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Inheritance of resistance to *Yam mosaic virus*, genus *Potyvirus*, in white yam (*Dioscorea rotundata*)

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Abstract *Yam mosaic virus* (YMV) causes the most-widespread and economically important viral disease affecting white yam (*Dioscorea rotundata*) in West Africa. The genetic basis of resistance in white yam to a Nigerian isolate of YMV was investigated in three tetraploid *D. rotundata* genotypes: TDr 93–1, TDr 93–2 and TDr 89/01444. F_1 progeny were produced using TDr 87/00571 and TDr 87/00211 as the susceptible parents. Segregation ratios indicated that a single dominant gene in a simplex condition governs the resistance in TDr 89/01444, while the resistance in TDr 93–2 is associated with the presence of a major recessive gene in duplex configuration. Segregation of progeny of the cross TDr 93–1×TDr 87/00211 fitted a genetic ratio of 2.48:1 resistant:susceptible, which can be expected when two simplex heterozygotes are crossed, indicating the possible modifying effect of the susceptible parent. A triple antibody immunosorbent assay (TAS-ELISA) was used for virus detection in inoculated plants. Slight mosaic symptoms appeared on most resistant individuals, while asymptomatic resistant genotypes with high ELISA (A_{405}) values were observed in all crosses. Such a heterogeneous response suggests the influence of additional modifier genes that segregate in the progeny. The finding that resistance can be inherited as a dominant or recessive character has important implications for YMV resistance breeding.

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Introduction

Yam mosaic virus (YMV) is a major constraint to the production of yam (*Dioscorea* spp.), with *Dioscorea rotundata* which accounts for most of the total world yam production, being particularly susceptible to the virus (Thouvenel and Dumont 1990; Goudou-Urbino et al. 1996). Severe chlorosis, green vein banding, shoe-stringing and severe stunting lead to a reduction in the photosynthetic ability of the foliage, with deleterious effects on tuber yield (Thouvenel and Dumont 1988; Odu et al. 2001).

Natural transmission of the virus is mainly through infected planting material (Thouvenel and Fauquet 1986; Brunt et al. 1989), but transmission may also be by aphid vectors such as *Aphis gossypii* and *Aphis craccivora* (Odu et al. 2001). Although chemical control of various aphid vectors may limit the local spread of YMV, and germplasm certification schemes may reduce inoculum level, genetic resistance is the only economically viable method of control (Fraser 1990).

Field evaluation of YMV resistance in the white yam (*D. rotundata*) germplasm is conducted annually at the International Institute of Tropical Agriculture (IITA), Ibadan-Nigeria, and sources of resistance to YMV in Nigeria have been found among landraces and breeding lines (IITA 1998a). Little is known concerning the inheritance of YMV resistance in yam, due to the lack of segregating yam populations. Hybridization of yam has become feasible due to a better understanding of the reproductive biology of cultivated yam (Asiedu et al. 1998).

Bousalem et al. (2000) recently hypothesized that YMV originated from Africa on *D. rotundata* and *Dioscorea cayenensis*, followed by independent transfers to *Dioscorea alata* and *Dioscorea trifida* during virus evolution. Considerable genetic diversity is known to exist among West African populations of YMV (Duterme et

al. 1996; Goudou-Urbino et al. 1996; Bousalem et al. 2000). Goudou-Urbino et al. (1996) identified six distinct groups based on symptomatology, Western immunoblotting and ELISA. Sequence data and phylogenetic analysis revealed that YMV had the most-variable coat protein when compared to eight other potyviruses, with YMV from Africa representing the most-diversified and divergent group of isolates (Bousalem et al. 2000). In addition to YMV, two other potyviruses *D. alata* virus (DaV) and *Dioscorea dumetorum* virus (DdV) also infect *D. rotundata* (Odu et al. 2001; Olatunde et al. 2001). YMV-resistant *D. rotundata* genotypes usually show mild mosaic symptoms in the field, and a high degree of resistance, such as immunity, has not been observed (IITA 1998a). Knowledge on the genetic control of resistance to YMV will help yam breeders design more-effective breeding strategies for the incorporation of potyvirus resistance genes into farmers' preferred varieties.

