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Distribution, Pathogenicity, and Interactions of Two Strains of *Rice yellow mottle virus* in Forested and Savanna Zones of West Africa

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ABSTRACT

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In Côte d'Ivoire, the S2 strain of *Rice yellow mottle virus* (RYMV) predominated in the forested zones, including the "rice belt" to the west, in each of the cropping systems where rice was grown. The S1 strain occurred more frequently in the northern Guinean savanna, and only S1 isolates were found further north in the Sahelo-Soudanian zones. In mixed infection, S2 dominated over S1 both in viral capsid and RNA contents under temperature regimes encompassing those observed in savanna and forested zones of Côte d'Ivoire. There was no evidence of interactions in virus accumulation between the West African strains S1 or S2 with the more distantly related East African strain S4. Field trials emphasized the impact of RYMV, which induced yield losses of 40 to 60% in several widely grown cultivars of *Oryza sativa indica* and *O. sativa japonica*. We report the high resistance of the *O. indica* cv. Gigante under field conditions which was apparent with all the S1 and S2 isolates tested. Responses to RYMV infection of several cultivars were isolate dependent. With most differential cultivars, responses were not strain specific, with the exception of the *O. japonica* cv. Idsa6, in which the S2 isolates always induced higher yield losses than the S1 isolates.

Additional keywords: host plant resistance, *Sobemovirus,* strain competition

Rice (*Oryza sativa*) is widely grown in Africa and is the most cultivated cereal in Côte d'Ivoire, where annual production exceeds 700,000 metric tons (20). First reported in Kenya and in Côte d'Ivoire in the 1970s (6,8), *Rice yellow mottle virus* (RYMV) is now present in most of the African continent, where it induces severe yield losses (1). RYMV is a member of the genus *Sobemovirus* (10). Under natural conditions, RYMV is transmitted by chrysomelid beetles and, under artificial conditions, it is also sap transmissible. Infected plants show yellow discoloration and mottling of leaves, stunting, reduced tillering, poor panicle exertion, and sterility. Early infection of susceptible varieties can cause the death of the plant; severe yield losses of 20 to 100% have been reported in many countries (4,5,12,22).

The existence of strains of RYMV with contrasted geographical distribution between East and West Africa has been reported (19). In West Africa, three strains with overlapping distributions were identified and named S1, S2, and S3. In Côte d'Ivoire, the isolates were assigned to the S1 or S2 strains (18,19). These strains were determined on the basis of their coat protein (CP) sequence, and also differed serologically using discriminating monoclonal antibodies (MAbs; 17,18). S2 was more prevalent in Côte d'Ivoire, whereas S1 isolates were mainly found in the savanna zones of the north (18). There was unilateral antagonism between S1 and S2 strains, because coinoculation of S1 and S2 isolates led to S2 dominance irrespective of the isolates or the cultivar tested. S2 dominance over S1 did not relate to crossprotection because it occurred whatever the sequence of inoculation (18).

In this study, (i) S2 prevalence in Côte d'Ivoire was reassessed on a larger survey, especially in the "rice belt" to the west of the country, in different cropping systems, and S1/S2 coexistence was assessed in the savanna zones in neighboring countries to the north of Côte d'Ivoire; (ii) S2 dominance over S1 was checked at the RNA level and in plants grown at different temperatures to test whether differences between strains in thermosensitivity were involved; in addition, S2 and S1 interactions with the more distantly related East-African S4 strain were tested; and (iii) differences in pathogenicity among 15 S1 and S2 isolates were assessed in field trials conducted during three consecutive years by recording symptom intensity and yield losses among 12 cultivars. Implications for RYMV epidemiology and control are considered.

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MATERIALS AND METHODS

Isolate collection. In all, 91 isolates, 77 from Côte d'Ivoire and 14 from four neighboring countries (Mali, Burkina-Faso, Ghana, and Guinea), were collected from affected *O. sativa indica* plants in rainfed lowland fields. Isolates were recovered by mechanical inoculation on the susceptible cultivars BG90-2 or Bouaké189, which induced the characteristic yellow discoloration and mottling of leaves. Of the 91 isolates, 57 were collected before 1997 and 34 after. The two main agro-ecological zones surveyed were the forested south and center of Côte d'Ivoire and the Guinean savanna to the north. Below latitude 8°N are forests with annual rainfall exceeding 1,100 mm, and to the north is savanna vegetation with less rainfall and higher temperatures (24). In Abidjan, in the forested zone of the south of Côte d'Ivoire, average maximum monthly temperatures range from 23 to 29°C; in Bouaké, in the center of the country, from 21 to 32°C; in Man at the west, from 21 to 28°C; and in Ferkessedougou, Bondoukou, and Odienné in the Guinean savanna zone at the north, from 20 to 34, 21 to 31, and 20 to 33°C, respectively (20,24).

