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HIGH-YIELDING *japonica*-RICE LINES CARRYING *Ur1* (Undulate rachis-1) GENE, POSSESSING VARIOUS HEADING TIMES

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SUMMARY

An incompletely dominant gene *Ur1* (Undulate rachis-1) increases spikelet number per panicle, resulting in a larger sink size and enabling increase of yield in rice. Murai 79 (denoted by "79") and four other prospective *Ur1*-carrying inbred lines were used, which possess various heading times from extremely late line 79 to the early line "J3", together with four check varieties, viz. a representative variety of southern Japan 'Hinohikari', early 'Koshihikari' and late 'Nishihikari', and one super high-yielding *indica*-type variety 'Takanari'. Five and eight of all lines-varieties were grown using various fertilizer levels in a paddy field at Kochi University in two years, and eight of them at one fertilizer level in another year, and yield and its related traits were measured. The five *Ur1*-carrying lines were significantly higher in yield than the three *japonica* varieties (30 to 36% higher than Hinohikari), which was due to their larger sink sizes resulting from their higher spikelet numbers per panicle. In yield, line 79 was similar to Takanari in 2003, while the former was lower than the latter in 2005. Amount of carbohydrates transferred from leaf sheaths and culms to panicles during grain filling can be estimated by the difference on dry-matter basis between total brown rice yield and increase of total plant weight after heading. This trait contributed 26 or 32% of total brown rice yield including unripened grains in line 79. On the other hand, high yields of Takanari and an *Ur1*-carrying line 53 depended mostly on increase in total plant weight after heading. In addition, Takanari and 53 had the highest values of harvest index. An extraordinarily high yield by 79 (784 g/m^2) was recorded in a farmer's paddy field. Consequently, the 79 and the other four *Ur1*-carrying lines could be candidates for high-yielding varieties with various maturities and/or mid-mother lines to develop new varieties.

Keywords: High yield, rice breeding, *Ur1* gene, commercial variety, sink size, spikelet number per panicle, heading time, *Oryza sativa*

Key findings: An incompletely dominant gene *Ur1* on chromosome 6 increases spikelet number per panicle and sink size in rice. Five *Ur1*-carrying lines were developed, which were 30 to 36% higher in yield than 'Hinohikari', a representative variety of southern Japan, suggesting that they could be candidates for high yielding varieties with various maturities and/or mid-mother lines to develop new varieties.

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INTRODUCTION

Ur1 (Undulate rachis-1) is an incompletely dominant gene on chromosome 6, being characterized by undulation of primary and secondary rachis branches (Nagao *et al.*, 1958; Nagao and Takahashi, 1963; Sato and Shinjyo, 1991), even though the degree of undulation varies from typical to little according to genetic backgrounds (Murai *et al*., 2014). Imai *et al*., (2009) found two SSR markers closely linked with the *Ur1* locus and suggested that they are available for the marker-assisted selection targeting *Ur1. Ur1* increases spikelet number per panicle due to the increases in the number of secondary branches per primary branch, number of spikelets per single secondary branch and number of primary branches per panicle (Murai and Iizawa, 1994; Murai, 1999; Murai *et al*., 2014). This genic effect increased grain yield in both the *Ur1*/*Ur1* and *Ur1*/+ genotypes by enlarging sink size on several *japonica* genetic backgrounds, although the diminution of ripened-grain percentage (Murai *et al*., 1997, 1999, 2002, 2003, 2004 and 2005 b).

The high-yielding line Murai 79, denoted by "79" in the present study, was developed from the F_1 of 'Nishihikari' x the isogenic line of Taichung 65 carrying both *Ur1* and *sd1-d* (Dee-geo-wo-gene dwarf gene), which originates from one plant of the F_2 carrying *Ur1*/*Ur1* genotype, and any intentional selection was not performed from F_3 and the following generations (Murai *et al*., 2005 a). 79 is characterized by high yield and extremely late heading.

A newly-developed high-yielding line carrying *Ur1*, denoted by "7E", is a sister line of 79 originating from another F_3 plant from the same F_2 plant as that of 79. 7E was earlier in heading than 79 (Table 1-(3)), which can be regarded as the late heading in southern Japan.

Lines denoted by "53" (Malangen *et al*., 2013) and "47", both carrying *Ur1*, can be regarded as the middle and rather early in heading, and the middle in heading, respectively, in Kochi prefecture, which originate from two different plants in the same F_2 population as that mentioned above.

In addition, an early-heading *Ur1*-carrying line "J3" has been developed from the F_1 hybrid of 'Koshihikari' × 79.

Table 1. 80%-heading dates and number of days to 80%-heading of the five *Ur1*-carrying lines (79, 53, 7E, 47 and J3) and the four varieties (Hi, Ni, Ta and Kos). Five of the nine lines-varieties were grown in both 2003 and 2005, and all of them except for Ta in 2010.

(1) 2003.

Traits	Fertilizer level	53	79	Ta	Ni	Hi
80%-heading dates	N16	29th July	22th Aug.	31th July	13th Aug.	9th Aug.
	N8	28th July	22th Aug.	— [1]	12th Aug.	9th Aug.
	N4	29th July	22th Aug.	—	12th Aug.	9th Aug.
Number of days to 80%-heading from sowing	N16	104	128	106	119	115
	N8	103	128	—	118	115
	N4	104	128	—	118	115

(2) 2005.

Traits	Fertilizer level	53	79	Ta	Ni	Hi
80%-heading dates	N21	21th July	24th Aug.	25th July	11th Aug.	7th Aug.
	N12	21th July	23th Aug.	25th July	11th Aug.	7th Aug.
Number of days to 80%-heading from sowing	N21	92	126	96	113	109
	N12	92	125	96	113	109

(3) 2010.

Traits	53	79	7E	47	J3	Kos	Ni	Hi
80%-heading dates	28th July	20th Aug.	15th Aug.	3rd Aug.	23th July	23th July	13th Aug.	6th Aug.
Number of days to 80%-heading from sowing	93	116	111	99	88	88	109	102

Ta, Ni, Hi and Kos : Takanari, Nishihikari, Hinohikari and Koshihikari , respectively.

[1] Ta was not grown at N8 and N4.

The above-mentioned five *Ur1*-carrying lines were grown in a paddy field, together with three check varieties early, middle and late in heading. Yield and related traits were measured to examine whether *Ur1*-carrying varieties with various heading times are possible for practical use.

Moreover, 53, 79, the middle and late varieties, and a super high-yielding *indica*-type variety 'Takanari' were grown at various fertilizer levels in two years. Weng *et al.* (1982) demonstrated that carbohydrates (mainly sugars and starch) stored in leaf sheaths and culms before heading contributed to yield more or less in rice varieties. The amount of carbohydrates transferred from leaf sheaths and culms to panicles during grain filling can be estimated by the difference on a dry-matter basis between the total brown rice weight and increase of total plant weight after heading (Amano *et al.*, 1993). This trait was measured in addition to yield, yield components and other traits such as harvest index. From the obtained data, we examine the yielding abilities of 79 and 53 by comparing them with the middle and late varieties, and the *indica*-type variety.

Additionally, 79 was grown in paddy fields of two farmers, to try to grow it in the actual fields of production.

From the results obtained, we examine the characteristics of 79 and the other four *Ur1*-carrying lines, and discuss their availabilities for candidates for commercial varieties possessing various heading times from the extremely late to early in warm regions of Japan.

MATERIALS AND METHODS

High yielding prospective lines carrying *Ur1* gene

The "79" (Murai 79, Murai *et. al.*, 2005 a) was developed through the process described as follows. The highest-yielding F_1 in the yield tests for various F_1 hybrids with the *Ur1* / + genotype (Murai *et al.,* 1997 and 2003) was used to develop recombinant inbred lines (RILs) with and without *Ur1*. Its maternal and paternal parents were 'Nishihikari' and an isogenic line of Taichung 65 carrying both *Ur1* and *sd1-d* (dee-geo-woo-gen dwarf), respectively. The F_2 population was grown in 1992; the 108 F_3 populations from respective 108 F_2 plants were grown in a glasshouse; and generations were advanced to F_8 without any intentional selection. In 1999, the 108 F_9 RILs originating from the 108 F_2 plants were grown in a paddy field; one of the most well-ripened lines carrying *Ur1*, viz. 79 was selected from *Ur1*-carrying lines by field observation. In 79, any genic segregations in heading and other traits between lines and within each line were not observed from 2000 (F_{10}) to 2003 (F_{14}), indicating its fixation practically. Its generations in the present study were F_{14} and more advanced generations. Its heading time can be regarded as extremely late, which was later in 80%-heading by 13 to 17 days than a check variety 'Hinohikari' in the three experimental years (Table 1).

"53" (Malangen *et al*., 2013) and "47" are other well-ripened RILs carrying *Ur1*, which were intermediate in 80%-heading between Koshihikari and Hinohikari (Table 1-(3)), and can be regarded as the middle and rather early, and the just middle, respectively, in heading in Kochi prefecture. The generation of 47 was F_{13} in 2010. Generations of 53 in the three experimental years were F_{13}, F_{14} and F_{15} in 2003, 2005 and 2010, respectively.