In this paper, we examine the inheritance of resistance to a Nigerian isolate of YMV identified in two *D. rotundata* landraces (TDr 93–1 and TDr 93–2) and one breeding line (TDr 89/01444).

Materials and methods

Plant material

The resistant yam accessions used in this study were the landrace cultivars TDr 93–1 and TDr 93–2, and the breeding line TDr 89/01444. The breeding lines TDr 87/00571 and TDr 87/00211 served as susceptible parents. Three crosses were made between the tetraploid yam accessions with contrasting reactions to YMV: TDr 93–1×TDr 87/00211 (cross 5), TDr 87/00571×TDr 89/01444 (cross 6), and TDr 93–2×TDr 87/00211 (cross 7). The resistant parents used in this study have consistently shown field resistance across locations. The parents were planted and crossed in the field. Progenies from these crosses were sown in seedling nurseries to generate minitubers. Minitubers were later planted in pots in the screenhouse for in vitro multiplication using nodal cuttings. In vitro shoot cultures were grown according to the method of Ng (1992). Mature plantlets were transferred into sterile peat pellets in a post-flask establishment chamber for 4 weeks, after which plants were transplanted into pots containing sterile soil. The plants were used in the screening experiments after a growth period of 2 weeks, at which stage they had developed at least three young, but fully expanded, leaves.

Yam mosaic virus isolate

A YMV isolate from *D. rotundata* was obtained from the Biotechnology Research Unit, IITA, and maintained in *Nicotiana benthamiana* plants by mechanical inoculation in a screenhouse at 18–32°C. Leaves from YMV-infected plants showed typical mosaic and green vein banding symptoms, and tested positive for YMV in TAS-ELISA (see below).

Virus inoculation

Sap extracts were prepared by homogenising infected *N. benthamiana* leaves (1:10 w/v) in 10 mM phosphate buffer (pH 7.7) containing 1 mM EDTA and 0.1 mM cysteine. Parental and progeny lines of the three crosses 5, 6 and 7 were dusted with carborundum (600 mesh) and inoculated with sap-extract prepared from the YMV-infected *N. benthamiana* leaves. Five plants of each cross were mock-inoculated with buffer to serve as healthy controls. Following this treatment, inoculation was repeated twice at 2-week intervals to reduce the possibility of 'escapes' and ensure the establishment of YMV infection. Air temperatures were between 18°C and 32°C during the course of the experiments. In another experiment, progeny of cross 7 were exposed to natural YMV infection in the field during the growing season (March–November).

Symptom evaluation

Plants were scored visually for YMV infection at 2 and 4 weeks after the third inoculation. Disease severity was evaluated on a scale of 1 to 5 (IITA 1998a), where 1 indicates plants with symptomless leaves; 2=1–25% of the leaves with mosaic or green banding symptoms; 3=26–50% of the leaves with mosaic or green vein banding; 4=51–75% of the leaves with mosaic or green vein banding symptoms; 5=plants with very severe mosaic, green vein banding and chlorosis covering >75% of the leaf. Evaluation of plants exposed to natural infection was carried out on the same scale, 4 and 6 months (July and September) after field exposure. Genotypes with symptom severity scores ≤2 were considered to be resistant, while those with severity scores ≥3 were considered susceptible (IITA 1998a). In addition, leaf samples were taken from individual parental and F_1 plants to confirm infection by the virus.

