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Assignment of a Brown Planthopper (*Nilaparvata lugens* Stål) Resistance Gene *bph4* to the Rice Chromosome 6

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A Sri Lankan *indica* rice (*Oryza sativa* L.) cultivar Babawee harboring a brown planthopper (BPH) (*Nilaparvata lugens* Stål) resistance gene *bph4* was crossed as a male parent with two susceptible cultivars, either *indica* IR24 or *japonica* Tsukushibare. Segregation of the BPH resistance in the two crosses was studied by directly assaying the F_2 phenotypes and by determining the F_2 genotypes based on the F_3 phenotypes. In both cross combinations, the segregation of the BPH resistance significantly deviated from the ratio expected for the single recessive gene model. Using bulked DNAs of homozygous resistant and susceptible F_2s and the parents, seven out of 214 RFLP markers were selected as linked markers, of which six on chromosome 6 were common in the two cross combinations. Two microsatellite markers on chromosome 6 were also linked to *bph4*. Although the map position of *bph4* could not be determined, the gene was assigned to the distal region of the short arm of rice chromosome 6 based on the bulked segregant analysis and linkage analysis.

Key Words: ***Oryza sativa* L., brown planthopper, resistance gene, *bph4*, RFLP, microsatellite.**

Introduction

The brown planthopper (BPH), *Nilaparvata lugens* Stål (Homoptera: Delphacidae), is one of the most serious insect pests of rice throughout the Asian rice-growing countries. To solve the BPH problem, naturally evolved resistance system(s) should provide a promising and readily acceptable means of control. Genetic and breeding research on BPH resistance has been conducted since the mid-1960s (Athwal *et al.* 1971). So far at least 12 major BPH resistance genes from *indica* cultivars and two wild relatives have been identified and characterized. Five genes (*Bph1*, *bph2*, *Bph10(t)*, *bph11(t)* and *bph12(t)*) have been mapped on the rice chromosomes 12, 4 and 3 using RFLP markers (Ishii *et al.* 1994, Hirabayashi and Ogawa 1995, Huang *et al.* 1997, Murata *et al.* 1997, 1998, Hirabayashi *et al.* 1998, 1999).

A recessive BPH resistance gene *bph4* was first identified in a Sri Lankan *indica* rice cultivar Babawee (Lakshminarayana and Khush 1977). The *bph4* gene was reported to be either allelic or closely linked to a dominant BPH resistance gene *Bph3* (Sidhu and Khush 1979). These two resistance genes were first assigned to rice chromosome 10 based on trisomic analysis (Ikeda and Kaneda 1981). Later, however, it was suggested that *Bph3* was located on chromosome 4 (Khush, personal communication). We therefore attempted to determine the *bph4* locus on the rice linkage map. For this, we made two independent crosses using Babawee as a pollen donor parent of *bph4* and two susceptible cultivars of *indica* and *japonica* rice as seed parents.

Materials and Methods

Plant materials

The following two crosses were made using a BPH-resistant Sri Lankan *indica* rice (*Oryza sativa* L.) cultivar Babawee as a donor of *bph4* (Lakshminarayana and Khush 1977). Babawee was crossed as a pollen parent with two BPH-susceptible rice cultivars, i.e. an *indica* cv. IR24 and a *japonica* cv. Tsukushibare as seed parents. F_2 and F_3 progenies were obtained from these *indica*/*indica* and *japonica*/*indica* crosses.

BPH resistance bioassay

Methods for the maintenance of a BPH colony (biotype 1) and the bioassay of BPH resistance and susceptibility in F_2s and F_3s followed those described by Murata *et al.* (1998). Briefly, F_2 phenotypes (resistant or susceptible) were determined by assaying the F_2 individuals using the mass seedling test (Kaneda *et al.* 1981), a modified version of the original bulk seedling method developed by Pathak *et al.* (1969). To determine F_2 genotypes (homozygous resistant: RR, heterozygous: RS, or homozygous susceptible: SS), 17

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F_3 seedlings from each of the F_2 plants were planted in a 12 cm-row plot of a row spacing of 2.2 cm with two replications in a tray (24.5 × 29.5 × 1.5 cm). Two rows each of the resistant and susceptible cultivars were grown as controls together with two rows each of eight F_3 lines in a tray. The tray was placed in a ventilated cage and incubated in a growth chamber under a 16-h photoperiod and at day-night temperatures of 30-25°C. At the 1st to the early 2nd leaf stages, the seedlings were infested with the 2nd to the 3rd instar nymphs at a density of 7 nymphs per seedling. At 13 days after infestation, the damage caused to the seedlings was compared with that in the control rows to determine their phenotypes.

