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Resistance to *Ditylenchus africanus* present in peanut breeding lines

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Abstract: Peanut is an important cash crop both for commercial and small-scale farmers in South Africa. The effect of *Ditylenchus africanus* on peanut is mainly qualitative, leading to downgrading of consignments. This nematode is difficult to control because of its high reproductive and damage potential. The objective of this study was to identify peanut genotypes with resistance to *D. africanus* that would also be sustainable under field conditions. Selected peanut genotypes were evaluated against *D. africanus* in microplot and field trials. The inbred lines PC254K1 and CG7 were confirmed to be resistant to *D. africanus*. The resistance expressed by these two genotypes was sustainable under field conditions. The breeding line PC287K5 maintained low nematode numbers in some trials, but its level of resistance was not as strong or as sustainable as that of PC254K1 or CG7. However, PC287K5 could still play an important role in the peanut industry where lower *D. africanus* populations occur.

Key words: Arachis hypogaea, *Ditylenchus africanus*, management, peanut, peanut pod nematode, resistance.

Peanut (*Arachis hypogaea* L.) is an important cash crop for both commercial and small-scale farmers in South Africa (Mc Donald et al., 2005). Many plant-parasitic nematode species have been associated with peanut in this country (Venter et al., 1992) but were disregarded as serious pests. *Ditylenchus africanus* Wendt, Swart, Vrain and Webster (1995) was first identified as *Ditylenchus destructor* (Jones and De Waele, 1988; De Waele et al., 1989). *D. africanus* is considered one of the economically most important plant parasites in peanut production (Jones and De Waele, 1988; Venter et al., 1991; Swanevelder, 1997; Mc Donald et al., 2005). *D. africanus* is omnipresent in peanut producing areas in South Africa (De Waele et al., 1989; Mc Donald et al., 2005) and it may occur in other southern African countries as well (De Waele and Elsen, 2007). For example, symptomatic peanuts have been reported from Mozambique, Malawi and the Democratic Republic of Congo (De Waele et al., 1997).

Penetration of *D. africanus* near the basis of the pod (De Waele et al., 1989; Jones and De Waele, 1990) weakens the peg and pod connection so that pods break off during lifting of the crop and remain behind in the soil (Jones and De Waele, 1990), causing losses of 40% to 60% of pods (Jones and De Waele, 1988). The main effect of *D. africanus* on peanut is qualitative (Jones and De Waele, 1988 and 1990; De Waele et al., 1989; Mc Donald et al., 2005). The breakdown of the hull by *D. africanus* with increased water penetration leads to split pods and may result in the occurrence of second-generation seedlings (Venter et al., 1995; De Waele et al., 1997). Feeding of the nematodes near or in the vascular bundles of the seed testa can lead to unattractive appearance of infected seed, and in severe cases can lead to leaching of chemical compounds that function as inhibitors of seed germination (Svamv and Narasimhareddy, 1977; Jones and De Waele, 1990; Venter et al., 1995), that in turn leads to the initiation of growth of the hypocotyls (De Waele et al., 1997). These symptoms of *D. africanus* infections affect high percentages of unsound, blemished and soiled (UBS %) kernels (Venter et al., 1991; Van der Merwe and Joubert, 1992; Mc Donald et al., 2005) that are highly correlated with the number of nematodes found in the testa of the peanut seed (Venter et al., 1991; Mc Donald et al., 2005).

Kernels of peanut consignments in South Africa are by law classified into (i) choice edible, (ii) standard edible, (iii) diverse, or (iv) crushing grade. The economic importance of *D. africanus* depends on current market prices for the grading classes (Venter et al., 1991; Van der Merwe and Joubert, 1992; Mc Donald et al., 2005). For sustainable, economically feasible production highly effective control measures are needed to manage *D. africanus* (Mc Donald et al., 2005). *D. africanus* is difficult to control because of its ability to survive in the absence of peanut (Basson et al., 1990; De Waele et al., 1990 and 1991; Swart and Jones, 1994), its high reproductive potential and its short life cycle (De Waele and Wilken, 1990).

Chemical, cultural and biological management tools currently implemented as well as current crop rotation systems are not adequate to keep *D. africanus* numbers below damage-threshold levels (Basson et al., 1990 and 1993; Mc Donald et al., 2005). Cultivation of resistant crops or cultivars often provides an effective alternative for the management of various plant-parasitic nematodes (Timper et al., 2003; Dickson and De Waele, 2005). This principle should be applicable to the management of *D. africanus* on peanut (De Waele et al., 1990). Previously more than 600 genotypes had been evaluated for resistance to this nematode without the identification of useful resistance (Basson et al., 1991; Van der Merwe and Joubert, 1992), and no resistant cultivars are currently on the market. The objectives of this study were (i) to identify *D. africanus* resistance in selected peanut genotypes in microplot trials over two consecutive growing seasons and (ii) to verify the sustainability of the resistant host plant responses of the peanut genotypes identified in the microplot trials under field conditions.

