

Growth and Yield of New Rice for Africa (NERICAs) under Different Ecosystems and Nitrogen Levels

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Abstract : Scarcity of water and N fertilizer are major constraints to rice production, particularly in developing countries where rainfed upland condition dominates. Improvement of genetic adaptability to inadequate water and N fertilizer is one option to maintain productivity in these regions. NERICAs are expected to yield higher under low input conditions, but growth and yield responses of the cultivars to different ecosystems and N levels remain unknown. The objectives of this study were to characterize the growth and yield performance of NERICAs, in comparison with selected Japanese rice cultivars. The two NERICAs (NERICA 1 and NERICA 5), two Japanese upland cultivars (Toyohatamochi and Yumenohatamochi), and a Japanese lowland cultivar Hitomebore were grown under two ecosystems (irrigated lowland (IL) and rainfed upland (RU)) with two N levels (high (H) and low (L)) for two years. The cultivar difference in the aboveground dry weight and grain yield was the largest in the in RU×L plot, where the values of NERICAs were similar to those in the other plots, but the values of other cultivars were substantially reduced. Regardless of cultivar, N contents of the plants at maturity correlated significantly with the aboveground dry weight at maturity, spikelet number and grain yield per area. These results indicate that NERICAs, compared with the selected Japanese upland cultivars that were bred for drought tolerance, have a higher ability to absorb N under upland conditions, which may contribute to higher biomass production and sink formation, resulting in increased gain yield.

Key words : Growth, Irrigated lowland, NERICA, Nitrogen absorption, Nitrogen level, Rainfed upland, Rice, Yield.

Advances in technologies such as irrigation and N fertilization along with genetic improvement have largely contributed to the continuous increase in rice production for the last several decades. Currently, about 150 million ha of land is used for rice production worldwide (FAO, 2008). Regarding water availability, rice-producing environments can be classified into four ecosystems: irrigated lowland, rainfed lowland, rainfed upland and flood-prone upland (Maclean et al., 2002). Among these ecosystems, irrigated lowland is the most productive, which provides 75% of global rice production with about 50% of the global harvested rice area (Bouman et al., 2007). The other ecosystems are less productive, but dominant systems in parts of subhumid and humid tropics where rice is a crucially important staple food. However, increasing competition of fresh water among agriculture and other industrial or nonindustrial sectors threatens a continuous utilization of water for rice production in any region. In addition, future global warming would accompany scarce and/or erratic precipitation depending on the region (IPCC, 2007); therefore, the capacity of rice production might be impaired in many rice-producing regions.

Rice plants are sensitive to water availability in soil, but the magnitude of damage caused by inadequate availability varies with the growth stage (O'Toole, 1982). Water stress reduces leaf area, leading to a reduction of a photosynthetic capacity of a whole plant, and hence a reduction of total biomass production. On the other hand, water stress during reproductive stage impairs sink capacity (Tajima, 1995). Many previous studies showed that rice plants grown under upland condition are more prone to water stress than those grown under irrigated lowland condition (McCauley, 1990; Bouman et al., 2005; Yang et al., 2005). Excess dosage of chemical fertilizers, especially N fertilizer, can cause environmental pollution. In addition, an ever-increasing rise of oil price in recent years is raising the expenditure to fertilization, along with other costs such as mechanization and transport, and thereby the total cost of rice production. Thus, there is growing need for the development of novel technologies and production systems that enable rice productivity to be maintained or increased with less water and N fertilizer. Improvement of genetic adaptability to inadequate water and fertilizer supply is one option to meet the necessity.

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Abbreviations : H, High N level; IL, Irrigated lowland; L, Low N level; NERICAs, Rice cultivars bred from interspecific cross between *O. sativa* and *O. glaberrima*; RU, Rainfed upland.

