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The semidwarf gene, *sd-1*, of rice (*Oryza sativa* L.). I. Linkage with the esterase locus, *Estl-2*

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Abstract The linkage relationship between the semidwarf gene (*sd*-1) and the isozyme locus *Estl*-2 was elucidated using segregating populations derived from crosses between several semidwarf testers and tall rice varieties. Bimodal distributions for culm length were observed in F_2 populations of three cross combinations, including Shiokari/Shiokari (*sd*-1), Taichung 65 (*A,Pn,Pau*)/Taichung 65 (*sd*-1), and Milyang 23/Kasalath. Taking the valley of the distribution curves as the dividing point, two height classes were apparent with a segregation ratio of 3 tall:1 short, demonstrating this character to be under the control of a single recessive gene. An inheritance study of esterase isozymes, based on isoelectric focusing (IEF), showed that the *Estl*-2 locus had two active allozymes of monomeric structure and one null form, which were designated "a", "b", and "n", respectively (Eun et al. 1990). Semidwarf testers such as Shiokari (*sd*-1), Taichung 65 (*sd*-1) and Milyang 23 have an active allozyme designated as *Estl*-2^{aa}, while the tall parents, Shiokari and Taichung 65 (*A,Pn,Pau*), have the active allozyme, *Estl*-2^{bb}, and Kasalath has a null form of the allozyme, *Estl*-2^{nn}. By dividing F_2 populations based on *Estl*-2 allozyme patterns, culm-length distributions exhibited trimodal curves. Most of the short plants had the homozygous *Estl*-2^{aa} pattern of the short parents, most of the tall plants had the homozygous pattern, *Estl*-2^{bb} or *Estl*-2^{nn}, and most of the intermediate plants had the heterozygous *Estl*-2^{ab} or *Estl*-2^{an} banding pattern. Linkage analysis indicated that *sd*-1 and *Estl*-2 were tightly linked. These findings were also confirmed by segregation analyses in F_3 progenies. No recombinants among 171 F_3 families from the Shiokari/Shiokari (*sd*-1) combination, five recombinants among 267 F_3 families from Taichung 65 (*A,Pn,Pau*)/Taichung 65(*sd*-1), and only two recombinants out of 237 F_3 families from Milyang 23/Kasalath, were found. The recombination values were 0, 1.87 and 0.8%, respectively.

Key words Rice · Semidwarf gene · Isozyme marker
Esterase · Isoelectric focusing

Introduction

The introduction of the semidwarf gene (*sd*-1) into cultivars of rice (*Oryza sativa* L.) and wheat (*Triticum aestivum*) formed the basis of the high-yielding "green revolution" varieties that served to double grain yield in much of the world (David 1991). This gene confers semidwarf stature or reduced culm lengths, has a major effect on harvest index (Walcott and Laing 1976), improves lodging resistance (Pinthus 1973), and is associated with increased responsiveness to nitrogen fertilizer (Suh and Heu 1978).

The first improved semidwarf cultivar of indica rice was 'Taichung Native 1' (TN-1), developed in Taiwan in 1956 from the Chinese cultivar 'Dee-geo-woo-gen'(DGWG) (Aihwai 1971). The semidwarf cultivar 'IR 8' was developed in the early 1960s from the cross Peta/DGWG at the International Rice Research Institute (IRRI) in the Philippines. IR 8 subsequently broke all existing yield records throughout Asia (IRRI 1967). The DGWG source of semidwarfism has since been used extensively in the development of short-statured rice cultivars.

In the late 1960s, the high-yielding rice variety, Tongil, was developed at the Rural Development Administration in Korea and at the IRRI in the Philippines as a shuttle breeding from the cross IR 8 //Yukara/Taichung Native 1 (Choi et al. 1974). Since that time, a number of other high-yielding varieties have been released which have played

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vital roles in helping Korea to achieve self-sufficiency for this staple food. Most of these high-yielding varieties carry the same single recessive semidwarf gene, *sd*-1 (Aquino and Jennings 1966; Suh and Heu 1978).

At least 60 dwarfing genes have been identified in rice. They are designated *d*-1 to *d*-60 (Kinoshita 1990). Of these, *d*-47, or *sd*-1, has been most widely used in rice breeding. Most of the others have been used as phenotypic markers in genetic studies, but rarely used in plant breeding.

