Root-knot Nematode Resistance in Sweetpotato and Development of Sweetpotato Differential Host Genotypes for *Meloidogyne* spp.

By

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Abstract

Cervantes-Flores, Jim Carlos. Root-Knot Nematode Resistance in Sweetpotato and Development of Sweetpotato Differential Host Genotypes for *Meloidogyne* spp. (Under the direction of G. Craig Yencho and Eric L. Davis).

Root-knot nematodes represent a significant problem in sweetpotato, *Ipomoea batatas* (L.) Lam., causing reduction in yield and quality of the storage roots. The following experiments were conducted to: (1) test the use of an alternative screening method for root-knot nematode resistance; (2) assess the effect of different root-knot nematode spp. on sweetpotato cultivars; and (3) develop a set of sweetpotato differential host genotypes for *Meloidogyne* species. In the first study, five sweetpotato cultivars were selected and evaluated for resistance to *Meloidogyne incognita* race 3, *M. arenaria* race 2, and *M. javanica*. Screening was conducted in 400-cm^3 square pots and 150-cm^3 Conetainers™. Nematode infection was measured as the percentage of root system galled, percentage of root system necrosis, and the number of nematode eggs per gram of root tissue. Means of dependent variables were not significantly different between the two container types. Conetainers™ were the more efficient pot type, because they required less space and permitted an easier assessment of nematode infection. Resistance responses differed depending on the nematode species and sweetpotato cultivar. All cultivars were resistant to *M. arenaria* race 2, while 'Hernandez', 'Excel' and 'Jewel' were also resistant to *M. incognita* race 3 and *M. javanica*. In the second study, twenty-seven sweetpotato genotypes were evaluated for their resistance to North Carolina root-knot nematode populations: *M. arenaria* (races 1 and 2), *M. incognita* (races 1, 2, 3, and 4), and *M. javanica*. Sweetpotato plants were evaluated in 150-cm^3

Conetainers™. Nematode infection was assessed as the number of egg masses per root system. Different sweetpotato genotypes were hosts for different *Meloidogyne* populations. Five out of the 27 genotypes ('Beauregard', L86-33, PDM P6, 'Porto Rico', and 'Pelican Processor') were selected as sweetpotato differential hosts because of their resistance reaction to the *Meloidogyne* spp. These genotypes were tested against twelve *M. incognita* populations belonging to the four standardized host races collected from different geographical locations worldwide. Virulence of the *M. incognita* populations varied depending on the sweetpotato genotype and did not always correspond to host race as classified by the North Carolina Differential Host Test. 'Beauregard', L86-33, and PDM P6 were hosts for the 12 nematode populations, but differences in the aggressiveness of the populations were observed among the three sweetpotato genotypes. 'Porto Rico' and 'Pelican Processor' had differential host status to the *M. incognita* populations irrespective of their host race. These results suggest that: 1) multiple factors might be responsible for conferring virulence in the nematodes; 2) multiple genes could be involved in the resistance to root-knot nematodes in sweetpotato; and 3) the final outcome of root-knot nematode resistance in sweetpotato would depend on the specific interaction of these two factors. Further, these results suggest that *Meloidogyne* populations should be tested against sweetpotato differential hosts in order to determine the pathotypes affecting sweetpotato. This would help to standardize the evaluation of resistance to root-knot nematodes in sweetpotato breeding programs, and possibly identify reliable sources of resistance to numerous pathotypes of *Meloidogyne* spp.

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“I dedicate this work to my beloved parents for their unconditional support and patience.”

Biography

Jim C. Cervantes-Flores was born on January 9, 1973, in Lima, Peru. Jim is the second child of five children. By 1976, the family moved to Bolivia, where he spent his childhood in several cities like Santa Cruz and Cochabamba. He attended different schools and got the opportunity of growing up in places in direct contact with nature, and acquiring a great interest in biological sciences.

In 1985, his family moved back to Peru and established in Arequipa, where Jim completed his high school and undergraduate studies in Biological Sciences at the 'Universidad Nacional San Agustin'. He obtained his B.Sc. in Biology in July of 1995.

After finishing his studies, he joined the sweetpotato research team at the International Potato Center (CIP). First, conducting his thesis research to obtain his Professional certificate as Biologist and later working in the Molecular Biology Laboratories under the supervision of Dr. Dapeng Zhang and Dr. Marc Ghislain.

In 1997, he decided he needed further studies and he applied to the graduate school at North Carolina State University. He was accepted in the Department of Horticultural Science as a Master's student majoring in Plant Breeding and Genetics, with minors in Plant Pathology and Statistics under the advisement of Dr. G. Craig Yencho and Dr. Eric L. Davis, sponsored by the Fulbright Commission.

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Introduction

Sweetpotato, *Ipomoea batatas* (L.) Lam., with a production of more than 135 million tons ranks seventh in production among the food crops in the world, and fifth in developing countries (Clark and Moyer, 1988; FAO, 1999). Asia and Africa grow and consume more than 95% of the world's sweetpotatoes (FAO, 1999). In the southern U.S., sweetpotato is an important vegetable crop ranking first in North Carolina in terms of acreage and production in 1999 (N.C. Dept. Agr., 2000).

It has been estimated that 10% of world crop production is lost as a result of plant nematode damage. This represents one third of the total losses attributed to pests and diseases (Whitehead, 1998). The worldwide distribution of root-knot nematodes (RKN), *Meloidogyne* species, and their extensive host ranges, and associations with fungi and bacteria in disease complexes rank RKNs amongst the major pathogens affecting crops (Sasser, 1980). However, paradoxically much of the damage caused by RKNs goes undetected. Further, because of the difficulty and complexity of associating yield losses to RKNs, only a few estimations of crop losses due to RKNs have been calculated.

Scientists participating in the International *Meloidogyne* Project (IMP) estimated that the average crop loss due to RKNs in sweetpotato was 15%, 24% and 6% for South America, West Africa, and Southeast Asia respectively (Sasser, 1979). In North Carolina, the losses of sweetpotato due to RKNs were estimated at 6% in a 1991 survey (Toth et al., 1996). These estimates are conservative because RKNs are probably responsible for crop losses in many cases where environmental conditions such as soil moisture and fertility are blamed. In

addition, RKN infestation also may increase the susceptibility of plants to other diseases, such as those produced by bacteria and fungi (Tyler, 1933a; Dropkin, 1980).

The most important and predominant RKN species that infect sweetpotato are *Meloidogyne incognita* (Kofoid & White) Chitwood, *M. javanica* (Kofoid & White) Chitwood, and *M. arenaria* (Neal) Chitwood. *M. incognita* is the most widely spread and damaging nematode species attacking sweetpotato, and it occurs in most areas where sweetpotato is cultivated (Hammett et al., 1982, Johnson et al., 1996). *M. incognita* prefers warm temperatures for completion of its life cycle, and on sweetpotato it generally undergoes 4 to 5 generations per growing season. Therefore, nematode population numbers can increase significantly in a short time (Jatala, 1988), especially in light sandy soils where nematode infection is often most serious (Rosa, 1925).

Sweetpotatoes, even when susceptible to RKNs, are typically poor hosts when compared to other vegetables (e.g. melons, beans, tomatoes) which cannot be grown in heavily-infested soils. In sweetpotato, infection by RKN causes galls on fibrous roots and fleshy roots, suppresses the yield and quality of fleshy storage roots, and causes cracking with accompanying necrosis that decreases the market value of the storage roots (Poole and Schmidt, 1929; Lawrence et al., 1986; Clark and Moyer, 1988).

Sweetpotato was first reported as a host of RKNs in 1911 (Giamalva et al., 1963). Damage to sweetpotatoes produced by RKNs was likely underestimated in early studies because of the difficulty or unavailability of clean soils for a proper comparison of infested and non-infested plants. However, with the advent of nematicides, the impact of root-knot nematodes on yield and quality could be observed and quantified.

Roberts and Scheuerman (1984) noted that resistance to *M. incognita* in sweetpotato clones prevented damage to the storage roots, and growth and yield were increased significantly in fumigated plots compared with yields from non-fumigated plots of susceptible sweetpotatoes (Nielsen and Sasser, 1957). Satar and Phills (1982) observed greater sweetpotato yields in fumigated plots than in infested plots irrespective of level of resistance. However, the resistant variety was more vigorous and higher yielding than the susceptible cultivar when grown in non-fumigated RKN-infested soils. These studies point out that host plant resistance can be an effective, economical, and environmentally safe means of reducing losses from diseases caused by pests (Fassuliotis, 1979).

In the past, because the existence of different species and physiological races among RKNs was not determined, variable RKN resistance responses among the same sweetpotato cultivars were reported by different breeding programs (Rolston et al., 1986; Pecota, K.V, personal communication). Nevertheless, it was determined that resistance to RKN in sweetpotato ranged from highly susceptible to highly resistant.

In a study of field populations of *M. incognita* in sweetpotato, Davide and Struble (1966) hypothesized that RKN populations might be composed of a number of physiological races. They suggested that because potentially more pathogenic races are present in a field, the continued production of 'resistant' sweetpotato plants in that site might select for an increase in the most pathogenic nematode races. They also observed that at least one of the more virulent nematode isolates reproduced at a higher rate and earlier than the less virulent isolates. Similarly, Giamalva et al. (1963) observed significant differences in sweetpotato root gall ratings among isolates of *M. incognita acrita*. These results represent some of the earlier

indications of 'races' of RKN and may explain differences reported among investigators as to injury caused by RKNs in sweetpotatoes.

Considerable variation occurs in field populations of *M. incognita*, and cultivars are known to react differently to the various species and physiological races of RKNs. The symptoms of disease reactions to infection by RKN generally observed in other crops have also been observed in sweetpotato (Jones and Dukes, 1980). Lawrence and Clark (1986) reported that several RKN populations varied in their virulence on sweetpotato, and that trends in virulence were not correlated with the RKN races as identified by the NC Host Test (Hartmant and Sasser, 1985). They also observed that several RKN populations were capable of overcoming the resistance in the sweetpotato cultivars they studied. Netscher and Taylor (1979) pointed out that variation in pathogenicity to hosts among populations of the same RKN species might be very common. Similarly, Davis et al. (1996) noted that the origin of the nematode population was critical in evaluating soybean lines for nematode resistance.

Successful RKN management in sweetpotato includes one or a combination of several practices including crop rotation, selection of RKN-free propagation material, nematicide treatment, and use of resistant cultivars (Clark and Moyer, 1988). Studies of resistance to RKN in sweetpotato have been conducted with primarily one species, *M. incognita* (Struble et al., 1966; Dukes et al., 1978; Satar and Phills, 1982; Thomas and Clark, 1983; Dukes and Jones, 1985; Lawrence et al., 1986; Dukes et al., 1987; Dukes and Bohac, 1994). The response of RKN-resistant sweetpotato genotypes to multiple species of RKN has rarely been reported (Giamalva et al., 1963).

Because the success of a breeding program designed to develop sweetpotatoes with resistance to RKN depends on the identification of suitable resistance genes, it is necessary to

study in more detail the response of sweetpotato germplasm with different genetic backgrounds to multiple populations of RKN. This is particularly important for populations of *M. incognita* from different geographical origins. Thus, continued improvement of screening procedures for RKN resistance is critical for developing new resistant cultivars (Bonsi and Phills, 1979; Gentile et al., 1962). Efficient screening for root-knot nematode resistance should allow an initial screening of large germplasm collections to select promising resistant genotypes, as well as of breeding materials.

Additionally, in sweetpotato there is a need to develop sweetpotato host differentials for *M. incognita* because the NC Differential Host Test (Hartmant and Sasser, 1985) does not provide race information that may be applicable to the evaluation of sweetpotato germplasm. These differentials would, ideally, represent distinct sources of resistance to *M. incognita* that could be standardized and used by sweetpotato breeders.

The research presented in this thesis was designed:

(a) to evaluate the relative efficiency and accuracy of two methods of screening sweetpotato genotypes for resistance to RKNs,

(b) to determine the response of selected sweetpotato genotypes to three *Meloidogyne* species,

(c) to develop a set of sweetpotato differential host lines for the three most important *Meloidogyne* species, and

(d) to assess the response of these sweetpotato differential genotypes to several *M. incognita* populations collected from different areas of the world.

Literature review

Sweetpotato

Sweetpotato belongs to the family Convolvulaceae, and it is a hexaploid with 90 somatic chromosomes (2n=6x=90). Due to its ploidy level, self-incompatibility, and high heterozygosity, the genetics of inheritance of many important traits remain unclear in this crop. Recent studies suggest that sweetpotatoes are autopolyploids (Ukoskit et al., 1997). Because sweetpotato is able to adapt to many different environments, it has become an excellent supplement to staple foods, and in some areas (e.g. Rwanda, Tanzania, Uganda, and Papua New Guinea) it is a food staple (Yen, 1974). According to FAO (1999) and CIP (1999a), developing countries produce approximately 98% of the total sweetpotato world production (approximately 133 million tons), ranking this crop in terms of production fifth after rice, wheat, maize, and cassava.

