WFL Publisher
Science and Technology
Meri-Rastilantie 3 B, FI-00980
Helsinki, Finland
e-mail: info@world-food.net

Journal of Food, Agriculture & Environment Vol.6(2) : 227-233. 2008 *www.world-food.net*

Genetic variation and genotype × environment interaction in yams (*Dioscorea* spp.) for root colonization by arbuscular mycorrhiza

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Received 8 January 2008, accepted 25 March 2008.

Abstract

Root colonization by arbuscular mycorrhiza (AM) enhances nutrient acquisition by plants and could benefit the production of yam (*Dioscorea* spp.). The variation in AM colonization in yam genotypes was evaluated in two experiments at four locations (Ibadan, Onne, Abuja and Ubiaja) in different agroecologies of Nigeria in 2004 and 2005. Twenty-seven genotypes of *D. rotundata* and 28 of *D. alata* were investigated in a randomized complete block design with three replicates. Arbuscular mycorrhizal fungi colonized all yam genotypes. Root length colonization ranged from 24 to 95% in *D. rotundata* and from 21 to 95% in *D. alata*. Colonization was observed to be high in locations with lower soil available P but was not precluded by relatively high soil acidity. Highly significant ($P< 0.001$) effects were observed in *D. rotundata* for genotype and location, as well as genotype × location, location × year and in *D. alata* for genotype, location and year. The location × genotype × year interaction was significant ($P < 0.05$) in both experiments. The broad sense heritability estimates for AM colonization were 0.60 in *D. rotundata* and 0.87 in *D. alata*. Further analysis of genotype × environment interactions using a GGE biplot for the two-year data showed that the most stable genotypes for AM colonization across locations were TDr 93-32 (*D. rotundata*) and TDa 98/01183 (*D. alata*). The highest percentage AM colonization mean were found in TDr 93-32 (*D. rotundata*) and TDa 01/00204 in (*D. alata*). Generally, the highest mean colonization values were obtained at Abuja and Ubiaja. The results of this study reveal that AM colonization in yam is host-dependent and influenced by the environment.

Key words: Arbuscular mycorrhizal colonization, breeding, genotype by environment interaction, GGE biplot, yam.

Introduction

Yam is an important tuber crop with major food, commercial and sociocultural values. *Dioscorea rotundata* (white Guinea yam) is the dominant species cultivated and used in Africa, a region that accounts for over 95% of the world's annual production of about 49 million tons. Globally, *Dioscorea alata* is the most widely cultivated species but it is second to *D. rotundata* in terms of the quantity produced in Africa. Raising and sustaining productivity requires a solution to the problem of declining soil fertility in the yam growing regions. Soil fertility was reported as a major constraint to production by farmers in an on-farm survey conducted in Nigeria [2]. Some of the other problems militating against production have been solved by selecting and breeding for desired traits but little progress has been made in mineral nutrition-related constraints. Mycorrhizae help plants to acquire nutrients such as P, N, Zn and Cu [6, 7] from soils with low plant available nutrients. Hence, sustaining productivity through root colonization by arbuscular mycorrhizal (AM) fungi for enhanced nutrient acquisition could be a useful objective for yam breeders. Breeding for sustainability has been defined as a process of fitting cultivars to an environment instead of altering the environment (e.g., by adding fertilizer, water, pesticides, etc.) to fit cultivars [8].

Plant response to mycorrhizal colonization varies with species and genotype and genotypic variations have been observed in the mycorrhizal colonization of many crops [15, 23]. Environmental conditions, such as density of inoculum, temperature, light and availability of soil nutrients, especially P, have been observed to influence colonization [29, 30]. Most of the field trials previously reported on AM colonization of crops were restricted to one location and consequently leave no clue about the genotype × environment (G × E) interactions that have been employed in assessing the ecological adaptations of yam [3, 11, 12]. Investigation of this aspect would improve our knowledge of AM fungus-yam associations under different environments. Multilocational evaluation of genotypes has been adopted for various traits in yam breeding programmes [3] with a primary goal of identifying superior cultivars for the target locations and developing an understanding of the target regions.

Biplot analyses have been used for the analysis and graphical presentation of G × E interaction in agronomic studies [19]. Recently, the GGE biplot was developed to graphically visualize and address specific questions in relation to genotype × environment interaction [32]. The GGE concept is based on the understanding that genotype main effect (G) and genotype × environment interaction (G × E) are the two sources of variation that are relevant to genotype evaluation and must be considered simultaneously (not alone or separately) for appropriate genotype evaluation [32].

Therefore, GGE biplot analysis can be used to improve our understanding of the AM colonization of yam in different environments.

The aims of this research were to study variations in root colonization by AM in *D. rotundata* and *D. alata* and the effects of environment and genotype × environment interactions on this trait.

