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RFLP mapping of a brown planthopper (*Nilaparvata lugens* Stål) resistance gene *bph2* of *indica* rice introgressed into a *japonica* breeding line 'Norin-PL4'

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A rice gene *bph2* for resistance against brown planthopper (BPH), *Nilaparvata lugens* Stål, was reported to be recessive and either allelic or closely linked to a dominant BPH resistance gene, *Bph1*. *bph2* was introgressed from an *indica* resistance donor variety, 'IR1154-243', into a *japonica* breeding line, 'Norin-PL4'. A segregation analysis of BPH resistance in F_2 and F_3 progenies from a cross of a *japonica* susceptible variety, 'Tsukushibare', and 'Norin-PL4', however, showed that the resistance gene in 'Norin-PL4' behaved as a dominant gene. Genotyping of 'Norin-PL4' using 99 RFLP markers covering all 12 rice chromosomes showed that 'Norin-PL4' possessed a large segment of chromosome 12 introgressed from 'IR1154-243'. Six RFLP markers on the introgressed segment was cosegregated with BPH resistance and *bph2* was mapped at 3.5 cM from the closest RFLP marker, G2140. The position of *bph2* on the standard 'Nipponbare'/'Kasalath' map was at a considerable distance (about 30 cM) from that of *Bph1* previously mapped using a different population. Despite this, no susceptible recombinants were obtained in a large number of F_3 progeny from crosses between two *Bph1* carrier lines and 'Norin-PL4'. Problems of dominance/recessiveness and no recombinations between the two loci were discussed.

INTRODUCTION

Brown planthopper (BPH), *Nilaparvata lugens* Stål (Homoptera: Delphacidae), is one of the most destructive insect pests of rice throughout the tropic, subtropic and temperate rice-growing areas in South to Southeast Asia and Oceania. BPH sucks phloem saps of rice plants and causes a severe damage symptom known as hopper-burn. BPH also acts as vectors of rice tungro virus, grassy stunt virus, and rugged stunt virus (Heinrichs, 1979; Saxena and Khan, 1989). Both of the direct feeding and the transmitted viral diseases cause considerable yield losses in rice production.

Genetic analysis of BPH resistance was first conducted by Athwal et al. (1971) at the International Rice Research Institute, Philippines. In this study, BPH resistance in an Indian local variety, 'Mudgo', and two other breeding lines, 'CO22' and 'MTU15', was concluded to be controlled by a single dominant gene, *Bph1*, and the resistance in a breeding line, 'Karsamba Red ASD7', by a single recessive gene, *bph2*. Further, *bph2* was shown to be either closely linked or allelic to *Bph1*, because no recombinants were obtained (Athwal et al., 1971). Two additional BPH resistance genes were identified, i.e., *Bph3* in a Sri Lankan local variety, 'Rathu Heenati', and *bph4* in another Sri Lankan local variety, 'Babawee' (Lakshminarayana and Khush, 1977). These two genes were also reported to be either closely linked or allelic. Kabir and Khush (1988) further identified *bph5* in 'ARC10550', *Bph6* in 'Swarnalata' and *bph7* in 'T12', using BPH biotypes from Bangladesh. Ikeda and Kaneda (1986) and Nemoto et al. (1989a), using three different laboratory biotypes and two resistant varieties that carry *Bph3* and *bph4*, identified a new recessive resistance gene, *bph8*, in 'Thai Col. 5', 'Thai Col. 11' and 'Chin Saba', and a new dominant gene, *Bph9*, in three Sri Lankan local varieties, 'Pokkali',

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'Balamawee' and 'Kaharamana'. A wild relative of rice, *Oryza australiensis*, was also shown to possess a dominant resistance gene, *Bph10(t)*, that was introgressed into an *indica* breeding line (Ishii et al., 1994).