Immunological typing. The immunological profile of the isolates was determined using the full range of MAbs M, C, G, E, B, F, D, and A (18). S1 isolates reacted with all MAbs except D, whereas S2 isolates reacted with all MAbs except A and F (17,18). MAbs were used in triple-antibody sandwich-enzyme-linked immunosorbent assay (TAS-ELISA) essentially as given in Thomas et al. (23) following the protocol of N'Guessan et al (18). RYMV-Mg polyclonal antiserum, prepared against an S4 isolate from Madagascar, was used as primary antibody in TAS-ELISA because it detected S1 and S2 isolates similarly (18); MAbs in tissue supernatant fluids were used as secondary antibodies. Bound MAbs were detected with goat antimouse globulin-alkaline phosphate conjugate.

Molecular typing. Genome fragments with the CP gene and part of the 3′ untranslated region (UTR) were transcribed and amplified by reverse transcriptase-polymerase chain reaction (RT-PCR) after extraction of total RNA from leaves. The

protocol was that of Pinel et al. (19). Primers A2 and B2 directed to S1/S2-conserved regions were used to amplify a 870-bp region, including the 720-bp CP gene of S1 and S2 isolates. Sequencing was carried out with the *Taq* terminator sequencing kit (Applied Biosystems, Inc., Foster City, CA) and analyzed on an Applied Biosystems 373 A sequencer. Two readings per base (3′ to 5′ and 5′ to 3′ directions) led to sequence accuracy >99.9%. Sequences were assembled and analyzed by autoassembler software (Applied Biosystems, Inc.).

Growth chamber tests. Competition between S1 isolate CI4 and S2 isolate CI24 in mixed infection was studied at different growth temperatures. CI4 and CI24, which are representative of all S1/S2 pairing (18), were coinoculated in four growth chambers with regimes of night-day temperatures set at 22 and 30°C (I), 28 and 30°C (II), 26 and 32°C (III), and 26 and 40°C (IV). Previous experiments (18) on interactions were conducted in growth chamber I, approximating the forest conditions of southern Côte d'Ivoire. The temperature regime of growth chamber II was intermediate for the south and north of Côte d'Ivoire, whereas conditions of growth chamber III were similar to those in the north of the country. Growth chamber IV approximated the savanna-Sudanese zones of countries north of Côte d'Ivoire.

Virus titer was assessed 2 and 4 weeks after inoculation in the highly susceptible cv. Bouaké189 (high virus titer and pronounced symptoms) and in the partially resistant cv. Ita212 (low virus titer and moderate symptoms). Each inoculation (single and dual) was applied to five plants pooled together and each treatment was replicated three times. The entire experiment was repeated twice. RYMV-Mg polyclonal antiserum was used as primary antibody in TAS-ELISA. MAbs A and F and MAb D specific to S1 and S2 strains, respectively, were used as secondary antibody to assess the respective amount of S1 or S2 isolates used to coinoculate the plants. In addition, the nondiscriminant MAb C, which has the same affinities for all RYMV strains (18), quantified the overall virus titer independently of the serological properties of the isolates.

Field tests. Fifteen isolates were selected and their pathogenicity assessed in field trials. This sample consisted of 5 S1 and 10 S2 isolates (determined serologically and molecularly, as described above). Experiments were conducted in four large 5-by-20-m insect-proof cages at the WARDA experimental station, 35 km from Bouaké (center of Côte d'Ivoire). Each isolate was inoculated to 12 cultivars, a sample representative of the differential reactions to RYMV infection of *O. sativa indica, O. sativa japonica,* and *O. glaberrima* species, but which had never been tested simultaneously and using the same criteria over several years. The sample consisted of *O. glaberrima* cv. Tog5672, *O. sativa indica* cv. Gigante, *O. sativa japonica* cv. Fkr27, *O. sativa indica* cvs. Ita212 and Tox3211, the closely related cvs. *O. sativa japonica* Idsa6 (originating from an *indica* × *japonica* cross) and Wab56-50 (= Idsa6 × Iac165), cvs. Ngoyumabol and Bogudi (land races from Sierra-Leone), the closely related natural *O. sativa indica* cvs. Wita8 and Wita7, and the widely grown *O. sativa indica* cv. Bouaké189. The trial was arranged as a factorial design with four replicated plots, one plot per cage, and repeated in three consecutive years (1995, 1996, 1997). Each plot contained 16 subplots which were inoculated by one of the 15 isolates randomly allocated; one virus-free subplot served as control. Each subplot consisted of 12 rows, 1 row of 10 plants for each of the 12 cultivars tested. The distance between and within rows was 20 by 20 cm. An unplanted strip of 50 cm was left between replicates and between subplots.

