COMPARISON OF PATHOGENICITY OF GEOGRAPHICALLY SEPARATE POPULATIONS OF *SCUTELLONEMA BRADYS* ON YAM (*DIOSCOREA* SPP.) IN WEST AFRICA

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ABSTRACT

Coyne, D., V. Williamson, A. Tchabi, H. Baimey, and I. Rotifa. 2012. Comparison of pathogenicity of geographically separate populations of *Scutellonema bradys* on yam (*Dioscorea* spp.) in west Africa. Nematropica 42:181-190.

Nine Nigerian populations of *Scutellonema bradys*, obtained from infected yam (*Dioscorea* spp.), were assessed following inoculation onto susceptible yam (*Dioscorea rotundata*) cv. TDr131 in pot and field experiments in Nigeria between 2002 and 2004. In addition, geographically separated populations, two each from Benin, Burkina Faso, Côte d'Ivoire, Ghana, Mali, Nigeria and Togo, were compared in pot assays in Benin between 2003 and 2004. The effect of different nematode populations on tuber yield was variable and depended on the experiment. Moreover, *S. bradys* damage and yield reduction was more pronounced when plants were under stress as evidenced by production of small tubers Nematode numbers increased for all *S. bradys* populations during storage, by as much as 37.3 times for one population from Nigeria. Similarly, up to 44.5% tuber weight loss was observed during storage compared with control tubers (28%), with differences in weight loss evident among some *S. bradys* population treatments. Dry rot symptoms occurred on both *S. bradys* infected and also uninfected tubers, indicating that dry rot is an unreliable diagnostic for yam nematode infection. However, dry rot severity was higher on infected tubers, varying with some *S. bradys* populations. In conclusion, this study demonstrates that nematode densities and yam dry rot severity (following infection with the different nematode populations) was variable and differed between years, but did not identify any populations that had higher pathogenicity. Results imply, however, that greater variability of *S. bradys* damage may occur because of the effects of environment and host differences, rather than between the pathogenicity of these populations.

Key words: Benin, Burkina Faso, Côte d'Ivoire, dry rot disease, Ghana, Mali, Nigeria, plant parasitic nematodes, Togo, yam belt, yield loss.

RESUMO

Coyne, D., V. Williamson, A. Tchabi, H. Baimey, y I. Rotifa. 2012. Comparación de la patogenicidad de poblaciones geográficamente separadas de *Scutellonema bradys* en ñame (*Dioscorea* spp.) en el oeste de África. Nematropica 42:181-190.

Nueve poblaciones nigerianas de *Scutellonema bradys*, obtenidas de ñames infectados (*Dioscorea* spp.), fueron evaluadas después de la inoculación en ñame susceptible (*Dioscorea rotundata*) cv. TDr131 en macetas y experimentos en campo en Nigeria entre 2002 y 2004. En adición, poblaciones geográficamente separadas, dos de cada una de Benin, Burkina Faso, Costa de Marfil, Ghana, Mali, Nigeria y Togo, fueron comparadas en ensayos en macetas en Benin entre 2003 y 2004. El efecto de diferentes poblaciones de nematodos en el rendimiento del tubérculo fue variable y dependió del experimento. Más aún, *S. bradys* daño y reducción en el rendimiento fue más pronunciado cuando las plantas estuvieron bajo estrés como evidenció la producción de tubérculos pequeños. Los números de nematodos se incrementaron para todas las poblaciones de *S. bradys* durante el almacenamiento, hasta 37.3 veces para una población de Nigeria. Similarmente, hasta un 44.5% de pérdida en el peso del tubérculo se observó durante el almacenamiento comparado con los tubérculos control (28%), con diferencias en pérdida de peso evidente entre tratamientos de algunas poblaciones de *S. bradys*. Síntomas de pudrición seca ocurrieron en ambos *S. bradys* tubérculos infectados y también en los no infectados, indicando que la pudrición seca no es un diagnóstico confiable de la infección del ñame por el nematodo. Sin embargo, la severidad de la pudrición seca fue más alta en tubérculos infectados, variando con algunas poblaciones de *S. bradys*, después de la infección con las diferentes poblaciones del nematodo. En conclusión, este estudio demuestra que las densidades del nematodo y severidad de la pudrición seca del ñame (después de

la infección con las diferentes poblaciones del nematodo) fue variable y difirió entre años, pero no identificó ninguna de las poblaciones que tuvieron una patogenicidad más alta. Los resultados implican sin embargo, que una mayor variabilidad del daño de *S. bradys* puede ocurrir debido a los efectos del ambiente y diferencias de hospedante, más bien que entre la patogenicidad de estas poblaciones.

