



Resistance of *Oryza sativa* and *Oryza glaberrima* Genotypes to RBe24 Isolate of Rice Yellow Mottle Virus in Benin and Effects of Silicon on Host Response

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Rice yellow mottle virus (RYMV) is the most harmful virus that affects irrigated and lowland rice in Africa. The RBe24 isolate of the virus is the most pathogenic strain in Benin. A total of 79 genotypes including susceptible IR64 (*Oryza sativa*) and the resistant TOG5681 (*O. glaberrima*) as checks were screened for their reactions to RBe24 isolate of RYMV and the effects of silicon on the response of host plants to the virus investigated. The experiment was a three-factor factorial consisting of genotypes, inoculation level (inoculated vs. non-inoculated), and silicon dose (0, 5, and 10 g/plant) applied as CaSiO₃ with two replications and carried out twice in the screen house. Significant differences were observed among the rice genotypes. Fifteen highly resistant and eight resistant genotypes were identified, and these were mainly *O. glaberrima*. Silicon application did not affect disease incidence and severity at 21 and 42 days after inoculation (DAI); it, however, significantly increased plant height of inoculated (3.6% for 5 g CaSiO₃/plant and 6.3% for 10 g CaSiO₃/plant) and non-inoculated (1.9% for 5 g CaSiO₃/plant and 4.9% for 10 g CaSiO₃/plant) plants at 42 DAI, with a reduc-

tion in the number of tillers (12.3% for both 5 and 10 g CaSiO₃/plant) and leaves (26.8% for 5 g CaSiO₃/plant and 28% for 10 g CaSiO₃/plant) under both inoculation treatments. Our results confirm *O. glaberrima* germplasm as an important source of resistance to RYMV, and critical in developing a comprehensive strategy for the control of RYMV in West Africa.

Keywords : Benin, *Oryza glaberrima*, rice, RYMV, silicon

Rice (*Oryza* sp.) is one of the most important food crops in the world. Africa accounts for 4% of world production. Average rice yield of 2.6 t/ha in Africa falls considerably short of the average world yield of 4.6 t/ha (Food and Agriculture Organization of the United Nations, 2019), although, rice production, which was 21 million tonnes in 2007, increased to 31.1 in 2017 (Food and Agriculture Organization of the United Nations, 2019). Notwithstanding this increase, many countries in the continent continue to rely heavily on rice imports as local production has not been able to meet up the growing consumption needs (Food and Agriculture Organization of the United Nations, 2017a).

As a source of calories, rice ranks third for most of the countries in West Africa (Fiamohe et al., 2018; Food and Agriculture Organization of the United Nations, 2017b). In Benin Republic, despite several efforts made to increase local production, yields of irrigated rice rarely exceeded 2.07 t/ha (Diagne et al., 2013). This is largely due to biotic stresses, among which are viruses. Rice yellow mottle virus (RYMV), a Sobemovirus (Hull, 1988), is one of the

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most destructive viruses affecting rice cultivation in both irrigated and lowland ecologies in Africa (Abo et al., 1997; Kouassi et al., 2005, Séré et al., 2013). Yield losses due to RYMV in smallholder farms range from 10% to 100%, depending on the time of infection, level of susceptibility of rice varieties cultivated and the prevailing climatic conditions (Issaka et al., 2012; Kam et al., 2013; Kouassi et al., 2005; Laha et al., 2017; Séré et al., 2013). The virus was first reported in Kenya (Bakker, 1970). Extensive characterization of the viral strains revealed different genetic groups with gradual differentiation from East to West Africa (Pinel-Galzi et al., 2015). Due to its complex epidemiology, varietal resistance has been the major management method used to control the disease (Traoré et al., 2009).

Among accessions of the two cultivated rice species, *O. sativa* (originating from Asia and cultivated worldwide) and *O. glaberrima* (endemic to Africa and locally cultivated in West Africa), several resistant accessions were found mostly among the African rice species (Thiémélé et al., 2010). Researches in molecular rice breeding have led to the identification of three major resistance genes named RYMV1, RYMV2, and RYMV3 in *O. sativa* and *O. glaberrima*, the two cultivated species. The first resistance gene (RYMV1) encodes the eukaryotic translation initiation factor eIF(iso)4G (Albar et al., 2006) with five allelic variants. These include one susceptible allele *rymv1-1* carried by IR64, and four resistance alleles viz. *rymv1-2*, *rymv1-3*, *rymv1-4*, and *rymv1-5*, carried by Gigante (*O. sativa*), tropical *Oryza glaberrima* (TOG) 5681, TOG5672, and TOG5674, respectively (Albar et al., 2006; Thiémélé et al., 2010). The second resistance gene (RYMV2) is governed by a recessive allele and codes for CPR5-1, a probable component of the nuclear pore complex involved in the regulation of defense mechanisms (Pidon et al., 2017). The third gene (RYMV3), with NB-LRR as a very convincing candidate gene, is probably involved in the virus recognition mechanism (Pidon et al., 2017).

Attempts at the introgression of resistance alleles from *O. glaberrima* sources into high yielding but susceptible *O. sativa* varieties by conventional breeding have met with limited success because of genetic barriers (Heuer et al., 2003; Jones et al., 1997). Although, the interspecific lowland rice varieties, the NERICAs (New Rice for Africa), were obtained using TOG5681 (*O. glaberrima*) and IR64 (*O. sativa*) as parents (Sié et al., 2005), these varieties did not exhibit the high resistance to RYMV of their *O. glaberrima* parent (Agnoun, 2013; Ndjiondjop et al., 2008). In addition, breakdown of the resistance in some rice genotypes carrying *rymv1-2* and *rymv1-3* alleles has been observed in experimental stations (Pidon et al., 2017).

This raises concerns on the durability of the known RYMV resistance genes (Hébrard et al., 2018; Kobayashi et al., 2014). These observations suggest that available rice varieties may be vulnerable to RYMV in areas where a great diversity of the virus exists, such as in Benin Republic (Oludare et al., 2016).

