Effects of a Major Gene *Ur1* Characterized by Undulation of Rachis Branches on Yield and its Related Traits in Rice

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An incompletely dominant gene *Ur1* is characterized by undulation of primary and secondary rachis branches. The gene increases spikelet number per panicle owing to increase of secondary branches. The *Ur1/Ur1*, *Ur1/+* and *+/+* genotypes with *sd1* (denoted by u, h and d, respectively, viz. three dwarfs) and those without *sd1* (U, H and T, respectively, viz. three tall) were produced under the common genetic background of a *japonica* variety Taichung 65. The six genotypes were grown in 2000. Yield and its related traits were measured. Analysis of variance on yield indicated that the effect of *Ur1* was significant whereas the effects of *sd1* and the *Ur1* × *sd1* interaction were nonsignificant. Genotypes u and h had significantly higher yields than d; h showed the highest yield of all genotypes. The three tall had yields in the order of H ≥ U ≥ T (H > T). Regarding spikelet number per panicle, the genotypes were in the order of u = U > h ≥ H > T > d, reflecting the principal effect of *Ur1*. Regarding panicle number per m², the effect of *Ur1* was not significant. The ripened-grain percentages of the six genotypes were almost in the reverse order of spikelet number per panicle. The 1000 grain weight of the genotypes was in the order of U ≈ u ≤ h ≤ H ≤ d < T. Sink size-2 (single grain weight × fertilized-spikelet number per m²) showed a high positive correlation with yield. As for LAI, there were no significant differences among the six genotypes. The total weight per m² at maturity for the three dwarf genotypes were in the order of h ≥ u ≥ d (h > d). As for harvest index, u and h were higher than d. Similar results were obtained for the three dwarf genotypes under three fertilizer levels in 1998. Thus, *Ur1* enlarged sink size through increase of spikelet number per m² resulting in higher yield. Consequently, *Ur1* may be utilized for developing high yielding inbred varieties and F₁ varieties at the *Ur1/+* genotype.

Key Words: *Oryza sativa*, *Ur1*, *sd1*, spikelet number per panicle, yield, sink size, harvest index.

Introduction

The first-released *indica* semidwarf variety IR8 carrying *sd1* (dee-geo-woo-gen dwarf) and its descendants developed at the International Rice Research Institute and in Korea such as IR24 and 'Milyang 23' possess larger panicles and higher yielding abilities with large spikelet numbers per m² than ordinary Japanese varieties (De Datta *et al.* 1968, Osada *et al.* 1973, Sun *et al.* 1979, Komatsu *et al.* 1983, Sugimoto 1983, Saito *et al.* 1990, Peng *et al.* 1999 and 2000), although *sd1* itself and its allele(s) have a pleiotropic effect of decreasing spikelet number per panicle (Murai *et al.* 1982, 1995 and 2002, Murai and Kinoshita 1983, Murai 1999, and Murai and Yamamoto 2001). However, it is not easy to introduce genes with increasing effects on spikelet number per panicle from an *indica* variety into Japanese *japonica* varieties, since the hybrid sterility and hybrid lethality between *indica* and *japonica* cause reproductive isolation (Kato *et al.* 1928, Terao and Midushima 1939, Oka 1954 and 1957, Oka and Doida 1962). So, if a major gene known to increase spikelet number per panicle can enlarge sink size per unit area and is contained in a *japonica* variety or line, we could utilize it for developing high yielding *japonica* varieties.

Ur1 (Undulate rachis-1) is a incompletely dominant gene of rice, being characterized by undulation of primary and secondary rachis branches (Nagao *et al.* 1958). In addition, primary branches of the panicles at the *Ur1/Ur1* genotype are more open at maturity than the ordinary (observation by one of us, Murai). Moreover, *Ur1* increases not only the number of secondary branches per panicle but also spikelet number per secondary branch, resulting in a large spikelet number per panicle; nevertheless, *Ur1* decreases both spikelet fertility and 1000 kernel weight, and large panicles facilitate lodging (Murai and Iizawa 1994, Murai 1999).

A preliminary experiment suggested that *Ur1* can increase grain yield by enlarging spikelet number per m² under the genetic background of a *japonica* variety, 'Taichung 65' (Murai *et al.* 1997). In the present study, the *Ur1/Ur1*, *Ur1/+* and *+/+* genotypes with *sd1* (three dwarfs) and those without *sd1* (three tall) were prepared under the common genetic background of 'Taichung 65'. Besides yield and its components, percentage of unfertilized spikelets, sink size, harvest index, leaf area and other traits were measured for the six genotypes in one year. The three genotypes with *sd1* were grown under three fertilizer levels in another year.