NERICAs (new rice for Africa) are the product of interspecific hybridization between the cultivated rice species of Africa and Asia. From 1990s, a plenty of efforts to utilize *Oryza glaberrima* genes to improve *O. sativa* have been made mainly by Africa Rice Center (formerly West Africa Rice Development Association (WARDA)), which attempted to develop new rice ecotypes that adapted to input-limited, weed- and drought-prone production systems (Jones et al., 1997a, 1997b). In 2000, first NERICAs, NERICA 1 to NERICA 7, were released. Since then, additional NERICAs, which were adaptable not only to upland condition but also to lowland ecosystem, have been available to farmers (Kaneda, 2007a, 2007b; Africa Rice Center, 2007; Futakuchi, 2008).

NERICAs, compared to improved *O. sativa* cultivars, are expected to yield higher under resource-limited conditions. Futakuchi and Jones (2005) evaluated growth and yield performance of NERICAs in various growing ecologies (upland, rainfed lowland and irrigated lowland), and revealed their better growth and yield performance than their parental *O. sativa* cultivar WAB56-104. Tamamura et al. (2007) compared yield of NERICAs with that of Japanese upland and lowland cultivars for three years, and revealed that NERICAs could outyield selected Japanese cultivars under rainfed upland condition, depending on the year. NERICAs were also characterized by exhibiting higher water use efficiency under limited soil water availability (Fujii et al., 2006; Onyango et al., 2007). However, information on the combined effects of different water availability and N level, which are both major limiting resources in developing countries, on growth and yield performance of NERICAs is very limited (Sakagami and Ito, 2008). The objectives of the present study were to evaluate the growth and yield performance of NERICAs under different ecosystems and N levels.

Materials and Methods

1. Plant materials

Two Japanese upland rice cultivars (Toyohatamochi and Yumenohatamochi), a Japanese lowland cultivar Hitomebore and two NERICAs (NERICA 1 and NERICA 5) were used. NERICAs are progenies of interspecific hybridization between the cultivated rice species of *O. sativa* and *O. glaberrima* (Africa Rice Center, 2007). The two NERICAs used in this study were selected among the progenies as adaptable to the climatic condition in Sendai based on the preliminary tests conducted by other experimental institutes. Yumenohatamochi is one of the most drought-tolerant cultivars in Japan (Hirasawa et al., 1998). Hitomebore is a Japanese lowland cultivar currently grown dominantly in the Tohoku district in Japan.

Table 1. Soil properties of the two ecosystems (irrigated lowland (IL), rainfed upland (RU) used in the experiment.

Property	IL	RU
pH (H ₂ O)	5.8	6.3
Cation-exchange capacity (cmolc kg ⁻¹)	26.4	22.6
Exchangeable cations		
Ca	16.9	14.3
Mg	1.4	1.3
K	0.6	1.2
Na	0.9	0.1
Total carbon (g kg ⁻¹)	24.3	19.9
Total nitrogen (g kg ⁻¹)	1.8	1.5
Available phosphate (Bray II, P ₂ O ₅ mg kg ⁻¹)	867	1160
Phosphate absorption coefficient (P ₂ O ₅ , g kg ⁻¹)	9.8	6.7

2. Experimental design and cultural practices

Field experiments were conducted at the experimental field of Graduate School of Agricultural Science, Tohoku University, located in Sendai, Japan (38°16'N). The soil of experimental field is classified in a fine-textured clayey Terrace Yellow soil (Classification Committee of Cultivated Soils, 1996). The soil chemical properties are shown in Table 1. The soil had been used, for about 60 yr, for growing rice under irrigated condition, or for growing various upland crops under rainfed condition. Plants were grown under two ecosystems (irrigated lowland (IL) and rainfed upland (RU)), combined with two N application levels (high (H): 7 g N m⁻² and low (L): 2 g N m⁻²). Plots were arranged using a split-split-plot design; ecosystem as a main plot, N level as a sub-plot, and cultivar as a sub-sub-plot. Each cultivar consisted of six rows×4.8 m long in IL plot, five rows×6.0 m long in RU plot. Experiments were repeated for two yr (2006, 2007).

