High Temperature Enhances the Resistance of Cultivated African Rice, *Oryza glaberrima*, to Bacterial Blight

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Abstract

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Rice bacterial blight (BB) is caused by *Xanthomonas oryzae* pv. *oryzae* and is responsible for substantial yield loss worldwide. Host resistance remains the most feasible control measure. However, pathogen variability leads to the failure of certain resistance genes to control the disease, and climate change with high amplitudes of heat predisposes the host plant to pathogen invasion. Due to pressure in natural selection, landrace species often carry a wide range of unique traits conferring tolerance of stress. Therefore, exploring their genetic background for host resistance could enable the identification of broad-spectrum resistance to combined abiotic and biotic stresses. Nineteen *Oryza glaberrima* accessions and *O. sativa* rice variety SUPA were evaluated for BB resistance under high temperature (35 and 31°C day and night, respectively) using 14 *X. oryzae* pv. *oryzae* strains originated from the Philippines. Under normal temperature,

most of the accessions showed resistance to 9 strains (64.3%) and accession TOG6007 showed broad-spectrum resistance to 12 strains (85.7%). Under high temperature, most accessions showed a reduction in BB disease, whereas, accession TOG5620 showed disease reduction from all the *X. oryzae* pv. *oryzae* strains under high temperature. Molecular characterization using gene-based and linked markers for BB resistance genes *Xa4*, *xa5*, *Xa7*, *xa13*, and *Xa21* revealed the susceptible alleles of *Xa4*, *xa5*, *xa13*, and *Xa21* in *O. glaberrima*. However, no allele of *Xa7* was detected among *O. glaberrima* accessions. Our results suggest that *O. glaberrima* accessions contain a BB resistance different from the *Xa* gene type. Genome-wide association mapping could be used to identify quantitative trait loci that are associated with BB resistance or combined BB resistance and high-temperature tolerance.

Rice bacterial blight (BB) caused by *Xanthomonas oryzae* pv. *oryzae* is one of the most important bacterial diseases in rice. Reported in several rice-producing countries in Asia and Africa, rice BB affects rice production worldwide. Thus, rice-*X. oryzae* pv. *oryzae* interaction leads to severe yield losses in major rice ecosystems. Host resistance is still the most economically effective control measure against the disease and, thus far, 39 rice resistance (*R*) genes have been identified against Asian *X. oryzae* pv. *oryzae* populations (Khan et al. 2014; Natraj Kumar et al. 2012; Zhang et al. 2015). However, in Africa, up till now, there has been no *R* gene identified to control this disease. The effectiveness or durability of host-plant resistance may be affected by climate change (Reddy 2015).

Climate change, with air temperature increase and water scarcity, will affect world agricultural production. Several reports have shown the effects of global warming on pathogen and host plant alike. Increase in temperature predisposes the host plant to pathogen colonization. Webb et al. (2010) reported an increase in BB disease on rice near-isogenic lines carrying single *Xa3*, *Xa4*, *xa5*, and *Xa10* genes, with *Xa4* *R* genes mostly under high temperature; however, the effectiveness of BB *R* gene *Xa7* was enhanced under the same conditions. Similarly, the wheat stripe rust *R* gene *Yr36* confers broad-spectrum resistance to *Puccinia striiformis* f. sp. *tritici* at high temperature (25 to 35°C) and shows susceptibility to the pathogen at low temperature (15°C) (Uauy et al. 2005). Therefore, there is an urgent need to

develop cultivars with resistance to or tolerance of BB to sustain rice production under changing climate conditions. *Oryza glaberrima* is known to possess many important traits.

Oryza glaberrima (2n = 14, AA) is the second most important cultivated rice worldwide. It was domesticated in West Africa in the Niger River Delta more than 3,500 years ago (Yves et al. 2012). Because of its low-yielding characteristic, *O. glaberrima* was progressively abandoned for *O. sativa*, the Asian cultivated rice, which has a higher yield (Jones et al. 1997). However, because of its adaptation to African climate conditions, *O. glaberrima* is still grown in some West African countries. Although the high-yielding cultivars of *O. sativa* are preferred, their adaptation to the adverse conditions of the local environment is not satisfactory. *O. glaberrima* is well known to possess many useful traits, such as resistance to blast, Rice yellow mottle virus, sheath blight, nematodes, stem borer, hispa, stalk-eyed fly, the African gall midge for weed competitiveness, and BB (Alam and Efron 1986; Albar et al. 2006; Baggie et al. 2002; Djedatin et al. 2011; Lorieux et al. 2003; Maji et al. 2001; Ndjondjop et al. 1999; Nipah et al. 1997; Nwilene et al. 2002; Sahrawat and Sika 2002; Silue and Notteghem 1991; Thiémélé et al. 2010; Wang et al. 1996); and tolerance of drought, submergence, soil acidity, salt, iron, and aluminum. Interestingly, notable traits from *O. glaberrima* have been combined with high-yielding traits of *O. sativa* to generate the New Rice for Africa (Jones et al. 1997). Vikal et al. (2007) have identified 13 *O. glaberrima* accessions with resistance to Indian *X. oryzae* pv. *oryzae* pathotypes, and a narrow genetic base for resistance to *X. oryzae* pv. *oryzae* among 107 accessions of *O. glaberrima* was reported (Djedatin et al. 2011).

Natural selection often generates wild species with diverse traits, such as disease resistance, that could be inherited by wild relatives (Das et al. 2014). Thus, *R* genes were identified from wild rice. For example, BB *R* gene *Xa21*, which confers resistance to several Philippine *X. oryzae* pv. *oryzae* races, was identified from African rice *O. longistaminata*. Identification of *R* genes from African rice would enable breeding of resistance cultivars not only against the

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African *X. oryzae* pv. *oryzae* population but also against the Asian *X. oryzae* pv. *oryzae*. Discovery of new, large-spectrum *R* genes will contribute to the control of rice BB disease in the future. To our knowledge, there is no report available on the combination of high temperature and BB stress on *O. glaberrima*. This study aims to

evaluate selected accessions of the cultivated *O. glaberrima* to a combination of high temperature and BB stresses.