"7E" is a sister line of 79 originating from the same F_2 plant as that of 79. The F_3 population (27 plants) from the F_2 plant was grown in the paddy field in 2002, and three low-amylose-content plants were selected, which were earlier in heading than 79. From this generation and thereafter, selection for higher panicle weight per plant and better appearance of brown rice was performed on plant basis. In one of the three F_4 lines from the three F_3 plant, two plants were selected among the 35 plants in 2003. The two F_5 lines from the two F_4 plants were grown in 2004, and three plants were selected among the 189 plants of the earlier-heading F_5 line. Any genic segregations in heading and other traits between lines and within each line were not observed from F_6 (2005) to F_{10} (2008), indicating its fixation practically. It was 9 days later in 80% heading than Hinohikari in 2010 (Table 1-(3)). The yield test was conducted for the F_{11} generation in 2010.

"J3" is an inbred line derived from the F_1 hybrid of Koshihikari × 79. The 342 F_2 plants were grown in the paddy field in 2003. From this generation and thereafter, plants were selected for early-heading, low-amylose-content, higher panicle weight per plant as well as better appearance of brown rice. Three plants possessing better performances in these characteristics were selected. The three F_3 populations from the three selected plants were grown in 2004. In one of the F_3 populations, all the 120 plants possessed the *Ur1/Ur1* genotype, and six plants were selected. The six F_4 lines from the six F_3 plants were grown in 2005. One of the six lines was selected, and two plants were selected within the line (15 plants). The two F_5 lines from the two plants were grown in 2006, and five plants were selected from one of the lines (54 plants). This line had a heading time similar to that of Koshihikari. The five F_6 lines from the five selected F_5 plants were grown in 2007. One of the five lines was selected. However, segregation in culm length was observed in this line (20 plants), and one short-culm plant was selected. In the F_7 line from the plant, all of 20 plants were uniformly short-culmed. Any genic segregations in heading and other traits between lines and within each line were not observed in the F_8 generation (from the autumn of 2008 to the winter of 2009 in a growth chamber) and the F_9 generation (in the paddy field in 2009), indicating its fixation practically. The yield test was conducted for the F_{10} generation in 2010. Its heading time was identical with that of Koshihikari (Table 1-(3)).

Three *japonica* varieties and one *indica*-type variety

'Hinohikari' (abbreviated as "Hi") is a representative variety for normal season cropping in southern Japan, which possesses high eating-quality, low amylose content, and a rather long culm; and is of partial panicle-weight type (The Miyazaki Breeding Group, 2005). Its maturity is classified as the middle in Kyushu District, and as the middle and rather late in Kochi prefecture (Agricultural Production Bureau, Ministry of Agriculture, Forestry and Fisheries, Japan, 1997, and Table 1-(1) to –(3)).

'Nishihikari' ("Ni") is a short-culmed and panicle-number type variety possessing the highest lodging resistance in Kyushu District, which exerts high yielding-ability in fertile lands (Nishiyama, 1982). Its maturity is classified as the middle and rather late in Kyushu District, and as late in Kochi prefecture (Agricultural Production Bureau, Ministry of Agriculture, Forestry and Fisheries, Japan, 1997, and Table 1-(1) to –(3)).

'Koshihikari' ("Kos") is a representative high eating-quality variety in Japan, but is long-culmed and readily lodged (Agricultural Production Bureau, Ministry of Agriculture, Forestry and Fisheries, Japan, 1997). It is cultivated almost over Japan except the northern part of Northeast Japan, Hokkaido prefecture and Okinawa prefecture, and occupied 35.0% of the total rice area of Japan in 2018 (Rice Stable Supply Support

Organization, 2019). Its maturity is classified as the early and rather late in Kochi prefecture (Table 1-(3)).

'Takanari' ("Ta") is a super high-yielding and extra panicle-weight-type *indica*-type variety (Imbe *et al*., 2004). Its eating quality is low and less sticky, compared with ordinary Japanese varieties. Its rice is used for feeding livestock and for processed foods such as rice cracker. The maturity of Ta can be regarded as middle and rather early in Kochi prefecture (Table 1-(1) and (2)).

Cultivations in the experimental field in 2003, 2005 and 2010

Yield test was conducted for 53, 79, Ta, Ni and Hi in 2003. Twenty three-day seedlings, grown in a natural-light growth chamber, were transplanted to an experimental paddy field of Faculty of Agriculture (present name: Faculty of Agriculture and Marine Science), Kochi University (Nankoku 33°35′N, 7 m above sea level), at a spacing of 30 cm × 15 cm (22.2 hills/m^2) with two seedlings per hill, on 9th May. Three fertilizer levels were set in the paddy field. Chemical fertilizers containing N, P_2O_5 and K_2O were applied at the total nitrogen levels of 4.00, 8.00 and 16.00 g/m^2, being denoted by "N4", "N8" and "N16", respectively, for 53, 79, Ni and Hi (Table 2). Ta was grown only in N16. Just before ploughing, an ordinary chemical fertilizer containing N, P_2O_5 and K_2O was applied as basal application at the rate of 2.0 g/m^2 for each of the three nutrient elements. Additional basal application was performed 6 days after transplanting at the rates of 2.00 and 6.00 g/m^2 for N8 and N16, respectively, with a slow release and coated fertilizer ECOLONG® 424-100 type (7% of each nutrient element is readily available) manufactured by Chisso-Asahi Fertilizer Co., Ltd. Top-dressing application was performed at the rates of 2.00, 4.00 and 8.00 g/m^2, respectively, for N4, N8 and N16 with the same coated fertilizer 26 to 33 days before 80%-heading for the five varieties-lines. Three replications were set for all combinations of the three fertilizer levels and the four lines-varieties, and Ta at N16, on the experimental field, according to the randomized block design. Each plot comprised 27 hills × 4 rows (108 hills).

The object of the yield test in 2005 was the same five lines-varieties as in 2003. Eighteen-day seedlings raised by a similar way to that in 2003 were transplanted to the experimental field with the same planting density as in 2003, on 8 May. Chemical fertilizers containing N, P_2O_5 and K_2O was applied with total nitrogen levels of 12.00 and 21.00 g/m^2, denoted by "N12" and "N21", respectively (Table 2). Just before ploughing, the same ordinary chemical fertilizer as in 2003 containing N, P_2O_5 and K_2O was applied as a basal application at 4.0 g/m^2 for each of the three nutrient elements. The additional basal application for N21 was performed 6 days after transplanting at the rate of 3.00 g/m^2 with ECOLONG® 424-100 type 6 days after transplanting. Top-dressing was applied at the rates of 8.00 and 14.00 g/m^2, respectively, for N12 and N21, with another slow release and coated fertilizer ECOLONG® 424-180 type (3% of each nutrient element is readily available) manufactured by the same corporation, 62 or 63 days before 80%-heading for the five varieties-lines. Three replications were set for all combinations of the five lines-

Table 2. Chemical fertilizers applied to the experimental field at Kochi University in the three experimental years.

Years	Fertilizer levels	Basal or top-dressing	Chemical fertilizers applied	N (g/m^2)	P_2O_5 (g/m^2)	K_2O (g/m^2)
2003	N16	Basal	Ordinary chemical fertilizer	2.00	2.00	2.00
		Additional basal	ECOLONG® 424-100 type	6.00	6.00	6.00
		Top-dressing	ECOLONG® 424-100 type	8.00	8.00	8.00
		Total		16.00	16.00	16.00
	N8	Basal	Ordinary chemical fertilizer	2.00	2.00	2.00
		Additional basal	ECOLONG® 424-100 type	2.00	2.00	2.00
		Top-dressing	ECOLONG® 424-100 type	4.00	4.00	4.00
		Total		8.00	8.00	8.00
	N4	Basal	Ordinary chemical fertilizer	2.00	2.00	2.00
		Top-dressing	ECOLONG® 424-100 type	2.00	2.00	2.00
		Total		4.00	4.00	4.00
2005	N21	Basal	Ordinary chemical fertilizer	4.00	4.00	4.00
		Additional basal	ECOLONG® 424-100 type	3.00	3.00	3.00
		Top-dressing	ECOLONG® 424-180 type	14.00	14.00	14.00
		Total		21.00	21.00	21.00
	N12	Basal	Ordinary chemical fertilizer	4.00	4.00	4.00
		Top-dressing	ECOLONG® 424-180 type	8.00	8.00	8.00
		Total		12.00	12.00	12.00
2010	N18	Basal	Ordinary chemical fertilizer	6.00	6.00	6.00
		Top-dressing	ECOLONG® 424-180 type	12.00	12.00	12.00
		Total		18.00	18.00	18.00

ECOLONG® 424-100 type and ECOLONG® 424-180 type: see text.

varieties and the two fertilizer levels on the experimental field, according to the randomized block design. Each plot comprised 27 hills × 4 rows (108 hills).

J3, 7E, 47, 53, 79, Kos, Ni and Hi were used for the yield test in 2010. Twelve-day seedlings, grown in a natural-light growth chamber, were transplanted to the same paddy field with the same planting density on 8th May. Chemical fertilizers containing N, P_2O_5 and K_2O were applied with a the total nitrogen level of 18.00 g/m^2 (Table 2). The basal application was applied with the ordinary chemical fertilizer at 6.00 g/m^2 for each of the three nutrient elements. Top-dressing was applied at 12.00 g/m^2 for each of the three nutrient elements with ECOLONG® 424-180 type 65 to 74 days before 80%-heading for the eight varieties-lines. Each plot comprised 29 hills × 3 rows (87 hills).