Bulked segregant analysis and linkage analysis using RFLP and microsatellite markers

After the determination of the *bph4*-genotypes of F_2s, DNAs were extracted and bulked from 8 RR and 8 SS F_2 plants from the IR24/Babawee cross. Six F_2 plants were used to construct both RR and SS bulk DNAs in the case of the Tsukushibare/Babawee cross. These RR and SS bulk DNAs were used together with the parental DNAs in a bulked segregant analysis (Michelmore *et al.* 1991) to detect linked markers. Bulked DNAs were digested with 8 restriction enzymes (*Bam*HI, *Bgl*II, *Eco*RV, *Hind*III, *Apa*I, *Dra*I, *Eco*RI and *Kpn*I), fractionated by electrophoresis through 0.6% agarose gel, and blotted onto nylon membranes (Boehringer Mannheim) in 0.4 N NaOH. Southern blot hybridization and signal detection were performed according to the method of Murata *et al.* (1998) using 214 RFLP markers as probes. The markers were provided by the National Institute of Agrobiological Resources, Tsukuba, Japan, and by Cornell University, U.S.A. Four and six microsatellite markers (McCouch *et al.* 1997) located respectively on the rice chromosomes 4 and 6 (see Results) were also used in the bulked segregant analysis in the following way. The microsatellites were PCR-amplified, fractionated by electrophoresis through 4% polyacrylamide gel, and visualized by staining with Bio-Rad Silver Staining Kit as previously described (McCouch *et al.* 1997).

A linkage analysis was performed using RFLP and microsatellite markers, which were selected by the bulked segregant analysis, in 64 F_2s derived from the IR24/Babawee cross and in 74 F_2s from the Tsukushibare/Babawee cross. Recombination values were calculated using MAPMAKER Version 2.0 with LOD scores higher than 3.0 (Lander *et al.* 1987) and linkage maps were constructed.

Results

Segregation of BPH resistance/susceptibility

Segregation of BPH resistance (R) and susceptibility (S) in the two F_2 populations was studied by directly assaying the phenotypes of F_2 individuals. Individuals without detectable damage were estimated to be resistant, while those that withered and died were estimated to be susceptible. In the bioassay of 258 F_2 seedlings from the IR24/Babawee cross, the resistance segregation deviated significantly from the single recessive gene ratio of 1R:3S, with more resistant progenies than expected (Table 1). In the Tsukushibare/Babawee cross, a similar deviation towards more resistant progenies was observed. We next performed genotyping of F_2 individuals by assaying the phenotypes of F_3 progenies. In this analysis, F_2s showing more than 90% of resistant F_3 progenies were estimated to be homozygous resistant (RR), those showing less than 10%, homozygous susceptible (SS), and all the others, heterozygous (RS). In the IR24/Babawee cross, the segregation ratio thus determined in 138 F_2 seedlings deviated from the expected 1RR:2RS:1SS ratio (Table 1). The segregation ratio in 160 F_2s in the Tsukushibare/Babawee cross also showed a deviation. In both crosses, the numbers of F_2 seedlings that were estimated to be RS were much larger than expected. In the bioassay, we noted considerable numbers of seedlings (up to 18.3% of F_3s per F_2) that showed intermediate levels of resistance. In the intermediate types, the first leaves either withered or remained alive but the second leaves did not develop during the bioassay period. No such intermediate types were observed among the resistant and susceptible parent plants, which were tested together with the segregating populations in the same bioassay cage. All the intermediate types were classified as susceptible in the present analysis based on the judgment that they did not carry a major resistance gene *bph4*. Fig. 1 shows the distribution of the percentage frequency of resistant F_3 progenies from F_2 individuals. The frequency distribution of F_3 progenies in F_2s that were estimated to be heterozygous was continuous in both cross combinations. In the IR24/Babawee cross, the mode of the percentage of resistant progenies was 30-40%, supporting that *bph4* is a recessive gene. The mode of the resistance frequency in the Tsukushibare/Babawee cross deviated towards a larger value (50-60%).