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Materials and Methods

Peanut genotypes evaluated possessed characteristics preferred by the local peanut-breeding program, which included suspected resistance to *D. africanus*, high oleic-acid contents or resistance to various diseases (Table 1; Cilliers et al., 2001). In all trials the commercial cv. Sellie served as *D. africanus*-susceptible standard (Mc Donald, 1998) and commercial cv. Kwarts, classified as tolerant to *D. africanus* (Mc Donald, 1998), as the other standard because no source of resistance to *D. africanus* was available. Prior to planting, five 5-g sub-samples of the seed of each genotype were soaked in water for 24 h (Bolton et al., 1990) to ascertain that the seed was *D. africanus*-free. The rest of the seed was treated with the fungicide Tiram (dithiocarbamate) at 120 g per 500 kg seed (Thiolin®, Almond Agro Chemicals (Edms) Bpk, Van Riebeeck Park, South Africa) and inoculated with *Bradyrhizobium arachis* nitrogen-fixing bacteria at 250 g per 50 kg seed (Soygro (Edms) Bpk, Potchefstroom, South Africa).

The genotypes were evaluated over two consecutive seasons (2003-2004 and 2004-2005) in microplots at the Agricultural Research Council – Grain Crops Institute (ARC-GCI) near Potchefstroom; 26.74° S, 27.08° E. Twenty clay-brick enclosures of 1.1 x 2.1 x 0.5 m were filled with EDB-fumigated (at an equivalent of 50 l/ha three weeks before planting), sandy-loam, Hutton soil (93.6% sand; 3.9% clay; 1.9% silt and 0.6% organic material, pH (H_2O) 6.28). Nutrients were added to the soil according to a soil analysis and nutrient guidelines for this crop (Swanevelder, 1997). Treatments were planted in a randomized complete split-plot design with five replicates, which were re-randomized during the second season. The main factor included plots that were not inoculated and plots inoculated at planting with 3,000 + *D. africanus* per plant. Nematodes used for inoculation were obtained from *in vitro* peanut callus tissue cultures of a population of *D. africanus* from Vaalharts (Van der Walt and De Waele, 1989). The sub-factor was genotype (eight test lines and the two standard cv.'s) evaluated during each season. Four rows of 20 seeds of each peanut genotype were planted in each trough at an inter-row spacing of 45 cm, an intra-row spacing of 5 cm and a depth of 5 cm. Irrigation of the trials was adapted according to rainfall.

Table 1. Origin and preferred characteristics of peanut genotypes evaluated for resistance to *Ditylenchus africanus* over two consecutive growing seasons in microplot and field trials.

Genotype	Origin	Most important characteristics
Kwarts	Local	tolerant standard
Sellie	Local	susceptible standard
PC254K1	Local	high oleic-acid content and suspected resistance to *D. africanus*
PC287K5	Local	suspected resistance to *D. africanus*
CG7	Malawi	resistant to a variety of diseases
Harts	Local	resistant to black pod rot
JL24	Democratic Republic of Congo	resistant to tomato spotted wilt virus
PC223	Local	high oleic-acid content
PC299K5	Local	high oleic-acid content
UF85	USA	high oleic acid content
73-30	Senegal	high oleic-acid content
453	Senegal	high oleic-acid content

Sustainability of resistance of genotypes was tested in two separate field sites naturally infested with plant-parasitic nematodes. Field trials were conducted during 2004-2005 at Jan Kempdorp; 27.95° S, 24.85° E and Hartswater; 27.83° S, 24.79° E where peanut is grown commercially under irrigation. The soil type at Hartswater and Jan Kempdorp was a sandy-loam Hutton, consisting of 7.3% clay; 85.6% sand; 6.22% silt, 0.82% organic material, pH (H_2O) 7.18) at Hartswater and of 8.7% clay; 82.8% sand, 7.8% silt, 0.69% organic material, pH (H_2O) 6.25) at Jan Kempdorp. Preparation of the trial sites was done according to commercial practices, rates of nutrients were applied based on soil analyses, and herbicides were applied when required. No nematicide or fumigant was applied because of the risk of contamination of adjacent plots by chemical treatments, particularly under irrigation, which could have interfered with results (Hough and Thomason, 1975). In each of the trials the eight treatments were arranged in a randomized complete block design with six replicates. Each replicate consisted of eight 1-m rows planted at an inter-row spacing of 45 cm, an intra-row spacing of 5 cm, and 5 cm deep. Each row was planted to 20 seeds of each respective genotype. The fields were irrigated once a week with 30 mm water from the Vaal River.