Measurements of yield, its components and other traits

Yield, yield components and other traits were measured for the lines-varieties. All panicles of 23 hills in 2003 and 2005, and 25 hills in 2010 were sampled from the third row in 2003 and 2005 and the second row in 2010 of each plot of each line/variety at maturity, and were dried in a drying oven with a temperature between 30 and 45°C for 20 h to 30 h until the moisture content of the rough rice decreased to 11% or less. The panicle weight of each hill was checked after cutting at 1.5 mm below the panicle bases. Of the nine hills randomly selected from 23 or 25 hills of each plot of each line/variety, five hills having intermediate panicle weights were selected. The panicles of the five hills were threshed, and all spikelets from each hill were counted. Each spikelet was examined for development of endosperm by handling with fingers or by opening the hulls: a spikelet with developed endosperm containing starch (layer and/or powder) was regarded as fertilized in the present study. Grains after hulling (hereafter "grains") were sieved at 1.7 mm to select ripened grains by thickness, and the weight and number of ripened grains were measured on hill basis. Unripened grains (fertilized and partially filled) with thickness less than 1.7 mm were counted and weighed. The percentage of ripened-grain weight to panicle weight in the five selected hills of each plot was calculated; then the ripened-grain weight (yield) of the 23 or 25 hills of each plot was estimated from this percentage. The moisture content of the ripened grains was measured in each plot, and yield at 15% moisture was estimated from the moisture content. The total brown-rice yield was the total weight of the ripened grains and unripened grains. The ripened-grain percentage is the ratio of the number of ripened grains to the total number of spikelets. The percentage of ripened grains to fertilized spikelets, without unfertilized spikelets, was also calculated. This trait and the fertilized-spikelet percentage (fertilized spikelets ÷ all spikelets) enable to examine whether the failure of spikelet fertilization or insufficient grain-filling lowered the ripened-grain percentage. The mean spikelet number per hill of the 23 or 25 hills in each plot was estimated from both that of the five hills and the ratio of the mean panicle weight of the 23 or 25 hills to that of the five hills. "Sink size" was calculated by single grain weight × spikelet number per m^2.

Measurements of dry matter and leaf area

At each of 80%-heading stage and maturity, nine hills were sampled from each plot in 2003 and 2005. Five hills, which had intermediate panicle numbers per hill, were selected from the nine hills at each stage. Dry weight excluding roots of each of the five hills was measured after drying at 75°C for 2 days. At the former stage, the total area of living leaves in each hill was measured.

Amount of translocated carbohydrates from culms and leaf sheaths to panicles

Rice yield at maturity is composed of both carbohydrates produced after heading and those translocated from culms and leaf sheaths to panicles (Weng *et al.*, 1982). The former component can be approximated by the difference between the total dry matter weight at heading and that at maturity, viz. the increase of total dry weight after heading (ΔW) (Amano *et al.*, 1993). The latter component can be estimated by the difference between the dry matter weight of the total brown-rice yield and ΔW, according to Amano *et al.* (1993). This estimation of the amount of translocation is employed in the present study.

Table 3. Chemical fertilizers applied to the two farmers' fields at NOICH and TOSA.

Year	Location[1]	Basal or top-dressing	Chemical fertilizers applied	Date of top-dressing	N (g/m^2)	P_2O_5 (g/m^2)	K_2O (g/m^2)
2009	NOICHI	Basal	Hai-banto-ippatsu-48® [2,3]		12.00	7.80	6.00
		Top-dressing	Ordinary chemical fertilizer	13th Sep.	1.12	1.12	1.12
		Top-dressing	Ordinary chemical fertilizer	5th Oct.	0.35	0.35	0.35
		Total			13.47	9.27	7.47
2010	TOSA	Basal	New-Hai-LPV50® [2,4]		8.00	2.40	2.80
		Top-dressing	High grade organic rice® [5,6]	10th July	5.20	2.80	2.80
		Total			13.20	5.20	5.60

[1] See the MATERIALS AND METHODS.
[2] Manufactured by JCAM AGRI. CO., LTD.
[3] 50% of the total amount of N element is by three kinds of slow-release coated urea, and the remaining 50% of N is readily available.
[4] 50% of the total amount of N element is by two kinds of slow-release coated urea, and the remaining 50% of N element is readily available.
[5] Katakura & Co-op Agri Corporation.
[6] 50.8% of the total amount of N element is by organic nitrogen; 24.6% of that is by a kind of slow-release coated urea; 10.0% of that is by a kind of IB fertilizer; and the remaining 14.6% is readily available.

Cultivation of 79 at two farmers' fields in Kochi prefecture, and measurements of yield and related traits

The 79 was cultivated at two farmers' fields at two sites in Kochi prefecture. One was located at Doi 1660, Noichi, Konan city (33°34'N, 8 m above sea level); the other was at Nakayama 4301-i-22, Jizoji, Tosa (33°44'N, 578 m above sea). The former and latter were denoted by "NOICHI" and "TOSA", respectively, the areas of which were about 0.3 ha at both locations. Thirty two-day and 40-day seedlings were transplanted at the spacing of 30.0 cm × 23.6 cm and 30.1 cm × 20.7 cm, with 5.1 and 3.5 seedlings per hill in average by transplanting machine, on 23th June 2009 and 17th June 2010, respectively, at NOICHI and TOSA. Table 3 shows the chemical fertilizers applied and ways of application at the two locations. The total amounts of N element applied were 13.47 and 13.20 g/m^2, together with P_2O_5 and K_2O elements, at NOICHI and TOSA, respectively. At each of the two locations, seven sampling points were set at a distance of about 11 m along the diagonal line of the paddy field, excluding a 5 m margin. All panicles of ten hills were sampled at each of the seven points (70 hills in total) at maturity. Panicle weight and panicle number were measured for each of the 70 hills. In the ten hills of each of four points randomly selected from the seven points, four hills having intermediate panicle weights were selected. The number and weight of ripened grains, fertility of spikelets, etc., were measured for the panicles of the four hills of each of the four points (16 hills in total) by the same way as the yield tests at Kochi University. The yield based on the 70 hills and other traits were calculated.

RESULTS

Experiment in 2003

Table 4 shows yield, yield components and other traits related with yield in 53, 79, Ta, Ni and Hi in 2003. Regarding yield at N16, 79 and Ta were higher than the other line-varieties, followed by 53. Hi was lower than Ni. At N8 as well as at N4, the four lines-varieties except Ta were in the same order 79 > 53 > Ni > Hi as at N16 (">" indicates statistically significant difference at the 5% level). It is noticed that the higher the fertilizer level, the higher the yield in each of the four lines-varieties except Ta. As for spikelet number per panicle, the five lines-varieties were in the order Ta > 53 >79 > Hi ≥ Ni at N16, where "≥" indicates that the former is higher than the latter but being not significant statistically. Ta was outstandingly higher than the other four lines-varieties. The 53 and 79 were higher than Ni and Hi, which was principally due to the effect of *Ur1*. Similar results for the four lines-varieties except Ta were obtained in N8 and N4. Positive response to fertilizer level was noticed in each of 53, Ni and Hi, whereas significant differences were not noticed among the three fertilizer levels in 79. Regarding panicle number per m^2, Ta was noticeably lower than the other four lines-varieties at N16. 79 and Ni were higher than Hi in each of the three fertilizer levels. Nevertheless, the percentages of 53, 79 and Ni to Hi were between 97% of 53 at N16 and 111% of Ni at N4, suggesting that the varietal differences among the four varieties-lines in this trait were lower than those in spikelet number per panicle. Positive fertilizer response was noticed in each of the four lines-varieties. In 1000-grain weight, Ni was highest among the five lines-varieties at N16. Differences among the other four lines-variety were not significant or significant but low. Differences among the three fertilizer levels in each of 53 and 79 were not significant, and those were not significant or significant but low in each of Ni and Hi. Regarding ripened-grain percentage, the lines-varieties were in the order Ni ≥ 79 ≥ 53 > Ta > Hi at N16: significant differences were not noticed among the former three variety-lines, and Hi was the lowest. Similarly, significant differences were not noticed among Ni, 79 and 53, and Hi was the lowest at each of N8 and N4. Differences among the three fertilizer levels were not significant or significant but low in each of the four lines-varieties. As for fertilized-spikelet percentage, Hi was the lowest, and the other four lines-varieties were not significantly different from each other at N16. In each of the four lines-varieties, significant differences were not noticed among the three fertilizer levels. In percentage of ripened grains to fertilized spikelets, 53, Ni and 79 were significantly higher than Ta and Hi. Significant differences among the three fertilizer levels were not noticed in each of the three lines-variety except Hi. Regarding spikelet number per m^2 as well as sink size, the five lines-varieties were in the order Ta > 79 > 53 > Ni ≥ Hi at N16: Ta was the highest; and 79 and 53 were higher than Ni and Hi in each of N8 and N4. Positive fertilizer response was noticed in each of four lines-varieties in each of the two traits.

As shown in Table 5, the five lines-varieties were in the order of Hi > Ni ≥ 79 ≥ 53 ≥ Ta at N16 in LAI at heading. In total dry weight at

Table 4. Yield, yield components and other traits of 53, 79, Ta, Ni, and Hi at three fertilizer levels in 2003.

