High Yielding F₁ Hybrid Carrying *Ur1* (Undulate rachis -1) Gene in *Japonica* Rice

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An incompletely dominant gene *Ur1* (Undulate rachis -1) increases spikelet number per panicle owing to increase of secondary branches. This genic effect on spikelet number can increase grain yield in either the *Ur1/Ur1* or *Ur1/+* genotype by enlarging sink size. We examined whether the yield-increasing effect of *Ur1* in the heterozygous genotype can be superimposed upon the high yield ability of a *japonica* F₁ hybrid. Two F₁s with and without *Ur1* (H^U and H⁺) were produced by the hybridization between 'Nishihikari' (common maternal parent, short-culm variety) and the isogenic line of Taichung 65 possessing both *Ur1* and *sd1* or that carrying *sd1* only. In 1999, H^U, H⁺ and 'Hinohikari', a leading variety in southern Japan, were grown under three fertilizer levels. 'Nishihikari' was included in the experiment only at the middle fertilizer level. In 2000, H^U and 'Hinohikari' were grown at the twofold (heavy) fertilizer level. H⁺ had a 21% higher yield than 'Nishihikari', revealing its heterobeltiosis. The yield of H⁺ was 12 to 15% higher under the three fertilizer levels than that of the check variety 'Hinohikari'. H⁺ had a higher ripened-grain percentage than either 'Hinohikari' or 'Nishihikari'. H^U had a 7, 10 and 11% higher yield, respectively, at the low, middle and high fertilizer levels than H⁺. Among the four yield components, spikelet number per panicle alone contributed to the higher yield of H^U, even though its ripened-grain percentage was lower than that of H⁺. In yield, both F₁s showed positive responses from the middle to high fertilizer levels but little response from the low to middle fertilizer levels. H^U showed 22, 25 and 24% (116, 126 and 137 g/m²) higher yield, respectively, at the low, middle and high fertilizer levels in 1999 than 'Hinohikari'. H^U gained the highest yield, 723 g/m² at the twofold fertilizer level in 2000 which was 14% (88 g/m²) higher than that of 'Hinohikari'. Thus, the yield-increasing effect of *Ur1* was superimposed upon the high yield ability of H⁺. Consequently, *Ur1* could be utilized for developing high yielding F₁ varieties in the *Ur1/+* genotype.

Key Words: *Oryza sativa*, *japonica*, *Ur1*, heterosis, hybrid rice, spikelet number per panicle, yield.

Introduction

Hybrid rice varieties were grown for about half of the total rice area of China in 2001, contributing greatly to increased production (Yuan 1997, China National Rice Research Institute 2002). Most of the widely-grown F₁ varieties such as 'Shan You 63' are regarded as *indica* (Hibino and Kokawa 1993). However, the requirements for eating quality in Japan are too high to accept the present F₁ varieties (Maruyama 1989, Hibino and Kokawa 1993). Moreover, *indica* varieties are hardly usable in northern Japan, since they are more susceptible to the chilling injury at the seedling stage and the sterile-type cool-damage at the booting stage, compared with *japonica* varieties (Chuong and Omura 1980, Morishima and Oka 1981, Nagamine and Nakagahra 1990, Kabaki 1993). Heterosis over the better parent, viz. heterobeltiosis, in grain yield was recognized in F₁s between *japonica* varieties (Murayama 1972, 1973, Kawase and Harada 1982, Murai and Kinoshita 1986, Murai *et al.* 1992, Murai 1999). However, it is assumed that the magnitude of heterosis in *japonica/japonica* hybrids is smaller than that in *indica/indica* hybrids or that in *indica/japonica* hybrids, owing to the limited genetic diversity within *japonica* (Araki 1990).

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). *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 (Murai and Iizawa 1994, Murai 1999). This genic effect increased grain yield in both *Ur1/Ur1* and *Ur1/+* genotypes by enlarging sink size under the genetic background of a *japonica* variety, 'Taichung 65', despite reduction in ripened-grain percentage, and the extent of yield increase in the *Ur1/+* genotype was similar to that in the *Ur1/Ur1* genotype (Murai *et al.* 1997, 2002b). Nevertheless, *Ur1* increases culm length, and the long culms below large panicles are ready to lodge (Murai

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and Iizawa 1994, Murai *et al.* 1997, 2002b, Murai 1999). An effective countermeasure against the lodging is the use of *sd1* (dee-geo-woo-gen dwarf) (Murai *et al.* 2002b).