Materials and Methods

Plant materials. In all, 19 accessions of *O. glaberrima* (Table 1) were obtained from the Africa Rice Center gene bank (Cotonou, Benin), with the help of Dr. Drissa Silue. The 19 accessions, which originated from West African countries (Ghana, Liberia, Mali, Nigeria, and Senegal), were selected according to their resistant reaction to African *X. oryzae* pv. *oryzae* strain Mai1 and Asian *X. oryzae* pv. *oryzae* race 2 strain PXO86 (Djedatin et al. 2011). We also included *O. sativa* variety SUPA (accession IRGC 69789) because it is one of the most preferred varieties in East Africa. One set of plants was grown under greenhouse conditions (12-h day length). To evaluate the combination of high temperature and *X. oryzae* pv. *oryzae*, the plants were grown under greenhouse conditions for 21 days and then transferred into a growth chamber (12 h of light and 12 h of darkness; 35 and 31°C day and night temperatures, respectively; and 80% relative humidity).

BB inoculation and evaluation. Fourteen strains (Table 1) representative of 10 *X. oryzae* pv. *oryzae* races from the Philippines (Cottyn and Mew 2007) were used in this study. Strains were grown on Modified Wakimoto's medium, as described by Leach et al. (1992), for 72 h. The inocula were prepared by suspending the harvested bacterial cells in demineralized sterile water. Approximately 10⁸ CFU/ml of each inoculum was used to inoculate the plants with the use of the leaf-clipping inoculation method (Kauffman et al. 1973) 4 weeks after sowing, under greenhouse conditions and in a growth chamber at 35 and 31°C (day and night, respectively). Disease assessment was done by measuring lesion length 14 days after inoculation. Two replicated trials were performed, each trial consisting of three replicates with six plants per strain. The average lesion length was classified as follows: resistant (lesion length 0 to 5 cm), moderately resistant (lesion length 5.1 to 10 cm), moderately susceptible (lesion length 10.1 to 15 cm), and susceptible (lesion length >15 cm). In total, 10 accessions, including SUPA, were selected for resistance to BB under high temperature after evaluating 20 rice accessions in the greenhouse.

***O. glaberrima* genotyping using *Xa* gene markers.** All the accessions were genotyped for the presence or absence of the resistance alleles of *Xa4*, *Xa5*, *Xa7*, *xa13*, and *Xa21*. Rice genotypes IRBB4, IRBB5, IRBB7, IRBB13, and IRBB21 with resistance alleles *Xa4*, *Xa5*, *Xa7*, *xa13*, and *Xa21*, respectively, were used as controls. IR24 was used as a susceptible allele control. Genomic DNA was extracted from each sample and control using the cetyltrimethylammonium bromide DNA extraction protocol. The genomic DNA was purified with RNase. The primer pairs used for *Xa* gene detection and their corresponding product size are listed in Table 2.

For *Xa4* detection, 50 to 100 ng of genomic DNA was used to detect resistant and susceptible alleles in a 10-μl polymerase chain reaction (PCR) according to the following cycles: initial denaturation at

Table 1. List of rice accessions and *Xanthomonas oryzae* pv. *oryzae* strains

Sample number	Accession or strain name ^a	Accession number or race ^b	Origin
Africa			
1	CG17 ^c	IRGC 86741	Senegal
2	RAM90	na	Mali
3	RAM98	na	Mali
4	SUPA ^c	IRGC 69789	Tanzania
5	TOG5293	IRGC 96725	Nigeria
6	TOG5447	IRGC 96756	Nigeria
7	TOG5458	na	Mali
8	TOG5464 ^c	IRGC 96760	Nigeria
9	TOG5473 ^c	IRGC 104534	Nigeria
10	TOG5523 ^c	IRGC 86757	Nigeria
11	TOG5566 ^c	IRGC 96779	Nigeria
12	TOG5620 ^c	IRGC 86764	Ghana
13	TOG5650	IRGC 104543	Nigeria
14	TOG5675	IRGC 96791	Nigeria
15	TOG5810	IRGC 86784	Liberia
16	TOG5953 ^c	IRGC 96811	Nigeria
17	TOG5989 ^c	na	Nigeria
18	TOG6007	IRGC 96824	Nigeria
19	TOG6231	IRGC 96854	Mali
20	TOG7173 ^c	IRGC 96893	Nigeria
Asia			
1	PXO61	Race 1	Philippines
2	PXO86	Race 2	Philippines
3	PXO79	Race 3b	Philippines
4	PXO340	Race 3c	Philippines
5	PXO71	Race 4	Philippines
6	PXO112	Race 5	Philippines
7	PXO99	Race 6	Philippines
8	PXO145	Race 7	Philippines
9	PXO280	Race 8	Philippines
10	PXO339	Race 9a	Philippines
11	PXO349	Race 9b	Philippines
12	PXO347	Race 9c	Philippines
13	PXO363	Race 9d	Philippines
14	PXO341	Race 10	Philippines

^a Accession name according to AfricaRice (Cotonou, Benin).

^b Accession number according to the International Rice Research Institute (Los Baños, Philippines) germplasm database; na = not available.

^c Accessions selected for combined high temperature and bacterial blight experiment.

Table 2. *Xa* gene-based and linked markers and size of their polymerase chain reaction (PCR) products

Gene	Primer name	Sequence (5' to 3')	Type of marker	PCR products (bp) ^a
<i>Xa4</i> ^b	MP1_F	ATCGATCGATCTTCACGAGG	Linked	S = 120
	MP2_R	dTG CTA TAA AAG GCA TTC GGG	Linked	R = 150
<i>Xa5</i> ^c	Xa5_F2_Sus	GCTCGCCATTCAAGTTCTTGTC	Gene-based	198
	Xa5-F2-Res	GCTCGCCATTCAAGTTCTTGAG	Gene-based	...
	Xa5_R2	CCTTGATAGAAACCTTGCTCTTGAC	Gene-based	...
<i>Xa7</i> ^b	M5_F	CGATCTTACTGGCTCTGCAACTCTGT	Linked	S = 1170
	M5_R	GCATGTCTGTGTCGATTGGTCCGTACGA	Linked	R = 294
<i>Xa13</i> ^b	Xa13F_130-140	CCT GAT ATG TGA GGT AGT	Gene-based	S = 1326
	xa13R_1678-1662	GAG AAA GGC TTA AGT GC	Gene-based	R = 1523
<i>Xa21</i> ^b	Xa21 Forward	ATA GCA ACT GAT TGC TTG G	Gene-based	S = 1200
	Xa21 Reverse	CGA TCG GTA TAA CAG CAA AAC	Gene-based	R = 1400

^a S = sensitive and R = resistant.