Materials and Methods

Locations and plot history: Two experiments (one on *D. rotundata* and the other on *D. alata*) were conducted in 2004 and 2005 at selected sites in four agroecological zones of Nigeria: Ibadan (3º45´E, 7º30´N; rainfall, 1119.55 mm; solar radiation, 13.55 MJ/m²/day) in the forest-savanna transition zone; Onne (7ºE, 4º48´N; rainfall, 2356.80 mm; solar radiation, 6.10 MJ/m²/day) in the high rainfall area of the coastal region; Ubiaja (6º25´E, 6º40´N; rainfall, 1534.56 mm; solar radiation, 13.05 MJ/m²/day) in the humid forest and Abuja (7º20´E, 9º16´N; rainfall, 1302.38 mm; solar radiation, 13.75 MJ/m²/day) in the Guinea savanna. The minimum and maximum temperatures were 22 and 33ºC at Abuja; 21 and 31ºC at Ibadan; 23 and 31°C at Onne and 21 and 33°C at Ubiaja. The experimental fields were under crop rotation at Abuja, Ibadan and Ubiaja. Cover crops (*Pueraria*) were grown for 3 years at Abuja and Ibadan. Before the introduction of cover crops, yam was the last crop grown at Ibadan and maize at Abuja. Cassava was the last crop at Ubiaja, followed by natural vegetation for 3 years before yam was planted. At Onne, the plot used for *D. rotundata* was planted with tree legumes (*Dactyladenia barteri*) from 1985 to 1997 as an experimental site for an alley cropping project. Five cowpea varieties were later planted in the alley between 1998 and 2001 and thereafter it was left to natural vegetation between 2001 and 2004. The *D. alata* plot at Onne was under natural vegetation until 1998 when it was used for plantain sucker multiplication for one year. During this period, a high amount of triple super phosphate fertilizer was applied. The land was under natural vegetation from 1999 to 2004.

Plant materials and experimental design: Twenty-seven genotypes of *D. rotundata* and 28 of *D. alata* were planted at the four research sites. These genotypes were advanced IITA hybrids selected for good yields and resistance to foliage diseases and a few landrace cultivars. The *D. rotundata* and *D. alata* genotypes were established in separate fields. At each location, 30 setts of each genotype were planted at spacing of 1 m × 1 m on plots of 6 m × 5 m, arranged in a randomized complete block design with three replicates. Each sett weighed 200–300 g. The experiments were first conducted in 2004 and repeated in 2005 in new fields in all locations, except Onne. Planting was carried out at Onne in mid-February in 2004 and mid-March in 2005; at Ibadan, in late March 2004 and early April 2005; at Ubiaja, in late April of both years; and at Abuja, in early May of both years. The dates were determined by the commencement of rainfall. In 2005, two genotypes of *D. rotundata,* TDr 97/01817 and TDr 04-211, were not planted at Abuja and were treated as missing data in the statistical analysis. Neither fertilizer nor pesticide was applied. There was no staking except at Onne in the coastal high rainfall area where it is the cultural practice. Soil characteristics of the locations were determined.

Data collection: Root samples were collected at 4 months after planting from five plants of each genotype, randomly selected from middle rows in each plot and assessed for percentage root colonization. The roots were cleared with KOH [26] and stained with Chlorazol black E [4]. Colonization by AM was measured using the method of Giovanetti and Mosse [13].

Data analyses: The values obtained for percentage mycorrhizal colonization were arc sine transformed before analysis. Analysis of variance was conducted using Proc GLM of SAS [27]. Genotype was fixed while location and year were assumed to be random effects. The model for the experiment for each yam species was $P_{ijkr} = m + G_k + L_j + Y_i + B_r(L_j Y_i) + YL_{ij} + GY_{ki} + GL_{kj} + GLY_{kji} + e_{ijkr}$, where P_{ijkr} = percentage AM colonization of genotype k in replication r, location j, and year i; m is the overall mean of the trial; G_k is the effect of genotype k ; L_j is the effect of location j; Y_i is the effect of year i; B_r is the effect of block r; YL_{ij} is the interaction between year *i* and location *j*; GY_{ki} is the interaction between genotype k and year i; GL_{kj} is the interaction between genotype k and location j; GLY_{kij} = the interaction between genotype k, year i, and location j; and e_{ijkr} is the residual effect.

Variance components were estimated from the mean squares in the analysis of variance. Broad-sense heritability estimates (H^2_{bs}), were calculated using the standard formulae outlined by Singh and Chaudaury [28].

GGE biplot analysis [32] was conducted using an environment-centered model $p_{ij} = (y_{ij} - \mu - \beta_j) = \alpha_i + \phi_{ij}$ where p_{ij} is matrix P (a multiplication of matrices G and E); y_{ij} is mycorrhizal colonization of genotype i in environment j; m is grand mean; a_i is genotype main effect; b_j is environment main effect; and f_{ij} is specific genotype × environment interaction.

Data were based on environment-centered (scaling = 2) and G × E table without scaling (scaling = 0). The relationship between environments was based on environment metric preserving (SVP = 2) while the relationship between genotypes was based on genotype-metric preserving (SVP = 1). The goodness of fit of the biplot for all tables was based on principal components (PC)1 and 2.

Results

The soil analyses revealed highly to moderately acidic soils at all locations (Table 1). Onne soils were highly acidic and had the most organic matter. Soil available P was about 10-fold higher at Onne and Ibadan than at Ubiaja and Abuja in *D. rotundata* fields and very much higher in the *D. alata* field at Onne than at the other locations. The soil organic matter contents were lowest at Abuja; Ibadan soils had the highest concentrations of Ca, K, Zn, Mn and Cu. The soils at all locations were loamy sand.

