stem, plant length, SLA at hull heading, maximum number of tillers, number of productive tillers, and productive tiller ratio in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three different water management regimes during 2011 and 2012: continually flooded (FL), supplementary irrigation (IR), and non-irrigation (NIR).

		2011				2012		
Growth parameter	Variety	FL	IR	NIR		FL	NIR	
Final leaf number on main stem	N1	14.0 b	13.8 b	13.6 c	n.s.	14.4 b	14.8 b	n.s.
	N5	12.3 c	13.0 c	12.6 d	**	12.3 c	12.3 c	n.s.
	YHM	14.1 b	14.3 b	13.7 b	n.s.	14.3 b	14.3 b	n.s.
	HH	15.9 a	15.9 a	15.6 a	n.s.	15.9 a	16.1 a	n.s.
Plant length (cm)	N1	104 a	102 a	99 a	n.s.	122 a	111 a	n.s.
	N5	111 a	103 a	102 a	n.s.	107 c	102 *ab*	n.s.
	YHM	100 a	97 a	105 a	n.s.	103 c	107 *ab*	n.s.
	HH	108 a	99 a	95 a	n.s.	114 b	88 b	*
Maximum number of tillers (m^{-2})	N1	291 b	262 c	315 d	n.s.	275 c	342 b	n.s.
	N5	273 b	278 c	342 c	*	277 c	311 b	n.s.
	YHM	335 *ab*	349 b	424 b	n.s.	354 b	446 a	n.s.
	HH	384 a	462 a	500 a	**	424 a	464 a	n.s.
Number of productive tillers (m^{-2})	N1	240 c	175 d	186 d	**	181 d	179 b	n.s.
	N5	229 c	215 c	220 c	n.s.	213 c	205 b	n.s.
	YHM	273 b	260 b	311 b	*	283 b	302 a	n.s.
	HH	342 a	335 a	355 a	n.s.	334 a	364 a	n.s.
Productive tiller ratio (%)	N1	82.5 a	67.1 b	59.2 c	**	67.9 a	52.8 c	*
	N5	83.7 a	77.6 a	64.3 bc	**	77.1 a	67.2 b	n.s.
	YHM	82.0 a	74.5 a	73.3 a	n.s.	80.3 a	67.7 b	*
	HH	89.0 a	72.6 *ab*	71.1 *ab*	**	79.0 a	79.0 a	n.s.
SLA (cm^2 g^{-1})	N1	142 b	143 b	144 b	n.s.	199 *ab*	201 bc	n.s.
	N5	134 b	144 b	144 b	n.s.	168 a	178 c	n.s.
	YHM	214 a	218 a	215 a	n.s.	222 a	228 a	n.s.
	HH	157 b	143 b	148 b	n.s.	208 *ab*	209 *ab*	n.s.

Note: Within each water management column, values followed by the same letter do not differ significantly at $p < 0.05$ (LSD test).
* and ** indicate significance at $p < 0.05$ and $p < 0.01$ within each variety.
n.s. indicates not significant.

Table 4. Yield and yield components in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three different water management regimes during 2011 and 2012: continually flooded (FL), supplementary irrigation (IR), and non-irrigation (NIR).