^b Codominant primers.

^c Dominant primers.

94°C for 4 min; 32 cycles of denaturation at 94°C for 1 min, annealing at 58°C for 1 min, and extension at 72°C for 2 min; and a final extension step at 72°C for 8 min.

For *xa5* allele detection, 10 to 20 ng of genomic DNA was used in a 10-μl PCR according to the following cycles: initial denaturation at 94°C for 3 min; 34 cycles of denaturation at 94°C for 1 min, annealing at 68°C for 1 min, and extension at 72°C for 1 min; and a final extension step at 72°C for 4 min.

For *Xa7*, 50 to 100 ng of genomic DNA was used in a 10-μl PCR according to the following cycles: initial denaturation at 94°C for 4 min; 30 cycles of denaturation at 94°C for 30 s, annealing at 60°C for 30 s, and extension at 72°C for 2 min; and a final extension step at 72°C for 8 min.

The *xa13* alleles were detected with 10 to 20 ng of genomic DNA in a 10-μl PCR according to the following cycles: initial denaturation at 94°C for 4 min; 30 cycles of denaturation at 94°C for 1 min, annealing at 60°C for 1 min, and extension at 72°C for 2 min; and a final extension step at 72°C for 8 min.

Some 50 to 100 ng of genomic DNA was used for *Xa21* alleles in a 10-μl PCR according to the following cycles: initial denaturation at 94°C for 4 min; 32 cycles of denaturation at 94°C for 1 min, annealing at 52°C for 1 min, and extension at 72°C for 2 min; and a final extension step at 72°C for 8 min.

The PCR products were separated in 1% agarose gel for *Xa7*, *xa13*, and *Xa21* and 2% for *Xa4* and *xa5*, then visualized under UV light.

Data analysis. The mean value from two replicated experiments was used for analysis of variance of BB lesion length. The significant difference ($P < 0.001$) in lesion length between accessions was assessed using the *F* test. Statistical analysis was performed using the R package.

Results

Identification of *O. glaberrima* accessions with broad-spectrum resistance to Philippine *X. oryzae* pv. *oryzae* strains. *O. glaberrima* accessions and SUPA showed different reactions in response to the 14 *X. oryzae* pv. *oryzae* strains (Fig. 1). *O. sativa* variety SUPA was susceptible to all the strains (Table 3; Supplementary Table S1). For the *O. glaberrima* accessions, all of them showed resistance to moderate resistance to PXO86 (race2), PXO79 (race3B), PXO347 (race9c), and PXO341 (race10). The majority of accessions were resistant to moderately resistant to PXO340 (race3C), PXO112 (race5), PXO145 (race7), PXO339 (race9A), and PXO349 (race9B). Strains PXO61, PXO71, PXO99, PXO363, and PXO280 were the most

virulent, with 18, 16, 19, 12, and 10 accessions, respectively, being moderately susceptible to susceptible to them (Table 3). *X. oryzae* pv. *oryzae* strains PXO86, PXO79, PXO347, and PXO341 were less virulent on *O. glaberrima* accessions. Race 3 strains (PXO79, race 3B and PXO340, race 3C) induced different reactions on *O. glaberrima*. All the accessions were resistant and moderately resistant to PXO79.

O. glaberrima accessions TOG5953 and TOG6007 showed broad-spectrum resistance to 12 *X. oryzae* pv. *oryzae* strains and TOG5810, TOG5566, and TOG7173 were resistant to 11 *X. oryzae* pv. *oryzae* strains. *O. glaberrima* accessions TOG5458 and TOG5523 were susceptible to six *X. oryzae* pv. *oryzae* strains (Table 3).

Accessions TOG5989 and TOG5473 were moderately susceptible and susceptible, respectively, to PXO340. Among race 9 strains, PXO363 (race 9d) was the most virulent, with only seven accessions showing resistance. Accessions CG17 and TOG5447 were moderately susceptible to race 9a, and accession TOG5523 was moderately susceptible to race 9b. All the accessions were resistant to moderately resistant to race 9c. Significant differences in lesion length were observed among all the accessions and differences were also significant among strains ($P < 2.20E-16$; Table 4).

High temperature enhances *O. glaberrima* resistance to *X. oryzae* pv. *oryzae*. *O. glaberrima* resistance to *X. oryzae* pv. *oryzae* was found to be enhanced under high temperature (HT; 35 and 31°C). BB resistance was evaluated in nine *O. glaberrima* accessions and SUPA. A majority of the accessions showed disease lesion length reduction and HT compared with the greenhouse study (Tables 5 and 6). Accession TOG5620 showed broad-spectrum resistance to all *X. oryzae* pv. *oryzae* strains, with moderate resistance to strains PXO71 and PXO99 under HT. Increase in lesion length under HT was observed in the accession-strain combinations CG17–PXO71; TOG5464–PXO339, PXO341, and PXO347; TOG5953–PXO71, PXO112, and PXO339; TOG7173–PXO339, PXO340, and PXO341; and SUPA–PXO61 and PXO145. Although most of the accessions showed lesion length reduction under high temperature, average lesion lengths induced by *X. oryzae* pv. *oryzae* strains PXO61, PXO71, and PXO99 were generally higher compared with lesion lengths induced by other strains.

The lesion lengths under each treatment were significantly different among treatments and among accessions and strains ($P = 3.44E-11$; Tables 5 and 6). Accession TOG5523 showed the strongest BB disease reduction under HT and TOG5620 was the most resistant to majority of the *X. oryzae* pv. *oryzae* strains under HT.