Palabras clave: Benin, Burkina Faso, Costa de Marfil, enfermedad de la pudrición seca, Ghana, Mali, Nigeria, nematodos parásitos de plantas, Togo, cinturón del ñame, pérdidas en rendimientos.

INTRODUCTION

Yam (*Dioscorea* spp.) is an important starch staple food produced throughout Africa, but mainly in an area spanning West and Central Africa, essentially between Guinea and Cameroon. Over 90% of global yam is produced in the 'yam belt', where Nigeria, Ghana and Côte d'Ivoire are the largest producers (FAOSTAT, 2010). Production therefore occurs across a range of agro-ecological zones (AEZ) and climates, and includes different yam species. In terms of bulk, the most important yams cultivated across the region are *D. rotundata* Poir. (white yam), followed by *D. alata* L. (water yam) and *D. cayenensis* Lam. (yellow yam) (Degras, 1993).

Numerous pests and diseases are associated with yam in West Africa, but the yam nematode, Scutellonema bradys (Steiner & LeHew) Andrássy, which occurs throughout the region and affects all the main yam species and cultivars, is one of the most important (Kwoseh, 2000; Coyne *et al.*, 2006). Damage symptoms begin with light yellow or brown lesions below the outer skin, which gradually progress deeper into the tuber as the nematodes feed and multiply turning infected tissues brown to black. The outer cortex may crack and flake exposing the necrotic tissue, but may remain intact, presenting the appearance of an otherwise healthy tuber. Dry rot is mainly observed during storage but may develop in the field prior to harvest. Infected tubers, which are used for planting, but are not treated, provide inoculum to infect the new crop resulting in the cyclical perpetuation of the disease from store back to the field. This results in the persistent decline in yam quality and production and even total loss of susceptible cultivars.

Scutellonema bradys, *S. clathricaudatum* Whitehead and *S. cavenessi* Sher, all occur in West Africa, are closely related and comprise the "S. bradys complex" referred to by Baujard and Martiny (1995). These three species are morphologically similar but *S. bradys* alone affects yam (Bridge *et al.*, 2005). *Pratylenchus coffeae* (Zimmerman) Filipjev & Schuurmans Steckhoven and Radopholus similis (Cobb) Thorne infection also cause dry rot of yam tubers (Bridge *et al.*, 2005), but not in Africa. *Pratylenchus sudanensis* (Loof & Yassin) infection results in similar symptoms in Uganda (Mudiope *et al.*, 2008). A number of studies have been undertaken on the biology and pathogenicity of *S. bradys*, which was also recently recorded causing damage to potato (*Solanum tuberosum*) (Coyne and Claudius-Cole, 2009; Coyne *et al.*, 2011). Baimey *et al.* (2009) found pathogenic variability within three Benin populations, but otherwise there has been no assessment of *S. bradys* variability from across the 'yam belt'. Such studies are important, since selection of representative and/or aggressive nematode populations is critical to the development of robust screening procedures. The current study reports on the pathogenicity and multiplication of populations of *S. bradys* from within Nigeria in both field and pot experiments, while populations from seven countries from across West Africa were examined in pots under contained conditions in Benin.

MATERIALS AND METHODS

Experimental details and design

During 2002-2004, three separate experiments were conducted: two in Nigeria and one in Benin, with each repeated a second time. Experiments in Nigeria were carried out in pots in a screenhouse and on the experimental farm of the International Institute of Tropical Agriculture (IITA), Ibadan Station. The experiment in Benin was carried out in pots under greenhouse and screenhouse conditions at IITA, Cotonou Station. IITA Ibadan is located within the forest-savanna transition zone in south-western Nigeria (7.30°N, 3.54°E; altitude 243 m asl), 120 km north of Lagos and IITA Cotonou in the coastal savanna zone near the town of Abomey-Calavi (6.25°N, 2.19°E; altitude 23 m above sea level [asl]), 12 km north of Cotonou.

Throughout the study, seed tubers, weighing 100-150 g each, of the *S. bradys*-susceptible yam cv. TDr 131 (*D. rotundata*) were used. These were obtained from IITA Ibadan and selected for absence of symptoms of nematode infection. All seed tubers were hot water-treated at 50°C for 30 min prior to planting (Smit, 1967) to eliminate any *S. bradys* present, then allowed to sprout in shredded coconut husk in wooden trays to allow for uniform selection of sprouted plants.