Traits	Fertilizer levels	53	79	Ta	Ni	Hi	LSD (5%)
Yield (g/m^2)	N16	612 b (136)	673 a (149)	690 a (153)	554 c (123)	451 de	38
	N8	549 c (145)	626 b (165)	—[1]	478 de (126)	379 f	
	N4	481 d (148)	553 c (170)	—	442 e (136)	326 g	
Spikelets/panicle	N16	107.4 b (128)	103.8 bc (124)	203.6 a (243)	80.6 ef (96)	83.6 e	5.5
	N8	101.8 cd (130)	101.4 cd (130)	—	76.5 fg (98)	78.3 efg	
	N4	96.6 d (130)	102.0 bcd (137)	—	74.1 g (100)	74.3 g	
Panicles/m^2	N16	309 b (97)	338 a (107)	190 f (60)	336 a (106)	317 b	14
	N8	288 cd (100)	317 b (110)	—	314 b (109)	287 cd	
	N4	268 e (98)	289 c (105)	—	304 b (111)	274 de	
1000-grain weight (g)	N16	20.2 e (97)	20.4 cde (98)	20.1 e (97)	21.7 a (105)	20.8 c	0.4
	N8	20.2 e (98)	20.4 cde (99)	—	21.3 b (103)	20.6 cd	
	N4	20.1 e (99)	20.3 de (100)	—	21.1 b (104)	20.3 de	
Ripened-grain percentage	N16	91.6 b (112)	94.0 ab (115)	88.4 c (108)	94.1 ab (115)	82.0 d	2.8
	N8	93.0 ab (114)	95.3 a (117)	—	93.2 ab (114)	81.6 de	
	N4	92.4 b (117)	92.4 b (117)	—	92.7 ab (117)	78.9 e	
Fertilized-spikelet percentage	N16	95.8 bc (107)	97.0 ab (108)	95.6 bc (107)	96.4 abc (108)	89.6 d	1.6
	N8	95.9 abc (106)	97.5 a (107)	—	96.0 abc (106)	90.9 d	
	N4	95.3 c (106)	96.4 abc (107)	—	96.2 abc (107)	90.3 d	
Percentage of ripened grains to fertilized spikelets	N16	95.6 a (104)	96.9 a (106)	92.4 b (101)	97.6 a (107)	91.5 bc	2.3
	N8	96.9 a (108)	97.8 a (109)	—	97.0 a (108)	89.8 c	
	N4	96.9 a (111)	95.9 a (110)	—	96.4 a (110)	87.4 d	
Spikelets/m^2 (×100)	N16	331 c (125)	351 b (132)	388 a (147)	271 e (102)	265 e	19
	N8	293 d (130)	321 c (143)	—	240 fg (107)	225 g	
	N4	259 ef (127)	294 d (145)	—	225 g (111)	203 h	
Sink size [2] (g/m^2)	N16	668 c (122)	717 b (130)	781 a (142)	588 de (107)	549 ef	40
	N8	590 d (127)	656 c (141)	—	513 fg (110)	465 h	
	N4	520 f (126)	598 d (145)	—	477 gh (115)	413 i	

( ) : Percentage to Hi.
Values followed by the same letter within each trait are not significantly different at 5% level of significance, determined by LSDs in the table.
[1] Ta was not grown at N8 and N4.
[2] Single grain weight × Spikelets/m^2.

Table 5. LAI, total dry weights, harvest index, amount of translocation, culm length and other traits of 53, 79, Ta, Ni, and Hi at three fertilizer levels in 2003.

Traits	Fertilizer Levels	53			79			Ta			Ni			Hi		LSD (5 %)
LAI at heading	N16	3.8	bcd	(81)	4.0	bc	(85)	3.3	de	(71)	4.1	b	(86)	4.7	a	0.5
	N8	3.4	de	(97)	3.2	ef	(92)	— [1]			3.4	de	(98)	3.5	cde	
	N4	2.8	f	(87)	2.7	f	(84)	—			3.1	ef	(96)	3.2	ef	
Total dry weight at heading (g/m^2)	N16	832	fg	(77)	1205	a	(111)	910	e	(93)	1007	c	(93)	1086	b	69
	N8	774	g	(81)	1093	b	(115)	—			922	de	(97)	951	cde	
	N4	688	h	(77)	990	cd	(111)	—			883	ef	(99)	889	ef	
Total dry weight at maturity (g/m^2)	N16	1304	fg	(83)	1636	a	(104)	1427	cd	(91)	1444	cd	(92)	1573	ab	89
	N8	1186	h	(85)	1498	bc	(107)	—			1328	efg	(95)	1397	de	
	N4	1070	i	(85)	1383	def	(110)	—			1242	gh	(99)	1256	gh	
Harvest index (%)	N16	39.9	ab	(164)	35.0	c	(144)	41.1	a	169)	32.6	d	(134)	24.4	f	1.9
	N8	39.3	ab	(170)	35.5	c	(154)	—			30.6	e	(132)	23.1	fg	
	N4	38.2	b	(173)	34.0	cd	(154)	—			30.2	e	(137)	22.1	g	
Dry weight of total brown rice (g/m^2) (a)	N16	531	b	(136)	580	a	(148)	607	a	(155)	474	c	(121)	392	de	32
	N8	473	c	(142)	538	b	(161)	—			410	de	(123)	333	f	
	N4	415	d	(142)	478	c	(164)	—			380	e	(130)	292	g	
Increase of total dry weight after heading (g/m^2) (b)	N16	472	abc	(97)	431	bcd	(89)	517	a	(106)	437	bcde	(90)	487	ab	77
	N8	412	bcdef	(92)	406	cde	(91)	—			406	cdef	(91)	446	abcd	
	N4	382	def	(104)	393	def	(107)	—			359	f	(98)	367	ef	
Amount of translocation (g/m^2) (c)	N16	59	cd		149	a		90	abc		38	cd		−95	e	72
	N8	62	bcd		132	ab					5	d		−112	e	
	N4	32	cd		86	abc					22	cd		−75	e	
Culm length (cm)	N16	65.9	e	(87)	73.5	ab	(97)	65.2	ef	(86)	63.6	fg	(84)	75.6	a	2.1
	N8	63.5	fg	(88)	70.6	cd	(98)	—			62.1	gh	(86)	72.2	bc	
	N4	60.6	hi	(87)	69.6	d	(100)	—			59.5	i	(85)	69.8	d	
Panicle length (cm)	N16	19.7	cde	(107)	20.3	bc	(110)	25.9	a	(141)	20.5	b	(112)	18.4	fg	0.8
	N8	19.3	de	(106)	20.1	bcd	(110)	—			19.6	cde	(107)	18.3	fg	
	N4	19.1	ef	(106)	20.4	bc	(113)	—			19.7	cde	(109)	18.0	g	

( ) : Percentage to Hi.
Values followed by the same letter within each trait are not significantly different at the 5% level, determined by LSDs in the table.
Note: c = a - b.
[1] Ta was not grown at N8 and N4.

heading and that at maturity, the five lines-varieties were in the order 79 > Hi > Ni > or ≥ Ta > or ≥ 53 at N16. Nevertheless, significant correlations were not noticed between yield and these traits at N16 (r = −0.143 and −0.152, respectively). Positive fertilizer response was noticed in each of four lines-varieties in each of the above three traits. Regarding harvest index, Ta and 53 were the highest at N16, while Hi the lowest. Correlation coefficient between this trait and yield was 0.942 at N16, and was 0.881 among the 12 combinations of the four lines-varieties except Ta and the three fertilizer levels (significant at the 5% level in both cases). Hence, it is suggested that the higher yields for Ta and 53 depended principally on the higher values of harvest index. In this trait, significant fertilizer response was not noticed in 53 and 79, while positive fertilizer response was noticed in Ni and Hi.

Dry weight of total brown rice per m^2, shown in Table 5, was highly correlated with yield among the five lines-varieties at N16 as well as among the 12 combinations between the four lines-varieties except Ta and the three fertilizer levels (r = 0.999 identically in both cases, significant at the 1% level). The increase of total dry matter after heading was in the order Ta ≥ Hi ≥ 53 ≥ Ni ≥ 79 (Ta > Ni): Ta was the highest but varietal difference is lower in this trait than in yield. Positive fertilizer response was noticed in each of the four lines-varieties in this trait. Regarding amount of translocation at N16, the lines-varieties were in the order 79 ≥ Ta ≥ 53 ≥ Ni > Hi (79 > 53), and the lowest value of Hi was negative. The four lines-varieties except Ta were in the same order at each of N8 and N4 as at N16. The minus values for Hi imply that carbohydrates produced after heading stagnated in culms and leaf sheaths to some degree, and/or were used for growth of tillers. In Hi, it is inferred that the low ability of its panicles to draw carbohydrates from leaf blades through leaf sheaths and culms was related with the lowest ripened-grain percentages caused by both the lowest fertilized-spikelet percentages and the lowest percentages of ripened grains to fertilized spikelets (Table 4). On the other hand, it is suggested that the higher yields of 79, 53 and Ta depended on the amounts of translocation, more or less. Significant fertilizer response was not noticed in the four lines-varieties in this trait.

At N16, culm length was in the order Hi ≥ 79 > 53 ≥ Ta ≥ Ni (53 > Ni) (Table 5). Positive fertilizer response was noticed in each of the four lines-varieties. Panicle length was in the order Ta > Ni ≥ 79 ≥ 53 >Hi (Ni > 53) at N16; and Ta was outstandingly higher than the other four lines-varieties. Significant fertilizer response was noticed in each of the three lines-variety except Ni.

