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Kumagai, Etsushi
NARO Tohoku Agricultural Research Center

Araki, Takuya
Faculty of Agriculture, Ehime University

Kubota, Fumitake
Emeritus Professor, Kyushu University

Ueno, Osamu
Emeritus Professor, Kyushu University

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Effects of Nitrogen Deficiency on Dry Matter and Grain Productions of Six Rice (*Oryza sativa* L.) Cultivars

Etsushi KUMAGAI[1]*, Takuya ARAKI[2], Fumitake KUBOTA[3] and Osamu UENO

Laboratory of Plant Production Physiology, Division of Agricultural Bioresource Sciences,
Department of Bioresource Sciences, Faculty of Agriculture,
Kyushu University, Hakozaki, Fukuoka 812–8581, Japan
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Effects of limited nitrogen (N) supply on dry matter and grain productions were investigated in the pot–grown six rice cultivars, Kasalath (a traditional *indica*), IR36 (an improved *indica*), Shirobeniya (a conventional *japonica*), Nipponbare (an improved *japonica*), BSI429 (an improved tropical *japonica*, a new plant type line) and Akenohoshi (an improved *japonica–indica* cross). At maturity, N limitation caused significant decreases in aboveground dry weight (DW), DW increased during heading to maturity (ΔDW), grain weight, panicle number per plant, fertility % and sink size in the six cultivars, and there were significant "cultivar × N" interactions; the magnitudes of these decreases caused by limited N supply were smallest in Akenohoshi. There were significant positive correlations between grain weight and aboveground DW at maturity under both standard–N (SN) and low–N (LN) conditions, whereas there was a significant positive correlation between grain weight and ΔDW under the LN condition but not under the SN condition. Grain weight was more closely correlated with sink size under both N conditions. Among the cultivars examined, Akenohoshi showed the highest ΔDW, fertility % and sink size under the LN condition, leading the highest grain weight. It is suggested that Akenohoshi is a breeding material useful for the improvement of adaptability to LN environment.

Key words: Grain yield, Nitrogen deficiency, Rice, Yield components

INTRODUCTION

Over the last 50 years, rice production in Asia has kept pace with the increasing population. The rice production system consisting of high yielding cultivars, high input of fertilizers and agrochemicals, and irrigation contributed to great yield increases in both developed and developing countries during the past decades (Evans, 1993). However, adverse effects of high input agriculture have been recognized. Nitrate and agrochemicals discharged from agriculture cause both surface and underground water pollution (Jarvis, 1996). Nitrogen (N) fertilizer is one of the most important inputs in the production package. Fertilizers account for almost half of the energy used in world agriculture, and the manufacture of N fertilizer is about 10 times more energy–intensive than that of other fertilizers such as phosphate (P) and potassium (K) (Evans, 1993). Recently, the soaring world oil prices also raise a problem of N fertilizer cost. In rice, reduced rate of N fertilizer application can diminish the occurrence of blast disease and several insect pests such as planthoppers and can reduce the use of the fungicides and insecticides. In addition, reduced application of N fertilizer can contribute to reducing dinitrogen monoxide (N_2O) emission from agricultural soils resulting in global warming.

The main goals of the rice production system are the optimization of grain yield, the reduction of production cost and the minimization of the pollution risk for the environment. At present, genetic improvements of crops that will be used in low input sustainable agricultural system are required, but most of the previous genetic improvements were conducted presupposing cultivation under high input conditions. In wheat, Austin *et al.* (1980) found that high yielding cultivars performed better than traditional ones in both fertile and less fertile soils. Ortiz–Monasterio *et al.* (1997) also found that newly released wheat cultivars attained higher grain yield than old cultivars even without application of N fertilizer. Newly released maize hybrids also outperformed traditional ones even at reduced N application rates (Ding *et al.*, 2005). In spite of these studies, there are still some opinions that high yielding cereal cultivars may not be used in low input cropping systems. With respect to this, Evans (1993) stated that "there are more strong opinions than strong data". Actually, there are few comparative studies on the production of rice under LN input conditions (Hasegawa, 2003). In order to elucidate the adaptability to LN environment in rice cultivars, we investigated some characteristics of dry matter and grain productions in several traditional and newly improved rice cultivars grown under the SN and LN conditions.

