Variation in Root Architecture Attributes at the Onset of Storage Root Formation among Resistant and Susceptible Sweetpotato Cultivars Infected with *Meloidogyne incognita*

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Abstract. In sweetpotato (*Ipomoea batatas*), the successful emergence and development of lateral roots (LRs), the main determinant of root system architecture (RSA), determines the competency of adventitious roots (ARs) to undergo storage root formation. The present study investigated the effect of three levels of root-knot nematode (RKN) inoculum of race 3 of *Meloidogyne incognita* on LR length, number, area, and volume in ‘Beauregard’, ‘Evangeline’, and ‘Bayou Belle’, sweetpotato cultivars which are highly susceptible, moderately resistant, and highly resistant, respectively, to *M. incognita*. The three RKN levels were control (untreated), medium (500 eggs/pot), and high (5000 eggs/pot). In general, the number of galls after 20 days for each cultivar was consistent across RKN levels and two planting dates (PDs). ‘Beauregard’ inoculated with medium and high RKN levels showed 2.9 and 18.9 galls on each AR, respectively. ‘Evangeline’ had 0.5 and 3.4 galls at medium and high RKN levels, respectively. By contrast, ‘Bayou Belle’ showed only 0.9 galls at the high inoculum level. There was a significant PD × cultivar effect and cultivar × RKN level effect for all root attributes. LR attributes varied within and among resistant and susceptible cultivars with a general trend for increase in all root growth attributes in response to RKN infection in the first (PD1) and second PD (PD2). ‘Evangeline’ showed relatively consistent within-cultivar increase across PD1 (medium and high RKN levels) and PD2 (medium RKN level only). LR length, number, area, and volume within ‘Evangeline’ plants subjected to high RKN increased 122%, 126%, 154%, and 136%, respectively, relative to the untreated control plants in PD1. ‘Evangeline’ (PD1 and PD2) and ‘Bayou Belle’ (PD1 only) showed significant increase in all root attributes relative to the susceptible ‘Beauregard’ at medium or high RKN levels. In PD1, LR length, number, area, and volume in ‘Evangeline’ plants subjected to high RKN increased 165%, 167%, 176%, and 190%, respectively, relative to ‘Beauregard’ plants at the same RKN level. These findings are consistent with some data in other systems wherein nematode infection is associated with cultivar-specific root compensatory growth and demonstrate how genotype and environment interact to modify root development responses. These data can be used to further understand the role of cultivar-specific responses to nematode infection and can lead to the consideration of root traits in selection strategies.

The southern RKN (*M. incognita*) is a major biotic stress to sweetpotato (*I. batatas*) production in many regions (Overstreet, 2013). In addition to causing reductions in yield in susceptible cultivars, the nematode can diminish the quality of the storage roots by inducing the formation of cracks on some cultivars or pimple-like bumps on other cultivars and by the presence of dark areas within the flesh of the sweetpotato associated with the presence of enlarged females and their egg masses (Lawrence et al., 1986; Overstreet, 2013). Cracks induced by the nematodes can also provide an opportunity for decay organisms to enter the root and cause secondary storage rots. Current management options for *Meloidogyne* spp. in

sweetpotatoes include cultural practices, nematicides, and resistance (Lawrence et al., 1986; Overstreet, 2013). Of these, resistance is one of the primary approaches for managing RKN in sweetpotatoes (Overstreet, 2013). Resistance is usually identified in sweetpotato germplasm by determining the incidence of galls and egg masses following standardized inoculation of plants in greenhouse evaluations (Cervantes-Flores et al., 2002). While RKN effects on storage root yield have been demonstrated in field plots (Dukes et al., 1994; Lawrence et al., 1986), there is a lack of information on how infection affects RSA in either susceptible or resistant genotypes. Thus, it is important to understand the relationship between RSA and nematode resistance in sweetpotato.