The use of varietal resistance combined with appropriate agronomic management, one of which is the use of silicon (Si), may offer a very practical and cost-effective solution to overcome RYMV. Silicon is known to play a beneficial role in achieving healthy growth and development in many plant species and also improves tolerance to abiotic stresses such as salinity, drought, chilling, freezing, iron toxicity etc. (Epstein, 1994, 1999; Liang, 1999; Liang et al., 2005, 2007; Ma et al., 2001; Mbonankira, 2014). It is also known to improve mineral nutrient uptake and alleviate metal toxicity in plant species (Frantz et al., 2011; Liang et al., 2007; Mbonankira, 2014). The beneficial role of silicon in improving resistance to biotic stresses has also been reported (Tsujimoto et al., 2014). Many members of the family Poaceae, especially rice, are known to accumulate silicon (Tamai and Ma, 2003), which is abundant in the soil (Janislampi, 2012). Plants can accumulate silicon at concentrations higher than those of many essential macronutrients, often in excess of 1,000 mg/kg (Epstein, 1999; Tsujimoto et al., 2014). It is, however, not required by most plant species for the completion of their life cycle (Marschner, 1995). Silicon taken up by the rice plant is usually deposited in various organs such as husks, leaves, leaf sheath, culm and roots (Zhu et al., 2004). Its presence in cell wall fiber makes the cell wall tough, reduces plant transpiration and improves photosynthesis rate due to its association with leaf ultrastructure, chlorophyll content and ribulose biphosphate carboxylase activity (Epstein, 1994). In effect, silicon deposition in leaves improves resistance/tolerance to pests and diseases (Meyer and Keeping, 2001) and remediates nutrient imbalances (Epstein, 1994; Ma et al., 2001; Savant et al., 1996). Silicon has been reported to increase rice yield under multiple stress conditions of lowland ecosystems (Meharg and Meharg, 2015).

The first study on silicon nutrient in relation to viral disease control was reported by Zellner et al. (2011). These authors observed that silicon-fertilized plants of tobacco (*Nicotiana tabacum*) inoculated with tobacco ringspot virus (TRSV) exhibited higher foliar Si-content with lower TRSV systemic symptom formation. No previous study to date has reported the effects of silicon on the control of viral disease on important food security crops. The objectives of this study were to evaluate the reaction of diverse rice genotypes to the RBe24 isolate of RYMV and determine

Table 1. List of the 79 genotypes screened for disease resistance with RBe24 isolate of rice yellow mottle virus under silicon fertilizer

No.	Code	Genotypes	Species	Source	No.	Code	Genotypes	Species	Source
1	VB1	WAB 2066-6-FKR4-WAC1-TGR1-B-WAT-B16	Interspecific ^a	INERA	41	V23	PL55-2	<i>O. glaberrima</i>	AfricaRice
2	VB2	WAB 2066-WAT21-1-B-1-3	Interspecific	INERA	42	V24	PL55-7	<i>O. glaberrima</i>	AfricaRice
3	VB5	WAB 2152-TGR2-WAT1-2	Interspecific	INERA	43	V25	PL57-4	<i>O. glaberrima</i>	AfricaRice
4	VB9	WAB 2066-6-FKR4-WAC1-TGR1-B-WAT-B11	Interspecific	INERA	44	V26	PL57-5	<i>O. glaberrima</i>	AfricaRice
5	VB10	SAHEL 177	Interspecific	INERA	45	V27	S2-6	<i>O. glaberrima</i>	AfricaRice
6	VB11	SAHEL 328	Interspecific	INERA	46	V29	PL58-1	<i>O. glaberrima</i>	AfricaRice
7	VB14	ORYLUX 4	Interspecific	INERA	47	V30	PL58-2	<i>O. glaberrima</i>	AfricaRice
8	VB15	ORYLUX 2	Interspecific	INERA	48	V31	PL62-1	<i>O. glaberrima</i>	AfricaRice
9	VB17	WAB 2066-WAT20-1-B-1-1	Interspecific	INERA	49	V33	PL67-1	<i>O. glaberrima</i>	AfricaRice
10	VB18	WAB 2066-6-FKR4-WAC1-TGR1-B-WAT-B1	Interspecific	INERA	50	V34	PL68-1	<i>O. glaberrima</i>	AfricaRice
11	VB19	WAB 2066-WAT21-1-B-1-TGR2	Interspecific	INERA	51	V35	PL68-6	<i>O. glaberrima</i>	AfricaRice
12	VB20	SAHEL 309	Interspecific	INERA	52	V36	PL68-8	<i>O. glaberrima</i>	AfricaRice
13	VB21	WAB 2081-WAC2-2-TGR2-WAT1-9-TGR3	Interspecific	INERA	53	V37	PL75-2	<i>O. glaberrima</i>	AfricaRice
14	VB22	WAB 2138-WAC B-2-TGR2-WAT-B1	Interspecific	INERA	54	V38	PL75-3	<i>O. glaberrima</i>	AfricaRice
15	VB24	NIL 16	Interspecific	INERA	55	V39	PL75-6	<i>O. glaberrima</i>	AfricaRice
16	VB25	WAB 2066-WAT20-1-B-1-TGR1	Interspecific	INERA	56	V40	PL82-7	<i>O. glaberrima</i>	AfricaRice
17	VB26	WAB 2066-WAT21-1-B-1-1	Interspecific	INERA	57	V41	PL85-1	<i>O. glaberrima</i>	AfricaRice
18	VB27	WAB 2066-6-FKR4-WAC1-TGR1-B-WAT-B6	Interspecific	INERA	58	V42	PL85-2	<i>O. glaberrima</i>	AfricaRice
19	VB28	WAB 2066-WAT20-1-B-1-TGR3	Interspecific	INERA	59	V43	PL85-3	<i>O. glaberrima</i>	AfricaRice
20	V1	TOG5672	<i>O. glaberrima</i>	AfricaRice ^b	60	V45	PL85-5	<i>O. glaberrima</i>	AfricaRice
21	V2	TOG5681	<i>O. glaberrima</i>	AfricaRice	61	V46	PL87-1	<i>O. glaberrima</i>	AfricaRice
22	V3	TOG7291	<i>O. glaberrima</i>	AfricaRice	62	V47	PL87-3	<i>O. glaberrima</i>	AfricaRice
23	V4	S2-4	<i>O. glaberrima</i>	AfricaRice	63	V48	PL87-4	<i>O. glaberrima</i>	AfricaRice
24	V5	S2-5	<i>O. glaberrima</i>	AfricaRice	64	V49	PL87-5	<i>O. glaberrima</i>	AfricaRice
25	V6	S5-8	<i>O. glaberrima</i>	AfricaRice	65	V50	PL87-6	<i>O. glaberrima</i>	AfricaRice
26	V7	S6-9	<i>O. glaberrima</i>	AfricaRice	66	V51	PL87-8	<i>O. glaberrima</i>	AfricaRice
27	V8	S7-1	<i>O. glaberrima</i>	AfricaRice	67	V52	PL88-3	<i>O. glaberrima</i>	AfricaRice
28	V9	S19-4	<i>O. glaberrima</i>	AfricaRice	68	V53	PL92-1	<i>O. glaberrima</i>	AfricaRice
29	V10	S21-6	<i>O. glaberrima</i>	AfricaRice	69	V54	PL92-4	<i>O. glaberrima</i>	AfricaRice
30	V11	S24-9	<i>O. glaberrima</i>	AfricaRice	70	V56	S19-3	<i>O. glaberrima</i>	AfricaRice
31	V12	PL49-7	<i>O. glaberrima</i>	AfricaRice	71	V57	Moroberekan	<i>O. sativa</i>	INRAB
32	V13	PL50-4	<i>O. glaberrima</i>	AfricaRice	72	V58	CG14	<i>O. glaberrima</i>	INRAB
33	V15	PL51-1	<i>O. glaberrima</i>	AfricaRice	73	V60	WAB 56-50	<i>O. sativa</i>	INRAB
34	V16	PL51-2	<i>O. glaberrima</i>	AfricaRice	74	V61	ARICA 1	Interspecific	INRAB
35	V17	PL51-3	<i>O. glaberrima</i>	AfricaRice	75	V62	ARICA 2	Interspecific	INRAB
36	V18	PL 52-2	<i>O. glaberrima</i>	AfricaRice	76	V63	ARICA 3	Interspecific	INRAB
37	V19	PL 52-4	<i>O. glaberrima</i>	AfricaRice	77	V64	ARICA 6	Interspecific	INRAB
38	V20	PL 52-5	<i>O. glaberrima</i>	AfricaRice	78	V66	IR 64	<i>O. sativa</i>	INRAB
39	V21	PL 52-7	<i>O. glaberrima</i>	AfricaRice	79	V69	NERICA L-19	Interspecific	INRAB
40	V22	PL 52-8	<i>O. glaberrima</i>	AfricaRice					