Pot experiments at IITA Ibadan and IITA Cotonou

At four weeks after planting sprouted tubers were transplanted from the coconut husk into 5.5-litre plastic pots in May 2002 and 2003 in Ibadan and March 2003

and 2004 in Cotonou. For both experiments, pots were arranged in a completely randomized block design with ten replicates for each nematode population in Ibadan, and five in Cotonou (due to scarcity of planting material). One sprouted tuber was planted per pot, filled with steam sterilised topsoil originating at each station. Plants were watered with tap water as required and staked three weeks after planting (one stake per plant). During the period of the experiment, temperature ranged from 25 to 27°C in the screenhouse in Ibadan and in Cotonou from 25 to 33°C in 2003 and 25 to 29°C in 2004. The high temperatures experienced in the greenhouse in Cotonou in 2003 were considered as a reason for poor growth and so a screenhouse was used in 2004. All experiments were terminated at nine months after planting.

Field experiment at IITA Ibadan

Prior to transplanting sprouted tubers to the field, pre-plant soil nematode population densities were determined. Soil samples of *ca.* 100 g were removed from each 1 m² of the 40 m x 40 m area reserved for the experiments using a trowel. All samples were bulked and nematodes extracted from 9 x 100 ml sub-samples for 48 h using a modified Baermann method (Coyne *et al.*, 2007). The nematode suspension was collected, reduced to 50 ml and nematodes, identified to genus level, counted from 3 x 10 ml sub-samples using a Leica Wild MZ9.5 stereomicroscope returning the sub-sample after each count. Sprouted yam tubers were transplanted from the coconut husk at four weeks after planting, in May 2003 and 2004, in mounds spaced 1 m apart. Each mound was prepared by gathering the surrounding top layer of soil to *ca.* 50-75 cm high and arranged in a completely randomized block design replicated ten times, with one row per block. Three weeks after transplanting, plants were staked (one stake per plant). The experiment was maintained weed-free by regular hand weeding and harvested at nine months after transplanting.

Inoculum preparation and inoculation procedure

For the experiments in Ibadan, *S. bradys* was collected from heavily infected *D. rotundata* tubers from nine localities within Nigeria, which are representative of a range of major yam growing areas across AEZ's (Table 1). In Cotonou, *S. bradys* originated from heavily infected tubers collected during a survey of seven West African countries: Benin, Burkina Faso, Côte d'Ivoire, Ghana, Mali, Nigeria and Togo (Coyne *et al*., 2006) (Table 1). Two separate S. bradys populations (1 and 2) were selected for use from each country. To determine the nematode population density per weight of tuber peel, infected tubers were manually peeled using a kitchen peeler, chopped (*ca.* 0.5 cm x 0.3 cm) and 3 x 5 g sub-samples removed. Nematodes were extracted from each sub-sample for 48 h and nematode densities assessed as previously described (Coyne *et al.*, 2007). Number of nematodes per unit fresh peel was then calculated from motile adults and juveniles. Infected yam peel with weight equating to *ca*. 2000 and 1000 motile nematodes was used in Ibadan and Cotonou, respectively, for inoculations.

In all cases, *S. bradys* (juveniles and adults) were inoculated at four weeks after transplanting by gently excavating a shallow trench at *ca.* 5 cm radius around the stem of each plant, to a depth (5-10 cm) that exposed some of the roots. Nematodes were inoculated as chopped infected yam peel (*ca.* 0.5 x 0.3 cm), applied to the trench and covered with soil, according to Kwoseh (2000). Uninfected yam tuber peel equal to the average weight of infected peel was applied to the uninoculated control plants. Nematode inoculum for each location between the different years was maintained on inoculated yam grown in pots.

Crop growth parameters assessed

In Ibadan, for both pot and field experiments, the fresh weight of tubers and roots per plant was recorded at harvest. In Cotonou, the mean number of tubers per plant and the girth of the main stem at soil level were additionally recorded.