At harvest, four randomly selected plants from each row of the microplots and from all plots in the field trials were collected for nematode extraction. Separate extractions were made from peg, hull or kernel samples from the microplot trials, and from soil, root, peg, hull and kernel samples from the field trials. Soil and root samples were included in the field trial evaluations since assessments were made of all extracted plant-parasitic nematodes that occurred along with *D. africanus*. Nematodes were extracted from soil using the decanting and sieving method combined with sugar centrifugal flotation (Jenkins 1964) and from roots and pegs with the method described by De Waele et al. (1987). Hull and kernel tissue was extracted separately according to the procedures described by Bolton et al. (1990); counts with a research microscope of *D. africanus* per 5 g pegs, 5 g kernels and 5 g hulls were added and expressed as final population (Pf) of *D. africanus* per 15 g pods.

Plants from the microplot and field trials not used for nematode assessments were collected for quality assessments. For each replicate, a sub-sample of 500 g pods per replicate was shelled to determine yield quality by grading the kernels according to the Act on Agricultural Product Standards, 119 of 1990 (South Africa, 1997). Genotypes in the non-inoculated section of the microplot trials

served as nematode-free controls to distinguish between resistant and tolerant plant responses.

Statistical analysis: Nematode data were log-transformed ($\log_{10}$ (x+1)) before analysis of variance (ANOVA) with Stat Graphics Plus 5 for Windows (Statistical Graphics Corporation, Impresol, Garsfontein-East, Pretoria, South Africa). Means were separated by the LSD test ($P = 0.05$).

The percentage reproduction rate (RR) of *D. africanus* populations was determined on pods from each peanut genotype from the microplot and field trials. This allowed estimation of the reproduction percentage relative to the susceptible standard Sellie (RR = Pf (genotype)/Pf (Sellie) x 100) (Timper et al., 2003).

Yield quality was determined according to standard grading procedures and was calculated using Maksi Plan (ARC-GCI, Potchefstroom, South Africa), a computer program specifically developed for the evaluation of crop cultivars and breeding material.

Results

Microplot trials: Although the nematode numbers in pods of Kwarts, Sellie, PC254K1 and PC287K5 varied during both seasons, PC254K1 and PC287K5 sustained significantly lower Pf values compared to most of the genotypes (Table 2). CG7 tested during 2004-2005 maintained significantly lower Pf values in its pods compared to the rest of the genotypes, including PC254K1 and PC287K5. PC299K5 evaluated during the same season also had a significantly lower Pf than those of the susceptible standard Sellie but did not differ significantly from that of the tolerant standard, Kwarts (Table 2).

In spite of the low nematode numbers present during 2003-2004, the RR of PC254K1 was 1.9% and PC287K5 13.8% that of Sellie (Table 2). RR of Kwarts was 22.7% of Sellie, while the RR of line 453 and PC233 were 31.5% and 49.6%, respectively, of Sellie during the same season. The RR's of *D. africanus* for CG7, PC254K1 and PC287K5 during 2004-2005 were 1%, 3.7% and 7.5%, respectively, of Sellie (Table 2). The RR of tolerant Kwarts was more than half (53.1%) of Sellie under the much higher Pf during the same season.

Table 2. *Ditylenchus africanus* numbers (Pf) and reproduction rates (RR) in pods of eight peanut genotypes in consecutive microplot trials during 2003-2004 and during 2004-2005.

	2003-2004		2004-2005	
Genotype	Pf (15 g pods)	RR[a]	Pf (15 g pods)	RR
Sellie[b]	2,693 a[d]	100	28,116 a	100
Kwarts[c]	610 b	22.7	14,919 ab	53.1
PC254K1	50 c	1.9	1,046 c	3.7
PC287K5	372 c	13.8	2,095 c	7.5
CG7	-[e]	-	273 d	1.0
Harts	-	-	25,649 a	91.2
JL24	-	-	15,191 ab	54.0
PC233	1,335 ab	49.6	-	-
PC299K5	-	-	7,843 b	27.9
UF85	2,700 ab	100.3	-	-
73-30	1,742 ab	64.7	-	-
453	848 ab	31.5	-	-
P-value	0.0000	-	0.0000	-
F-ratio	10.0200	-	40.6900	-

[a]RR = Pf (genotype)/Pf (Sellie) x 100.
[b]*D. africanus*-susceptible standard.
[c]*D. africanus*-tolerant standard.
[d]Numbers in the same column followed by the same letter do not differ significantly at $P = 0.05$.
[e]Not grown during specific season.