Virus detection

The TAS-ELISA procedure used for virus detection was conducted essentially as reported in Martin and Stace-Smith (1984). Rabbit IgG against YMV (2 µg/ml) was used to coat microtiter plates (Dynatech) at 100 µl/well for 2–3 h at 37°C. The plates were washed three times with PBS-T (phosphate saline buffer, pH 7.4; 0.8% NaCl, 0.02% KH_2PO_4, 0.115% Na_2HPO_4, 0.02% KCl, 0.02% $NaNO_3$, plus 0.05% Tween-20) and blocked with 2% skimmed milk powder in PBS-T, at 200 µl/well for 1 h at 37°C. Composite leaves from each of the yam plants were ground in ELISA conjugate buffer [PBS-T+2% PVP+0.2% egg albumin (Sigma)] to a sap dilution of 1:10 (w/v). YMV-infected *N. benthamiana* and mock-inoculated tissue-cultured *D. rotundata* plants served as positive and negative controls, respectively. Each sap was applied in duplicate to drained plates at 100 µl/well, and incubated overnight at 4°C. The plates were washed again with PBS-T. Monoclonal antibodies (YMV-M20) produced against a Nigerian isolate of YMV at IITA were applied at 1:500 dilution (100 µl/well) and incubated at 37°C for 2–3 h. After washing three times in PBS-T, goat-anti-mouse IgG conjugated to alkaline phosphatase (Sigma) diluted 1:30,000 in conjugate buffer was applied at 100 µl/well and incubated at 37°C for 2 h. The plates were washed three times with PBS-T before 100 µl/well of substrate solution (*p*-nitrophenyl phosphate, Sigma) was applied. The plates were incubated at room temperature for 1 h and absorbance values (A_{405} nm) were read using a Dynatech model MR 500 ELISA reader. Samples were considered positive when the absorbance value was more than twice the average value of the healthy control plus three standard deviations.

The SAS statistical package (SAS Institute Inc 1989) was used to carry out chi-square (χ^2) analysis for Pearson's goodness-of-fit to specific genetic segregation ratios.

Results

The resistant parents TDr 93–1, TDr 93–2 and TDr 89/01444, showed mild or no symptoms of infection (scores <2) during the entire period of screenhouse evaluation. In contrast, plants of the susceptible breeding lines TDr 87/00211 and TDr 87/00571 showed typical mosaic symptoms (scores >3), which confirmed the viru-

Table 1 Segregation ratios of resistant and susceptible genotypes in crosses between resistant and susceptible breeding lines following mechanical inoculation with YMV

Cross, R×S[a] (code)	*n*	Observed (R:S)	Expected segregation[b]		*P*
			Ratio (R:S)[c]	χ^2	
TDr 93–1× TDr 87/00211 (5)	297	203:94	1:1	40.3	0.001
			2.48:1	1.01	0.31
			3:1	7.00	0.008
TDr 87/00571× TDr 89/01444 (6)	175	92:83	1:1	0.46	0.49
			13:15	3.04	0.08
TDr 93–2× TDr 87/00211 (7)	162	35:127	1:5	2.43	0.10
			3:11	0.04	0.85

[a] R=resistant, S=susceptible (S×R for cross 6)
[b] Frequencies of segregation expected assuming Mendelian inheritance of resistance genes
[c] Inferred genetic constitution for the different segregation ratios are: 1:1 (13:15)=one dominant gene in simplex, chromosome (chromatid) segregation; 1:5 (3:11)=one recessive gene in duplex, chromosome (chromatid) segregation; 2.48:1=one dominant gene in simplex, assuming random chromatid segregation (cross of two heterozygotes); 3:1=two dominant genes (Ra and Rb) in simplex, chromosome segregation

Table 2 Distribution of symptom ratings and ELISA A_{405} values following mechanical inoculation of progeny of crosses 5, 6 and 7 with YMV

Cross, R×S[a]	Percentage genotypes with symptom score				
	1	2	3	4	5
	Limit of TAS-ELISA A_{405} values (% genotypes in each class[b]				
	0.1	0.2	0.3	0.4	$0.4<x\leq2$
TDr 93–1× TDr 87/00211 (5)	30.0 (nd)[c]	38.4 (nd)	26.9 (nd)	3.7 (nd)	1.0 (nd)
TDr 87/00571× TDr 89/01444 (6)	37.2 (34.8)	15.4 (10.1)	46.8 (7.6)	0.6 (5.1)	– (42.4)
TDr 93–2× TDr 87/00211 (7)	3.7 (7.0)	17.9 (42.5)	62.4 (18.9)	14.8 (10.2)	1.2 (21.4)