INERA, Institute of Environment and Agricultural Research of Burkina-Faso; INRAB, National Institute of Agricultural Research of Benin.

^aInterspecific: *Oryza glaberrima* × *O. sativa*.

^bAfricaRice: Africa Rice Center (Benin).

the effects of silicon on the reaction to the virus.

Materials and Methods

Plant materials. A total of 79 rice genotypes obtained from three research institutions were used for the study: 51 from AfricaRice (Benin Republic); 9 from the National Institute of Agricultural Research of Benin (INRAB), and 19 from the Institute of Environment and Agricultural Research (INERA) of Burkina-Faso (Table 1). These genotypes included three *O. sativa*, four *O. glaberrima*, 24 interspecific rice varieties and 48 intraspecific *O. glaberrima* genotypes. Most of the interspecific rice are aromatic, and some of these have been released to rice farmers in West Africa (Wopereis, 2013). Two rice genotypes among the collections served as checks and these are IR64 (*O. sativa*; susceptible check) and TOG5681 (*O. glaberrima*; resistant check).

Source of RYMV inoculum. The 79 genotypes were screened using the most virulent RYMV isolate (RBe24) collected from northern-Benin Republic (Agnoun, 2013). The isolate belongs to the S1 serological diversity group, which is the most widespread in all the major rice growing areas of the country (Oludare et al., 2016).

Green house experiments. Two experiments were conducted in 2017 under screen house conditions at the AfricaRice-Benin station located in the Abomey Calavi District. The first experiment was from May to July while the second was from September to November. Plastic pots of 1 L capacity were filled with heat-sterilized soil. The experiment was a factorial involving three factors viz. genotypes, inoculation treatment (inoculated vs. non-inoculated) and silicon dose applied (0, 5, and 10 g/plot). In each case, experimental design was randomized complete block with two replications. Two to three rice seeds were sown per pot and seedlings were thinned to one plant per pot. The silicon was supplied as Calcium Silicate (CaSiO_3) at sowing. In addition, plants were fertilized with 1 g of NPK 15-15-15 per pot at sowing and 0.2 g of urea (46% of N) per pot at 21 and 42 days after sowing. The pots were watered and weeded regularly throughout the duration of the experiments.

Inoculation of rice plants and enzyme-linked immunosorbent assay test. The RBe24 isolate of RYMV was obtained from the Plant Pathology Unit of AfricaRice, Benin. To obtain fresh inoculum, the isolate was propagated on the susceptible *O. sativa* rice variety IR64 following the

procedure described by Fargette et al. (2002) and Oludare et al. (2016). The fresh infected leaves obtained were ground in phosphate buffer (0.01 M pH 7.0) at a ratio of 1:10 (w/v); 0.5 g carborundum (600-mesh) was added to the inoculum sap to increase the efficiency of the mechanical inoculation of the virus into leaves tissues (Pinel-Galzi et al., 2018). The viral solution was manually rubbed on the leaves of 21-day-old seedlings, from the base to the top of the plant. Indirect antigen-coated-plate enzyme-linked immunosorbent assay (ELISA) was performed on leaf samples collected at 42 days after inoculation (DAI) using the methodology described by Oludare et al. (2016).

Data collection. RYMV symptoms were assessed at 21 and 42 DAI on a scale of 0 to 9 (International Rice Research Institute, 2002) where ‘0’ represents normal plant growth with no visible symptoms and ‘9’ represents severe leaves symptoms or plant death (Fig. 1). In addition, data were collected on plant height, number of tillers and number of leaves at 21 and 42 DAI. Disease symptoms scores recorded at 21 and 42 DAI were used to calculate disease incidence (DI) and disease severity (DS) as follows:

Disease incidence (DI) = Total number of leaves with symptoms \times 100/Total number of leaves

Disease severity (DS) = $\{((n1 \times 1) + (n3 \times 3) + (n5 \times 5) + (n7 \times 7) + (n9 \times 9)) \times 100 / ((n1 + n2 + n3 + n5 + n7 + n9) \times 9)\}$, where, n1, n3, n5, n7, and n9 represent the number of leaves scored 1, 3, 5, 7, and 9, respectively;

Statistical analysis. Data were analyzed using Excel and JMP 12.01 (SAS Institute, Cary, NC, USA). Analysis of

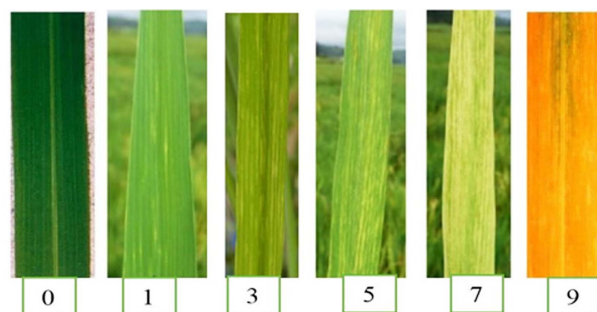


Fig. 1. Symptoms of rice yellow mottle virus corresponding to the 0 to 9 scoring scale (International Rice Research Institute, 2002; Koudamilo et al., 2015). 0, no symptom observed; 1, leaves greens, little yellow sparse dots or streaks; 3, leaves greens, abundant dots or streaks, < 5% height reduction; 5, leaves pale green with mottling, 6-25% height reduction, flowering slightly delayed; 7, leaves pale yellow with mottling, 26-75% height reduction, flowering delayed; 9, leaves turned yellow or orange, >75% height reduction, no flowering, plant dead.

variance (ANOVA) was carried out to determine if the differences among genotypes and silicon doses, inoculation treatments and interactions among the main effects were significant. Turkey's honestly significant difference test was then used to compare means of the inoculated plants with the control for significance. Principal component analysis (PCA) and Hierarchical Clustering were used to group the genotypes on the basis of their level of resistance to isolate RBe24 of the virus.