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Thus, the effects of *Ur1* on various traits, with and without *sd1*, were investigated. Relations between yield and its related traits were examined, in order to clarify how *Ur1* increase yield. On the basis of the results, we discuss the possibility of producing inbred varieties carrying *Ur1* and *F₁* varieties at the *Ur1/+* genotype.

Materials and Methods

Taichung 65 (abbreviated as “T”) is a tall Taiwanese *japonica* cultivar. T was the common recurrent parent of all the isogenic lines described below. An isogenic line carrying *Ur1*, which was developed after eight backcrosses with T (Sato and Shinjyo 1991), was crossed with T again, and a *Ur1-B₉* isogenic line (abbreviated as “U”) was selected from the progeny lines. The *F₁* between T and U was denoted by “H”, which possessed the *Ur1/+* genotype. An isogenic line for *sd1* originating from ‘Dee-geo-woo-gen’, which was developed after ten backcrosses with T (Murai *et al.* 1995, 2002), was abbreviated as “d” in the present study. Murai *et al.* (1997) used another isogenic line carrying both *Ur1* and *sd1* which was derived from a plant in the *F₂* population of a cross between an *sd1-B₁₀* isogenic line and a *Ur1-B₈* isogenic line. This line was crossed with T in order to add one backcross, and a progeny line at the *Ur1/Ur1 sd1/sd1* genotype (“u”) was selected. The *F₁* between d and u provided the *Ur1/+ sd1/sd1* genotype, being denoted by “h”.

In 2000, 26-day-old seedlings of u, h, d, U, H and T were transplanted to a paddy field of the Faculty of Agriculture, Kochi University, Japan with two seedlings per hill at a spacing of 30.0 × 15.0 cm (22.2 hills per m²), on June 1. A single fertilizer level with three replications was adopted, using the randomized blocks design (Table 1). In 1998, the three dwarf genotypes with *sd1*, viz. u, h and d, were grown at three fertilizer levels (Table 1). On June 11 in 1998, 24-day-old seedlings of the three genotypes were transplanted to a paddy field of the faculty with the same planting density as in 2000. In 1998, we adopted the split-plot design to the

experimental field, applying the main-plot and sub-plot to the fertilizer levels and the genotypes, respectively. In both years, each plot comprised 132 hills (33 hills × 4 rows), and samplings described below were conducted for the central two rows except for the first three and last three hills in each row. The 80%-heading stages of the three genotypes in both years are shown in Table 1. Some hills of U and H started bending at the middle stage of ripening, and all hills over the three replications in the two genotypes lodged or bended completely to the ground at maturity in 2000.

In both years, all panicles of about 30 hills were sampled from each plot at maturity, and panicle weight of each hill was checked after cutting just at their panicle bases and air drying. Out of seven hills randomly selected from 30 hills of each plot, five hills having intermediate panicle weights were selected. The panicles in the five hills were threshed, and all spikelets in each hill were counted. Each spikelet was examined for endosperm development by handling with fingers or by opening hulls; a spikelet containing no developed endosperm was regarded as unfertilized in the present study. This trait was not measured in 1998. Grains after hulling (hereafter “grain”) were sieved at 1.7 mm to select ripened grains by thickness. All ripened grains in each of the five hills were counted, and were weighed. Percentage of ripened-grain weight to panicle weight in the five selected hills of each plot was calculated; then, ripened-grain weight (yield) of 30 hills of each plot was estimated from this percentage. The moisture content (%) of ripened grains of each plot was measured; and yield at 15% moisture was estimated and used in the present study.

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

Table 1. Fertilizer applications for the experiments in 2000 and 1998, and heading stages of the six genotypes

Year	Fertilizer level	Basal dressing (N ²) g/m ²)	Top dressing ¹⁾ (N ²) g/m ²)	80%-heading stage (date in August)					
				u	h	d	U	H	T
2000 ³⁾	Middle	4.8	3.2 ⁵⁾	13	13	11	13	10	9
1998 ⁴⁾	High	7.2	4.8 ⁶⁾	19	18	18	—	—	—
	Middle	4.8	3.2 ⁶⁾	19	18	18	—	—	—
	Low	2.4	1.6 ⁶⁾	18	18	18	—	—	—

u, h, d, U, H and T (Taichung 65): see text.

¹⁾ A slow-release coated fertilizer (NUTRICOTE®, presented from Chisso Asahi Fertilizer Co., Ltd.), about 3% of each element of which was readily available, was used.

²⁾ P₂O₅ and K₂O elements were supplied at the same level as N element.

³⁾ Date of transplanting: June 1.

