PANICLE CHARACTERISTICS IN HIGH-YIELDING *japonica* RICE LINES CARRYING *Ur1* (UNDULATED RACHIS-1) GENE

ABSTRACT

Ur1 (Undulate Rachis -1), an incompletely dominant gene on chromosome 6, being characterized by undulation of primary and secondary branches at the lowest part of a panicle, has the principal effect of increasing number of secondary branches per primary branch, and additional effects of increasing both spikelet number per single secondary branch and number of primary branches per panicle. This genic effect can increase grain yield by enlarging sink size. We examined the panicle traits of two high-yielding Ur1-carrying lines (MR79 and MR53) and two commercial varieties ('Hinohikari' and 'Nishihikari'). They were grown at high, middle and low fertilizer levels in a paddy field. In addition to the traits mentioned above, the numbers of differentiated (developed + degenerated) primary and secondary branches were measured. MR53 was outstandingly higher than the two commercial varieties in spikelet number per panicle, number of secondary branches per primary branch and number of differentiated secondary branches per primary branch. In each of these traits, MR79 was higher than the two commercial varieties, but lower than MR53 more or less. By number of differentiated secondary branches per primary branch, the spikelet twinning and the panicle opening in total, plants with the Ur1/Ur1 genotype could be selected in a segregating population like F_2 in a process of breeding by the use of Ur1, even if undulation is little or absent like in MR79.

Keywords : *rice, Ur1 gene, panicle, spikelet number, number of differentiated secondary branches.*

INTRODUCTION

Ur1 (Undulate Rachis -1), an incompletely dominant gene on chromosome 6 (Nagao *et al.* 1958 and 1963; Sato and Shinjyo 1991), being characterized by undulation of primary and secondary branches at the lowest part of a panicle (Fig.1), has the principal effect of increasing number of secondary branches per primary branch, viz. acceleration of secondary branching from primary branches, and additional effects of increasing both spikelet number per single secondary branch and number of primary branches per panicle (Murai and Iizawa 1994; Murai *et al.* 2012).

In addition to the panicle traits mentioned above, number of differentiated (developed + degenerated) secondary branches, pedicel length and other traits were investigated for an isogenic line of Taichung 65 carrying both *Ur1* and *sd1-d* (dee-geo-woo-gen dwarf), the *Ur1* isogenic line of 'Nishihikari', together with the *sd1-d* isogenic line of Taichung 65 and 'Nishihikari' (their respective genetic backgrounds) (Murai *et al.* 2012). Effect of *Ur1* on number of differentiated secondary branches per primary branch was higher than number of (developed) secondary branches per primary branch. They found twined spikelets at the tip of the uppermost primary branch of a panicle in the *Ur1/Ur1* genotype (Fig. 2), because *Ur1* shortened the pedicel length of the top spikelet but it elongated that of the second spikelet. This visual characteristic was recommended as one of indicators for the *Ur1/Ur1* genotype.

Murai *et al.* (2005) preliminarily reported that a *japonica Ur1*-carrying line Murai 79 (hereafter "MR79") had a higher yielding-ability exceeding the levels of ordinary *japonica* varieties in southern Japan; due to its higher sink size caused by more spikelets per panicle, which was derived from the cross of a Japanese commercial variety and an isogenic line of Taichung 65 carrying both *Ur1* and *sd1-d* (dee-geo-woo-gen dwarf). Another *Ur1*-carrying line "MR53" was developed from the same cross by Murai (Malangen *et al.* 2013). MR79 and MR53 possess extremely late and rather early heading times, respectively (Table 1). These two lines

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Fig. 1. Undulation of primary and secondary branches at the lowest part of a panicle in MR53 (*Ur1/Ur1*).

Fig. 2. Twinning of the top spikelet and next one in the uppermost primary branch of a panicle in an isogenic line of Taichung 65 carrying both *Ur1* and *sd1-d* (*Ur1/Ur1*).

Table 1. Fertilizer application levels and heading dates of the two *Ur1*-carrying lines and two commercial varieties.

