YIELD LOSS IN GUINEA YAM (*DIOSCOREA ROTUNDATA POIR.*) DUE TO INFECTION BY *YAM MOSAIC VIRUS* (YMV) GENUS *POTYVIRUS*.

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(Received: June 2012; Accepted: November 2012)

ABSTRACT

An experiment was conducted to investigate the influence of *Yam mosaic virus* (YMV) genus *Potyvirus* on the tuber yield of *Dioscorea rotundata* based on assessment of comparative performance of inoculated and uninoculated plants of two genotypes (TDr 93-31 and TDr 95-127). Symptoms of virus infection were evident on inoculated plants especially at four weeks after inoculation. Visual virus symptom severity scores had significant ($P<0.0001$) correlations with enzyme-linked immunosorbent assay (ELISA) readings ($r = 0.7$), leaf chlorophyll content ($r = -0.9$), and tuber yields ($r = -0.9$). Stomatal conductance results showed higher values ($P < 0.001$) of diffusive resistance in virus-infected leaves compared to virus-free leaves. The leaf area per plant, leaf dry weight, vine dry weight, and tuber dry weight were less ($P< 0.001$) in inoculated plants compared to uninoculated plants for both genotypes at 10, 18 and 24 weeks after inoculation. Similarly lower values for leaf area index ($P > 0.004$), harvest index ($P < 0.01$), leaf chlorophyll content, and intercepted photosynthetically active radiation ($P = 0.01$) were obtained from plots with inoculated plants.

YMV infection in *D. rotundata* resulted in a yield loss of 65.4% in TDr 93-31 and 52.6% in TDr 95-127. Reduced capacity for photosynthesis in YMV infected plants, due to increased diffusive resistance of stomata, as well as reduced leaf area and chlorophyll content, contributed significantly ($P < 0.001$) to their reduced tuber yields. The economic importance of the virus is thus established as it can result in significant loss to resource-poor farmers.

Key words: *Dioscorea rotundata*; TAS-ELISA; yield loss; *Yam mosaic virus* (YMV) genus *Potyvirus*.

INTRODUCTION

Yams (*Dioscorea spp.)* constitute a major staple in West and Central Africa as well as parts of the tropics and subtropics of Asia, America, and the Caribbean and Pacific islands (Degras, 1993). Cultivated yams are sources of carbohydrate, protein, amino acids, vitamins and mineral elements, while the amount of fats (lipids) is negligible in terms of food value (Degras, 1993). In yam-growing regions the crop provides over 240 calories and about 4 g of protein per person each day. Freshly harvested yam tubers consist of about 70% water, 25% starch, 1-2% protein and traces of vitamins (Onwueme and Sinha, 1991). The world production of yams in 2004 was 40 million metric tonnes of which about 92% was from West Africa, with Nigeria contributing about 66% of world total production (FAO, 2005). The average yield of yams is about 9 tons per hectare in the yam-growing areas (FAO, 2005). One of the key production constraints in yam cultivation is damage from pests and diseases, such as insects, nematodes, fungi, bacteria and viruses, which singly or in combination have direct adverse effects on the yield (Degras, 1993).

The viruses reported to infect yams include *Dioscorea latent virus* (DLV) genus *Potexvirus* Family Potexviridae; *Dioscorea alata virus* (DAV) genus *Potyvirus* Family Potyviridae; *Cucumber mosaic virus* (CMV) genus *Cucumovirus* Family Bromoviridae; *Dioscorea dumetorum virus* (DdV) genus *Potyvirus* Family Potyviridae; *Dioscorea bulbifera bacilliform virus* (DbBV) genus *Badnavirus* Family Caulimoviridae; *Dioscorea alata bacilliform virus* (DaBV), genus *Badnavirus* Family Caulimoviridae; and *Yam mosaic virus* (YMV) genus *Potyvirus* Family Potyviridae (Thouvenel and Fauquet, 1979; Brunt et al., 1990; Van Regenmortel and Dubs, 1993; Hughes et al., 1997; Odu et al., 1999).