Results

Incidence and severity of RYMV symptoms on rice.

Typical symptoms of RYMV were observed on the in-

oculated rice plants in both experiments. Infected plants exhibited yellow discoloration, necrosis and mottling of rice leaves. Severe symptoms manifested as stunting, and in some cases death of the plants. Differences among the 79 genotypes evaluated for DI and DS were significant ($P < 0.001$) at 21 and 42 DAI (Table 2). DI for the susceptible IR64 was 100% at 21 and 42 DAI, but severity was 48.2% and 50.9% at 21 and 42 DAI, respectively (Table 3). Three genotypes had disease severity values higher than that of IR64 at 42 DAI; these were ARICA 6 (V64) with DS of 61.3%, WAB 2081-WAC2-2-TGR2-WAT1-9-TGR3 (VB21) with DS of 61.7% and PL 52-2 (V18) with a DS of 66.5%. In contrast, the DI and the DS for the resistant check was 0 at 21 and 42 DAI. Averaged over the 79 geno-

Table 2. Analysis of variance test performed on the disease incidence and disease severity at 21 and 42 DAI

Source of variation	Degree of freedom	21 DAI				42 DAI			
		Disease incidence		Disease severity		Disease incidence		Disease severity	
		Mean square	F-value	Mean square	F-value	Mean square	F-value	Mean square	F-value
Block	1	13,169.6	26.4***	3,835.5	26.1***	2,727.3	4.2*	98	0.5 ns
Dose (of silicon)	2	297.6	0.6 ns	134.4	0.9 ns	1,017.6	1.6 ns	157.2	0.8 ns
Genotype	78	10,412.8	20.9***	2,736.0	18.6***	9,525.2	14.6***	2,616.7	12.8***
Dose (of silicon) × Genotype	156	268.9	0.5 ns	78.6	0.5 ns	330.6	0.5 ns	133.8	0.7 ns
Error	236	499.0		147.0		653.8		204.1	
Total	473								

Significant at $*P < 0.05$ and $***P < 0.001$, respectively; ns, non-significant. DAI, days after inoculation.

Table 3. Means of inoculation and non-inoculation treatments for agronomic traits at 21 and 42 days after inoculation

Days after inoculation	Treatments	Means	Plant height (cm)	No. of tillers (count/plant)	No. of leaves (count/plant)	Disease incidence (%)	Disease severity (%)
21	Non-inoculated	Overall	92.2 ± 0.6 a	4.2 ± 0.1 a	15.6 ± 0.2 a	-	-
		TOG5681	79.2	4.7	14.3	-	-
		IR64	87.0	8.2	30.5	-	-
	Inoculated	Overall	73.8 ± 0.6 b	3.4 ± 0.1 b	11.7 ± 0.2 b	59.5 ± 2.1	29.2 ± 1.1
		TOG5681	74.5	3.8	12.5	0	0
		IR64	55.8	4.5	16.2	100.0	48.2
42	Non-inoculated	Overall means	110.4 ± 1.4 a	5.9 ± 0.2 a	26.9 ± 0.4 a	-	-
		TOG5681	116.7	7.7	35.8	-	-
		IR64	94.2	9.8	48.5	-	-
	Inoculated	Overall	94.0 ± 1.3 b	6.7 ± 0.2 b	26.6 ± 0.4 a	61.9 ± 2.1	29.2 ± 1.1
		TOG5681	110.3	8.8	35.0	0	0
		IR64	78.5	8.2	36.3	100.0	50.9

Means within each day after inoculation followed by the same letter are not significantly different according to honestly significant difference test of Turkey at 5% level of probability.