Seeds of each cultivar were sown in beds and transplanted 2 weeks later. Mechanical inoculation was performed 2 weeks later. Disease severity was scored fortnightly from 2 to 8 weeks after inoculation using a 1-to-9 scoring system (11). Plant height was also recorded fortnightly. Yield losses (%) of each isolate–cultivar combination were determined by the following formula: $100 \times (Xh - Xi)/Xh$, where Xh and Xi were respectively the mean weights of 1,000 grains from healthy and infected cultivars collected 4 to 6 months after planting. Variance analyses were performed with the Winstat statistical software (version II, ITCF-CIRAD, Paris).

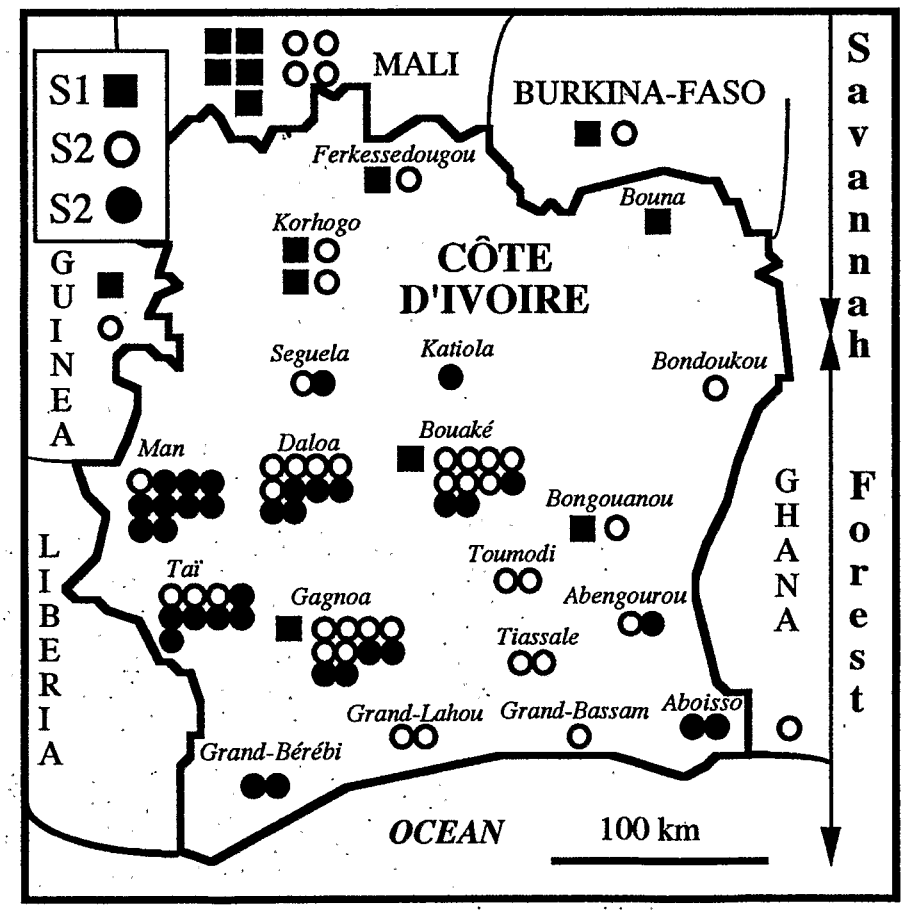

Fig. 1. Map of Côte d'Ivoire and of the neighboring countries showing the distribution of *Rice yellow mottle virus* (RYMV)-S1 (■) and RYMV-S2 isolates (○ and ●). The S2 isolates collected before 1997 are distinguished from those collected afterward (○ and ●, respectively). For isolates of Côte d'Ivoire, the nearest town to the sampling location is indicated; for the other isolates only the country of origin is mentioned.

RESULTS

Prevalence and distribution of strains. Immunological typing with the discriminating MAbs detected 77 S2 isolates, 70 of which were from Côte d'Ivoire, 4 from Mali, and 1 each from Burkina-Faso, Ghana, and Guinea (Fig. 1). Fourteen S1 isolates were detected; seven from Côte d'Ivoire, five from Mali, and one each from Guinea and Burkina-Faso. The western part of Côte d'Ivoire (Daloa, Gagnoa, and Grand-Lahou), the main rice-producing region of the country (the rice belt), is a forested zone where rainfed upland rice is cultivated in monoculture. All isolates, except one, were identified as S2 isolates. In the central region (Bouaké, Bongouanou, and Toumodi), an intermediate

forested-savanna zone, lowland irrigated rice and yam are cultivated. All but two isolates were of the S2 strain. Thus, in these two regions, the two strains coexist with S2 predominating overwhelmingly, with 3 S1 compared with 33 S2 isolates detected in surveys conducted before 1997 and no S1 compared with 34 S2 isolates subsequently. S2 was also found to the west of Côte d'Ivoire in Guinea and to the east in Ghana (Fig. 1).