One-month-old seedlings were transplanted on 19 May in 2006 and 23 May in 2007, at a density of 22.2 hills m⁻² (three plants per hill) with a 30 cm row spacing×15 cm intra-row spacing. In H plot, mixed fertilizer (N: P₂O₅:K₂O=12:16:18) was applied at a rate of 5 g N m⁻² before transplanting and ammonium sulfate was additionally applied at the panicle formation stage and booting stage each at a rate of 1 g N m⁻², respectively. In L plot, the mixed fertilizer was applied at a rate of 2 g N m⁻² and no additional N was applied. In IL, irrigated water was kept 3–5 cm deep after transplanting until maturity. In RU, the plots were irrigated during the first two weeks after transplanting to ensure establishment of seedlings, but not thereafter. Weeds were controlled by hand when necessary. Weather data were obtained from the website of Sendai District Meteorological Observatory.

Table 2. Monthly average of daily solar radiation, daily mean air temperature and monthly precipitation during growth period in 2006 and 2007.

Month	Solar radiation (MJ m ⁻² d ⁻¹)			Mean temperature (°C)			Precipitation (mm)		
	2006	2007	Normal	2006	2007	Normal	2006	2007	Normal
May	15.4	17.7	17.7	15.2	15.4	14.9	102	114	108
June	14.1	17.7	14.5	18.9	19.8	18.3	155	159	138
July	9.2	11.7	14.1	21.5	20.9	22.1	325	303	160
August	15.0	16.7	14.6	24.5	25.6	24.1	41	135	174
September	12.2	12.2	11.4	20.4	22.3	20.4	215	191	218
October	10.8	11.3	10.3	15.5	16.0	14.8	305	161	99

Normal: Average of 30 yr (1971–2000).

Table 3. Days from sowing to heading and maturity in five rice cultivars grown under two ecosystems with two N levels in 2006 and 2007.

Cultivar	Treatment		2006		2007	
	Ecosystem	N	Heading	Maturity	Heading	Maturity
Toyohatamochi	IL	H	94	135	94	134
		L	94	135	94	134
	RU	H	102	145	105	142
		L	103	145	105	142
Yumehatamochi	IL	H	104	140	104	141
		L	104	140	104	141
	RU	H	116	153	114	154
		L	116	155	114	154
Hitomebore	IL	H	105	142	106	141
		L	105	142	106	141
	RU	H	119	162	122	167
		L	119	167	114	167
NERICA 1	IL	H	107	147	109	154
		L	107	147	109	154
	RU	H	117	158	124	162
		L	117	158	124	162
NERICA 5	IL	H	103	140	106	142
		L	103	140	106	142
	RU	H	116	152	122	162
		L	116	152	122	162

IL, Irrigated lowland; RU, Rainfed upland; H, High N; L, Low N.

3. Measurements

At maturity, 12 hills in a row for each cultivar were harvested for the measurement of grain yield. The samples were dried for three weeks at room temperature, then separated into grain and straw, and weighed. Grain yield was adjusted as a moisture content of 14%. For the measurements of yield components, five hills of medium size were sampled, and panicle number per hill and spikelet number per panicle were counted. After threshing, ripened grains

were selected by soaking unhulled grains in tap water, and the percentage of ripened grains were estimated.

For determination of the N content of plants, the dried samples of grain and straw were ground, and N concentration was analyzed with an automated NC analyzer (Sumigraph 80, SCAS, Osaka, Japan).

Results

1. Weather conditions and growth periods

Generally, solar radiation was normal, though it

Table 4. Aboveground dry weight (DW) at maturity, grain yield and harvest index (HI) in five rice cultivars grown under two ecosystems with two N levels in 2006 and 2007.