The percentage AM colonization of *D. rotundata* genotypes ranged from 24.17 to 95.06 in 2004 and from 28.75 to 90.43 in 2005 (Table 2). The highest ranked genotypes by location in 2004 were TDr 93-32 at Abuja and Ubiaja, TDr 97/00588 at Ibadan, and TDr 04-213 at Onne. In 2005, the top genotypes were TDr 04-213 at Abuja, TDr 99-13 at Ibadan, TDr 96/01817 at Onne, and TDr 97/00917 at Ubiaja. TDr 04-212 had the lowest colonization in 2004 and TDr 96/00528 in 2005 (Table 2). Mean percentage AM colonization for *D. rotundata* was highest at Abuja in 2004 and at Ubiaja in 2005.

Table 1. Soil properties of the experimental sites for *D. rotundata* and *D. alata* genotypes.

Soil properties	2004				2005			
	Abuja	Ibadan	Onne	Ubiaja	Abuja	Ibadan	Onne	Ubiaja
D. rotundata								
pH(H_2O)	4.7	6.1	3.6	5.7	4.7	5	3.8	5.2
pH(KCl)	3.9	5.5	3.2	4.8	3.9	4.5	3.4	4.7
OM (%)	0.98	1.62	2.38	1.64	0.91	1.67	2.07	2.05
N (g/kg)	0.03	0.105	0.102	0.093	0.037	0.075	0.09	0.084
P (mg/kg soil)	2.68	20.28	20.76	2.13	2.58	13.02	22.16	4.71
Ca (cmol/kg)	0.65	2.25	0.46	1.44	0.68	2.6	0.38	1.7
Mg (cmol/kg)	0.13	0.56	0.10	0.60	0.26	0.67	0.1	0.79
K (cmol/kg)	0.10	0.24	0.06	0.08	0.18	0.25	0.07	0.11
Zn (mg/kg soil)	2.13	5.58	2.96	2.16	4.13	7.34	3.35	5.82
Cu (mg/kg soil)	1.39	2.23	1.15	0.94	1.28	2.97	1.44	1.75
Mn (mg/kg soil)	35.29	63.81	2.88	41.85	31.75	87.1	1.93	44.44
Fe (mg/kg soil)	36.69	62.42	143.74	27.27	34.51	54.5	161.02	23.61
Sand (g/kg)	780	820	720	800	780	800	740	840
Clay (g/kg)	100	80	80	60	120	100	40	40
Silt (g/kg)	120	100	200	140	100	100	220	120
D. alata								
pH(H_2O)	5.4	6.1	3.6	5.7	4.5	5.4	3.6	5.2
pH(KCl)	4.6	5.5	3.2	4.8	3.8	5.1	3.2	4.7
OM (%)	1.45	1.62	3.17	1.64	0.76	1.48	2.53	2.05
N (g/kg)	0.091	0.105	0.153	0.093	0.024	0.082	0.165	0.084
P (mg/kg soil)	19.72	20.28	171.54	2.13	2.78	16.05	194.25	4.71
Ca (cmol/kg)	1.6	2.25	1.11	1.44	0.46	2.14	0.59	1.7
Mg (cmol/kg)	0.39	0.56	0.21	0.6	0.13	0.67	0.11	0.79
K (cmol/kg)	0.14	0.24	0.19	0.08	0.13	0.28	0.15	0.11
Zn (mg/kg soil)	4.0	5.58	3.88	2.16	2.94	3.94	2.22	5.82
Cu (mg/kg soil)	1.43	2.23	1.23	0.94	0.83	2.81	1.06	1.75
Mn (mg/kg soil)	55.88	63.81	4.75	41.85	39.23	83.22	3.39	44.44
Fe (mg/kg soil)	48.72	62.42	158.52	27.27	35.54	36.2	172.7	23.61
Sand (g/kg)	840	820	760	800	800	760	760	840
Clay (g/kg)	80	80	40	60	100	120	40	40
Silt (g/kg)	80	100	200	140	100	120	200	120

Table 2. Percentage AM colonization of *D. rotundata* genotypes at four locations in the yam growing region of Nigeria.