Table 1. Segregation of BPH resistance in F_2 and F_3 progenies derived from the IR24/Babawee and Tsukushibare/Babawee crosses

F_2 test[1]	Number of F_2 individuals		
	Resistant	Susceptible	Total[2]
IR24/Babawee	112	146	258*
Tsukushibare/Babawee	85	150	235*
F_3 test	Number of F_2 individuals		
	RR	RS	SS	Total[2]
IR24/Babawee	14	93	31	138*
Tsukushibare/Babawee	12	133	15	160*

[1] IR24 (a total of 260 seedlings) and Tsukushibare (272) were susceptible, while Babawee (268) was resistant in the bioassay.

[2] *indicates significant deviation at the 0.1% level from the 1R:3S ratio in the F_2 test and the 1RR:2RS:1SS ratio in the F_3 test.

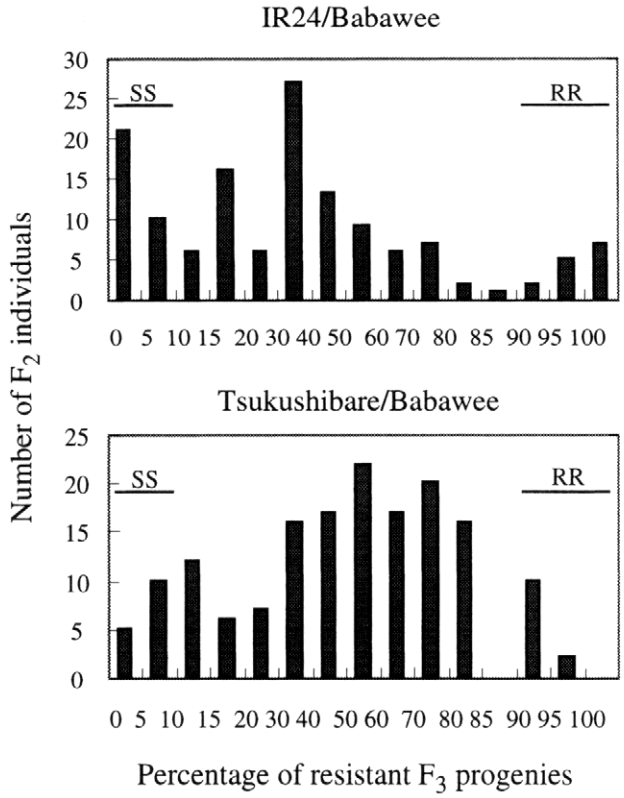

Fig. 1. Frequency distribution of resistant F_3 progenies derived from individual F_2s. The upper panel indicates the results obtained from the IR24/Babawee cross and the lower panel from the Tsukushibare/Babawee cross. RR: homozygous resistant, SS: homozygous susceptible. All the others were estimated to be RS.

Bulked segregant analysis and linkage analysis using RFLP and microsatellite markers

In the bulked segregant analysis, DNAs extracted from 8 RR and 8 SS F_2s of the IR24/Babawee cross and those from 6 RR and 6 SS F_2s of the Tsukushibare/Babawee cross were used. The RR bulks were constructed from the F_2s that showed an average of 96.3% resistant F_3s in the IR24/Babawee cross and 93.2% resistant F_3s in the Tsukushibare/Babawee cross. The SS bulks were constructed from the F_2s that showed 98.0% and 96.9% susceptible F_3s for the IR24/Babawee and Tsukushibare/Babawee crosses, respectively. Southern blot profiles that were generated by a combination of 214 RFLP markers and eight restriction enzymes were compared among the parental DNAs and the RR and SS bulk DNAs. The RFLP markers were randomly selected to cover the 12 rice chromosomes. As expected, the *japonica-indica* combination was more polymorphic (68 polymorphic markers) than the *indica-indica* combination (51 polymorphic markers). Six RFLP markers on chromosome 6 (C76A, RZ516, R1954, RZ588, R2147 and R2171) and one on chromosome 4 (C76B) were commonly polymorphic and associated with R/S in the two cross combinations. Another marker R2869 on chromosome 6 was polymorphic and associated with R/S in the IR24/Babawee cross but monomorphic in the Tsukushibare/Babawee cross. R2170 on chromosome 3 was also polymorphic and R/S-associated, but it was monomorphic in the Tsukushibare/Babawee cross. An example of the segregation of two RFLP markers, R2147 and RZ588, in F_2 seedlings is shown in Fig. 2. A probe C76 generated a polymorphic marker fragment that was designated as C76A on chromosome 6 and C76B on