Fertilizer level	Basal dressing (N [2] g/m^2)	Top dressing [1] (N [2] g/m^2)	80%-heading date in 2003			
			MR 53	MR79	Ni	Hi
High	8	8 [3]	July 29	Aug. 22	Aug. 13	Aug. 9
Middle	4	4 [3]	July 28	Aug. 22	Aug.13	Aug.9
Low	2	2 [3]	July 29	Aug. 22	Aug.13	Aug.9

1) A slow-release coated fertilizer (LONG ®, 100-day type presented from Chisso Asahi Fertilizer Co., Ltd.), about 7% of each element of which was readily available, was used.
2) P_2O_5 and K_2O elements were supplied at the same level as N element., an ordinary chemical fertilizer was used.
3) Applied on June 30 for MR53, July 27 for MR79, July 9 for Hi, July 14 for Ni in 2003.

and two commercial varieties were grown under various fertilizer levels in a paddy field of Kochi University in southern Japan in 2003 and 2005 in the previous study (Malangen *et al.* 2013). High yields of 728 and 723 g/m^2, respectively, were obtained by MR79 and MR53 through a heavy fertilizer application. Furthermore, MR79 was the highest-yielding in every combination of fertilizer levels and years, suggesting that MR79 involves a high yielding-ability stable to variation of fertilizer level.

In the present study, panicles of MR79, MR53 and the two commercial varieties grown at three fertilizer levels in 2003 (Malangen *et al* 2013) were used for measurements of above-mentioned panicle traits inclusive of number of differentiated secondary branches. On the basis of the data, we examine:

1) Which traits can classify the two *Ur1*- carrying lines from the two commercial varieties?

2) Whether the classification was influenced by fertilizer level or not?

3) Which differences were detected between MR79 and MR53? and

4) Combination of measurable trait(s) and visual characteristics enable gentypic determination at the *Ur1* locus in a segregating population like F_2?

MATERIALS AND METHODS

Ur1-carrying lines

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 for developing recombinant inbred lines with and without *Ur1* (Murai *et al.* 2005; Malangen *et al.* 2013). 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, and the generation was progressed to F_8 without selection in glasshouse condition. In 1999, the 108 F_9 lines originating from the respective 108 F_2 plants were grown in a paddy field; the two well-ripened lines carrying *Ur1*, viz. MR53 and MR79 were selected from *Ur1*-carrying lines by field observation. The uniformity (non-segregation) in MR53 and MR79 was confirmed from 2000 to 2003 (F_{10} to F_{14} generations).

Fig. 3. Panicles of MR53, MR79 and Hi ('Hinohikari'), from left to right. MR 53 and MR 79 carry *Ur1* gene (*Ur1/Ur1*).

Appearances in panicles of two *Ur1*-carrying lines

Fig. 3 exhibits matured panicles of MR53, MR79 and 'Hinohikari'. The undulation of primary and secondary rachis branches at the lowest part of panicles was noticed in MR53 (Fig. 1), whereas little or no undulation was observed in MR79. The panicles of the two *Ur1*-carriers, particularly MR53, were more open at maturity than the ordinary, being in agreement with the observation by Murai *et al*, (2002). Moreover, twined or semi-twined spikelets at the tip of the uppermost primary branch, which is caused by *Ur1* (Murai *et al.* 2012), were observed in at least one panicle within every hill of both MR 53 and MR 79 (Fig. 3). Such spikelets were more frequently observed in MR53 than in MR79. Accordingly, MR53 had typical panicle appearance of the *Ur1/Ur1* genotype. On the other hand, MR79 had many panicles which were hardly decided as *Ur1*–carrying from their appearances.

Commercial varieties for comparison to *Ur1*-carriers

'Nishihikari' and 'Hinohikari', (abbreviated as "Ni" and "Hi" respectively) were used for the field experiments. Ni is a short-culm and panicle-number type variety possessing the highest lodging tolerance in southern Japan (Nishiyama 1982). Hi is a leading variety in southern Japan, which possesses rather late heading, rather long culm and rather many panicles.