From the classical linkage map, *sd*-1 is known to be located on chromosome 1 (Suh and Heu 1978), and linked to both a dominant shattering habit (Yokoo and Saito 1986), and a recessive shattering habit (Oba et al. 1990), as well as to *A* (anthocyanin activator), *Pp* (purple pericarp), *Pn* (purple node) and *Pau* (purple auricle) (Suh and Heu 1978).

In recent years, the development of protein and DNA markers has stimulated interest in new approaches to plant improvement. While both morphological characters and molecular markers have been widely used for the construction of linkage maps of rice chromosomes, molecular markers have several advantages in genetic studies or breeding schemes.

Isozyme and DNA markers are numerous, discrete, codominant, and almost entirely free of environmental and epistatic interactions. For these reasons, they are widely used in gene-tagging studies aimed at identifying tight linkages to agronomically desirable genes (Yu et al. 1991; Ahn et al. 1992; Ronald et al. 1992; Mackill et al. 1993) and have also been used as selection tools in breeding programs (Tanksley 1983; Helentjaris et al. 1985; McCouch et al. 1988).

This study was undertaken to determine the linkage relationship between the *sd*-1 gene and the *Est1*-2 locus in rice.

Materials and methods

Plant materials

Eighteen near-isogenic dwarf and semidwarf lines were developed by the introgression of 18 different dwarfing genes into the recurrent parent, Shiokari, based on 4–8 generations of backcrossing (Kinoshita and Shinbashi 1982). Each near-isogenic line (NIL) contained one dwarfing gene, symbolized *d*-1 to *d*-47, and each gene was introgressed from a different donor. Table 1 lists the NILs, the specific gene contained in each, the donor, and the number of backcrosses used to construct the lines analyzed in this study. *d*-47 is the symbol of the gene, *sd*-1, which was backcrossed into isoline 'ID-47' from IR 8 (I-120).

Three different populations were developed in order to resolve the linkage relationship between *sd*-1 and the *Est1*-2 locus. One-hundred-and-seventy-one F_2 and F_3 progenies from the cross, Shiokari/Shiokari (*sd*-1), 267 F_2 and F_3 progenies from Taichung 65 (*A,Pn,Pau*)/Taichung 65 (*sd*-1), and 237 F_2 and F_3 progenies from Milyang 23/Kasalath, were used for segregation analysis of esterase isozyme patterns and culm length. Shiokari (*sd*-1) was a BC4 F_3 selection from the cross Shiokari/IR 8. It was used as the paternal parent in a cross to the recurrent parent, Shiokari. Taichung 65 (*sd*-1) was a BC8 selection from the cross Taichung 65/T(N)-1 and was used as the paternal parent in a cross to Taichung 65 (*A,Pn,Pau*). Milyang 23 was a Korean variety, released in 1976, which contained *sd*-1.

Enzyme extraction

Rice seed, and leaves harvested at the early tillering stage, were used for the detection of enzymes. When a single rice seed was used as the source of enzyme, a brown rice kernel was ground with a mortar and pestle at room temperature, mixed with 100 µl of deionized water on ice, and centrifuged at 12000 rpm for 3 min. The supernatant was decanted into new microtubes and used for electrofocusing (Eun et al. 1988).

Est1-2 allozymes were analyzed in young leaf tissue by grinding 6–8-week-old leaves in deionized water with a mortar and pestle and centrifuging at 12000 rpm for 15 min. The supernatant was decanted into new microtubes and used in electrophoresis.

Electrophoresis

Isozyme electrophoresis was performed using isoelectric focusing in polyacrylamide gels (pH 4–6.5 and pH 3–7) (Ainsworth et al. 1984; Cho et al. 1989). To generate the pH gradient, ampholytes (Pharmacia products) of several pH ranges were added to 5% polyacrylamide slab gels (22 cm×7 cm×0.75 mm). A saturated calcium hydroxide solution and 0.1% phosphoric acid were used as cathodic and anodic solutions, respectively. Electrode strips were applied as reservoirs for both electrode solutions. Isoelectric focusing was carried out at 100 V for the first 30 min and was continued at 200–500 V for 3 h.