Sweetpotato is a perennial vine, usually cultivated as an annual crop. Sweetpotato storage roots are high in energy, and are an important source of carbohydrates, vitamins A and C, fiber, iron, copper, calcium, and folic acid, especially the orange-fleshed sweetpotatoes (Collins et al., 1999; Woolfe, 1992). Germplasm characterization and evaluation studies indicate that considerable variation exists in morphological and horticultural traits, such as dry matter, starch, sugar, protein content, and disease and insect resistance. The inheritance of most traits is severally quantitative with only a few traits (e.g. vine color, internodal length) controlled by one or two genes (Collins et al., 1999). Studies have shown that the protein content and the amino acid balance of sweetpotato proteins vary depending upon cultivar, environment, cultural practices and growth duration. Sweetpotatoes are also

generally high in lysine and therefore represent a good protein supplement to cereals (Yang, 1982).

Early development of superior sweetpotato varieties was primarily based on new plant introductions selected from varieties and/or landraces from the tropics. Indeed, until the early 1930's selection of advantageous somatic mutations and the maintenance of stocks by selection against deleterious mutation were the only forms of plant breeding used in this crop (Edmond and Ammerman, 1971; Yen, 1974). The potential for sweetpotato improvement by varietal hybridization of sweetpotato was recognized in the 1930's (Tioutine, 1935; Miller, 1938, 1939). However, many of the early genotypes introduced did not produce flowers outside the tropical zone. Thus, most of the early work on sweetpotato breeding was focused on investigating flowering (Burnette, 1894; Miller, 1939). Since the development of sweetpotato flower induction in long-day environments, great progress has been made in sweetpotato breeding.

The center of origin of sweetpotato is unclear, but it is generally accepted to be in northwestern South America, in the territories of Peru, Ecuador, Colombia, Venezuela, and Bolivia. The oldest remains of sweetpotato storage roots were found in Chilca Canyon (Peru), and they were radiocarbon-dated at 8,000 BC (Yen, 1974). Sweetpotato was among the earliest crops introduced to Europe from America by the Spaniards, and by the early 16th century sweetpotato was cultivated by elite gardeners in England and in the warmer areas of the Mediterranean. Sweetpotato was unknown to the Greeks, Romans and Arabians, and it was not cultivated in Egypt until two centuries ago (Morgan and Ross, 1892; Yen, 1974).

In a recent study, Zhang et al. (1999) analyzed sweetpotato samples from South America and Central America using AFLP and SSR markers, and observed that there is a

greater molecular variability among the samples from Central America in comparison with the South American samples. This suggests that the geographical origin of sweetpotatoes might be somewhere in the Caribbean or Central American region. Therefore, the exact origin of sweetpotato remains unclear.

Root-knot nematodes

Most plant-parasitic nematodes feed on root tissue and damage their host mainly by: 1) reducing root nutrient and water uptake; 2) promoting microbial or fungal infections through wound sites; 3) serving as vectors for pathogenic viruses. In some cases, nematode infection intensifies the disease caused by a primary pathogen (Hollis, 1964; Ohl et al., 1997). RKNs are the most abundant and damaging of the plant-parasitic nematodes (Sasser, 1979). RKNs damage plants by disrupting root vascular tissue, where they form swellings (galls) on the roots that serve as a nutrient sink and as pathogen infection courts. They also reduce the market value of the crops by direct infection of the below-ground parts (Sasser, 1979)

Second-stage juveniles (J2) hatch from eggs in the soil and are the infective stage of *Meloidogyne* (Hussey, 1985). The J2 enter plant roots near the tip, migrate intercellularly to the root vascular tissue, and modify selected plant cells into an elaborate, permanent feeding sites called “giant cells”. Hypertrophy and hyperplasia of plant cells surrounding the feeding site produce the gall that is characteristic of RKN infection. The J2 feed, swell, and become sedentary as they progress through three more molts to the adult stage. Most RKN become adult females, especially in parthenogenic species. However, some vermiform males are produced within the swollen juvenile body.

RKNs are a serious problem in sweetpotato production areas throughout the United States, and they are especially damaging in sandy soils (Clark and Moyer, 1988). Heavy soils are less favorable for the development of RKN disease compared to sandy and sandy-loam soils. The warm, well-aerated sands of the Norfolk series are most favorable for the disease (Poole and Schmidt, 1929). Neither very dry nor wet soils are favorable for RKN development (Poole and Schmidt, 1929; Tyler, 1933a).

The most dramatic symptom of RKN infection on sweetpotato is on the storage roots, where they cause the formation of longitudinal cracks on the root surface (Clark and Moyer, 1988). Although cracking has been associated with many environmental factors, especially soil moisture fluctuations, Lawrence et al. (1986) observed that the number of cracked roots was correlated with the initial RKN population number. But, when rainfall was more uniform, although nematodes were present in the storage roots, the storage roots did not crack. This suggested that the nematode may be a predisposing rather than a causal factor of cracking in sweetpotato (Lawrence et al., 1986).

In the southern U.S., the most abundant nematode populations affecting sweetpotatoes are *M. incognita* races 1 and 3 as defined by the NC Host Differential Test (Clark and Moyer, 1988; Taylor et al., 1982). Giamalva et al. (1963) showed that *M. javanica* and *M. ha*pla also infect sweetpotato. Fortunately, the distribution of *M. hapla* is limited to cooler regions where sweetpotato production is minimal. Bonsi and Phills (1979) noted that sweetpotatoes are not as highly resistant to *M. javanica* as previously observed. Giamalva et al. (1963) noted that *M. arenaria* did not cause galling and mature females did not develop on any of the sweetpotato cultivars they studied.

The most predominant RKNs that reproduce by mitotic parthenogenesis, such as *M. javanica*, some members of *M. incognita*, and some members of *M. arenaria* have an extensive host range and are widely distributed geographically, especially in the tropical and subtropical regions of the world (Triantaphyllou, 1979). Triantaphyllou (1979), hypothesized that RKNs are capable of adaptation to a great variety of environments because apomixis maintains extensive heterozygosity, especially when it is combined with polyploidy. Thus, any beneficial gene mutations and most non-deleterious chromosomal mutations that occur tend to accumulate in the genome and are proliferated within the population. This makes the individual nematodes highly heterozygous for many loci and thus capable of broad adaptation.

Different races of plant pathogens arise by mutation, genetic recombination, genetic reassortment via mitotic recombination, and heterokaryosis (Nelson, 1973). Races can arise totally independently of the relative resistance or susceptibility of their hosts. However, host genotypes may influence the ultimate frequency or the sustained presence of new races. Successive cropping with resistant cultivars can shift the allele frequency of a population from non-virulent to virulent. Such shifts have led to the increasing prevalence of races capable of attacking widely used and presumably resistant germplasm (Nelson, 1973).

In the absence of a host, *Meloidogyne* spp. can survive in the soil for as long as two years, depending on the environment (Carter and Sasser, 1982). Geographic distribution of species is correlated with climatic factors: average yearly temperatures, average temperatures of the coldest and warmest months of the year, total annual precipitation, and distribution of precipitation by months (Carter and Sasser, 1982).

Several strategies have been effective in controlling RKNs in sweetpotato. The most efficacious control is via the use of highly neurotoxic nematicides, in combination with

cultural control practices. Although nematicides are effective, their high cost is prohibitive for small-scale growers because of the relatively low market value of sweetpotato (Gasapin, 1984). In addition, because nematicide toxicity and persistence creates a serious threat to the environment with consequent health risks, nematicide use has decreased in the past decades. Indeed, some countries have adopted policies aimed at the further reduction of nematicide use, creating an increasing need for the development of resistant crop varieties.

Resistance to root-knot nematodes (*Meloidogyne* spp.)

Measurements of host resistance and nematode virulence are typically based on the level of reproduction of the nematode on a plant, or on the degree of symptoms expressed by a plant. RKN reproduction is measured by extraction and counting of total nematodes (or eggs) in a root system or per unit weight of root, and sometimes by changes in soil population density. The extent of root galling by RKNs, root necrosis, and/or number of egg masses, are frequently used to measure RKN resistance because of their ease of assessment (Roberts et al., 1998). Relative resistance is indexed against susceptible and resistant controls (Bridge and Page, 1980; Roberts et al, 1998).

In addition to accurate measures of resistance, Fassuliotis (1979) mentions that the selection of resistant plants requires a basic understanding of the nematode, the host plant, the types of interactions that may occur, and the environmental relationships between the plant and the nematode that affect resistance. Active RKN resistance responses occur postinfection, following penetration into the root or other host tissues by the nematodes. Postinfection resistance is expressed by delayed or retarded development of the nematodes after penetration into the plant, or by non-development of the nematode to maturity in the

plants (Gasapin, 1986). Typically, resistant plants carrying major R genes for resistance to RKNs are invaded like susceptible plants. Preinfection (non-host) resistance may be manifested as physical or chemical barriers, or as nutritional inadequacies. Some resistance (incompatibility) results in a hypersensitive response (HR) and accumulation of toxic metabolites, and some resistance results in the degeneration of nematode feeding sites (Veech, 1981). After invasion into the plant, the activation of incompatible interactions can result in nematodes emigrating from the roots or nematode death within resistant roots (Roberts et al., 1998). This results in a lower number of egg masses and reduced size of egg-laying females in resistant cultivars as compared to susceptible cultivars (Gasapin, 1986). Dean and Struble (1953) reported that on resistant and susceptible sweetpotato varieties, juveniles (J2) enter the roots in equal number, but fewer nematodes develop to egg-laying maturity on resistant varieties. They speculated that resistance to RKN in sweetpotato was related to an extensive necrosis of root tissues. Histological studies of 'Porto Rico' sweetpotato showed that the primary root penetration by J2 occurred at the tips of young roots in the region of tissue differentiation. Another major nematode penetration site in sweetpotato occurred through the loose ruptured cells of enlarging roots where lateral roots emerged (Krusberg and Nielsen, 1958).

Several types of host-parasite reactions are associated with RKN resistance in sweetpotato. These are: 1) none to trace amounts of galling on the host; 2) moderate to severe root tip necrosis; 3) general inability of nematode larvae to reach mature stages; 4) little or no reproduction by the nematode; and 5) reduced number of eggs where reproduction does occur (Davide and Struble, 1966). Resistance to RKN in sweetpotato is influenced by plant genotype, nematode population, environmental factors, and nematode species (Bonsi and Phills, 1979). For example, Fassuliotis (1985) observed that sweetpotato

loses its resistance in elevated soil temperatures above 28°C. Dukes and Bohac (1994) indicated that although yield of 'Beauregard' sweetpotato in RKN-infested soils was not affected or reduced, the internal necrosis observed upon storage was more severe than in other cultivars.

Breeding for RKN resistance in sweetpotato

The most critical factor in the development of crops with RKN resistance is the availability of resistant genetic material within a plant species. In sweetpotato, there is a wide gene pool for disease resistance and many other traits. Currently, approximately 6500 *Ipomoea* accessions are maintained in the International Potato Center (CIP), Lima, Peru, sweetpotato germplasm bank. Wild species, cultivated and advanced breeding lines are included in this genebank (CIP, 1999b).

The presence of multiple species and races of RKN greatly complicates the task of developing nematode-resistant cultivars. Breeding RKN resistant sweetpotatoes is also complicated by the genetics of the crop. The use of wild relatives to incorporate resistance to RKN has been successful in some crop species (Smith, 1944; Havis et al., 1950; Clayton et al., 1958; Shepherd, 1974). However, in sweetpotato this rarely has been the case because wild sweetpotatoes are not as readily accessible due to incompatibility factors and difference in ploidy levels. Iwanaga (1988) indicated that the use of wild germplasm is important as a genetic source to provide specific beneficial traits to adapted germplasm and to widen the genetic background of cultivated germplasm. However, due to the difficulties in this process, wild germplasm should be used only when the desired trait is not present in adapted material. Based on this observation, Iwanaga (1988) concluded that there was not enough justification

to use wild germplasm as a source of resistance to RKN in sweetpotato, because resistant commercial cultivars are available.

Despite the difficulty encountered when introgressing genes from wild sweetpotatoes into cultivated sweetpotatoes, the Japanese sweetpotato breeding program, conducted work with a putative hexaploid *I. trifida* (K123) wild relative. This genotype was crossed to established cultivars and after several generations of backcrossing, the cultivar called 'Minamiyutaka' was developed (Iwanaga, 1988). 'Minamiyutaka' was resistant to *M. incognita* and high-yielding. It was the first successful use of wild sweetpotato germplasm to transfer desirable traits like RKN resistance into sweetpotato cultivars, and this success had a major impact on the sweetpotato breeding program in Japan (Iwanaga, 1988).

Cordner et al. (1954) and Giamalva et al. (1961) observed in the progeny of selected sweetpotato parents that the resistance response to RKN segregated quantitatively. Likewise, Struble et al. (1966) suggested that RKN resistance in sweetpotato might be inherited as multiple factors, not as simple Mendelian characters.