Cultivation and sampling

The two *Ur1*-carrying lines and the two commercial varieties were seeded on April 16 and transplanted on May 9 in 2003 to a paddy field of the faculty of Agriculture, Kochi University, Japan (Malangen *et al*, 2013). Two seedlings per hill were transplanted at a spacing of 30.0 × 15.0cm. They were grown under high, middle and low fertilizer levels (Table 1). The randomized block design with three replications was adopted for all combinations of the lines-varieties and fertilizer levels. Each plot comprised 108 hills (4 rows × 27 hills). The largest panicle in each of ten hills from each plot (a total of 30 panicles per line/variety at each fertilizer level from three replications) was used for the measurements of traits described below.

Panicle traits measured

Table 2 shows 12 panicle traits adopted in the present study. There is the following relationship between spikelet number per panicle and the four components (Murai and Kinoshita 1983; Murai and Iizawa 1994). NS = SB1 × NB1 + SB2 × NB2 × NB1 (NB2 × NB1 = number of secondary branches per panicle). Thus, spikelet number per panicle can be equated by NB1 (the number of primary branches), NB2 (the number of secondary branches per primary branch), SB1 (the number of spikelets per primary branch) and SB2 (the number of spikelets per secondary branch). Beside the numbers of developed primary and secondary branches, the numbers of degenerated primary and secondary branches were measured, being denoted by DNB1 and DB2, respectively. The number of differentiated primary branches (TNB1) is calculated by NB1 + DNB1. Similarly, TB2 is calculated by B2 + DB2. TNB2 equals TB2/NB1.

Table 2: List of panicle traits assessed in this study

Trait (abbreviation)	Explanation
1. No. of spikelets per panicle **(NS)**	Measured by the largest panicle in each hill.
2. No. of primary branches **(NBI)**	Ditto
3. No. of secondary branches **(B2)**	Ditto
4. No. of secondary branches per primary branch **(NB2)**	No. of secondary branches / No. of primary branches per panicle.
5. No. of spikelets per primary branch **(SB1)**	No. o f spikelets setting on primary branches / No. of primary branches.
6. No. of spikelets per secondary branch **(SB2)**	No. of spikelets setting on secondary branches / No. of secondary branches.
7. **SB2** %	Percentage of spikelet setting on secondary branches to No. of spikelets per panicle.
8. **DNB1**	No. of degenerated primary branches per panicle.
9. **DB2**	No. of degenerated secondary branches per panicle.
10. **TNB1**	Total number of differentiated primary branches = **NB1 + DNB1**
11. **TB2**	Total number of differentiated secondary branches = **B2 + DB2**
12. **TNB2**	Total number of differentiated secondary branches per primary branch = **TB2 /NB1**

Statistical analysis

Analysis of variance was conducted using EXCEL Toukei Version 5.0 (ESUMI Co., Ltd., Tokyo, Japan), and Least Significant Difference (LSD) was calculated from error variance.

RESULTS

Table 3 shows results of analysis of variance for the panicle traits of the two *Ur1*- carrying lines and two commercial varieties at the three fertilizer levels. For NS, the effects of the lines and the fertilizer levels were statistically significant whereas the interaction was not significant. This trait was in the order MR53 > MR79 > Hi ≧ (or >) Ni at each of the fertilizer levels (Table 4). At every fertilizer level, MR53 and MR79 were significantly higher than Hi and Ni. MR53 and MR79 were 34 to 43% and 23 to 37%, respectively, higher in NS than Hi in all fertilizer levels. There was non-significant or small difference between Ni and Hi. Ns of each line/variety increased with the enhancement of fertilizer level.

For NB1, the effects of the lines and the fertilizer levels were statistically significant but the interactive effect was not significant (Table 3). At every fertilizer level, MR79 was the highest among all lines-varieties in this trait, while Ni was the lowest. Differences between MR53 and Hi at the middle and low fertilizer levels were not statistically significant. Hence, the two *Ur1*-carriers were not distinctly classified from the two non-carriers by this trait. Every line/variety showed positive fertilizer response.