Four BPH resistant *japonica* breeding lines have been registered in Japan until now: 'Norin-PL3' with *Bph1* from 'Mudgo' (Kaneda et al., 1985), 'Norin-PL4' with *bph2* from 'IR1154-243' (Kaneda et al., 1986), 'Norin-PL7' with *bph4* from 'Babawee' (Nemoto et al., 1988), and 'Norin-PL10' with *Bph3* from 'Rathu Heenati' (Nemoto et al., 1989b). 'Norin-PL7', however, has recently been withdrawn from the registration, because of the finding that it carries *Bph1* from 'Mudgo' instead of *bph4* from 'Babawee', this being apparently due to mis-introgression (Murata et al., 1997). *Bph1* and *bph2* were first assigned to chromosome 4 and *Bph3* and *bph4* to chromosome 10 by trisomic analyses and linkage analyses using morphological marker stocks (Ikeda and Kaneda, 1983; Ikeda, 1985). However, *Bph1* from a breeding line, 'TKM6', was later mapped on chromosome 12 by a linkage analysis using RFLP markers (Hirabayashi and Ogawa, 1995). This result was confirmed by studies using different mapping populations (Huang et al., 1997; Murata et al., 1997). *Bph10(t)* from *O. australiensis* introgressed into *indica* line was also mapped on chromosome 12 by RFLP analysis (Ishii et al., 1994).

In this paper we report the result of segregation analysis of BPH resistance using the progeny from a cross between a susceptible *japonica* variety, 'Tsukushibare', and the resistant *japonica* introgression line, 'Norin-PL4'. RFLP mapping was conducted to locate *bph2* on the rice linkage map.

MATERIALS AND METHODS

Plant materials. The following two *japonica* introgression lines were used: 'Norin-PL4' (pedigree: Asominori*3/IR1154-243, BC_2F_{11}) with *bph2* derived from an *indica* variety, 'IR1154-243' (Kaneda et al., 1986), and 'Norin-PL3' (pedigree: $F_6$324 [Houyoku/Mudgo//Kochikaze///IR781-1-94/4/Houyoku]/Akitsuho//Tsukushibare) with *Bph1* from an Indian local variety, 'Mudgo' (Kaneda et al., 1985). 'Norin-PL7' originally registered as a *bph4* introgression line (Nemoto et al., 1988) was used as an additional *Bph1* carrier (Murata et al., 1997). Two susceptible *japonica* cultivars, 'Tsukushibare' and 'Asominori', and the *bph2* donor variety, 'IR1154-243', were used as controls. F_2 and F_3 progenies obtained from a cross of 'Tsukushibare'/'Norin-PL4' were used in a segregation analysis of BPH resistance and RFLP mapping of *bph2*. F_3 progenies of crosses of 'Norin-PL3'/'Norin-PL4' and 'Norin-PL7'/'Norin-PL4' were used in an allelism test for *bph2* and *Bph1*.

BPH resistance test. A BPH colony used in the resistance bioassay was a mixture of two colonies provided by Kyushu Agricultural Experiment Station and Hyogo Agriculture Research Center. The colony was maintained in a growth chamber under a 15 h photoperiod and day-night temperatures of 30–25°C. Genotypes of F_2 plants were determined using F_3 progenies in the following way. Seventeen F_3 seedlings from each of F_2 plants were planted in a 12 cm-row plot with row spacing of 2.2 cm with two replications in a tray (22.5 × 29.5 × 1.5 cm). Two rows each of the resistant breeding lines, the resistance donor and the susceptible cultivar were grown together as controls with F_3 progenies in a tray. At the 1st leaf stage, the 2nd to the 4th instar nymphs were released for infestation at a density of 10 to 12 nymphs per seedling. At day 9–10 after infestation, damages on the seedlings of each row were compared with the control rows to judge their phenotypes, either resistant or susceptible. Phenotypes of F_2 individuals were also determined directly under the same bioassay conditions.

Genotyping of 'Norin-PL4' and linkage analysis. Genotyping of 'Norin-PL4' was made using 99 RFLP markers covering 12 chromosomes of the rice genome. DNAs from 'IR1154-243', 'Asominori', and 'Tsukushibare' were used as references. In the linkage analysis, bulked DNA of about 20 F_3 individuals from each of 90 F_2s derived from a cross of 'Tsukushibare'/'Norin-PL4' was used. Total DNA was digested with eight restriction enzymes (*Bam*HI, *Bgl* II, *Eco*RV, *Hin*dIII, *Apa*I, *Dra*I, *Eco*RI, and *Kpn*I), electrophoresed through 0.6% agarose gel, and blotted onto nylon membranes (Boehringer Mannheim) in 0.4 N NaOH. The membranes were washed in 2 × SSC, air-dried and baked at 120°C for 20 min. DNA probes used for Southern hybridization were obtained after PCR amplification of cloned rice RFLP markers provided by Rice Genome Research Program, National Institute of Agrobiological Resources, Japan. Southern hybridization and signal detection were made by ECL™ Direct Nucleic Acid Labeling and Detection System (Amersham). Recombination values between *bph2* and RFLP markers were calculated by MAPMAKER Version 2.0 (Lander et al., 1987).