⁴⁾ Date of transplanting: June 11.

⁵⁾ Applied on July 14.

⁶⁾ Applied on July 23.

Results

Effects of *Ur1* with and without *sd1*

Table 2 shows results of analysis of variance for yield and other traits of u, h, d, U, H and T in 2000: we investigated the effect of the six genotypes on each trait by the one-factor analysis, and the genic effects of *Ur1* and *sd1* on each trait by the two-factor analysis. As for yield, the effect of *Ur1* was significant whereas the effects of *sd1* and the *Ur1* × *sd1* interaction were nonsignificant. Table 3 shows the yield, yield components and other traits of the six genotypes in 2000. Genotypes u and h had significantly higher yields than d; h showed the highest yield of the six genotypes. H had a significantly higher yield than T, and U had an intermediate yield between those of H and T. Besides, the yields of u and h were higher than those of the corresponding tall genotypes, U and H, whereas the yield of d was lower than that of T; nevertheless, these differences were nonsignificant.

The spikelet number per panicle was in the order of $u > h \geq H > T > d$, reflecting the principal effect of *Ur1*. The effect of *sd1* was not significant: u and h were equal or similar to U and H, respectively, but d was significantly smaller than T.

As for panicle number per m^2 , the effect of *sd1* was significant: u and d showed significantly larger values than the corresponding tall genotypes, U and T, although h and H had

the same value. On the other hand, the effect of *Ur1* was not significant.

The ripened-grain percentage of the three dwarf and three tall genotypes was in the order of $u < h < d$ and $U \leq H < T$, respectively, which was consistent with the significant effect of *Ur1*. The effects of *sd1* and the interaction were significant: in fact, h and d had significantly higher values than H and T, respectively, although u and U had similar values.

Fertilized-spikelet percentage was highly significantly correlated with the ripened-grain percentage in all six genotypes ($r=0.972$); the former trait was 3.2 to 6.2% lower than the latter trait in each genotype. Moreover, the percentage of ripened grains to fertilized spikelets, excluding unfertilized spikelets, was calculated for the six genotypes. There were no significant differences in this trait among all genotypes except U. The range of this trait in the six genotypes (3.9%) was narrower than that of fertilized-spikelet percentage (10.5%). Hence, the variation in ripened-grain percentage was due to unfertilization rather than insufficient grain filling.

The 1000 grain weight of the three dwarf genotypes was in the order of $u \leq h < d$; similarly, the three tall genotypes were in the order of $U < H < T$. U and H were similar to u and h, respectively, although T was significantly larger than d.

The spikelet number per m^2 of the genotypes was in the order of $u > U \geq h \geq H > T \geq d$ (Table 3); in fact, the effect

Table 2. Analysis of variance for yield and other traits of u, h, d, U, H and T (Taichung 65) in 2000

Trait	Source of Variation ¹⁾			
	Genotypes ²⁾	<i>Ur1</i>	<i>sd1</i>	<i>Ur1</i> × <i>sd1</i>
Yield (g/m ²)	5.35* ⁶⁾	11.35** ⁶⁾	1.40 ⁶⁾	1.33 ⁶⁾
Spikelets/panicle	50.71**	122.93**	1.73	2.99
Panicles/m ²	3.31	2.87	7.11*	1.87
Ripened grains (%)	23.03**	47.11**	9.87*	5.53*
Fertilized spikelets (%)	32.79**	67.55**	3.06	12.90**
Percentage of ripened grains ³⁾	3.72*	4.43*	8.04*	<1
1000 grain weight (g)	20.53**	39.25**	10.95*	6.60*
Spikelets/m ² (× 100)	34.86**	84.30**	<1	2.40
Sink size-1 ⁴⁾ (g/m ²)	22.74**	50.61**	<1	6.21*
Sink size-2 ⁵⁾ (g/m ²)	6.64**	14.66**	<1	1.92
LAI at 80% heading	<1	1.38	<1	<1
Leaf weight at 80% heading (g/m ²)	<1	<1	<1	<1
LAI at maturity	6.70**	15.20**	<1	1.35
Total weight at 80% heading (g/m ²)	<1	1.06	<1	<1
Total weight at maturity (g/m ²)	14.56**	6.84*	58.00**	<1
Harvest index (%)	7.39**	2.77	30.45**	<1
Culm length (cm)	628.66**	183.66**	2772.14**	1.92
Panicle length (cm)	63.69**	25.44**	254.26**	6.66*

¹⁾ Degrees of freedom for genotypes, *Ur1*, *sd1*, the *Ur1* × *sd1* interaction, blocks and error are 5, 2, 1, 2, 2 and 10, respectively.