It has also been noted that sweetpotato genotypes screened with different RKN have expressed resistance in varying degrees. Dean and Struble (1953) observed that RKN resistance was of high frequency in seedling populations from selected resistant parents. Similar observations were made by Giamalva et al. (1961) when they crossed sweetpotato lines with different degrees of resistance to *M. incognita*, and they obtained different ratios in the resistance responses among the progeny. In susceptible x intermediate-resistant crosses, seedlings were 22% intermediate-resistant and 78% susceptible. In intermediate-resistant x intermediate-resistant crosses, seedlings were 0.7% resistant, 15.3% intermediate-resistant, and 84% susceptible. In susceptible x resistant crosses, seedlings were evenly distributed

among the three classes. And in susceptible selfed crosses, seedlings were 2.6% resistant, 21.1% intermediate-resistant, and 76.3% susceptible.

In another set of RKN inheritance studies, Jones and Dukes (1980) studied the inheritance of resistance in sweetpotato to *M. incognita* and *M. javanica*. They used three measures of resistance (number of egg masses, gall index, and necrosis index) and reported heritability estimates of 0.69, 0.78 and 0.72, respectively. They found that resistance to the two species was not correlated, and suggested independent inheritance involving different genes. Gasapin (1984) suggested that the different degrees of resistance exhibited by different sweetpotato cultivars to *M. incognita* and *M. javanica* could be attributed to the differences in genes for resistance possessed by the different cultivars. They also observed a linear correlation between resistance rating and number of egg masses and root galls. They preferred to use the egg mass index since galling was less pronounced, and thus more difficult to assess.

Resistance genes to several plant-nematodes have been identified and cloned in other crop species. The Mi gene for RKN resistance was cloned from tomato, *Lycopersicon esculentum*, being originally transferred from *Lycopersicon peruvianum* (Williamson et al., 1998) The $Hs1^{pro\text{-}1}$ gene, conferring resistance to beet cyst nematode, was cloned from a wild species and transferred to cultivated sugar beets successfully (Jung et al., 1998). In sweetpotato, Ukoskit et al. (1997) using random amplified polymorphic DNA (RAPD) identified a single RAPD marker ($OP15_{1500}$) linked to RKN resistance. However, due to the limited number of RAPD markers available, the estimated recombination fraction between the marker $OP15_{1500}$ and the resistance gene was of 0.2421 ± 0.057. Subsequently, several recombinants for the marker were observed among the different progeny tested. Thus, much

work remains before any resistance genes for RKN are cloned or even tightly linked in sweetpotato.

In summary, sweetpotato breeding has experienced great progress since the induction of flowering was developed during the late 1930's (Miller, 1939). Recent studies have increased our understanding of the genetics of sweetpotato (Ukoskit et al., 1997; Zhang et al, 1999). While, resistance to many important diseases has been introgressed into several cultivated lines, including resistance to RKN (Jones et al., 1989; LaBonte et al., 1992; Pope et al., 1971). The variability in sources of RKN resistance is sweetpotato, however, combined with the variability and lack of uniformity of *Meloidogyne* populations used in breeding programs, presents an unclear picture of the nature of sweetpotato resistance to RKNs. The results presented in this thesis should help to clarify this picture.

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Chapter One

Efficient Evaluation of Resistance to Three Root-Knot Nematode Species in Selected Sweetpotato Cultivars

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(In the format appropriate for submission to HortScience from the American Society of Horticultural Science)

Efficient Evaluation of Resistance to Three Root-Knot Nematode Species in Selected Sweetpotato Cultivars

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Plant breeding

Efficient Evaluation of Resistance to Three Root-Knot Nematode Species in Selected Sweetpotato Cultivars

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Abstract. Five sweetpotato [Ipomoea batatas (L.) Lam.] cultivars ('Beauregard', 'Excel', 'Jewel', 'Hernandez', and 'Porto Rico') were evaluated for resistance to three root-knot nematode species: Meloidogyne arenaria (Neal) Chitwood (race 2), M. incognita (Kofoid & White) Chitwood (race 3), and M. javanica (Treub) Chitwood. Resistance screening efficiency was assessed in 400-cm³ square pots and 150-cm³ Conetainers™. Nematode infection was assessed as the percentage of root system galled, percentage of root system necrosis, and the number of nematode eggs produced per gram of root tissue. Means of these dependent variables were not significantly different between container types, with Conetainers™ being more efficient to use. Root necrosis was not significantly related to nematode infection, but was significant among cultivars (P=0.0005). The resistance responses of the cultivars differed depending on the nematode species. All five cultivars were resistant to M. arenaria race 2. 'Hernandez', 'Excel' and 'Jewel' were also resistant to M. incognita race 3 and M. javanica.

Plant-parasitic nematodes, especially root-knot nematodes (RKN), *Meloidogyne* species, represent a significant problem in sweetpotato production, causing reduction in yield and quality of the storage roots in Asia, South America and southern U.S. (Clark et al., 1992; Sasser and Carter, 1985; Ukoskit et al., 1997). The average damage to field crops by plant-parasitic nematodes is estimated at 10% worldwide (Whitehead, 1998). Three species of RKN -*Meloidogyne incognita*, *M. arenaria*, and *M. javanica*- are particularly important pathogens of sweetpotato (Sasser, 1980). The most characteristic symptoms of RKN are round to spindle-shaped swellings (galls) on fibrous roots and cracks on fleshy storage roots (Lawrence et al., 1986). Nematode injury inflicted during early root development predisposes storage roots to the formation of cracks in the cortex (Thomas and Clark, 1983a), a major determinant of decreased root quality.

Successful nematode management in sweetpotato includes one or a combination of several practices including crop rotation, selection of nematode-free propagation material, nematicide treatment, and use of resistant cultivars (Clark and Moyer, 1988). Studies of resistance to RKN in sweetpotato have been conducted with primarily one species, *M. incognita* (Struble et al., 1966; Dukes et al., 1978; Satar and Phills, 1982; Thomas and Clark, 1983b; Dukes and Jones, 1985; Lawrence et al., 1986; Dukes et al., 1987; Dukes and Bohac, 1992, 1994). The response of RKN-resistant sweetpotato genotypes to multiple species of RKN has rarely been reported (Giamalva et al., 1963). In most studies no information was provided on the nematode host race used, causing confusion among breeders on the specificity of resistance of sweetpotato genotypes to RKN.

Continued improvement of screening procedures for RKN resistance is critical for developing new resistant cultivars (Bonsi and Phills, 1979; Gentile et al., 1962). Screening for resistance to RKN should allow efficient initial screening of large germplasm collections

to select promising lines. The sweetpotato breeding program at North Carolina State University, presently uses 400-cm^3 (9 cm per side) containers for greenhouse evaluations of sweetpotato genotypes for RKN resistance, demanding significant greenhouse space. Efficient and reproducible greenhouse screening of tobacco and soybean germplasm for resistance to RKN has been achieved using the 150-cm^3 Conetainer™ system (Davis et al., 1988, 1998). Resistance to the three major species of *Meloidogyne* was assessed in several commercial sweetpotato cultivars in two greenhouse screening systems in the study reported here.

Materials and Methods

Five sweetpotato cultivars (Beauregard, Hernandez, Jewel, Porto Rico and Excel)(Table 1) with reported resistance to *M. incognita* (Clark et al., 1992; Thies, 1999) were evaluated for resistance to *M. arenaria* race 2, *M. incognita* race 3 and *M. javanica*. Fifteen-cm-long cuttings were planted in both 400-cm^3 pots, model LAPOT (Landmark Plastic Corporation, Orlando, Fla.), and 150-cm^3, model SC-10 Super Cell Conetainers™ (Stuewe & Sons, Inc., Corvallis, Ore.), containing a 3 : 1 pasteurized mix (by volume) of coarse sand and field soil (loamy sand: 88.9% sand, 8.3% silt, and 2.8% clay), respectively.

Meloidogyne arenaria race 2, *M. incognita* race 3, and *M. javanica* were cultured on roots of 'Rutgers' tomato plants (*Lycopersicon esculentum* Mill.). Eggs of the RKN populations were extracted using Hussey and Barker's (1973) NaOCl extraction technique and approximately 10,000 eggs were injected into the soil to infest each plant. The inoculation was done two weeks after planting each cutting. Inoculated plants were grown under greenhouse conditions of 25° C - 28° C and watered once a day.

Plants were harvested at 56 days after inoculation and rated visually for the percentages of total root system that were galled or necrotic. Root fresh weights were recorded at harvest. Eggs of RKN were extracted from a maximum of 5 g of each root system with NaOCl (Hussey and Barker, 1973). A subsample of the extracted eggs was stained with acid fuchsin (Daykin and Hussey, 1985), and eggs were counted using a stereoscopic microscope to estimate total eggs per gram of root system based upon total root fresh weight.

Each treatment combination (container type, nematode species, and sweetpotato cultivar) was replicated five times, and the same experiment was conducted at two different times. All experiments were arranged in a split-plot design with container type as the main treatment and nematode species as the subplot treatment. Sweetpotato cultivars were distributed randomly within each subplot. Nematode data were transformed by log (x+1) to standardize the variance. All data were subjected to analysis of variance (ANOVA) using the SAS GLM Procedure (SAS Institute Inc., Cary, NC). Main effects and interactions were analyzed for all dependent variables mentioned above. To simplify the statistical analysis, and to prevent variations due to missing data, the ANOVA was performed on the means of the five plants for each cultivar within each subplot, with the two experiments serving as replications. Fisher's LSD procedure (alpha=0.05) was used to compare treatment means. Back-transformed data are presented in Table 3 for clarity.

Results

No significant differences in root necrosis, root galling, or nematode egg production were observed between the two container types (Table 2). Subsequently, data of the square

pots and Conetainers™ were pooled for statistical analyses of sweetpotato response to nematode infection. Some effect in the growth of the root system was visible between the two types of containers, but this did not affect the resistance rating between containers (Table 2).

The analysis of variance on all three nematode species demonstrated significant interactions between cultivar and RKN species ($P<0.0001$) for root galling and number of eggs per gram of root, but not for root necrosis (Table 2). Root necrosis, averaged across nematode species and container type (data not shown), were significantly different ($P=0.0368$). This difference was mainly explained by the cultivar effect ($P=0.0007$). 'Porto Rico' showed on average the higher degree of necrosis (> 8%), compared with values below 3% for the other four cvs. But the degree of response also changed with the nematode species (Table 3), and root necrosis was not correlated with the number of eggs per gram of root.

The number of nematode eggs produced per gram of root tissue was highly correlated ($r=0.9$) with galling. Differences in the level of resistance to the RKN reproduction were observed among the sweetpotato cultivars tested. The number of eggs per gram of root system produced by *M. incognita* race 3 was higher in 'Beauregard' (1,214 eggs) and in 'Porto Rico' (1,571 eggs), compared to the other 3 cultivars (20 eggs). *M. javanica* was highly pathogenic to 'Beauregard', producing over 5,000 eggs per gram of root system. *M. javanica* also formed eggs, significantly fewer though, in 'Jewel' (54 eggs per gram of root system), but did not affect 'Excel', 'Hernandez' or 'Porto Rico'. *M. incognita* race 3 caused significant galling in 'Porto Rico' and 'Beauregard', but not in the other 3 cultivars. Galling ranged from 0 to 20% of the root system affected, with 'Porto Rico' having the higher value (Table 3). *M. javanica* produced significant galling only in

'Beauregard' (20% of root system galled). 'Excel', 'Jewel', 'Hernandez', and 'Porto Rico' were resistant to the formation of galls by *M. javanica* (Table 3). All sweetpotato cultivars evaluated in this experiment were resistant to *M. arenaria* race 2, which did not produce galls or eggs in the root system.

Discussion

The results of these tests indicate that the response of the sweetpotato cultivars evaluated differs among the *Meloidogyne* species studied. Our results are similar to those observed on other sweetpotato germplasm by Bonsi and Phills (1979). The data suggest the presence of different genes for resistance to the different root-knot nematode species, and this is supported by the differences in cultivar pedigree (Table 1). For example, both 'Excel' and 'Hernandez' are resistant to *M. incognita* race 3 and *M. javanic*a, but they have different pedigrees. The difference in source of resistance is evident when comparing the susceptible responses of 'Beauregard' and 'Porto Rico'. 'Beauregard' was highly susceptible to M. incognita race 3 and to *M. javanica*, but 'Porto Rico' was susceptible to *M. incognita* race 3 and resistant to *M. javanica* in our study (Table 3).

Levels of galling and amount of eggs per gram of root system produced in 'Beauregard' by *M. incognita* and *M. javanica* were significantly higher compared to the other cultivars. 'Beauregard' is the cultivar preferred by growers for its agronomic qualities in the southern U.S., representing approximately 70% of the sweetpotatoes grown in the U.S. (Schultheis, J., personal communication). 'Beauregard' is also a popular parent in many breeding programs in the U.S. and other countries. However, because of the high

susceptibility of 'Beauregard' to RKN, its use as a parental genotype should viewed cautiously.