Fig. 1. Reaction of 20 rice accessions to 14 strains of *Xanthomonas oryzae* pv. *oryzae* from the Philippines. Bacterial blight lesion lengths were evaluated under greenhouse conditions at 2 weeks after inoculation. Lesion lengths were scored 14 days after inoculation. Lesion lengths: resistant (R) = <5 cm, moderately resistant (MR) = >5 to 10 cm, moderately susceptible (MS) = >10 to 15 cm, and susceptible (S) = >15 cm.

Table 3. *Oryza glaberrima* reaction to 14 strains of *Xanthomonas oryzae* pv. *oryzae* from the Philippines under greenhouse conditions^a

Strains	R	MR	MS	S
PXO61 (race 1)	...	TOG6007	TOG5293, TOG5620, TOG7173	CG17, RAM90, RAM98, SUPA, TOG5447, TOG5458, TOG5464, TOG5473, TOG5523, TOG5566, TOG5650, TOG5675, TOG5810, TOG5953, TOG5989, TOG6231
PXO86 (race 2)	TOG7173	TOG6007, CG17, RAM90, RAM98, TOG544, TOG5458, TOG5464, TOG5473, TOG5523, TOG5566, TOG5650, TOG5675, TOG5810, TOG5953, TOG5989, TOG6231, TOG5293, TOG5620	...	SUPA
PXO79 (race 3B)	TOG5650, TOG5810,	CG17, RAM90, RAM98, TOG5293, TOG5447, TOG5458, TOG5464, TOG5473, TOG5523, TOG5566, TOG5620, TOG5675, TOG5953, TOG5989, TOG6007, TOG6231, TOG7173	...	SUPA,
PXO340 (race 3C)	TOG5566, TOG5953, TOG6231	CG17, RAM90, RAM98, TOG5293, TOG5447, TOG5458, TOG5464, TOG5523, TOG5620, TOG5650, TOG5675, TOG5810, TOG6007, TOG7173	TOG5989,	SUPA, TOG5473,
PXO71 (race 4)	...	CG17, RAM90, TOG5810, TOG5953,	TOG5523, TOG5566, TOG5620, TOG5675, TOG5989, TOG6231	RAM98, SUPA, TOG5293, TOG5447, TOG5458, TOG5464, TOG5473, TOG5650, TOG6007, TOG7173
PXO112 (race 5)	RAM90, TOG5566, TOG5675, TOG5810, TOG5953, TOG5989, TOG6007, TOG6231, TOG7173	CG17, TOG5293, TOG5447, TOG5458, TOG5473, TOG5523, TOG5620, TOG5650,	TOG5464,	RAM98, SUPA,
PXO99 (race 6)	...	...	...	CG17, RAM90, RAM98, SUPA, TOG5293, TOG5447, TOG5458, TOG5464, TOG5473, TOG5523, TOG5566, TOG5620, TOG5650, TOG5675, TOG5810, TOG5953, TOG5989, TOG6007, TOG6231, TOG7173
PXO145 (race 7)	TOG5650, TOG5810, TOG7173	CG17, RAM90, RAM98, TOG5293, TOG5464, TOG5473, TOG5523, TOG5566, TOG5620, TOG5675, TOG5953, TOG5989, TOG6007, TOG6231	SUPA, TOG5447,	TOG5458
PXO280 (race 8)		RAM98, TOG5293, TOG5464, TOG5566, TOG5675, TOG5810, TOG5953, TOG6007, TOG7173	TOG5447, TOG5473, TOG5523, TOG5620, TOG5650, TOG5989, TOG6231	CG17, RAM90, SUPA, TOG5458
PXO339 (race 9a)	TOG5293, TOG5464, TOG5473, TOG5566, TOG5810, TOG5953, TOG7173	RAM90, RAM98, TOG5458, TOG5523, TOG5620, TOG5650, TOG5675, TOG5989, TOG6007, TOG6231	CG17, TOG5447	SUPA
PXO349 (race 9b)	TOG5293, TOG5464, TOG5473, TOG5620, TOG5810, TOG6231, TOG7173	CG17, RAM90, RAM98, TOG5447, TOG5458, TOG5566, TOG5650, TOG5675, TOG5953, TOG5989, TOG6007	TOG5523	SUPA
PXO347 (race 9c)	TOG5953, TOG6231, TOG7173	CG17, RAM90, RAM98, TOG5293, TOG5447, TOG5458, TOG5464, TOG5523, TOG5566, TOG5620, TOG5650, TOG5675, TOG5810, TOG5989, TOG6007	...	SUPA
PXO363 (race 9d)	TOG5464, TOG5473, TOG5566, TOG5953, TOG5989, TOG7173	RAM98	TOG5810, TOG6007	CG17, RAM90, SUPA, TOG5293, TOG5447, TOG5458, TOG5523, TOG5620, TOG6231, TOG5650, TOG5675
PXO341 (race 10)	TOG5566, TOG5675, TOG5953, TOG7173	CG17, RAM90, RAM98, TOG5293, TOG5447, TOG5458, TOG5464, TOG5473, TOG5523, TOG5620, TOG5650, TOG5810, TOG5989, TOG6007, TOG6231	...	SUPA

^a Bacterial blight lesion lengths were evaluated under greenhouse conditions at 2 weeks after inoculation. Lesion lengths were scored 14 days after inoculation. Lesion lengths: resistant (R) = <5 cm, moderately resistant (MR) = >5 to 10 cm, moderately susceptible (MS) = >10 to 15 cm, and susceptible (S) = >15 cm.

Rice *Xa* gene detection from 10 *O. glaberrima* accessions. All of the *O. glaberrima* accessions—SUPA, IR24, IRBB4, IRBB5, IRBB7, IRBB13, and IRBB21—were genotyped for the presence and absence of the *Xa4*, *xa5*, *Xa7*, *xa13*, and *Xa21* alleles. All of the *O. glaberrima* accessions carried the susceptible alleles *Xa4*, *xa5*, *xa13*, and *Xa21*. No *Xa7* alleles were detected among *O. glaberrima* accessions and SUPA (Table 7). The *Xa4*-resistant allele was detected in SUPA. As expected, IRBB4, IRBB5, IRBB7, IRBB13, and IRBB21 showed resistant alleles *Xa4*, *xa5*, *Xa7*, *xa13*, and *Xa21*, respectively. The susceptible alleles were detected in IR24.