YMV is the most important virus infecting both cultivated and wild yams especially *D. rotundata*, *D. alata*, *D. cayenensis* and *D. praehensilis* in the yam-growing areas of the world (Thouvenel and Fauquet, 1979; Theberge, 1985; Porth et al., 1987).

It causes several symptoms including mottling, chlorosis (leaf and vein), mosaic of different shades, leaf distortion and malformation. It is naturally transmitted through infected planting materials, insect vectors such as *Aphis craccivora* and experimentally by mechanical inoculation (Thouvenel and Dumont, 1988). Viral infection could result in a 29-41% yield reduction in *D. alata* species, as reported by Mantel and Haque (1979). Thouvenel and Dumont (1990) estimated crop losses to amount to 27% for *D. alata* cv, Florido. In *D. rotundata*, yam viruses were reported to cause a yield loss of about 40% (IITA, 1981) based on symptomatology and Direct antibody sandwich enzyme-linked immunosorben assay (DAS-ELISA), which are not sufficiently reliable (Njukeng, 1998). Various viruses infecting yams would have contributed significantly to the reported losses. Yield reduction due to single infection by YMV remains to be adequately quantified.

Yield loss assessment largely involves statistical comparisons between yields of virus-diseased plants with those of virus-free ones. This study was designed to investigate the influence of YMV on the growth and development of *D. rotundata*, and to quantify the yield loss in these two most cultivated of the *Dioscorea* species (TDr 93-31 and TDr 95-127) due to infection by the virus.

MATERIALS AND METHODS

Planting of yam tubers

Two *D. rotundata* genotypes (TDr 93-31 and TDr 95-127) were selected based on their performance in a previous trial as moderately resistant and susceptible, respectively, to YMV (Odu *et al.*, 2004a). The experiment was carried out for two years in the planting seasons of 2002 and 2004. Mini tubers of these genotypes, produced in a screenhouse from virus-tested *in vitro* plantlets, were obtained from the Tissue Culture Unit of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. The mini tubers were buried in propagating medium until sprouting had just begun. These were then transplanted into mounds at a spacing of 1 m between rows and 0.75 m within rows in a screenhouse that was purpose-built on an experimental plot at IITA to protect the plants from insect vectors. Virus-free tubers of the two genotypes derived from virus-free tissue culture plantlets were cut into sett sizes of 100 to 150 g, pre sprouted and transplanted. The plants and the screenhouse environment were sprayed once a week with an insecticide, Sherpa plus R (30 g l^{-1} cypermethrin, 250 g l^{-1} dimethoate at 5 ml l^{-1} water), for protection. Each plot was 5.25 m long, 5 m wide and consisted of 7 rows at 0.75 m apart, giving a total of 35 plants per plot. The experimental design was a 2 x 2 factorial (2 varieties and 2 levels of inoculation with YMV) laid out in a Randomised Complete Block Design (RCBD) with four treatments in three replications. The four treatment combinations were: uninoculated TDr 93-31; uninoculated TDr 95-127; inoculated TDr 93-31 and inoculated TDr 95-127. Each plant was staked with a 2 m stake for maximum exposure of the shoot to sunlight so as to prevent shade effects and facilitate easy observation of leaf symptoms and data collection.

Serological indexing of test plants

Test plants were serologically indexed in the laboratory at four weeks after planting using Triple antibody sandwich enzyme linked immunosorbent assay (TAS-ELISA), as described by Njukeng (1998) so as to ensure that the plants were free from YMV before inoculation. This was followed by a second laboratory screening 10 weeks after inoculation, using TAS-ELISA to detect the presence of YMV and PAS-ELISA to detect DAV, CMV, DaBV essentially as described by Odu *et al.* (2004b).

Inoculation of test plants with YMV

YMV was isolated from leaves of previously infected plants of *D. rotundata* maintained in a screenhouse. The infected leaves were ground in a blender (model 35BL59, Christison Scientific Equipment) after adding 10 mM phosphate buffer pH 7.7 containing 1 mM ethylene diamine-tetra acetic acid (EDTA) and 0.1 mM cysteine. The ground material (inoculum; 1g mL^{-1}) was kept in an ice bucket containing ice cubes. Plants in plots designated for inoculation were inoculated with inoculum at six weeks after planting in the first instance and at eight weeks after plant at the second instance. At both instances, young fully expanded leaves of test plants were dusted with carborundum (600 mesh) and rubbed with a finger previously dipped in the inoculum. The inoculated leaves were then rinsed with water to prevent them from scorching. Healthy control plants were mock inoculated with inoculation buffer alone.