		2011				2012		
Yield parameter	Variety	FL	IR	NIR		FL	NIR	
Panicle number (m^{-2})	N1	200 c	170 (85) c	167 (83) d	n.s.	192 c	181 (94) d	n.s.
	N5	252 bc	181 (72) c	204 (81) c	*	204 c	207 (102) c	n.s.
	YHM	289 b	266 (92) b	281 (97) b	n.s.	285 b	307 (108) b	n.s.
	HH	366 a	359 (98) a	370 (101) a	n.s.	359 a	370 (103) a	n.s.
Spikelet number per panicle	N1	122.8 a	104.4 (85) b	91.8 (75) b	n.s.	151.5 a	102.2 (67) a	n.s.
	N5	122.0 a	122.1 (100) a	107.3 (88) a	**	126.0 a	110.1 (87) a	n.s.
	YHM	83.0 b	80.6 (97) c	70.4 (85) c	*	84.6 b	87.4 (103) b	n.s.
	HH	88.9 b	73.2 (82) d	64.2 (72) c	*	86.7 b	51.3 (59) c	**
Spikelet number (m^{-2})	N1	24,080 b	17,660 (73) c	14,992 (62) d	*	29,123 *ab*	18,337 (63) c	n.s.
	N5	30,566 a	21,982 (72) b	21,756 (71) b	**	25,493 *ab*	22,404 (88) b	*
	YHM	23,795 b	21,475 (90) bc	19,777 (83) c	**	24,020 b	26,836 (112) a	**
	HH	32,438 a	26,266 (81) a	23,684 (73) a	n.s.	31,076 a	18,881 (61) c	*
Grain filling ratio (%)	N1	71.3 a	83.2 (117) a	83.9 (118) a	n.s.	65.4 a	77.6 (119) a	n.s.
	N5	60.5 b	67.3 (111) b	62.1 (103) b	n.s.	67.9 a	67.6 (100) *ab*	n.s.
	YHM	68.3 *ab*	67.8 (99) b	71.1 (104) *ab*	n.s.	63.8 a	63.9 (100) b	n.s.
	HH	69.8 *ab*	71.2 (102) b	78.0 (112) *ab*	n.s.	73.9 a	74.4 (101) *ab*	n.s.
1000-grain weight (g)	N1	24.1 b	23.6 (98) b	22.9 (95) b	n.s.	25.0 b	22.5 (90) b	n.s.
	N5	23.8 b	23.5 (99) b	22.1 (93) b	n.s.	22.4 c	21.9 (98) c	n.s.
	YHM	26.7 a	27.1 (101) a	27.0 (101) a	n.s.	27.3 a	26.1 (96) a	n.s.
	HH	22.5 c	21.7 (97) c	21.8 (97) b	n.s.	23.9 bc	22.5 (94) b	**
Brown rice yield (g m^{-2})	N1	413 b	346 (84) a	287 (69) c	*	466 b	318 (68) b	*
	N5	440 b	348 (79) a	298 (68) bc	n.s.	387 c	331 (85) b	**
	YHM	434 b	393 (91) a	379 (87) *ab*	n.s.	418 bc	447 (107) a	n.s.
	HH	508 a	406 (80) a	402 (79) a	*	548 a	314 (57) b	**

Note: Within each water management column, values followed by the same letter are not significantly different at $p < 0.05$ (LSD test).
* and ** indicate significance at $p < 0.05$ and $p < 0.01$ within each variety.
n.s. indicates not significant.
Numbers in parentheses indicate, for each variety, the relative values of each yield parameter under IR or NIR to those under FL.

effect on panicle number per square meter in the two Japanese varieties.

For all varieties except YHM in 2012, FL resulted in the highest number of spikelets per square meter and per panicle (Table 4). These two components also tended to decrease with decreasing soil water availability in every variety except YHM in 2012. Under NIR in 2011, the relative value of spikelet number per panicle for N1, N5, YHM, and HH was 75, 88, 85, and 72% of the number under FL, respectively. Similarly, under NIR in 2012, the relative value was 67, 87, 103, and 59%, respectively, of the number under FL.

Irrespective of water management, N1 and N5 had higher spikelet numbers per panicle than did YHM and HH (Table 4). However, NERICAs had similar or lower numbers of spikelets per square meter as compared to that of the Japanese varieties.

In 2011, N1 had the highest grain filling ratio, followed by HH and YHM, and then by N5 (Table 4). However, there was no clear varietal difference in the grain filling rate in 2012. For all varieties, FL resulted in slightly lower grain filling ratios than those under IR and NIR, except N5 and YHM in 2012.

Across both years, YHM had the highest 1000-grain weight among the four varieties, whereas no clear varietal difference was observed among the other three varieties (Table 4). When examining the effect of water management, FL tended to result in greater 1000-grain weight than did IR and NIR, but a clear trend was not very apparent. In all varieties, brown rice yield under FL was the highest and tended to decrease as soil water availability declined, except YHM in 2012. Under IR and NIR, YHM showed a lower reduction in brown rice yield compared with N1, N5, and HH in both years. Under FL in both years, HH had a higher brown rice yield than YHM, N1, and N5. In 2011, brown rice yields under IR and NIR tended to be higher in HH than in the other three varieties. However, in 2012, the brown rice yield of HH under NIR was comparable to that of the NERICA varieties and lower than that of YHM.