MATERIALS AND METHODS

Plant materials and N treatment

Six rice cultivars, Kasalath (a traditional *indica*), IR36 (an improved *indica*), Shirobeniya (a traditional

[1] NARO Tohoku Agricultural Research Center, Akahira, Shimokuriyagawa, Morioka 020–0198, Japan
[2] Faculty of Agriculture, Ehime University, Tarumi, Matsuyama, Ehime 790–8566, Japan
[3] Emeritus Professor, Kyushu University
* Corresponding author (E–mail: ekumagai@affrc.go.jp)

japonica), Nipponbare (an improved *japonica*), BSI429 (an improved tropical *japonica*, a new plant type (NPT) line) and Akenohoshi (an improved *japonica–indica* cross), were used in this experiment. Imbibed seeds of these cultivars were sown in nursery boxes in a glass house of the Hakozaki Campus of Kyushu University at the beginning of June 2006. At three weeks after sowing, the seedlings (a seeding per pot) were transplanted into 8–L pots filled with sandy loam. The total N of the soil was 1.35 mg g^{-1}. They were divided into the SN (Control) and LN (50% of SN) groups. In the SN group, N fertilizer was applied at a rate of 0.96 g pot^{-1} at transplanting, followed by 0.64 g pot^{-1} at panicle initiation. For the LN group, 0.48 g pot^{-1} of N was applied at transplanting, followed by 0.32 g pot^{-1} at panicle initiation. Ammonium sulfate was used as N fertilizer. In both groups, 1.6 g pot^{-1} of P and 1.6 g pot^{-1} of K were also applied in form of calcium superphosphate and potassium chloride, respectively. Pots were arranged without mutual–shading in the glass house under natural sunlight. Water was supplied sufficiently throughout. Weeds were removed manually when necessary.

Measurements

The dates of heading and maturity of each pot were recorded. The heading date was defined as the date when 50% of the panicles had fully emerged. The maturity date was determined as the date when 80% of spikelets became yellow. The aboveground parts of three plants per cultivar were sampled at heading for each N condition, and leaf blades were detached from the rest of the plant parts. The leaf area (LA) of samples was measured with an automatic area meter (AAM–8, Hayashi Denko Co. Ltd., Tokyo, Japan). Their DWs were determined after drying in an oven at 80˚C for 3 days. At maturity, three plants per cultivar were harvested for each N condition and air dried, and the aboveground DW of the plants was measured. And then, the panicle number per plant and spikelet number per panicle were counted. After threshing, ripened grains were selected by soaking unhulled grains in a salt solution of 1.06 specific gravity, and the percentage of ripened grains (fertility %) was estimated. After air–drying in the grain moisture range of 13–14%, grain weight per plant and 1000–grains weight were estimated. Sink size is the product of the spikelet number per plant multiplied by an average weight of grain with moisture of 13–14%.

Statistical analysis

Data were statistically analyzed by a two–way analysis of variance (ANOVA) using a Sigmastat software (Sigmastat 3.1, Systat Software, Inc., Richmond, USA). Then, the significance of mean values was analyzed using Fisher's LSD test (P<0.05).

RESULTS AND DISCUSSION

Table 1 shows days from transplanting to heading, LA at the heading stage, aboveground DW at the heading and mature stages, and ΔDW in the six cultivars grown

Table 1. Days from transplanting to heading, leaf area (LA) at the heading stage, aboveground dry weight (DW) at the heading and mature stages, and DW increased from heading to mature stages (ΔDW) for the six cultivars grown under two nitrogen (N) levels. SN, standard–N; LN, low–N. Values are given as the mean ± SE (n=3). Values followed by the same letters in the column had no significant difference as determined by Fisher's LSD test at 5% level. Values in parentheses represent the ratio compared to SN. Results of two–way ANOVA: ***, P<0.001; **, P<0.01; *, P<0.05