Genotype	2004					2005				
	Abuja	Ibadan	Onne	Ubiaja	Mean	Abuja	Ibadan	Onne	Ubiaja	Mean
TDr 04-211*	76.20	17.97	56.16	65.24	46.45		40.65	38.11	71.32	50.03
TDr 93-32*	95.06	40.04	35.62	81.70	63.11	71.93	66.83	39.02	86.59	66.09
TDr 04-212*	33.18	30.53	28.83	44.25	34.20	75.90	52.76	28.75	79.04	59.11
TDr 04-213*	89.26	38.42	79.44	65.72	68.21	83.23	49.46	43.94	66.18	60.70
TDr 99-13*	53.07	61.08	61.62	52.47	57.06	54.60	67.62	36.69	72.95	57.96
TDr 96/00428	73.48	52.25	63.69	68.85	64.57	57.63	49.35	56.28	76.57	59.96
TDr 96/00528	53.73	49.57	52.90	31.25	46.86	69.77	52.17	32.04	56.76	52.68
TDr 96/00582	68.68	35.68	69.92	39.36	53.41	80.43	38.88	29.94	75.34	56.15
TDr 96/00609	78.58	32.75	63.39	43.06	54.45	62.07	58.09	31.24	78.94	57.58
TDr 96/00629	80.68	39.56	51.38	68.38	60.00	68.90	59.15	39.38	73.86	60.32
TDr 96/01393	54.88	49.85	46.53	59.35	52.65	64.03	63.34	51.53	82.55	65.36
TDr 96/01395	70.24	50.21	69.49	28.05	54.50	64.03	43.96	43.86	80.33	58.05
TDr 96/01621	66.98	45.75	52.20	45.57	52.63	73.66	46.12	41.11	70.28	57.79
TDr 96/01724	51.77	35.31	58.10	69.43	53.65	58.47	56.51	40.51	69.14	56.16
TDr 96/01750	62.81	24.16	63.56	51.79	50.58	74.47	62.15	32.74	75.91	61.32
TDr 96/01799	79.03	47.67	77.33	69.00	68.26	67.93	47.42	30.49	85.32	57.79
TDr 96/01817	56.20	48.02	56.53	52.86	52.47		58.45	61.49	83.75	67.89
TDr 96/01818	51.54	43.54	46.43	75.08	54.15	61.07	47.20	30.78	81.48	55.13
TDr 97/00205	82.35	41.78	51.40	52.63	57.04	75.60	45.11	35.47	73.60	57.45
TDr 97/00585	77.89	33.10	66.69	56.88	58.64	72.10	30.28	33.92	80.32	54.16
TDr 97/00588	85.42	78.89	58.38	81.23	75.98	68.03	32.91	35.53	83.82	55.07
TDr 97/00632	56.73	31.45	51.37	40.47	45.00	67.83	53.69	38.04	89.16	62.18
TDr 97/00777	74.65	46.17	42.01	61.16	56.00	78.53	50.97	27.31	74.53	57.84
TDr 97/00793	49.97	50.39	53.32	69.31	55.75	66.97	40.60	58.68	86.93	63.29
TDr 97/00903	62.38	47.53		69.78	45.20	71.70	55.63	36.31	88.30	62.99
TDr 97/00917	71.03	48.92	63.20	71.42	63.64	79.40	53.40	30.19	90.43	63.36
TDr 97/00960	68.58	53.73	52.76	77.76	63.21	59.17	52.50	33.21	75.42	55.07
Mean	67.68	43.49	54.57	58.97		69.10	50.93	38.39	78.10	
SE	2.81	2.36	3.07	2.92		1.50	1.85	1.80	1.50	
CV (%)	21.16	27.63	28.04	25.25		11.5	18.49	23.86	9.96	

*Landrace cultivar.

In the *D. alata* experiment, percentage AM colonization ranged from 21.18 to 91.70 in 2004 and from 24.76 to 95.08 in 2005 (Table 3). The highest ranked genotypes by location in 2004 were TDa 98/01168 at Abuja, TDa 85/00250 at Ibadan, TDa 01/00012 at Onne, and TDa 98/01176 at Ubiaja (Table 3). In 2005, they were TDa 01/00004 at Abuja, TDa 98/01183 at Ibadan and Onne, and TDa 00/00364 at Ubiaja. In both years, TDa 93-36 had the lowest colonization across the locations; TDa 85/00250 had the highest one in 2004 and TDa 98/01183 in 2005. There were significant differences ($P < 0.05$) in AM colonization among genotypes within and across locations. Ubiaja had the highest mean in both years for *D. alata* (Table 3).

Analysis of variance for 2004 and 2005 combined data showed significant effects for all sources of variation except year in the *D. rotundata* experiment (Table 4). In terms of relative contributions to the total variation observed (based on the total sum of squares), the major effects were attributable to location (38.91%), genotype × location (18.63%), location × year (15.43) and genotype × location × year (12.43%). Genotype accounted for 7.30% of the sum of squares. Table 4 also shows significant effects for all sources of variation in the *D. alata* experiment except for the location × year and genotype × year interactions. The contributions to the sum of squares were: location 70.02%, genotype 5.30% and genotype × location interaction 7.86%. Variance components of mycorrhizal colonization trait in yam are shown in Table 5. In *D. rotundata* and *D. alata*, the genotypic variance (δ^2g) was higher than the variance for genotype × location (δ^2gl), genotype × year (δ^2gy) and genotype × location × year (δ^2gly). The broad sense heritability estimate of mycorrhizal colonization was 0.87 in *D. alata* genotypes and 0.60 in *D. rotundata*.

Table 4. Results of combined analysis of variance for AM colonization of *Dioscorea rotundata* and *D. alata* in 2004 and 2005.