Of the four varieties, N1 had the highest number of primary rachis-branches per panicle, followed by N5, HH, and finally YHM (Table 5). Further, N1 and N5 had higher counts of primary rachis-branches per panicle than did HH and YHM. In N1 and HH, the number of primary rachis-branches per panicle decreased under IR and NIR as compared to that with FL during both years, whereas water management did not affect this trait in N5 and YHM. In contrast, the number of secondary rachis-branches per panicle decreased with decreasing soil water availability in all varieties across both years, except YHM in 2012. The reduction rate in the number of secondary rachis-branches was greater than the reduction in the number of primary rachis-branches. Additionally, low soil moisture had a stronger effect on the number of primary and secondary rachis-branches in N1 and HH compared with N5 and YHM. However, low soil moisture appeared to have little effect on spikelet number per primary and secondary rachis-branches. Comparing across varieties, N1 and N5 had more spikelets per primary rachis-branches than HH and YHM, whereas YHM had more spikelets per secondary rachis-branches than HH, N1, or N5.

Table 5. Number of primary and secondary rachis-branches per panicle, and spikelet number per primary and secondary rachis-branches in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three different water management regimes during 2011 and 2012: continually flooded (FL), supplementary irrigation (IR), and non-irrigation (NIR).

		2011				2012		
Parameter	Variety	FL	IR	NIR		FL	NIR	
Number of primary rachis-branches per panicle	N1	14.1 a	12.3 (87) a	11.6 (82) a	*	14.1 a	12.0 (85) a	*
	N5	11.5 b	12.1 (105) a	11.6 (101) a	n.s.	12.4 b	12.1 (98) a	n.s.
	YHM	7.5 c	7.3 (98) a	7.2 (97) c	n.s.	7.4 d	7.4 (100) b	n.s.
	HH	9.7 b	9.1 (94) b	9.1 (93) b	*	0.3 c	7.9 (76) b	**
Number of secondary rachis-branches per panicle	N1	11.7 b	10.4 (89) b	6.4 (55) b	n.s.	23.7 a	11.0 (46) b	n.s.
	N5	18.2 a	17.6 (97) a	13.0 (72) a	*	20.1 *ab*	15.1 (75) a	n.s.
	YHM	14.4 *ab*	14.8 (102) a	11.8 (82) a	*	15.3 bc	16.2 (106) a	n.s.
	HH	12.4 b	8.8 (71) b	6.0 (48) b	*	12.4 c	3.8 (30) c	*
Spikelet number per primary rachis-branch	N1	6.7 a	6.3 (94) a	6.4 (95) a	n.s.	6.2 a	6.1 (98) a	n.s.
	N5	6.1 b	6.1 (100) a	6.0 (99) b	n.s.	5.7 b	5.6 (97) b	n.s.
	YHM	5.2 d	5.0 (97) c	4.9 (95) d	n.s.	5.1 c	4.9 (97) c	n.s.
	HH	5.7 c	5.6 (97) b	5.5 (95) c	n.s.	5.7 b	5.4 (95) b	*
Spikelet number per secondary rachis-branch	N1	2.4 c	2.5 (106) b	2.5 (107) b	n.s.	2.7 b	2.5 (95) b	n.s.
	N5	2.8 *ab*	2.7 (96) b	2.8 (101) a	n.s.	2.7 b	2.7 (99) b	n.s.
	YHM	3.1 a	3.0 (98) a	3.0 (97) a	n.s.	3.1 a	3.1 (103) a	n.s.
	HH	2.6 bc	2.5 (97) b	2.4 (92) b	n.s.	2.2 c	2.3 (102) c	*

Note: Within each water management column, values followed by the same letter are not significantly different at $p < 0.05$ (LSD test).
* and ** indicate significance at $p < 0.05$ and $p < 0.01$ within each variety.
n.s. indicates not significant.
Numbers in parentheses indicate the relative values of each parameter under IR or NIR to those under FL for each variety.

Table 6. Correlation coefficients obtained from regression analyses between brown rice yield and each yield component in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three different water management regimes during 2011 and 2012: continually flooded (FL), supplementary irrigation (IR), and non-irrigation (NIR).

Variety	Panicle number (m^{-2})	Spikelet number per panicle	Spikelet number (m^{-2})	Grain filling ratio (%)	1000-grain weight (g)
N1	0.512 n.s.	0.828 **	0.874 **	−0.656 *	0.921 ***
N5	0.637 *	0.686 *	0.876 **	0.061 n.s.	0.701 *
YHM	0.587 n.s.	0.600 n.s.	0.733 *	−0.453 n.s.	−0.187 n.s.
HH	−0.245 n.s.	0.942 ***	0.937 ***	−0.236 n.s.	0.616 n.s.