There has been some progress in understanding the genetic basis of resistance to RKN (Cervantes-Flores et al., 2002, 2008) and the potential role of molecular markers as tools for improving selection for nematode resistance (Mcharo et al., 2005; Ukoskit et al., 1997). In comparison, there is relatively limited information about how the root system responds to nematode infection, especially during the critical storage root formation stage, defined as the appearance of cambia around the protoxylem and secondary xylem elements (Togari, 1950; Wilson and Lowe, 1973). Recent evidence has implicated LR development, a key determinant of RSA, as being fundamentally associated with the competency of ARs to undergo storage root formation (Villordon et al., 2012). RSA has been referred to as the integrative result of LR initiation, morphogenesis, emergence, and growth (Dubrovsky and Forde, 2012). LRs facilitate the extraction of soil-based resources such as water and nutrients (Casimiro et al., 2003). Understanding of the variables that control RSA development can lead to a more systematic approach to determining and managing biotic and abiotic yield constraints of this globally important root crop. The roles of water and nitrogen availability in altering RSA during the critical storage root initiation period have been validated in the cultivar ‘Beauregard’ (Villordon et al., 2012, 2013). Recently, it has been shown that virus infection directly influenced LR development in ‘Beauregard’ sweetpotato plants infected with a complex of viruses (Villordon and Clark, 2014). Such findings provide evidence about the potential influence of biotic factors on RSA development in sweetpotato. The primary objective of this work was to investigate RSA response of resistant and susceptible sweetpotato cultivars infected with RKN. RSA attributes such as root length have been used as an important characteristic to determine nematode damage or plant tolerance (Pang et al., 2011; Rawsthorne and Brodie, 1986).

Materials and Methods

Nematodes. A population of race 3 of *M. incognita* originally isolated from Beauregard sweetpotato in Louisiana was provided by Charles Overstreet (Dept. Plant Pathology and Crop Physiology, LSU AgCenter, Baton Rouge, LA). The population was maintained in a greenhouse on ‘Yolo Wonder’ pepper plants (*Capsicum annuum*). Inoculum was harvested from roots of the pepper plants at ≈45–60 d after inoculation by washing the roots with tap water, extracting eggs from egg masses by immersion in 0.525% NaOCl for 4 mins, and collecting the eggs on a 500-mesh (25 µm opening) sieve. Egg suspensions were diluted to deliver either 500 (medium) or 5000 (high) eggs per pot. To enhance infiltration of inoculum, three holes, 7 mm in diameter by 50 mm deep, were made in the soil equally spaced at ≈3 cm from the planted stem and the inoculum was added to

the surface of each pot at 25 mL volume per pot immediately after planting.

Plant material. Source plants (G0) for cuttings for experiments were produced in a greenhouse at the Sweet Potato Research Station, Chase (lat. 32.0984394°N, long. -91.6996033°W). This facility is a component of the Louisiana State University Agricultural Center sweetpotato foundation seed program. All experiments used cuttings that were 25–30 cm long, with five to six fully opened leaves, ≈ 5 mm diameter at the basal cut (cut end) and with uniform distribution of nodes. Three commercially grown cultivars were used: ‘Bayou Belle’ (LaBonte et al., 2013), ‘Beauregard’ (Rolston et al., 1987), and ‘Evangeline’ (La Bonte et al., 2008). ‘Bayou Belle’ is considered highly resistant to RKN (LaBonte et al., 2013), whereas ‘Evangeline’ and ‘Beauregard’ are considered moderately resistant and susceptible, respectively (La Bonte et al., 2008).

Experimental design and incubation conditions. The experiments were conducted in a greenhouse at the Louisiana State University Agricultural Center, Baton Rouge (lat. 30.411380°N, long. 91.172807°W). There were two replication experiments, and the PDs were 2 Mar. 2015 (PD1) and 19 Apr. 2016 (PD2). Cuttings were planted (two nodes under the growth substrate surface) in 10-cm-diameter polyvinyl chloride pots (height = 30 cm) with detachable plastic bottoms. The growth substrate and experimental conditions in the study were based on previously developed approaches for measuring the effect of water availability, nitrogen, and virus infection at the onset of storage root initiation in ‘Beauregard’ sweetpotato (Villordon et al., 2012, 2013, 2014). The growth substrate was washed sand of uniform particle size (majority in the 0.05- to 0.2-mm range). Plants were inoculated with the RKN treatments immediately after transplanting. Half-strength Hoagland’s nutrient solution (150 mL) was added to the pots twice a week until the conclusion of the study. The greenhouse temperature regime was 29 °C for 14 h (day) (PD1 SD = 5.9; PD2 SD = 6.7) and 18 °C for 10 h (night) (PD1 SD = 1.2; PD2 SD = 10.1). Photosynthetic photon flux (PPF)