Cultivar	Treatment	Days to heading		LA at heading (m^2 $plant^{-1}$)		Aboveground DW (g $plant^{-1}$)				ΔDW (g $plant^{-1}$)	
						Heading		Maturity			
Kasalath	SN	66±0.3c		1.13±0.02a		152±5.7a		191±5.4a		39±4.4cde	
	LN	60±0.3ef	(91)	0.56±0.01d	(50)	91±1.5cd	(60)	108±3.6d	(57)	17±3.0g	(43)
IR36	SN	65±0.0d		0.74±0.04b		95±3.0bc		145±9.1bc		50±7.4bc	
	LN	62±0.3e	(95)	0.33±0.02f	(45)	63±4.1e	(66)	83±3.3f	(57)	20±2.7fg	(40)
Shirobeniya	SN	65±0.3cd		0.61±0.02d		80±1.2d		141±5.1bc		61±4.2ab	
	LN	59±0.3g	(91)	0.30±0.02f	(49)	55±0.4f	(69)	76±3.4fg	(54)	21±2.8defg	(34)
Nipponbare	SN	55±0.3i		0.62±0.02cd		68±1.2d		117±3.5de		48±2.9bc	
	LN	53±0.3j	(97)	0.32±0.01f	(52)	45±0.3f	(66)	67±2.8g	(58)	22±2.3defg	(46)
BSI429	SN	77±0.3a		0.58±0.01d		96±3.2b		135±1.5c		39±4.7cd	
	LN	73±0.5b	(95)	0.31±0.01f	(53)	65±1.0de	(68)	85±2.2f	(63)	20±1.8efg	(51)
Akenohoshi	SN	60±0.0fg		0.64±0.02cd		83±2.9cd		153±1.5b		70±1.2a	
	LN	57±0.0h	(95)	0.38±0.01e	(59)	65±1.7e	(78)	102±1.5e	(67)	38±1.3cdef	(55)
Results of two–way ANOVA											
Cultivar (C)		***		***		***		***		***	
Nitrogen (N)		***		***		***		***		***	
C×N		***		**		***		**		*	

under the SN and LN conditions. Days from transplanting to heading ranged from 53 to 77 days. The days were shortest in Nipponbare, followed by Akenohoshi, Shirobeniya, IR36, Kasalath and BSI429. Moreover, days to heading were longer in the SN plants than in the LN plants for all the cultivars. LA and aboveground DW at the heading stage of the LN plants were decreased to 45–59% and 60–78% of the SN plants in all cultivars, respectively. The magnitude of decreases differed among the cultivars: Akenohoshi showed the smallest decreases of LA and aboveground DW at the heading stage under the LN condition (59% and 78%, respectively). However, there were no relationships between LA and aboveground DW, and days to heading under the two N conditions (data not shown), indicating that the dry matter production before heading was not associated with the duration of vegetative stage.

At maturity, N limitation significantly decreased aboveground DW (54–67%), and there was a significant "cultivar × N" interaction; the magnitude of the decrease in aboveground DW caused by N limitation was smallest in Akenohoshi (67%) and largest in Shirobeniya (54%). In addition, ΔDW was significantly affected by N limitation, and there was a significant "cultivar × N" interaction; the decrease in ΔDW was smallest in Akenohoshi (55%) and largest in Shirobeniya (34%). There was no difference in the duration of ripening regardless of the differences in cultivar and N application (data not shown). As shown in Table 2, N limitation significantly decreased grain weight, and there was a significant "cultivar × N" interaction. The decrease in grain weight was smallest in Akenohoshi (62%) and largest in Shirobeniya (47%). Furthermore, Akenohoshi has the highest grain weight under the LN condition. Grain weight was significantly correlated with LA and aboveground DW at the heading

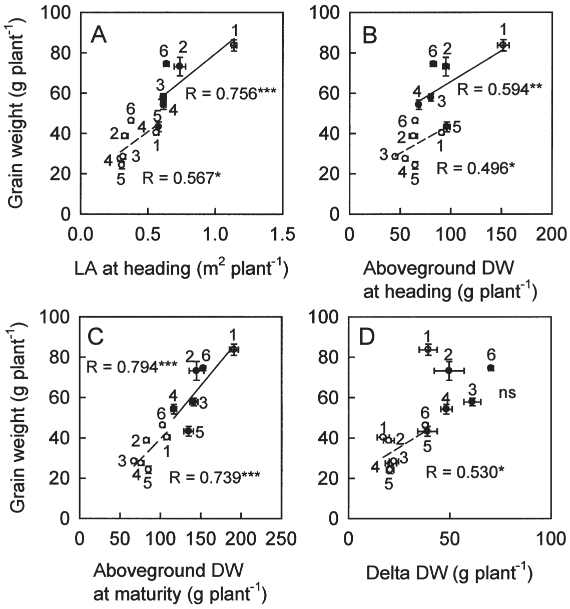

Fig. 1. Relationships between grain weight and leaf area (LA) at the heading stage (A), aboveground dry weight (DW) at the heading stage (B), aboveground DW at the mature stage (C), and increased DW from heading to mature stages (ΔDW) (D) in the six rice cultivars grown under the standard–N (SN) and low–N (LN) conditions. Closed circle; SN, Opened circle; LN. ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$; ns, not significant. 1, Kasatah; 2, IR36; 3, Shirobeniya; 4, Nipponbare; 5, BSI429; 6, Akenohoshi.