Source	Degrees of freedom	Sum of squares	Mean squares	Variation (%)†
D. rotundata				
Location (L)	3	28067.15	9355.72***	38.91
Genotype (G)	26	5269.80	202.69***	7.30
Year (Y)	1	312.22	312.22 ns	0.43
G × L	78	13440.54	172.32***	18.63
L × Y	3	11128.11	3709.37***	15.43
G × Y	26	4952.88	190.50***	6.87
L × G × Y	77	8970.45	116.50*	12.43
Residual error	422		86.81	
CV (%)			18.65	
D. alata				
Location (L)	3	65089.90	21696.63***	70.02
Genotype (G)	27	4768.37	176.61***	5.13
Year (Y)	1	5873.87	5873.87***	6.32
G × L	81	7308.70	90.23*	7.86
L × Y	3	352.36	117.45 ns	0.38
G × Y	27	2320.77	85.95ns	2.50
L × G × Y	81	7249.18	89.50*	7.80
Residual error	440		68.32	
CV			15.32	

ns - not significant at $P<0.05$, *** - significant at $P<0.0001$, * - significant at $P<0.05$
† - proportion of variation due to the total sum of squares of all treatment effects.

Table 3. Percentage AM colonization of *D. alata* genotypes at four locations in the yam growing region of Nigeria.

	2004					2005				
Genotype	Abuja	Ibadan	Onne	Ubiaja	Mean	Abuja	Ibadan	Onne	Ubiaja	Mean
TDa 291*	67.92	31.76	37.69	78.2	53.89	82.00	51.89	56.52	89.47	69.97
TDa 297*	73.42	61.20	52.88	81.74	67.31	90.16	49.32	52.92	87.11	69.88
TDa 00/00060	80.34	44.06	53.58	70.89	62.22	86.79	60.49	47.77	88.98	71.01
TDa 00/00064	78.23	45.09	61.06	88.84	68.31	86.12	50.74	62.72	86.33	71.48
TDa 00/00103	76.33	55.01	48.08	82.59	65.50	85.03	51.52	58.77	85.59	70.23
TDa 00/00104	75.55	55.58	51.98	89.23	68.09	79.43	53.62	51.29	85.16	67.38
TDa 00/00194	70.76	43.23	49.51	75.73	59.81	78.76	50.02	61.75	90.29	70.20
TDa 00/00204	76.54	62.29	50.97	74.05	65.96	70.59	57.97	57.83	95.08	70.37
TDa 00/00364	75.66	64.02	30.48	73.02	60.80	93.10	57.55	46.19	86.86	70.93
TDa 01/00004	68.96	42.11	63.37	75.48	62.48	92.71	53.50	44.28	91.28	70.44
TDa 01/00012	56.63	60.09	36.43	77.49	57.66	68.99	51.45	58.51	88.20	66.79
TDa 01/00024	61.43	42.90	58.10	82.06	61.12	79.25	53.77	56.38	91.82	70.31
TDa 01/00081	74.84	51.96	44.24	73.64	61.17	81.27	59.51	65.24	92.06	74.52
TDa 01/00210	66.89	57.95	33.64	83.85	60.58	85.01	57.23	44.81	89.28	69.08
TDa 85/00250	68.00	84.72	39.94	88.32	70.24	83.12	52.79	48.92	78.23	65.76
TDa 92-2*	72.90	20.91	34.65	75.77	51.06	81.18	53.86	44.82	79.43	64.82
TDa 93-36*	50.54	28.47	32.48	82.38	48.47	79.88	44.37	24.76	76.12	56.28
TDa 95/00010	70.39	32.86	22.96	80.08	51.57	86.63	42.98	41.03	81.72	63.09
TDa 95/00328	72.73	21.18	46.86	81.68	55.61	79.86	56.77	68.54	86.97	73.03
TDa 98/01166	72.31	37.52	35.50	85.02	57.58	78.78	50.30	61.25	83.99	68.58
TDa 98/01168	84.00	33.82	31.03	75.68	56.13	74.97	59.29	56.11	84.34	68.68
TDa 98/01174	62.92	29.47	41.31	74.78	52.12	73.52	57.39	48.28	86.83	66.51
TDa 98/01176	61.03	47.79	44.74	91.70	61.32	76.47	54.37	50.34	89.07	67.56
TDa 98/01183	62.43	53.25	58.04	74.28	62.00	83.84	64.50	68.71	85.25	75.57
TDa 99/00199	67.67	45.28	46.50	82.32	60.44	79.16	45.84	59.58	81.71	66.57
TDa 99/00395	44.49	45.69	34.78	77.29	50.56	78.09	51.31	46.82	80.76	64.25
TDa 99/00528	75.86	57.46	44.03	78.67	64.01	60.52	52.45	46.38	89.49	62.21
TDa 99/01169	66.43	31.13	27.09	79.75	51.10	79.77	55.25	64.77	83.18	70.74
Mean	69.11	45.96	43.28	79.81		80.54	53.57	53.4	86.24	
SE	1.69	2.81	2.05	1.05		1.34	0.93	1.86	0.86	
CV (%)	12.74	31.72	24.67	6.81		8.67	9.07	18.13	5.19	

* Landrace cultivar.

Table 5. Estimates of variance components and broad sense heritability (H^2_{bs}).