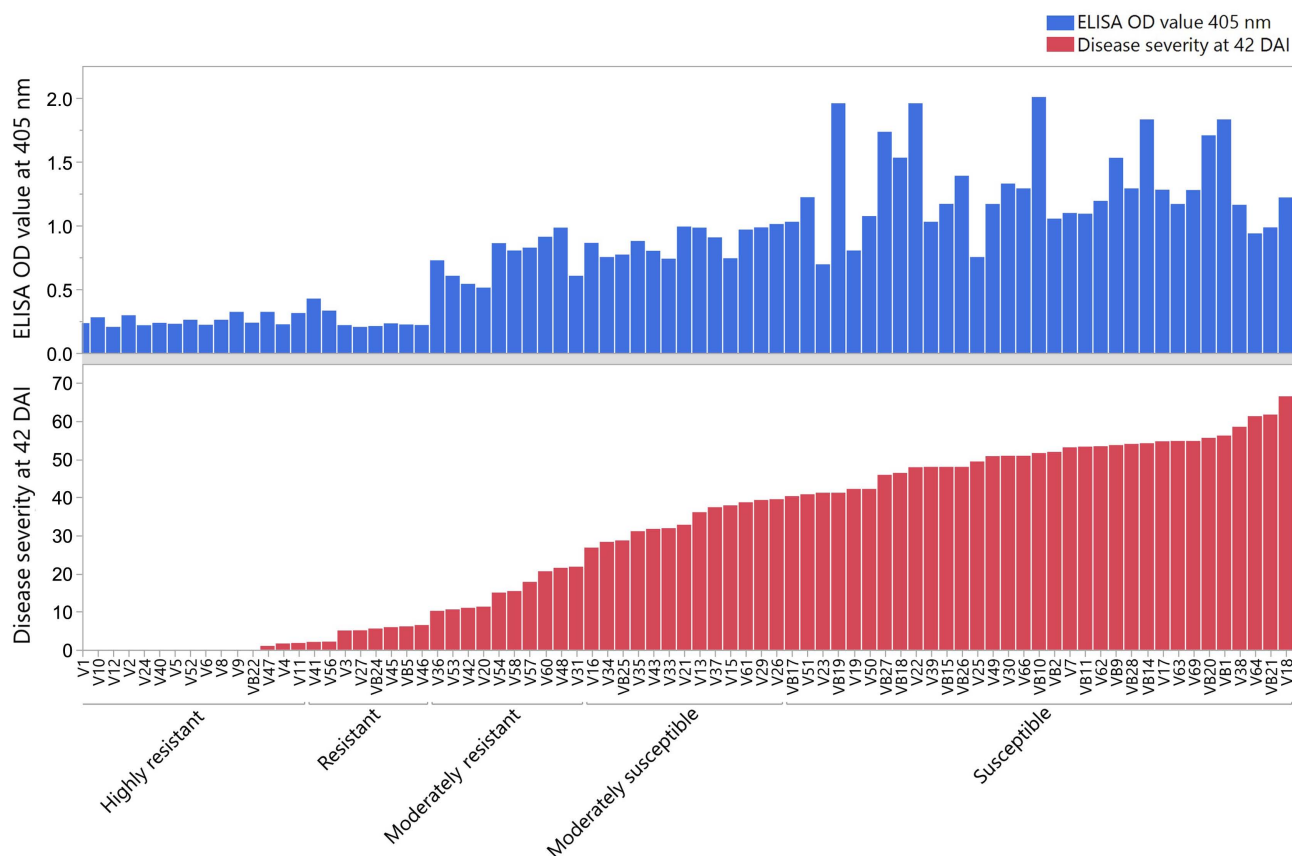


Fig. 2. Classification of tested rice genotypes for their resistance to rice yellow mottle virus (RYMV) using the disease severity score (DS) at 42 days after inoculation (DAI) and enzyme-linked immunosorbent assay (ELISA) optical density value measured for the tested rice genotypes at 42 DAI. Rice materials were categorized as follow based on the disease severity: susceptible, 40% and above; moderately susceptible, DS = 26-39%; moderately resistant, DS = 10-25%; resistant, DS = 2-9%; highly resistant, DS < 2. ELISA OD value at 405 nm, ELISA optical density value measured at absorbance of 405 nm after 3 h of incubation with para NitroPhenylPhosphate tablets dissolved in 1× phosphate buffer saline Tween (1 mg/ml).

types, DI increased from 59.5% at 21 DAI to 61.9% at 42 DAI, while average DS was unchanged from 21 DAI to 42 DAI (Table 3). On the basis of the DS score at 42 DAI, the 79 genotypes were grouped into five viz. highly resistance (DS score < 2%), resistant (DS score = 2-9%), moderately resistant (DS score = 10-25%), moderately susceptible (DS score = 26-39%), susceptible (DS score > 40%). The numbers of genotypes in these groups were 15, 8, 10, 13, and 33, respectively (Fig. 2). When the average DS of the two most resistant groups (highly resistant and resistant) was compared to that of the two susceptible groups (susceptible and moderately susceptible), a major difference was observed. The average DS of the resistant groups (comprising 23 genotypes) was 1.1 and 2.2% at 21 and 42 DAI in contrast to 48.8 and 51.0% at 42 DAI for the susceptible groups (a total of 46 genotypes). The highest DS at 42 DAI were recorded for the genotypes VB21 (61.7%), V64 (61.3%), and V18 (66.5%).

Effects of RYMV on agronomic traits of rice. RYMV significantly ($P < 0.001$) affected the height, the number of tillers and the number of leaves of the rice plant at 21 DAI (Table 4). At this time, reduction in the plant height due to RYMV ranged from 5.9% for TOG5681 to 35.9% for IR64 and averaged 19.9%. Reductions, which ranged from 19.1% to 45.1% for the number of tillers, and 12.6% to 46.9% for the number of leaves averaged 19.0% and 25.0%, respectively. Inoculum × genotype interaction was significant ($P < 0.001$) for plant height, number of tillers and number of leaves at 21 DAI, indicating that the genotypes differed in their response patterns to inoculation treatments at this time.

At 42 DAI, overall plant height reduction was 14.9% (range, 5.5 to 16.7), a somewhat lower value than the reduction at 21 DAI (Table 3); this reduction was, however, significant (Table 4). Different from the general trend of the result at 21 DAI, the average number of tillers was

Table 4. Mean square from the analysis of variance for agronomic traits at 21 and 42 days after inoculation

Source of variation	Degree of freedom	Days after inoculation														
		21						42								
		Mean square	F-value	No. of tillers (count/plant)	Mean square	F-value	No. of leaves (count/plant)	Mean square	F-value	Plant height (cm)	Mean square	F-value	No. of tillers (count/plant)	Mean square	F-value	No. of leaves (count/plant)
Block	1	23,590.1	132.4***	782.0	322.9***	8,853.0	348.4***	54,008.7	68.2***	1,523.8	102.4***	3,408.1	1.371	5***		
Inoculum	1	80,780.6	599.4***	136.0	69.0***	3,583.0	168.7***	59,570.3	75.2***	98.5	6.6**	24.6	0.3	ns		
Dose (of silicon)	2	35.8	0.2 ns	15.5	6.4**	209.6	8.3***	3,398.1	4.3***	203.4	13.7***	2,077.0	22.6***			
Genotype	78	1,254.6	7.0***	11.62	4.8***	149.2	5.9***	2,609.8	3.3***	45.9	3.1***	556.3	6.1***			
Inoculum × Dose (of silicon)	2	89.8	0.5 ns	0.1	0.0 ns	0.1	0.0 ns	64.0	0.1 ns	70.5	4.7**	103.1	1.1	ns		
Inoculum × Genotypes	78	476.6	2.7***	4.9	2.0***	51.6	2.0***	1,202.0	1.5**	25.8	1.7***	210.0	2.3***			
Dose (of silicon) × Genotype	156	159.4	0.9 ns	2.1	0.8 ns	23.5	0.9 ns	541.4	0.7 ns	16.6	1.1 ns	95.4	1.0	ns		
Inoculum × Dose (of silicon) × Genotype	156	94.0	0.5 ns	2.0	0.8 ns	21.1	0.8 ns	522.8	0.7 ns	14.8	1.0 ns	78.9	0.9	ns		
Error	473	178.2		2.4		25.4		782.2		14.6		90.5				
Total	947															

Significant at ** $P < 0.01$ and *** $P < 0.001$, respectively; ns, non-significant.

significantly lower (13.6%) in non-inoculated pots than in inoculated pots. Difference in number of leaves between plants in infected and non-infected pots was not significant (Table 4). As with the results obtained at 21 DAI, differences in response patterns of the rice genotypes to RYMV infection at 42 DAI were significant. This was evidenced by the significant inoculum × genotype interaction (Table 4).

At 42 DAI, when the differences in symptoms among the inoculated genotypes were highest; the serological tests from ELISA, using leaves, confirmed the former. Optical density (OD) values (measured at absorbance of 405 nm) varied from 0.1 to 2.0 for the 79 genotypes. Nine genotypes which showed no visible symptoms and had no or very low virus load in their leaf samples were more resistant than TOG5681 (Fig. 2); these included PL55-7 (V24), S7-1 (V8) and S19-4 (V9), in that order. Genotypes considered susceptible with DI value of 100% had an OD values as high as 2.0 (Fig. 2). The highest OD value measured at absorbance of 405 nm (Fig. 2), were recorded for the genotypes VB19 (1.9), V22 (1.9), and VB10 (2.0).