Discussion

Because resistance loss can occur any time due to pathogen adaptation and variability, a continuous search for new resistance traits is necessary. Continuous exploring of existing BB *R* genes or, alternatively, the search among cultivated and wild rice genotypes to discover new *R* genes with broad-spectrum resistance would assist in containing the disease in the future, particularly under climate change. In this study, 19 cultivated African rice accessions evaluated for reaction to BB and combined BB and heat stresses showed different responses

Table 4. Variance analysis of average lesion length from 20 rice accessions inoculated with 14 *X. oryzae* pv. *oryzae* strains under greenhouse conditions^a

Variable	Sum of squares	Df	F value	Pr (>F)
Accession	10,029.7	19	68.5506	<2.20E-16***
Strain	20,340.7	13	203.1897	<2.20E-16***
Accession × strain	9,691.4	247	5.0953	<2.20E-16***
Residuals	4,312.3	560	...	...

^a Degrees of freedom = Df: 14 *X. oryzae* pv. *oryzae* strains (Df = 13) were used to inoculate 20 rice accessions (Df = 19) under greenhouse conditions. Asterisks (***) indicate the level of significance of each factor or between factors at *P* value of 0.001.

to BB. One accession with broad-spectrum resistance to at least 12 Philippine strains was identified, suggesting that more *O. glaberrima* accessions should be evaluated to identify more accessions with broad-spectrum resistance to BB. Nevertheless, four, five, and six accessions were identified as having resistance to moderate resistance to 11, 10, and 9 *X. oryzae* pv. *oryzae* strains, respectively, among the 14 strains. Our results are supported by previous reports which showed *O. glaberrima* accessions with broad-spectrum resistance to seven Indian *X. oryzae* pv. *oryzae* strains (Vikal et al. 2007) and resistance to West African *X. oryzae* pv. *oryzae* strains and the Philippine strain PXO86 (Djedatin et al. 2011). Moreover, the *O. glaberrima* accessions with broad-spectrum resistance reported by Vikal et al. (2007) were not included in this study, suggesting that *O. glaberrima* could be a store of resistance to several BB populations. Therefore, future studies are required to explore the *O. glaberrima* gene pool for the development of new resistance cultivars. A new *R* gene for controlling BB in Asia, particularly in the Philippines, could be identified among *O. glaberrima* accessions. Furthermore, the use of broad-spectrum BB *R* genes would reduce the development of new virulent strains, and broad-spectrum resistance traits among *O. glaberrima* could be introduced into *O. sativa* elite varieties through hybridization. Although a majority of the accessions ranged from moderately susceptible to susceptible to PXO61, accession TOG6007 showed susceptibility to only PXO71, PXO99, and PXO363.

Rice BB *R* gene *Xa4* confers resistance to IRBB4 against PXO61 and has been widely used in Asia; however, the occurrence of new virulent strains affects the durability of *Xa4* (Vera Cruz et al. 2000). We suggest that accession TOG6007 could be useful in areas dominated by Philippine race 1 strain. A majority of the accessions were susceptible to PXO61, PXO71, PXO99, PXO280, and PXO363. This could be explained by (i) the presence of conserved transcription activator-like (TAL) effectors in these strains that activate susceptibility genes among the selected *O. glaberrima* accessions (*n* = 4) and

Table 5. Bacterial lesion length on 10 rice accessions evaluated under greenhouse (GH) and high temperature (HT) conditions^a