RESULTS

Segregation of BPH resistance in a cross of 'Tsukushibare'/'Norin-PL4'. Segregation of BPH resistance was studied using F_2 and F_3 progenies derived from a cross of 'Tsukushibare'/'Norin -PL4'. The BPH resistance assay showed that the segregation of resistance in 52 F_2s was significantly deviated from the recessive, single gene ratio of 1 resistant (R): 3 susceptible (S) but fitted to the dominant, single gene ratio of 3R : 1S (Table 1). On the other hand, the F_2 ratio evaluated from the assay of 159 F_3 lines did not fit to the single gene ratio of 1RR : 2RS : 1SS, showing more heterozygotes than expected. A test for the homogeneity of ratio showed that the F_3 popula-

Table 1. Segregation of BPH resistance in F_2 and F_3 progenies derived from a cross of 'Tsukushibare'/'Norin-PL4'

F_2 test	Number of F_2 individuals		
	Resistant	Susceptible	Total
'Tsukushibare'/'Norin-PL4'	35	17	52[a]
'Norin-PL4'	51	0	51
'Tsukushibare'	0	51	51

F_3 test	Number[b] of F_3 lines	F_2 genotype	Number of F_3 plants		
			Resistant	Susceptible	Total
	28	RR	1,786	24	1,810
	96	RS	4,360	1,762	6,122[c]
	35	SS	4	1,959	1,963
Total	159		6,150	3,745	9,895

[a] χ^2 of 3R: 1S = 1.64 (p = 0.18).
[b] An average of 61 individuals per line were assayed for BPH resistance in triplicated tests. χ^2 for 1RR : 2RS : 1SS = 7.47 (p = 0.025), for 3R : 1S = 0.76 (p = 0.38).
[c] χ^2 for 3R : 1S = 46.7 (p < 0.001).
More than 500 plants of 'Asominori' studied were all susceptible.

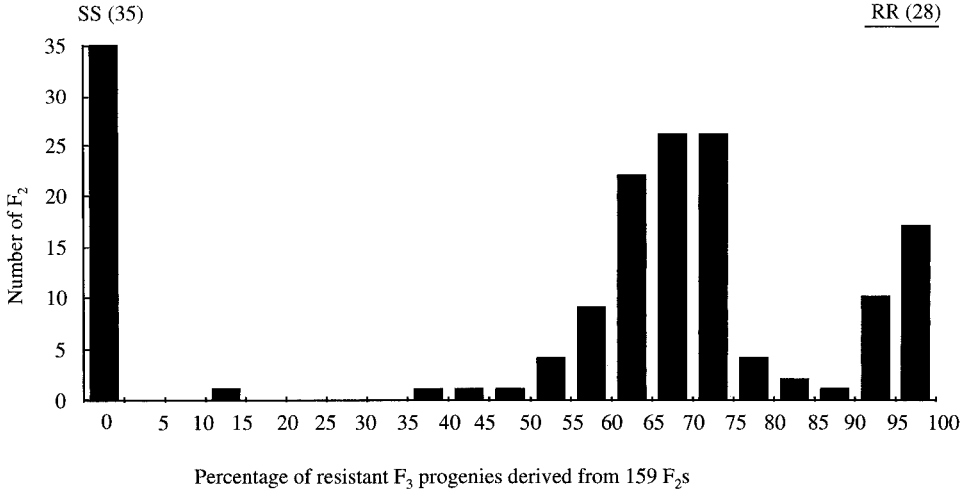

Fig. 1. The frequency distribution of resistant F_3 progenies derived from 159 F_2s from a cross of 'Tsukushibare'/'Norin-PL4'.

tion was heterogeneous. Thus the segregation ratio was deviated significantly from 3R : 1S in 29 out of 96 F_3 lines derived from the heterozygous F_2s. The frequency distribution of resistant F_3 progeny from 159 F_2s was skewed towards the lower percentage of resistant progenies than that expected based on a single dominant gene (Fig. 1).