Evaluation of disease symptoms

Virus infection was diagnosed by visual inspection of the shoot for symptoms and complemented with TAS-ELISA to check for latent infection. Each of 20 plants (excluding the ones on the boarder rows) in a plot was assessed for severity of virus infection symptoms on a scale of 1 (negligible) to 5 (very severe) as reported by Odu *et al.* (2004a), where 1: no symptoms, 2: moderate or mild symptoms, 3: severe symptoms, 4: very severe symptoms, and 5: distortion, malformation of leaf or stem. This was done four weeks after the second inoculation and repeated six weeks later.

Assessment of stomatal conductance

Estimates of stomatal conductance of leaves of inoculated and uninoculated plants were measured with a steady state porometer (Licor Instrument Corporation, Model LI-1600 Li-cor Inc. 1989). Data were collected from three leaves per plant and three plants selected at random per plot around the middle portion of the canopy, from about 12.45 hr until 14.00 hr on days when the sky was clear so clouds did not interfere with direct solar radiation. The following data were recorded: Relative humidity, Quantum, Leaf temperature, Diffusive resistance, Transpiration and flow.

Determination of photosynthetically active radiation

Photosynthetically active radiation (PAR) was determined with a 1 m long Decagon sunfleck ceptometer (Decagon Devices, Inc., Pullman, WA 99163 USA). Measurements were made under clear-sky conditions at solar noon (±2 hours) at nine and 18 weeks after the second inoculation. This was done at nine and 18 weeks after inoculation to make time for inoculum to have effects on the inoculated plants. The incident photosynthetically active radiation (IPAR) above the yam canopy was taken twice at opposite angles in a plot and the average was recorded. Transmitted photosynthetically active radiation (TPAR) was measured below the yam canopy at 20 cm above the ground, by taking four readings perpendicular to the yam plant row, on two-fixed diagonal transects across each plot. The average from the replicated readings per plot represented the TPAR value for each treatment combination within a replicate. Percentage transmittance (TPAR/IPAR x 100) and the percentage of PAR intercepted by the yam canopy (100 - % transmittance) were calculated.

Determination of chlorophyll content

The chlorophyll content of leaves was determined using a lightweight hand held chlorophyll meter (Minolta SPAD 502 Konica Minolta Sensing, Inc., Japan.). These data were taken at eight and 16 weeks after the second inoculation. Readings ranging from 0 to 80 SPAD (Yadava, 1986) were taken randomly from five plants per plot and five leaves per plant at the middle portion of the leaf midway between the central vein and the leaf edge.

Measurement of growth characteristics

Five plants per plot were harvested at 10, 18 and 24 weeks after the second inoculation for measurement of leaf area per plant, and fresh and dry weights of leaves, vines, and tubers as detailed below. Each plant was separated into leaves, vines, and tubers. The areas of thirty leaves per plant from five plants per plot were measured at each sampling period using a Leaf Area Meter (Model Li 3100 LI-COR, Nebraska, USA). Total leaf area per plant was obtained by multiplying the calculated mean area per leaf by total number of leaves per plant. Leaf area index (LAI) was estimated as: total leaf area per plant divided by land area per plant.

All leaves per plant were weighed, dried using Hotpack oven (PA, USA, model 217300) at 70 ^{o}C for 3 days and weighed again to obtain leaf dry weight. Vines were similarly weighed, dried and re-weighed to obtain vine dry weight. Tubers were washed, weighed, sliced into small bits, and dried in an oven at 70 ^{o}C for three days to obtain tuber dry weight.

Harvest index: Harvest index was calculated as the ratio of fresh tuber weight per plot to total plant weight per plot (weight of leaf + vine + tuber).