[a] R=resistant, S=susceptible (S×R for cross 6)
[b] ELISA readings (A_{405nm}) were scored as follows: negative (>twice that of the healthy control plus three standard deviations, ≤0.1), positive (>0.1)
[c] nd=not determined

lence of the YMV isolate used and the reliability of the mechanical inoculation method. An excess of resistant F_1 individuals was observed in progeny of crosses 5 and 6, while progeny of cross 7 had a considerable excess of susceptible individuals, indicating that the resistant accessions carry different genes for YMV resistance. One feature that emerged from exposure of cross 7 progeny to natural infection in the field is the number of susceptible genotypes that escaped infection. Mechanical inoculation of several genotypes considered resistant in the field showed that these genotypes were highly susceptible to YMV under controlled inoculation conditions.

The analysis of the segregation of the three crosses following mechanical inoculation is presented in Table 1. An excess of resistant genotypes was observed in progeny of crosses 5 and 6, while progeny of cross 7 had a considerable excess of susceptible individuals. After the inoculation of 297 F_1 plants from cross 5, 203 resistant and 94 susceptible plants were identified. The observed segregation pattern fits neither a 1:1 (χ^2=40.30, *P*=0.001) nor a 3:1 (χ^2=7.00, *P*=0.008) ratio, but fits to a 2.48:1 ratio, which can be expected when two simplex heterozygotes are crossed, assuming chromatid segregation.

Progeny of cross 6 segregated 92 resistant: 83 susceptible, which fits a simplex dominant resistance model in TDr 89/01444. The observed ratio was compared with an expected chromosome segregation ratio of 1:1 and with an expected random chromatid segregation ratio of 13:15. The observed ratio was consistent with both segregation ratios; however, a better fit was obtained assuming chromosome segregation (Table 1).

Segregation into 35 resistant and 127 susceptible individuals for progeny of cross 7 fitted a 1:5 ratio (assuming chromosome segregation) and a 3:11 ratio (assuming random chromatid segregation), both of which are consistent with the presence of a single recessive resistance gene in duplex configuration. An almost perfect fit was obtained assuming chromatid segregation (χ^2=0.04, *P*=0.85).

ELISA tests detected YMV in parental resistant accessions at mostly low but above background levels, while susceptible parents generally gave higher ELISA values. Completely asymptomatic F_1 plants with high ELISA values were observed in the two crosses tested. Negative ELISA values for over 60% of cross-7 progeny exposed to natural infection in the field further confirmed the fact that these genotypes had escaped infection. The frequency distribution for cross-6 progeny according to ELISA values showed that 65.2% of the genotypes tested positive, while only 47.4% had symptom severity scores >2 (Table 2). Similarly, 93% of mechani-

cally inoculated cross-7 progeny tested positive, while only 78.4% could be considered susceptible by symptom evaluation.

Discussion

We studied the inheritance of resistance to *Yam mosaic virus* in tetraploid *D. rotundata*. As a source of resistance to YMV, TDr 93–1, TDr 93–2 and TDr 89/01444 did not provide a high degree of resistance, such as immunity to viral infection or complete absence of symptoms. Segregation into resistant and susceptible individuals in progenies of the three crosses investigated indicated that resistance is manifested differentially as a dominant (crosses 5 and 6) and recessive (cross 7) character. Our results are in agreement with those of Boiteux et al. (1996), who found that two single major genes (one dominant, the other recessive) control resistance in *Capsicum* spp. to a pepper strain of PVY (pathotype 1–2). The availability of genotypic diversity for YMV resistance is extremely interesting to breeding programs because both genes could be pyramided in the same genetic background or used separately against infection by this virus.