Jones and Dukes (1980) reported that 'Jewel' was susceptible to *M. javanica*. However, our results indicate that 'Jewel' is moderately resistant to *M. javanica*, since galling is not higher than 5%, and the number of eggs•g^{-1} is considerably lower than that corresponding to 'Beauregard'. Differences in *M. javanica* isolates may account for some discrepancies between the two studies. 'Hernandez' represents approximately 20% of the sweetpotatoes produced in North Carolina (Schultheis, J., personal communication). Its high degree of resistance to the three *Meloidogyne* spp. should be taken into account in future breeding programs as a possible source of resistance to RKN. 'Hernandez' is, however, a poor flowering genotype under N.C. conditions, and it may be difficult to use it as a parent.

It is surprising that all five cultivars were resistant to *M. arenaria* race 2. *M. arenaria* race 2 is very aggressive on many crop species, including genotypes that are resistant to *M. incognita* (Davis et al., 1988, 1998). Resistance to *M. arenaria* in sweetpotato, however, has been observed previously (Giamalva et al., 1963).

The lack of correlation between necrosis and nematode infection suggests that root necrosis is not a good indicator of sweetpotato resistance to RKN. Traditionally, localized root necrosis has been associated with resistance by a hypersensitive response (Gentile et al., 1962; Bonsi and Phills, 1979). However, the root necrosis observed here appears to be a function of plant genotype.

The difference in root system development among cultivars grown in the Conetainers™ versus the square pots is probably due to the area where the roots could develop. Although, the difference in root development between containers did not affect

RKN infection, the roots in the Conetainers™ tended to be thicker, longer, and less dense than those formed in the square pots. This growth difference in the Conetainers™ made the resistance assessment of the roots easier and faster compared to those grown in the square pots. This characteristic could be used to the advantage of researchers when screening large numbers of breeding lines or accessions for nematode resistance.

Our studies indicate that for a successful RKN-resistance breeding program, breeders need to consider the nematode species predominant to a production region. Our results also suggest that susceptible and resistant control sweetpotato genotypes need to be identified for each *Meloidogyne* species. Further studies are also needed to better understand the resistance to RKN in sweetpotato and the impact of the different RKN host races (Hartman and Sasser, 1985) on sweetpotato genotypes.

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Table 1. Traceable pedigrees of the sweetpotato genotypes evaluated for resistance to root-knot nematodes.

Cultivar	Parentage[1]	Reference
Beauregard	L78-21>L70-197>L67-69>L59-89	Rolston et al., 1987
Excel	Regal>W-99>SC-1166	Jones et al., 1989
Hernandez	L70-323>L63-2217>L41-212 (Mameyita x L4-6)	LaBonte et al., 1992
Jewel	[Centennial (>(Unit 1 Porto Rico x Pelican Processor))] x Nugget [(NC-53 (>Tinian) x NC-65) x (NC-41 x NC-1)]	Pope et al., 1971
Porto Rico	Selection derived from 'Mameyita'	Nielsen and Pope, 1960

[1] Parents showed alone or after a '>', represent an open-pollination cross (the parent shown is the maternal parent and the male parent is unknown).

Table 2. ANOVA[z] table of main effects and interactions for root necrosis, root galling and eggs produced by *Meloidogyne incognita* race 3, *M. javanic*a and *M. arenar*ia race 2 in sweetpotato cultivars in two greenhouse pot types.

Source of variation	D.F.	Mean Square		
		Necrosis[y]	Galling[x]	Eggs•g^{-1} [w]
RKN[v]	2	0.0145	1.4088*	11.2129*
Pot[u]	1	0.0511	0.0199	0.0055
Pot x RKN	2	0.1449	0.0324	0.2536
Cultivar[t]	4	0.4745**	1.3872**	7.2462**
Cultivar x Pot	4	0.0525	0.0099	0.1759
Cultivar x RKN	8	0.0749	0.6726**	4.5852**
Cv. x Pot x RKN	8	0.0152	0.0124	0.0504

[z] ANOVA was performed on the log (x+1) transformed data.

[y] The percentage of total root system necrosis.

[x] The percentage of total root system with galls.

[w] The total number of eggs per gram of root.

[v] Effect of the nematode species averaged across pots and sweetpotato cultivars.

[u] Effect of the type of containers used averaged across RKN and sweetpotato cultivars. The pots are the following : a 400 cm^3 container, model LAPOT (Landmark Plastic Corporation, Orlando, Fla.), and a 150 cm^3, SC-10 Super Cell Conetainer™ (Stuewe & Sons, Inc., Corvallis, Ore.).

[t] Cultivar effect averaged across RKN and pot type. The sweetpotato cultivars evaluated were 'Beauregard', 'Excel', 'Hernandez', 'Jewel', and 'Porto Rico'.

*, ** Significant at $P<0.05$ or $P<0.01$, respectively. No symbol was used when effect was non-significant.

Table 3. Root necrosis, root galling and eggs produced by *Meloidogyne arenaria* race 2, *M. incognita* race 3 and *M. javanica* on selected sweetpotato cultivars in two container types.

Cultivar	Necrosis[z]				Galling[y]				Eggs•g^{-1} [x]			
	Pot[w]	Cone[v]	Mean	S.E.	Pot	Cone	Mean	S.E.	Pot	Cone	Mean	S.E.
M. arenaria race 2												
Beauregard	2.4	4.5	3.4 a[u]	0.5	0.0	0.0	0.0 a	0.0	0.4	0.6	0.5 a	0.3
Excel	3.1	3.7	3.4 a	0.5	0.0	0.4	0.2 a	0.2	1.2	2.9	1.9 a	0.6
Hernandez	1.4	4.5	2.7 a	0.3	0.0	0.0	0.0 a	0.0	0.0	0.6	0.3 a	0.3
Jewel	3.0	1.2	1.9 a	0.4	0.0	0.0	0.0 a	0.0	0.3	4.6	1.7 a	1.3
Porto Rico	5.7	7.0	6.3 a	0.2	0.3	0.3	0.3 a	0.2	0.4	1.0	0.7 a	0.2
M. incognita race 3												
Beauregard	1.6	1.8	1.7 b	0.5	10.4	14.6	12.3 a	0.3	2664.6	553.5	1214.8 a	1.2
Excel	1.7	2.1	1.9 b	0.2	0.4	0.0	0.2 b	0.2	2.1	0.5	1.2 c	0.3
Hernandez	1.4	1.2	1.3 b	0.4	0.0	0.6	0.3 b	0.1	23.8	19.2	21.4 b	0.3
Jewel	3.1	1.8	2.4 b	0.4	0.6	0.6	0.6 b	0.3	2.4	10.3	5.2 bc	1.9
Porto Rico	12.0	14.2	13.1 a	0.1	24.9	17.6	20.1 a	0.2	2564.5	962.8	1571.5 a	0.4
M. javanica												
Beauregard	4.6	3.5	4.0 ab	0.3	25.3	15.7	20.0 a	0.5	6720.9	4373.1	5421.4 a	0.2
Excel	2.5	0.7	1.5 c	0.5	0.4	0.0	0.2 b	0.1	0.4	1.0	0.7 c	0.2
Hernandez	2.9	2.2	2.5 bc	0.4	0.2	0.0	0.1 b	0.1	0.4	0.9	0.6 c	0.2
Jewel	3.5	1.0	2.0 bc	0.5	0.4	0.2	0.3 b	0.2	55.4	54.0	54.7 b	1.6
Porto Rico	10.1	3.5	6.0 a	0.6	0.4	0.0	0.2 b	0.2	1.4	1.0	1.2 c	0.6

(Continuation Table 3)

[z] Necrosis values are the mean of two replications of five plants each. It is expressed as the percent of necrotic root tissue. Values were not significantly different between types of container ($P>0.05$).

[y] Galling values in pot and cone are the mean of two replications of five plants each. It is expressed as the percent of root galled. Values were not significantly different between types of container ($P>0.05$).

[x] Eggs•g^{-1} values are the mean of two replications of five plants each. It is expressed as the number of eggs found per gram of root tissue. Values were not significantly different between types of container ($P>0.05$).

[w] Pot, represents the 400 cm^3 container, model LAPOT (Landmark Plastic Corporation, Orlando, Fla.)

[v] Cone, represents the 150 cm^3, SC-10 Super Cell Conetainer™ (Stuewe & Sons, Inc., Corvallis, Ore.)

[u] For each RKN species, values within a column followed by the same letter are not significantly different (Fisher's protected-LSD test, alpha=0.05.

Transformation of the data used for the corresponding ANOVA was log (x+1).

Chapter Two

Sweetpotato Differential Host Genotypes for Root-Knot Nematodes and Variation in Virulence of *Meloidogyne incognita*

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(In the format appropriate for submission to HortScience from the American Society of Horticultural Science)

Sweetpotato Differential Host Genotypes for Root-Knot Nematodes and Variation in Virulence of *Meloidogyne incognita*

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Plant breeding

Sweetpotato Differential Host Genotypes for Root-Knot Nematodes and Variation in Virulence of *Meloidogyne incognita*

Additional index words. *Ipomoea batatas, Meloidogyne arenaria, Meloidogyne javanica*, host plant resistance, differential hosts, pathogenicity, physiological race, plant breeding

Abstract. **Sweetpotato [***Ipomoea batatas* **(L.) Lam.] genotypes were evaluated for their resistance to North Carolina root-knot nematode populations**: *Meloidogyne arenaria* **(Neal) Chitwood (races 1 and 2),** *M. incognita* **(Kofoid & White) Chitwood (races 1, 2, 3, and 4), and** *M. javanica* **(Treub) Chitwood. Resistance screening was conducted using 150-cm³ Conetainers™ containing 3 sand : 1 soil mix. Nematode infection was assessed as the number of egg masses produced by root-knot nematodes per root system. Host preference of the root-knot nematode populations differed among the sweetpotato genotypes. Five out of twenty-seven genotypes ('Beauregard', L86-33, PDM P6, 'Porto Rico', and 'Pelican Processor') were selected as potential sweetpotato differential hosts for root-knot nematode so host status of these five genotypes was tested against 12 populations of** *M. incognita***, belonging to four host races, collected from different geographical regions. Virulence of root-knot nematode populations of the same host race varied among and within sweetpotato genotypes. 'Beauregard', L86-33, and PDM P6 were hosts for all twelve** *M. incognita* **populations, but differences in the aggressiveness of the isolates were observed. 'Porto Rico' and 'Pelican Processor'**

had different reactions to the *M. incognita* **populations regardless of the host race. Two other genotypes ('Tanzania' and 'Wagabolige') were observed to have resistance to all twelve** *M. incognita* **populations tested. These responses suggest that different factors might be responsible in conferring virulence in the nematodes, and that several different genes could be involved in the resistance to root-knot nematode in sweetpotato. The results suggest that** *Meloidogyne* **populations should be tested against sweetpotato differential hosts to determine the pathotypes affecting sweetpotato and to standardize the evaluation of resistance to root-knot nematodes in sweetpotato breeding programs.**

The worldwide distribution of root-knot nematodes, their extensive host ranges, and their interactions with pathogenic fungi and bacteria in plant disease complexes rank root-knot nematodes among the major pathogens affecting crops (Sasser, 1980). In sweetpotato, *Ipomoea batatas*, root-knot nematodes represent a significant problem, causing reductions in yield and quality of the storage roots (Clark et al., 1992). In North Carolina, losses of sweetpotato due to root-knot nematode were estimated at 6 % in a 1991 survey (Toth et al, 1996). Root-knot nematode symptoms on sweetpotato are round- to spindle-shaped swellings (galls) on fibrous roots and cracks on fleshy storage roots (Lawrence et al., 1986). In less developed countries in the tropics where sweetpotato is a staple crop (Yen, 1974), use of resistant cultivars may be the only economically practical management alternative (Roberts, 1992). Because of the wide host range of root-knot nematodes, accurate identification of the species and race is important for the selection of appropriate plant resistant management strategies (Sasser and Carter, 1985).

Greater than fifty species of root-knot nematodes have been described, but *Meloidogyne incognita, M. javanica, M. arenaria,* and *M. hapla* Chitwood account for more than 95% of the species detected in agricultural soils worldwide (Sasser and Carter, 1985; Taylor et al., 1982). Four races have been recognized in *M. incognita* and two in *M. arenaria*. These races have been proposed based on the ability or inability of a root-knot nematode population to reproduce in the North Carolina Differential Host Test (Hartmant and Sasser, 1985). However, it is important to note that the assignment of these races was based on a particular set of host plants that does not include sweetpotato, and that if different host plants were used, the characterized variation could also change.

Triantaphyllou (1987) indicated that differential hosts should be selected carefully they should represent the simplest cases of the inheritance of resistance. Further, they should

preferably have resistance that is controlled by major genes and should, as a set, include all useful sources of resistance that are actually used in breeding programs. Triantaphyllou (1987) suggested that hosts with polygenic resistance should be avoided, because two or more differential hosts of the set may share common genes for resistance, which could affect the differentiation of biotypes and races.