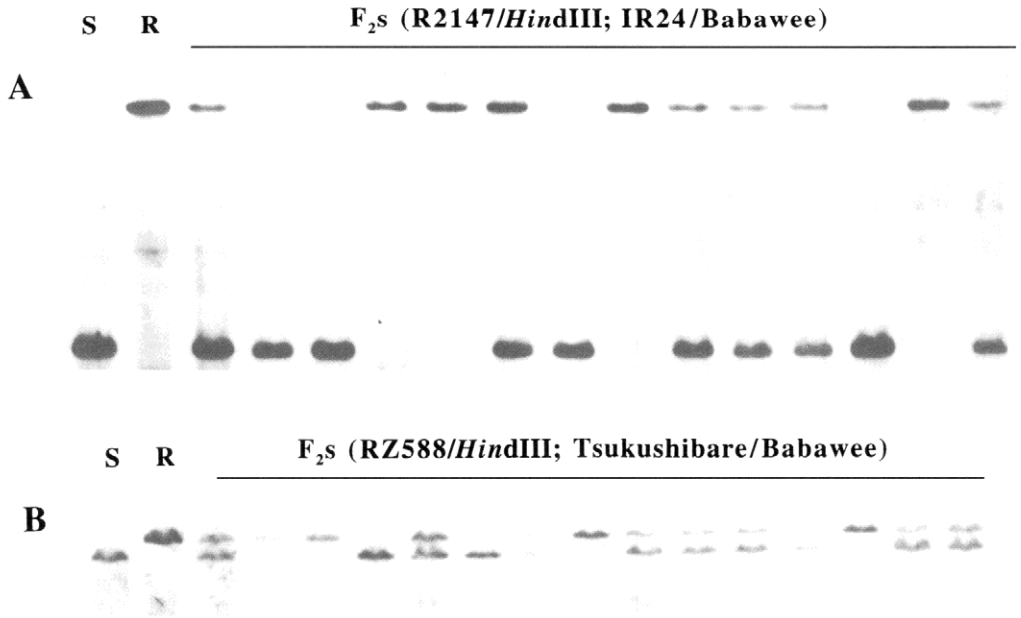

Fig. 2. R/S-associated RFLP markers and their segregation in F_2 plants. A. Southern blot profile of R2147/*Hin*dIII in F_2s from the IR24/Babawee cross. B. Southern blot profile of RZ588/*Hin*dIII in F_2s from the Tsukushibare/Babawee cross. S: susceptible parents, IR24 or Tsukushibare and R: resistant parent, Babawee.

chromosome 4 (Harushima *et al.* 1998). C76 gave an identical Southern blot profile, and thus the two markers could not be distinguished.

To confirm the chromosome assignment of *bph4*, we employed microsatellite markers in the bulked segregant analysis using the same RR and SS bulks prepared from the IR24/Babawee cross. In this analysis, we used four microsatellite markers that were located on chromosome 4 (RM261, RM252, RM241 and RM255) and six markers on chromosome 6 (RM204, RM225, RM217, RM238B, RM3 and RM30) (McCouch *et al.* 1997). The analysis showed that two of the microsatellite markers on chromosome 6 (RM225 and RM217) were associated with R/S.

Linkage analysis was attempted using the polymorphic markers on the rice chromosome 6. Linkage analysis was also attempted for chromosome 4. In these analyses, 64 F_2s (7 RR:38 RS:19 SS) and 74 F_2s (12 RR:44 RS:18 SS) were used for the IR24/Babawee cross and the Tsukushibare/Babawee cross, respectively. The mapping populations showed significant deviations from the expected 1 RR:2 RS:1 SS ratio for BPH resistance segregation, while segregation of all the polymorphic markers was normal. The segregation of markers on chromosome 6 is shown in Table 2. In the linkage maps constructed for chromosome 4, the marker C76B selected from the bulked segregant analysis was located at the distal end (data not shown), which differed largely from the position in the standard Nipponbare/Kasalath map (Harushima *et al.* 1998). In the linkage maps constructed for chromosome 6, the order of all the markers agreed with that of the standard map. However, the estimated distances of some markers were much larger than those of the standard map, particularly in the IR24/Babawee cross (Fig. 3). The locus of *bph4* thus could not be determined, but it was suggested that it might be located in the distal region of the marker C76A on the short arm of rice chromosome 6.