In a preliminary experiment, six F_1 hybrids between *japonica* varieties and *japonica* *Ur1* lines were examined, and it was found that the F_1 between a short-culm variety 'Nishihikari' and the isogenic line of Taichung 65 possessing both *Ur1* and *sd1* showed the highest grain yield (Murai *et al.* 1997, Murai unpublished). On the other side, the F_1 of 'Nishihikari' $\times$ the *sd1* isogenic line of Taichung 65 without *Ur1* had a higher yield than the better parent 'Nishihikari', indicating the heterobeltiosis in this F_1 . The F_1 with *Ur1* had a 12% higher grain yield than the F_1 without *Ur1*, suggesting that the yield-increasing effect of *Ur1* can be superimposed upon the heterobeltiosis. However, further experiments should be performed to verify this assumption.

In the present study, the above-mentioned two F_1 s with and without *Ur1*, 'Nishihikari', and 'Hinohikari', a leading variety in southern Japan were grown at various fertilizer levels in the same year. Furthermore, the F_1 with *Ur1* and 'Hinohikari' were grown under a heavy fertilizer condition in another year, for examining the maximum yield level in this F_1 . Besides yield, its components, sink size, harvest index and other traits were measured in both years. On the basis of the results, we discuss the possibility of high yielding F_1 varieties possessing the *Ur1/+* genotype.

Materials and Methods

Taichung 65 is a tall *japonica* variety developed in Taiwan: its parents were Japanese varieties 'Kameji' and 'Shinriki' (Iso 1947). Two isogenic lines of Taichung 65 with and without *Ur1* were used as the paternal parents of the two F_1 s, being denoted by "u" and "d", respectively, according to Murai *et al.* (2002b) (Table 1). The d is the isogenic line for *sd1* originating from 'Dee-geo-woo-gen', which was developed after ten backcrosses (Murai *et al.* 1995, 2002a). The u carries both *Ur1* and *sd1*, which was produced after the hybridization between an *sd1*-B₁₀ isogenic line and a *Ur1*-B₈ isogenic line (Murai *et al.* 1997). Fig. 1 shows the panicles of u and d at maturity. 'Nishihikari', the common maternal parent of the two F_1 s, is a short culm and panicle-number type variety possessing the highest lodging tolerance in southern Japan (Table 3, Nishiyama 1982). It is presumed that this variety carries a dwarfing allele at the *sd1* locus originating from 'Jikkoku' (Nishiyama 1982). Crossed seeds for the F_1 s were obtained by the emasculation with pincette. 'Nishihikari' was included in the present study to evaluate the heterobeltiosis in H^+ . Moreover, 'Hinohikari', a leading variety in southern Japan, was used as the check variety for the two F_1 s, which possesses a rather long culm, rather many panicles and medium maturity (Table 2 and Table 3, Yagi 1989). H^U and H^+ showed heading behavior similar to that of 'Hinohikari' (Table 2). 'Nishihikari' had a two days later heading date than 'Hinohikari'.

In 1999, 24-day-old seedlings of H^U , H^+ , 'Hinohikari'

Table 1. Two isogenic lines of Taichung 65 with and without *Ur1*, and two F_1 s with and without *Ur1*

Line or F_1	Genotype at <i>Ur1</i> locus	Explanation
u	<i>Ur1/Ur1</i>	The isogenic line of Taichung 65 carrying both <i>Ur1</i> and <i>sd1</i>
d	+/+	The <i>sd1</i> isogenic line of Taichung 65
H^U	<i>Ur1/+</i>	F_1 , 'Nishihikari' $\times$ u
H^+	+/+	F_1 , 'Nishihikari' $\times$ d

Fig. 1. Panicles of u (left) and d (right), viz. the isogenic lines of Taichung 65 with and without *Ur1*, respectively. The isogenic lines carry *sd1*.

and 'Nishihikari' 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 $\times$ 15.0 cm (22.2 hills per m²), on May 26. Low, middle and high fertilizer levels were applied (Table 2): we adopted the split-plot design to the experimental field, applying the main-plot and sub-plot to fertilizer level and genotype, respectively, with three replications. 'Nishihikari' was included in the field experiment only at the middle fertilizer level. In 2000, on June 1, 26-day-old seedlings of H^U and 'Hinohikari' were transplanted to a paddy field of the faculty with the same planting density as in 1999. A fertilizer level twofold higher than the middle fertilizer level in 1999 was applied to the paddy field in 2000 (Table 2). Three replications were set in the paddy field. In both years, each plot comprised 132 hills (33 hills $\times$ 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.