The difference in yield quality in the inoculated and corresponding non-inoculated sections of the microplot trials varied between genotypes and over seasons (Figs. 1 and 2). The UBS% of most genotypes in the inoculated section was generally higher than those in the corresponding uninoculated section during both seasons. During 2003-2004 PC254K1, PC287K5 and Kwarts (tolerant) had UBS% lower than 10 and were comparable between the inoculated and uninoculated sections in this regard (Fig. 1). Greater reduction in UBS% from nematode inoculated to non-inoculated were only apparent in PC223, Sellie, UF85 and 73-70. The grades from choice to crushing corresponded with the trend in UBS% (Fig. 1). Choice grade kernels were obtained from the inoculated and the non-inoculated plots of PC254K1, PC287K5 and Kwarts. The lines 453 and 73-70 produced standard grade kernels in the inoculated and uninoculated plots, while PC233, Sellie and UF85 only yielded standard grade kernels in the uninoculated plots. Only diverse and crushing grade were obtained from the inoculated plots of the rest of the genotypes. During 2004-2005 the UBS% of inoculated Harts, Sellie, PC254K1 and JL24 were substantially higher than those of their respective non-inoculated counterparts (Fig. 2). The UBS% of all the other genotypes did not differ much between the inoculated and uninoculated pairs, although both sections of CG7 were higher than 10%. Only Kwarts and PC287K5 had UBS lower than 10% in this trial. Also in this trial the grading from choice to crushing corresponded with the respective UBS% (Fig. 2). Choice grade kernels were obtained from the inoculated and the uninoculated sections of PC287K5 as well as from non-inoculated Kwarts. Standard grade was obtained only from Kwarts in the inoculated plots and from JL24 and Sellie from the non-inoculated plots. The rest of the genotypes produced only diverse and crushing grade in the inoculated and the uninoculated sections of the microplot trial.

Field trials: Nematode populations in the soil from Hartswater and Jan Kempdorp consisted of non-parasitic species and mainly the plant-parasitic spp. *Meloidogyne* and *Helicotylenchus*. At both localities, the peanut genotypes did not differ significantly from each other in terms of the numbers of either *Meloidogyne* spp. or *Helicotylenchus* spp. per 200 cm^3 soil (data not shown). *Meloidogyne* spp. numbers were low in the roots of the genotypes at both sites. The genotypes did not differ significantly from each other in terms of root-knot nematode numbers per 50 g roots (data not shown). *D. africanus* was present in the roots of the peanut genotypes at the Hartswater trial but

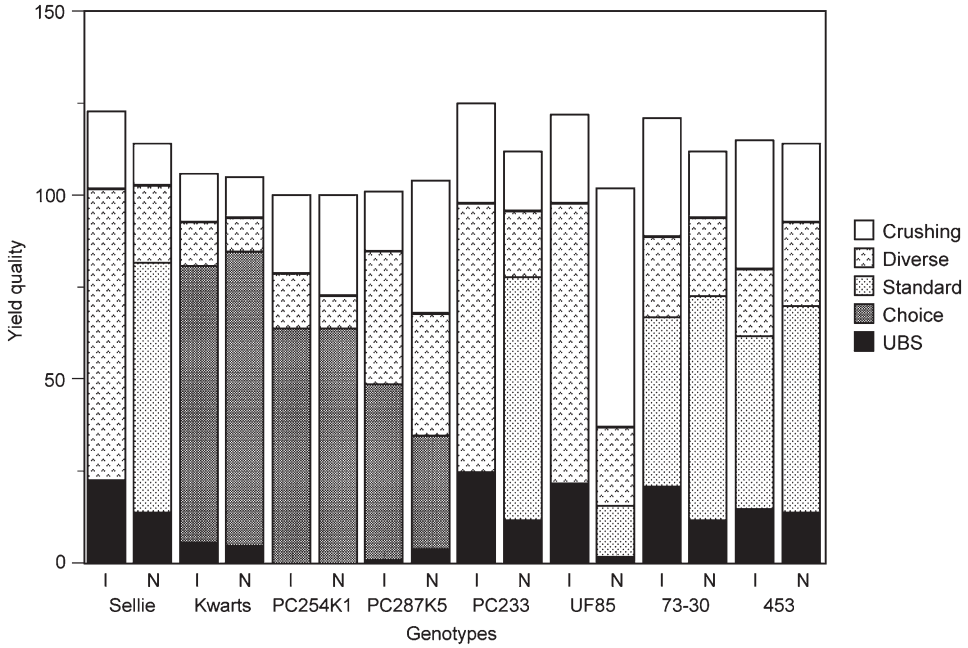

FIG. 1. Yield quality of eight inoculated (I) and uninoculated (N) peanut genotypes in a microplot trial during 2003-2004.

not in roots of the genotypes from the Jan Kempdorp trial. *D. africanus* numbers in the roots of CG7 and PC254K1 at Hartswater did not differ significantly from those in the roots of Sellie and JL24 but were significantly lower than those in roots of the other genotypes (data not shown).