Assessment of nematode damage and population density at harvest

For field experiments, 10 tubers were randomly selected per *S. bradys* population (weighing 796-1158 g each) for assessing dry rot severity on an arbitrary scale of 0-4 where 0 = clean tuber; 1 = 1-25% tuber skin showing dry rot symptoms (low level of damage); 2 = 26-50% (low to moderate level); 3 = 51-75% (moderate to severe level); 4 = 76-100% (high level). For pot experiments conducted in Ibadan, 5 tubers per treatment weighing 25-50 g each were used to score for dry rot symptoms in 2002 and 5 weighing 100-150 g each in 2003. In Cotonou, 3 tubers weighing 10-15 g each and 3 weighing 100-150 g each were used for dry rot assessment, respectively, in 2003 and 2004. The difference in number and weight of tubers selected for assessment reflected the variation in number of replicates per experiment and the lack of uniformity in tuber size. Nematode density (numbers per 5 g fresh weight of peel) was assessed from tubers selected for dry rot assessment as previously described, and for soil (per 100 ml) and roots (per 5 g fresh weight root) from all Ibadan pots and from the 2003 Benin pot experiment. Plant roots were cut to *ca.* 0.5 cm, thoroughly mixed and nematodes extracted from 3 x 5 g sub-samples of chopped roots per pot. Soil around the roots of each of the selected plants was thoroughly mixed and nematodes extracted from 100 ml soil sub-samples.

Table 1. Origins of *Scutellonema bradys* populations used in the study.

Country	*S. bradys* populations[x]	Origin site	Yam cultivar[y]	AEZ[z]
Benin	Benin1	Assiou	Gagni	NGS
	Benin2	Djougou	Yorubadoundou	NGS
Burkina Faso	Burkina Faso1	Sikasso	Koudje	SS
	Burkina Faso2	Banfora	Americano	SS
Côte d'Ivoire	Côte d'Ivoire1	Northern	Koudje	-
	Côte d'Ivoire2	Northern	Koudje	-
Ghana	Ghana1	Nogtedo	Kokoro	NGS
	Ghana2	Nkawkaw	Kokoro	NGS
Mali	Mali1	Bougouni	Koudje	NGS
	Mali2	Manakoro	Koudje	NGS
Nigeria	Nigeria1	Ekiti	Sogbe	DS
	Nigeria2	IITA-Ibadan	Tdr131	HF
	Abuja	Kubwa	Adanacha	SGS
	AbujaFCT	FCT	Omacha Ibaji	SGS
	Borno	Stadia side	Ogomaka	SS
	Delta	Umunebe	Asoko	HF
	Kogi	Lokoja	Awana	SGS
	Nassarawa	Lafia	Danacha	SGS
	Niger	Bida	Lapai	SGS
	Oyo	Saki	Ehuru	DS
	Rivers	Kpite	Birasiae	HF
Togo	Togo1	Aouda	Kokoro	NGS
	Togo2	Awandjolo	Foudouabalo	NGS

[x] nematode populations are referred to by country of origin, recovered from the site indicated; populations followed by 1 or 2 were studied in pots in Cotonou, while the remainder constitute the nine Nigerian populations studied in Ibadan;
[y] all yam species are *Dioscorea rotundata* except for Americano, which is *D. Alata*;
[z] AEZ = Agro ecological zone; NGS = Northern Guinea savannah, SGS = Southern Guinea savannah, SS = Sudan savannah, HF = Humid forest, DS = Derived savannah.

Tuber assessment following three months storage

At harvest, 5 tubers weighing 796-1158 g each were randomly selected per treatment from field experiments for storage in an open-sided yam barn at an average temperature of 25-27°C for three months. The tubers were weighed at harvest and on a monthly basis following storage to determine weight loss, dry rot severity and nematode density, as previously described.

Data analyses

Differences in nematode population density, nematode damage and percentage weight loss in tubers between treatments were compared with ANOVA, using the SAS system, Version 8 for Windows 1999, following $\log_{10}(x+1)$ transformation of nematode densities, arcsine(x) transformation of percentage weight loss and Arcsin(sqrt(x/100)) transformation

of nematode damage assessment data. Means were separated by Fisher's Protected Least Significant Difference Test (LSD), $P \leq 0.05$.

RESULTS

Pot experiments conducted at IITA Ibadan

In 2002, the tuber weight at harvest of plants inoculated in pots with S. bradys was significantly lower than for uninoculated control plants for all populations tested ($P \leq 0.05$), but tuber weight was similar between S. bradys populations. In 2003, tubers were heavier than those harvested in 2002, and the tuber weight was not significantly different for infected and control plants; however, tubers of plants infected with the Abuja FCT population of *S. bradys* had the lowest weight in both years (Table 2).

In 2002, plant root weights for all but two S. bradys treatments (Nassarawa and Abuja) were lower ($P \leq 0.05$) than control plants. However, in 2003, root weights of plants were not lower for infected plants, and, in fact, those from Rivers- and Niger-inoculated pots were heavier than on control plants (Table 2). As with the tubers, the weight of roots infected with Abuja FCT was lower than with the population from Abuja.