A different distribution pattern occurred in the drier and hotter northern Guinea savanna zones of Côte d'Ivoire and in the neighboring countries to the north (Burkina-Faso, Guinea, and Mali), where rice is mainly cultivated in rainfed systems together with maize and sorghum. The S1 strain was found more frequently than in the forested zones, and isolates of S1 and S2 strains occurred with similar prevalence (11 S1 compared with 9 S2 isolates). In Mali and Burkina-Faso, the five S2 isolates originated exclusively from the Guinean savanna zone at the south of the countries, whereas two of the six S1 isolates were from the Office du Niger in Mali, located further north in Sahelo-Soudano zones where irrigated rice was grown intensively.

Interactions between RYMV strains. There was no apparent correlation between temperature and symptom expression or virus content assessed serologically because responses with the nondiscriminant MAb C were similar in S1 and S2 monoinoculated plants whatever the growth conditions (*data not shown*). S2 strain dominance over S1 was not temperature dependent because unilateral antagonism of S2 over S1 occurred in each temperature regime (Fig. 2), cultivar, or test (*data not shown*). For S1, using S1-specific MAb A, the ratio of absorbances ([S1 in doubly infected plants]/[S1 in singly infected plants]) was always less than 0.5 and often below 0.1 (Fig. 2). By comparison with a dilution curve, S1 CP content in coinoculated plants was less than a tenth that of S1 in singly inoculated plants (*data not shown*). In S2, using S2-specific MAb D, there was neither decrease nor increase after coinoculation with S1, because ratios of absorbances ([S2 in doubly infected plants]/[S2 in singly infected plants]) were approximately 1, indicating that the extracts did not differ significantly in CP content between singly and doubly infected plants (Fig. 2). No differences in pathogenicity (see below) and in rate of CP accumulation (*data not shown*) between the S2 isolate (CI24) and the S1 isolate (CI4) in singly infected plants were apparent to account for S2 dominance over S1.

S2 dominance over S1 was not only found through capsid protein content, as estimated serologically, but also occurred at the RNA level. Sequences of the RNA extracted from plants monoinoculated with S1 and S2 isolates were typical of the S1 and S2 strains, respectively. There was a 6% divergence in nucleotide sequence of the CP gene between the CI4 (S1) and CI24 (S2) isolates, which is well within the known 5-to-7% range of S1-S2 divergence (19). The sequence of the RNA extracted from the coinoculated plants and amplified by RT-PCR, representing the consensus sequence of the leaf extract, was >99.9% homologous to that of the CI24 (S2) isolate inoculated. Thus, the RNA of the S2 strain was predominant in the S1-S2 coinoculated plants.

MAbs had been raised against an S4 isolate. Consequently, interactions between S4 isolates and either S1 or S2 isolates could only be tested unilaterally, (i.e., whether S4 virus content decreased when coinoculated with S1 using MAb D, which does not detect S1, or when coinoculated with S2 using MAb A, which does not detect S2). There was no interaction between S4 and either S1 or S2 because absorbances values were invariably similar in S4 mono or S1-S4 and S2-S4 coinfected plants (*data not shown*).