Strains	CG17	SUPA	TOG5464	TOG5473	TOG5523
PXO61 (race 1) GH	25.5 ± 2.43 (S)	25.05 ± 2.7 (S)	19.4 ± 2.02 (S)	17.6 ± 0.98 (S)	16 ± 1.49 (S)
PXO61 (race 1) HT	9.97 ± 0.21 (MR)	27.03 ± 2.03(S)	4.31 ± 0.50 (R)	9.37 ± 0.98 (MR)	12.24 ± 0.84 (MS)
PXO86 (race 2) GH	7.11 ± 0.79 (MR)	19.04 ± 2.11 (S)	6.43 ± 1.19 (MR)	7.15 ± 1.42 (MR)	6.59 ± 1.43 (MR)
PXO86 (race 2) HT	2.40 ± 0.1 (R)	11.14 ± 0.92 (MS)	3.66 ± 0.41 (R)	6.42 ± 0.02 (MR)	2.91 ± 0.31 (R)
PXO79 (race 3B) GH	5.09 ± 0.25 (MR)	16.11 ± 1.02 (S)	7.08 ± 0.93 (MR)	6.12 ± 0.23 (MR)	7.17 ± 0.55 (MR)
PXO79 (race 3B) HT	2.88 ± 0.77 (R)	7.63 ± 0.88 (MR)	4.35 ± 0.13 (R)	3.13 ± 0.83 (R)	6.44 ± 1.41 (MR)
PXO340 (race 3C) GH	7.17 ± 1.57 (MR)	21.17 ± 1.76 (S)	5.31 ± 0.93 (MR)	17.13 ± 0.23 (S)	8.15 ± 0.84 (MR)
PXO340 (race 3C) HT	2.18 ± 0.58 (R)	11.48 ± 1.23 (MS)	4.08 ± 0.48 (R)	7.56 ± 1.31 (MR)	2.53 ± 1.13 (R)
PXO71 (race 4) GH	7.68 ± 0.89 (MR)	27.99 ± 0.71 (S)	21.65 ± 0.84 (S)	18.14 ± 2.33 (S)	12.95 ± 2.12 (MS)
PXO71 (race 4) HT	14.74 ± 0.74 (MS)	15.75 ± 1.99 (S)	13.75 ± 0.13 (MS)	15.06 ± 1.11 (S)	6.11 ± 0.36 (MR)
PXO112 (race 5) GH	6.01 ± 2.52 (MR)	24.91 ± 0.24 (S)	13.46 ± 0.65 (MS)	5.91 ± 2.27 (MR)	5.44 ± 1.97 (MR)
PXO112 (race 5) HT	2.61 ± 0.69 (R)	18.56 ± 2 (S)	3.99 ± 0.57 (R)	8.43 ± 0.93 (MR)	3.26 ± 0.59 (R)
PXO99 (race 6) GH	25.81 ± 2.78 (S)	28.92 ± 1.12 (S)	25.16 ± 1.93 (S)	25.19 ± 0.74 (S)	27.45 ± 2.45 (S)
PXO99 (race 6) HT	5.19 ± 0.34 (MR)	26.55 ± 0.30 (S)	12.33 ± 0.21 (MS)	10.48 ± 1.25 (MS)	3.45 ± 0.21 (R)
PXO145 (race 7) GH	7.89 ± 1.66 (MR)	13.76 ± 1.5 (MS)	6.6 ± 1.36 (MR)	5.58 ± 0.45 (MR)	8.63 ± 0.1 (MR)
PXO145 (race 7) HT	2.47 ± 0.76 (R)	17.01 ± 1.08 (S)	3.55 ± 0.65 (R)	5.26 ± 0.25 (MR)	4.64 ± 0.16 (R)
PXO280 (race 8) GH	17.88 ± 3.32 (S)	28.26 ± 2.42 (S)	5.99 ± 0.56 (MR)	14.5 ± 2.46 (MS)	10.95 ± 2.75 (MS)
PXO280 (race 8) HT	5.68 ± 0.68 (MR)	13.97 ± 0.92 (MS)	4.62 ± 0.74 (R)	4.49 ± 1.04 (R)	4.06 ± 0.01 (R)
PXO339 (race 9a) GH	10.75 ± 1.66 (MS)	29.22 ± 2.81 (S)	4.1 ± 0.41 (R)	4.94 ± 0.65 (R)	7.1 ± 0.69 (MR)
PXO339 (race 9a) HT	2.31 ± 0.55 (R)	23.27 ± 1.76 (S)	13.87 ± 1.09 (MS)	7.4 ± 0.87 (MR)	7.49 ± 1.21 (MR)
PXO349 (race 9b) GH	7.25 ± 2.79 (MR)	37.56 ± 3.43 (S)	4.78 ± 1.03 (R)	4.87 ± 0.97 (R)	12.34 ± 1.65 (MS)
PXO349 (race 9b) HT	3.10 ± 0.88 (R)	24.99 ± 1.01 (S)	3.31 ± 0.44 (R)	5.48 ± 0.55 (MR)	4.51 ± 0.33 (R)
PXO347 (race 9c) GH	7.35 ± 1.96 (MR)	28.46 ± 2.45 (S)	5.27 ± 0.97 (MR)	4.92 ± 0.80 (R)	5.32 ± 1.41 (MR)
PXO347 (race 9c) HT	1.92 ± 0.58 (R)	19.02 ± 1.87 (S)	23.62 ± 0.37 (S)	3.97 ± 0.7 (R)	3.27 ± 0.84 (R)
PXO363 (race 9d) GH	20.85 ± 1.66 (S)	17.15 ± 1.2 (S)	3.87 ± 1.71 (R)	3.57 ± 1.03 (R)	16.89 ± 2.55 (S)
PXO363 (race 9d) HT	6.79 ± 0.92 (MR)	9.22 ± 2.03 (MR)	3.81 ± 0.19 (R)	4.44 ± 0.24 (R)	3.93 ± 0.96 (R)
PXO341 (race 10) GH	9.1 ± 2.23 (MR)	23.13 ± 2.62 (S)	5.53 ± 0.95 (MR)	5.58 ± 0.67 (MR)	6.02 ± 0.51 (MR)
PXO341 (race 10) HT	2.38 ± 0.48 (R)	23.71 ± 0.22 (S)	8.43 ± 1.13 (MR)	3.66 ± 0.68 (R)	7.16 ± 0.76 (R)

(continued on next page)

^a Bacterial blight lesion lengths were evaluated under greenhouse (GH) and high temperature (HT) conditions at 2 weeks after inoculation. Lesion lengths were scored 14 days after inoculation. Each value is the mean ± standard error. Mean values are followed by the standard error. Letters in parentheses are reaction categories based on lesion length. Lesion lengths: resistant (R) = <5 cm, moderately resistant (MR) = >5 to 10 cm, moderately susceptible (MS) = >10 to 15 cm, and susceptible (S) = >15 cm.

(ii) the lack of resistant genes among these accessions that could recognize the avirulence protein of these strains. TAL effectors play an important role in the successful colonization of the host plant.

In this study, high temperature had generally shown positive effects on *O. glaberrima* resistance to BB. The lesion lengths induced by different *X. oryzae* pv. *oryzae* strains were generally reduced under high temperature in comparison with the greenhouse study, suggesting that *O. glaberrima* tolerance of abiotic stress enhanced its biotic stress response under high temperature. Resistance to abiotic and biotic stresses has been reported in *O. glaberrima* (Alam and Efron 1986; Albar et al. 2006; Baggie et al. 2002; Djedatin et al. 2011; Lorieux et al. 2003; Maji et al. 2001; Ndjonjop et al. 1999; Nipah et al. 1997; Nwile et al. 2002; Sahrawat and Sika 2002; Silue and Notteghem 1991; Thiémélé et al. 2010; Wang et al. 1996); however, none of the previous reports had shown a dual stress (abiotic and biotic) response. Thus, we suppose that *O. glaberrima* possesses traits that respond to combined stresses and could be useful for the improvement of *O. sativa* varieties. Although a reproductive barrier between *O. glaberrima* and *O. sativa* has been a major constraint to exploring the gene pool offered by *O. glaberrima*, further studies involving development of chromosome segment substitution lines to reduce hybrid sterility (Lorieux et al. 2013) are recommended to identify quantitative trait loci (QTL) responsible for abiotic and biotic stress in *O. glaberrima* to be used for development of interspecific hybridization between *O. glaberrima* and *O. sativa* (Ghesquière et al. 1997).