RFLP genotyping of 'Norin-PL4'. 'Norin-PL4' was genotyped to confirm the introgression of chromosome segment(s) from the donor variety, 'IR1154-243', using 99 RFLP markers chosen from all 12 chromosomes of the rice genome. A comparison of RFLP patterns among 'Norin-PL4', 'IR1154-243', 'Asominori', and 'Tsukushibare' suggested that a large segment spanning more than 51.4 cM on chromosome 12 in 'Norin-PL4' was identical to that of 'IR1154-243', based on the 'Nipponbare'/Kasalath' map (Kurata et al., 1994) (Fig. 2). Six polymorphic markers were detected in this introgressed region, and four other smaller regions were also suggested to be derived from 'IR1154-243'. Among them three regions, each on chromosomes 1, 4, and 11, were polymorphic between 'Tsukushibare' and 'Norin-PL4' and also between 'Asominori' and 'IR1154-243', but a region on chromosome 2 was monomorphic among the resistant lines and 'Tsukushibare'. Regions defined by 15 markers were monomorphic among all the lines tested.

Linkage analysis. Segregation of RFLP markers was studied using bulked DNAs of about 20 F_3 plants derived from each of the randomly selected 90 F_2s and the result

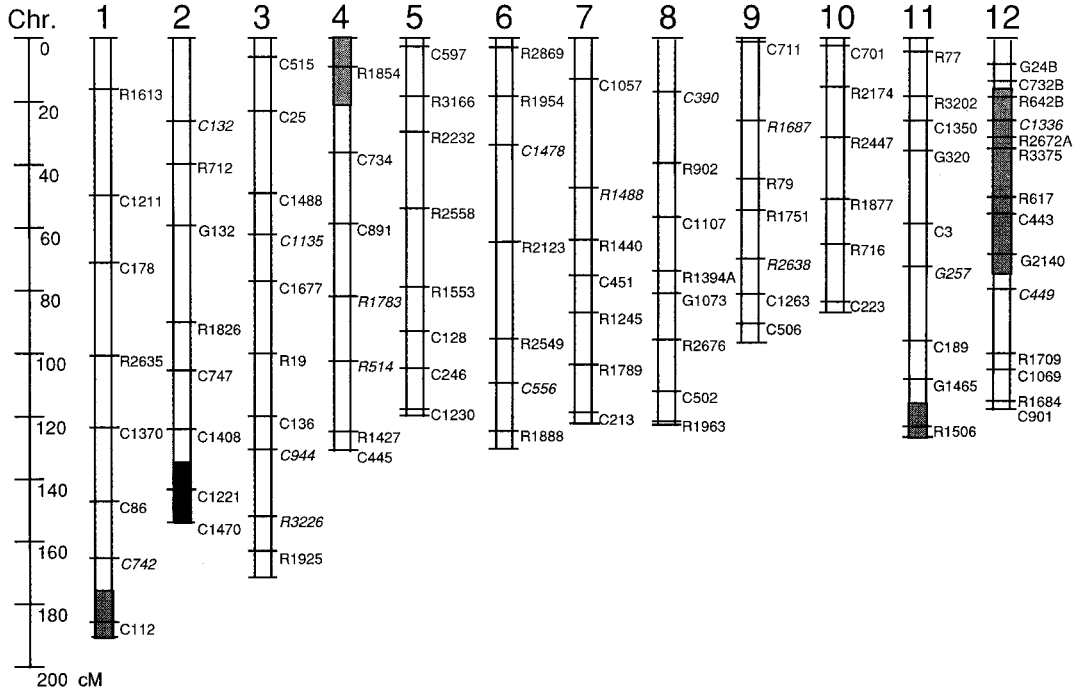

Fig. 2. A graphical genotype of Norin-PL4'. Hatched boxes on chromosomes 1, 4, 11 and 12 indicate the regions commonly polymorphic between 'Tsukushibare' and 'Norin-PL4' and between 'Asominori' and 'IR1154-243', but monomorphic between 'IR1154-243' and 'Norin-PL4'. A black box on chromosome 2 indicates the region monomorphic among the resistant lines and 'Tsukushibare' and polymorphic between 'Asominori' and all other lines. Italicized markers were monomorphic among all the lines. Among seven RFLP markers in the region on chromosome 12, C1336 was monomorphic among the lines. Proximal ends of the boxed regions are arbitrarily placed at the middle of the two flanking markers. The map was positioned in a way that the short arms are on the top.