Pathogenicity of S1 and S2 isolates. The pathogenicity of 15 isolates, 5 S1 and

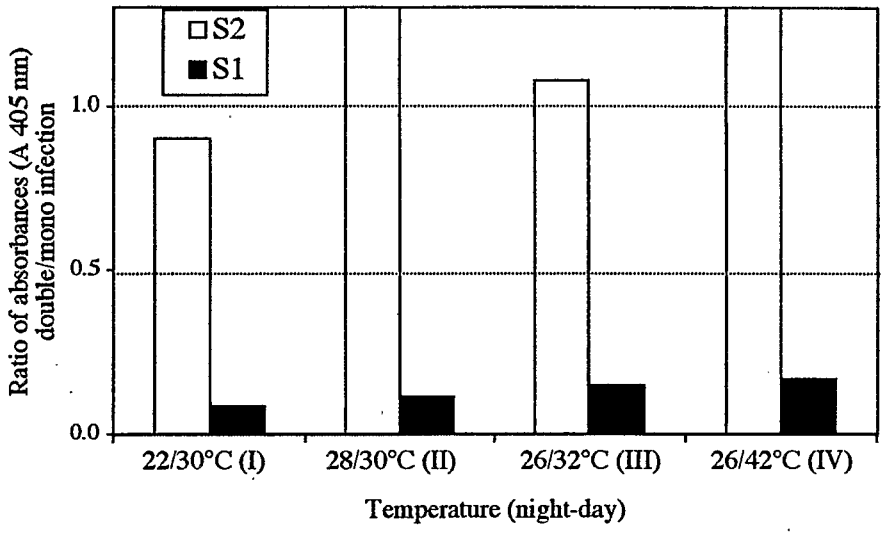

Fig. 2. Relative virus titers of S1 and S2 strains of *Rice yellow mottle virus* (RYMV) in singly and doubly infected plants in four growth chambers, each having different day-night temperature regimes. The virus titer of S1 and S2 strains was assessed serologically in triple-antibody sandwich enzyme-linked immunosorbent assay using, respectively, S1-specific monoclonal antibody (MAb) A (black histograms) and S2-specific MAb D (open histograms) as secondary antibodies. The results for S1 and S2 were expressed, respectively, as the ratio of absorbances ([S1 in doubly infected plants]/[S1 in singly infected plants] and [S2 in doubly infected plants]/[S2 in singly infected plants]). A ratio <1 indicates a decrease in coat protein content in coinfected plants, whereas a ratio of approximately 1 indicates that the extracts do not differ in coat protein content between monoinfected and doubly infected plants. The response was assessed 14 days after inoculation.

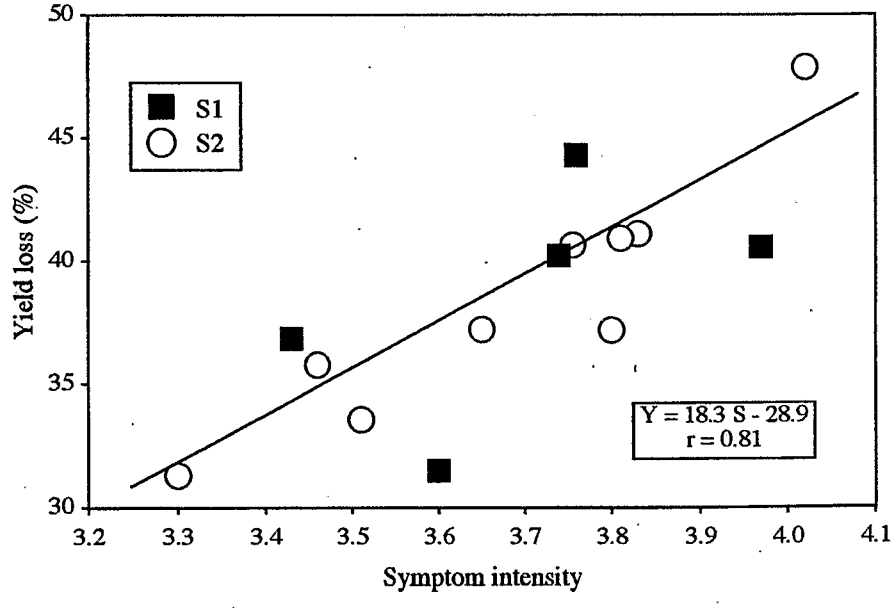

Fig. 3. Relationship and regression line between symptom intensity and yield loss induced by each of nine S2 isolates (○) and of five S1 isolates (■) for all of the 12 cultivars confounded.

10 S2, was assessed each of three consecutive years against a group of 12 cultivars. There was a significant linear relationship (r = 0.81) between symptom intensity and yield loss (Fig. 3), with the possible exception of one isolate (CI21), which induced conspicuous symptoms but limited losses. However, yield loss data allowed a better discrimination between isolates and cultivars than symptom expression or plant height (*data not shown*). Consequently, yield loss data were analyzed further.

Three-way variance analysis of yield losses (Table 1) indicated significant effects of isolate (F = 23.0, df = 14, 1620; P < 0.001), cultivar (F = 665.4, df = 11, 1620; P < 0.0001), and year (F = 3.1; df = 2, 1620; P = 0.04). There were no isolate–year or cultivar–year interactions, indicating that the effects of isolates and of cultivars were consistent from year to year. By contrast, there was an overall significant isolate–cultivar interaction (F = 9.5, df = 154, 1620; P < 0.0001), indicating that the response to isolates was cultivar dependent.

Average yield losses of approximately 60%, with maxima of up to 80%, were found in the four cultivars Bouaké189, Bogudi, Wita7, and Wita8, subsequently referred to as highly susceptible (Fig. 4). Yield losses of approximately 45% were recorded in the susceptible cvs. Idsa6, Wab56-50, and Ngoyumaboi. Yield losses of approximately 20% occurred in cvs. Fkr27, Ita212, and Tox3211, subsequently referred to as partially resistant. Yield losses below 10% were recorded in the highly resistant cvs. Tog5672 and Gigante. Variation in yield loss between years was either low or nonsignificant (Table 1, Fig. 4).