Species	δ^2g	δ^2gl	δ^2gy	δ^2gly	δ^2p	δ^2e	H^2_{bs}
D. rotundata	38.63	28.50	34.56	9.90	64.27	86.81	0.60
D. alata	36.10	7.30	5.88	7.06	41.75	68.32	0.87

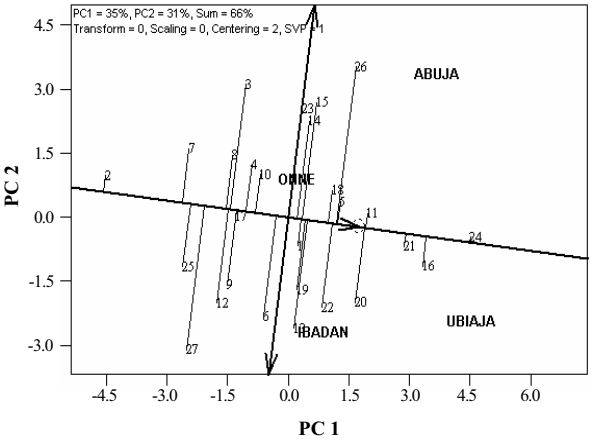

Figure 1. GGE biplot of the mean performance and stability of *Dioscorea rotundata* genotypes with respect to AM colonization for 2004 and 2005 combined analysis.
D. rotundata genotypes (each with accession prefix TDr)
1, 96/00428; 2, 96/00528; 3, 96/00582; 4, 96/00609; 5, 96/00629; 6, 96/01393; 7, 96/01395; 8, 96/01621; 9, 96/01724; 10, 96/01750; 11, 96/01799; 12, 96/01817; 13, 96/01818; 14, 97/00205; 15, 97/00585;16, 97/00588; 17, 97/00632; 18, 97/00777; 19, 97/00793; 20, 97/00903; 21, 97/00917; 22, 97/00960; 23, 04-211; 24, 93-32; 25, 04-212; 26, 04-213; 27, 99-13.

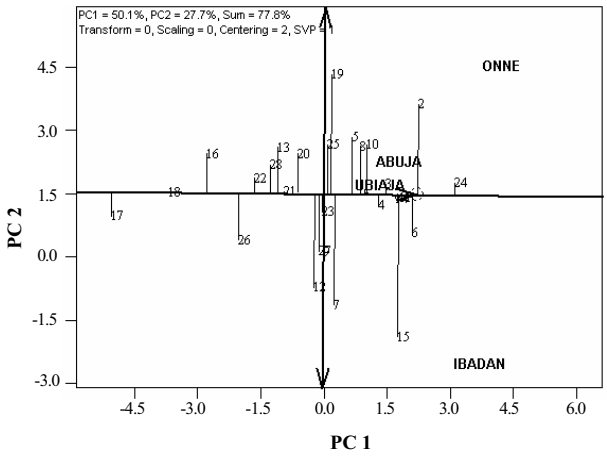

Figure 2. GGE biplot of the mean performance and stability of *Dioscorea alata* genotypes with respect to AM colonization for 2004 and 2005 combined analysis.
D. alata genotypes (each with accession prefix TDa)
1, 00/00060; 2, 00/00064; 3, 00/00103; 4, 00/00104; 5, 00/00194; 6, 00/00364; 7, 01/00004; 8, 01/00012; 9, 01/00024; 10, 01/00081; 11, 01/00204; 12, 01/00210; 13, 291; 14, 297; 15, 85/00250; 16, 92-2; 17, 93-36; 18, 95/00010; 19, 95/00328; 20, 98/01166; 21, 98/01168; 22, 98/01174; 23, 98/01176; 24, 98/01183; 25, 99/00199; 26, 99/00395; 27, 99/00528; 28, 99/01169.

Principal components (PC) 1 and 2 for the combined (2004 and 2005) analysis (GGE bi-plot) explained 66.0% of the variation in *D. rotundata* (Fig. 1) and 77.8% of the variation in *D. alata* (Fig. 2). The highest mean percentage AM root colonization was observed in TDr 93-32 for *D. rotundata* and in TDa 98/01183 for *D. alata*; TDr 96/00528 had the lowest mean percentage AM root colonization for *D. rotundata* (Fig. 1) and TDa 93-36 for *D. alata* (Fig. 2). Figs 1 and 2 represent the average-tester coordination views. These views show the performance of yam genotypes across the locations, whereby the genotypes were ranked along the average-tester axis based on their mean performance and with the arrow pointing towards genotypes with greater performance. From the figures, the average location in terms of AM colonization was between Ubiaja and Abuja for *D. alata*, while the locations under *D. rotundata* performed either below or above average.

TDr 93-32 (*D. rotundata*) and TDa 01/00204 (*D. alata*) were the most stable for the two species and had their mean percentage AM colonization values above the general average. In *D. rotundata*, the highest ranked genotype was a landrace cultivar, TDr 93-32, and three out of the five landraces had their AM colonization mean higher than the average (Fig. 1). However, in *D. alata,* three out of the four landrace cultivars had lower values than the location mean (Fig. 2).

Discussion

Genotypes of *D. rotundata* such as TDr 93-32, TDr 04-213, TDr 97/00588, and of *D. alata* such as TDa 85/00250, TDa 00/00064 and TDa 98/01183, gave promising results with high percentages of AM colonization. Contrary to earlier findings that the hybrids of some crops had reduced ability to form mycorrhiza [14], some of the hybrids in this study exhibited a high percentage of AM colonization. In fact, many of the *D. alata* hybrids had higher level of AM colonization than the landraces used in this study.