Significantly lower *D. africanus* numbers were extracted from CG7 and PC254K1 pods than from those of the rest of the genotypes evaluated at both Hartswater and Jan Kempdorp (Table 3). At Jan Kempdorp, *D. africanus* numbers in PC287K5 pods were significantly higher than those in CG7 and PC254K1 but were significantly lower than those in pods of the rest of the genotypes (Table 3). The RR of CG7 was 0% of that of Sellie at both Hartswater and Jan Kempdorp (Table 3). RR of PC254K1 was 0% of that of Sellie at Jan Kempdorp and 10.8% at Hartswater. For PC287K5 the RR was 75.3% of that of Sellie at Hartswater and 36.6% at Jan Kempdorp.

At Hartswater, the UBS% of Harts was 39% and that of Sellie was 12% (Fig. 3). The yields of these latter two

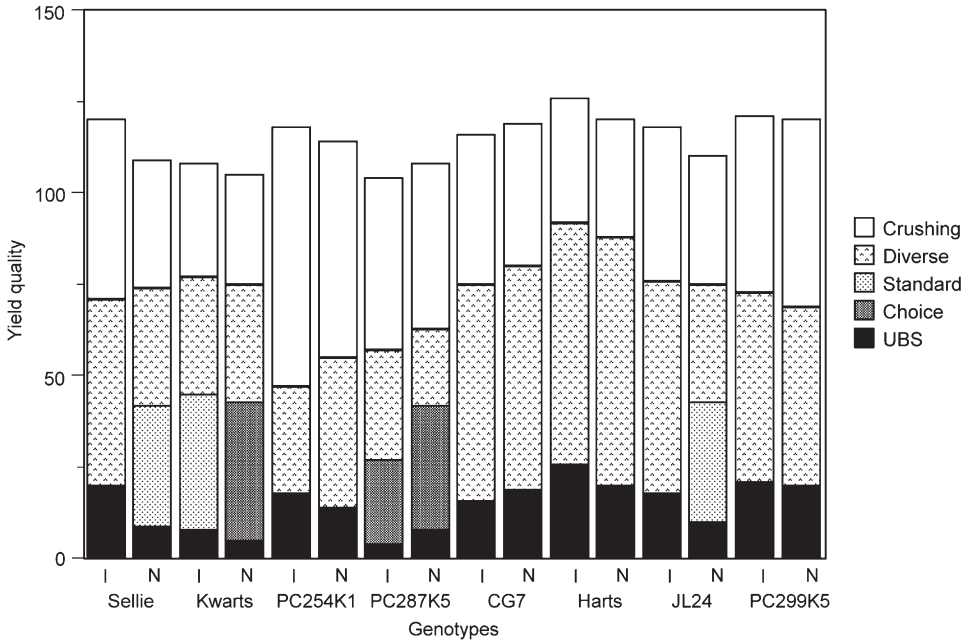

FIG. 2. Yield quality of eight inoculated (I) and uninoculated (N) peanut genotypes in a microplot trial during 2004-2005.

TABLE 3. *Ditylenchus africanus* numbers (Pf) and reproduction rates (RR) in pods of eight peanut genotypes from field trials planted at Hartswater and Jan Kempdorp during 2004-2005.

	Pf (15 g pods)		RR[a]	
Genotype	Hartswater	Jan Kempdorp	Hartswater	Jan Kempdorp
Sellie[b]	1,042 a[d]	142 a	100	100
Kwarts[c]	851 a	150 a	81.6	105.6
PC254K1	112 b	0 c	10.8	0
PC287K5	785 a	52 b	75.3	36.6
CG7	3 c	0 c	0	0
Harts	371 a	180 a	35.6	126.8
JL24	328 a	105 a	31.5	73.9
PC299K5	805 a	148 a	77.3	104.2
P-value	0.0000	0.0000	-	-
F-ratio	15.38	44.06	-	-

[a] RR = Pf (genotype)/Pf (Sellie) x 100.
[b] *D. africanus*-susceptible standard.
[c] *D. africanus*-tolerant standard.
[d] Numbers in the same column followed by the same letter do not differ significantly.

genotypes were downgraded to diverse and crushing grade. For the rest of the genotypes, the UBS% was lower than 10%. CG7 (4%), PC287K5 (3%) and PC254K1 (4%) had the lowest UBS% and they also produced choice grade kernels. The rest of the genotypes, including the tolerant Kwarts produced standard, diverse or crushing grade. At Jan Kempdorp (Fig. 3) the UBS% of Harts was 23% and it was downgraded to diverse and crushing grade. The UBS% of the rest of the genotypes was all below 10% and all produced choice grade kernels.