Isozyme staining

Esterase (EST). After electrophoresis, EST was stained by submerging the gel in a staining solution of 250 ml of phosphate buffer (0.2 M, pH 7.0) containing 40 mg of alpha-naphthyl acetate and 100 mg of Fast blue RR salt. The gel was incubated in the staining solution at 37 °C for 30 min.

Phosphoglucose isomerase (PGI). PGI was stained by submerging the gel in a staining solution of 20 mg of fructose-6-phosphate, 45 ml of Tris-HCl buffer (pH 8.5), 2 ml of 0.1 M magnesium chloride, 1 ml of NADP (5 mg/ml), 1 ml of glucose-6-phosphate dehydrogenase (10 units/ml), 1 ml of MTT (5 mg/ml) and 1 ml of phenazine methosulfate (PMS) (1 mg/ml). The gel was incubated in the staining solution at 40 °C for 30 min.

Malic enzyme (ME). ME was stained by submerging the gel in a staining solution of 100 mg of malic acid, 46 ml of 0.2 M Trisma base solution (adjusted to pH 7.0 with 1 N HCl), 1 ml of NADP (5 mg/ml), 25 ml of 0.2 M magnesium chloride, 1 ml of MTT (5 mg/ml), and PMS (1 mg/ml). The gel was incubated in the staining solution at 40 °C for 30 min.

Hexokinase (HK). HK was stained by submerging the gel in a staining solution of 100 ml of 50 mM Tris (pH 8.4), 2 ml of 1 M magnesium chloride, 180 mg of glucose, 130 mg of ATP Na^+, 15 mg of NADP, 20 mg of MTT, 4 mg of PMS, and 25 units of glucose-6-phosphate dehydrogenase. The gel was incubated in the staining solution at 40 °C for 60 min or until blue bands appear.

The stained gel was fixed and destained for 1 h in 5% acetic acid.

Results and discussion

Isozyme analyses using dwarf near-isogenic lines

As summarized in Table 1, no isozyme variation was observed among the 18 dwarf and semidwarf NILs, or their recurrent parent, Shiokari, for the isozymes malic enzyme (ME), phospho-glucose isomerase (PGI), and hexokinase (HK). Isozyme patterns ME *III*, PGI *IV*, and HK *I*, respectively, were observed for these enzymes using isoelectric focusing (Eun et al. 1989). For esterase (EST), 17 of the

Table 1 Specific characteristics and isozyme phenotypes of the 18 near-isogenic lines and the recurrent parent used in the experiment

Isogenic lines	Gene symbols	Dwarf donors	No. of back-crossings	Isozyme phenotype[a]			
				EST	*ME*	*PGI*	*HK*
ID-1	*d-1*	H-86	8	IIC	III	IV	I
ID-2	*d-2*	H-85	7	IIC	III	IV	I
ID-3	*d-3*	H-2	4	IIC	III	IV	I
ID-6	*d-6*	H-126	6	IIC	III	IV	I
ID-7	*d-7*	N-7	8	IIC	III	IV	I
ID-10	*d-10*	N-70	8	IIC	III	IV	I
ID-11	*d-11*	N-58	6	IIC	III	IV	I
ID-12	*d-12*	N-62	5	IIC	III	IV	I
ID-13	*d-13*	M-51	5	IIC	III	IV	I
ID-14	*d-14*	H-147	7	IIC	III	IV	I
ID-17	*d-17*	I-71	5	IIC	III	IV	I
ID-18^h	*d-18^h*	N-71	8	IIC	III	IV	I
ID-18^k	*d-18^k*	Fl-26	8	IIC	III	IV	I
ID-19	*d-19*	N-56	6	IIC	III	IV	I
ID-27	*d-17*	Fl-86	6	IIC	III	IV	I
ID-30	*d-30*	Fl-3	5	IIC	III	IV	I
ID-42	*d-42*	M-341	4	IIC	III	IV	I
ID-47	*d-47*	I-120	4	IIB	III	IV	I
Shiokari	Recurrent parent			IIC	III	IV	I

[a] *EST*, esterase; *PGI*, phosphoglucose isomerase; *ME*, malic enzyme; *HK*, hexokinase

NILs, and Shiokari, showed the EST *IIC* pattern (Eun et al. 1988). Only the line containing *d*-47 (*sd*-1) showed the EST *IIB* pattern (Table 1). This polymorphism provided the first evidence that the semidwarf gene, *sd*-1, might be linked to the *EstI*-2 locus.