Table 2. Segregation of BPH resistance (*bph2*) and six *bph2*-liked RFLP markers on chromosome 12 in 90 F_2s derived from a cross of 'Tsukushibare'/'Norin-PL4'

Marker	Number of F_2s with genotypes of 'Tsukushibare' homo : Hetero : '*IR1154-243*' homo	χ^2 values
bph2	21 : 53 : 16 (90)	3.4
G2140	22 : 49 : 19 (90)	0.9
C443	24 : 42 : 16 (82)	1.6
R617	26 : 45 : 17 (88)	1.9
R3375	10 : 27 : 9 (46)	1.4
R2672A	25 : 48 : 16 (89)	2.4
R642B	19 : 32 : 12 (63)	1.6

F_2 genotypes for 6 RFLP markers were determined using bulked DNAs from 20 F_3 plants per F_2. χ^2 values are not significant for all markers in this mapping population. Figures in parentheses indicate numbers of F_2s analyzed.

was combined with the genotype of *bph2*. In this mapping population, *bph2* genotype determined using F_3s did not deviate from the single gene ratio of 1 : 2 : 1 (Table 2). The study showed that six RFLP markres on rice chromosome 12 were cosegregated with *bph2*, while RFLP markers on four other chromosomes were segregated independently. It was also shown that the segregation ratio of the six RFLP markers did not deviate from the expected ratio (Table 2).

bph2 was mapped at 3.5 cM from the closest RFLP marker, G2140, on chromosome 12 (Fig. 3). The map distance covering the introgressed region was about 29 cM which was shorter than that (more than 51.4 cM) of the corresponding region on the standard 'Kasalath'/'Nipponbare' map. The position of *bph2* on the standard map was about 30 cM apart from that of *Bph1* previously mapped using the population derived from a cross of 'Tsukushibare'/'Norin-PL7' (Murata et al., 1997). How-

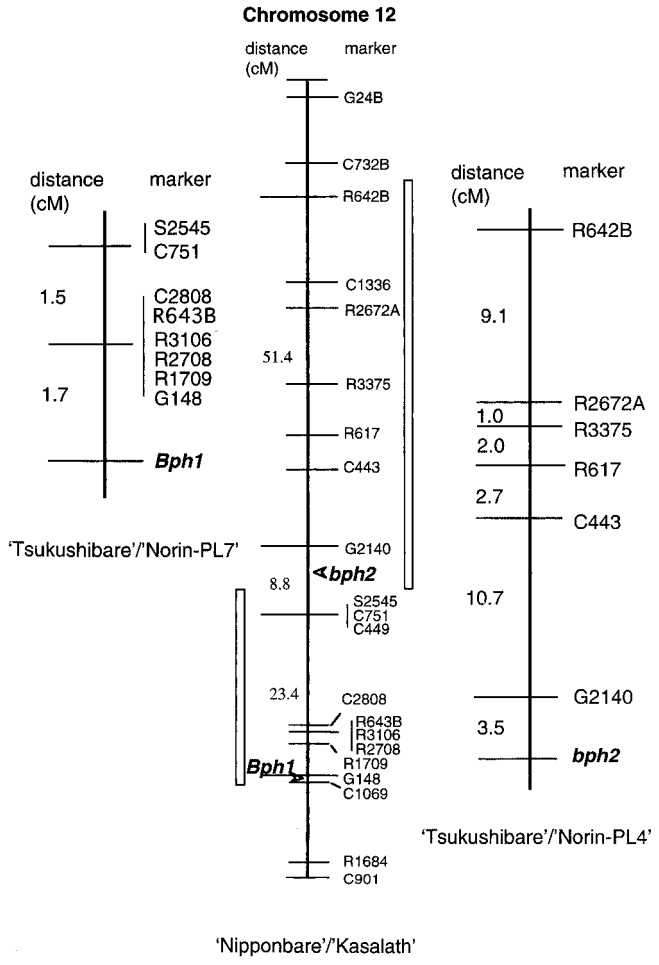

Fig. 3. Map positions of *bph2* and *Bph1*. A central map is the standard 'Nipponbare'/'Kasalath' map of the rice chromosme 12 (Kurata et al., 1994), and the right and left are the extended maps covering *bph2* and *Bph1*, respectively. The open boxes indicate the regions introgressed from the resistance donors to the two breeding lines, 'Norin-PL4' (*bph2*) and 'Norin-PL7' (*Bph1*). The map position of *Bph1* is from Murata et al. (1997).

ever, the estimated distance (about 8.5 cM) covering these two BPH resistance genes was much shorter than that on the standard map.

Allelism test of *bph2* and *Bph1*. An allelism test was conducted to examine the non-allelic relationship between *bph2* and *Bph1* and to further pyramid them by crossing 'Norin-PL4' as a male parent with two *Bph1* carrier lines, i.e. 'Norin-PL3' and 'Norin-PL7'. Contrary to the expectation based on the estimated distance between the two BPH resistance genes, neither susceptible F_2 homozygotes nor segregating F_2s could be detected after bioassay of about 8,600 F_3s obtained from these crosses (Table 3).