Assessment of yield at final harvest

All yam tubers were harvested at senescence of shoots, about eight months after sprout emergence. The following data were collected: number of stands/plot, number of tubers/stand and weight of tubers/stand. The percentage yield loss was calculated as $(Y_o - Y_1)/Y_o \times 100$, where Y_o = yield of uninoculated plot, and Y_1 = yield of inoculated plot.

Data analysis

Data obtained from the experiments were

analyzed using SAS (SAS Inc., USA) statistical package, version 6.12. Analysis of variance (ANOVA) was used to test the hypothesis that there was difference in yields of inoculated and uninoculated yam genotypes.

RESULTS

Serological indexing of test plants

TAS-ELISA and PAS-ELISA at first serological indexing of test plants showed that the plants were free from infection by yam viruses known in West Africa before inoculation. The presence of YMV in inoculated plants was detected in the second laboratory screening. Leaves of inoculated plants also showed visual symptoms of virus infection (Figure 1). A positive correlation ($r = 0.7$; $P < 0.0001$) was obtained between the visual virus severity scores at 10 weeks after inoculation and ELISA absorbance readings for the virus, and tuber yield was negatively correlated ($r = -0.8$; $P < 0.0001$) with the visual virus symptom severity scores (Table 1). Mean and maximum virus symptom severity scores were higher for inoculated plants compared to uninoculated plants for both genotypes at four and 10 weeks after inoculation (Table 2).

Figure 1. Symptoms exhibited by *Dioscorea rotundata* genotype TDr 95-127 inoculated (A) with *Yam mosaic virus* (YMV) genus *Potyvirus* and healthy uninoculated leaves (B) of the same genotype.

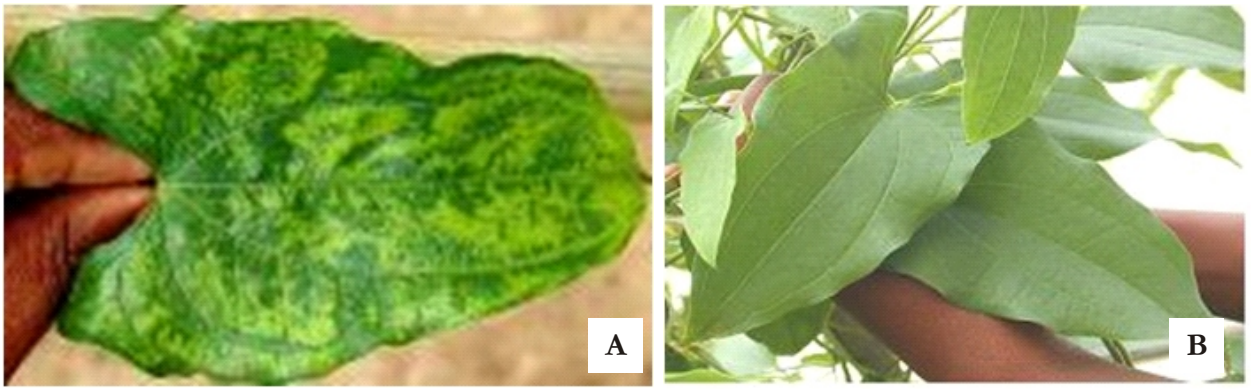


Table 1. Correlation coefficients (probabilities in parenthesis) between mean virus scores*, ELISA absorbance and tuber yield of two genotypes of *D. rotundata* (TDr 93-31 and TDr 95-127).

	Score 1	Score 2	Tuber yield	ELISA absorbance
Score 1	1			
Score 2	0.9307 (<0.0001)	1		
Tuber yield	-0.8675 (<0.0001)	-0.8723 (<0.0001)	1	
ELISA absorbance	0.6478 (<0.0001)	0.6478 (<0.0001)	-0.6191 (<0.0001)	1

*Scores obtained on a scale of 1-5, where 1: no symptom, and 5: distortion, malformation of leaf or stem, complete plant infection (Odu *et al.*, 2004a)

Score 1 = Virus symptom severity scores of plants at 4 WAI

Score 2 = Virus symptom severity scores of plants at 10 WAI

Table 2: Mean and maximum virus symptom severity scores* of *D. rotundata* inoculated or uninoculated with YMV.