Table 2. Grain weight, panicle number per plant, spikelet number per panicle, fertility %, 1000–grains weight, sink size for the six cultivars grown under two nitrogen (N) levels. SN, standard–N; LN, low–N. Values are given as the mean ± SE (n=3). Values followed by the same letters in the column had no significant difference as determined by Fisher's LSD test at 5% level. Values in parentheses represent the ratio compared to SN. Results of two–way ANOVA: ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$; ns, not significant

Cultivar	Treatment	Grain weight (g plant^{-1})		Panicle number per plant		Spikelet number per panicle		Fertility %		1000–grains weight (g)		Sink size (g plant^{-1})	
Kasalath	SN	84±2.8a		41±1.3a		135±3.3a		81.2±0.6a		18.3±0.3de		103±2.3a	
	LN	40±0.7e	(48)	26±0.3d	(63)	132±1.3a	(98)	66.7±0.6ef	(82)	17.9±0.1e	(98)	60±0.5f	(58)
IR36	SN	73±4.6bc		38±1.2b		124±6.7abc		78.8±3.0ab		19.7±0.3d		93±2.5b	
	LN	38±1.0f	(52)	23±1.4e	(60)	117±2.5bc	(95)	73.8±2.2cd	(94)	19.3±0.2d	(98)	53±2.2g	(57)
Shirobeniya	SN	57±1.8bc		41±0.6ab		84±2.7d		70.4±1.5de		23.6±0.4b		82±2.3c	
	LN	27±1.1fg	(47)	24±0.3de	(59)	84±2.3d	(94)	63.9±0.5fg	(91)	23.3±0.4b	(99)	46±1.2h	(56)
Nipponbare	SN	54±2.4de		40±0.0ab		79±2.1d		79.4±1.6ab		21.5±0.3c		68±1.6de	
	LN	28±1.0g	(52)	22±0.7ef	(55)	78±2.1d	(99)	75.8±1.7bc	(95)	22.1±0.6c	(103)	37±0.7i	(54)
BSI429	SN	43±2.4de		20±1.5f		115±10.1c		60.6±0.7g		31.8±0.5a		71±2.7d	
	LN	24±1.8f	(56)	13±0.3h	(65)	110±4.5c	(96)	52.9±3.1h	(87)	31.2±0.6a	(98)	45±1.8h	(63)
Akenohoshi	SN	74±1.1b		30±2.4c		130±6.9ab		82.5±1.1a		23.7±0.1b		90±1.9b	
	LN	46±1.0d	(62)	21±0.0f	(70)	130±5.7ab	(100)	81.9±0.7a	(99)	23.6±0.2b	(100)	65±2.2e	(72)
Results of two–way ANOVA													
Cultivar (C)		***		***		***		***		***		***	
Nitrogen (N)		***		***		ns		***		ns		***	
C×N		***		***		ns		*		ns		**	

stage under the two N conditions (Fig. 1–A and –B), which indicates that at least dry matter production and LA expansion before heading would be contributors for the increase in grain weight of rice cultivars regardless of N levels. There were significant correlations between grain weight and aboveground DW at maturity under both SN and LN conditions (Fig. 1–C), whereas there was a significant correlation between grain weight and ΔDW under the LN condition but not under the SN condition (Fig. 1–D). Among the six cultivars examined, Akenohoshi (No. 6) produced the highest dry matter during ripening under the LN condition, leading the highest grain weight.

Grain yield of rice is the final product of a combination of different yield components, such as panicle number per plant, spikelet number per panicle, fertility % and 1000–grains weight (Yoshida, 1981). In transplanted rice plants, spikelet number per plant is usually the most variable yield component, accounting for about 74% of the variation of yield. Both fertility % and 1000–grains weight account for 26% of the yield variation (Yoshida and Parao, 1976). This relative importance of each component varies with the cultural system. As shown in Table 2, limited N supply significantly decreased panicle number per plant, fertility % and sink size, and there were significant "cultivar × N" interactions; the magnitude of these decreases was smallest in Akenohoshi among the cultivars examined. On the other hand, the effects of limited N supply on spikelet number per panicle and 1000–grains weight were not significant. Grain weight was significantly correlated with panicle number per plant, spikelet number per panicle, fertility % and sink size under both the SN and LN conditions (Fig. 2–A, –B, –C and –E). However, there was no correlation between grain weight and 1000–grains weight under each N condition (Fig. 2–D). Grain weight was more closely correlated with sink size under both N conditions, and this result agrees with those from many previous reports on rice (e.g., Takeda *et al.*, 1984). Among the cultivars examined, Akenohoshi (No. 6) showed the highest fertility % and sink size, leading the highest grain weight under the LN condition (Table 2). As mentioned above, sink size is the product of the spikelet number per plant multiplied by weight of a grain. The size of rice grain is physically restricted by the size of the hull, and its weight is very stable under most environmental conditions (Yoshida, 1981). It has been reported that N uptake before heading is a critical factor in spikelet production (Hasegawa *et al.*, 1994). It was previously observed that Akenohoshi has higher N uptake capacity than Nipponbare at the late–vegetative stage (Kumagai, 2007). Therefore, this cultivar may efficiently utilize N absorbed from soil for spikelet production under the LN condition. Fertility % is mainly affected by the amount of carbohydrates available for grain filling (Kobata *et al.*, 2000). The contribution of carbohydrates assimilated after heading to grain carbohydrates ranges from 60% to 100% under most environmental conditions (Yoshida, 1981). Nagata *et al.* (2001) studied the effects of dry matter produced after heading and carbohydrates stored in stems before heading on grain filling and reported that the former had a stronger effect on fertility % than the latter. Therefore, Akenohoshi could produce the highest dry matter after heading, leading the highest fertility % under the LN condition.