Note: *, **, and *** indicate significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.
n.s. indicates not significant.

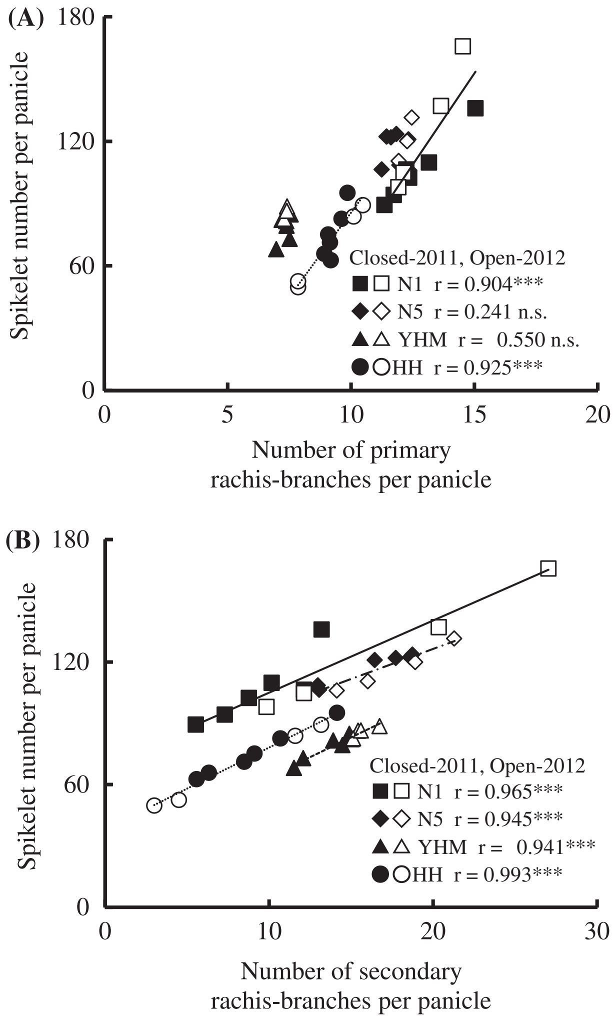

Figure 3. Relationship between spikelet number per panicle and the number of primary and secondary rachis-branches per panicle in NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under three different water management regimes during 2011 and 2012: continually flooded (FL), supplementary irrigation (IR), and non-irrigation (NIR).
*** Significant at $p < 0.001$; n.s. not significant.

3.5. Relationship between yield and yield components

Brown rice yield exhibited a positive and significant correlation with spikelet number per square meter in all varieties (Table 6). A positive and significant correlation was also observed between brown rice yield and spikelet number per panicle in all varieties except YHM. However, brown rice yield was not correlated with panicle number per square meter, except in N5. No clear relationship existed between brown rice yield and grain filling ratio. A positive and significant correlation was found between brown rice yield and 1000-grain weight in NERICAs, but not in the Japanese varieties.

The spikelet number per panicle was positively and significantly correlated with the number of primary rachis-branches per panicle in N1 and HH, but not in N5 and YHM (Figure 3(A)). In contrast, a strong positive correlation was observed between spikelet number per panicle and number of secondary rachis-branches in all varieties (Figure 3(B)).

3.6. Average soil water potential (ASWP) during determination period for each yield component

In both years and treatments, ASWP during the determination period (subsequently,'ASWP') of panicle number tended to be lower for YHM and HH than for N1 and N5, except for YHM under IR in 2011 (Table 7). Under IR in 2011, ASWP of spikelet number per panicle remained greater than −14.4 kPa for all varieties. In 2012, ASWP of spikelet number per panicle for N1 and HH was considerably lower than that for N5 and YHM, and was 3.5–8.8 times lower than the ASWP for N1 and HH in 2011. For YHM specifically, ASWP under NIR in 2011 was more than two times lower than ASWP under IR in 2011 and under NIR in 2012. Under NIR in 2012, ASWP of grain filling ratio and 1000-grain weight for N5 was over two times lower than ASWP of YHM and HH (Table 7). Furthermore, under NIR in 2011, ASWP for N5 and YHM tended to be lower than ASWP for N1 and HH. Finally, under NIR in 2012, ASWP for YHM was more than 2.5 times higher than that for YHM under IR and NIR in 2011.