Table 2. Fertilizer application for H^U, H⁺, 'Hinohikari' and 'Nishihikari' in 1999, and that for H^U and 'Hinohikari' in 2000, together with their heading dates

Year	Fertilizer level	Basal dressing (N ² g/ m ²)	Top dressing ¹⁾ (N ² g/ m ²)	80%-heading date in August			
				H ^U	H ⁺	'Hinohikari'	'Nishihikari'
1999	High	7.2	4.8 ³⁾	15	13	15	—
	Middle	4.8	3.2 ^{3,4)}	14	13	15	17
	Low	2.4	1.6 ³⁾	14	12	14	—
2000	Twofold	9.6	6.4 ⁵⁾	19	—	18	—

¹⁾ A slow-release coated fertilizer (NUTRICOTE®, presented from Chisso Asahi Fertilizer Co., Ltd.), about 7% 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⁾ Applied on July 22 for H^U, H⁺ and 'Hinohikari'.

⁴⁾ Applied on July 26 for 'Nishihikari'.

⁵⁾ Applied on July 24.

Table 3. Percentage of H⁺ to 'Nishihikari' or 'Hinohikari' in yield and other traits in 1999, together with actual values in the two varieties at the middle fertilizer level

Trait	Percentage of H ⁺ to				Actual value at the middle fertilizer level	
	'Nishihikari'		'Hinohikari'		'Nishihikari'	'Hinohikari'
	Middle ¹⁾	Low ¹⁾	Middle	High		
Yield (g/m ²)	121**	115**	113**	112**	488	523
Spikelets/panicle	126**	105*	104*	103	66.6	80.4
Panicles/m ²	84**	97	95*	95*	376	332
Ripened-grain percentage	113**	108**	109**	109**	82.7	85.4
1000 grain weight (g)	102*	105**	105**	105**	23.6	23.0
Culm length ²⁾ (cm)	114**	93**	93**	92**	65.9	80.8
Panicle length ²⁾ (cm)	101	101	99	102	18.1	18.4

¹⁾ Fertilizer level.

²⁾ Measured for the longest culm of each hill at maturity.

*** Difference between H⁺ and 'Nishihikari' or 'Hinohikari' was significant at the 5 and 1% levels, respectively.

In both years, all panicles of about 30 hills were sampled from each plot at maturity, and the panicle weight of each hill was checked after cutting just at their panicle bases and air-drying. Out of seven hills randomly selected from about 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. 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. 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 30 hills of each plot was estimated from this percentage. The moisture content (%) of ripened grains of each plot was measured; and the yield at 15% moisture was estimated and used in the present study.

Nine hills were sampled from each plot at maturity in both years. Five hills, which had intermediate panicle numbers per hill, were selected from the nine hills. The total dry weight excluding roots of each hill was measured after drying at 75°C for two days.

Results

Performance of H⁺

In 1999, H⁺ had a 21% (102 g/m²) higher yield than 'Nishihikari' at the middle fertilizer level, which was due to its larger spikelet number per panicle and higher ripened-grain percentage compared with those of 'Nishihikari' despite its smaller panicle number per m² (Table 3). The yield of H⁺ was 15, 13 and 12% (77, 67 and 66 g/m²) higher, respectively, at the low, middle and high fertilizer levels than that of 'Hinohikari', resulting from its higher ripened-grain percentage and larger 1000 grain weight. Consequently, H⁺ has a higher yield ability than the two inbred varieties well-adapted to southern Japan. It is notable that H⁺ has a higher grain-filling ability than either 'Hinohikari' or 'Nishihikari'. H⁺ had a culm length intermediate between those of 'Nishihikari' and 'Hinohikari'. Regarding panicle length, the three genotypes were similar to one another.