²⁾ All of the six genotypes.

³⁾ To fertilized spikelets, excluding unfertilized spikelets.

⁴⁾ Single grain weight × spikelets/m².

⁵⁾ Single grain weight × fertilized spikelets/m².

⁶⁾ Numerals in the table indicate F-values.

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

Table 3. Yield and other traits of u, h, d, U, H and T (Taichung 65) in 2000

Trait	u	h	d	U	H	T	LSD _(5%)
Yield (g/m ²)	604 ^{ab}	619 ^a	546 ^c	577 ^{bc}	599 ^{ab}	557 ^c	39
Spikelets/panicle	115.5 ^a	108.8 ^b	83.6 ^d	115.5 ^a	107.5 ^b	91.1 ^c	5.9
Panicles/m ²	314 ^{ab}	312 ^{abc}	327 ^a	297 ^c	312 ^{abc}	309 ^{bc}	16
Ripened grains (%)	74.8 ^d	80.9 ^b	86.3 ^a	75.7 ^{cd}	77.9 ^c	81.5 ^b	2.8
Fertilized spikelets (%)	79.0 ^d	84.5 ^b	89.5 ^a	81.9 ^c	81.8 ^c	86.4 ^b	2.1
Percentage of ripened grains ¹⁾	94.7 ^a	95.8 ^a	96.4 ^a	92.5 ^b	95.2 ^a	94.3 ^{ab}	2.2
1000 grain weight (g)	22.3 ^d	22.5 ^{cd}	23.2 ^b	22.2 ^d	22.9 ^{bc}	24.3 ^a	0.5
Spikelets/m ² (× 100)	362 ^a	339 ^b	273 ^c	343 ^b	336 ^b	281 ^c	19
Sink size-1 ²⁾ (g/m ²)	807 ^a	765 ^{ab}	633 ^d	762 ^b	769 ^{ab}	684 ^c	43
Sink size-2 ³⁾ (g/m ²)	637 ^a	646 ^a	566 ^c	624 ^{ab}	629 ^a	591 ^{bc}	38
LAI at 80% heading	4.0 ^a	4.1 ^a	4.4 ^a	4.3 ^a	4.0 ^a	4.4 ^a	0.7
Leaf weight at 80% heading (g/m ²)	204 ^a	201 ^a	213 ^a	212 ^a	201 ^a	213 ^a	29
LAI at maturity	2.0 ^c	2.2 ^c	3.0 ^a	2.3 ^c	2.4 ^{bc}	2.8 ^{ab}	0.5
Total weight at 80% heading (g/m ²)	1002 ^a	1002 ^a	944 ^a	1042 ^a	1026 ^a	978 ^a	138
Total weight at maturity (g/m ²)	1357 ^{de}	1394 ^{cd}	1311 ^e	1497 ^{ab}	1531 ^a	1448 ^{bc}	67
Harvest index (%)	37.8 ^a	37.7 ^a	35.3 ^{ab}	32.7 ^b	33.2 ^b	32.7 ^b	2.7
Culm length ⁴⁾ (cm)	78.6 ^c	78.9 ^c	67.0 ^d	113.5 ^a	113.7 ^a	99.2 ^b	2.5
Panicle length ⁴⁾ (cm)	19.4 ^d	20.5 ^c	19.0 ^d	22.1 ^a	22.0 ^a	21.2 ^b	0.5

¹⁾ To fertilized spikelets, excluding unfertilized spikelets.

²⁾ Single grain weight × spikelets/m².

³⁾ Single grain weight × fertilized spikelets/m².

⁴⁾ Measured for the longest culm of each hill at maturity.

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

Table 4. Analysis of variance of the split-plot experiment applying the fertilizer levels and the three dwarf genotypes (u, h and d) to main- and sub-plots, respectively, for yield and other traits in 1998

Trait	Source of Variation ¹⁾		
	Fertilizer levels	Genotypes	Interaction (F. × G.)
Yield	8.82 ^{*3)}	117.38 ^{**3)}	1.08 ³⁾
Spikelets/panicle	2.78	745.02 ^{**}	3.51 [*]
Panicles/m ²	10.80 [*]	< 1	1.26
Ripened grains (%)	7.54 [*]	215.96 ^{**}	8.83 ^{**}
1000 grain weight (g)	4.29	2.07	1.42
Spikelets/m ² (× 100)	6.19	136.73 ^{**}	1.09
Sink size-1 ²⁾ (g/m ²)	7.39 [*]	142.76 ^{**}	1.09
Total weight at 80% heading (g/m ²)	15.70 [*]	3.09	1.17
Total weight at maturity (g/m ²)	10.39 ^{**}	15.46 ^{**}	< 1
Harvest index (%)	3.16	113.65 ^{**}	2.30
Culm length (cm)	39.19 ^{**}	708.51 ^{**}	< 1

¹⁾ Degrees of freedom for fertilizer levels (main-plot), genotypes (sub-plot), the interaction, blocks, main-plot error and sub-plot error are 2, 2, 4, 2, 4 and 12, respectively.