3.7. Effect of deficient soil moisture conditions on spikelet number

Under conditions with ASWP greater than approximately −30 kPa, the relative spikelet number per panicle (ratio of

Table 7. Average soil water potentials (ASWP) under supplementary irrigation (IR) and non-irrigation (NIR) conditions during determination periods for each yield component of NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) in 2011 and 2012.

	ASWP from the beginning of water treatment to full heading[a] (kPa)			ASWP from 25 to 10 days before heading[b] (kPa)			ASWP from full heading to maturity[c] (kPa)		
	2011		2012	2011		2012	2011		2012
Variety	IR	NIR	NIR	IR	NIR	NIR	IR	NIR	NIR
N1	−15.3	−13.1	−13.1	−5.5	−9.3	−48.6	−29.2	−28.1	−24.0
N5	−16.7	−22.9	−19.4	−12.3	−21.9	−23.9	−32.5	−41.5	−39.8
YHM	−20.5	−26.2	−32.1	−14.4	−33.0	−14.3	−36.9	−43.4	−14.7
HH	−31.5	−27.3	−31.5	−8.1	−18.2	−62.9	−21.8	−30.8	−17.7

[a] During determination period for panicle number.
[b] During determination period for spikelet number per panicle.
[c] During determination period for grain filling rate and 1000-grain weight.

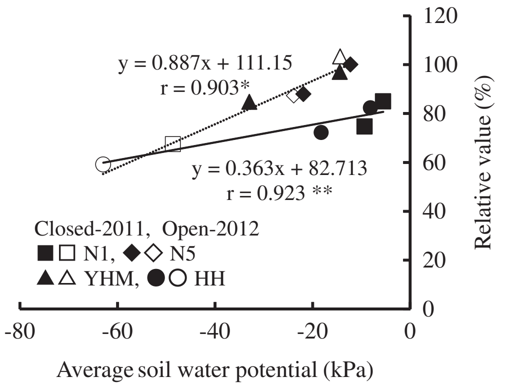

Figure 4. Relationship between relative value of spikelet number per panicle and ASWP during the determination period for spikelet number per panicle (from 25 to 10 days before heading). The relative value refers to the ratio of spikelet numbers under supplementary irrigation (IR) and non-irrigation (NIR) conditions to spikelet numbers under continually flooded (FL) conditions. Data for NERICA 1 (N1), NERICA 5 (N5), Yumenohatamochi (YHM), and Hinohikari (HH) grown under IR and NIR conditions in 2011 and 2012 are shown. The solid line represents data from N1 and H, and the dotted line represents N5 and YHM.
* Significant at $p < 0.05$; ** Significant at $p < 0.01$.

spikelets per panicle under IR/NIR to spikelets per panicle under FL) of N5 and YHM was higher than that of N1 and HH (Figure 4). For all varieties, the relative spikelet number per panicle was positively and significantly correlated with ASWP of spikelet number per panicle (Figure 4). Decreases in relative spikelet number per panicle were greater for N5 and YHM than for N1 and HH.

Panicle number per square meter, grain filling ratio, and 1000-grain weight were not correlated with ASWP (data not shown).

4. Discussion

4.1. *Characterization of NERICAs as affected by soil water conditions*

To understand the inconsistent responses of NERICAs grown in uplands vs. lowlands, information about growth and yield characteristics is essential. In the present study, we thus compared NERICA varieties with Japanese upland and lowland varieties, in terms of their responses to soil water conditions.

Soil moisture under IR and NIR during a particular growing period varied across rice varieties, because each variety differs in growing length (Table 2), and the SWP is always fluctuating (Figure 2). Therefore, we used the ASWP during the determination periods for every yield component of each variety under IR and NIR to eliminate the effect of growing length (Table 7). There were three determination periods depending on the component: (1) panicle number, from the start of the water management treatments until full heading; (2) spikelet number per panicle, from 25 to 10 days before heading (Hoshikawa, 1975; Matsushima, 1962); (3) grain filling ratio and 1000-grain weight, from full heading to maturity.

4.1.1. *Heading time*

When soil moisture content is low, the degree of heading delay is directly proportional to the cumulative pre-heading water stress (Tsuda & Takami, 1991). In the present study, water management showed little influence on the time of heading in both NERICA and Japanese varieties (Table 2). During the growing period, rainfall was greater than 1500 mm in both years, considerably higher than normal (Table 1). As a result, ASWPs under IR and NIR remained around or exceeded −30 kPa from the start of the experiment to full heading in all varieties (Table 7). Lampayan et al. (2015) reported that alternate wetting and drying irrigation with over −30 kPa of SWP had little effect on the growth and yield of rice. Thus, water management might not have changed the heading date because the rice varieties did not experience severe cumulative water stress before heading.