Experiment in 2005

Table 6 shows the results of analysis variance for yield, yield components, sink size and other related traits in 53, 79, Ta, Ni and Hi at N21 and N12 in 2005. Effect of the lines-varieties was statistically significant through all the nine traits. Effect of the fertilizer levels was significant in all of seven traits except 1000-grain weight and fertilized-spikelet percentage. The interaction between the lines-varieties and the fertilizer levels was significant in yield, panicle number per m^2, ripened-grain percentage, fertilized-spikelet percentage and percentage

Table 6. Analysis of variance for yield, yield components and other traits of 53, 79, Ta, Ni and Hi at the two fertilizer levels in 2005, in which numerals show F-values.

Traits	Lines-varieties (A)		Fertilizer levels (B)		Interaction A × B		Replications
Yield (g/m^2)	152.85	**	133.37	**	3.09	*	2.37
Spikelets/panicle	353.60	**	32.57	**	2.78		2.24
Panicles/ m^2	61.95	**	58.19	**	3.14	*	< 1
1000-grain weight (g)	197.66	**	< 1		< 1		< 1
Ripened-grain percentage	31.13	**	11.83	**	6.33	**	< 1
Fertilized-spikelet percentage	31.41	**	4.08		3.83	*	< 1
Percentage of ripened grains to fertilized spikelets	15.42	**	8.49	**	3.62	*	< 1
Spikelets/m^2	89.07	**	134.26	**	1.23		1.70
Sink size [1] (g/m^2)	94.26	**	172.29	**	1.58		< 1

Degrees of freedom for lines-varieties, fertilizer levels, the interaction, replication, and error are 4, 1, 4, 2 and 18, respectively.
*, ** Significant at the 5% and 1% levels, respectively.
[1] Single grain weight × Spikelets/m^2.

of ripened-grains to fertilized spikelets. Effect of the replication was not significant through all the nine traits.

The Table 7 shows yield, yield components and other related traits in 53, 79, Ta, Ni and Hi at the two fertilizer levels in 2005. Regarding yield, the five lines-varieties were in the order Ta > 79 ≥ or > 53 ≥ or > Ni > Hi at N21 as well as at N12. Ta was the highest, followed by 79 and 53. The highest increase from N12 to N21 was 123 g/m^2 in Ni, while increases were 51 to 97 g/m^2 in the other four lines-varieties, suggesting the high fertilizer responsiveness of Ni. Spikelet number per panicle was in the order Ta > 79 > 53 > Hi ≥ or > Ni at N21 as well as at N12: Ta and the two *Ur1*-carrying lines were higher than the two varieties. Positive fertilizer responses were noticed in the lines-varieties; particularly, those were statistically significant in 79 and Ta in this trait. Panicle number per m^2 was in the order Ni ≥ Hi ≥ 53 ≥ 79 > Ta (Ni > 53, and Hi > 79) at N21, and Ni ≥ Hi ≥ 79 ≥ 53 > Ta (Ni > 79, and Hi >53) at N12. Ta was the lowest at N21 and N12, while the percentages of the other three lines-variety to Hi were between 92% of 53 at N12 to 104% of Ni at N21, suggesting that the varietal differences among the four varieties-lines except Ta in this trait were lower than those in spikelet number per panicle. Significant positive fertilizer response was noticed in each of the four lines-varieties except Ta. The 1000-grain weight was in the order Ni > Ta > 53 > or ≥ Hi > 79 at each of N21 and N12. Significant fertilizer responses were not noticed in the five lines-varieties. The ripened grain percentage was in the order Ta ≥ 53 > Ni ≥ 79 > Hi at N12. In this trait, significant decreases from N12 to N21 were noticed in 53 and 79; no significant fertilizer responses in both Ta and Hi; however, significant increase in Ni. As the result, Hi at both N12 and N21, and 79 at N21 were low in this trait (79.2 to 81.3%); because both fertilized-spikelet percentages and percentages of ripened grains to fertilized spikelets were low in the three cases of the two lines (89.5 to

Table 7. Yield, yield components and other traits of 53, 79, Ta, Ni and Hi at the two fertilizer levels in 2005.

Traits	Fertilizer levels	53			79			Ta			Ni			Hi		LSD (5%)
Yield (g/m²)	N21	723	c	(130)	728	c	(130)	843	a	(151)	695	cd	(125)	558	f	34
	N12	626	e	(123)	662	d	(131)	767	b	(151)	572	f	(113)	507	g	
	Average	675	b	(127)	695	b	(130)	805	a	(151)	633	c	(119)	533	d	24
Spikelets/panicle	N21	116.0	e	(123)	132.7	c	(140)	159.6	a	(169)	90.5	fg	(96)	94.5	f	5.9
	N12	111.2	e	(121)	123.8	d	(134)	145.1	b	(158)	85.2	g	(93)	92.1	f	
	Average	113.6	c	(122)	128.3	b	(138)	152.4	a	(163)	87.8	e	(94)	93.3	d	4.2
Panicles/ m²	N21	360	bc	(96)	354	cd	(95)	279	g	(75)	389	a	(104)	374	ab	19
	N12	312	f	(92)	326	ef	(96)	274	g	(81)	349	cd	(103)	339	de	
	Average	336	b	(94)	340	b	(95)	277	c	(78)	369	a	(103)	357	a	13
1000 grain weight (g)	N21	20.4	c	(102)	19.5	e	(98)	21.6	b	(108)	22.2	a	(111)	20.0	d	0.4
	N12	20.3	cd	(102)	19.3	e	(97)	21.5	b	(108)	22.5	a	(113)	20.0	d	
Ripened-grain percentage	N21	85.0	b	(107)	79.8	c	(101)	87.6	ab	(111)	88.9	a	(112)	79.2	c	2.7
	N12	88.9	a	(109)	84.9	b	(104)	89.9	a	(111)	85.5	b	(105)	81.3	c	
Fertilized-spikelet percentage	N21	91.6	cd	(102)	90.6	de	(101)	95.9	a	(107)	93.8	b	(105)	89.5	e	1.7
	N12	93.5	b	(104)	93.1	be	(103)	95.9	a	(106)	92.4	bc	(103)	90.1	de	
Percentage of ripened grains to fertilized spikelets	N21	92.8	abcd	(105)	88.0	f	(100)	91.4	cde	(103)	94.8	ab	(107)	88.4	f	2.4
	N12	95.0	a	(105)	91.2	de	(101)	93.7	abc	(104)	92.5	bcde	(103)	90.2	ef	
Spikelets/m² (×100)	N21	417	c	(118)	469	a	(132)	446	b	(126)	351	d	(99)	354	d	23
	N12	347	d	(111)	404	c	(129)	398	c	(128)	297	e	(95)	312	e	
Sink size [1] (g/m²)	N21	852	c	(121)	913	b	(129)	962	a	(136)	782	d	(111)	706	e	42
	N12	705	e	(113)	780	d	(125)	854	c	(137)	669	e	(107)	624	f	

( ) : Percentage to Hi.
Values followed by the same letter within each trait are not significantly different at 5% level of significance, determined by LSDs in the table.
[1] Single grain weight × Spikelets/m².

Table 8. Analysis variance for LAI at heading, total dry weights, harvest index, amount of translocation and other traits of 53, 79, Ta, Ni, and Hi at the two fertilizer levels in 2005, in which numerals show F-values.

Traits	Lines-varieties (A)		Fertilizer levels (B)		Interaction A X B		Replications
LAI at heading	18.92	**	48.73	**	<1		3.15
Total dry weight at heading (g/m^2)	227.87	**	80.39	**	4.86	**	1.37
Total dry weight at maturity (g/m^2)	42.10	**	113.36	**	<1		2.97
Harvest index (%)	453.33	**	<1		1.47		<1
Dry weight of total brown rice (g/m^2)	172.07	**	162.68	**	2.44		2.79
Increase of total dry weight after heading (g/m^2)	32.28	**	28.61	**	2.18		1.78
Amount of translocation (g/m^2)	52.56	**	<1		3.08	*	1.37
Culm length (cm)	133.29	**	39.14	**	1.67		5.94 *
Panicle length (cm)	114.72	**	<1		<1		2.98

Degrees of freedom for lines-varieties, fertilizer levels, the interaction, replication and error are 4, 1, 4, 2 and 18, respectively.
*, ** Significant at the 5% and 1% levels, respectively.

90.6% and 88.0 to 90.2%, respectively, in the former and latter traits).

The order in spikelet number per m^2 was 79 > or ≥ Ta > 53 > Hi ≥ Ni at N21 and N12. Sink size was in the order Ta > 79 > 53 > or ≥ Ni > Hi at N21 and N12. Significant positive fertilizer response was noticed in each of the five lines-varieties in the two traits. Correlation coefficient between yield and spikelet number per m^2, and that between yield and sink size are 0.815 and 0.956 respectively, and are significant at the 1% level, indicating that correlation with yield was higher in the later trait than in the former trait.