Genotype	Treatment	4 WAI				10 WAI			
		Mean		Maximum		Mean		Maximum	
TDr 93-31	Inoculated	2.36	0.2	3.33	0.17	2.82	0.28	4.67	0.08
	Uninoculated	1.00		1.00		1.00		1.00	
TDr 95-127	Inoculated	2.41	0.02	3.00	0	2.57	0.13	3.00	0
	Uninoculated	1.00		1.00		1.00		1.00	

Table 3: Stomatal conductance as determined by a steady state porometer in two genotypes of *D. rotundata* at 10 weeks after inoculation with YMV.

Genotype	Treatment	Diffusive resistance (s cm^{-1})	Transpiration rate (ug cm^{-2} s^{-1})	Leaf temperature (^oC)	Flow (cm^2s^{-1})
TDr 93-31	Inoculated	14.63 1.8	2.02 0.3	28.46 0.3	0.44 0.1
	Uninoculated	2.87 0.7	6.80 1.1	28.01 1.1	1.30 0.1
TDr 95-127	Inoculated	24.16 2.5	1.05 0.2	29.21 0.8	0.24 0.1
	Uninoculated	2.43 0.3	7.13 0.6	28.25 0.4	1.44 0.1

Assessment of stomatal conductance and photosynthetically active radiation (PAR)

Values obtained from porometer readings at 10 weeks after inoculation showed that the uninoculated plants had lower diffusive resistance and higher transpiration rates (Table 3). However the treatment had no effect on the leaf temperature. Intercepted PAR of the inoculated plots was less ($P < 0.01$) than in uninoculated plots for both genotypes at nine and 18 WAI.

Chlorophyll content of leaves

Virus infection caused reduction in chlorophyll content of the leaves in both genotypes. At eight WAI SPAD meter reading for inoculated plants was 16.2 in both genotypes. By 16 WAI the values were 12.8 SPAD for TDr 93-31 and 14.4 for TDr 95-127. Uninoculated plants had SPAD values of 43 and 45 SPAD units respectively for TDr 93-31 and TDr 95-127 at 16 WAI. A negative correlation ($r = -0.9$; $P < 0.0001$) was obtained between the chlorophyll level and both the first and second visual virus symptom scores.

Growth characteristics

Leaf area per plant at 10 weeks after inoculation was higher ($P < 0.001$) in uninoculated plants compared to the inoculated plants for both genotypes (Table 4). This trend was maintained as leaf area increased through 18 and 24 WAI. Leaf Area Indices (LAI) were higher in uninoculated plants compared to inoculated plots at 10 and 18 WAI ($P < 0.03$). Inoculated plants had lower harvest indices than uninoculated ones at 10 and 18 WAI ($P < 0.03$). Similarly inoculated plants had lower leaf, vine, and tuber dry weights than uninoculated plants (Tables 4 and 5) at 10, 18 and 24 weeks after inoculation.

Components of yield at harvest

Higher mean fresh tuber yield of 27.6 kg/plot was recorded from uninoculated compared with 9.55 kg/plot from inoculated plants of TDr 93-31. Corresponding values for TDr 95-127 were 30.2 kg/plot for uninoculated plants compared to 14.31 kg/plot for inoculated plants. Visual observation showed that the tuber yield from uninoculated plants were bigger in sizes than those from inoculated plants (Figure 2). With about the same number of tubers produced per plant by both uninoculated plants and inoculated plants, mean sizes of tubers were larger in the former than in the latter. The genotype (TDr 93-31) with higher maximum virus symptom rating also had the higher percent yield loss (Table 6).

Table 4: Leaf dry weight and leaf area of two *D. rotundata* genotypes at 10 and 18 weeks after inoculation (WAI) with *Yam mosaic virus* (YMV), genus *Potyvirus*.