ranged from 300 to 800 $\text{m}^{-2}\cdot\text{s}^{-1}$. High-intensity mercury vapor lamps were used to extend daylength to 14 $\text{h}\cdot\text{d}^{-1}$. PPF was measured at the canopy level with a quantum sensor (Model QSO-S; Decagon Devices, Inc., Pullman, WA). The relative humidity averaged 60%. Temperature and relative humidity were monitored at the canopy level using an integrated temperature and relative humidity sensor (Model RHT; Decagon Devices, Inc.). The moisture of the growth substrate was maintained at $\approx 65\%$ to 75% of field capacity ($\approx 12\%$ volumetric water content). Growth substrate moisture was measured with ECH2O soil moisture sensors (Model EC-5; Decagon Devices, Inc.) inserted vertically at 2–7 cm depth.

All experiments were arranged in a randomized complete block design where a pot (one plant per pot) was considered a replication. There were five replications. The experiment was ended after 20 d. Prior work has shown that this stage corresponds to the onset of storage root formation in ‘Beauregard’ under these culture conditions (Villordon et al., 2012). Entire root systems were extracted by pre-wetting the pots, removing the detachable plastic bottoms, tilting the pots, and gradually removing the growth substrate. Individual ARs were detached and washed before image acquisition.

Root architecture measurements. Measurement of root architectural attributes followed the procedures described in prior work on the cultivar Beauregard (Villordon et al., 2012, 2013, 2014). Intact ARs that were 5 cm or greater in length were floated on waterproof trays and scanned using a specialized Dual Scan optical scanner (Regent Instruments, Inc., Quebec, Canada). The acquisition and image analysis software was WinRHIZO Pro (v. 2009c; Regent Instru-

ments, Inc.). Image acquisition parameter was set to “high” accuracy (600 dpi; image size ≈ 18 MB), whereas analysis precision was set to “high.” Debris removal among scanned images was performed manually using the WinRHIZO Pro Edition working mode. Debris consisted mostly of sand particles and occasionally broken root segments (≤ 1 cm in length). Root types (main root, first-order LRs, and second-order LRs) were automatically classified based on root diameter, which was in turn based on predetermined size intervals that were dynamically adjusted between samples. In the present work, three intervals were initially used: 0–0.2, 0.2–1.0, and 1.0–20 mm. After the scanning phase, it was determined that the intervals for classifying root classes in ‘Beauregard’ had to be adjusted frequently because of increased complexity of the root systems of ‘Bayou Belle’ and ‘Evangeline’. It was determined that pooling the first-order and second-order LR measurements reduced experimental variability and more accurately reflected genotype and treatment effects. In addition, it was determined that using WinRHIZO’s manual method (value = 212) for pixel classification increased the efficacy of the software to detect faint pixels. LR attributes that were measured from scanned images included LR length, LR number (pooled first-order and second-order LRs), surface area, and volume. Nematode galls were unambiguously detected on scanned gray-scale images of LRs, allowing the use of the nodule counting feature in WinRHIZO Pro (v. 2009c; Regent Instruments, Inc.). Galls were also visible on the main roots, especially in the susceptible cultivar ‘Beauregard’. However, these galls could not be unambiguously visualized on the scanned images because of the thickness of the main roots. Thus, only galls on

Fig. 1. Scanned color image of ‘Beauregard’ sweetpotato adventitious root obtained from a plant subjected to high *Meloidogyne incognita* inoculum level (A). The same sample was scanned in gray scale for image analysis using WinRHIZO (B), showing nematode galls on lateral roots (LR) (inset, C). These galls were counted using the nodule counting feature of WinRHIZO. Scale bar = 5 cm. MR = main root; G = gall.

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LRs were counted each time an AR image was analyzed.