Treatment		Cultivar	2006			2007		
Ecosystem	N		DW (g m ⁻²)	Yield (g m ⁻²)	HI (%)	DW (g m ⁻²)	Yield (g m ⁻²)	HI (%)
IL	H	Toyohatamochi	929 b	462 b	50 bc	853 b	412 b	48 c
		Yumehatamochi	1084 ab	488 b	46 c	944 ab	545 a	58 b
		Hitomebore	1264 a	655 a	52 ab	1046 a	634 a	61 a
		NERICA 1	1296 a	664 a	51 ab	1000 a	574 a	57 b
		NERICA 5	1229 a	658 a	54 a	1049 a	624 a	59 ab
	L	Toyohatamochi	782 b	380 b	48 ab	584 d	265 c	45 d
		Yumehatamochi	774 b	362 b	47 b	702 cd	371 b	53 c
		Hitomebore	1048 a	504 a	48 b	887 a	524 a	59 a
		NERICA 1	707 b	350 b	49 ab	849 ab	492 a	58 ab
		NERICA 5	740 b	379 b	51 a	736 bc	408 b	55 bc
RU	H	Toyohatamochi	1201 a	536 ab	44 b	976 b	509 b	52 a
		Yumehatamochi	1349 a	667 ab	49 a	1307 a	693 a	53 a
		Hitomebore	1177 a	509 b	43 b	997 b	293 c	30 c
		NERICA 1	1170 a	520 b	44 b	1370 a	715 a	52 a
		NERICA 5	1502 a	761 a	50 a	1491 a	672 a	45 b
	L	Toyohatamochi	940 ab	415 bc	44 b	750 b	360 c	48 c
		Yumehatamochi	1061 a	519 ab	49 a	941 b	524 b	56 a
		Hitomebore	671 b	253 c	38 c	802 b	306 c	38 d
		NERICA 1	1235 a	565 ab	45 d	1525 a	771 a	51 bc
		NERICA 5	1230 a	643 a	52 a	1517 a	811 a	54 ab
Significance	Ecosystem (E)		***	**	***	***	***	***
	N level (N)		***	***	**	***	***	n.s.
	Cultivar (C)		**	***	***	***	***	***
	E×N		n.s.	n.s.	n.s.	**	***	***
	N×C		n.s.	n.s.	n.s.	**	***	***
	C×E		***	***	***	***	***	***
	E×N×C		***	***	n.s.	**	***	***

For denotation of ecosystem and N level, refer to Table 3. Values followed by the same letter in a column within each treatment are not significantly different at $P < 0.05$. Level of significance: **significant at $P < 0.01$, ***significant at $P < 0.001$, n.s.= not significant at $P < 0.05$.

was substantially lower than the normal in July in both years (Table 2). Temperature in 2006 was within a small variation from the normal throughout the growth period, while that in 2007 markedly varied with month: it was lower than the normal in July, but was higher in other months. Precipitation was substantially different from the normal in both years; it was markedly greater than the normal in July and October, but extremely lower than the normal in August.

The period from sowing to heading and maturity was longer in RU than in IL condition; the difference in the period to heading and to maturity between the two ecosystems was 8–16 and 8–26 d, respectively (Table 3). The longer period in RU condition was most

obvious in Hitomebore, which is the only cultivar bred for IL condition. Effects of N levels on the period were negligible. NERICAs exhibited growth duration similar to that of Hitomebore which is a leading rice cultivar in Tohoku district.

2. Growth, yield and yield components

Significant effects of ecosystem, N level and cultivar on the aboveground dry weight (DW), grain yield and harvest index (HI) were observed in both years, except that N level effect on HI was not significant in 2007 (Table 4). Interactions of the two or three sources were also significant in many cases. Within each treatment, cultivar ranking in DW was similar to that in grain

Table 5. Yield components of five rice cultivars grown under two ecosystems with two N levels.