Effects of Ur1 under the genetic background of H⁺ in different fertilizer levels

H^U and H⁺ were compared in yield and its related traits at each fertilizer level in 1999, in order to investigate the heterozygous effects of *Ur1* under the genetic background of

H⁺ (Table 4). The analysis of variance for the two F₁s in the three fertilizer levels was conducted to each trait in accordance with the split-plot design, excluding the data of 'Hino-hikari' (Table 5). H^U had a 7, 10 and 11% (39, 57 and 71 g/m²) higher yield, respectively, at the low, middle and high fertilizer levels than H⁺. The yield of both F₁s increased from the middle to high fertilizer levels but hardly increased from the low to middle levels. In fact, the effect of fertilizer level

was significant, whereas the fertilizer level $\times$ *Ur1* interaction was not significant. In addition, the yield of 'Hino-hikari' was 534, 523 and 545 g/m², respectively, at the low, middle and high fertilizer levels (data not included in Table 4), showing a fertilizer response similar to that of H⁺.

The spikelet number per panicle in H^U was 18, 21 and 26% larger, respectively, at the low, middle and high fertilizer levels than that in H⁺. The effect of fertilizer level and its

Table 4. Yield and other traits of H^U and H⁺ at the three fertilizer levels in 1999

Trait	Fertilizer level	H ^U	H ⁺	LSD _(5%) ¹⁾
Yield (g/m ²)	High	682** (111) ²⁾	611	26
	Middle	647** (110)	590	
	Low	640** (107)	601	
Spikelets/panicle	High	107.5** (126)	85.4	2.7
	Middle	101.3** (121)	83.6	
	Low	95.5** (118)	80.9	
Panicles/m ²	High	326 (101)	324	15
	Middle	310 (98)	315	
	Low	315 (96)	329	
Ripened-grain percentage	High	85.0** (93)	91.8	3.4
	Middle	88.4* (95)	93.2	
	Low	91.2 (97)	94.2	
1000 grain weight (g)	High	22.8** (95)	24.1	0.4
	Middle	23.3** (97)	24.0	
	Low	23.3* (97)	24.0	
Spikelets/m ² ($\times 100$)	High	351** (127)	277	21
	Middle	314** (119)	263	
	Low	301** (113)	266	
Sink size ³⁾ (g/m ²)	High	801** (120)	666	39
	Middle	733** (116)	633	
	Low	702** (110)	638	
Total weight at maturity (g/m ²)	High	1570* (108)	1455	103
	Middle	1477 (107)	1384	
	Low	1452 (101)	1437	
Harvest index (%)	High	36.9 (103)	35.7	1.6
	Middle	37.3 (103)	36.2	
	Low	37.5* (105)	35.5	
Culm length ⁴⁾ (cm)	High	89.8** (117)	76.6	1.7
	Middle	85.9** (115)	75.0	
	Low	86.2** (116)	74.0	
Panicle length ⁴⁾ (cm)	High	20.6** (109)	19.0	0.6
	Middle	20.5** (112)	18.3	
	Low	20.2** (110)	18.4	

¹⁾ Calculated from sub-plot errors of the analysis of variance in 1999 (Table 5).

²⁾ H^U/H⁺ (%).

³⁾ Single grain weight $\times$ spikelets/m².

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

*,** Difference between H^U and H⁺ was significant at the 5 and 1% levels, respectively.

Table 5. Analysis of variance for the split-plot experiment applying the fertilizer levels and the two F₁s (H^U and H⁺) to main-plot and sub-plot, respectively, in yield and other traits in 1999

Trait	Source of Variation ¹⁾		
	Fertilizer levels	<i>Ur1</i> ²⁾	Interaction (F. × <i>Ur1</i>)
Yield (g/m ²)	19.73** ³⁾	94.60** ³⁾	3.51 ³⁾
Spikelets/panicle	34.30**	785.40**	10.54*
Panicles/m ²	3.58	1.50	2.66
Ripened-grain percentage	5.15	35.85**	1.69
1000 grain weight (g)	1.81	66.89**	2.76
Spikelets/m ² (× 100)	8.08*	124.98**	6.56*
Sink size ⁴⁾ (g/m ²)	9.78*	128.71**	6.54*
Total weight at maturity (g/m ²)	13.42*	11.59*	2.08
Harvest index (%)	< 1	13.81**	< 1
Culm length (cm)	7.96*	910.63**	2.72
Panicle length (cm)	4.16	205.19**	1.45

¹⁾ Degrees of freedom for fertilizer level (main-plot), *Ur1* (sub-plot), the interaction, block, main-plot error and sub-plot error are 2, 1, 2, 2, 4 and 6, respectively.