Statistical analyses. Root length and counts were transformed using log 10 and square root transformation, respectively. The unbalanced data set was analyzed using SAS Proc Mixed (SAS 9.4; SAS, Inc., Cary, NC). Fisher's least significant difference test at the 0.05 *P* level was used to test for statistical significance. The data presented were means and standard error of the means from non-transformed data. There was a significant PD × cultivar effect and cultivar × RKN level effect for all root attributes; hence, data were presented according to PD.

Results and Discussion

Cultivar response to *M. incognita* infection on LRs. Galls were visible on LRs from scanned color (Fig. 1A) and gray-scale images of ARs (Fig. 1B and C). In general, the number of galls for each cultivar was consistent across RKN levels and two PDs (PD1 and PD2) (Fig. 2A and B). Within cultivars, 'Beauregard' plants subjected to high RKN level (19 galls per AR) showed 601% increase in number of galls relative to plants subjected to the low inoculum level (2.7 galls per AR) across PD1 and PD2. 'Evangeline' treated with high RKN level showed only increase in number of galls relative to the control and medium inoculum levels in PD1. 'Bayou Belle' plants did not show any within-cultivar differences across treatments in both PDs. Among cultivars, 'Beauregard' plants treated with the highest rate of RKN inoculum showed the highest number of galls, increasing by 400% and 1900%, respectively, relative to 'Evangeline' (3.4 galls per AR) and 'Bayou Belle' (0.9 galls per AR) at the same inoculum level across PD1 and PD2. At medium inoculum levels, the only among-cultivar difference observed was between 'Beauregard' and 'Bayou Belle' and only in PD1. These results corroborate available data about the relative response of these cultivars to RKN infection (La Bonte et al., 2008, 2013).

Root architecture attributes. There were inherent cultivar and PD effects for the measured root attributes as evidenced by the variation in LR length, number, area, and volume in untreated plants across cultivars and within and among PDs (Figs. 3 and 4). In PD1, LR length, number, area, and volume in the resistant 'Bayou Belle' control plants increased 117%, 138%, 121%, and 110% relative to the susceptible 'Beauregard' control plants. In PD2, the trends were reversed. There were no differences in root attributes between 'Evangeline' and 'Beauregard' control plants across PDs. LR attributes varied within and among resistant and susceptible cultivars, with a general trend for increase in all root growth attributes in response to RKN infection in PD1 and PD2 (Figs. 3 and 4). 'Evangeline' showed relatively consistent within-cultivar increase across PD1 (medium and high RKN levels)

Fig. 2. Number of galls observed on lateral roots on planting dates 1 (A) and 2 (B) for sweetpotato cultivars Bayou Belle (BB), Beauregard (BX), and Evangeline (EV) previously inoculated with 0 (Control), 500 (Medium), or 5000 (High) eggs of *Meloidogyne incognita* per pot.

and PD2 (medium RKN level only). LR length, number, area, and volume within 'Evangeline' plants subjected to high RKN increased 122%, 126%, 154%, and 136%, respectively, relative to the untreated controls in PD1. In PD2, LR length, number, area, and volume within 'Evangeline' plants treated with medium RKN level increased by 42%, 33%, 33%, and 24%, respectively, relative to the untreated plants. 'Bayou Belle' showed moderate but nonstatistically significant within-cultivar increases for all root attributes in PD1. 'Evangeline' (PD1 and PD2) and 'Bayou Belle' (PD1 only) showed among-cultivar increase for all root attributes relative to the susceptible 'Beauregard' at medium or high RKN levels. When comparing among cultivars treated with high inoculum level in PD1, LR length, number, area, and volume in 'Evangeline' increased by 165%, 167%, 176%, and 190%, respectively, relative to 'Beauregard' plants with

similar RKN level. In PD1, LR length, number, area, and volume in 'Bayou Belle' plants treated with high inoculum levels increased by 122%, 91%, 158%, and 203%, respectively, relative to 'Beauregard'.