Treatment		Cultivar	Panicle number (m ⁻²)	Spikelet number (panicle ⁻¹)	Spikelet number (×100 m ⁻²)	Percentage of ripened grains (%)	1000-grain weight (g) ¹
Ecosystem	N						
IL	H	Toyohatamochi	271 b	74 b	200 b	74.1 b	25.8 c
		Yumenohatamochi	355 a	55 c	195 b	83.5 ab	29.0 ab
		Hitomebore	382 a	69 bc	263 a	90.0 a	26.7 c
		NERICA 1	204 c	111 a	227 ab	83.6 ab	30.4 a
		NERICA 5	240 b	113 a	270 a	76.9 b	27.5 bc
	L	Toyohatamochi	244 b	61 b	150 b	73.2 c	25.8 d
		Yumenohatamochi	317 a	49 b	156 ab	83.8 abc	27.3 bc
		Hitomebore	320 a	58 b	184 a	95.3 a	26.5 cd
		NERICA 1	155 c	107 a	164 ab	86.7 ab	30.2 a
		NERICA 5	160 c	94 a	150 b	80.0 bc	28.0 b
RU	H	Toyohatamochi	258 c	82 b	211 b	84.7 a	25.8 bc
		Yumenohatamochi	400 a	67 b	267 ab	75.7 ab	29.2 a
		Hitomebore	306 b	72 b	215 b	83.6 a	23.9 c
		NERICA 1	204 d	147 a	299 a	71.1 b	29.4 a
		NERICA 5	253 c	130 a	329 a	76.3 ab	27.7 ab
	L	Toyohatamochi	224 bc	70 b	156 bc	87.5 a	24.5 c
		Yumenohatamochi	302 a	62 b	187 b	82.0 a	31.5 a
		Hitomebore	198 c	61 b	118 c	87.4 a	24.4 c
		NERICA 1	224 bc	127 a	284 a	78.8 a	29.7 a
		NERICA 5	251 b	115 a	289 a	79.3 a	27.3 b
Significance	Ecosystem (E)		n.s.	***	***	n.s.	n.s.
	N level (N)		***	***	***	**	n.s.
	Cultivar (C)		***	***	***	***	***
	E×N		n.s.	n.s.	n.s.	n.s.	n.s.
	N×C		***	n.s.	*	n.s.	n.s.
	C×E		***	**	***	***	***
	E×N×C		***	n.s.	**	n.s.	***

For denotation of ecosystem and N level, refer to Table 3. Values for individual traits are shown as average of the two yr (2006 and 2007). ¹Unhulled grain. Values followed by the same letter in a column within each treatment are not significantly different at $P < 0.05$. Level of significance: *significant at $P < 0.05$, **significant at $P < 0.01$, ***significant at $P < 0.001$, n.s.= not significant at $P < 0.05$.

yield, and the results for the two yr were consistent. In the IL×H plot, DW and grain yield were greater in Hitomebore and two NERICAs than the other two cultivars; while they were greater only in Hitomebore under IL×L plot, indicating that Hitomebore is most adaptable to irrigated condition regardless of N level. Under RU condition, NERICA 5 exhibited the greatest grain yield regardless of N level. Under the RU×L condition, the cultivar differences in DW and grain yield became larger; NERICAs could maintain those values whereas other cultivars substantially reduced them compared with other plots. Among Japanese cultivars, Yumenohatamochi produced the greatest DW and grain yield, while Hitomebore exhibited the lowest DW and grain yield under this condition (RU×L).

Compared to DW and grain yield, HI varied less with the treatment, except that it was significantly low in Hitomebore when grown under the RU condition.

Since the results of yield components and N contents were consistent in the two yr, averaged values of the two yr are shown in Tables 5 and 6. The ecosystem exhibited a significant effect on spikelet number per panicle and spikelet number per unit area, while N level had a significant effect on all the yield components measured except 1000-grain weight (Table 5). The effects of cultivars on the components were all significant. Regarding yield components, the two NERICAs were characterized by having smaller number of panicles per unit area but larger number of spikelet number per panicle regardless of ecosystem

Table 6. N content of five rice cultivars grown under two ecosystems with two N levels.