The effect of lines alone among the three factors was significant in B2. This trait was in the order MR53 > MR79 > Ni ≧ (or ≦) Hi at each of the fertilizer levels. The B2s of MR53 and MR79 were about twofold and about one and half of that of Hi, respectively, at every fertilizer level. Ni was not significantly different from Hi at every fertilizer level.

Regarding NB2, the effect of lines was significant, while those of fertilizer levels and the interaction were not significant. It was in the order

Table 3. Analysis of variance for all panicle traits of the two *Url*-carrying lines and two commercial varieties at the three fertilizer levels

	Source of Variation [1]			
Trait (Abbreviation)	**Lines (A)**	**Fertilizer levels (B)**	**Interaction (A X B)**	**All combinations of lines and fertilizer levels**
NS	186.69 ** [2]	10.95 ** [2]	1.02 [2]	53.46**[2]
NB1	52.31 **	6.58**	2.03	16.57**
B2	306.92 **	2.61	<1	84.48**
NB2	381.50 **	<1	<1	104.35**
SB1	278.10**	<1	<1	76.25**
SB2	58.54**	<1	<1	16.62**
SB2 %	97.59**	<1	2.24	27.96**
DNB1	4.41*	<1	<1	1.38
DB2	210.27**	6.93**	3.70*	60.62**
TNB1	50.01**	8.76**	2.54	16.62**
TB2	383.49**	7.06**	1.14	106.49**
TNB2	371.97**	<1	<1	102.01**

[1] Degrees of freedom for fertilizer levels, lines, interaction, all combinations of lines and fertilizer levels and error are 3,2,6,11 and 22, respectively.

[2] Numbers in the table indicate F-values.

*,** Significant at the 5% and 1% levels, respectively.

MR53 > MR79 > Ni ≧ (or >) Hi at every fertilizer level. MR53 and MR79 were 107 to 117% and 36 to 43%, respectively, higher in this trait than Hi in all fertilizer levels. Ni was not significantly different from Hi at middle and low fertilizer levels.

As for SB1, the effect of lines alone was significant. At every fertilizer level, it was in the order MR53 < MR79 < (or ≦) Ni ≦ Hi. According to Murai *et al* (1994 and 2012), *Ur1* accelerates secondary branching toward the tip of each primary branch, resulting in decrease of spikelets directly set on a primary branch. This may cause the lower SB1s in the two *Ur1*-carriers.

As for SB2, the effect of lines alone was significant. It was in the order MR53 > MR79 > (or ≧) Ni ≧ (or >) Hi at each of the fertilizer levels. Thus, the two *Ur1*-carriers were higher in SB2 than the two non-carriers.

Regarding SB2%, the effect of lines alone was significant. At every fertilizer level, it was in the order MR53 > MR79 > Ni ≧ (or >) Hi. Thus, the two *Ur1*-carriers were distinctly higher than the two non-carriers; particularly, MR53 was the highest.

Table 5 shows the panicle traits concerning degeneration and differentiation of branches (Table 2) in the two *Ur1*-carrying lines and two commercial varieties at the three fertilizer levels. For DNB1, the effect of lines alone was significant at the 5% level (Table 3). This trait ranged from 0.03 to 0.30 overall combinations of lines-varieties and fertilizer levels; no or at most one degenerated primary branch per panicle was observed in all measured panicles of all lines-varieties. MR79 had little more degenerated primary branches than the other three line-varieties at each fertilizer level.

Regarding DB2, the effects of lines, fertilizer levels and the interaction were all significant. It was in the order MR79 > MR53 > Hi > Ni at every fertilizer level. MR53 and MR79 were 35 to 74% and 105 to 140%, respectively, higher in this trait than Hi in all fertilizer levels. This trait was higher at the high fertilizer level than at the low fertilizer level in both MR53 and MR79, but

Ni and Hi showed no significant fertilizer responses.