In this study, the trend for inherent genotypic variability for RSA attributes corroborates the data reported by Pardales and Yamauchi (2003) wherein five sweetpotato cultivars showed inherent variation in LR number among controls and after imposition of drought treatments. Pardales and Yamauchi (2003) suggested that opportunities exist for manipulating root systems of sweetpotato in agronomy and breeding for stable production under stressful environments. In terms of root system compensatory growth response to *M. incognita* infection, evidence for genotype-specific increase in root volume has also been reported in barley (*Hordeum vulgare*) (Haase et al., 2007), cotton (*Gossypium hirsutum*) (Ma et al., 2013), and tobacco (*Nicotiana*

Fig. 3. Lateral root length, count, volume, and surface area for sweetpotato cultivars Bayou Belle (BB), Beauregard (BX), and Evangeline (EV) previously inoculated with 0 (Control), 500 (Medium), or 5000 (High) eggs of *Meloidogyne incognita* per pot (planting date 1).

tabacum) (Johnson and Nusbaum, 1970). In particular, Haase et al. (2007) documented that low levels of *M. incognita* infection resulted in elongated LRs. This is similar to the within-cultivar variation in LR length observed in the present study in the resistant ‘Evangeline’ subjected to medium inoculum treatment in PD2. The mechanism that causes compensatory root growth in response to nematode infection is still unknown (Ma et al., 2013). Presently, there are no data from field trials on the effect of *M. incognita* on the storage root yield of cultivars used in this study. However, Lawrence et al. (1986) reported that with comparable low levels of *M. incognita* inoculum under field conditions, ‘Centennial’, a susceptible cultivar, show reduced storage root number and weight relative to ‘Jasper’, a moderately resistant cultivar. Lawrence et al. (1986) noted that root proliferation appeared to be a response to nematode infection and cited prior work (Wallace, 1973) that speculated that root proliferation may indicate that the plant is responding to root destruction by the production of new roots.

The significant PD × cultivar effect and cultivar × RKN interaction effects in this study are consistent with prior findings regarding the role of environment and cultivar effects on the variability of *M. incognita*

infection response in sweetpotato (Lawrence et al., 1986; Ukoskit et al., 1997). Although the current work was conducted in a greenhouse environment, the plant materials used in each of the two PDs were obtained from different sets of virus-tested source plant stock of varying ages in each of 2015 and 2016. Recent data indicate that sweetpotato source plant nutrient status associated with plant age can exert a significant effect on root development in the daughter plants and this effect can vary with cultivar (Villordon et al., 2018).

Taken together, the evidence suggests that RSA traits can be harnessed to help improve sweetpotato tolerance to *M. incognita* infection. However, the incorporation of RSA as a breeding objective is subject to practical difficulties associated with the lack of tools for monitoring and visualizing RSA development and screening for such traits under field conditions (Villordon et al., 2014). The root scanning and WinRHIZO-based image analysis approach used in the present study is time-consuming and tedious, suitable for detailed root architecture and plant stress or physiology studies (Pang et al., 2011), but not appropriate for screening large numbers of entries associated with a breeding program. However, an alternative method has been developed for rapidly measuring root volume using water displacement (Pang et al., 2011),

and there are ongoing studies to develop noninvasive imaging approaches for monitoring and visualizing RSA development based on X-ray computed tomography and magnetic resonance imaging technologies (Spalding and Miller, 2013). Noninvasive imaging methods are essential tools not only for crop improvement but also for functional genomics research that will help shed light on the genetics and physiology of compensatory root growth in response to nematode infection.

Conclusions

We have generated evidence that corroborates past data regarding the existence of inherent genotypic variation in RSA attributes in sweetpotato. We have also corroborated findings in other crop species that *M. incognita* infection leads to genotype-specific modification of RSA attributes such as root volume and LR length. In the present study, the highly resistant ‘Bayou Belle’ demonstrated this compensatory root growth through increased LR length in response to an intermediate level of RKN infection. Taken together, the evidence suggests that RSA can be manipulated to increase resistance to biotic stress such as nematode infection. The integration of RSA traits into

Fig. 4. Lateral root length, count, volume, and surface area for sweetpotato cultivars Bayou Belle (BB), Beauregard (BX), and Evangeline (EV) previously inoculated with 0 (Control), 500 (Medium), or 5000 (High) eggs of *Meloidogyne incognita* per pot (planting date 2).

current breeding programs will depend on the development and availability of tools that permit routine screening of desirable root architecture traits.

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