Resistance to root-knot nematodes in sweetpotato is not well understood. Cordner et al. (1954) and Giamalva et al. (1961) indicated that root-knot nematode resistance segregated quantitatively and that a relatively large number of genes were involved. Likewise, Struble et al. (1966) suggested that root-knot nematode resistance in sweetpotato might be inherited as multiple factors, not as simple Mendelian characters. When Jones and Dukes (1980) studied the inheritance of resistance in sweetpotato to *M. incognita* and *M. javanica*, they used three measures of resistance (number of egg masses, gall index, and necrosis index) and reported heritability estimates of 0.69, 0.78 and 0.72, respectively. They found that resistance to the two species was not correlated, and suggested independent inheritance involving different genes. In recent studies, Ukoskit et al. (1997) hypothesized that resistance to root-knot nematodes was inherited qualitatively, and using random amplified polymorphic DNA (RAPD) identified a single RAPD marker ($OP15_{1500}$) linked to root-knot nematode resistance in a cross between a resistant ('Regal') and a susceptible ('Vardaman') sweetpotato. However, the marker was not tightly linked to the resistance gene and several recombinants for the marker were observed among the progeny tested.

Because the success of a breeding program designed to develop sweetpotatoes with resistance to root-knot nematode depends on the identification of suitable resistance genes, it is necessary to study in more detail the response of sweetpotato germplasm with different genetic backgrounds to multiple populations of root-knot nematodes. This is particularly

important for populations of *M. incognita* from different geographical origins. Because the most commonly encountered species of *Meloidogyne* exhibit considerable physiological variation, it has been suggested that the only satisfactory approach to determine races of root-knot nematode is to determine the reaction of potential host plants to individual field populations. However, this approach is not realistic, thus a better solution would be to test as many populations as possible and to extrapolate from the results obtained whenever a recommendation is required for the field (Netscher and Taylor, 1979).

The objectives of this study were to develop sweetpotato differential host genotypes for *Meloidogyne incognita, M. arenaria and M. javanica*, and to assess different populations of *M. incognita* collected from different areas worldwide using these differentials. This work will provide a better understanding of the relationships between sweetpotato and *Meloidogyne* populations, identify sweetpotato genotypes that can be used as a potential source of root-knot nematode resistance genes, and contribute to the standardization of the evaluation of resistance to root-knot nematodes in sweetpotato breeding programs.

Materials and Methods

A. Development of differential hosts

Twenty-six sweetpotato genotypes of economic importance or present in the pedigree of modern cultivars (Table 1), were evaluated for resistance to greenhouse-cultured North Carolina populations of *Meloidogyne arenaria* (races 1 and 2), *M. incognita* (races 1, 2, 3 and 4), and *M. javanica* as classified by the NC Differential Host Test (Hartmant and Sasser, 1985). Fifteen cm-long cuttings were transplanted into 150-cm^3 pots, model SC-10 Super Cell Conetainers™ (Stuewe & Sons, Inc., Corvallis, Ore.), containing a 3 : 1 pasteurized mix (by volume) of coarse sand and field soil (loamy sand: 88.9%, 8.3% silt, and 2.8% clay), respectively (Cervantes-Flores et al, in press).

Root-knot nematodes were cultured on 'Rutgers' tomato plants (*Lycopersicon esculentum* Mill.). Eggs were extracted using NaOCl (Hussey and Barker, 1973) and approximately 10,000 eggs were injected into the soil to infest each plant. The inoculations were applied two weeks after planting each cutting. Plants were grown under greenhouse conditions of 25°C – 28°C and watered as needed.

Plants were harvested at 56 days after inoculation and rated by counting the number of egg masses (EM) present on the root system. The rating was done after staining the egg masses with phloxine B as described by Daykin and Hussey (1985). The experiment was arranged in a split-plot design with each nematode population as main treatments, and each sweetpotato genotype replicated five times within each nematode plot. Number of egg mass per root system counts were transformed by $\sqrt{(x+0.5)}$ and the analysis of variance (ANOVA) was performed for each root-knot nematode population using PROC GLM (SAS

Institute, Cary, N.C.). Means were separated using the Waller-Duncan *k*-ratio *t*-test (*k*-ratio = 100) procedure (alpha=0.05) (Table 2).

A subset of sweetpotato genotypes that differentiated the nematode populations was selected for conducting a second test under the same conditions as explained above. The experiment was arranged similarly to the first test, but only with the selected sweetpotato genotypes (Table 3). Data were transformed by $\sqrt{(x+0.5)}$ and the data from both tests were analyzed by ANOVA using SAS. The two tests were used as whole plot replications. Means were separated using the Waller-Duncan *k*-ratio *t*-test (*k*-ratio = 100) procedure (alpha=0.05), and the best set of sweetpotato differential hosts for *Meloidogyne* species were selected (Table 4). Non-transformed data are presented in tables for clarity.

A. Nematode population variation

Eight *M. incognita* populations (Table 5) kept under cryo-preservation from the collections of the International *Meloidogyne* Project (Hartman and Sasser, 1985) were defrosted and cultured on 'Rutgers' tomatoes. Since only a few hundred nematodes were revived from each population, they were cultured for four months and re-cultured over six months to increase the population levels to conduct the tests below. The thawed nematode populations corresponded to the 4 host races of *Meloidogyne incognita* as classified by the NC Differential Host Test (Table 5). Also, the North Carolina *Meloidogyne incognita* populations of the four host race (Table 5) used in the previous tests to develop sweetpotato differentials were used as a comparison for nematode infection.

The differential host genotypes selected from the first experiment (section A) (Table 4) were tested against the twelve *M. incognita* populations described above. Conditions and the screening procedures were the same as in the differential host studies. 'Rutgers' tomatoes

were also inoculated to check the viability and pathogenicity of the nematode populations. The experiment was arranged in a split-plot design with nematode population as main treatment, and genotype as the subplot treatment. Sweetpotato differential genotypes were distributed randomly within each nematode plot. Each treatment combination (nematode population and cultivar) was replicated 5 times and the same experiment was conducted at two different times. Data were transformed by $\sqrt{(x+0.5)}$ and analyzed with ANOVA using SAS (SAS Institute, Cary, N.C.). Means were separated using the Fisher's LSD procedure (alpha=0.05). Non-transformed data are presented in tables for clarity.

Results

A. Development of differential hosts

The initial screen of sweetpotato germplasm demonstrated that host status depended on the *Meloidogyne* species and race evaluated (Table 2). Sweetpotato genotype had a highly significant ($P < 0.001$) effect in each *Meloidogyne* species. A mean value of ten egg masses per root system or more, as used by the NC Differential Host Test (Hartman and Sasser, 1985) delineated a positive host plant reaction. All nematode populations were successful at infecting at least one sweetpotato cultivar, with the exception of *M. arenaria* race 1. *M. arenaria* race 1 was only able to infect and reproduce slightly on L86-33. *M. arenaria* race 2 only reproduced successfully on L86-33 (egg mass = 38) and relatively poorly on 'Nancy Hall' (egg mass = 8). Only L86-33 was a host for the other five *Meloidogyne* populations. 'Beauregard' was a host for *M. incognita* races 1, 2, 3 and 4, and *M. javanica*. The other cultivars varied in response depending on the nematode population. Interestingly, 'Pelican Processor' was only a host for *M. incognita* race 2. Sweetpotato genotypes such as 'Excel',

'Triumph', 'Regal', 'Tinian', 'Resisto', 'Tanzania', and 'Wagabolige' were also hosts for only a limited number of *Meloidogyne* populations (Table 2).

Due to their differential responses to the *Meloidogyne* populations tested, 'Beauregard', 'Centennial', 'Eureka', 'Jewel', L86-33, 'Nancy Hall', PDM P6, 'Pelican Processor', 'Porto Rico', 'Tanzania', 'Triumph', and 'Wagabolige' were selected as a set of differential sweetpotato hosts (Table 3). The results of the evaluations from the two tests (Tables 2 and 3) were not significantly different ($P>0.05$). The analysis of the combined data shows that nematode and cultivar effects were significant ($P=0.0033$ and $P<0.0001$, respectively). Also, the nematode x cultivar interaction was found to be significant ($P<0.0001$), and the results observed in the preliminary test were confirmed in the second test (Table 3).

M. incognita race 1 (Table 3) produced the greatest number of egg masses on 'Centennial' and 'Porto Rico'. *M. incognita* race 1 also produced a significant number of egg masses ($P<0.05$) on 'Beauregard', 'Eureka', L86-33, 'Nancy Hall', and PDM P6. The other cultivars were not infected by *M. incognita* race 1, except 'Tanzania' on which race 1 reproduced only slightly.

'Centennial', 'Pelican Processor' and 'Porto Rico' were hosts for *M. incognita* race 2 (Table 3). In contrast, 'Jewel', 'Tanzania', and 'Wagabolige' were not hosts for *M. incognita* race 2. The other genotypes were infected, but significantly less than 'Centennial'. *M. incognita* race 3 produced the greatest number of egg masses on 'Porto Rico' and 'Centennial', but failed to infect 'Pelican Processor', 'Tanzania', 'Triumph', and 'Wagabolige' (Table 3).

'Beauregard', PDM P6, 'Nancy Hall', and L86-33 were hosts for *M. incognita* race 4 (Table 3). All other cultivars, except 'Jewel' which was slightly affected, were non-hosts for this nematode population.

L86-33, 'Nancy Hall', and 'Beauregard' were hosts for *M. javanica* compared to 'Jewel' and 'Eureka' which were only slightly infected (Table 3). All the other cultivars were non-hosts for *M. javanica*.

From the sweetpotato clones evaluated, 'Beauregard', L86-33, PDM P6, 'Porto Rico', and 'Pelican Processor' were selected as a final set of sweetpotato differential hosts (Table 4). L86-33 was chosen as a genotype susceptible to *M. incognita*, *M. javanica*, and *M. arenaria*. No sweetpotato differential host was found to distinguish clearly between *M. incognita* race 1 and *M. incognita* race 3. 'Pelican Processor' was chosen as a key differential host for *M. incognita* race 2.

A. Nematode population variation

The results of the two nematode population variation tests were not significantly different ($P=0.08$). Analysis of the combined data showed that cultivar, place of origin of the nematode (site), nematode race x cultivar interaction, and cultivar x site interaction had significant ($P<0.001$) effects on *M. incognita* infection of sweetpotato. Data from the combined tests are presented in Table 6. Variation in host status was dependent on the sweetpotato genotype and the nematode population evaluated did not necessarily correspond to the designated nematode host race.

When analyzed by *Meloidogyne* race, cultivar effect and the cultivar x site interaction were significant for *M. incognita* race 1. Due to problems during the increase of the population from China, only two populations of *M. incognita* race 1 were evaluated in the

second test. Since data from both tests did not differ significantly, results on the population from China were drawn from test 1 only. For *M. incognita* race 2, cultivar, site and cultivar x site interaction were significant. For *M. incognita* race 3, cultivar and the cultivar x site interaction were significant. For *M. incognita* race 4, cultivar, site and the cultivar x site interaction were significant.

'Beauregard' and PDM P6 were infected by the three *M. incognita* race 1 populations from different geographical origins. In contrast, L86-33 and 'Porto Rico' had different reactions to the *M. incognita* race 1 populations. Based on their egg mass counts, 'Pelican Processor', 'Tanzania', 'Wagabolige' were considered as non-hosts for *M. incognita* race 1. 'Porto Rico' distinguished among the three *M. incognita* race 1 populations, with the population from NC being the most aggressive.

'Beauregard' was susceptible to the three *M. incognita* race 2 populations. L86-33 was minimally infected by the three *M. incognita* race 2 populations. PDMP6 was a host for the *M. incognita* race 2 populations from NC and Nigeria, but not *M. incognita* race 2 from Trinidad. 'Pelican Processor' and 'Porto Rico' were only hosts for *M. incognita* race 2 from NC.

'Beauregard' was susceptible to the three *M. incognita* race 3 populations. L86-33 was a host for the three *M. incognita* race 3 populations, but the *M. incognita* race 3 population from NC was the least aggressive. PDM P6 was a host for *M. incognita* race 3 populations from Louisiana and Uruguay. The *M. incognita* race 3 population from NC was able to reproduce in PDM P6, but the infection was low. 'Pelican Processor' was a non-host for the three *M. incognita* race 3 populations. 'Porto Rico' was only a host for *M. incognita* race 3 population from NC.

'Beauregard', L86-33, and PDMP6 were hosts for the three *M. incognita* race 4 populations and did not distinguish among the different populations. In contrast, 'Pelican Processor' was a host for the *M. incognita* race 4 populations from TX and Ghana, with the population from Ghana being more aggressive. 'Porto Rico' was only a host for *M. incognita* race 4 from Ghana.

Overall, 'Beauregard' was the most susceptible of the genotypes evaluated, being a host for all the *M. incognita* populations tested. L86-33 and PDM P6 were also hosts for almost all *M. incognita* populations tested, but the infection was generally lower than in 'Beauregard' (Table 6). 'Pelican Processor' and 'Porto Rico' had a different reaction to the *M. incognita* populations, being only hosts for certain isolates of the host races (Table 6). Also, for their particular traits of interest, 'Tanzania' and 'Wagabolige' were evaluated for their resistance to these 12 populations of nematodes, and both sweetpotato genotypes were non-hosts for all *M. incognita* populations tested.