Three patterns of interactions between cultivars and isolates were distinguished (Table 1). First, the "isolate effect" was not significant with the highly resistant cvs. Tog5672 and Gigante and the partially resistant cvs. Fkr27 and Tox3211, possibly because a minimal level of susceptibility is necessary to detect interactions, and with the highly susceptible cv. Wita78. With each of these five cultivars, there were no differences in response to infection between the isolates inoculated.

Second, there was a differential response in six other cultivars (Ita212, Ngoyumaboi, Wab56-50, Wita7, Bogudi, and Bouaké189), where the isolate effect was significant but with no strain–pathogenicity relationship (Table 2). Interactions between isolates and cultivars were complex. Wab56-50 discriminated clearly between two groups of isolates with yield losses of 32 to 40% caused by isolates of the first and between 56 and 72% by those of the second. With the other cultivars, differences in pathogenicity between isolates were less clear cut, which resulted in partial overlapping of the ranking of the isolates (Table 2). For all differential cultivars, large differences in pathogenicity were observed between isolates. For instance, yield losses ranged from 1 to 49% in Ita212 and from 10 to 78% in Ngoyumaboi. Accordingly, Ita212 would be scored highly resistant, with less than 10% yield loss when inoculated with isolates CI2, CI3, CI21, or CI24 and susceptible with yield losses exceeding 40% with isolates CI4, CI1, or CI23 (Table 2). Similarly, Ngoyumaboi would be scored resistant with losses of 10% when inoculated with isolate CI20 and highly susceptible with yield losses >60% with isolates CI24, CI5, CI8, or CI23.

Overall, isolates CI23 and CI5 induced the highest yield losses (averaging 70 and 65%, respectively) and were ranked as the most severe isolates against all six differential cultivars (Table 2). By contrast, pathogenicity of the other isolates was cultivar dependent and any overall ranking for all cultivars is inappropriate and not statistically valid. In these cultivars collectively, there was no relationship between pathogenicity and strain because there were mild and severe isolates of both S1 and S2 strains (Table 2). Moreover, pathogenicity was not geographically related and, for instance, the most severe isolates CI5 and CI23 originated from savanna and forest, respectively (Table 2).

By contrast, a third type of response occurred with the *O. sativa japonica* cv. Idsa6, which clearly differentiated S1 from S2 isolates (Table 3). Significantly higher yield losses (Newman-Keuls tests of mean comparison after two-way variance analysis) were induced by S2 than by S1 isolates in each year. Average yield losses were 44 to 49% in S2-infected plants, compared with 31 to 35% in S1-infected plants. The average S2-S1 difference was 12%, ranging from 8 to 18% depending on the year (Table 3). There was no overlap in pathogenicity between isolates of the two strains, and each year the minimum difference in yield losses between the milder S2 isolate and the most severe S1 ranged from 1 to 9%.

DISCUSSION

The overwhelming prevalence of strain S2 in the forested zones in the south, in the

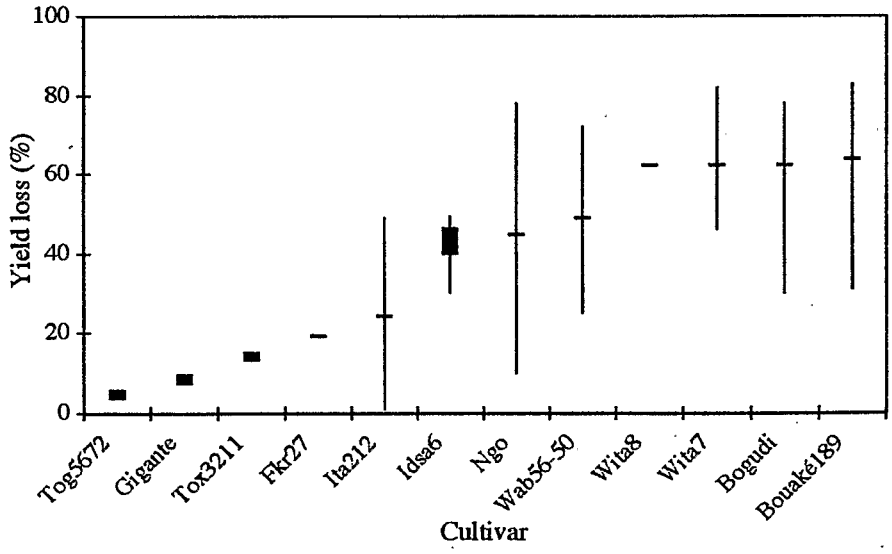

Fig. 4. For each of the 12 cultivars tested, the average yield losses induced by the 15 isolates taken together across the 3 years of experiments (horizontal bars), the year-to-year variation of the annual average (black rectangles), and the range of variation of yield loss among the isolates (vertical bars) are indicated.