²⁾ Single grain weight × spikelets/m².

³⁾ Numerals in the table indicate F-values.

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

of *Ur1* was significant (Table 2). This trait was highly significantly correlated with spikelet number per panicle ($r = 0.978$). Sink size-1 (single grain weight × spikelet number per m²) was highly significantly correlated with spikelet number per m² ($r = 0.979$). Furthermore, sink size-2 (single grain weight × fertilized-spikelet number per m²) was used in the present study to estimate sink capacity more exactly than sink size-1. Sink size-2 showed a higher correlation with yield ($r = 0.957$, significant at the 1% level) than sink size-1 did ($r = 0.873$, significant at the 5% level). The sink size-2 of

the genotypes was in the order of $h \geq u \geq H \geq U > T \geq d$; thus, h had the largest value. However, u had the largest sink size-1.

At the 80%-heading stage, there were no significant differences in either LAI (Leaf Area Index) and leaf weight per m² among the six genotypes (Table 2 and Table 3). At maturity, however, u and h had significantly smaller values than d in both traits; similarly, the three tall genotypes were in the order of $U \leq H < T$.

There were no significant differences in total weight per m² at the 80%-heading stage among the six genotypes,

Table 5. Yield and other traits of the three dwarf genotypes at the three fertilizer levels in 1998

Trait	Fertilizer level	u	h	d	LSD _(5%) ¹⁾
Yield (g/m ²)	High	614 ^a (117) ⁴⁾	632 ^a (120) ⁵⁾	525 ^b	29
	Middle	593 ^a (121)	581 ^a (119)	490 ^b	
	Low	567 ^a (126)	561 ^a (125)	449 ^b	
Spikelets/panicle	High	132.9 ^a	125.0 ^b	94.2 ^c	3.7
	Middle	129.2 ^a	124.5 ^b	94.8 ^c	
	Low	127.5 ^a	116.8 ^b	93.1 ^c	
Panicles/m ²	High	275 ^a	288 ^a	284 ^a	18
	Middle	263 ^a	253 ^a	260 ^a	
	Low	244 ^a	253 ^a	244 ^a	
Ripened grains (%)	High	74.4 ^c	79.2 ^b	88.4 ^a	2.0
	Middle	78.4 ^c	82.6 ^b	89.2 ^a	
	Low	82.2 ^c	86.7 ^b	89.6 ^a	
1000 grain weight (g)	High	22.6 ^a	22.2 ^b	22.2 ^b	0.4
	Middle	22.3 ^a	22.4 ^a	22.3 ^a	
	Low	22.1 ^b	22.6 ^a	22.1 ^b	
Spikelets/m ² (× 100)	High	366 ^a	360 ^a	268 ^b	22
	Middle	340 ^a	315 ^b	247 ^c	
	Low	312 ^a	295 ^a	227 ^b	
Sink size-1 ²⁾ (g/m ²)	High	828 ^a	799 ^a	594 ^b	50
	Middle	756 ^a	704 ^a	550 ^c	
	Low	690 ^a	647 ^{ab}	501 ^b	
Total weight at 80% heading (g/m ²)	High	924 ^{ab}	1008 ^a	896 ^b	93
	Middle	897 ^a	866 ^a	857 ^a	
	Low	819 ^a	872 ^a	811 ^a	
Total weight at maturity (g/m ²)	High	1375 ^{ab}	1449 ^a	1321 ^b	75
	Middle	1318 ^a	1330 ^a	1227 ^b	
	Low	1233 ^{ab}	1254 ^a	1159 ^b	
Harvest index (%)	High	38.0 ^a	37.1 ^a	33.8 ^b	1.3
	Middle	38.2 ^a	37.2 ^a	34.0 ^b	
	Low	39.1 ^a	38.0 ^a	32.9 ^b	
Culm length ³⁾ (cm)	High	81.6 ^a	80.9 ^a	67.1 ^b	1.6
	Middle	80.9 ^a	80.1 ^a	66.4 ^b	
	Low	78.6 ^a	79.2 ^a	64.9 ^b	

¹⁾ Calculated from sub-plot errors of the analysis of variance in 1998 (Table 4).