Treatment		Cultivar	N concentration (%)		N content (g m ⁻²)
Ecosystem	N		Grain	Straw	
IL	H	Toyohatamochi	1.28 a	0.55 ab	8.1 b
		Yumehatamochi	1.20 ab	0.61 ab	9.3 ab
		Hitomebore	1.00 d	0.65 a	9.7 a
		NERICA 1	1.08 cd	0.52 b	9.5 ab
		NERICA 5	1.12 bc	0.52 b	9.8 a
	L	Toyohatamochi	1.22 a	0.53 a	5.8 b
		Yumehatamochi	1.12 b	0.53 a	6.1 b
		Hitomebore	0.94 c	0.51 a	7.2 a
		NERICA 1	1.05 b	0.54 a	6.3 b
		NERICA 5	1.05 b	0.51 a	5.9 b
RU	H	Toyohatamochi	1.40 a	0.86 a	11.9 bc
		Yumehatamochi	1.27 ab	0.81 a	13.9 ab
		Hitomebore	1.18 b	0.83 a	10.3 c
		NERICA 1	1.43 a	0.98 a	15.3 a
		NERICA 5	1.27 ab	0.94 a	16.4 a
	L	Toyohatamochi	1.28 ab	0.71 a	8.1 b
		Yumehatamochi	1.19 ab	0.67 a	9.4 b
		Hitomebore	1.03 c	0.68 a	6.0 c
		NERICA 1	1.29 a	0.77 a	13.9 a
		NERICA 5	1.18 b	0.74 a	13.3 a
Significance	Ecosystem (E)		***	***	***
	N level (N)		***	***	***
	Cultivar (C)		***	n.s.	***
	E×N		n.s.	***	n.s.
	N×C		n.s.	n.s.	n.s.
	C×E		**	***	***
	E×N×C		n.s.	n.s.	*

For denotation of ecosystem and N level, refer to Table 3. Values for individual traits are shown as average of the two years (2006 and 2007). Values followed by the same letter in a column within each treatment are not significantly different at $P < 0.05$. Level of significance: *significant at $P < 0.05$, **significant at $P < 0.01$, ***significant at $P < 0.001$, n.s.= not significant at $P < 0.05$.

and N level. This characteristic resulted in larger spikelet number per unit area under RU condition. The 1000-grain weight was significantly larger in Yumehatamochi and the two NERICAs. Percentage of ripened grains was markedly higher in Hitomebore in IL plot, but it was not true in RU plot.

3. N content of plants and its relation to yield-relating traits

N concentration of plants at maturity was significantly affected by ecosystems and N levels (Table 6). Generally, RU and H plots had higher N content of grain than IL and L plots regardless of cultivar, except NERICAs grown in the IL condition. Among cultivars,

Hitomebore exhibited the lowest N content of grain, but ranking in N content of grain among the other four cultivars varied with the ecosystem and N level. The N content of straw was not significantly different among cultivars except NERICAs in the IL regime where NERICAs had lower values than Hitomebore.

N content of the plant (aboveground part) was higher in RU than IL, and in a high N level than low N level (Table 6). Among cultivars, it was obvious that Hitomebore contained the smallest amount of N in the RU condition, while it contained the largest amount in the IL×low N plot. In contrast, NERICAs exhibited higher N contents in the RU condition regardless of N level; but not in the IL condition.

Table 7. Correlation coefficients between grain yield and yield components in five rice cultivars grown under two ecosystems with two N levels.

Yield components	Toyohatamochi	Yumenohatamochi	Hitomebore	NERICA 1	NERICA 5	All cultivars
Panicle number	0.464	0.704*	0.781*	0.840**	0.961**	0.237
Spikelet number per panicle	0.590	0.815**	0.419	0.581	0.857**	0.592**
Spikelet number per area	0.586	0.953**	0.857**	0.845**	0.961**	0.896**
Percentage of ripened grains	0.537	-0.504	0.518	-0.674*	-0.104	-0.103
1000-grain weight	0.419	0.439	0.823*	0.456	0.037	0.523**

Data of the two yr (2006 and 2007) were combined for calculation of the coefficients. Level of significance: *significant at $P < 0.05$, **significant at $P < 0.01$.

Table 7 shows the correlation coefficients among yield components calculated for each cultivar. In all the cultivars combined, grain yields were significantly correlated with spikelet number per panicle, spikelet number per area and 1000-grain weight. Spikelet number per area had the highest coefficients in most cultivars.