Table 8 shows results of analysis of variance for LAI, total dry weight at maturity, harvest index, amount of translocation and other traits of 53, 79, Ta, Ni and Hi at both N21 and N12 in 2005. Effect of the lines-varieties was statistically significant through all the nine traits. Effect of the fertilizer levels was significant in the six traits except harvest index, amount of translocation and panicle length. The interaction between the lines-varieties and the fertilizer levels was significant in total dry weight at heading and amount of translocation. The effect of the replication was significant only in culm length.

As shown in Table 9, LAI at heading was in the order Hi ≥ Ni ≥ 79 ≥ 53 ≥ Ta (Hi > 79) at N21, and Hi ≥ Ni ≥ Ta ≥ 79 ≥ 53 (Hi >Ta, and Ni > 79) at N12. Total dry weight at maturity was in the order 79 ≥ Hi ≥ Ni ≥ (or ≤) Ta > 53 at N21 and N12. Significant correlation between this trait and yield was not noticed among the ten combinations of the five lines-varieties and the two fertilizer levels as well as among the eight combinations of the four lines-varieties except Ta and the two fertilizer levels (r = 0.148 and 0.176). This trait was significantly correlated with total dry weight at heading among the ten combinations of the

Table 9. LAI at heading, total dry weights, harvest index, amount of translocation and other traits of 53, 79, Ta, Ni and Hi at two fertilizer levels in 2005.

Traits	Fertilizer levels	53			79			Ta			Ni			Hi		LSD (5%)
LAI at heading	N21	4.2	bc	(81)	4.3	bc	(83)	4.0	ab	(77)	5.0	ab	(96)	5.2	a	0.5
	N12	3.5	ef	(78)	3.6	de	(80)	3.6	de	(80)	4.2	bc	(93)	4.5	b	
Total dry weight at heading (g/m^2)	N21	900	g	(73)	1455	a	(118)	1011	f	(82)	1291	b	(105)	1233	cd	58
	N12	765	h	(66)	1263	bc	(110)	982	f	(85)	1175	de	(102)	1151	e	
Total dry weight at maturity (g/m^2)	N21	1517	f	(83)	1884	a	(104)	1714	cd	(94)	1766	bc	(97)	1818	ab	88
	N12	1332	g	(81)	1676	d	(102)	1558	ef	(95)	1503	f	(92)	1636	de	
Harvest index (%)	N21	40.5	b	(155)	32.9	cd	(126)	41.8	a	(160)	33.5	cd	(128)	26.1	e	1.2
	N12	40.0	b	(152)	33.6	c	(127)	41.9	a	(159)	32.3	d	(122)	26.4	e	
Dry weight of total brown rice (g/m^2) (a)	N21	626	c	(128)	651	bc	(133)	735	a	(150)	598	d	(122)	490	f	28
	N12	539	e	(122)	584	d	(132)	665	b	(150)	495	f	(112)	442	g	
Increase of total dry weight after heading (g/m^2) (b)	N21	618	b	(106)	428	c	(73)	704	a	(120)	475	c	(81)	585	b	77
	N12	567	b	(117)	413	c	(85)	576	b	(119)	327	d	(68)	484	c	
Amount of translocation (g/m^2)(c)	N21	9	ef		223	a		32	de		124	bc		−95	g	63
	N12	-29	ef		171	ab		89	cd		168	ab		−43	fg	
Culm length (cm)	N21	66.1	cde	(87)	77.0	a	(101)	67.9	c	(89)	64.6	de	(85)	75.9	a	2.1
	N12	64.0	e	(89)	75.0	a	(104)	66.2	cd	(92)	60.0	f	(83)	72.0	b	
Panicle length (cm)	N21	21.6	d	(106)	22.8	b	(112)	26.4	a	(130)	20.5	e	(101)	20.3	e	1.0
	N12	21.7	cd	(110)	22.6	bc	(114)	26.1	a	(132)	20.4	e	(103)	19.8	e	

( ) : Percentage to Hi.
Values followed by the same letter within each trait are not significantly different at 5% level of significance, determined by LSDs in the table.
Note: c = a - b.

Table 10. Yield, yield components and other traits of 79, 7E, 47, 53, J3, Kos, Ni and Hi in 2010.

Traits	79			7E			47			53			J3			
Yield (g/m^2)	584	a	(135)	587	a	(136)	584	a	(135)	564	a	(130)	585	a	(135)	[138]
Total brown rice yield (g/m^2)	596	a	(135)	595	a	(134)	597	a	(135)	569	a	(128)	593	a	(134)	[137]
Spikelets/panicle	103.4	ab	(127)	99.9	b	(123)	105.9	a	(130)	106.2	a	(130)	98.8	b	(121)	[124]
Panicles/m^2	309	a	(100)	311	a	(101)	329	a	(107)	279	b	(90)	316	a	(102)	[118]
1000-grain weight (g)	20.9	b	(102)	22.2	a	(109)	19.6	d	(96)	20.7	b	(101)	20.1	cd	(98)	[91]
Ripened-grain percentage	87.2	bc	(104)	85.1	c	(101)	85.4	c	(102)	92.2	a	(110)	93.4	a	(111)	[103]
Fertilized-spikelet percentage	93.4	cd	(101)	90.4	e	(98)	92.2	d	(100)	94.6	bc	(102)	96.2	a	(104)	[101]
Percentage of ripened grains to fertilized spikelets	93.4	abc	(103)	94.2	abc	(104)	92.6	c	(102)	97.5	a	(107)	97.1	ab	(107)	[102]
Spikelets/m^2 (×100)	320	b	(127)	311	bc	(123)	349	a	(139)	296	c	(118)	311	bc	(124)	[146]
Sink size [1] (g/m^2)	670	ab	(130)	689	a	(134)	683	a	(133)	611	c	(119)	626	bc	(122)	[134]
Culm length (cm)	72.3	c	(89)	71.2	cd	(88)	63.5	f	(78)	67.5	e	(83)	70.5	d	(87)	[80]
Panicle length (cm)	22.1	a	(117)	21.9	a	(116)	20.1	c	(107)	20.8	b	(111)	17.5	f	(93)	[90]

Traits	Kos			Ni			Hi		LSD (5%)
Yield (g/m^2)	424	c	(98)	482	b	(112)	432	c	43
Total brown rice yield (g/m^2)	433	c	(98)	492	b	(111)	443	c	40
Spikelets/panicle	79.9	c	(98)	73.9	d	(91)	81.5	c	5.1
Panicles/m^2	267	b	(86)	330	a	(107)	308	a	23
1000-grain weight (g)	22.0	a	(108)	22.3	a	(109)	20.4	bc	0.5
Ripened-grain percentage	90.4	ab	(108)	88.6	abc	(105)	84.1	c	4.9
Fertilized-spikelet percentage	94.9	ab	(103)	95.2	ab	(103)	92.5	d	1.4
Percentage of ripened grains to fertilized spikelets	95.2	abc	(105)	93.1	bc	(102)	91.0	c	4.4
Spikelets/m^2 (×100)	213	e	(85)	244	d	(97)	252	d	22
Sink size [1](g/m^2)	469	e	(91)	545	d	(106)	514	de	46
Culm length (cm)	88.0	a	(109)	60.7	g	(75)	81.0	b	1.7
Panicle length (cm)	19.4	d	(103)	20.2	c	(108)	18.8	e	0.4

() : Percentage to Hi.
[] : Percentage to Kos.
Values followed by the same letter within each trait are not significantly different at 5% level of significance, determined by LSDs in the table.
[1] Single grain weight × Spikelets/m^2.

five lines-varieties and the two fertilizer levels as well as among the eight combinations of the four lines-varieties except Ta and the two fertilizer levels (r = 0.842 and 0.900, significant at 1% level in both cases). Positive fertilizer response was noticed in each of the five lines-varieties in total dry weights at heading and that at maturity, and LAI. Regarding harvest index, Ta was the highest followed by 53 at each of the two fertilizer levels, while Hi was the lowest. Correlation coefficient between this trait and yield was significant at the 5% level (0.798) among the ten combinations of the five lines-varieties and the two fertilizer levels; however, it was positive but not significant at the 5% level (0.674) among the eight combinations of the four lines-varieties except Ta and the two fertilizer levels. Hence, it is suggested that the higher yields of Ta and 53 depended considerably on the higher values of harvest index. Significant fertilizer response was not noticed in the five lines-varieties in this trait.

Dry weight of total blown rice per m^2, shown in Table 9, was highly correlated with yield among the ten combinations between the five lines-varieties and the two fertilizer levels (r = 0.997, significant at the 1% level).

Increase of total dry matter after heading was in the order Ta > 53 > Hi > Ni > 79 (or 79 > Ni) at both N21 and N12 (Table 9). Ta was higher than the other lines-varieties at both N21 and N12, which is in accordance with its highest yield. In this trait, however, 79, which was the second highest in yield, was the lowest or the second lowest; and the lowest-yielding Hi was intermediate.

The amount of translocation was in the order 79 ≥ Ta ≥ 53 ≥ Ni > Hi (79 > 53) at each of N21 and N12, and the lowest value of Hi was negative (Table 9). Correlation coefficient between this trait and yield among the ten combinations between the five lines-varieties and the two fertilizer levels was 0.333. It was 0.536 among the eight combinations of the four lines-varieties except Ta and the two fertilizer levels. The correlation coefficients were not significant at the 5% level. In this trait, the lowest-yielding Hi was the lowest; the second highest-yielding 79 was highest; however, the highest-yielding Ta was intermediate.