DISCUSSION

This is the first report of peanut genotypes that express high-level, sustainable resistance to *D. africanus* under microplot as well as field conditions. PC254K1 could play an important role in peanut-breeding programs because of its evidently high level of resistance, even at high nematode infestation levels. Although this line may lack many desirable traits required for an agronomically acceptable cultivar, e.g., high yield potential, desired kernel size, color and form it should be acceptable for introgressing resistance into preferred breeding material. Although only tested in one part of this study, there are strong indications that CG7 may also have superior resistance to *D. africanus*. As it is a parental line of PC254K1 it warrants further investigation should a comprehensive program on the introgression of nematode resistance in peanut be initiated. A high-yielding cultivar developed from these lines should be able to produce better kernel quality, which may increase the net income per ha of peanut crops (Mc Donald et al., 2005).

Contrary to the high Pf of *D. africanus* in the susceptible standard Sellie and most of the other genotypes tested during this study, PC254K1 and CG7 pods consistently maintained significantly lower Pf values at harvest under microplot as well as field conditions. This is fair proof of their resistance (Bos and Parlevliet, 1995) to *D. africanus*. Low Pf in PC287K5 in the microplots also indicated resistance but the high Pf value in the field showed that the resistance in this line may be lower or less sustainable under field conditions. This was substantiated by the corresponding RR values that remained below 10% (Abdel-Momen et al., 1998; Hussey and Janssen, 2002; Timper et al., 2003) for these two lines under microplot as well as field conditions. The field trials provided solid confirmation of the resistance or susceptibility levels of the genotypes tested (De Waele et al., 1989; Venter et al., 1992; Mc Donald, 1998). Although the presence of multiple

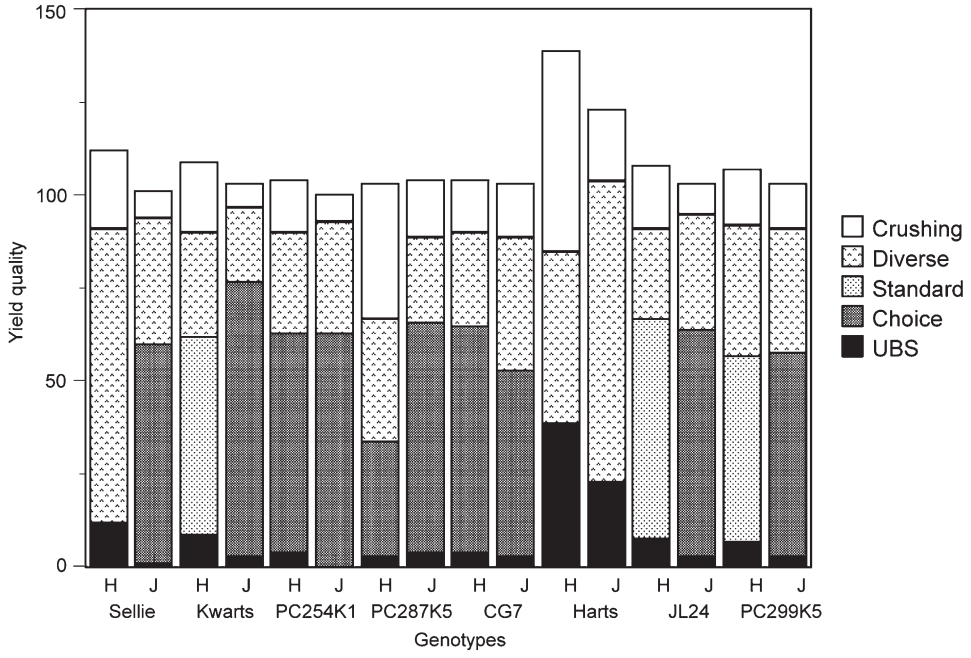

FIG. 3. Yield quality of eight peanut genotypes in field trials planted at Hartswater (H) and Jan Kempdorp (J) during 2004-2005.

plant-parasitic nematode species in a field may affect the expression of resistance (Barker and Olthof, 1976; Eisenback, 1985) this did not seem to be applicable to *D. africanus* resistance in PC254K1 and CG7.