Genotype	Treatment	Leaf dry weight/plot (g)						Leaf area/plant (cm^2)					
		10 WAI		18 WAI		24 WAI		10 WAI		18 WAI		24 WAI	
TDr 93-31	Inoculated	21.5	5.3	64.1	7.3	64.7	8.5	416	117.6	1355	30.6	1345	36.2
	Uninoculated	42.9	3.7	97.5	4.6	108.4	7.3	782	25.5	1826	130	1856	122.2
TDr 95-127	Inoculated	39.2	6.2	52.4	11.9	54.5	5.8	610	161.7	1344	24.8	1307	53.5
	Uninoculated	68.1	4.8	88.3	5.3	96	4.7	1281	67.4	1863	96.7	1916	84.7

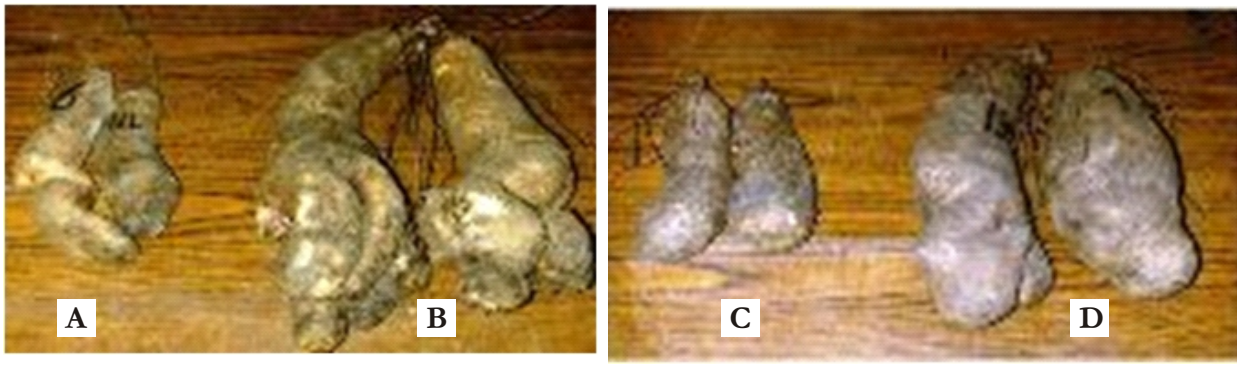
Table 5: Tuber and vine dry weight of two *D. rotundata* genotypes showing the effects of inoculation with *Yam mosaic virus* (YMV), genus *Potyvirus*.

Genotype	Treatment	Tuber dry weight/plot (g)						Vine dry weight/plot (g)					
		10 WAI		18 WAI		24 WAI		10 WAI		18 WAI		24 WAI	
TDr 93-31	Inoculated	0.56	0.1	144	11.5	182	15.7	31.6	6.6	55.5	3.7	59.9	7.6
	Uninoculated	7.78	0.3	242	13.6	351	10.7	58.6	5.4	82.2	3.3	89.1	1.9
TDr 95-127	Inoculated	29.05	3.2	175	16.0	226	13.9	37.5	6.0	45.7	4.3	45.4	4.8
	Uninoculated	83.11	2.1	309	12.8	360	20.2	63.5	4.1	66.4	3.7	71.7	3.3

Table 6: Yield losses at final harvest in two genotypes of *D. rotundata* when inoculated with YMV

Genotype	Treatment	Yield parameters			Sett weight (kg)	
		Yield/plot (kg)		% yield loss		
TDr 93-31	Inoculated	9.55	1.1		2.60	0.2
	Uninoculated	27.60	1.2	65.39	2.54	0.2
TDr 95-127	Inoculated	14.31	0.9		2.74	0.2
	Uninoculated	30.20	1.9	52.62	2.85	0.1

Figure 2. Final tuber yield of *Dioscorea rotundata* genotypes TDr 95-127 (A-inoculated with *Yam mosaic virus* (YMV) genus *Potyvirus* and B-uninoculated) and TDr 93-31 (C-inoculated and D-uninoculated)



DISCUSSION

Effectiveness of mechanical inoculation as earlier reported by Thouvenel and Dumont (1988) and Odu (2002) was demonstrated by the appearance of classical symptoms of virus disease in yams and the serological confirmation of infection. There was consistent disease progression from four to 10 weeks after inoculation, and the observable mean and maximum symptom severity scores were higher in inoculated plots compared with uninoculated ones. The positive correlation (r = 0.7) between the visual virus severity scores and ELISA absorbance readings at 4 and 10 WAI suggests a correspondence between virus concentration and severity of symptom expression. The influence of the infection on the yam plant is evident in the negative correlation established between tuber yield and the visual virus severity scores.