²⁾ Single grain weight × spikelets/m².

³⁾ Measured for the longest culm of each hill at maturity.

⁴⁾ u/d (%).

⁵⁾ h/d (%).

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

although d and T tended to have smaller values than the other four genotypes (Table 2 and Table 3). Regarding total weight per m² at maturity, the effects of *Ur1* and *sd1* were significant although the interaction was not significant: the

three dwarf and three tall genotypes were in the order of $h \geq u \geq d$ ($h > d$), and $H \geq U \geq T$ ($H > T$), respectively. Each dwarf genotype was smaller than the corresponding tall genotype. As for harvest index, u and h were significantly higher than

(1) u.

(2) h.

Fig. 1. Percentages of the yield and its components of u or h to those of d in 2000 and at the high fertilizer level in 1998.

—2000. ---1998.

*, ** Difference between u or h and d was significant at the 5 and 1% levels, respectively.

U and H, respectively, whereas difference between d and T was not significant. Moreover, u and h were higher than d although not significantly.

Regarding culm length, the effect of *Ur1* as well as *sd1* was highly significant (Table 2). Both U and H had culm lengths at about 114 cm, being about 14 cm longer than that of T (Table 3). Culm lengths of both u and h (about 79 cm) were about 12 cm longer than that of d. The panicle length was in the order of $H \geq U > T > h > u > d$; these differences were smaller than those in culm length.

Effects of *Ur1* under different fertilizer levels

Table 4 shows results of analysis of variance for data of u, h and d grown at the high, middle and low fertilizer levels in 1998. As for yield, the effects of genotype and fertilizer level were significant whereas the interaction between them was not significant. The yield in all three genotypes increased with the enhancement of fertilizer level (Table 5). At each fertilizer level, the yields of u and h were significantly higher than that of d, and difference between u and h was not significant. The yield of h at the high fertilizer level was the highest in 1998.

The spikelet number per panicle was in the order of $u > h > d$ at all fertilizer levels. The effect of fertilizer level on this trait was not significant but the interaction was significant (Table 4): u and h showed consistent increases with the enhancement of fertilizer level whereas d showed almost no fertilizer response.

There were no significant differences in panicle number per m^2 among the three dwarf genotypes at each fertilizer level; and each genotype showed a positive fertilizer response.

The ripened-grain percentage was in the order of $u < h < d$ at each of the fertilizer level. In this trait, the values of u and h decreased consistently with the enhancement of fertilizer level whereas d showed little or no fertilizer response, being in accordance with the significant effects of fertilizer level and the interaction.

As for 1000 grain weight, the effects of genotype, fertilizer level and the interaction were nonsignificant.

The spikelet number per m^2 and sink size-1 were both in the order of $u > h > d$ at each fertilizer level; the three genotypes showed similar positive responses to fertilizer level (Table 4 and Table 5).

The effect of fertilizer level on total weight at the 80%-heading was significant but the effect of genotype was not significant (Table 4). The total weight at maturity, the genotypes were in the order of $h > u > d$ at each fertilizer level, although the differences between h and u were nonsignificant. The genotypes showed similar positive fertilizer responses (Table 4 and Table 5). As for harvest index, u and h were significantly higher than d at all fertilizer levels, and there were no significant differences between u and h. The effect of fertilizer level was not significant.

At all fertilizer levels, u and h had similar culm lengths which were about 14 cm longer than that of d (Table 4 and Table 5). Each genotype showed a positive fertilizer response.

Relations between yield and yield components

Yields of u and h exceeded $600 g/m^2$ in the experiment in 2000 and at the high fertilizer level in 1998 (Table 3 and Table 5). The percentages of yield and yield components of u or h to those of d were calculated from the data under the two growing conditions, in order to investigate how *Ur1* increased yield at the homozygous and heterozygous genotypes. As illustrated in Fig. 1-(1), the yield of u was 111 and 117% of that of d in 2000 and 1998, respectively. The spikelet number per panicle in u was 38 and 41% larger than that

in d in 2000 and 1998, respectively. The panicle number per m² in u was 96 and 97% of that in d in 2000 and 1998, respectively. The ripened-grain percentage of u was 13 and 16% lower than that of d in 2000 and 1998, respectively. The 1000 grain weight of u was 96 and 102% of that of d in 2000 and 1998, respectively.

As shown in Fig. 1-(2), h had a 13 and 20% higher yield than d in 2000 and 1998, respectively. The spikelet number per panicle in h was 30 and 33% larger than that in d in 2000 and 1998, respectively. The panicle number per m² in h was 95 and 101% of that in d in 2000 and 1998, respectively. In 2000 and 1998, respectively, the ripened-grain percentage of h was 94 and 90% of that of d, and the 1000 grain weight of h was 97 and 100% of that of d.