Table 1. Variance analysis of yield losses induced in twelve cultivars by 15 isolates of RYMV over three consecutive years

		Cultivar																					
Source of		Tog 5672		Gigante		Tox3211		Fkr27		Ita212		Idsa6		Ngo		Wab56-50		Wita8		Wita7		Bogudi		Bouaké189	
variation	df	F[z]	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Isolate	14	1.6	NS	1.3	NS	1.1	NS	1.6	NS	13.5	0.000	11.3	0.000	18.6	0.000	17.5	0.000	0.4	NS	3.3	0.000	13.8	0.000	11.0	0.000
Year	2	5.6	0.004	5.3	0.006	5.5	0.005	1.0	NS	0.4	NS	25.0	0.000	0.2	NS	0.0	NS	1.5	NS	0.3	NS	0.2	NS	1.4	NS
Interaction	28	0.2	NS	0.6	NS	1.0	NS	0.3	NS	0.2	NS	0.90	NS	0.2	NS	0.2	NS	0.2	NS	0.1	NS	0.9	NS	0.3	NS
Residual	135																								

[z] Fisher value (F) and significance level (P) of each factor; P < 0.01 indicates a significant effect; NS a nonsignificant effect.

center, and in the rice belt of western Côte d'Ivoire (annual rainfall >1,100 mm) occurred in all cropping systems in which rice is grown. S2 also occurred in neighboring countries, in Ghana to the east and in Guinea to the west. Strains S1 and S2 coexisted with a greater proportion of S1 isolates in the dryer Guinean savanna zones (900 to 1,100 mm rainfall) in the north of Côte d'Ivoire, and to the south of Mali and Burkina-Faso. Only S1 isolates were found further north in the Sahelo-Soudanian zones of Mali (200 to 600 mm rainfall), where irrigated rice is grown intensively.

Differences in thermosensitivity between virus strains have often been reported (15). It might be speculated that differences in heat sensitivity between S1 and S2 explain both the contrasting south/north distribution of S1 and S2 isolates and the S2 dominance over S1 after coinoculation at the temperature used in earlier experiments (18), which approximated that of forest zones. Based on this hypothesis, the lower temperatures of the south and center of Côte d'Ivoire would favor S2, whereas the hotter temperatures in the north would favor S1. However, our experiments did not support this hypothesis and showed that S2 dominance over S1 cannot be attributed to differences in thermosensitivity because stable unilateral antagonism of S2 over S1 in coinoculated plants was observed in each temperature regime.

Our results indicate that S2 dominated S1 both in viral capsid and RNA contents. S2 dominance was not due to higher pathogenicity of S2 isolates: in most cultivars tested, pathogenicity of the isolates was not strain specific, with the exception of Idsa6. Nor was it due to a higher rate of CP accumulation of S2 isolates. A similar example of such a strain-selective advantage occurred with *Cauliflower mosaic virus* strain S (Cabb S), which dominated in mixed infections, although Cabb S and other strains induced symptoms of similar severity in turnip plants inoculated concurrently and accumulated to similar levels in singly infected plants (25). There was no evidence of interactions in virus accumulation between the West African strains S1 or S2 of RYMV with the more distantly related East African strain S4. This is consistent with the general finding that the more closely related the strains, the greater the degree of interaction (9).

There was a significant relationship between symptom intensity and yield loss which confirmed the importance of making symptom assessments in screening tests. However, yield loss estimates, although more time consuming, gave more consistent results and greater discrimination, possibly because symptoms are masked in some cultivars and with some isolates or in specific growing conditions. This is consistent with results of Coulibaly (7), who found that yield parameters discriminated better than vegetative growth parameters in screening tests. The results of the field trials further emphasized the potential impact of RYMV, which induced yield losses of 40 to 60% in several widely grown *O. indica* and *O. japonica* cultivars.

High resistance was observed in *O. glaberrima* cv. Tog5672 and in *O. sativa indica* cv. Gigante, in which yield losses were <10% with each isolate inoculated. Similarly, Tog5672 was found to be highly resistant in previous field trials in Burkina-Faso (7,14). With Gigante, in earlier greenhouse tests, no visible symptoms occurred and no virus was detected, although Gigante was not immune because virus was recovered by mechanical inoculation back to susceptible cultivars (16). This is the first detailed report of the high resistance of Gigante in field conditions and to a range of isolates. Indeed, the 7 to 9% yield loss observed in infected Gigante may not even have been due to RYMV infection because it could have resulted from damage caused by the inoculation, because the plants in the virus-free control plots were not mock inoculated with virus-free buffer. These field data establishing the high resistance of the *O. sativa indica* cv. Gigante emphasize the importance of the current plant breeding projects to transfer this type of resistance to the currently susceptible irrigated and lowland cultivars (16).