Fig. 1 shows the correlation of N content of aboveground part with DW, spikelet number per unit area, and grain yield in five cultivars. The correlation of the aboveground N content with the other components was significant in most cultivars except Hitomebore and Toyohatamochi, in which the correlations among the components were not consistently significant. Across all cultivars, DW was significantly correlated with spikelet number per unit, and similarly spikelet number per unit area was significantly correlated with grain yield. Among cultivars, NERICAs had higher values than the other cultivars in all the yield components examined.

Discussion

NERICAs used in this study were released based on trials in West Africa including Ivory Coast and Nigeria where latitude ranges from 5 to 15°N. Generally, the rice cultivars that are bred for areas in low latitude exhibit a long growth period and are not able to reach maturity in the areas in higher latitude. However, the scientists of WARDA have successfully and substantially shortened the life span in attempts to breed NERICAs (Jones et al., 1997a, 1997b). The two NERICAs used in this study exhibited growth period comparable to that of Japanese cultivars that are adaptable to Tohoku area, Japan (>35°N) (Table 3), indicating their adaptability to wide areas where daylength and temperature markedly differ from their origin.

The growth and yield of NERICAs were superior to those of representative Japanese cultivars that were bred for tolerance to drought, which was more pronounced in water and N-limited condition (Table 4, Fig. 1). Futakuchi and Jones (2005) evaluated growth and yield performance of NERICAs in various growing ecologies (upland, rainfed lowland and irrigated lowland). They found that NERICAs generally had

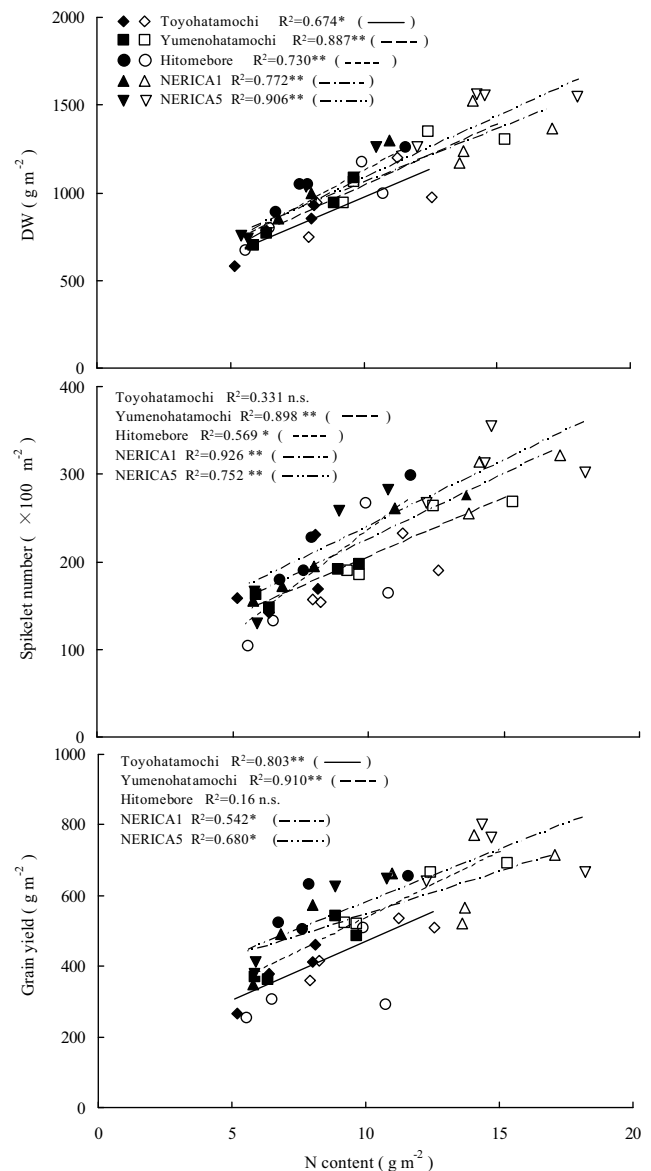


Fig. 1. Relation of aboveground N content with aboveground dry weight (DW), spikelet number per unit area and grain yield in five rice cultivars grown under two ecosystems (IL, RU) with two N levels (H, L). Values of the two years are combined. Closed symbols: IL plots. Open symbols: RU plots. Level of significance: *significant at $P < 0.05$, **significant at $P < 0.01$.

better growth and yield than their parental *O. sativa* cultivar WAB56-104. Tamamura et al. (2007) found that NERICAs exhibited a high and stable yield under rainfed upland condition, but their yield superiority to Japanese cultivars varied with year.