Tuber dry rot symptoms were relatively low, and surprisingly, tubers from control pots expressed (mild) dry rot symptoms during both years. In 2002, tubers from five nematode-inoculated plants had more dry rot than control plants; however, tubers inoculated with Borno *S. bradys* presented no obvious symptoms. In 2003, dry rot symptoms on tubers were higher for the noninoculated plants than in plants infested with seven of the nine *S. bradys* populations (Table 2).

Over both years, nematode densities recovered from tuber peel were consistently greater than from either roots or soil. The one exception was that in 2002 no nematodes were recovered from tuber peel of pots inoculated with *S. bradys* populations from Abuja and Abuja FCT (Table 3). A possible explanation, which has previously been suggested, is that severely deteriorated tubers may not support nematodes (Bridge *et al.*, 2005). A few nematodes were also recovered from control pots. In 2002, nematode densities in root tissues were very low for all *S. bradys* populations, while tuber peel densities of two populations (Borno and Nassarawa) were higher than from a number of other treatments. In 2003, nematode density of tuber peels from six populations were statistically higher than the control but Kogi-, Oyo- and Rivers-inoculated pots were not (Table 3).

Field experiments conducted at IITA Ibadan

Analysis of soil samples from the experimental area prior to planting detected no *S. bradys*. At harvest in 2002, no significant difference in tuber weight was measured for plants inoculated with any of the *S. bradys* populations (Table 4). In 2004, only tuber weights from mounds inoculated with Borno *S. bradys* population were significantly lower than from controls (Table 4). During storage, tubers from all treatments, including controls, lost weight during both years (Table 4). Tubers from Abuja FCT-inoculated mounds lost over 40% weight during three months storage, compared with 28% in controls. In 2004, control tubers lost 26% weight compared with over 40% weight losses from Borno- and Abuja-inoculated mounds.

In 2002, only tubers from Abuja FCT- and Rivers-inoculated mounds showed dry rot symptoms that were statistically higher than for control tubers after storage (Table 4). In 2004, control tubers again presented symptoms of dry rot, although four nematode-inoculated treatments (Abuja, Abjua FCT, Delta, Kogi and Niger) had greater tuber dry rot.

At harvest nematode yam tuber peel densities were generally low (mean of 38 and 30 nematodes per 5 g of peel across treatments, for 2002 and 2004 respectively) with no differences observed among inoculum populations (data not shown). Although densities increased for all treatments during the storage period, by as much as 37.3 times in the case of the Delta *S. bradys* population, the differences among populations were not significant (data not shown). In addition, nematodes were also recovered from control tubers and densities on yams of inoculated plants were not statistically higher either before or after storage.

Pot experiments conducted in Cotonou

There were few differences in the number of tubers produced among treatments in either year, with the highest being two per plant (Table 5). In 2003 tuber weights across treatments were low, possibly due to the high temperatures in the greenhouse, although all *S. bradys* population treatments had significantly lower tuber weight than the control. Tubers were heavier in 2004, and there were no significant differences in weights between inoculated and control plants. For both years, tuber weights were similar from plants inoculated with each of the geographic populations. In 2003, the stem girth was less for all nematode-inoculated plants compared to control plants, however, inoculated and control plants did not differ in girth in 2004. Dry rot symptoms were assessed only for 2004 and were significantly higher than controls for five S. bradys population treatments. Symptom severity differed between populations from within the countries of Burkina Faso, Côte d'Ivoire, Ghana, Mali and Togo (Table 5). As with experiments in Nigeria, control plants produced tubers presenting dry rot symptoms even though few, if any, nematodes were recovered (Table 6). Nematodes recovered from roots and peel were significantly higher in number than controls for all inoculated populations for both years.

Table 2. Effect of Scutellonema bradys populations originating from different localities of Nigeria on mean tuber weight, plant root weight, and tuber dry rot during pot experiments in 2002 and 2003 in Nigeria.[y]