Differences in pathogenicity between isolates were detected in several cultivars,

Table 2. Yield losses (%) induced by the *Rice yellow mottle virus* (RYMV) isolates in rice cultivars[z]

			Cultivar						
Isolate	Strain	Origin	Ita212	Ngo	Wab 56-50	Wita7	Bogudi	Bouaké189	Mean
CI23	S2	Forest	49 a	78 a	61 a	70 abc	76 a	83 a	70
CI5	S1	Savannah	35 abc	70 a	71 a	69 abc	77 a	66 a-e	65
CI1	S1	Forest	49 a	35 bc	56 a	72 ab	57 bc	79 ab	58
CI24	S2	Forest	5 e	66 a	57 a	67 abc	78 a	65 b-e	56
CI8	S2	Forest	11 de	72 a	57 a	46 c	78 a	72 a-d	56
CI3	S1	Savannah	3 e	70 a	62 a	67 abc	71 ab	59 cde	55
CI22	S2	Forest	32 abc	38 bc	72 a	57 bc	61 bc	67 a-e	55
CI4	S1	Savannah	18 cde	40 bc	63 a	82 a	70 ab	31 f	51
CI18	S2	Forest	43 ab	20 cd	38 b	60 abc	58 bc	75 abc	49
CI19	S2	Forest	29 abc	36 bc	37 b	58 bc	57 bc	77 ab	49
CI9	S2	Forest	32 abc	48 b	27 b	62 abc	55 bc	56 de	47
CI10	S2	Forest	31 abc	31 bc	35 b	48 bc	47 c	59 cde	42
CI21	S2	Forest	4 e	23 cd	40 b	55 bc	64 ab	52 e	40
CI2	S1	Forest	1 e	37 bc	25 b	62 abc	56 bc	52 e	39
CI20	S2	Forest	22 cd	10 d	32 b	60 abc	30 d	64 b-e	36

[z] Ranking of the pathogenicity of the isolates was determined from the yield loss data of each cultivar with significant isolate effect in variance analysis. Different letters indicates that isolates differed significantly at 5% level in Newman-Keuls test.

Table 3. Yield losses (%) induced by five S1 and 10 S2 isolates of *Rice yellow mottle virus* (RYMV) in the *Oryza sativa japonica* cultivar Idsa6 over three consecutive years

	Yield losses (%)															Δ(%)[z] S2 - S1	
	S2										S1						
Year	CI8	CI22	CI21	CI24	CI19	CI23	CI9	CI20	CI18	CI10	CI4	CI2	CI5	CI3	CI1	Mean	Min
1995	55	55	53	53	50	53	50	52	49	48	39	37	40	32	31	18	8
1996	47	43	40	39	44	40	43	40	40	40	34	35	32	38	33	8	1
1997	46	47	45	45	42	43	43	42	44	43	34	33	32	33	29	11	9
Mean	49	48	46	46	45	45	45	45	44	44	35	35	35	34	31	12	6

[z] Respectively, mean and minimal differences of yield losses induced by S2 compared with S1 isolates.

but the relationship was complex and resistance was often isolate specific, as observed with many other viruses (13). Only two isolates were consistently more severe in all cultivars. With the others, there was a significant isolate–cultivar interaction and ranking of the pathogenicity of the isolates differed according to the cultivar inoculated, even between the two closely related and similarly susceptible cultivars Wita7 and Wita8. A difference in pathogenicity between isolates is also likely to explain why Wita7 and Wita8 were found to be highly susceptible in our tests and previously in Burkina-Faso (7) and yet were tolerant elsewhere (3). Cvs. Ita212 and Ngoyumaboi were ranked either resistant or susceptible according to the isolate inoculated. Several other examples of differential responses to RYMV infection are suspected to be isolate dependent (1,7), including reports of the high susceptibility of Ita212 (21), whereas it is most often considered to be partially resistant. These differential responses to infection fit with the hypothesis that different resistance genes or groups of resistance genes are involved in virus–host interactions (2,14). Practically, this indicates that breeding projects should include a screening against a range of isolates differing in pathogenicity.

For all cultivars of *O. sativa indica* that were tested, there was no relationship between pathogenicity and strain or between pathogenicity and geographic origin. By contrast, in the *O. sativa japonica* cv. Idsa6, which is grown widely in the south of Côte d'Ivoire and has the shortest growth cycle of those cultivated under rainfed systems, S2 isolates always induced higher yield losses than S1 isolates. This occurred whatever the isolate tested and during each year. Thus, in Idsa6, severe and mild isolates coincided exactly with the S2 and S1 strains, respectively. However, the relationships between pathogenicity and strain in Idsa6 cannot be generalized to all *O. sativa japonica* cultivars because pathogenicity and strains did not coincide in the closely related and similarly susceptible *O. sativa japonica* cv. Wab56-50.

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