Culm length was in the order 79 ≥ or > Hi > Ta ≥ or > 53 ≥ or > Ni at each of N21 and N12 (Table 9). Positive fertilizer response was noticed in each of the lines-varieties. Ta was outstandingly higher than the other four lines-varieties in panicle length; the other four lines-varieties were in the order 79 > or ≥ 53 > Ni ≥ Hi at N21 and N12. Significant fertilizer responses were not noticed in the five lines-varieties.

Experiment in 2010

Table 1-(3) shows 80%-heading dates and number of days from sowing to heading in 53, 79, 7E, 47, J3, Kos, Ni and Hi at 2010. In the former trait, they were in the order 79, 7E, Ni, Hi, 47, 53, and J3 = Kos, from the latest to the earliest. As shown in yield Table 10, the five *Ur1*-carrying lines had yields significantly higher than those of the three varieties examined, which corresponded to 130 to 136% of that of Hi. J3 was 38% higher than Kos in this trait. The order in the three varieties was Ni > Hi ≥ Kos. Correlation coefficient between this trait and total brown-rice yield was significant at the 1% level (0.999). In spikelet number per panicle, the five

Ur1-carrying lines were significantly higher than the three varieties; they were 121 to 130% of that of Hi, and J3 was 24% higher than Kos. The order in the three varieties was Hi ≥ Kos > Ni. Correlation coefficient between this trait and yield was significant at the 5% level (0.887). In panicle number per m^2, the lines-varieties were in the order Ni ≥ 47 ≥ J3 ≥ 7E ≥ 79 ≥ Hi > 53 ≥ Kos. The five *Ur1*-carrying lines were not significantly different with the three varieties in this trait, according to t-test. The 1000-grain weight was in the order Ni ≥ 7E ≥ Kos > 79 ≥ 53 ≥ Hi ≥ J3 ≥ 47 (53 > J3, and Hi > 47). The lines-varieties can be classified into two groups: the three varieties-line with 1000-grain weights higher than 21.4 g and the five lines-variety with 1000-grain weights lower than 21.3 g. 7E belongs to the former group, suggesting that *Ur1*-carrying varieties with higher single-grain weights can developed. Ripened-grain percentage was in the order J3 ≥ 53 ≥ Kos ≥ Ni ≥ 79 ≥ 47 ≥ 7E ≥ Hi (53 > 79, and Ni > 47). Hi, 7E and 47 were the lowest, resulting from both their lower fertilized-spikelet percentages (90.4 to 92.5%) and their lower percentages of ripened grains to fertilized spikelets (91.0 to 94.2%). On the other hand, J3, 53 and Kos had ripened-grain percentages higher than 90.0%, resulting from both their higher fertilized-spikelet percentages (94.6 to 96.2%) and their higher percentages of ripened grains to fertilized spikelets (95.2 to 97.5%). However, correlation coefficient between this trait and yield is low (0.112). Spikelet number per m^2 was in the order 47 > 79 ≥ J3 ≥ 7E ≥ 53 > Hi ≥ Ni > Kos. Sink size was in the order 7E ≥ 47 ≥ 79 ≥ J3 ≥ 53 > Ni ≥ Hi ≥ Kos (79 > 53, and Ni > Kos). The five *Ur1*-carrying lines were 18 to 39% and 19 to 34%, respectively, higher than Hi in the former and latter traits. Kos was the lowest in the two traits. Correlation coefficient between yield and spikelet number per m^2, and that between yield and sink size are 0.929 and 0.958, respectively, and are significant at the 1% level. Culm length was in the order Kos > Hi > 79 ≥ 7E ≥ J3 > 53 > 47 > Ni. 47 was the second shortest, following short-culmed Ni. The 79 was the highest among the five *Ur1*-carrying lines, but was lower than rather long-culmed Hi. The order in panicle length was 79 ≥ 7E > 53 > Ni ≥ 47 > Kos > Hi > J3. Significant difference was not noticed between the five *Ur1*-carrying lines and the three varieties in this trait.

Yields of 79 in farmers' fields

Table 11 shows yield, yield components, related traits and 50%-heading date of 79 at NOICHI in 2009 and those at TOSA in 2010. The yield at NOICHI (673 g/m^2) was identical with that of 79 at N16 in 2003 (Table 4). Hence, yield components in the former and latter are compared with each other. Panicle number per m^2 was higher in the former than in the latter. Little difference between the former and latter was noticed in spikelet number per panicle as well as 1000-grain weight. As a result, the former was higher than the latter in spikelet number per m^2 as well as sink size. Nevertheless, these increases were canceled by the decrease in ripened-grain percentage in the former, mainly due to the decrease in percentage of ripened grains to fertilized spikelets. The yield at TOSA (784 g/m^2) exceeded the highest yield of 79 at N21 in 2005 (728 g/m^2) at Kochi University (Table 7). Yield

Table 11. Yield, yield components, 50%-heading date, and other traits of 79' cultivated at NOICHI in 2009 and at TOSA in 2010.

Traits	NOICHI	TOSA
Yield (g/m^2)	673	784
Total brown rice yield (g/m^2)	737	807
Spikelets/panicle	105.3	122.3
Panicles/m^2	417	371
1000-grain weight (g)	20.5	21.0
Ripened-grain percentage	74.5	82.7
Fertilized-spikelet percentage	91.6	89.7
Percentage of ripened grains to fertilized spikelets	81.3	92.2
Spikelets/m^2 (×100)	439	454
Sink size [1] (g/m^2)	903	952
Culm length (cm)	77.9	81.7
Panicle length (cm)	20.9	21.1
50%-heading date	12th Sep.	10th Sep.

[1] Single grain weight × Spikelets/㎡

Table 12. Daily maximum temperature and daily minimum temperature in each of the second 10-days of September to the second 10-days of October in 2009 at NOICHI and in 2010 at TOSA.

Month	10-day duration of month	NOICHI [1]		TOSA [2]	
		Max. temp. (°C)	Min. temp. (°C)	Max. temp. (°C)	Min. temp. (°C)
Sep.	Second	29.1	18.5	26.6	16.0
	Third	28.0	20.0	22.4	14.5
Oct.	First	25.1	17.8	20.8	13.1
	Second	24.2	12.5	21.2	10.3

Source: Japan Meteorological Agency (http://www.jma.go.jp/jma/menu/report.html).
[1]Site of observation: Nankoku-Nissho meteorological-observation point which is the nearest to NOICH.
[2]Site of observation: Hongawa meteorological-observation point in Kochi prefecture, the height above sea level (550 m) of which is similar to that of TOSA.

components in the former and latter are compared with each other. The former was higher than the latter in panicle number per m^2, 1000-grain weight, ripened-grain percentage and sink size; on the other hand, the former was lower than the latter in spikelet number per panicle. In other words, the increases in the three yield components exceeded the decrease in the one yield component, resulting in the higher yield in the former.

Regarding spikelet number per m^2, 79 was far higher than 40000 at NOICHI and TOSA. Moreover, both the ripened-grain percentage higher than 80% and the higher 1000-grain weight brought about the high yield of almost 800 g/m^2 at TOSA; on the other hand, the lower ripened-grain percentage caused the lower yield at NOICHI than that at TOSA. Table 12 shows the daily maximum temperature and daily minimum temperature (average of ten days) in each of the second 10-days of

September to the second 10-days of October in 2009 at NOICHI, and those in 2010 at TOSA. This period almost overlapped the maturing durations of 79 at both NOICHI in 2009 and TOSA in 2010. The daily maximum temperatures and daily minimum temperatures were not too high to inflict damage to brown-rice appearance at both locations.

Accordingly, higher sink size and higher grain-filling resulting in higher ripened-grain percentage and higher 1000-grain weight should coexist to obtain an extraordinarily high yield by 79. Condition and traits of soil, and root characteristics were not investigated in the two locations and the experimental paddy field of Kochi University. These investigations should be performed for paddy fields cultivated by 79 in which high sink size resulting from high spikelet number per m^2 is obtained, in addition to using data of meteorological observation, in order to peruse high yield by the use of 79.

DISCUSSION

At the International Rice Research Institute, seven improved varieties such as IR8, IR36 and IR72 had rough (unhulled) rice yields from 708 to 932 g/m^2 in two dry seasons (Peng *et al*. 2000), which correspond to 566 to 746 g/m^2 of brown rice, by assuming that 80% of rough rice is brown rice. At the Shikoku National Agricultural Experiment Station (Senyu 1-3-1, Zentuji, Kagawa, 34°13′N, 26 m above sea level), a Korean *indica*-type variety Suweon 258 had brown-rice yields from 827 to 1010 g/m^2 in the May-transplanting cultivation by applying fertilizers at high levels of nitrogen, which corresponded to 146 to 161% of those of 'Nipponbare', a representative Japanese *japonica* variety, and IR36 had a yield (773 g/m^2) intermediate between those of the two varieties in a field test, probably reflecting its yielding ability (Komatsu *et al*. 1984). At the same agricultural experiment station, Ta had brown-rice yields from 787 to 861 g/m^2 which corresponded to 124 to 143% of those of Nipponbare. Similar differences between the two varieties were reported by Taylaran *et al.* (2009). Therefore, it seems that the potential yielding-ability of Ta is far higher than that of Nipponbare but lower than that of Suweon 258.