Discussion

The results of these experiments confirm that the host status of sweetpotatoes for root-knot nematodes depends upon the sweetpotato genotype and *Meloidogyne* population. These results agree with those observed in other studies (Giamalva et al., 1963; Bonsi and Phills, 1979; and Cervantes-Flores et al. (in press)). The results of the evaluations of *Meloidogyne* populations from NC, suggest that there are probably different genes responsible for the resistance to the different *Meloidogyne* species and even races. This can be observed in the response of L86-33 to *M. arenaria* race 2 and *M. arenaria* race 1. *M. arenaria* race 2 is relatively aggressive on L86-33 as compared to *M. arenaria* race 1.

Another example was 'Pelican Processor' which supported a relatively high population of *M. incognita* race 2, but not any other *Meloidogyne* population. Netscher and Taylor (1979) also observed that sweetpotatoes did not have a uniform response to populations of the same species of *Meloidogyne*.

It is interesting to note that *M. arenaria* an aggressive pathogen of many plant species (Davis et al., 1988, 1998). However, our results have confirmed that most sweetpotato genotypes are resistant to *M. arenaria*, except for L86-33, which was susceptible to *M. arenaria* race 2. Cervantes-Flores et al., (in press) in a companion study did not observe infection in several sweetpotato genotypes by *M. arenaria* race 2. Similarly, Giamalva et al. (1963) did not observe *M. arenaria* developing to mature females on different sweetpotato varieties.

Breeding for resistance to *M. javanica* may not be a problem in sweetpotato, since good sources of resistance were observed in most cultivated varieties. However, 'Beauregard', L86-33 and 'Nancy Hall' were highly susceptible to *M. javanica*. This is important because *M. javanica* is the second most common nematode found in cultivated lands worldwide, especially in the tropics (Sasser, 1980; Taylor et al., 1982), and because 'Beauregard' and L86-33 are commonly used as breeding parents. Distinct host races of *M. javanica* using the NC Differential Host Test have not been identified (Hartman and Sasser, 1985). However, Sasser (1980) observed that a few populations of *M. javanica* parasitize 'California Wonder' pepper.

The importance of a clear assessment of the effect of the different root-knot nematode populations on specific plant genotypes, in order to establish better nematode control practices, has been debated (Sasser, 1980). In breeding for resistance to any pathogen, it is important for the plant breeder to have information on the physiological races or biotypes to

which the resistant varieties may be subjected in the field (Goplen et al., 1959). The problem of races among root-knot nematodes is quite different from the race problem in other diseases, because the rate of spread of virulent biotypes of nematodes is very slow (Goplen et al., 1959). Thus, a resistant cultivar could be efficiently deployed with the appropriate knowledge of the nematode pathotypes present in the field (Goplen et al., 1959). However, the outcrossing nature, heterozygosity and hexaploidy of sweetpotato, complicates the analysis of the genetic basis of root-knot nematode resistance in sweetpotato, which may translate into a very complex combination of the resistance genes. Thus, many different relationships can be expected when newly-released cultivars are subjected to pathogens highly heterozygous in their virulence genes, as is predicted in parthenogenic root-knot nematodes (Triantaphyllou, 1979).

During our development of the sweetpotato differential host genotypes, no genotypes could differentiate between races 1 and 3 of the North Carolina populations of *M. incognita*. But a clear differentiation was observed for the other *Meloidogyne* populations. However, when these proposed sweetpotato differential host genotypes were tested against the twelve populations of *M. incognita*, differences in virulence were observed within each designated *M. incognita* host race (Hartman and Sasser, 1985). Unfortunately, 'Beauregard' was a host for all twelve *M. incognita* populations. 'Beauregard' is the predominant variety in the U.S. and it has been used as a parental line in the U.S. and in many countries. Because resistance is the most economically efficient alternative in controlling nematodes in a low-valuable crop such as sweetpotato, this susceptibility of 'Beauregard' should be taken into account by breeders,

The egg mass values of L86-33 for *M. incognita* race 2 and PDM P6 for *M. incognita* race 3 were not consistent with egg mass values obtained during the selection of the sweetpotato differential host genotypes (Tables 2, 3 and 6). We suspect this could be due to a

change in the greenhouse conditions, or because the viability of the larvae was affected in the second experiment, probably during egg extraction. This is probably the case why the level of infection due to *M. incognita* race 3 was lower in the latter experiments, compared to the experiments in part A (Table 2 and 3). Also, we observed that in the qualitative analysis the host status of some genotypes, such as in the case of PDM P6 for *M. incognita* race 3, changed from '+' to '-' ('-' when egg mass <10 and '+' when egg mass >= 10). Which may be due to the expected variation in the number of egg masses of the samples around the critical value of 10.

Our results suggest that a better understanding of the relationships of the genes for plant resistance in sweetpotato and the nematode virulence genes is warranted given the differences in virulence observed among the *M. incognita* populations on the proposed sweetpotato differential genotypes. It is very interesting that several sweetpotato genotypes (e.g. 'Tanzania' and 'Wagabolige') possessed high levels of resistance to all *Meloidogyne* populations tested. These genotypes need to be further investigated to determine the nature of this multiple resistance. These genes are potentially valuable and they could be used to improve the levels of root-knot nematode resistance in adapted sweetpotato cultivars, with the possibility of conferring resistance to multiple *Meloidogyne* species.

The set of sweetpotato differential host genotypes selected in this work demonstrates the need to use sweetpotato differential host genotypes to identify distinct *Meloidogyne* populations present in regions of interest. They also demonstrate that the current classification of root-knot nematodes into host races (Hartman and Sasser, 1985), may not be applicable to host status of sweetpotato genotypes. This was demonstrated by the inconsistency of the ability of the *M. incognita* populations, classified as same host race, from different geographical origins (Hartman and Sasser, 1985) to infect the sweetpotato

differential genotypes. Further, the differential susceptibility (i.e. none, low, medium, and high infection levels) of the selected host suggests that root-knot nematode resistance in sweetpotato is probably quantitative. The different combinations of resistance genes in sweetpotato interacting with virulence genes in the nematode might determine the degree of the resistance. This observation is supported by studies of Giamalva et al. (1963), Davide and Struble (1966), Lawrence and Clark (1986).

The results presented in this study may explain differences in the resistance to root-knot nematodes observed by the different breeding programs (Pecota K.V., personal communication), and the apparent lack of resistance when clones are tested in different countries with varying root-knot nematode populations. Further studies of the genetic basis of sweetpotato resistance to root-knot nematode and tests against more *Meloidogyne* populations are needed to select the best set of sweetpotato differential host genotypes, and to incorporate additional differential genotypes to represent all sources of root-knot resistance available in sweetpotato germplasm. Our studies suggest that 'Beauregard' can be used as a susceptible control for resistance evaluations to *M. incognita* populations. Finally, this work contributes to the standardization of the evaluation of root-knot nematode resistance in sweetpotato breeding programs, and will promote a more efficient incorporation and exchange of sweetpotato germplasm when breeding for root-knot nematode resistance.

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Table 1. Pedigree of the sweetpotato genotypes evaluated for resistance to *M. are*naria (race 1 and 2), *M. incognita* (race 1, 2, 3 and 4), and *M. javanica*.

Cultivar	Pedigree[z]
Beauregard	L78-21>L70-197>L67-69>L59-89
Carogold	Unknown
Centennial	L-130>Unit 1 PR x Pelican Processor
Eureka	L9-163>L0-132(Centennial x Unit 1 PR)
Excel	Regal
Heartogold	Mameyita x Yellow Yam
Hernandez	L70-323>L63-217>L41-212
Jewel	Centennial x Nugget
L86-33	L82-508(Beauregard)
Nancy Hall	Unknown
Nugget	NC-124[NC-53(Tinian) x NC-65(NC-41 x NC-24)] x NC-63[NC-41(SC32-149 x 6-42-1) x NC-1(B5965)]
PDM P4	PI from Southeast Asia
PDM P6	PI from Southeast Asia
Pelican Processor	Americano
Porto Rico	PR varieties (derived from Mameyita)
Regal	W-99
Resisto	W-56 (derived from I/6 USDA population[y])
Southern Delite	W-99
Tanzania	African landrace
Tinian	Unknown
Triumph	Unknown
W-250	Unknown
W-271	Unknown
W-274	W-233
W- 99	SC-1166
Wagabolige	African landrace
Minamiyutaka	KS x KY-58[KA-48 x LM-17(Pelican Processor x K123-11(6X trifida))]

[z] Parents showed alone or after a '>' represent an open-pollination cross (the parent shown is the maternal parent and the male parent is unknow).

[y] Mass selected population created by the USDA sweetpotato breeding program (Jones et al., 1991).

Table 2. Host status of 27 sweetpotato genotypes for selected North Carolina *Meloidogyne* populations[z] in Test 1.

Cultivars	***M. arenaria*** Race 1		***M. arenaria*** race 2		***M. incognita*** race 1		***M. incognita*** race 2		***M. incognita*** race 3		***M. incognita*** race 4		***M. javanica***	
	EM[y]	S.D.[x]	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.
Beauregard	0.0 b[w]	0.0	0.0c	0.0	38.8b	1.2	27.4cd	1.2	4.7de	0.7	21.8 a	1.0	23.8a	0.5
Carogold	0.0 b	0.0	0.0c	0.0	0.3ef	0.1	0.3g	0.1	0.3f	0.1	0.0 f	0.0	0.0d	0.0
Centennial	0.0 b	0.0	0.3c	0.1	51.7b	5.3	90.2a	6.0	40.6a	2.7	0.0 f	0.0	0.3d	0.1
Eureka	0.0 b	0.0	0.0c	0.0	23.2c	3.0	10.7e	7.0	12.2bc	4.2	0.0 f	0.0	0.0d	0.0
Excel	0.0 b	0.0	0.2c	0.1	0.3ef	0.1	0.0g	0.0	0.0f	0.0	0.0 f	0.0	0.0d	0.0
Heartogold	0.0 b	0.0	0.0c	0.0	0.4ef	0.3	0.2g	0.1	3.5de	2.9	3.2 bcd	0.7	0.0d	0.0
Hernandez	0.0 b	0.0	0.0c	0.0	0.7ef	0.1	1.2g	0.7	1.8ef	0.2	0.0 f	0.0	0.0d	0.0
Jewel	0.0 b	0.0	0.0c	0.0	1.0ef	0.3	0.7G	0.1	6.8cd	0.7	2.3 cde	0.8	1.7c	0.6
L86-33	2.7 a	1.6	38.0a	0.2	22.1c	4.2	2.2fg	1.0	12.6bc	1.3	6.3 b	2.1	23.7a	0.2
Nancy Hall	0.0 b	0.0	8.8b	0.7	21.2c	3.3	15.6de	1.0	15.1b	0.9	17.9 a	0.7	20.5a	2.1
Nugget	0.0 b	0.0	0.0c	0.0	0.5ef	0.1	0.0g	0.0	0.2f	0.1	0.7 def	0.1	3.2b	0.0
PDM P4	0.0 b	0.0	0.0c	0.0	0.0f	0.0	0.0g	0.0	0.0f	0.0	0.0 f	0.0	0.0d	0.0
PDM P6	0.0 b	0.0	0.0c	0.0	19.4c	0.8	7.7ef	0.9	2.3ef	0.6	18.4 a	5.5	0.0d	0.0
Pelican Processor	0.0 b	0.0	0.0c	0.0	0.0f	0.0	35.7c	1.1	0.0f	0.0	0.0 f	0.0	0.0d	0.0
Porto Rico	0.0 b	0.0	0.0c	0.0	85.4a	4.8	60.2b	7.7	49.5a	6.1	0.0 f	0.0	0.0d	0.0
Regal	0.0 b	0.0	0.0c	0.0	0.0f	0.0	0.2g	0.1	0.0f	0.0	0.0 f	0.0	0.0d	0.0
Resisto	0.0 b	0.0	0.0c	0.0	0.0f	0.0	0.3g	0.1	0.0f	0.0	0.0 f	0.0	0.0d	0.0
Southern Delite	0.0 b	0.0	0.0c	0.0	0.6ef	0.3	3.0fg	4.4	0.0f	0.0	4.9 bc	4.4	0.0d	0.0
Tanzania	0.0 b	0.0	0.0c	0.0	7.0d	0.3	0.5g	0.1	0.2f	0.1	0.3 ef	0.1	0.0d	0.0
Tinian	0.0 b	0.0	0.0c	0.0	0.0f	0.0	0.0g	0.0	0.0f	0.0	0.0 f	0.0	0.0d	0.0
Triumph	0.0 b	0.0	0.0c	0.0	0.3ef	0.1	7.2ef	0.3	0.0f	0.0	0.2 ef	0.1	0.0d	0.0
W 250	0.0 b	0.0	0.0c	0.0	0.0f	0.0	0.6g	0.3	0.2f	0.1	0.0 f	0.0	0.0d	0.0
W 271	0.0 b	0.0	0.0c	0.0	0.0f	0.0	0.0g	0.0	0.0f	0.0	0.0 f	0.0	0.0d	0.0
W 274	0.0 b	0.0	0.0c	0.0	0.0f	0.0	2.3fg	0.8	0.3f	0.1	0.0 f	0.0	0.0d	0.0
W 99	0.0 b	0.0	0.0c	0.0	3.0de	0.4	0.0g	0.0	1.5ef	0.3	0.5 ef	0.1	0.0d	0.0
Wagabolige	0.0 b	0.0	0.0c	0.0	0.3ef	0.1	0.2g	0.1	0.0f	0.0	0.9 def	0.2	0.0d	0.0

(Continuation Table 2)

[z] Populations maintained in pure greenhouse culture on 'Rutgers' tomato and race determined by NC Differential Host Test (Hartman and Sasser, 1985).