Relationship between culm length and the *EstI*-2 locus

Semidwarf testers such as Shiokari (*sd*-1), Taichung 65 (*sd*-1), and Milyang 23 have the active allozyme form *EstI*-2^{aa}, tall parents such as Shiokari, and Taichung 65 (*A,Pn,Pau*) have the active form *EstI*-2^{bb}, and Kasalath, also a tall-stature variety, has the null allele at this locus *EstI*-2^{nn}. Figure 1 illustrates the migration pattern of the *a* and *b* alleles at the *EstI*-2 locus and segregation with culm lengths in F_3 families of Shiokari/Shiokari (*sd*-1).

Shiokari/Shiokari (*sd*-1)

The F_2 population derived from Shiokari/Shiokari (*sd*-1) was evaluated for culm length and showed a bimodal distribution (Fig. 2-Ia). Out of 185 plants investigated, 137 were tall and 48 were short, giving the expected ratio of 3 tall to 1 short, and providing evidence that the semidwarf stature in this population is conferred by a single recessive gene.

When the F_2 population was grouped in terms of *EstI*-2 allozyme patterns, culm-length distributions exhibited a trimodal form (Fig. 2-Ia). All short plants were homozygous for *EstI*-2^{aa}, like the short parent, all tall plants were homozygous for *EstI*-2^{bb}, and the intermediate plants were heterozygous, *EstI*-2^{ab}. These results indicated that *EstI*-2 and the semidwarf gene, *sd*-1, were closely linked.

These findings were confirmed by evaluating *EstI*-2 and culm length in F_3 progenies from the Shiokari/Shiokari (*sd*-1) combination. A total of 1700 F_3 individuals (171 F_3 families) were evaluated for culm length using *EstI*-2 scores to predict the phenotype. The F_3 progenies derived from the F_2 lines with the *EstI*-2^{aa} band were short, all plants derived from the lines with the *EstI*-2^{bb} band were tall, and all plants derived from the lines with *EstI*-2^{ab} segregated 1 short: 3 tall (Fig. 1 and Fig. 2-IIa).

Based on all the segregation data from 185 F_2 lines and 171 F_3 families evaluated from this cross, no recombinants were observed, giving a recombination value of 0% (Table 2A) and providing evidence that the linkage relationship between *EstI*-2 and *sd*-1 is very tight.

Taichung 65 (*A,Pn,Pau*)/Taichung 65 (*sd*-1)

To further resolve this relationship, we investigated a different population derived from the NILs, Taichung 65 (*A,Pn,Pau*) and Taichung 65 (*sd*-1). As can be seen in Fig. 2-Ib, the distribution of culm lengths based on isozyme analysis of *EstI*-2 alleles in 267 F_2 lines was bimodal and similar to that observed in the Shiokari/Shiokari (*sd*-1) combination.

The culm lengths of 2670 F_3 plants were evaluated and compared to *EstI*-2 isozyme scores of F_2 lines. The result

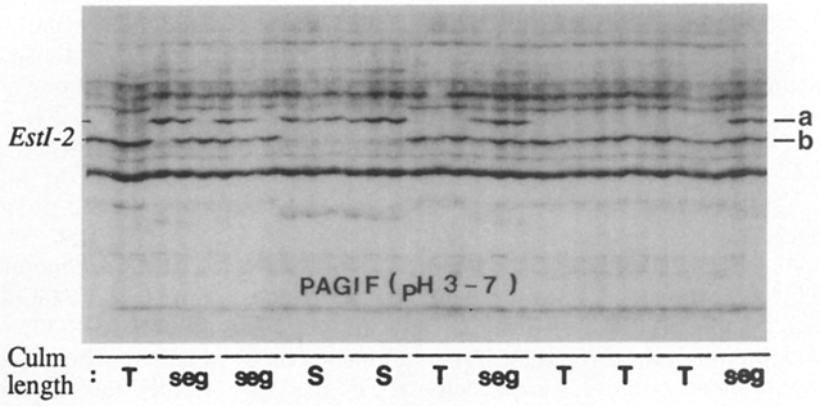

Fig. 1 Migration pattern of alleles at the *EstI-2* locus in semidwarf and tall testers. *a*, semidwarf allele from Shiokari (*sd*-1), Taichung 65 (*sd*-1), and Milyang 23; *b*, tall allele from Shiokari, Taichung 65 (*A,Pn,Pau*), and Kasalath. Segregation of *EstI-2* alleles with culm lengths in F_3 families of Shiokari /Shiokari (*sd*-1): *T*, tall; *S*, short; *seg*, segregating for tall and short