4.1.2. *Tillering ability*

NERICAs exhibited poorer tillering ability than that of Japanese varieties, (i.e. lower maximum tiller number per square meter and productive tiller number per square meter across all treatments) (Table 3). Previous research has suggested that rice varieties with a shorter plant length show greater tillering ability because they produce shorter and thinner leaves, resulting in lower competition for dry matter and nitrogen among tillers (Nuruzzaman et al., 2000). Furthermore, varieties with shorter leaf blade length may have greater tillering ability because the briefer leafing intervals may cause individual tillers to develop simultaneously with leaves on the main culm at definite intervals (Katayama, 1951). In our experiment, NERICAs and YHM did not differ in plant length or in the final leaf number in main stem (Table 3). However, the SLA of NERICAs at full heading was significantly lower than the SLA of YHM, indicating that NERICAs have thicker leaves than the Japanese upland variety (Table 3). These thicker leaves might contribute to the lower tillering ability found in NERICAs.

In addition, NERICAs exhibited the highest maximum number of tillers and the lowest ratio of productive tillers under NIR than in the other two treatments (Table 3). However, ASWP during tillering (from treatment start to full heading) was higher for NERICAs than for either Japanese variety (Table 7). These results imply that the observed differences in tillering ability under NIR were due to variety-specific characteristics, and not due to variation in the intensity of water stress during tillering.

4.1.3. Numbers of spikelets, primary rachis-branches, and secondary rachis-branches

Our results revealed that both NERICAs produced more primary rachis-branches than the Japanese varieties, whereas N5 had more secondary rachis-branches (Table 5). Further, both NERICAs also showed slightly more spikelets per primary rachis-branch, and thus, more spikelets per panicle, than the Japanese varieties (Tables 4 and 5). However, the inferior tillering ability of NERICAs meant that they showed fewer panicles per square meter than did the Japanese varieties, resulting in fewer or a similar number of spikelets per square meter (Tables 3 and 4). Our results agreed with previous findings (Matsunami et al., 2009; Wainaina et al., 2015) showing that NERICAs have more spikelets per panicle and fewer panicles per plant than some Japanese varieties, including YHM.

Rice is most sensitive to water stress during the meiosis stage of growth (Tajima, 1995), and the resultant yield reduction is attributed mainly to the decreased spikelet number per panicle (Wada, Baba, & Furuya, 1945). Our study supports this explanation, as spikelet number per panicle was the yield component most severely affected by water management, even though ASWPs during the determination periods for spikelet number per panicle, grain filling ratio, and 1000-grain weight were all comparable (Tables 4 and 7).

We observed that lower ASWP during the determination period for spikelet number per panicle resulted in a higher reduction rate of spikelet number per panicle across varieties, water management methods, and years (Tables 4 and 7). Furthermore, we found significant correlations between ASWP during the determination period for spikelet number per panicle and the reduction rate of spikelet number per panicle (Figure 4), indicating that spikelet number per panicle decreases as soil water availability decreases during the determination period for this component.

The reduction in spikelet number was primarily responsible for yield decreases in the two NERICAs under IR and NIR (Table 6), consistent with the results of Matsumoto et al. (2014). Moreover, decreases in spikelet number per panicle for N1 and HH were due to reductions in the number of both primary and secondary rachis-branches, whereas similar decreases in spikelet number for N5 and YHM were mainly caused by secondary rachis-branch decline (Figure 3). A mild drought stress (−20 kPa) during determination period for spikelet number per panicle appeared to be sufficient for secondary rachis-branch reduction in NERICAs, as ASWPs of spikelet number per panicle for N5 did not drop below −24 kPa across water management and year. This finding corroborates that of Kato et al. (2008), who found that even mild drought stress (<20% reduction in shoot dry weight) was sufficient to reduce secondary rachis-branches and consequently, spikelet number per panicle.