²⁾ Difference between H^U and H⁺.

³⁾ Numerals in the table indicate F-values.

⁴⁾ Single grain weight × spikelets/m².

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

interaction with *Ur1* were both significant (Table 5): either F₁ showed a consistent increase with the enhancement of fertilizer level, and H^U was more responsive than H⁺.

There was no significant difference in panicle number per m² between the F₁s at every fertilizer level; and the effect of fertilizer level was not significant.

Regarding ripened-grain percentage, H^U was lower than H⁺ at every fertilizer level. The value of H^U consistently decreased from the low to high fertilizer levels, although not significantly. H⁺ showed little fertilizer response.

As for 1000 grain weight, H^U was lower than H⁺ at every fertilizer level, although the difference was small. There was no significant fertilizer response.

Consequently, spikelet number per panicle alone among the four yield components contributed to the higher yield of H^U, even though H^U had a lower ripened-grain percentage. In H^U, the increase of yield from the low to high fertilizer levels was principally due to the positive fertilizer response in spikelet number per panicle.

H^U had a 13 to 27% higher spikelet number per m² and 10 to 20% larger sink size than H⁺. The effect of fertilizer level and the interaction were both significant in either trait: H^U was more responsive than H⁺.

Regarding the total weight at maturity, the effect of *Ur1* was significant and H^U was larger than H⁺ at every fertilizer level. The effect of fertilizer level was significant; in fact, the value of H^U became larger with the increase of fertilizer level, but such a consistent response was not noticed in H⁺. On the other side, H^U had a higher harvest index than H⁺ at every fertilizer level. Neither F₁ showed any significant fertilizer response in this trait.

H^U had a culm length 10.9 to 13.2 cm longer than H⁺. Either F₁ showed a positive fertilizer response. In panicle length, H^U was longer than H⁺ at every fertilizer level; and

the effect of fertilizer level was not significant.

Comparison between H^U and the check variety 'Hinohikari'

H^U gained the highest yield in the present study (723 g/m²) at the twofold fertilizer level in 2000 which was 14% (88 g/m²) higher than that of 'Hinohikari' (Table 6). In 1999, H^U showed a 22, 25 and 24% (116, 126 and 137 g/m²) higher yield, respectively, at the low, middle and high fertilizer levels than 'Hinohikari', resulting from its larger panicles despite its smaller number of panicles per m². Regarding ripened-grain percentage as well as 1000-grain weight, there was no significant difference between H^U and 'Hinohikari' at all fertilizer levels except the low fertilizer level in both years. At the twofold fertilizer level, however, about 10% of all hills in H^U lodged or bent to the ground at maturity owing to its long culm (87.2 cm) and heavy panicles.

Discussion

A rice F₁ hybrid reported by Murai *et al.* (1992) had about 10% higher yields than 'Ishikari', a formerly leading variety in Hokkaido, viz. the northernmost prefecture of Japan. Being calculated from data reported by Murayama *et al.* (1974), the best two *japonica* F₁s in the experiment had 20 and 3% higher yields than 'Reiho', a representative variety grown in southern Japan in the 1970s. In the present study, H⁺ exceeded the check variety 'Hinohikari' by 12 to 15% in yield, indicating its high yield ability (Table 3).

Another field experiment conducted under the same three fertilizer levels at Kochi University showed that the heterozygous effect of *Ur1* increased the yield of d by 19 to 25% (Murai *et al.* 2002b). This extent of yield increase by *Ur1* was larger than that from H⁺ to H^U (7 to 11% in Table 4), which may be due to the lower yield ability of d (449 to

Table 6. Percentage of H^U to 'Hinohikari' in yield and other traits at the three fertilizer levels in 1999, and those at the twofold fertilizer level in 2000, together with actual values of H^U in 2000

Trait	Percentage of H ^U to 'Hinohikari'				Actual value in H ^U
	Low ¹⁾	Middle ¹⁾	High ¹⁾	Twofold ²⁾	Twofold ²⁾
Yield (g/m ²)	122**	125**	124**	114**	723
Spikelets/panicle	124**	130**	126**	139**	105.5
Panicles/m ²	93**	96*	93**	87*	373
Ripened-grain percentage	104*	101	104	94	82.6
1000 grain weight (g)	102*	99	102	100	22.2
Culm length ³⁾ (cm)	108**	106**	108**	106*	87.2
Panicle length ³⁾ (cm)	111**	111**	111**	114*	21.4

¹⁾ In 1999.²⁾ In 2000.³⁾ Measured for the longest culm of each hill at maturity.*** Difference between H^U and 'Hinohikari' was significant at the 5 and 1% levels, respectively.