Conversely, a few combinations of strains and four accessions (CG17, TOG5464, TOG5953, and TOG7173), including SUPA, showed an increase in BB disease with high temperature, which suggests that more attention should be given for resistance durability under combined stresses through abiotic and biotic factors. This result was more often observed with *X. oryzae* pv. *oryzae* strains PXO71, PXO339, PXO341, and PXO347.

Previous reports have shown temperature effects on plant responses to pathogens. In rice, Webb et al. (2010) reported an increase in BB disease on IRBB4 and a reduction on IRBB7 under high temperature. A wheat variety with *R* gene *Yr36* showed broad-spectrum

resistance to the wheat stripe rust (*P. striiformis* f. sp. *tritici*) at high temperature (25 to 35°C) but susceptibility at low temperature (15°C) (Uauy et al. 2005). This suggests that identification of accessions that increase plant resistance and, thus, reduce pathogen aggressiveness under high-temperature conditions could play an important role in breeding rice varieties for combined stresses.

In this study, molecular characterization of *O. glaberrima* accessions and SUPA revealed that none of the *O. glaberrima* accessions possessed the resistance alleles *Xa4*, *xa5*, *Xa7*, *xa13*, and *Xa21*. Interestingly, *Xa7* alleles were not detected in any of the accessions, suggesting that *O. glaberrima* lacks *Xa7*. Moreover, resistance to PXO86 (*avrXa7*) may be conferred by a different type of *R* gene in *O. glaberrima*. The absence of resistance alleles *Xa4*, *xa13*, and *Xa21* correlate with the phenotype data, because all the accessions were susceptible to PXO61 (except TOG6007) and PXO99. Although SUPA was susceptible to all *X. oryzae* pv. *oryzae* strains, the molecular characterization of SUPA was revealed to be homozygous for the *Xa4* resistant allele. This suggests that the *Xa4* resistant allele in SUPA is defective and, moreover, the *Xa4* marker used in this study is not a linked marker.

The use of resistant cultivars remains the most effective control measure. Thirty-nine *R* genes have been identified in rice (Khan et al. 2014; Natraj Kumar et al. 2012; Zhang et al. 2015), among which some of them, such as *Xa21*, derived from wild rice, originate from *O. longistaminata* (Khush et al. 1990; Song et al. 1995), *Xa23* from *O. rufipogon* (Zhang et al. 1998), *Xa27* from *O. minuta* (Gu et al. 2004, 2005), and *Xa30(t)* from *O. nivara* (Cheema et al. 2008). Wild rice genotypes are highly diverse due to natural selection and possess several traits that could be used for introgression of disease resistance in rice cultivars. Thus, mutations due to selection pressure could be transmitted from the ancestor to various cultivated accessions. Therefore, more attention should be given to African cultivated rice and its ancestor, *O. longistaminata*, and to other wild rice species, to identify traits of combined BB resistance and abiotic stress tolerance. PCR-based detection of *Xa* genes revealed no resistance alleles of *R* genes studied here that could be associated with BB resistance. Therefore, we suggest the use of genome-wide association

Table 5. (continued from preceding page)

TOG5566	TOG5620	TOG5953	TOG5989	TOG7173
18.7 ± 1.88 (S)	14.3 ± 1.74 (MS)	17.3 ± 2.26 (S)	19.04 ± 1.83 (S)	13.81 ± 0.75 (MS)
10.33 ± 0.95 (MS)	5.31 ± 0.89 (MR)	9.70 ± 0.40 (MR)	16.07 ± 2.53 (S)	11.53 ± 0.78 (MS)
5.42 ± 0.96 (MR)	8.04 ± 0.74 (MR)	6.28 ± 0.96 (MR)	5.88 ± 0.84 (MR)	4.7 ± 1.8 (R)
3.22 ± 0.53 (R)	2.98 ± 0.25 (R)	2.83 ± 0.53 (R)	2.29 ± 0.47 (R)	5.04 ± 0.07 (MR)
7.31 ± 1.47 (MR)	6.31 ± 0.62 (MR)	6.49 ± 1.53 (MR)	5.74 ± 0.76 (MR)	6.5 ± 1.01 (MR)
3.61 ± 0.85 (R)	2.63 ± 0.48 (R)	2.74 ± 0.59 (R)	3.14 ± 0.66 (R)	2.85 ± 0.78 (R)
4.53 ± 0.36 (R)	7.24 ± 0.59 (MR)	4.93 ± 0.73 (R)	13.05 ± 0.5 (MS)	5.03 ± 1.66 (MR)
2.48 ± 1.47 (R)	5.44 ± 0.32 (MR)	2.27 ± 0.61 (R)	4.55 ± 0.13 (R)	15.37 ± 1.79 (S)
11.63 ± 2.98 (MS)	14.47 ± 1.4 (MS)	9.91 ± 2.35 (MR)	12.52 ± 0.58 (MS)	15.38 ± 1.58 (S)
13.15 ± 0.97 (MS)	13.01 ± 0.15 (MS)	14.84 ± 0.86 (MS)	3.84 ± 0.29 (R)	10.63 ± 0.25 (MS)
4.18 ± 1.44 (R)	5.21 ± 0.95 (MR)	4.82 ± 1.65 (R)	4.16 ± 1.25 (R)	3.84 ± 1.35 (R)
3.12 ± 0.39 (R)	3.28 ± 0.63 (R)	7.70 ± 0.80 (MR)	4.78 ± 0.77 (R)	3.56 ± 0.44 (R)
17.29 ± 0.5 (S)	24 ± 2.49 (S)	20.15 ± 2.37 (S)	24.44 ± 3.57 (S)	19.24 ± 1.8 (S)
6.81 ± 0.27 (MR)	12.08 ± 1.98 (MS)	9.86 ± 0.7 (MR)	5.08 ± 0.7 (MR)	14.05 ± 0.98 (MS)
7.31 ± 2.44 (MR)	8.5 ± 1.77 (MR)	6.53 ± 1.02 (MR)	8.73 ± 0.93 (MR)	4.88 ± 0.75 (R)
4.39 ± 1.02 (R)	3.42 ± 0.12 (R)	4.15 ± 0.0 (R)	7.28 ± 0.48 (MR)	4.56 ± 0.48 (R)
6.96 ± 1 (MR)	10.17 ± 1.45 (MS)	9.1 ± 0.84 (MR)	13.13 ± 1.75 (MS)	7.3 ± 0.5 (MR)
1.94 ± 0.19 (R)	4.10 ± 0.85 (R)	13.92 ± 1.62 (MS)	3.89 ± 0.47 (R)	4.89 ± 0.54 (R)
4.93 ± 1.11 (R)	5.86 ± 0.86 (MR)	5 ± 1.25 (R)	6.4 ± 0.78 (MR)	3.65 ± 0.8 (R)
2.99 ± 0.16 (R)	5.75 ± 0.35 (MR)	2.82 ± 0.67 (R)	4.03 ± 0.63 (R)	7.63 ± 0.57 (MR)
7.22 ± 1.14 (MR)	4.68 ± 0.27 (R)	6.38 ± 2.41 (MR)	5.76 ± 0.56 (MR)	3.45 ± 0.73 (R)
2.04 ± 0.17 (R)	5.27 ± 0.34 (MR)	1.92 ± 0.82 (R)	1.86 ± 0.66 (R)	2.49 ± 0.36 (R)
6.22 ± 0.84 (MR)	5.31 ± 0.10 (MR)	4.75 ± 1.13 (R)	6.2 ± 0.80 (MR)	4.53 ± 0.59 (R)
6.0 ± 0.11 (MR)	5.29 ± 0.53 (MR)	16.07 ± 2.04 (S)	7.17 ± 1 (MR)	5.36 ± 0.63 (MR)
4.56 ± 1 (R)	19.45 ± 2.59 (S)	3.53 ± 1.23 (R)	4.96 ± 1.33 (R)	4.76 ± 1.65 (R)
7.62 ± 1.34 (MR)	4.96 ± 0.2 (R)	2.86 ± 0.05 (R)	3.01 ± 0.92 (R)	2.64 ± 0.67 (R)
4.39 ± 0.33 (R)	6.18 ± 1.18 (MR)	3.8 ± 0.64 (R)	6.31 ± 1.47 (MR)	4.58 ± 0.41 (R)
3.91 ± 0.29 (R)	3.98 ± 0.82 (R)	2.07 ± 0.52 (R)	5.78 ± 0.28 (MR)	5.63 ± 0.14 (MR)