Table 3. BPH resistance assay in F_3 progenies derived from crosses between two *Bph1* carriers ('Norin-PL3' and 'Norin-PL7') and 'Norin-PL4'

Cross	Number of F_2s			
	RR	RS	SS	Total[a]
'Norin-PL3'/'Norin-PL4'	309	0	0	309
'Norin-PL7'/'Norin-PL4'	264	0	0	264

[a] An average of 15 F_3 plants were assayed to determine the genotype of each F_2 in both crosses.

DISCUSSION

Our finding that *bph2* introgressed into a *japonica* breeding line, 'Norin-PL4', from an *indica* resistance donor, 'IR1154-243', behaved as a dominant gene (Table 1 and Fig. 1) was surprising. *bph2* was first found in an *indica* line, 'Karsamba Red ASD7' (Athwal et al., 1971). A study on the resistance segregation in a large number of F_2 and F_3 progenies from a cross of 'Taichung Native 1'/'Karsamba Red ASD7', clearly demonstrated the recessive nature of *bph2* (Athwal et al., 1971). In our study, nearly 10,000 F_3 individuals were tested for BPH resistance in addition to some F_2s derived from the cross of 'Tsukushibare'/'Norin-PL4'. Our result agrees with the report that BPH resistance introgressed from 'Norin-PL4' into two other *japonica* breeding lines is controlled by a single dominant gene (Takita, 1996). A similar result was obtained with another recessive BPH resistance gene, *bph4* (Lakshminarayana and Khush, 1977); i.e., *bph4* from 'Babawee' behaved as a dominant gene in crosses of 'Tsukushibare'/'Babawee' and 'IR24'/'Babawee' (unpublished data). A criterion for the dominance or recessiveness depends on the phenotype of the heterozygotes and might well be determined by the penetrance of the gene. The problem of dominance/recessiveness of *bph2* could be ascribed to different environments, different genetic backgrounds, or different BPH biotypes used in the bioassay. To test these possibilities, phenotypes of the heterozygotes must directly be determined using genetically defined BPH biotypes.

A segregation of *bph2* in 159 F_2s studied using F_3 progenies of 'Tsukushibare'/'Norin-PL4' was deviated significantly from the expected 1 : 2 : 1 ratio (Table 1). In 90 F_2s randomly selected and used in the mapping study, however, all the six RFLP markers linked to *bph2* were shown to be segregated normally (Table 2). The result at least suggests that no aberrant segregation distortion is occurring in the vicinity of these RFLP markers. A more detailed molecular map has to be constructed to test if any factor(s) closely linked to *bph2* are responsible for the apparent deviation towards the higher number of heterozygotes than expected. The deviation might also be ascribed to the presence of minor gene(s). To test this minor gene effect, a new bioassay method which can quantitatively evaluate the level of BPH resistance has to be developed and used in QTL analysis.

bph2 in 'Norin-PL4' was mapped at 3.5 cM from the

closest RFLP marker, G2140, on the rice chromosome 12 (Figs. 2 and 3). *bph2* was earlier reported to be either allelic or closely linked to a dominant BPH resistance gene, *Bph1* (Athwal et al., 1971). Our study, however, showed that the position of *bph2* on the standard map of 'Nipponbare'/'Kasalath' (Kurata et al., 1994) was ca. 30 cM apart from that of *Bph1* previously mapped using the different population, i.e., 'Tsukushibare'/'Norin-PL7' (Murata et al., 1997). Because of this considerable map distance we expected to obtain recombinants between these two BPH resistance genes, thus to achieve pyramiding of the genes. However, neither susceptible F_2 homozygotes nor segregating F_2s were obtained through BPH resistance assay of a large number of F_3 progenies obtained from the crosses between two *Bph1* carrier lines ('Norin-PL3' and 'Norin-PL7') and 'Norin-PL4' (Table 3). The result of no recombinations between the two genes was in agreement with the previous report (Athwal et al., 1971). The map distances in the introgressed regions covering *bph2* and *Bph1* estimated in the present study and the previous one (Murata et al., 1997) were much shorter than those in the corresponding regions on the standard map (Fig. 3). This indicates that crossing-over might be prevented in these regions. To examine this, marker genotypes have to be analyzed using the resistant progenies obtained in the above two crosses.

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