Both N1 and HH exhibited higher reduction rates in spikelet number per panicle than N5 and YHM in both years (Table 4), even though the latter two varieties had lower ASWPs than N1 and HH in 2011 (Table 7). In addition, under conditions wherein the ASWP during the determination period for spikelet number per panicle was greater than approximately −30 kPa, the spikelet number per panicle of N5 and YHM was more tolerant to water stress than that of N1 and HH (Figure 4). However, tolerance in N5 and YHM was comparable to that in N1 and HH when the ASWP was approximately −50 kPa. These results imply that NERICAs differ in the response of spikelet number per panicle to varying water stress levels.

4.1.4. Panicle number, 1000-grain weight, and grain filling ratio

In NERICAs, panicle number per square meter tended to decrease under low soil moisture conditions (IR and NIR), whereas the Japanese varieties were unaffected in terms of this yield component (Table 4). However, NERICAs had higher ASWP during the determination period for panicle number than the Japanese varieties (Table 7). Therefore, ASWP failed to explain differences in panicle number between NERICAs and the Japanese varieties under IR and

NIR. Instead, we hypothesize that panicle number is a yield component more susceptible to water stress in NERICAs than in Japanese varieties.

In our study, 1000-grain weight tended to decrease with decreasing soil water conditions (Table 4). However, the degree of reduction in 1000-grain weight did not correspond to the associated ASWP (Table 7). In contrast, the grain filling ratio of all four varieties remained unaffected by water management (Tables 4 and 7), despite being susceptible to drought stress (Bouman et al., 2007; Matsushima, 1962). Gendua et al. (2009) reported that the grain filling ratio could increase when cultivation methods reduce sink size (determined by multiplying spikelet number per panicle by one-grain weight). Therefore, we speculate that the grain filling ratio was maintained through decreases in spikelet number per panicle and 1000-grain weight that occurred as a result of ASWP declines.

4.2. Possible causes of inconsistent NERICA responses to soil water conditions

In the present study, the yield of NERICA under FL was found to be higher than that under IR and NIR (Table 4), consistent with the finding of Matsumoto et al. (2014), although the latter also suggested that when water supply is adequate in uplands, NERICA yield can be comparable to, or even exceed, that in irrigated lowlands. Similarly, Matsunami et al. (2009) reported that the NERICA yield was higher in uplands than in irrigated lowlands because rainfall supplied enough water. Thus, the ASWPs (−5.5–−48.6 kPa) associated with each NERICA yield component under IR and NIR were sufficiently low to reduce spikelet number per panicle, despite the considerable rainfall during trials (Table 7).

In the present study, NERICA spikelet number per panicle responded differently to low soil moisture (Table 5 and Figure 4). Specifically, N1 reduced both primary and secondary rachis-branches, whereas N5 reduced only secondary rachis-branches. This finding suggests that NERICAs vary in their yield response to certain soil water conditions. This variation may be partially responsible for the inconsistent NERICA performance under upland and lowland conditions. However, when ASWP was approximately −50 kPa, varietal differences in the reduction rate of spikelet number per panicle disappeared (Figure 4), implying that yield response variation in uplands could change depending on actual field SWP. Furthermore, Menge et al. (2016) reported that varietal differences in the plasticity of deep root and lateral root development exists among NERICAs subjected to moderate drought stresses. Therefore, graded availability of water along the vertical soil profile should also affect NERICA performances under upland conditions.

5. Conclusions

Our results demonstrated that NERICAs had lower yield than the Japanese upland and lowland varieties under low soil water conditions, despite similar growing periods. The lower yield potential of NERICAs appeared to be due primarily to inferior tillering ability, resulting in fewer panicles per square meter. However, spikelet number per panicle was considerably greater in NERICAs than in the Japanese varieties. We consider this parameter to be one of the most important determinants for grain yield under low soil moisture, because yield reduction under IR and NIR in all varieties, including NERICA, was due mainly to the reduction in spikelet number per panicle.

Our results demonstrated that water stress intensity was the primary factor for the reduction in spikelet number, and varietal differences in the reduction rate of spikelet number per panicle were caused mainly by the drought-stress-induced abortion of secondary rachis-branches. Variations in the yield response to low soil moisture may partially explain the inconsistency in NERICA performance across uplands and lowlands. Moreover, we suggest that the variation in NERICA performance under upland conditions could change depending on water stress intensity and the presence of an available water gradient along the vertical soil profile.

Because this was a field study, soil water conditions varied during the determination periods for each yield component. Therefore, future studies aiming to build on our existing findings will need to control for differences in soil moisture content and distribution along the vertical soil profile when examining NERICA yield and growth responses.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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