Regarding Ta in the present study (Tables 4 and 7), yield was lower in 2003 (N16) than in 2005 (average of N21 and N12, averaged nitrogen level = 16.5 g/m^2). This is caused by its lower panicle number per m^2 in 2003 than in 2005, despite a higher spikelet number per panicle in 2003. Table 13 shows the average of daily durations of sunshine for each of the first 10-days to the third 10-days of each month from May (transplanting) to September (maturity of 79) in 2003 and 2005. Daily duration of sunshine was lower in the second 10-days and the third 10-days of both May and June in 2003 than in 2005, suggesting that the rainy season in the former year was severe. This severe rainy season may have diminished to produce productive tillers, resulting in a lower panicle number per m^2 in 2003 than in 2005. Similarly, decrease of yield from 2005 (average of N21 and N12) to 2003 (N16) caused by decrease of panicle number per m^2 is noticed in Hi, Ni and 53, although the decreases of yield in them (82, 79 and 63 g/m^2, respectively) were lower than that in Ta (115 g/m^2). Nagata *et al*. (1997) reported that among-year fluctuation

Table 13. Daily duration of sunshine in each of the first 10-days to the third 10-days of each month from May (transplanting) to September (maturity of 79) in 2003 and 2005, and the averages of those from 2000 to 2009.

Months	10-day duration of month	Daily duration of sunshine (hours/day)		
		2003	2005	Average from 2000 to 2009
May	First	7.2	6.8	5.8
	Second	2.6	7.1	5.5
	Third	3.5	8.4	6.4
June	First	7.4	7.4	5.9
	Second	1.6	5.6	4.5
	Third	3.2	4.3	3.5
July	First	4.2	1.6	4.1
	Second	4.5	8.1	5.8
	Third	4.8	7.0	6.7
Aug.	First	7.3	8.7	7.5
	Second	3.3	7.7	6.5
	Third	6.7	5.2	6.1
Sep.	First	8.3	4.7	6.0
	Second	7.0	5.9	5.8
	Third	7.6	6.1	5.2

Source: Japan Meteorological Agency (http://www.jma.go.jp/jma/menu/report.html).
Site of observation: Kochi meteorological-observation point which is the nearest to the experimental paddy field of Kochi University, recording duration of sunshine.

in yield was higher in Ta than in Nipponbare, which is consistent with the above result. However, the between-year difference of yield in 79 is small (22 g/m^2), because 79 was 22 days later in heading than Ta in 2003 (Table 1-(1)), and its longer duration before heading may have contributed to produce more productive tillers.

Hybrid-rice varieties achieved brown-rice yields of about 1000 g/m^2 or higher in China, in which contribution of amount of translocation to total brown-rice yield was 38% at maximum (Amano *et al.*, 1993, 1996 a and 1996 b). For Ta and 53, the contributions of amount of translocation to dry weight of total brown rice were 15 and 11% at N16 in 2003, and 9 and −2% in 2005 (average of N21 and N12), respectively (calculated from data in Table 5 and Table 9). On the other hand, those in 79 were 26 and 32%, respectively, in 2003 (N16) and 2005 (average of N21 and N12). There is a possibility that the longer duration before heading enabled to store more amount of carbohydrates in leaf sheaths and culms to be translocated to panicles in 79. Hence, it is inferred that the higher yields in 79 depended considerably on the higher amounts of translocation, while the higher yields in 53 and Ta depended almost on the higher increases of total dry weight after heading, resulting in their higher values of harvest index despite their lower values in LAI as well as total dry weight at heading (Table 5 and Table 9). Moreover, it is suggested for the two *Ur1*-carring lines and Ta that their higher sink sizes owing to the higher spikelet numbers per panicle were indispensable to achieve the higher yields.

The line 79 was lower in yield than Ta in the desirable environmental condition in 2005 (Table 7), suggesting that the former may be lower in potential yielding-ability than the latter. Nevertheless, 79 was similar to Ta in yield in the rather undesirable environmental condition in 2003 (Table 4). The average yield of normal season cropping for the 20 years from 2000 to 2019 in Kochi prefecture was 422 g/m^2 (calculated from data via personal communication by Dr. Mototaka Sakata of Kochi Agricultural Research Station), which correspond to about half of the yield of 79 at TOSA (Table 11). In addition, the yield of 683 g/m^2 by 79 was obtained at the formerly place of Kagawa Prefectural Agricultural Experiment Station in 2008 (Ko 220, Busshozan, Takamatsu city, 34°16′N, 39 m above sea level) (Murai unpublished). Hence, it could be expected that 79 realizes high yields not only in Kochi prefecture but also in other warm regions of Japan such as Kagawa prefecture. 79 was later in heading by three days than 'Yumehikari', one of the latest varieties in Kyushu District, at a paddy field in Fukuoka prefecture in 2007 (data obtained at the Paddy field work research area of Kyushu Okinawa Agricultural Research Center, National Agriculture and Food Research Organization, Oaza-Izumi 496, Chikugo, 33°12′N, 9 m above sea level). In southern Japan, grains of brown rice damaged by high temperature such as white-backed and milky-white grains appeared when maturing temperature was too high in summer (Iwashita *et al*., 1973). In the case of Hinohikari, the ratio of first-class rice, as judged by the appearance of brown rice, to the total amount of prefectural rice production in Kochi prefecture as well as Fukuoka prefecture decreased to about 10% in 2010, in which the summer was unusually warm (Miyazaki, 2014; Sakata, 2014). Sakai *et al*. (2006) suggested that late-heading varieties of Kyushu District have the advantage of avoiding high-temperature damage of grain filling, because their maturing durations are mainly in September, during which the temperature is ordinarily lower than in August. Accordingly, 79 has higher possibility of avoiding high temperature damage of grain filling than middle-heading varieties, from the meteorological point of view. In a sensory eating quality test, 79 was higher in both overall evaluation and external appearance than Hi, even though 79 was lower in stickiness but higher in hardness than Hi (Kamimukai *et al*., 2017). Consequently, 79 could be a prospective candidate as a commercial variety not only for Kochi prefecture but also for other warm regions of Japan.

The 79, 7E, 47, 53 and J3 were 14 and 9 days later, and 3, 9 and 14 days earlier, respectively, than Hi in heading; and J3 was identical with Kos (Table 1-(3)). The five *Ur1*-carrying lines were 30 to 35% higher in yield than Hi, and J3 was 38% higher than Kos. In a sensory eating quality test, J3 had a similar score to Kos in overall evaluation and all the other test items such as taste, indicating its high eating quality (Murai unpublished). Hence, it is suggested that early-heading *japonica* varieties with high yielding-ability can be developed by the use of *Ur1*. In sensory eating quality tests (Murai unpublished), 7E and 47 were not significantly different from Hi regarding overall evaluation, taste, stickiness, and other test items. On the other hand, 53 was lower than Hi regarding these three test items and flavor, suggesting its lower

Table 14. Percentage of value in 2010 (N16) to that in 2005 (average of N21 and N12) regarding each of yield and yield components in each of 53, 79, Ni and Hi.

Traits	53	79	Ni	Hi
Yield (g/m^2)	78	80	69	77
Spikelets/panicle	92	78	82	86
Panicles/m^2	77	87	85	82
1000-grain weight (g)	101	107	101	102
Ripened-grain percentage	108	109	100	106

practical utility due to its lower eating quality. Consequently, 7E, 47 and J3 could be candidates for late-heading, middle-heading and early-heading commercial varieties, and also be mid-mother lines for developing high-yielding varieties with high eating quality.

The 79, 53, Ni and Hi were grown in 2010 and 2005. Their yields in 2010 (total nitrogen level of 18.00 g/m^2, Table 2) were 76 to 84% of those in 2005 (average of N21 and N12), being caused by their lower values in both spikelet number per panicle and panicle number per m^2 in 2010, even though their values in 2010 were similar to or rather higher than those in 2005 with respect to 1000-grain weight as well as ripened-grain percentage (Table 14, Table 7 and Table 10). The yields of 79 and Hi in 2009, grown with total nitrogen level of 18.00 g/m^2, are similar to those in 2010 (Murai unpublished). At Kochi Agricultural Research Station (Hataeda 1100, Nankoku city, 33°35′N, 22 m above sea), the average yield of Hi for the 20 years from 2000 to 2019 was 423 g/m^2, ranging from 318 to 539 g/m^2 (calculated from the data via personal communication by Dr. Mototaka Sakata). This range almost overlaps the range of yield in the three experimental years at Kochi University (Table 4, Table 7 and Table 10). In 2016, however, yield of 79 recovered to 645 kg/m^2 by supplying rapeseed meal at the rate of 476 g/m^2 to the same experimental field, together with the application of chemical fertilizers at the total nitrogen level of 8.00 g/m^2, while that of Hi was 415 g/m^2 (Bhattarai *et al*., 2016). The latter yield was similar to the average yield of Hi at Kochi Agricultural Research Station, probably because yielding ability of Hi is not high. At TOSA, where the high yield for 79 was obtained, organic nitrogen was applied (Table 3). Hence, the lower yields in 2010 may be due to diminution of land fertility since effective organic fertilizers were not supplied to the experimental field from 2000 to 2015. Consequently, it is suggested that land fertility should be sufficiently maintained to pursue high yield by using 79 and other *Ur1*-carrying lines.

The results of eating quality tests and traits related with eating quality such as amylose content for the five *Ur1*-carrying lines will be reported in detail in the next paper.

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