[y] Egg mass number per root system. Table values are the non-transformed mean of five replications per cultivar. Transformation used for data analysis was $\sqrt{(x+0.5)}$.

[x] Standard deviation for EM's values.

[w] Means within the same column followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, $k=100$).

Table 3. Host status of selected sweetpotato genotypes to North Carolina *Meloidogyne* populations[z].

Cultivars	***M. arenaria*** race1		***M. arenaria*** race 2		***M. incognita*** race 1		***M. incognita*** race 2		***M. incognita*** race 3		***M. incognita*** race 4		***M. javanica***	
	EM[y]	S.E.[x]	EM	S.E.	EM	S.E.	EM	S.E.	EM	S.E.	EM	S.E.	EM	S.E.
Beauregard	0.0b[w]	0.0	0.0c	0.0	24.3b	0.5	23.6 b	0.2	16.2cd	0.5	34.2a	0.4	28.5b	0.1
Centennial	0.0b	0.0	0.1c	0.1	48.4a	0.6	44.6 a	1.2	28.7ab	0.3	0.2d	0.0	0.2d	0.0
Eureka	0.0b	0.0	0.0c	0.0	25.8b	0.6	14.1 bc	0.4	22.7bc	0.5	0.5cd	0.0	2.8c	0.5
Jewel	0.0b	0.0	0.0c	0.0	1.2c	0.0	1.9 d	0.0	4.8e	0.1	3.0c	0.1	3.5c	0.1
L86-33	4.6a	0.1	43.5a	0.2	16.6b	0.3	3.4 d	0.1	10.2de	0.1	14.8b	0.3	48.1a	0.6
Nancy Hall	0.0b	0.0	8.2b	0.1	18.3b	0.2	24.5 b	0.2	19.2bc	0.2	29.6a	0.4	36.0b	0.5
PDM P6	0.0b	0.0	0.0c	0.0	26.0b	0.2	16.2 bc	0.3	14.2cd	0.6	32.0a	0.7	0.1d	0.0
Pelican Processor	0.0b	0.0	0.0c	0.0	0.3c	0.0	42.1 a	0.1	0.0f	0.0	0.3d	0.0	0.0d	0.0
Porto Rico	0.0b	0.0	0.0c	0.0	47.1a	0.9	40.2 a	0.7	38.0a	0.4	0.2d	0.0	0.0d	0.0
Triumph	0.0b	0.0	0.0c	0.0	0.3c	0.0	10.5 c	0.2	0.2f	0.0	0.1d	0.0	0.0d	0.0
Tanzania	0.0b	0.0	0.1c	0.0	3.3c	0.1	0.5 d	0.0	0.1f	0.0	1.0cd	0.0	0.2d	0.0
Wagabolige	0.0b	0.0	0.0c	0.0	0.1c	0.0	0.2 d	0.0	0.0f	0.0	0.9cd	0.0	0.0d	0.0

[z] Populations maintained in pure greenhouse culture on 'Rutgers' tomato and race determined by NC Differential Host Test (Hartman and Sasser, 1985).

[y] Egg mass number per root system. Table values are the non-transformed mean of two tests of five replications each. Transformation used for data analysis was $\sqrt{(x+0.5)}$.

[x] Standard error of the mean of egg masses.

[w] Means within a column followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, *k*=100).

Table 4. Proposed list of sweetpotato differential hosts[z], and their qualitative resistance response[y] to different *Meloidogyne* populations[x].

Root-knot nematode	Sweetpotato genotype				
	Beauregard	L86-33	PDM P6	Porto Rico	Pelican Processor
M. arenaria	-	+	-	-	-
M. incognita 1	+	+	+	+	-
M. incognita 2	+	-	+	+	+
M. incognita 3	+	+	+	+	-
M. incognita 4	+	+	+	-	-
M. javanica	+	+	-	-	-

[z] Sweetpotato genotypes selected for their differential resistance response to different races of *Meloidogyne*.

[y] Resistance response considered as (+) if the number of egg masses per root system were >= 10, and (-) if < 10.

[x] *Meloidogyne* populations were obtained from the Nematology program at NC State University. Raleigh, NC. Race classification of nematode was in according to the NC Differential Host Test (Hartmant and Sasser, 1985).

Table 5. *Meloidogyne incognita* populations[z] used to evaluate the suitability of the selected potential sweetpotato differential hosts.

Nematode host race[y]	Date of storage	Place of collection
M. incognita race 1	08/04/1988	Africa[x]
M. incognita race 1	06/03/1988	China
M. incognita race 1	Not stored[w]	NC, U.S.
M. incognita race 2	06/01/1990	Trinidad
M. incognita race 2	04/05/1985	Nigeria
M. incognita race 2	Not stored	NC, U.S.
M. incognita race 3	01/12/1989	Uruguay
M. incognita race 3	11/11/1988	La., U.S.
M. incognita race 3	Not stored	NC, U.S.
M. incognita race 4	09/09/1988	TX, U.S.
M. incognita race 4	08/12/1988	Ghana
M. incognita race 4	Not stored	NC, U.S.

[z] Populations were collected by scientists participating in the International *Meloidogyne* Project and stored frozen in liquid nitrogen (Hartman and Sasser, 1985).

[y] Race classification of nematode was in according to the NC Differential Host Test (Hartman and Sasser, 1985).

[x] For Africa, no specification of country was available in the collection data.

[w] Nematode populations from NC were not stored under cryogenic conditions. These were obtained from grenhouse cultures in the Nematology program at NC State University, Raleigh, NC.

Table 6. Host status of proposed sweetpotato differential hosts[z] to 12 populations of *Meloidogyne incognita*[y] collected worldwide.

RKN species and host race	Site of collection	Sweetpotato genotype													
		Beauregard		L86-33		PDM P6		Porto Rico		Pelican Processor		Tanzania[x]		Wagabolige[x]	
		EM[w]	S.E.[v]	EM	S.E.	EM	S.E.	EM	S.E.	EM	S.E.	EM	S.E.	EM	S.E.
M. incognita 1															
	Africa	37.2a[u]	0.3	5.8 b	0.3	30.2a	0.3	7.0b	0.2	1.6a	0.1	1.8a	0.1	1.4 a	0.0
	China[t]	21.4a	0.3	10.4 a	0.1	15.3a	0.5	0.3c	0.2	0.5a	0.0	0.2a	0.0	0.0 a	0.0
	NC - U.S.	37.3a	0.3	25.5 a	0.3	22.4a	0.3	42.9a	0.5	1.4a	0.0	0.4a	0.0	0.5 a	0.0
M. incognita 2															
	Nigeria	18.9b	0.9	6.1 b	0.3	12.6b	0.2	2.3b	0.1	0.2b	0.0	2.5a	0.1	0.1 a	0.0
	Trinidad	39.4a	0.3	12.6 a	0.2	8.3b	0.1	2.0b	0.1	0.0b	0.0	0.3b	0.1	0.0 a	0.0
	NC - U.S.	29.7ab	0.2	10.8 ab	0.1	27.6a	0.1	26.9a	0.2	41.2a	0.4	0.1b	0.0	0.2 a	0.0
M. incognita 3															
	La. - U.S.	39.5a	0.2	10.1 b	0.1	29.9a	0.4	2.8b	0.1	0.7a	0.0	2.0a	0.0	0.2 a	0.0
	Uruguay	48.4a	1.0	24.6 a	0.2	25.2a	0.3	0.3b	0.0	0.3a	0.0	2.0a	0.1	0.0 b	0.0
	NC - U.S.	25.9a	0.2	6.1 b	0.1	5.6b	0.1	12.7a	0.3	0.2a	0.0	0.0b	0.0	0.0 b	0.0
M. incognita 4															
	TX - U.S.	45.6a	0.7	13.0 ab	0.1	25.1a	0.3	2.1b	0.0	17.7b	0.2	0.8a	0.2	0.0 b	0.0
	Ghana	33.4a	0.3	11.4 b	0.1	24.5a	0.2	28.6a	1.4	42.8a	0.2	0.5a	0.2	0.6 a	0.3
	NC - U.S.	47.5a	0.5	21.1 a	0.2	27.5a	0.1	1.0b	0.0	0.2c	0.0	0.5a	0.3	0.1 ab	0.0

[z] Sweetpotato genotypes selected for their differential response to the 4 *Meloidogyne incognita* host races from the greenhouse cultures in the Nematology program at NC State University.

[y] Nematode populations were collected by scientists participating in the International *Meloidogyne* Project and kept frozen in liquid nitrogen. Populations from NC. were not subjected to cryogenic storage. Race designation is based upon NC Differential Host Test (Hartman and Sasser, 1985)

[x] African landraces of particular interest with virus resistance and high dry-matter content.

[w] Number of egg masses produced by the nematodes in the surface of the root system. EM is the mean of two tests of five replications each.

[v] Standard error of the mean for EM.

[u] For each RKN population, values within a column followed by the same letter are not significantly different (Fisher's protected-LSD test, alpha=0.05). Transformation of data used for the corresponding ANOVA was $\sqrt{(x+0.5)}$.

[t] EM mean and significance value for *M. incognita* race 1 from China is based only on one test of five replications.

Appendices

Appendix Table 1.1. Root necrosis, root galling and number of egg masses produced by *Meloidogyne arenaria* race 2, *M. incognita* race 3 and *M. javanica* on selected sweetpotato cultivars in two container types in Test 1.

Cultivar	Necrosis[z]				Galling[y]				Eggs•g^{-1} [x]			
	Pot[w]	Cone[v]	Mean	S.D.	Pot	Cone	Mean	S.D.	Pot	Cone	Mean	S.D.
M. arenaria race 2												
Beauregard	2.3	1.0	1.6	0.4	0.0	0.0	0.0	0.0	0.0	1.5	0.6	0.9
Excel	6.7	8.5	7.6	0.2	0.0	1.0	0.4	0.5	3.9	6.4	5.0	0.3
Hernandez	1.9	6.2	3.6	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jewel	3.7	0.0	1.2	2.0	0.0	0.0	0.0	0.0	0.8	30.2	6.5	6.5
Porto Rico	4.0	4.8	4.4	0.1	0.8	0.6	0.7	0.1	0.0	0.8	0.4	0.5
M. incognita race 3												
Beauregard	2.2	0.0	0.8	1.2	14.4	8.8	11.3	0.4	2925.2	117.5	587.9	8.6
Excel	3.2	2.6	2.9	0.1	1.0	0.0	0.4	0.6	3.2	0.0	1.1	1.7
Hernandez	4.2	0.7	2.0	1.2	0.0	0.6	0.3	0.4	37.0	13.1	22.2	1.0
Jewel	7.8	1.1	3.3	1.8	1.3	0.0	0.5	0.8	3.5	0.0	1.1	1.9
Porto Rico	11.3	15.8	13.4	0.3	21.8	11.1	15.6	0.6	1654.2	830.9	1172.4	0.6
M. javanica												
Beauregard	10.4	3.5	6.2	0.9	43.6	6.4	17.2	2.6	9169.3	3632.8	5771.6	0.9
Excel	7.7	1.1	3.3	1.7	0.6	0.0	0.3	0.4	1.1	1.2	1.1	0.1
Hernandez	7.0	3.7	5.1	0.5	0.4	0.0	0.2	0.2	0.9	0.9	0.9	0.0
Jewel	7.6	0.4	2.5	2.5	1.0	0.4	0.7	0.2	523.2	100.3	229.5	2.2
Porto Rico	22.9	2.0	7.4	3.3	1.0	0.0	0.4	0.6	4.8	0.0	1.4	2.5

[z] Necrosis values are the mean of five plants each. Necrosis is expressed as the percent of necrotic root tissue. Values were not significantly different between types of container ($P>0.05$).

[y] Galling values in pot and cone are the mean of five plants each. They are expressed as the percent of root galled. Values were not significantly different between types of container ($P>0.05$).

[x] Eggs•g^{-1} values are the mean of five plants each. They are expressed as the number of eggs found per gram of root tissue. Values were not significantly different between types of container ($P>0.05$).