To sum up, h and u had higher yields than d owing to their larger spikelet numbers per panicle, even though they had lower ripened-grain percentages than d.

Discussion

Percentage calculation for data in both years (Table 3 and Table 5) shows that *Ur1* increased spikelet number per panicle with *sd1* by 36 to 41% and 25 to 33%, respectively, at the homozygous and heterozygous genotypes, whereas *Ur1* increased it without *sd1* by 27 and 18%, respectively. Thus, the percentage increases at the *Ur1/Ur1* or *Ur1/+* genotype with *sd1* were larger than that without *sd1*; although the *Ur1* × *sd1* interaction was not significant (Table 2). Accordingly, the effect of *Ur1* on this trait may be enhanced with *sd1*. On the other side, d was significantly smaller than T, indicating that *sd1* reduces spikelet number per panicle, which is consistent with the reports by Murai *et al.* (1982, 1995 and 2002), Murai and Kinoshita (1983), Murai (1999), and Murai and Yamamoto (2001). This effect of *sd1* caused decrease of yield under the genetic backgrounds of T and another variety, ‘Shiokari’ (Murai *et al.* 2002). However, the spikelet number per panicle in u and h was similar to or rather larger than that in U and H, respectively, as if *Ur1* completely compensated the decreasing effect of *sd1*. Furthermore, the spikelet number per m² in u was significantly larger than that in U, resulting in the rather higher yield of u than that of U (Table 3). Thus, *Ur1* may produce a larger number of spikelets per unit area with *sd1* than without *sd1*.

Ur1 significantly reduced panicle number per plant under the genetic backgrounds of ‘Shiokari’ and other varieties (Nagao *et al.* 1958, Murai and Iizawa 1994, Murai 1999). However, no significant effect of *Ur1* on this trait was noticed under all the growing conditions, with and without *sd1*, in the present study. It seems that *Ur1* does not exert the reducing effect on this trait under some genetic backgrounds such as T.

Regarding ripened-grain percentage, u and h were 7.4 to 12.0% and 2.9 to 9.2%, respectively, lower than d in the experiments in both years (Table 3 and Table 5). The variation of this trait in 2000 was principally due to unfertilization. The sterile spikelet with whity-translucent hull

(“Hakufu” in Japanese) and cylindrical spikelet lacking its palea were frequently found in panicles at the *Ur1/Ur1* genotype under genetic backgrounds of Hokkaido varieties (Nagao *et al.* 1958, Murai and Iizawa 1994, Murai 1999). Hokkaido is one of the coolest rice-growing regions in the world, and the earliest maturing varieties of rice have been grown now and in the past. In such varieties, panicle development is initiated when the plant body is small (earlier leaf age); hence, excessive spikelet production at the *Ur1/Ur1* genotype may have led to deficiency of carbohydrates-supply to each developing panicle, inducing the said abnormal spikelets. On the other hand, the abnormal spikelets were rarely found in u and U in the experiments. Nevertheless, it can be assumed that *Ur1* induced some abnormality(s) in male or female organ(s) inside the spikelets resulting in increase of unfertilized spikelets in u, U, h and H. Besides, the percentage of insufficiently filled grains of U was greater than those of the other five genotypes (Table 3), which may have resulted from the most serious lodging in this genotype.

As for 1000 grain weight, u and h were 4 and 3%, respectively, smaller than d in 2000 (Fig. 1). According to Murai *et al.* (1997), two genotypes ($\cong$ u and h) were 8% smaller than d in this trait at Tsukuba, Japan. In 1998, however, the average for all fertilizer levels was similar in u, h and d, viz. 22.3, 22.4 and 22.2 g, respectively. Thus, the percentage decrease of u or h from d in this trait was altered with the location and year. Under genetic backgrounds of Hokkaido varieties, *Ur1* lowered 1000 grain weight by 10% or more, and reduced both length and width of spikelet by about 3% at both the homozygous and heterozygous genotypes (Murai and Iizawa 1994, Murai 1999). Hence, it is inferred that the decrease of this trait by *Ur1* is ascribable to both excessive number of spikelets and slightly smaller size of spikelet, and the extent of decrease is affected by not only genetic background but also environmental conditions, particularly weather condition after heading.

Regarding both LAI and leaf weight per m² at the 80%-heading, the six genotypes were similar to each other (Table 3), indicating that *Ur1* as well as *sd1* has almost no effect on the total amount of photosynthetic organ at heading. Murai *et al.* (2002) already reported that *sd1* had no effect on this character.