S.bradys populations	Tuber weight (g)		Root fresh weight (g)		Tuber dry rot[z]	
	2002	2003	2002	2003	2002	2003
Abuja	34.4b	228.7a	3.4a	4.4abc	1.8abc	1.5cd
Abuja FCT	18.7b	106.4b	0.3c	3.9abc	1.0cde	1.6bc
Borno	36.9b	161.1abc	0.6bc	3.2bc	0.0f	1.7bc
Delta	27.0b	166.0abc	0.5bc	2.9bc	2.1ab	2.2ab
Kogi	32.6b	156.5abc	1.0bc	2.3c	0.2ef	1.1dce
Nassarawa	35.6b	124.2bc	2.6ab	4.3abc	2.4a	0.9de
Niger	31.9b	148.8abc	0.8bc	5.9a	2.0ab	1.2cde
Oyo	27.0b	204.7ab	0.7bc	2.8c	1.4bcd	0.8e
Rivers	47.4b	138.8bc	0.3c	4.9a	2.0ab	2.7a
control	88.0a	147.0abc	4.7a	3.7bc	0.6def	2.4a

[y] N = 10; inoculum at 2000 nematodes per plant/pot; values with the same letter in a column not significantly different according to Fisher's Protected LSD test, $P \leq 0.05$; Statistical analyses and mean separations for dry rot undertaken on Arcsin(sqrt(x/100)) transformed data;
[z] Dry rot severity scored on a scale of 0-4: 0 = clean tuber; 1 = 1-25% (low level of damage); 2 = 26-50% (low to moderate damage); 3 = 51-75% (moderate to severe damage); 4 = 76-100% (high damage).

Table 3. *Scutellonema bradys* density at harvest on yam cv. TDr131 nine months after inoculation of nematode populations from different localities in Nigeria in pot tests in Nigeria.[z]

S. bradys populations	2002			2003		
	Tuber peel	Plant root	Soil	Tuber peel	Plant root	Soil
Abuja	0d	0a	5abc	465ab	14b	4b
Abuja FCT	0d	0a	4abc	402abc	27b	11b
Borno	369a	0a	1ab	272bcd	15b	13b
Delta	91cd	0a	2bc	511a	16b	13b
Kogi	79cd	1a	8ab	220cde	5b	5b
Nassarawa	328ab	2a	5abc	265bcd	113a	36ab
Niger	227abc	2a	1bc	250bcd	25b	69a
Oyo	178bc	0a	11a	139de	18b	10b
Rivers	98cd	2a	4abc	131de	22b	13b
control	4cd	0a	0c	11e	3b	12b

[z] Nematode numbers per 5 g tuber peel and root, and per 100 ml soil at harvest; N = 10; inoculum = 2000 *S. bradys* per plant/pot; values with the same letter in a column not significantly different according to Fisher's Protected LSD test, $P \leq 0.05$; Statistical analyses and mean separations for nematode densities undertaken on $\log_{10}(x+1)$ transformed data.

Table 4. Effect of *Scutellonema bradys* populations originating from different localities in Nigeria on mean tuber weight at harvest and tuber weight and dry rot three months.[y]

	2002			2003		
S. bradys populations	Harvest tuber weight (g)	Stored tuber weight (g)	Tuber dry rot	Harvest tuber weight (g)	Stored tuber weight (g)	Tuber dry rot[z]
Abuja	806a	580ba	0.8ba	191ba	112ba	1.8ba
Abuja FCT	796a	442b	1.1a	462a	297a	1.7ba
Borno	896a	720a	0.9ba	53b	31a	1.0d
Delta	935a	640ba	0.9ba	192ba	141ba	1.7ba
Kogi	1158a	810a	0.9ba	290ba	197ba	1.9a
Nassarawa	1077a	780a	0.8ba	446a	301a	1.4dcba
Niger	968a	700a	0.9ba	296ba	199ba	1.9a
Oyo	901a	590ba	0.8ba	130ba	82ba	1.6cba
Rivers	834a	510ba	1.1a	408a	281a	1.3dcb
control	898a	650ba	0.6b	424a	313a	1.1dc

[y]N = 10 and 5 tubers assessed per treatment, respectively, at harvest and during storage. inoculum = 2000 *S. bradys* per plant; values with the same letter in a column not significantly different according to Fisher's Protected LSD test, $P \leq 0.05$; Statistical analyses and mean separations for dry rot were undertaken on Arcsin(sqrt(x/100)) transformed data;
[z] Dry rot severity scored as for Table 2.

DISCUSSION

The current study provides the most extensive assessment yet of the variability of *S. bradys* pathogenicity across the yam growing belt of West Africa and within Nigeria. It complements the existing information on the biology of *S. bradys* (Bridge *et al*., 2005) and builds on the study by Baimey *et al.* (2009), who established that pathogenicity varied between three Benin populations. The current study indicates that while there may be differences in pathogenicity between populations, these differences appear to be relatively limited and vary with external factors, such as stressful conditions.