The higher UBS% of most genotypes in the inoculated sections of the microplot trials in relation to the non-inoculated sections agreed with several other studies in that the main effect of *D. africanus* on peanut yield was qualitative (Jones and De Waele, 1988 and 1990; De Waele et al., 1989; Venter et al., 1991; Venter et al., 1993; Mc Donald et al., 2005). Although environmental conditions can also play a role in kernel quality (Knauft & Wynne, 1995) the symptoms expressed as a result of these conditions often play a lesser role than those caused by the presence of aggressive nematodes (Mc Donald et al., 2005). This may also be applicable to *D. africanus* because UBS% of yields obtained from inoculated sections were generally higher compared to the non-inoculated counterparts of most genotypes. The generally lower UBS% of PC254K1 and CG7 yields compared to those of the other genotypes supported trends in Pf and RR, and confirmed the resistance, particularly of these two lines to *D. africanus* under microplot as well as field conditions.

Although PC287K5 also maintained low nematode numbers in some trials, its level of resistance did not seem to be as high as that of PC254K1 and CG7. However, it still performed well compared to the tolerant cultivar Kwarts, which might indicate that this line could also be tolerant. Therefore, it may still play an important role, particularly under less nematode population pressure.

This study produced useful new information because no useful resistant peanut sources had been identified since the discovery of *D. africanus* during 1987. PC254K1 and possibly CG7 were the first peanut genotypes identified with sustainable resistance to *D. africanus* under microplot as well as field conditions. In the presence of this nematode, these two genotypes consistently maintained low nematode numbers and produced yields with low UBS%. The strong characteristic of PC254K1 and CG7 in terms of *D. africanus* population suppression is of particular significance. This nematode is able to build up to damaging levels during a single growing season, even from a relatively small Pi. Both genotypes could, therefore, be used as a major source of resistance to *D. africanus* in a peanut-breeding programme for developing resistant cultivars.

Literature Cited

Abdel-Momen, S. M., Simpson, C. E., and Starr, J. L. 1998. Resistance of interspecific *Arachis* breeding lines to *Meloidogyne javanica* and an undescribed *Meloidogyne* species. Journal of Nematology 30:341–346.

Barker, K. R., and Olthof, T. H. A. 1976. Relationships between nematode population densities and crop response. Annual Review of Phytopathology 14:327–353.

Basson, S., De Waele, D., and Meyer, A. J. 1990. An evaluation of crop plants as hosts for *Ditylenchus destructor* isolated from peanut. Nematropica 20:23–29.

Basson, S., De Waele, D., and Meyer, A. J. 1991. Population dynamics of *Ditylenchus destructor* on peanut. Journal of Nematology 23: 485–490.

Basson, S., De Waele, D., and Meyer, A. J. 1993. Survival of *Ditylenchus destructor* in soil, hulls and seeds of groundnuts. Fundamental and applied Nematology 16:79–85.

Bolton, C., De Waele, D., and Basson, S. 1990. Comparison of two methods for extracting *Ditylenchus destructor* from hulls and seeds of groundnut. Revue de Nématologie 13:233–235.

Bos, L., and Parlevliet, J. E. 1995. Concepts and terminology on plant/pest relationships: Toward consensus in plant pathology and crop protection. Annual Review of Phytopathology 33:69–102.

Cilliers, A. J., Swanevelder, C. J., Joubert, H. L. N., and Barkel, R. G. 2001. Catalogue of groundnut germplasm available at the ARC-Grain Crops Institute Potchefstroom. Fourth revised edition. Potchefstroom, South Africa: Agricultural Research Council.

De Waele, D., and Elsen, A. 2007. Challenges in tropical plant nematology. Annual Review of Phytopathology 45:457–485.

De Waele, D., and Wilken, R. 1990. Effect of temperature on the in vitro reproduction of *Ditylenchus destructor* isolated from groundnut. Revue de Nématologie 13:171–174.

De Waele, E., De Waele, D., and Wilken, R. 1987. Effect of root mass on the efficacy of methods for extracting root-lesion nematodes from maize roots. Phytophylactica 19:473–474.

De Waele, D., Jordaan, E. M., and Basson, S. 1990. Host status of seven weed species and their effects on *Ditylenchus destructor* infestation of peanut. Journal of Nematology 22:292–293.

De Waele, D., Venter, C., and Mc Donald, A. H. 1997. The peanut pod nematode *Ditylenchus africanus*. Nematology Circular No. 218. March/April. Potchefstroom, South Africa, Agricultural Research Council.

De Waele, D., Wilken, R., and Lindeque, J. 1991. Response of potato cultivars to *Ditylenchus destructor* isolated from groundnut. Revue de Nématologie 14:123–126.