The result in TNB1 was similar to that in NB1 (Table 4), since every measured panicle had no or at most one degenerated primary branch.

Regarding TB2, the effects of the lines and the fertilizer levels were significant but the interactive effect was not significant. It was in the order MR53 > (or ≧) MR79 > Hi ≧ (or >) Ni at every fertilizer level. MR53 and MR79 were 91 to 109% and 75 to 81%, respectively, higher in this trait than Hi in all fertilizer levels. Significant and non-significant positive fertilizer responses were detected in the two *Ur-1* carriers and the two non-carriers, respectively.

The effect of lines alone was significant in TNB2. This trait was in the order MR53 > MR79 > Hi ≧ (or >) Ni at every fertilizer level. MR53 and MR79 were about twofold and about one and half of Hi, respectively, in this trait at every fertilizer level. There was non-significant or small difference between Ni and Hi at each of the fertilizer levels.

DISCUSSION

Regarding NB1, MR53 was similar to or lower than Hi; on the other hand, MR79 was higher than the two non-carriers (Table 4). According to Murai *et al.* (2012), *Ur1* increased NS by 38 and 35%, NB1 by 13 and 5%, NB2 by 45 and 58% and SB2 by 10 and 20%, but it decreased SB1 by 5 and 18%, respectively, on the genetic background of Ni and that of Taichung 65 with *sd1-d*. Thus, *Ur1* increased NB1 more on the former genetic background than on the latter genetic background. It is assumed that gene(s) accelerating primary branching in the cooperation with *Ur1* inherited from Ni to MR79 in the process of development.

MR53 was outstandingly higher than the two non-carriers in NS, NB2, SB2 and B2%, as well as TB2 and TNB2. In each of these traits, MR79 was higher than the two non-carriers, but

Table 4: No. of spikelets per panicle, its components and other traits of the two *Url*-carrying lines and two commercial varieties at the three fertilizer levels.

Trait	Fertilizer level	MR53	MR79	Ni	Hi	LSD(5%)
NS	High	134.7 a (134)[1)]	123.9 bc (123)[1)]	92.0 e (91)[1)]	100.6 d	7.5
	Middle	129.9 ab (143)	122.1 c (134)	88.7 e (97)	91.0 e	
	Low	122.9 bc (141)	120.1 c (137)	87.0 e (99)	87.4 e	
NB1	High	10.37 c (93)	11.90 a (107)	9.53 d (86)	11.10 b	0.65
	Middle	10.27 c (103)	11.50 ab (115)	9.53 d (95)	10.00 cc	
	Low	9.77 cd (102)	11.53 ab (121)	9.47 d (99)	9.53 d	
B2	High	29.86 a (205)	21.57 b (148)	14.33 c (98)	14.60 c	2.15
	Middle	29.50 a (225)	21.87 b (166)	13.70 c (104)	13.13 c	
	Low	27.90 a (216)	21.63 b (167)	13.17 c (102)	12.93 c	
NB2	High	2.87 a (217)	1.81 b (137)	1.51 c (114)	1.32 d	0.18
	Middle	2.87 a (217)	1.90 b (143)	1.45 cd (110)	1.32 d	
	Low	2.86 a (207)	1.88 b (136)	1.40 cd (101)	1.38 d	
SB1	High	3.84 d (67)	5.40 bc (94)	5.61 ab (98)	5.74 a	0.27
	Middle	3.76 d (66)	5.25 c (91)	5.58 ab (97)	5.74 a	
	Low	3.87 d (67)	5.18 c (90)	5.53 ab (96)	5.78 a	
SB2	High	3.18 a (126)	2.76 bc (110)	2.69 bcd (107)	2.51 c	0.16
	Middle	3.08 a (119)	2.82 b (109)	2.59 dc (100)	2.59 dc	
	Low	3.04 a (122)	2.81 b (112)	2.63 cde (105)	2.49 c	
SB2%	High	70.0 a (193)	47.8 b (132)	41.8 c (115)	36.4 d	4.0
	Middle	69.9 a (188)	50.7 b (137)	39.9 cd (108)	37.0 d	
	Low	68.8 a (188)	50.7 b (139)	39.7 cd (108)	36.6 d	

[1)] Percentage to Hi in parentheses

Values followed by the same letter within each trait are not significantly different at the 5% LSD level.