Table 6. Variance analysis of bacterial blight lesion lengths from 10 rice accessions inoculated with 14 *X. oryzae* pv. *oryzae* strains under 35/31°C (day/night) temperature conditions^a

Variables	Sum of squares	Df	F value	Pr (>F)
Strain	5,078.7	13	54.82	<2.20E-16***
Stress	5,799.2	1	813.808	<2.20E-16***
Variety	7,167.2	9	111.7523	<2.20E-16***
Strain × stress	1,025.6	13	11.0705	<2.20E-16***
Strain × accessions	3,321.7	117	3.9841	<2.20E-16***
Stress × accessions	685.1	9	10.6821	3.10E-16***
Strain × stress × accessions	2,097.0	117	2.5151	3.44E-11***
Residuals	1,995.3	280	...	...

^a Degrees of freedom = Df. 14 *X. oryzae* pv. *oryzae* strains (Df = 13) were used to inoculate 10 rice accessions (Df = 9) under greenhouse and high temperature conditions (Df = 1). Asterisks (***) indicate the level of significance of each factor or between factors at *P* value of 0.001.

Table 7. Allele analysis of *Oryza glaberrima* genotype using *Xa4*, *xa5*, *Xa7*, *xa13*, and *Xa21* markers^a

Accession	<i>xa4</i> (S)	<i>Xa4</i> (R)	<i>xa5</i> (R)	<i>Xa5</i> (S)	<i>xa7</i> (S)	<i>Xa7</i> (R)	<i>xa13</i> (R)	<i>Xa13</i> (S)	<i>xa21</i> (S)	<i>Xa21</i> (R)	Genotype				
											<i>Xa4</i>	<i>xa5</i>	<i>Xa7</i>	<i>xa13</i>	<i>Xa21</i>
CG17	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
RAM90	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
RAM98	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
SUPA	-	+	-	+	+	-	-	+	+	-	<i>Xa4/Xa4^b</i>	<i>Xa5/Xa5</i>	<i>xa7/xa7</i>	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5293	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5447	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5458	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5464	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5473	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5523	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5566	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5620	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5650	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5675	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5810	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5953	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG5989	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG6007	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG6231	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
TOG7173	+	-	-	+	-	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	-	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
IRBB4	-	+	-	+	+	-	-	+	+	-	<i>Xa4/Xa4</i>	<i>Xa5/Xa5</i>	<i>xa7/xa7</i>	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
IRBB5	+	-	+	-	+	-	-	+	+	-	<i>xa4/xa4</i>	<i>xa5/xa5</i>	<i>xa7/xa7</i>	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
IRRB7	+	-	-	+	-	+	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	<i>Xa7/Xa7</i>	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>
IRBB13	+	-	-	+	+	-	+	-	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	<i>xa7/xa7</i>	<i>xa13/xa13</i>	<i>xa21/xa21</i>
IRBB21	+	-	-	+	+	-	-	+	-	+	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	<i>xa7/xa7</i>	<i>Xa13/Xa13</i>	<i>Xa21/Xa21</i>
IR24	+	-	-	+	+	-	-	+	+	-	<i>xa4/xa4</i>	<i>Xa5/Xa5</i>	<i>xa7/xa7</i>	<i>Xa13/Xa13</i>	<i>xa21/xa21</i>

^a Symbols: + and - indicate presence or absence, respectively, of resistant (R) and susceptible (S) alleles.

^b Defective resistance allele in SUPA.

mapping to identify possible QTL that are associated with BB resistance observed from *O. glaberrima*.

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