Discussion

Based on the bulked segregant analysis and linkage analysis using RFLP and microsatellite markers, we assigned the *bph4* locus to the short arm of rice chromosome 6 (Fig. 3). However, we could not determine the position of *bph4* in the linkage maps, due to the significant deviations in the BPH resistance segregation in the two mapping populations (Table 1 and Fig. 1). Our results of BPH resistance segregation did not agree with the single recessive gene ratio reported by Lakshminarayana and Khush (1977) and Ikeda and Kaneda (1981) for *bph4*. Segregation of all the linked markers, however, showed the expected co-dominant gene ratio of 1:2:1 (Table 2). This finding suggested that no aberrant segregation distortion occurred in the region covering the *bph4* locus. A varying degree of sterility was observed (the average rate of sterile florets was 38.2 ± 13.2%) in the F_2s of the Tsukushibare/Babawee cross. No notable sterility was observed in the IR24/Babawee cross, although seed set data were not available. Sterility thus may not be responsible for the observed deviations in the BPH resistance segregation and the deviation may be ascribed to the accuracy of the BPH bioassay and/or to the presence of minor genes.

In the BPH bioassay, we observed considerable numbers of seedlings that showed intermediate levels of resistance in both crosses. No such intermediate types were observed in the resistant and susceptible parents and in the previous

Table 2. Segregation of 7 RFLP and 2 microsatellite markers linked to *bph4* on the rice chromosome 6 in F_2 progenies derived from the IR24/Babawee and Tsukushibare/Babawee crosses

Cross combination	Marker[1)]	Number of F_2s with genotypes of			χ^2 (1:2:1)[2)]
		IR24 or Tsukushibare	Hetero	Babawee	
IR24/Babawee					
	R2869	21	32	11	3.13
	C76A	17	35	12	1.06
	RZ516	22	30	12	3.38
	RM225*	19	32	13	1.13
	RM217*	20	29	15	1.34
	RZ588	20	27	17	1.84
	R1954	17	29	14	0.37
	R2147	25	26	13	3.94
	R2171	25	25	14	4.03
Tsukushibare/Babawee					
	C76A	17	42	15	1.46
	RZ516	21	36	17	0.49
	RZ588	21	34	19	0.59
	R1954	12	45	17	4.13
	R2147	17	33	24	2.19
	R2171	16	38	20	0.49

[1)] *indicates microsatellite markers. All the others are RFLP markers.

[2)] All the values do not significantly deviate from the 1:2:1 ratio.