Table 5: Traits concerning degeneration and differentiation of primary and secondary branches of the two *Url*-carrying lines and two commercial varieties at the three fertilizer levels.

Trait (abbreviation)	Fertilizer Levels	MR53	MR79	Ni	Hi	LSD (5%)
DNB1	High	0.03 b (50)[1]	0.30 a (450)[1]	0.03 b (50)[1]	0.07 ab	0.24
	Middle	0.10 ab (100)	0.23 ab (233)	0.03 b (33)	0.10 ab	
	Low	0.17 ab (125)	0.27 ab (200)	0.03 b (25)	0.13 ab	
DB2	High	9.83 c (159)	14.90 a (240)	2.70 f (44)	6.20 e	1.49
	Middle	9.83 c (174)	12.13 b (214)	3.13 f (55)	5.67 e	
	Low	7.70 d (135)	11.70 b (205)	3.17 f (56)	5.70 e	
TNB1	High	10.40 c (93)	12.12 a (109)	9.53 e (85)	11.17 b	0.71
	Middle	10.37 cd (103)	11.73 ab (116)	9.53 e (94)	10.10 cde	
	Low	9.93 cde (103)	11.77 ab (122)	9.50 e (98)	9.67 de	
TB2	High	39.70 a (191)	36.47 b (175)	17.03 e (82)	20.80 d	2.78
	Middle	39.33 a (209)	34.00 bc (181)	16.83 e (89)	18.80 de	
	Low	35.60 bc (191)	33.33 c (179)	16.33 e (88)	18.63 de	
TNB2	High	3.83 a (203)	3.06 b (162)	1.80 cd (95)	1.88 cd	0.25
	Middle	3.83 a (203)	2.96 b (156)	1.78 cd (94)	1.89 cd	
	Low	3.65 a (183)	2.90 b (145)	1.73 d (87)	1.99 c	

[1] Percentage to Hi in parentheses

Values followed by the same letter within each trait are not significantly different at the 5% level, determined by LSDs in the table.

lower than MR53 more or less. Yamagishi *et al.* (2002) found a QTL controlling number of secondary branches per panicle in a genetic difference between two ordinary Japanese varieties; even though its effect seems to be smaller than that of the major gene *Ur1*. It is inferred that allele(s) with minus-direction effect(s) at such QTL(s) diminished these traits in MR79, resulting in its less typical panicles compared with those of MR53.

MR53 had its typical panicle appearance caused by *Ur1*, while MR79 had panicles which cannot be distinguished distinctly from those of non-carriers (see Materials and Methods, Fig. 2). TB2, including degenerated secondary branches, can divide MR79 from the two non-carriers more distantly than B2 (Table 4 and Table 5). Similarly, TNB2 can divide the former from the latter more distantly than NB2. Besides, any lines-varieties did not show significant fertilizer response in this trait, suggesting that TNB2 can be an indicator for the *Ur1/Ur1* genotype stable to variation of fertilizer level. In a field observation, easier measurement than TNB2 would be needed; more conveniently, number of differentiated secondary branches per primary branch could be measured by the longest two or three primary branches in the largest panicle of a plant. Accordingly, number of differentiated secondary branches per primary branch could be a prospective tool to select high-yielding segregants of the *Ur1/Ur1* genotype like MR79 in a process of breeding by the use of *Ur1*. By this trait, and the spikelet twinning and the panicle opening in total, genotype of a plant or a line could be estimated to select those with the *Ur1/Ur1* genotype (Murai *et al.*, 2012), even if undulation is little or absent like MR79.

ACKNOWLEDGEMENTS

We are indebted to Mr. Y. Takemura and Mr. M. Urabe, Kochi University for their cooperation in carrying out the experiments.

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