Effects of silicon on DS and agronomic traits of RYMV-infected and non-infected rice plants. The application of silicon did not significantly influence the DI and DS of RYMV at 21 and 42 DAI (Table 2). Silicon dose × genotype interaction was also not significant for both DI and DS at 21 and 42 DAI (Table 2). The effect of silicon on rice plants manifested on the number of tillers and the number of leaves as early as 21 DAI ($P < 0.01$ to $P < 0.001$) but the effect was not significant for the plant height at this time (Table 2). The effect of silicon on the three traits was significant at 42 DAI ($P < 0.05$ to $P < 0.001$) (Table 4). Plant height at 42 DAI showed linear increase from 0 g CaSiO₃/plant to 10 g CaSiO₃/plant for plants in non-inoculated and inoculated pots. In non-inoculated pots, plant height at 5 g CaSiO₃/plant and 10 g CaSiO₃/plant increased by 1.9% and 4.9% over the height of plants in pots to which silicon was not applied (Fig. 3). In the inoculated pots, corresponding increases in the height of plants at these rates over those of plants in pots without silicon were 3.6% and 6.3%, respectively (Fig. 3).

The effect of silicon on the number of tillers and number of leaves was best demonstrated at 42 DAI, and the response patterns for both traits were similar and in contrast to the increases with rate observed for plant height. In effect, silicon reduced the number of tillers and number of leaves produced by rice plants in both inoculated and non-inoculated pots (Fig. 3).

Silicon dose × inoculation treatment was not significant

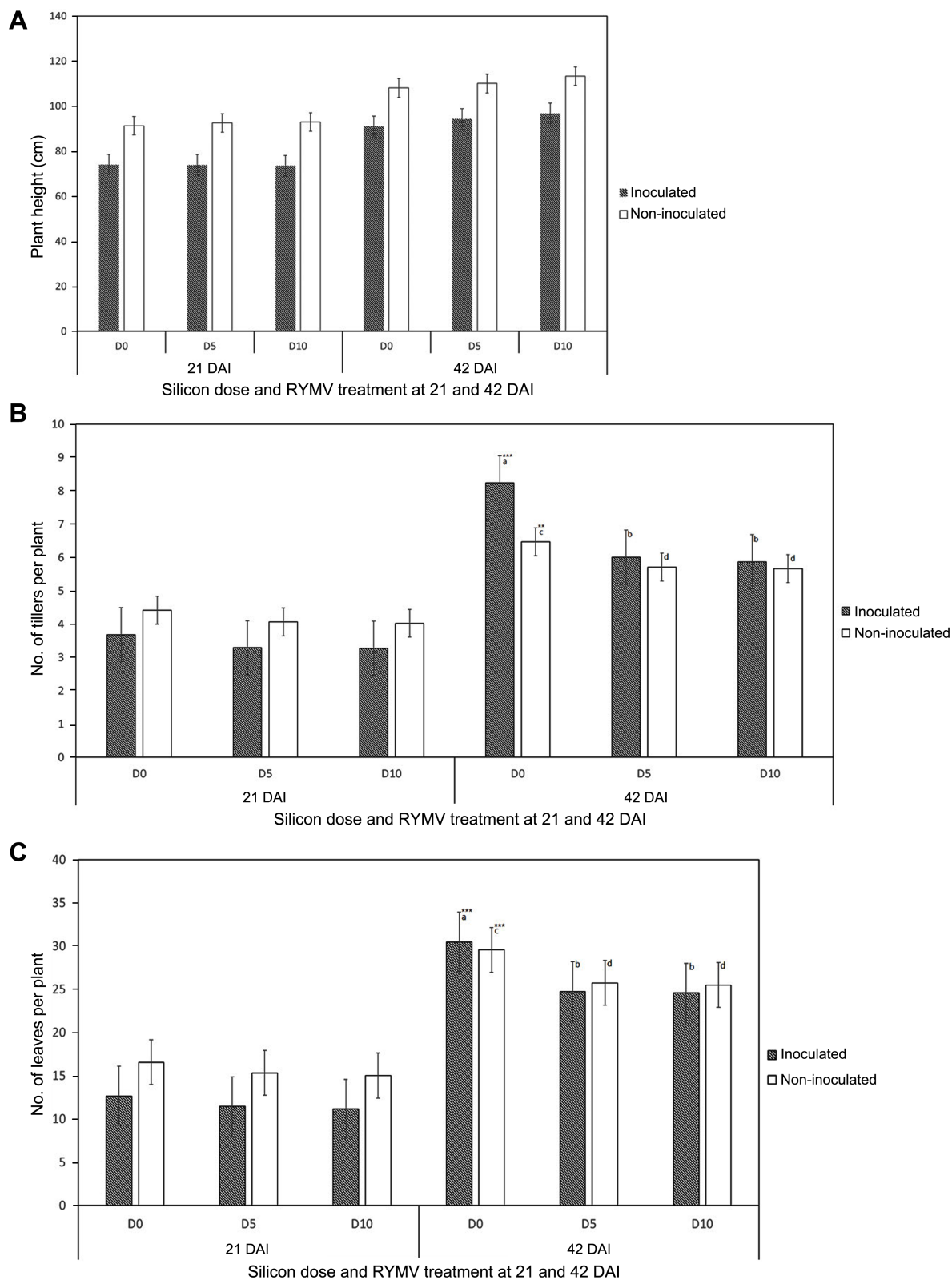


Fig. 3. Plant height (A), number of tillers (B), and number of leaves (C) at 21 and 42 days after inoculation (DAI) of inoculated and non-inoculated rice plants at three silicon levels. D0, 0 g of CaSiO_3 /plant; D5, 5 g of CaSiO_3 /plant; D10, 10 g of CaSiO_3 /plant; RYMV, rice yellow mottle virus. For inoculated and non-inoculated plants at 42 DAI, means followed by the same letter are not significantly different according to honestly significant difference test of Turkey at 5% level or probability. ***Significant at $P < 0.001$, **Significant at $P < 0.01$.

for the three agronomic traits at 21 DAI while it was significant for only number of tillers at 42 DAI. This result indicates that the effect of silicon on number of tillers produced at 42 DAI was influenced by the RYMV infection status of the plant. In comparison with pots to which silicon was not applied, the reduction was 12.3% for both 5 and 10 g CaSiO₃/plant for number of tillers in non-inoculated pots while the reductions in number of tillers were 26.8% for 5 g CaSiO₃/plant and 28% at 10 g CaSiO₃/plant for number of tillers in inoculated pots, respectively (Fig. 3).