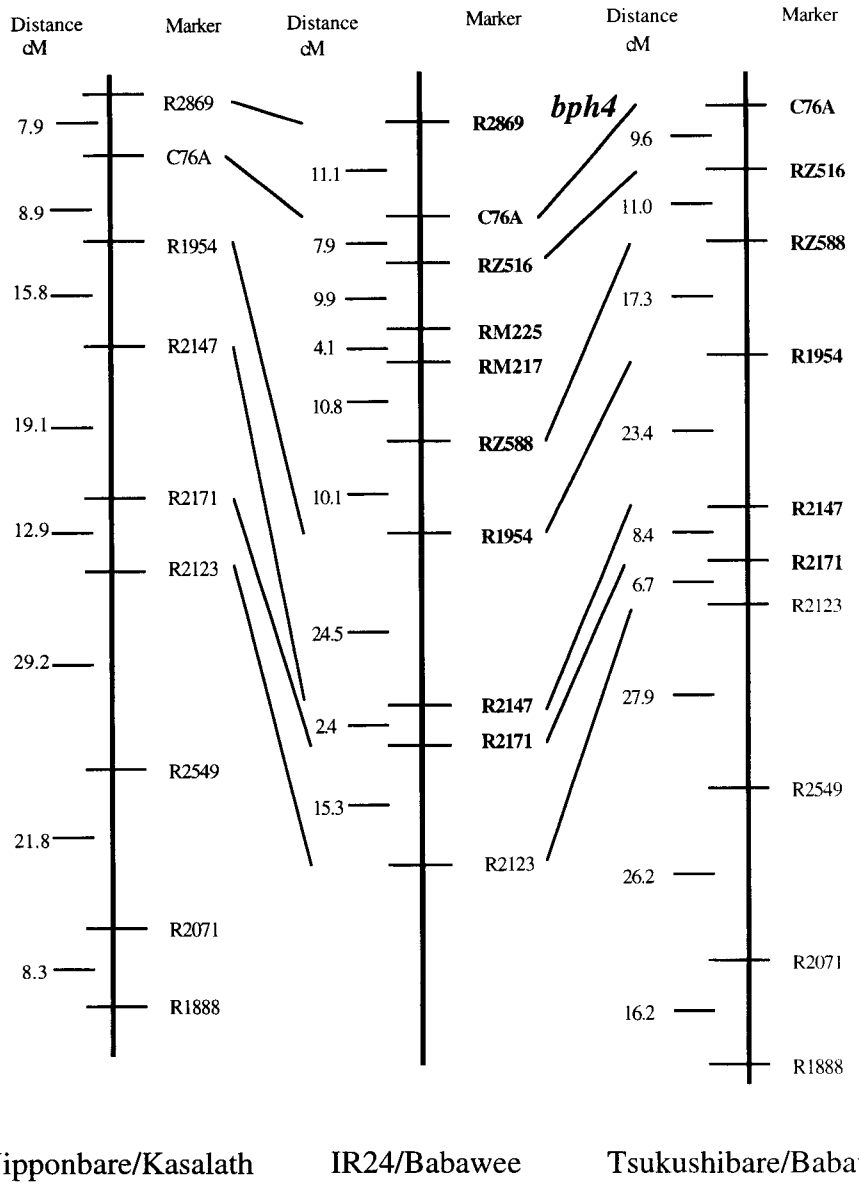

Fig. 3. Linkage maps of the rice chromosome 6. The left map represents a standard map of Nipponbare /Kasalath (Harushima *et al.* 1998), and the other two represent maps constructed in the present study. Bold-faced markers indicate R/S-associated regions detected by the bulked segregant analysis. The position of *bph4* is arbitrary because it could not be determined due to the deviation in the segregation in the mapping populations.

study with other BPH resistance genes, *Bph1* and *bph2* (Murata *et al.* 1997, 1998). In the present bioassay, it was difficult to prepare uniform seedlings at the first leaf stage for infestation with the BPH, due to the segregation of the seedlings with different rates of early growth. Growth stage of the test seedlings is known to be critical for the precision of the BPH bioassay, and the stage immediately preceding the development of the first leaf has been recommended (Athwal *et al.* 1971, Kaneda *et al.* 1981). The occurrence of the intermediate phenotypes could be due to the non-homogeneous assay populations including seedlings at different growth stages. The larger numbers of F_2 individuals that were estimated to be RS could also be attributed to the assay conditions.

Segregation of the BPH resistance in the F_3 progenies derived from F_2s that were estimated to be heterozygous showed a continuous distribution (Fig. 1). The results suggest that the BPH resistance in Babawee might be controlled by the major resistance gene *bph4* as well as by some other minor genes. One RFLP marker C76B on chromosome 4 was commonly associated with R/S genotypes in both cross combinations. Because of the identical RFLP patterns generated by this probe with those by C76A, it was not possible to determine whether C76B was actually associated

with the BPH resistance in Babawee. It was first reported that *bph4* was located on chromosome 10 (Ikeda and Kaneda 1981). Later, however, it was suggested that a dominant BPH resistance gene *Bph3* identified in another Sri Lankan variety Rathu Heenati was located on chromosome 4 (Khush, personal communication). Since *Bph3* is either allelic or closely linked to *bph4* in Babawee (Sidhu and Khush 1979), possible association of *bph4* with C76B could not be ruled out. Another RFLP marker R2170 on chromosome 3 was also associated with R/S in the Tsukushibare/Babawee cross. The marker association with R/S could not be determined in the IR24/Babawee cross, because of the monomorphic RFLP patterns produced in this cross combination. Whether Babawee harbors additional BPH resistance genes on chromosomes 4 and/or 3 besides the major recessive gene *bph4* on chromosome 6 must be further elucidated.

Moderate and durable level of BPH resistance conferred by polygenes was already reported in IR64 (Cohen *et al.* 1997). QTL mapping using a doubled haploid population showed that the BPH resistance in IR64 is controlled by seven loci located on six of the 12 rice chromosomes in addition to the major gene *Bph1* on chromosome 12 (Alam and Cohen 1998). To critically evaluate the polygenic nature of the BPH resistance in Babawee, a scoring method using criteria for tolerance, antixenosis and antibiosis (Kennedy *et al.* 1987) should be employed in a future QTL study.

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