Among leaves of rice plant, flag leaves are the primary

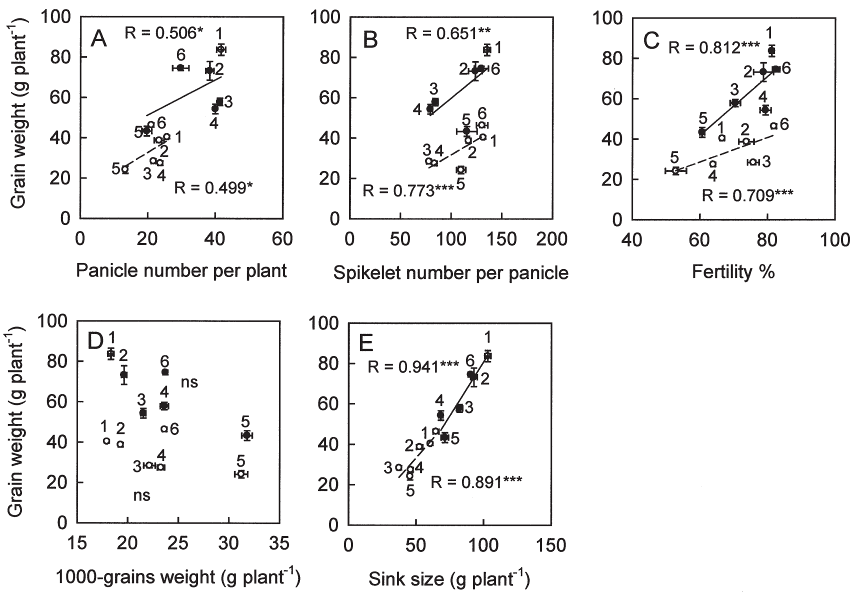

Fig. 2. Relationships between grain weight and panicle number per plant (A), spikelet number per panicle (B), fertility % (C), 1000–grains weight (D) and sink size (E) in the six rice cultivars grown under the standard–N (SN) and low–N (LN) conditions. Closed circle; SN, Opened circle; LN. ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$; ns, not significant. 1, Kasatah; 2, IR36; 3, Shirobeniya; 4, Nipponbare; 5, BSI429; 6, Akenohoshi.

contributor to the accumulation of dry matter in grains (Murata and Matsushima, 1975; Black *et al*., 1995). Previously, we investigated the difference in flag leaf photosynthesis during ripening stage of rice cultivars grown under the LN condition and showed that a prolonged high photosynthetic rate was observed during the ripening stage in the flag leaves of Akenohoshi grown under the LN condition (Kumagai *et al*., 2009). Therefore, high ΔDW in this cultivar under the LN condition could be explained by high photosynthetic productivity in the flag leaves after heading.

In conclusion, Akenohoshi significantly surpassed the other cultivars with respect to grain weight, ΔDW, fertility % and sink size under the LN condition. Hasegawa (2003) observed high–yielding temperate rice cultivars bred in Japan outyielded traditional ones not only at high N application but at a reduced N application, which was supported with our data. These findings are opposite to the suggestion by Evans (1993) that high yielding cereal cultivars would perform well only in the presence of sufficient amounts of N fertilizers. Since there is an increasing requirement to minimize the N application from environmental problems, it is suggested that Akenohoshi is a breeding material useful for improvement of the adaptability to LN environment.

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