Silicon dose x genotype interaction for the traits was not significant at 21 DAI and 42 DAI. In effect, the genotypes did not differ in the response pattern of their agronomic traits to silicon application. The inoculum x silicon dose x genotype interaction was not significant for any of the three traits at these times.

PCA and hierarchical clustering of 79 rice genotypes.
The PCA biplot (Fig. 4) showed that resistant genotypes

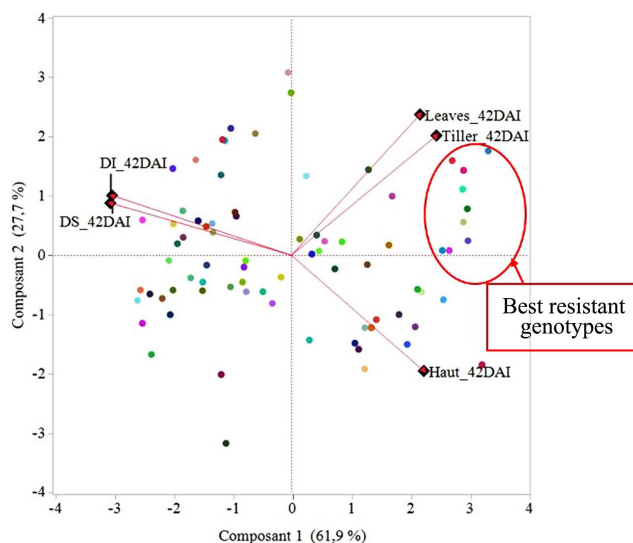
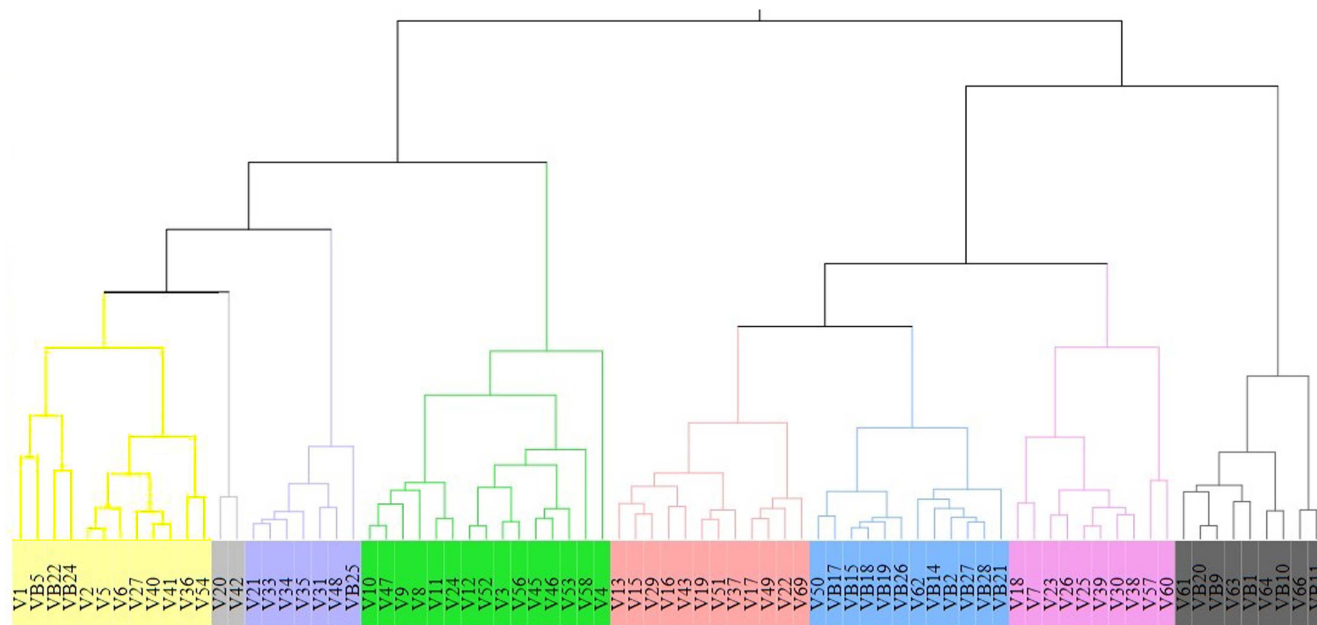


Fig. 4. Principal component analysis biplot of the 79 rice genotypes based on measured parameters. Haut, height; 42DAI, 42 days after inoculation; DI, disease incidence; DS, disease severity.



From the left (pale yellow clade) to the right (dark grey) the differences between cluster are summarized viz.

Cluster	Genotypes (Count)	Means of agronomic and disease traits at 42 days after inoculation				
		Disease severity	Disease incidence	Plant height	Plant tiller	Plant leave
1	12	2.7	7.2	108.5	9.6	37.0
2	2	11.2	30.7	113.4	9.2	30.0
3	7	22.7	57.7	106.5	7.4	30.7
4	15	3.8	11.8	113.9	6.2	25.6
5	12	36.5	73.6	104.5	5.5	23.5
6	12	49.7	100	88.1	5.4	24.1
7	10	46.6	96.3	100.8	3.9	17.7
8	9	51.8	99.7	84.6	7.8	34.7

Fig. 5. Dendrogram of the 79 rice genotypes based on measured parameters at 42 days after inoculation.

that exhibited high number of tillers and leaves with moderate plant height, had low score of DS and DI. The hierarchical clustering (Fig. 5) based on the measured parameters showed agreement with the PCA (Fig. 4) and differentiated the genotypes into eight groups based on the agro-morphological traits and physiological mechanism of the defense responses. The most resistant group (Cluster 1) contained the best nine genotypes viz. V1 (TOG5672), VB5 (WAB 2152-TGR2-WAT1-2), VB22 (WAB 2138-WAC B-2-TGR2WAT-B1), V2 (TOG5681), V5 (S2-5), V6 (S5-8), V27 (S2-6), V40 (PL82-7), and V41 (PL85-1). This cluster (Fig. 5) exhibited low average DS (2.7%) and DI (7.2%), with moderate plant height (108.5 cm), tillers (9.6), and the number of leaves (37.0) at 42 DAI in contrast to the most susceptible group (Cluster 8) (Fig. 5) which showed high DS (51.8%) and DI (99.7%), with average agro-morphological parameters at 42 DAI viz. plant height (84.6 cm), tillers (7.8) and the number of leaves (34.7). The highly resistant group (Cluster 1) included the resistant control TOG5681 while the susceptible control IR64 featured in the most susceptible group (Cluster 8).