Diffusive resistance, transpiration and flow were significantly influenced by the inoculation with YMV. The stomata are sensitive to light, relative humidity, carbon dioxide, water stress, pollutants and pathogens. The presence of the virus in leaves of infected plants must have influenced the extent of opening of the stomata leading to increased resistance to gas exchange between the air and the interior of the leaf, and lower transpiration and flow rates. This may have contributed to reduced rate of photosynthesis in virus infected leaves compared to virus free ones. This is in agreement with the observation of Matthews (1991) that the rate of photosynthesis and transpiration were reduced in virus-infected leaves. There was a higher level of light interception in the uninoculated plots compared to inoculated ones

at 18 WAI, confirming that there was reduction in amount of foliage produced by the inoculated plants. The reduction in amount of chlorophyll in leaves of inoculated plants (16 SPAD units) compared to uninoculated ones (43 SPAD units) at eight WAI may have also influenced the rate of photosynthesis. Van Loon (1987) reported severe reduction of photosynthesis related to many mosaic or yellowing disease symptoms when calculated on chlorophyll basis. The reductions in leaf area and shoot dry weight may have contributed to the reduced tuber dry weight in inoculated plants.

Sequential harvesting of the trial show that TDr 93-31 had a higher yield reduction due to inoculation with YMV of 92.8% compared to the 65.1% of TDr 95-127 by four months after planting. The fact that tuber initiation and bulking were slower in TDr 93-31 (late maturing genotype) than TDr 95-127 implies that the inoculation dates fell on different developmental stages for the two genotypes and this could be a factor in explaining the differential impact of the virus on yield. There was a partial recovery by 18 WAI, which reduced the yield loss to 40.5% in TDr 93-31 and 43.4% in TDr 95-127. By that time both genotypes had reached a peak in production and were more able to compensate for the reduction in photosynthetic capacity caused by the virus. Matthews (1991) observed that recovery is influenced by many factors such as environment and that the stage of development at which a plant is infected may have a marked effect on the extent to which symptoms are produced. The final yield depression levels due to the inoculation in this study (65.4% in TDr 93-31 and 52.6% in TDr 95-127) are higher than those of Mantel and Haque (1979) and Thouvenel and Dumont (1990) for *D. alata*. They are however similar to reports on other crops. About 50% decrease was reported in yellowing caused by *Beet yellow virus* (BYV), genus *Closterovirus* on sugar beet (Hall and Loomis, 1972). *Cassava mosaic disease* (CMD) has been reported to cause storage root yield reductions of 2060 %, and in some cases total crop failure (IITA, 1990; Otim-Nape et al., 1994).

In conclusion, YMV infection in *D. rotundata* caused yield loss of 65.4% in TDr 93-31 and 52.6% in TDr 95-127. The tuber yield reduction was higher at early stages of development (four months after planting) with some recovery as the plants approached maturity. The yield reductions could be attributed to reduction in photosynthesis caused by the reduced leaf area and leaf chlorophyll content which also impacted on light interception, shoot dry weight and tuber dry weight.

Host plant resistance to YMV and the health status of the planting material are the most important factors for control of the disease. Planting tubers obtained from plants with high symptom severity scores should be avoided to prevent the spread of virus infection, and curtail the progressive accumulation of virus particles in vegetatively propagated plants that could lead to stunting and very poor yields. Yam farmers need to be advised against storing small tubers harvested from infected plants as planting materials for subsequent season, as these tubers could serve as sources of infection. Dissemination of virus-free and resistant yam varieties to farmers and educating them on the classic symptoms of infection and subsequent tagging of diseased plants during growth for the non-seed use of their tubers would be very useful in reducing the impact of the disease on yam production.

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