[w] Pot, represents the 400 cm^3 container, model LAPOT (Landmark Plastic Corporation, Orlando, Fla.)

[v] Cone, represents the 150 cm^3, SC-10 Super Cell Conetainer™ (Stuewe & Sons, Inc., Corvallis, Ore.)

Appendix Table 1.2. Root necrosis, root galling and number of egg masses produced by *Meloidogyne arenaria* race 2, *M. incognita* race 3 and *M. javanica* on selected sweetpotato cultivars in two container types in Test 2.

Cultivar	Necrosis[z]				Galling[y]				Eggs•g^{-1} [x]			
	Pot[w]	Cone[v]	Mean	S.D.	Pot	Cone	Mean	S.D.	Pot	Cone	Mean	S.D.
M. arenaria race 2												
Beauregard	2.5	13.9	6.3	1.7	0.0	0.0	0.0	0.0	0.8	0.0	0.4	0.5
Excel	1.2	1.4	1.3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.4	0.6
Hernandez	1.0	3.2	1.9	0.7	0.0	0.0	0.0	0.0	0.0	1.5	0.6	0.9
Jewel	2.4	3.7	3.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Porto Rico	8.0	10.1	9.0	0.2	0.0	0.0	0.0	0.0	1.1	1.1	1.1	0.0
M. incognita race 3												
Beauregard	1.2	6.6	3.1	1.4	7.5	23.6	13.5	1.1	2427.3	2593.4	2508.9	0.1
Excel	0.8	1.5	1.1	0.3	0.0	0.0	0.0	0.0	1.3	1.2	1.3	0.0
Hernandez	0.1	1.9	0.8	0.9	0.0	0.6	0.3	0.4	15.2	27.9	20.7	0.5
Jewel	0.9	2.8	1.7	0.6	0.2	1.5	0.7	0.7	1.5	127.2	17.0	15.0
Porto Rico	12.8	12.8	12.8	0.0	28.4	23.6	25.9	0.1	3975.5	1115.7	2106.2	1.4
M. javanica												
Beauregard	1.7	1.2	2.5	0.4	14.5	36.8	23.2	0.9	4926.7	5264.2	5092.4	0.0
Excel	0.4	0.4	0.4	0.0	0.1	0.0	0.1	0.1	0.0	0.9	0.4	0.5
Hernandez	0.9	1.2	1.0	0.1	0.0	0.0	0.0	0.0	0.0	0.9	0.4	0.6
Jewel	1.3	1.8	1.6	0.1	0.0	0.0	0.0	0.0	5.1	28.8	12.5	2.1
Porto Rico	4.2	5.6	4.8	0.2	0.0	0.0	0.0	0.0	0.0	3.2	1.0	1.7

[z] Necrosis values are the mean of five plants each. Necrosis is expressed as the percent of necrotic root tissue. Values were not significantly different between types of container ($P>0.05$).

[y] Galling values in pot and cone are the mean of five plants each. They are expressed as the percent of root galled. Values were not significantly different between types of container ($P>0.05$).

[x] Eggs•g^{-1} values are the mean of five plants each. They are expressed as the number of eggs found per gram of root tissue. Values were not significantly different between types of container ($P>0.05$).

[w] Pot, represents the 400 cm^3 container, model LAPOT (Landmark Plastic Corporation, Orlando, Fla.)

[v] Cone, represents the 150 cm^3, SC-10 Super Cell Conetainer™ (Stuewe & Sons, Inc., Corvallis, Ore.)

Appendix Table 2.1. Host status of a selected group of sweetpotato genotypes to North Carolina *Meloidogyne* populations[z] in Test 2.

Genotypes	***M. arenaria*** race1		***M. arenaria*** race 2		***M. incognita*** race 1		***M. incognita*** Race 2		***M. incognita*** race 3		***M. incognita*** race 4		***M. javanica***	
	EM[y]	S.D.[x]	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.
Beauregard	0.0b[w]	0.0	0.0c	0.0	38.8cd	1.2	27.4cd	1.2	4.7ab	0.6	21.8a	1.0	23.8c	0.5
Centennial	0.0b	0.0	0.3c	0.2	51.7a	5.3	90.2d	6.0	40.6c	2.7	0.0c	0.0	0.3e	0.1
Eureka	0.0b	0.0	0.0c	0.0	23.2abc	3.0	10.7cd	6.9	12.2a	4.2	0.0c	0.0	0.0d	0.0
Jewel	0.0b	0.0	0.0c	0.0	1.0e	0.3	0.7ef	0.1	6.8de	0.8	2.3c	0.9	1.7d	0.6
L86-33	2.7a	1.6	38.0a	0.2	22.1d	4.2	2.2e	1.0	12.6d	1.3	6.3b	2.1	23.6a	0.2
Nancy Hall	0.0b	0.0	8.8b	0.7	21.2cd	3.3	15.6ab	1.0	15.1bc	0.9	17.9a	0.7	20.5b	2.1
PDM P6	0.0b	0.0	0.0c	0.0	19.4ab	0.8	7.7bc	0.8	2.3a	0.6	18.4a	5.5	0.0e	0.0
Pelican Processor	0.0b	0.0	0.0c	0.0	0.0e	0.0	35.7a	1.1	0.0f	0.0	0.0c	0.0	0.0e	0.0
Porto Rico	0.0b	0.0	0.0c	0.0	85.4bcd	4.7	60.2bcd	7.7	49.5abc	6.1	0.0c	0.0	0.0e	0.0
Triumph	0.0b	0.0	0.0c	0.0	0.3e	0.1	7.2d	0.3	0.0ef	0.0	0.2c	0.1	0.0e	0.0
Tanzania	0.0b	0.0	0.0c	0.0	7.0e	0.3	0.5f	0.1	0.2f	0.1	0.3c	0.1	0.0e	0.0
Wagabolige	0.0b	0.0	0.0c	0.0	0.3e	0.2	0.2f	0.1	0.0f	0.0	0.8c	0.2	0.0e	0.0

[z] Populations maintained in pure greenhouse culture on 'Rutgers' tomato and race determined by NC Differential Host Test (Hartman and Sasser, 1985).

[y] Number of egg masses per root of the *Meloidogyne* species. Table values are the non-transformed mean of five replications. Transformation used for data analysis was $\sqrt{(x+0.5)}$.

[x] Standard deviation of egg masses.

[w] Means within the same column followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, k=100).

Appendix Table 2.2. Host status of proposed sweetpotato differential hosts[z] genotypes to 12 populations of *Meloidogyne incognita*[y] collected worldwide in Test 1.

RKN species and host race	Site of collection	Sweetpotato genotype													
		Beauregard		L86-33		PDM P6		Porto Rico		Pelican Processor		Tanzania[x]		Wagabolige[x]	
		EM[w]	S.D.[v]	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.
M. incognita 1															
	Africa	28.1a[u]	3.8	0.8b	0.2	24.3a	3.4	13.6a	1.4	4.2a	0.5	4.2a	0.5	2.6a	0.4
	China	21.4a	0.3	10.4a	0.1	15.3a	0.5	0.3b	0.2	0.5b	0.0	0.2b	0.0	0.0b	0.0
	NC-U.S.	30.2a	1.0	15.2a	0.7	16.7a	1.6	21.4a	1.9	1.9ab	0.3	0.2b	0.1	0.8ab	0.2
M. incognita 2															
	Nigeria	5.7b	0.1	2.2a	0.9	6.9b	0.8	1.1b	0.6	0.3b	0.1	0.9a	0.4	0.0a	0.0
	Trinidad	22.1a	1.1	6.8a	0.5	7.5b	1.6	1.5b	0.6	0.0b	0.0	0.5a	0.2	0.0a	0.0
	NC-U.S.	21.8a	1.3	8.4a	1.5	27.2a	0.4	18.5a	1.2	23.4a	2.7	0.2a	0.1	0.4a	0.3
M. incognita 3															
	LA-U.S.	36.4a	2.4	12.6ab	0.7	17.6a	2.2	5.5ab	1.2	1.6a	0.0	2.2a	0.5	0.5a	0.1
	Uruguay	38.3a	1.9	17.8a	1.8	26.1a	0.9	0.6b	0.3	0.2b	0.1	1.1ab	0.6	0.0b	0.0
	NC-U.S	17.8a	2.0	5.5b	1.1	5.2b	0.5	7.6a	2.5	0.0b	0.0	0.0b	0.0	0.0b	0.0
M. incognita 4															
	TX-U.S.	32.9a	4.3	13.0ab	1.0	16.9a	1.3	3.4b	0.5	10.4b	2.0	1.3a	0.1	0.0a	0.0
	Ghana	25.4a	2.5	8.3b	1.7	21.2a	1.3	21.5a	1.1	38.3a	2.4	0.8a	0.2	0.3a	0.2
	NC-U.S.	31.8a	2.3	24.0a	0.7	24.4a	0.5	0.0c	0.0	0.5c	0.1	0.2a	0.1	0.2a	0.1

[z] Sweetpotato genotypes selected for their differential response to the 4 *Meloidogyne incognita* host races from the greenhouse cultures in the Nematology program at NC State University.

[y] Nematode populations were collected by scientists participating in the International *Meloidogyne* Project, and kept frozen in liquid nitrogen. Populations from NC-U.S. were not subjected to cryogenic storage. Race designation is based upon NC Differential Host Test (Hartman and Sasser, 1985)

[x] African landraces of particular interest with virus resistance and high dry-matter content.

[w] Number of egg masses produced by the nematodes in the surface of the root system. EM is the mean of five replications.

[v] Standard deviation of EM.

[u] For each RKN population, values within a column followed by the same letter are not significantly different (Fisher's protected-LSD test, alpha=0.05). Transformation of data used for the corresponding ANOVA was $\sqrt{(x+0.5)}$.

Appendix Table 2.3. Host status of proposed sweetpotato differential hosts[z] genotypes to 12 populations of *Meloidogyne incognita*[y] collected worldwide in Test 2.

RKN species and host race	Site of collection	Sweetpotato genotype													
		Beauregard		L86-33		PDM P6		Porto Rico		Pelican Processor		Tanzania[x]		Wagabolige[x]	
		EM[w]	S.D.[v]	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.	EM	S.D.
M. incognita 1															
	Africa	47.5a[u]	2.1	14.4b	1.0	36.8a	2.0	2.4b	1.2	0.0a	0.0	0.3a	0.2	0.5a	0.2
	NC-U.S.	45.2a	5.3	38.4a	1.8	28.9a	3.1	71.6a	0.7	0.9a	0.4	0.7a	0.7	0.2a	0.1
M. incognita 2															
	Nigeria	39.4a	11.3	11.5a	2.8	19.7ab	2.6	3.8b	0.5	0.0b	0.0	4.7a	0.7	0.3a	0.2
	Trinidad	61.6a	0.5	20.0a	1.2	9.2b	1.3	2.6b	1.3	0.0b	0.0	0.2b	0.1	0.0a	0.0
	NC-U.S.	38.7a	0.9	13.4a	0.7	27.9a	2.0	36.9a	0.6	64.5a	0.3	0.0b	0.0	0.0a	0.0
M. incognita 3															
	LA-U.S.	42.6a	1.5	7.9b	0.1	45.3a	2.1	0.9b	0.3	0.0a	0.0	1.8a	0.2	0.0a	0.0
	Uruguay	59.8a	18.5	32.6a	1.3	24.3a	6.4	0.0b	0.0	0.5a	0.1	3.0a	0.8	0.0a	0.0
	NC-U.S.	35.6a	1.0	6.8b	0.5	6.0b	0.7	19.1a	2.8	0.5a	0.2	0.0b	0.0	0.0a	0.0
M. incognita 4															
	TX-U.S.	60.2a	7.9	12.9a	0.3	34.8a	3.9	0.9b	0.3	26.8b	0.5	0.5a	0.2	0.0a	0.0
	Ghana	42.5a	2.8	14.9a	1.0	27.9a	2.0	36.7a	0.9	47.5a	2.1	0.2a	0.1	0.9a	0.5
	NC-U.S.	66.4a	5.5	18.4a	4.0	30.8a	1.0	2.5b	0.2	0.0c	0.0	1.0a	0.5	0.0a	0.0

[z] Sweetpotato genotypes selected for their differential response to the 4 *Meloidogyne incognita* host races from the greenhouse cultures in the Nematology program at NC State University.

[y] Nematode populations were collected by scientists participating in the International *Meloidogyne* Project, and kept frozen in liquid nitrogen. Populations from NC-U.S. were not subjected to cryogenic storage. Race designation is based upon NC Differential Host Test (Hartman and Sasser, 1985)

[x] African landraces of particular interest with virus resistance and high dry-matter content.

[w] Number of egg masses produced by the nematodes in the surface of the root system. EM is the mean of five replications.

[v] Standard deviation of EM.

[u] For each RKN population, values within a column followed by the same letter are not significantly different (Fisher's protected-LSD test, alpha=0.05). Transformation of data used for the corresponding ANOVA was $\sqrt{(x+0.5)}$.