That stress is an important factor in yield loss due to *S. bradys* is indicated by the finding in the current study of significantly lower tuber sizes obtained for yam after inoculation with each of the populations of *S. bradys* in years in which tuber size was small (2002 in Ibadan and 2003 in Cotonou), presumably due to stressful conditions. For the experiments in Cotonou, high temperature is a likely candidate for the causal stress. This result suggests that *S. bradys* is more of a threat to yam production when the crop is challenged by additional stress, such as that experienced under marginal conditions in drought prone and poor soil fertility areas. In further support of the role of stress, using *S. bradys* infected yam planting material in Nigeria, Claudius-Cole *et al.* (2004) experienced much greater field losses for untreated infected compared to treated yams at sites where rainfall following planting was low, compared to sites where rainfall was more favourable.

Previous studies have considered the damage and the physiological effects of *S. bradys* on yam (Bridge *et al.*, 2005). Few however, have assessed crop loss damage directly, and only recently has a comprehensive assessment of distribution of this nematode in West Africa been undertaken (Coyne *et al.*, 2006). Previous studies indicated that the importance of *S. bradys* in the yam belt varied with the yam cultivar/species and agro-ecological zone (Baimey, 2005; Coyne *et al.*, 2006) as well as with the nematode population (Baimey *et al.*, 2009). While the current study supports these findings of variable damage potential between populations, it does not clearly identify specific populations as more aggressive. The study by Coyne *et al.* (2006), identified central Nigeria, around Abuja, as the area in West Africa where the greatest nematode densities occurred on tubers, indicating possibly more aggressive populations. Although not conclusive, the two Abuja populations in the current study caused relatively high damage and had high final densities. Recent molecular studies on *S. bradys* populations collected from throughout the region revealed a relatively high degree of polymorphism both within and between populations

Table 5. Effect of *Scutellonema bradys* populations from seven countries in West Africa on yam cultivar TDr131 on number and weight of tubers, stem girth and dry rot symptoms in pots over two growing seasons in Cotonou, Benin.[y]

S. bradys populations	Number of tubers		Weight of tubers (g)		Stem girth (cm)		Dry rot[z]
	2003	2004	2003	2004	2003	2004	2004
Benin1	1.0b	1.8a	13.7b	253.5ab	2.2b	2.8ab	1.0de
Benin 2	1.3b	1.6ab	9.0b	243.8abc	1.9b	3.0a	2.8abc
Burkina Faso1	1.0b	0.8b	10.8b	229.7abc	2.2b	2.8ab	1.0de
Burkina Faso 2	2.0a	1.4ab	9.1b	242.1abc	1.9b	3.0a	2.8abc
Côte d'Ivoire1	1.0b	1.2ab	14.0b	213.5abc	1.8b	2.5ab	1.8cde
Côte d'Ivoire 2	1.0b	1.0ab	12.0b	142.2c	1.8b	2.4ab	3.8ab
Ghana1	1.0b	1.2ab	18.4b	219.6abc	1.9b	2.5ab	3.8ab
Ghana 2	1.0b	1.4ab	17.7b	239.6abc	1.8b	2.6ab	0.4e
Mali1	1.0b	1.0ab	13.8b	216.6abc	1.9b	2.1ab	2.0cd
Mali2	1.0b	1.2ab	11.0b	158.9bc	2.0b	2.4ab	4.0a
Nigeria1	1.0b	0.8b	19.7b	266.7a	1.7b	2.7ab	1.3cde
Nigeria 2	1.0b	1.8a	15.7b	279.1a	2.1b	2.2ab	2.2cd
Togo1	2.0a	1.2ab	27.2b	177.7abc	2.0b	2.7ab	3.8ab
Togo 2	1.0b	1.2ab	23.5b	150.8bc	2.1b	2.0b	2.0cd
control	1.2b	1.6ab	157.8a	223.3abc	3.0a	2.3ab	1.0de

[y] N = 5; inoculum = 1000 *S. bradys* per plant/pot; values with the same letter in a column not significantly different according to Fisher's Protected LSD test, $P \leq 0.05$; Statistical analyses and mean separations for dry rot were undertaken on Arcsin(sqrt(x/100)) transformed data;
[z] Dry rot severity scored as for Table 2.