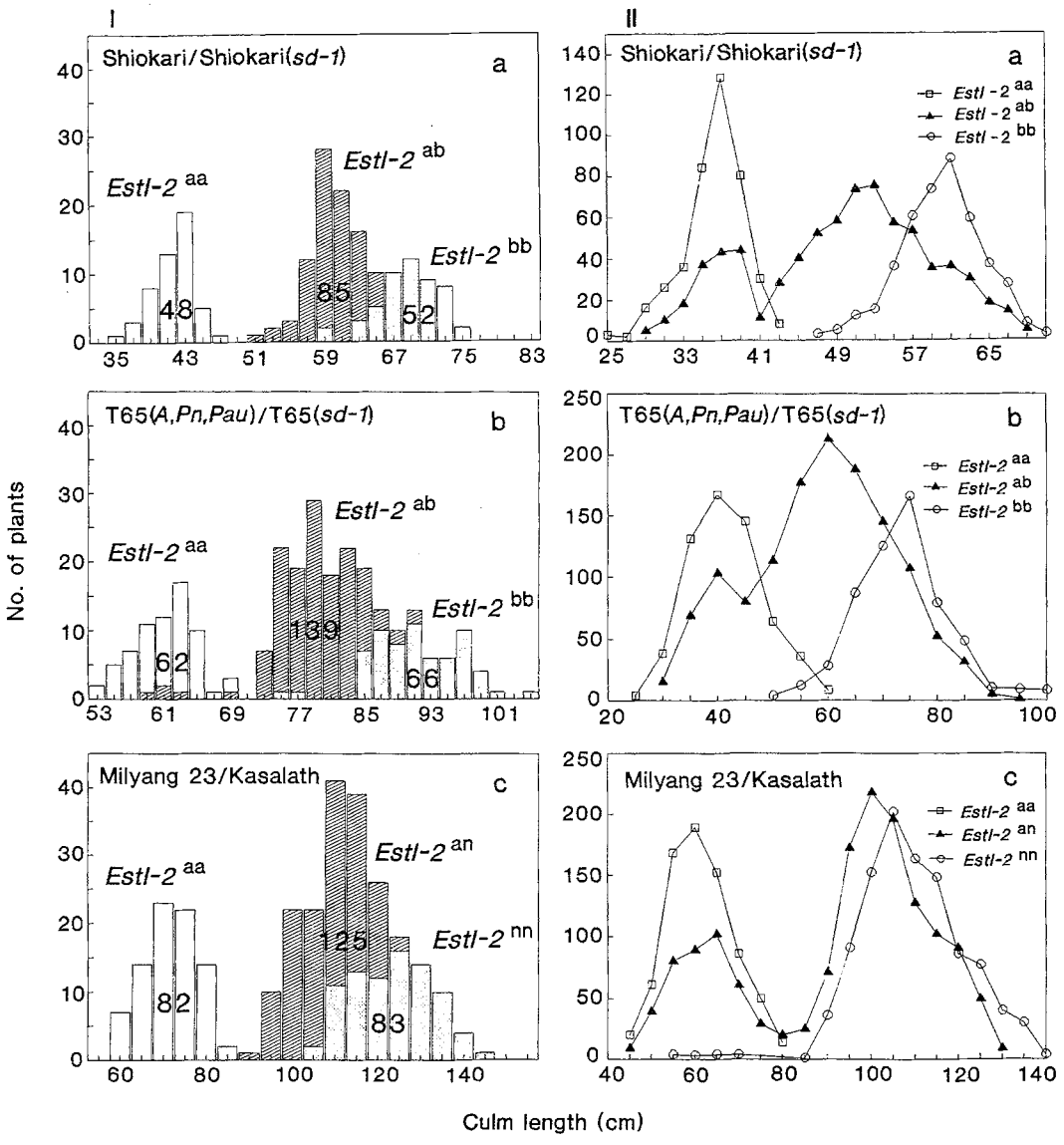

Fig. 2 I, II The distributions of semidwarf and tall culm lengths and *EstI-2* alleles in F_2 and F_3 families of (*a*) Shiokari /Shiokari (*sd*-1), (*b*) Taichung 65 (*A,Pn,Pau*)/Taichung 65 (*sd*-1) and (*c*) Milyang 23/Kasalath. **I** Segregation of *EstI-2* alleles in relation to culm length in F_2 populations. **II** Segregation of *EstI-2* alleles and culm lengths in F_3 families