525 g/m² in Murai *et al.* 2002b) than that of H⁺ (590 to 611 g/m² in Table 4). Nevertheless, the yield of H^U (640 to 682 g/m² in Table 4) was higher than the yield of the *Ur1*/+ genotype under the genetic background of d (561 to 632 g/m² in Murai *et al.* 2002b). Thus, the yield-increasing effect of *Ur1* was superimposed upon the high yield ability of H⁺.

The heterozygous effect of *Ur1* increased spikelet number per panicle, sink size, total weight per m² (biological yield) and harvest index but decreased ripened-grain percentage and 1000-grain weight under the genetic background of H⁺ (Table 4 and Table 5), which is consistent with the results obtained under the genetic background of d (Murai *et al.* 2002b). Nevertheless, the percentage increase of spikelet number per panicle by the heterozygous effect of *Ur1* under the genetic background of H⁺ (18 to 26% in Table 4) was smaller than that under the genetic background of d (25 to 33% in Murai *et al.* 2002b). A similar difference is noticed in sink size, which caused the smaller percentage of yield increase under the genetic background of H⁺ than that under the genetic background of d (Table 4, Murai *et al.* 2002b). The effect of *Ur1* seems to be modified by the difference in genetic background.

An unhulled grain (rough rice) yield higher than 1100 g/m² was gained by 'Shan You 63' in China or by an F₁ hybrid of the International Rice Research Institute in the Philippines (Amano *et al.* 1993, Peng *et al.* 1999); however, the nitrogen application as well as the hill density in both reports was higher than that in the present study. In a study conducted in Fukuoka prefecture in southern Japan (Song *et al.* 1990), 'Shan You 63' had a brown rice yield of 797 g/m² at a nitrogen fertilizer level intermediate between our high and twofold fertilizer levels with the same hill spacing and seedling number per hill as in the present study. The yield of H^U at the high and twofold fertilizer levels was 687 and 723 g/m², respectively (Table 4 and Table 6). Hence, the yield ability of H^U may not reach the level of the *indica* F₁ variety 'Shan You 63', although it is greater than that of 'Hinohikari', viz. the most representative variety of southern Japan (Table 6).

In the present study, we analyzed a high yielding F₁ hybrid possessing the *Ur1*/+ genotype. Further high-yielding F₁s could be found in various cross combinations between *Ur1* lines and *japonica* varieties/lines. H⁺ was higher in ripened-grain percentage than either 'Hinohikari' or 'Nishihikari' (Table 3). Moreover, H^U was similar to 'Hinohikari' in this trait even though this F₁ carried *Ur1* (Table 6). These results suggest that grain-filling ability is important for evaluating prospective F₁s in the *Ur1*/+ genotype.

H⁺ had a shorter culm length than 'Hinohikari', while H^U had a longer one resulting from the pleiotropic effect of *Ur1* (Table 3 and Table 6). H^U showed lodging at the twofold fertilizer level in 2000, indicating deficiency of lodging tolerance, even though this F₁ carried *sd1*. Hence, high lodging-tolerance is indispensable for developing F₁ varieties carrying *Ur1*.

Recently, rice F₁ varieties by the use of the thermo-sensitive or photoperiod-sensitive genic male sterility have begun to replace those by the cytoplasmic male sterility in China; because the former F₁ varieties do not need the restorer genes for their paternal parents making possible the use of various varieties/lines as the paternal parent, and the hybrid-seed production process in the former F₁ varieties is more simple than that in the latter F₁ varieties (Yuan 1997, Jiang *et al.* 2002). Jiang *et al.* (2002) reported that three lines out of the five thermo-sensitive or photoperiod-sensitive genic male sterile lines were *japonica*-like (not purely *japonica*). Hence, *japonica* lines carrying *Ur1* could be used as the paternal parent for prospective F₁ varieties, together with environment-sensitive genic male sterile (maternal) lines.

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