Table 6. Scutellonema bradys density on yam cultivar TDr131 of fourteen separate populations originating from seven different countries of West Africa in two pots over two growing seasons in Cotonou, Benin.[z]

S. bradys populations	2003			2004
	Tuber peel	Plant root	Soil	Tuber peel
Benin 1	680ab	21abcd	66a	396a
Benin 2	540a	15abcd	60a	187ab
Burkina Faso 1	933a	27ab	51ab	212ab
Burkina Faso 2	550abc	67abcd	32ab	148ab
Côte d'Ivoire 1	80f	12bcd	33ab	345ab
Côte d'Ivoire 2	115ef	9cd	13cde	89ab
Ghana 1	190cdef	16bcd	5cdef	448a
Ghana 2	190cdef	23abc	5cdef	104b
Mali 1	87ef	6d	40abc	187ab
Mali 2	153cdef	10bcd	1ef	144ab
Nigeria 1	433abcd	42a	15bcd	267ab
Nigeria 2	335abcde	19abcd	9cdef	378ab
Togo 1	160def	18abc	8cde	568a
Togo 2	127def	23abc	3def	284ab
control	0g	0e	0f	1c

[z] N = 5; inoculum = 1000 *S. bradys* per plant; values with the same letter in a column not significantly different according to Fisher's Protected LSD test, $P \leq 0.05$; Statistical analyses and mean separations undertaken on $\log_{10}(x+1)$ transformed data; nematode numbers per 5 g root and peel and 100 ml soil.

(Coyne *et al*., 2005). This molecular polymorphism is not necessarily indicative of pathogenic variability, but indicates genetic diversity within as well as between populations, possibly including differences in pathogenicity.

In the current study, the multiplication of pairs of *S. bradys* populations originating from different locations in the same country were significantly different only for some populations. However, differences in *S. bradys* final tuber population densities were not necessarily associated with corresponding differences in crop growth parameters and tuber yield. Similarly, when using a higher inoculum (density up to 5000 *S. bradys* per plant) in pot and field experiments, as compared with 1000 and 2000 in the current study, Baimey *et al.* (2009) found no effect on yield. This may indicate that the inoculum density that we used was insufficient to affect yam productivity.

Although some studies highlight the importance of *S. bradys* in yield reduction at harvest (e.g. Wood *et al.*, 1980), others mainly highlight the damage it incurs during storage (Adesiyan *et al.*, 1975; Bridge *et al.*, 2005). Our study indicates that under favourable conditions, its greater impact is through the deterioration of stored material, and the subsequent loss and fitness of material for planting is in agreement with the findings of Claudius-Cole *et al.* (2004). Evaluating inoculated plants at harvest may identify differences in aggressiveness of populations, but may not reliably assess the economic impact of *S. bradys.* In some of our experiments nematodes were recovered from control tubers, probably because the hot water treatment was not totally effective in eliminating nematodes, or in the case of the field study, through cross-contamination from neighbouring infected plots. Even though nematodes recovered were relatively few, their presence reduced our ability to assess the effects of inoculated populations.

During storage healthy yam tubers will gradually lose moisture (and weight) over time, while *S. bradys*-infected tubers will deteriorate to a greater degree due to increased dry rot disease (Bridge, 1973; Adesiyan *et al.*, 1975). Dry rot disease leads to a general decay of the tubers, especially when associated with fungal and bacterial pathogens (Adeniji, 1970; Ogundana *et al.*, 1970, Ekundayo and Navqi, 1972). However, while nematode presence was associated with increased dry rot symptoms in our study, symptoms were also apparent in control pots with few or no nematodes present. Although dry rot symptoms are strongly correlated with *S. bradys* tuber density (Kwoseh, 2000), occurrence in the absence of *S. bradys* has previously been reported (Coyne *et al.*, 2006; Baimey et al., 2009), and, conversely, *S. bradys* may be present without apparent symptoms (Bridge *et al.*, 2005). Dry rot symptoms are, therefore, an unreliable indicator for the presence or damage of *S. bradys*, even though we observed lowest yields in association with greatest dry rot in Cotonou.

Given the inconsistent relationship between dry rot and the presence of *S. bradys* in tubers, the development of a sensitive molecular method for the detection of *S. bradys* may prove useful. However, we conclude from this study, that although there are molecular polymorphisms among and between *S. bradys* populations (Coyne *et al.*, 2007; Humphriys, 2010), these are not so far associated with pathogenic variability, at least on yam and for the conditions of our assays. The recent finding that *S. bradys* can also cause serious damage to potato (Coyne and Claudius-Cole, 2009; Coyne *et al.*, 2011) raises greater concern regarding this nematode, and should further support the need for development of a molecular detection tool. The identification of molecular variation that correlates with plant host suitability would be particularly valuable.

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