again demonstrated that *EstI*-2 and *sd*-1 were tightly linked (Fig. 2-IIb). Out of 267 F_3 families, only five recombinants were identified, with a recombination value of 1.87% (Table 2B). This is equivalent to 1.87 cM (Kosambi 1944).

Milyang 23/Kasalath

A third cross combination was evaluated in order to compare the recombination value between *EstI*-2 and *sd*-1 in a cross which did not involve NILs. Milyang 23 and Kasalath, two unrelated varieties, were selected as parents. Milyang 23, a semidwarf tester, had the active allozyme *EstI*-2^{aa}, and the tall parent, Kasalath, had the null allozyme *EstI*-2^{nn}. In F_2 progenies of Milyang 23/Kasalath, culm length again showed a bimodal distribution (Fig. 2-Ic). Out of 290 plants tested, 208 were tall and 82 were short, giving the expected ratio of 3 tall to 1 short.

By dividing the F_2 (290 individuals) and F_3 (3230 individuals, or 237 families) populations based on *EstI*-2 allozyme patterns, culm-length distributions were the same as those observed for the Shiokari/Shiokari (*sd*-1) and Taichung 65 (*A,Pn,Pau*)/Taichung 65 (*sd*-1) populations (Fig. 2-Ic and Fig. 2-IIc). Most short plants had the homozygous *EstI*-2^{aa} pattern of the short parent, most tall plants had the homozygous *EstI*-2^{nn} pattern, and most intermediate plants had the heterozygous *EstI*-2^{an} allozyme pattern.

The recombination value between *EstI*-2 and *sd*-1, based on F_3 families of Milyang 23/Kasalath, was estimated to be 0.8% (2 recombinants out of 237 families; Table 2C). These results confirmed that the *sd*-1 gene was tightly linked to the *EstI*-2 locus, having a recombina-

Table 2 Linkage relationships between *EstI*-2 and *sd*-1 in F_3 families of (A) Shiokari/Shiokari (*sd*-1), (B) Taichung 65 (*A,Pn,Pau*)/ Taichung 65 (*sd*-1) and (C) Milyang 23/Kasalath

Culm length	*EstI-2* allozymes in F_3			Total	LX^2	Recombination value (%)
	aa	ab	bb			
A: Shiokari/Shiokari (*sd*-1)						
TT	0	0	47	47		
Tt	0	80	0	80	351.0**	0
tt	44	0	0	44		
Total	44	80	47	171		
B: Taichung 65(*A,Pn,Pau*)/Taichung 65(*sd*-1)						
TT	0	0	66	66		
Tt	1	133	1	135	504.5**	1.87
tt	63	3	0	66		
Total	64	136	67	267		
C: Milyang 23/Kasalath						
TT	0	0	67	67		
Tt	0	124	2	126	463.4**	0.8
tt	44	0	0	44		
Total	44	124	69	237		

tion value of 0–1.87%, and an average map distance of 0.89 cM.

Conclusion

We report here that an esterase isozyme locus, *EstI*-2, visualized by isoelectric focusing, is tightly linked to the semidwarf (*sd*-1) character in rice, with a recombination value of 0–1.87%, equivalent to approximately 0.89 cM. The *EstI*-2 marker could be used for precise in-vitro selection of individuals carrying the semidwarf gene using single seeds or very young leaf tissue, before this character is fully expressed. The use of a codominant marker to select for heterozygotes carrying *sd*-1 in a backcross or recurrent selection program offers the possiblity of avoiding a generation of progeny testing. Appropriate application of marker-assisted selection, using the *EstI*-2 marker for the semidwarf character in combination with other markers linked to genes of agronomic importance in rice, holds promise for improving the efficiency of a breeding program. This work also provides the basis for high-resolution genetic and physical mapping near *sd*-1, aimed at ultimately cloning this valuable gene.

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