Several of the agroclimatic factors that characterize the wide geographical range of the yam growing region in Nigeria would contribute to variation in AM colonization among crop genotypes [24, 31]. The values for soil available P, organic matter content and total N followed relatively the same patterns across the locations in this study. The soil pH of the locations ranged from highly acidic at Onne to moderately acidic at Ibadan. Despite the high acidity at Onne, substantial colonization was recorded there for both species of yam. Mycorrhizal colonization of up to 34% has been reported in soils with pH as low as 3.4 [5]. The higher AM colonization at Abuja and Ubiaja in many of the genotypes compared to that in Ibadan and Onne was possibly the result of the relatively lower soil available P in Abuja and Ubiaja [9]. However, AM colonization of yam roots was still recorded at Onne, despite the high available P, especially on the *D. alata* field, contrary to earlier reports that a high P concentration eliminates mycorrhizal colonization [1, 30]. These results suggest that yam roots can be colonized in soils of relatively high available P and low pH status.

Cropping management history is also known to influence the diversity of AM species and the extent of colonization [18, 20]. The heterogeneity of the crops preceding yam and the history of rotation probably influenced the AM colonization of yam in

different locations. High plant diversity in natural vegetation and the highly mycorrhizal cassava crop [16] preceding yam cultivation probably contributed to the higher colonization in genotypes of both crops at Ubiaja than in the other locations. High plant diversity or species-rich plant communities tend to favour AM species diversity and subsequently infectivity [30]. The higher AM colonization of most yam genotypes at Abuja compared to Ibadan, both with leguminous cover crop preceding yam, is perhaps explained by the lower soil available P at Abuja.

The foregoing discussion provides several of the likely reasons for the highly significant location effects on the AM colonization of yam roots in both experiments. The genotypes responded differently to the variations in environmental conditions as demonstrated by the significant first and second-order interactions with location and year, especially in the *D. rotundata* experiment. In the GGE biplots, TDr 97/00903 ranked best in AM colonization at Ibadan but was the poorest at Onne in 2004 and 2005. Among other factors, the interaction between genotypes and specific AM fungal species at the different locations could be responsible for this. Investigation of the diversity of these indigenous species or populations of AM fungi was not included in this study. The significant genotype x environment interactions would complicate broad recommendations of genotypes for target environments with respect to this trait. Previous work found significant interaction effects for genotype × location in *D. alata* and *D. rotundata* with respect to yield traits [11, 17] and also in cassava where genotype × location interaction was implicated in the analysis of heritability of most traits evaluated [10, 21].

The broad sense heritability (H^2_{bs}) estimates for AM colonization were relatively high for the two species; hence selection for the AM colonization trait could yield beneficial results. The ranges in percentage root colonization recorded in the two species offer opportunities to generate populations for detailed genetic studies on the trait.

Conclusions

The extent of AM root colonization varies significantly between yam genotypes and growing environments, and the relative performance of genotypes with respect to this attribute varies with the environment. AM fungi could be used to enhance nutrient acquisition in yam under conditions where low pH may limit soil P availability. The results from this study provide baseline information that would facilitate detailed genetic studies on AM root colonization of yam.

Acknowledgement

The authors thank IITA for funding the project.

References

[1]Amijee, F., Tinker, P. B. and Stribley, D. P. 1989. The development of endomycorrhizal root system VII. A detailed study of the effects of soil phosphorus on colonization. New Phytol. **111**:435–446.

[2]Asiedu, R., Ng, S. Y. C., Bai, K. V., Ekanayake, I. J. and Wanyera, N. M. W. 1998. Genetic improvement. In Orkwor, G. C. *et al*. (eds). Food Yams. Advances in Research. IITA and NRCRI, Nigeria, pp. 63–10.

[3]Asiedu, R., Bokanga, M., Carsky, R.J., Chikoye, D., Girardin, O., Green, K., Hughes, J. d'A., Manyong, V.M., Meerman, J.C., Mignouna, H., Ng, N.Q., Ng, S.Y.C., Quin, F.M., Speijer, P.R., Tian, G., Vernier, P. and Wanyera, N.M.W. 1997. Project 13. Improvement of Yam Based Production Systems. Annual Report. International Institute of Tropical Agriculture, Ibadan, Nigeria.

[4]Brundrett, M., Piche, Y. and Peterson, R. L. 1984. A new method for observing the morphology of vesicular arbuscular mycorrhiza. Can. J. Bot. **62**:2118–2134.

[5]Bunn, R. A. and Zabinski, C. A. 2003. Arbuscular mycorrhizae in thermal-influenced soils in Yellowstone National Park. Western North American Naturalist **63**(4):409–415.

[6]Cartmill, A.D., Alarcon, A. and Valdez-Aguilar, L.A. 2007. Arbuscular mycorrhizal fungi enhance tolerance of *Rosa multiflora* cv. Burr to bicarbonate in irrigation water. J. Plant Nutrition **30**(7-9):1517-1540.

[7]Cavallazzi, J.R.P., Filho, O.K., Stuermer, S.L., Rygiewicz, P.T. and de Mendonca, M.M. 2007. Screening and selecting arbuscular mycorrhizal fungi for inoculating micropropagated apple rootstocks in acid soils. Plant Cell Tissue and Organ Culture **90**(2):117-129.