The resistance would theoretically be more stable and durable (Johnson 1984) if two or more different genetic mechanisms are acting against the same pathogen. However, because resistance may be inherited independently as a dominant or recessive character, it will be necessary to employ an effective breeding strategy for simultaneous incorporation of such genes in a particular farmers' preferred variety. The recessive nature of the gene for YMV resistance in TDr 93–2 means that it cannot be identified at the phenotypic level, demanding refined diagnostic procedures such as molecular mapping for detailed genetic localization of specific genes and the identification of closely linked selectable markers. Efforts are currently underway in our laboratory to develop a genetic linkage map of *D. rotundata* based on amplified fragment length polymorphism (AFLP) markers (IITA 1998b; Mignouna and Asiedu 1999; Thottappilly et al. 2000).

Considerable genetic diversity exists among populations of YMV from West Africa (Aleman et al. 1996; Duterme et al. 1996; Goudou-Urbino et al. 1996; Bousalem et al. 2000). Also, two other potyviruses infect *Dioscorea* spp. in Nigeria (Odu et al. 2001). The presence of major dominant genes controlling resistance in *D. rotundata* to a member of the *Potyvirus* genus is thus an interesting feature from a practical breeding program standpoint. Dominant genes will greatly facilitate the transfer of this resistance into the genetic background of elite *D. rotundata* cultivars that are mostly lacking any effective resistance to YMV. The existence of simply inherited genes, or clusters of separate tightly linked genes that confer resistance to two or more distinct potyviruses, has been described in several crop species (Gilbert-Albertini et al. 1993; Fisher and Kyle 1994; Provvidenti and Niblett 1994; Kabelka and Grumet 1997; Anagnostou et al. 2000). In some instances, however, potyvirus resistance has been found to be virus- or pathotype-specific (Jones 1990; Provvidenti and Hampton 1992). Further studies are necessary to determine the spectrum of resistance afforded by the resistance genes reported in this study, relative to other YMV isolates and yam potyviruses.

Progeny of cross 5 gave a good fit to a 2.48:1 ratio, which can be expected when two simplex heterozygotes are crossed, assuming chromatid segregation (Flis 1995). This points to the possibility of some parents being genotypic mixtures, carrying both susceptibility and resistance determinants which interact (Flis 1995). To clarify the allelic or non-allelic nature of YMV resistance genes and to identify the best parents for resistance breeding, further research is needed on purifying parental lines, for instance via haploidization (Hutten et al. 1995).

The presence of mild mosaic symptoms on some parental resistant plants in all crosses and detection of YMV at low levels using TAS-ELISA may indicate the presence of modifier genes that segregate in the progeny; alternatively, environmental effects may have influenced the resistance phenotype (Anagnostou et al. 2000). Asymptomatic F_1 genotypes with high A_{405} values were observed in all the crosses tested. The resistant accessions studied have not been observed to show a hypersensitive or immune response to YMV in the field, and tolerance might be the mode of resistance involved (Ponz and Bruening 1986). Such tolerance could be the basis of 'field resistance' (Allen et al. 1982) and long-term plant protection (Ponz and Bruening 1986). The apparent lack of correlation between virus content and symptom expression indicates that asymptomatic plants may contribute to secondary spread of yam mosaic disease (Fargette et al. 1987). The possibility that resistance may be overcome when free systemic circulation of large amounts of viral particles exceeds a certain threshold (Munoz et al. 1975) means that sources of YMV resistance with the hypersensitive or immune response should also be sought. Several susceptible plants of the cross TDr 93–2×TDr 87/00211 escaped YMV infection in the field, stressing the need for careful mechanical inoculation in screening tests.

Besides searching for new sources of YMV resistance (IITA 1998a), we have developed strategies for marker-assisted selection for YMV resistance breeding in yam. The mapping populations described in the present study, together with other populations being developed, will be used to search for molecular markers closely linked to YMV resistance genes.

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