We expected that, regardless of cultivar, the growth and yield should be higher in IL than in RU condition where rice plants can be water-stressed because of limited water availability. Against our expectation, the yield in RU condition generally exceeded that in IL condition except Hitomebore (Table 4). Several previous studies revealed similar results. For example, Kato et al. (2006a, 2006b) reported that if the water supply was adequate and frequent, it was possible to produce a large amount of top dry matter under upland condition, which is comparable to that in irrigated lowland condition. Matsuo et al. (2007) examined the yield responses of rice cultivars to various water managements (irrigated lowland and different degrees of irrigation under upland condition), and indicated that some upland cultivars showed higher grain yield under upland condition than in irrigated lowland condition. The present study confirmed that the cultivars including NERICAs and Japanese cultivars that were bred for drought tolerance exhibit the superior yielding capacity under upland condition. In these studies, upland condition does not appear to have imposed a detrimental water stress to plants, because there was an adequate water supply by rainfall and/or irrigation. In the present study, there was plenty of rainfall during the vegetative stage (May-July) in both years (Table 2), and this might be partly responsible for the superior growth and yield under the upland condition. However, even under relatively favorable water availability, the yield of Hitomebore, which is the only cultivar bred for the irrigated lowland condition in the present study, was markedly reduced by upland condition regardless of N level (Table 4). There might be unknown mechanisms regulating the cultivar difference in the response to irrigated lowland and rainfed upland condition.

N acquisition was enhanced by RU condition, compared to IL condition, except Hitomebore (Table 6, Fig. 1). The same results have been obtained by several previous studies. For example, Wada et al. (2002) examined N absorption of japonica-indica hybrid rice cultivars under upland and irrigated lowland conditions, and found that N absorption of the cultivars was enhanced by upland condition compared to irrigated lowland condition. They ascribed the enhancement to soil temperature that might be higher in upland condition, and thereby have accelerated the dissolution of N from controlled N release fertilizer used in the experiment. Kato et al. (2006a) also found that N contents of plants at maturity were enhanced by upland condition compared to irrigated lowland condition; they estimated that it

was because of a longer growth period under upland condition. Another possibility is that there might exist mechanisms regulating genotypic difference in capability of N absorption, responding to water availability in soil. Further studies are needed to verify this possibility. For any reason, it is noteworthy that there exist rice genotypes that exhibit better growth and yield performance under rainfed upland condition than under irrigated lowland condition.

By contrast, there have been reports showing negative effects of upland condition on N acquisition. O'Toole and Baldia (1982) found that water-limited condition reduced transpiration of rice plants, resulting in the curbed absorption of major elements including N. Furthermore, Prasertsak and Fukai (1997) found that water-stressed rice plants produced a smaller biomass due to a reduction in N absorption. Apparently, water availability in soil was below the adequate level in these studies, which might have constrained the N absorption capacity of the plants. Thus, there should be a certain level of water availability for exhibiting better performance in an upland condition. Further study is needed to evaluate the adaptability of NERICAs to less water availability.

Grain yield was significantly correlated with spikelet number per unit area in all the cultivars except Toyohatamochi (Table 7). This high capacity for sink formation of NERICAs was associated with their higher capacity for N acquisition and biomass production under upland conditions (Fig. 1). The same was observed in japonica-indica hybrids. Yun et al. (1997) found that the superior yield of japonica-indica hybrids was associated with the higher capability of sink formation under the upland condition. NERICAs exhibited a higher capacity of sink formation under the upland condition, and this capacity appears to be a major trait contributing to a higher yielding capacity of these cultivars. The physiological traits of NERICAs associated with this capacity need to be studied in the future.

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* In Japanese with English abstract.

** In Japanese.