[8]Coffman, W. R. and Smith, M. E. 1991. Roles of the public, industry, and international research centre breeding programs in developing countries. In Sleper D. A. *et al.* (eds). Plant Breeding and Sustainable Agriculture: Considerations for Objectives and Methods. Proceedings of a symposium sponsored by Division C-1 of the Crop Science Society of America CSSA Special Publication No. 18. Crop Science Society of America, American Society of Agronomy, Madison, WI, USA.

[9]Covacevich, F., Echeverria, H.E. and Aguirrezabal, L.A.N. 2007. Soil available phosphorus status determines indigenous mycorrhizal colonization of field and glasshouse-grown spring wheat from Argentina. Applied Soil Ecology **35**(1):1-9.

[10]Egesi, C.N., Ilona, P., Ogbe, F.O., Akoroda, M.A. and Dixon, A. 2007. Genetic variation and genotype × environment interaction for yield and other agronomic traits in cassava in Nigeria. Agron. J. **99**:1137-1142.

[11]Egesi, C.N., Ogunyomi, S. and Asiedu, R. 2005 Genotype × environment interaction in water yam (*Dioscorea alata*) yield trials in five yam-growing sites in Nigeria. J. Genet. & Breed. **59**:81-88.

[12]Ekanayake, I. J. and Asiedu, R. 2003. Problems and perspectives of yam-based cropping systems in Africa. J. Crop Production **9**(1/2):531–558.

[13]Giovanetti, M. and Mosse, B. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. **84**:489–500.

[14]Hess, J. L., Shiffler, A. K. and Jolley, V. D. 2005. Survey of mycorrhizal colonization in native, open-pollinated, and introduced hybrid maize in villages of Chiquimula, Guatemala. J. Plant Nutrition **28**(10):1843–1852.

[15]Hetrick, B. A. D., Wilson, G. W. T. and Todd, T. C. 1996. Mycorrhizal response in wheat cultivars: Relationship to phosphorus. Can. J. Bot. **74**:19–25.

[16]Howeler, R. H. 1990. Phosphorus requirements and management of tropical root and tuber crops. In International Rice Research Institute Report. Phosphorus Requirements for Sustainable Agriculture in Asia and Oceania. Manila, The Philippines, pp. 427–444.

[17]IITA 1993. Root and Tuber Improvement Program. Archival Report 1989–1992. Part III Yam (*Dioscorea* spp.). Crop Improvement Division, IITA Ibadan, Nigeria, 118 p.

[18]Johnson, N.C., Copeland, P.J., Crookston, R.K. and Pfleger, F.L. 1992. Mycorrhizae: Possible explanation for yield decline with continuous corn and soybean. Agron. J. **84**:387–390.

[19]Kempton, R. A. 1984. The use of biplots in interpreting variety by environment interactions. J. Agric. Sci. **103**:123–135.

[20]Lekberg, Y. and Koide, R.T. 2005. Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. New Phytol. **168**:189–204.

[21]Mba, R. E. C. and Dixon, A. G. O. 1997. Heritability estimates for ACMD resistance for some newly developed cassava clones in Nigeria. African J. Root and Tuber Crops **2**:56–58.

[22]Menge, J. A. 1983. Utilization of vesicular arbuscular mycorrhizal

fungi in agriculture. Can. J. Bot. **61**:1015–1024.
[23]Mercy, M. A., Shivashankar, G. and Bagyaraj, D. J. 1990. Mycorrhizal colonization in cowpea is host dependent and heritable. Plant Soil **121**:292–294.
[24]Muthukumar, T. and Udaiyan, K. 2002. Seasonality of vesicular arbuscular mycorrhizae in sedges in a semi-arid tropical grassland. Acta Oecologica **23**:337–347.
[25]Orkwor, G. C. and Asadu, C. L. A 1998. Agronomy. In Orkwor, G. C. *et al.* (eds). Food Yams. Advances in Research. IITA and NRCRI, Nigeria, pp. 105-141.
[26]Philips, J. M. and Hayman, D. S. 1970. Improved procedure for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycolo. Soc. **55**:159–161.
[27]SAS 2003. SAS/STAT Guide for Personal Computers, Version 9.1 Edition. SAS Institute Inc., Cary, NC, USA, 1028 p.
[28]Singh, R. K. and Choudhary, B. D. 1985. Biometrical Methods in Quantitative Genetic Analysis. Kalyani Publishers, New Delhi, India, 318 p.
[29]Singh, S. 2005. Effect of elevated levels of carbon dioxide and light on mycorrhiza. Mycorrhiza News **16**(4):2–11.
[30]Smith, S. E. and Read, D. J. 1997. Mycorrhiza Symbiosis. 2nd edn. Academic Press, San Diego CA., USA, 605 p.
[31]Staddon, P. L., Thompson, K., Jakobsen, I., Grime, J. P., Askew, A. P. and Fitter, A. H. 2003. Mycorrhizal fungal abundance is affected by long-term climatic manipulations in the field. Global Change Biol. **9**:186–194.
[32]Yan, W. and Kang, M. S. 2003. GGE Biplot Analysis: A Graphical Tool for Breeders, Geneticists, and Agronomists. CRC Press, Boca Raton, FL, USA, 271 p.