De Waele, D., Jones, B. L., Bolton, C., and Van den Berg, E. 1989. *Ditylenchus destructor* in hulls and seeds of peanut. Journal of Nematology 21:10–15.

Dickson, D. W., and De Waele, D. 2005. Nematode Parasites of Peanut. Pp. 393–436 *in* M. Luc, R. A. Sikora, and J. Bridge, eds. Plant parasitic nematodes in subtropical and tropical agriculture. Second edition. Oxfordshire: CABI Publishing.

Eisenback, J. D. 1985. Interactions among concomitant populations of nematodes. Pp. 193–213 *in* J. N. Sasser and W. W. Carter, eds. An advanced treatise on Meloidogyne vol. 1. Biology and control. Raleigh: North Carolina State University Graphics.

Hussey, R. S., and Janssen, G. J. W. 2002. Root-knot nematodes: *Meloidogyne* species. Pp. 43–70 *in* J. L. Starr, R. Cook, and J. Bridge, eds. Plant resistance to parasitic nematodes. Egham: CABI Publishing.

Hough, A., and Thomason, I. J. 1975. Effects of aldicarb on the behaviour of *Heterodera schachtii* and *Meloidogyne javanica*. Journal of Nematology 7:221–229.

Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Disease 48:692.

Jones, B. L., and De Waele, D. 1988. First report of *Ditylencus destructor* in pods and seeds of peanut. Plant Disease 72:453.

Jones, B. L., and De Waele, D. 1990. Histopathology of *Ditylencus destructor* on peanut. Journal of Nematology 22:268–272.

Knauft, D. A., and Wynne, J. C. 1995. Peanut breeding and genetics. Advances in Agronomy 35:393–445.

Mc Donald, A. H. 1998. Management of *Ditylenchus africanus* (Nematoda: Tylenchidae) on groundnut (*Arachis hypogaea*). PhD Thesis, Potchefstroom University for Christian Higher Education, Potchefstroom, South Africa.

Mc Donald, A. H., Loots, G. C., Fourie, H., and De Waele, D. 2005. A microplot study on *Ditylenchus africanus* population densities and damage symptoms on groundnut in relation to commercial yields. Nematology 7:647–653.

South Africa. Department of Agriculture and Water Supply. 1997. Ontwikkelingsprogram vir grondbone. Olie- en Proteïensadesentrum, Navorsingsinstituut vir Graangewasse, Potchefstroom.

Svamv, P. M., and Narasimhareddy, S. 1977. Changes in the leakage of electrolytes from groundnut seeds (*Arachis hypogaea*) during afterripening. Seed Science and Technology 5:654–648.

Swanevelder, C. J. 1997. Grondbone – Altyd 'n wenner. Tegniese publikasie. Landbounavorsingsraad-Instituut vir Graangewasse, Potchefstroom. Potchefstroom, South Africa, Agricultural Research Council.

Swart, A., and Jones, B. L. 1994. Interaction between *Ditylenchus destructor* and the nematophagous fungus *Arthrobotrys dolioformis*. Pp 126 *in* Proc 32th Annual Congress of the South African Society of Plant Pathology, 23-26 January 1994, Christiana, Republic of South Africa.

Timper, P., Holbrook, C. C., and Anderson, W. F. 2003. Reproduction of *Meloidogyne* spp. on resistant peanut genotypes from three breeding programmes. Journal of Nematology 35:417–421.

Van Der Merwe, P. J. A., and Joubert, H. L. N. 1992. Tolerance of groundnut cultivars to the potato-rot nematode (*Ditylenchus destructor*). Pp 86–88 *in* Proc 10th South African Maize Breeding Symposium 1992. Technical communication 238, Department of Agriculture, Republic of South Africa.

Van der Walt, P. C. W., and De Waele, D. 1989. Mass culture of the potato rot nematode *Ditylenchus destructor* on grundnut callus tissue. Phytophylactica 21:79–80.

Venter, C., De Waele, D., and Meyer, A. J. 1991. Reproductive and damage potential of *Ditylenchus destructor* on peanut. Journal of Nematology 23:12–19.

Venter, C., De Waele, D., and Meyer, A. J. 1993. Reproductive and damage potential of *Ditylenchus destructor* on six peanut cultivars. Journal of Nematology 25:59–62.

Venter, C., De Waele, D., and Van Eeden, C. F. 1992. Plant-parasitic nematodes on field crops in South Africa. 4. Groundnut. Fundamental and Applied Nematology 15:7–14.

Venter, C., Van Aswegen, G., Meyer, A. J., and De Waele, D. 1995. Histological studies of *Ditylenchus africanus* within peanut pods. Journal of Nematology 27:284–291.