Discussion

The present study identified many genotypes that showed effective resistance, confirmed by low DS and low ELISA titre values at 42 DAI, to RBe24 isolate of RYMV—the most pathogenic strain on the virus in Benin. An indication of the effectiveness of the resistance in these lines was the disparity in DS score of the two most resistant groups and the two most susceptible groups. The number of highly resistant (15) and resistant (8) genotypes indicate the likelihood of developing broad-based resistance to RYMV from these sources. The consistent high incidence, DS as well as high ELISA titre value for IR64, demonstrate the effectiveness of the inoculation technique, and provide strong evidence of the reliability of the results obtained in this study. The close DS values of IR64 at 21 (48.2%) and 42 DAI (50.1%) indicate that reaction of rice genotypes to RYMV can be reliably assessed at 21 DAI using the inoculation technique deployed in the present study. The results of our study demonstrate *O. glaberrima* to have high frequency of resistance alleles to RYMV. This is in agreement with the results of Pidon et al. (2020) that *O. glaberrima* is an invaluable source of resistance to RYMV in rice. In our study, this was evidenced by the composition of the highly resistant and resistant groups. The highly resistant group consisted of two *O. glaberrima*, 1 *O. glaberrima* × *O. sativa* interspecific genotypes and 12 intraspecific *O. glaberrima* genotypes. Respective values for the resistant

group were 1, 2, and 5. *O. glaberrima* germplasm is considered critical in developing a comprehensive strategy for the control of RYMV in West Africa (Orjuela et al., 2013; Pidon et al., 2017, 2020). Information on the resistance gene(s) present in these genotypes will be useful for designing a breeding strategy to pyramid them.

RYMV reduced plant height and number of tillers at the initial stage of plant growth (21 DAI). In contrast to the reduction in plant height due to RYMV at 42 DAI, number of tillers, however, increased, indicating that infected plants showed some recovery from the effects of RYMV with age. Plant height and number of tillers are major yield components in rice (Akinwale et al., 2011; Huang et al., 2013; Li et al., 2019; Moldenhauer et al., 2004; Sakamoto and Matsuoka, 2008). Resistant genotypes used in this study also had high number of tillers and moderate plant height.

Although yield was not determined in the present study, the reduction in plant height and increase in the number of tillers under RYMV mirror the likely effects RYMV have on these traits, since plant height and number tillers are important yield components. Agahi et al. (2007) and Oladosu et al. (2018) reported a correlation of 0.6 and 0.7 between number of tillers and grain yield in rice. In general, the rice genotypes used in our study responded to RYMV infection by mitigating the effects of the virus. An indication of this was the lower percentage reduction observed for plant height at 42 DAI compared to 21 DAI, and the 13.6% increase in the number of tillers at 42 DAI relative to the 19.0% reduction in number of tillers at 21 DAI. The significant inoculum × genotype interaction observed for plant height and number of tillers at 42 DAI indicate that plant response under non-inoculated condition was not indicative of performance under RYMV infection. Consequently, an effective inoculation technique is crucial for breeding progress.

Integrated management, with host plant resistance as an important component, is usually more effective in the control of many pests and diseases. Although, several authors have investigated the beneficial effects of Si treatment in mitigating various biotic and abiotic stresses in plants (Datnoff et al., 2007; Dufey et al., 2014; Mbonankira, 2014), our study was the first to investigate the effects of Si on RYMV in rice. Epstein (1994) and Abed-Ashtiani et al. (2012) reported that the supply of soluble Si and its accumulation provide stronger and tougher cell walls that act as mechanical barrier to viruses in vegetables. In the present study, we did not find any effect of Si on RYMV infection and DS. Similar to our results, Zellner et al. (2011) reported that high levels of K_2SiO_3 had no effect on tobacco mosaic virus. Si supplementation in Cucumber infected

with Papaya ring spot virus, however, reduced to a larger extent the severity of this virus as well as its accumulation in the leaves (Elsharkawy and Mousa, 2015; Sakr, 2016). In contrast to these results, Bengsch et al. (1989) demonstrated that silicon application increased the incidence Belladonna mottle virus in infected tobacco plants. Sakr (2016) and Zellner et al. (2011) suggested that silicon effect may be virus-specific.

In this study, Si enhanced the plant height of rice in both inoculated and non-inoculated pots, with the highest percentage increases obtained at 10 g CaSiO₃ per plant, and with higher increase obtained in inoculated compared to non-inoculated pots. These results indicate that in terms of height, rice plants infected with RYMV benefitted more from Si application than non-inoculated plots. However, Si reduced the number of tillers in both inoculated and non-inoculated pots, with much higher reductions in inoculated pots (26.8% and 28.0% at 5 and 10 g CaSiO₃ per plant, respectively) compared to non-inoculated pots (12.3% at both 5 and 10 g CaSiO₃ per plant). These results indicate a major difference in the effects of Si on two major yield components in rice. Although grain yield was not determined in the present study, the reduction in number of tillers per plant suggests reduction in yield due to Si. Agahi et al. (2007) and Oladosu et al. (2018) reported a correlation of 0.6 and 0.7 between number of tillers and grain yield in rice. Kumar et al. (2011), Kumar and Nilanjaya (2014), and Sharifi (2018) from path analysis, also reported a direct effect of number of tillers on rice yield. The reductions of the Si dose on number of tillers was genotype-independent. This was indicated by the non-significant Si dose × genotype interaction, a result that suggests that both resistant and susceptible genotypes expressed similar responses.

Narayanaswamy et al. (2012), who studied the effect of Si on wheat and also used CaSiO₃, found a rate-dependent reduction in the yield of wheat, a result attributed to the negative effect of the high pH induced by the high application rates of CaSiO₃ on the solubility of several essential plant nutrients. Johnson et al. (2014) also reported that the application of CaSiO₃ induced an increase in soil pH; the release of large amounts of calcium ions prevent the bioavailability and absorption of silicon and other minerals by plants. Given that the source of Si used by these authors and in our studies are similar, it is plausible that the pH-induced effect of CaSiO₃ may have played a role in the reduction of number of tillers obtained under inoculated and non-inoculated conditions in the present study. Most of the previous studies on the beneficial effects of Si on plant growth, resistance and ability to withstand biotic and abiotic stresses were conducted using hydroponics, with periodic (daily

or weekly) correction of the pH of the solution (Dufey et al., 2009, 2012; Mbonankira, 2014; Zellner et al., 2011). The present study, carried out in pots, offered no opportunity for periodic pH correction of the growing medium. A repeat of the present study using hydroponics with periodic pH adjustment, other sources of Si and foliar application to increase the efficiency of absorption will offer more insight on the integrated management of RYMV with host plant resistant and Si.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

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