It is inferred that the serious lodging diminished the yields of U and H by affecting grain filling (see materials and methods, Table 3). So, the yields of the three dwarf genotypes are discussed in this paragraph. The sink size-2 in u and h, respectively, was 13 and 14% larger than that in d (percentages calculated from data in Table 3), indicating that *Ur1* exerts similar effects on the actual sink size at both the homozygous and heterozygous genotypes. Under all growing conditions in both years, u and h, respectively, had 11 to 26% and 13 to 25% higher yields than d (Table 5, Fig. 1). There were highly significant correlations between yield, and sink size-1 and total weight per m² at maturity, namely, $r=0.966$ and 0.870 , respectively, being calculated from the data of the three dwarf genotypes under the four growing

conditions. However, there were almost no significant differences in total weight at the 80%-heading among the three dwarf genotypes in either year. Accordingly, it is suggested that large sink size induced by *Ur1* increased dry matter production after heading, which made a contribution to the yield. On the other side, Amano *et al.* (1993) reported that translocation of accumulated carbohydrates from stems and leaves to panicles caused the high yield of 'Shan You 63', a widely cultivated Chinese *F₁* variety. It is assumed that the larger sink sizes in *u* and *h* accelerated such translocation contributing to the higher yields, which was accompanied with the small LAIs at maturity owing to withering of lower leaves (Table 3 and Table 5). Moreover, *u* and *h* were higher in harvest index than *d*, indicating that *Ur1* accelerated such translocation and/or dry matter production after heading (Table 3 and Table 5). However, further research is necessary to verify these assumptions.

We examined the grain appearance of the three dwarf genotypes. A large spikelet number per panicle made by *Ur1* is principally due to increase of spikelets setting on secondary branches (Murai and Iizawa 1994, Murai 1999). In ordinary Japanese varieties, thin, breakable and opaque grain ("shinimai" in Japanese) as well as underdeveloped green grain ("aomai") is more frequent in spikelets setting on secondary branches than in those directly setting on primary branches (Iwatsuki and Tatematsu 1934, Nagato and Chaudhry 1970). In brown rice before the sieving, these two kinds of incomplete grains appeared to be more frequent in *u* and *h* than in *d*. However, these incomplete grains were almost removed with the sieving. Two other kinds of incomplete grains, viz. white core and white belly rices were inconspicuous in *u*, *h* and *d*. Thus, *u* and *h* showed no serious problems regarding grain appearance. More detailed research is necessary to clarify the effect of *Ur1* on this characteristic.

Yagi *et al.* (2001) reported that the Korean high yielding variety 'Milyang 23' carries a gene with an increasing effect on spikelet number per panicle at a quantitative trait locus on chromosome 1. *Ur1* is different from this gene, because it is a marker gene on chromosome 6 (Nagao and Takahashi 1963, Sato and Shinjyo 1991). The present study suggests that *Ur1* can be a useful tool for developing high yielding *japonica* varieties. The same may be said of *indica* subspecies. Although *u* carries *sd1*, it showed apparent bending at maturity at the high fertilizer level in 1998, owing to not only its heavy panicles but also its longer culms than those of *d* (Table 5). Thus, *Ur1* have a pleiotropic effect of elongating culm. Hence, high lodging tolerance is indispensable for developing varieties carrying *Ur1*. The yield of *u* at the high fertilizer level (614 g/m²) was the highest in all growing conditions but the ripened-grain percentage was low (74.4%) (Table 5). Another *Ur1*-isogenic line of 'Nishihikari', a highly lodging-tolerant variety, showed a high ripened-grain percentage (88.9%) and a high yield (715 g/m²) in an experiment at Kochi University (Murai unpublished). Hence, genes or a combination of genes enhancing spikelet

fertility and grain filling should be accompanied to obtain high yield by the use of *Ur1*. Besides, *h* had a yield similar to that of *u*, due to its similar or rather larger sink size-2 (Table 3). Murai *et al.* (1997) reported an example of a high yielding *F₁* at the *Ur1/+* genotype, viz. 'Nishihikari' × the line almost equal to *u*. Hence, *Ur1* may be utilized for developing high yielding *F₁* varieties (hybrid rice). Recently, importance of LISA (Low Input and Sustainable Agriculture) is being recognized globally. The percentage increase in yield at the low fertilizer level was 26 and 25%, respectively, for *u* and *h* over *d*, and was greater than that at the middle or high fertilizer level (Table 5). Inbred and/or *F₁* varieties carrying *Ur1* may contribute towards rice cultivation in LISA.

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